# APPLICATION OF PYRIC-HERBIVORY IN THE NORTHERN MIXED-GRASS PRAIRIE TO ENHANCE BIODIVERSITY

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**Title**

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The Supervisory Committee certifies that this ***disquisition*** complies with North Dakota State University's regulations and meets the accepted standards for the degree of

**MASTER OF SCIENCE**

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# ABSTRACT

Pyric-herbivory is a naturally occurring disturbance that historically created shifting mosaics of heterogeneous plant communities and vegetation structure, supporting a biodiverse Great Plains ecosystem. Present land management has decoupled this interactive disturbance leading to homogenous grasslands, resulting in a reduction of biodiversity, which is exasperated by the dominance of non-native grasses. We believe reintroducing this disturbance will increase heterogeneity and enhance biodiversity. First, we compared the effects of a season-long grazing and two patch-burn grazing systems on plant communities. Second, we evaluated how small mammal communities were affected by each grazing system. Our findings show re-establishing pyric-herbivory, via patch-burn grazing, can enhance biodiversity compared to season-long grazing. We hypothesize further implementation of patch-burn grazing will continue to enhance biodiversity, as thatch and basal litter are further reduced. In conclusion, our findings support re-establishing pyric-herbivory to enhance biodiversity though further study is needed to determine what effect continued implementation will have.

# ACKNOWLEDGEMENTS

I would like to acknowledge all of those who started me on this path, fed my curiosity, challenged me, and got me to where I am today. Firstly, I would not be in this field of study if it had not been for my boss and friend, Jim Ghekiere, who first noticed my natural interest in plants and natural resources management and encouraged me to switch majors and study rangeland ecology and natural resources management at Montana State University (MSU). Thank you to all my professors at MSU, who continued to encourage me and provide me with opportunities, namely: Dr. Bok Sowell, the old goat, for challenging me to never take anything at face value and always dig deeper; Dr. Craig Carr for being instrumental in developing my plant identification abilities and for chatting with me about whatever was the subject of the day; and Dr. Clayton Marlow for helping me develop an interest in fire and disturbance ecology and encouraging me to go to graduate school, but more importantly for helping me not only become the best range scientist I could be, but also the best person I could be. Thank you to Ryan Limb, my advisor, for providing me with this research opportunity and for helping providing support and help through my time at North Dakota State University. I'd be remiss if I didn't thank my committee members as well. Kevin, Ned, and Torre, thank for serving on my committee, aiding me in this process, and being patient with me. You all provide me with unique and different perspectives on rangeland ecology for which I am grateful.

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who provided me with technical assistant (pulling me out of the mud) and with good conversation. I would not be where I am today without the exceptional work of my technicians, especially Joel Milos, Marina McCreary, and Paige Harman who I had the pleasure of working with.

My acknowledgements would not be complete if didn’t thank all my friends and family who have supported me through this time. My mother and best friend, Richie Hamel, helped develop me into the person I am today. She not only had steadfast support and helped me believe I could accomplish anything, but she also showed the same support for everyone in the community, and I is an example I hope to emulate. Thank you to my father, Steve Hamel, for pushing me to take chances and pursuing my master’s degree. You have been there for me through thick and thin, and taught me to be humble, respectful, but most importantly, dedicated. I also don’t believe I would’ve gotten to this point without my brother, Will Hamel. He and I have helped push and elevate each other throughout the years and have been each other’s biggest fans and best friends. I would also like to thank my dad and brother for putting up with my constant roadside and golf course plant ID of noxious weeds. To be sure, there are countless other people who have helped me along the way, for which I hope they know I am eternally grateful.

# DEDICATION

I dedicate this work to my late mother, Richie Lee Hamel, who always challenged me to be inquisitive and not to take life too seriously, and to all my other friends and family who are not here to share in my achievements.

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## Abstract

Fire and grazing are disturbances that have shaped grasslands for a millennia, creating heterogenous landscapes high in biodiversity. Present land management has removed this interaction from many fire-prone grassland ecosystems, creating homogenous landscapes low in biodiversity. Homogenization of landscapes is further compounded in the Northern Great Plains by the invasion and domination of non-native grass species, such as Kentucky bluegrass (*Poa pratensis*; hereafter bluegrass) and smooth brome (*Bromus inermis*). These grasses create monocultures by producing thick basal litter and thatch layers, which inhibit native species ability access resources and limits their propagation. To determine if reintroduction of the fire-grazing interaction (pyric-herbivory) could promote more heterogeneous and diverse plant communities, we conducted a study comparing the effects of two patch-burn grazing systems (PBG) that differed in size and season of fire to a season-long grazing treatment (SLG). Our first PBG consisted of 16 ha patches burned in the early-growing season (PB40). Similarly, our second PBG consisted of 16 ha patches, but with 8 ha burned during the early-growing season and 8 ha burned in the late-growing season (PB20). Treatments were assigned to twelve approximately 65-hectare pastures (160 acres) (*n* = 4). We conducted vegetation surveys over the course of four growing seasons to compare effects on plant communities amongst treatments. We determined plant community composition between the SLG and PBG systems were different, and became increasingly different with time. Plant community metrics (Shannon’s diversity, richness, and dissimilarity) were higher on the PBG systems by the end of this study phase and increased relative to SLG with time. Composition of forbs and native grasses reacted similarly to plant community metrics. Conversely, non-native grass cover, specifically bluegrass and smooth brome, was lower in PBG systems than SLG by the end of our study. We also observed decreases in diversity and richness, and composition of forbs and native grasses with time-since-fire, and increases in composition of non-native grasses, specifically bluegrass and smooth brome. We hypothesize that the initial underlining mechanisms driving changes in the plant community can be attributed to changes in bare ground, as focal disturbance reduces thick basal litter and thatch layers. These results indicate that reintroduction of pyric-herbivory in the form of PBG can be beneficial to plant communities within the novel ecosystems of northern mixed-grass prairie.

## Introduction

Fire and grazing are naturally-occurring disturbances that, along with climate and topo-edaphic differences, have shaped plant communities for millennia (Bowman et al. 2009; Bond & Keeley 2005; Fuhlendorf & Smeins 1998, 1999). Fire and grazing historically interacted in fire-prone grassland ecosystems, otherwise known as pyric-herbivory, creating spatial and temporal changes in plant communities (Fuhlendorf et al. 2009). This interaction occurs primarily when large herbivores, such as bison or cattle, preferentially graze recently burned areas due to more palatable and nutritious regrowth (Knapp et al. 1999; Fuhlendorf & Engle 2001; Vermeire et al. 2004; Allred et al. 2011). Because large herbivores focus their grazing efforts on recently burned patches, this allows patches that were previously burned and grazed to recover from focal disturbance (Fuhlendorf & Engle 2001; Gates et al. 2017; Starns et al. 2019). After several growing seasons, patches begin accumulating dead plant material due to lack of grazing, which leads to increased fuel loads and the probability of fire reoccurring, repeating the cycle (Fuhlendorf & Engle 2001).

Plant community composition and structure vary, both temporally and spatially, in response to pyric-herbivory (Fuhlendorf & Engle 2004; Fuhlendorf et al. 2009). Grassland fires create non-uniform, discrete burn patches that vary in successional stages, forming a shifting mosaic of plant communities through time and space, which produces an overall diverse landscape (Fuhlendorf et al. 2009). Recently burned and grazed sites experience increases in forbs, annual species, and bare ground with a reduction in litter and graminoid species, in line with heavily disturbed sites (Van der Maarel 1993; Hickman et al. 2004; Towne et al. 2005; Dorrough et al. 2007; Limb et al. 2010). Because large herbivores concentrate their grazing in burn patches, this allows for graminoids in past burn patches to recover from previous focal disturbance (Fuhlendorf & Engle 2004). The changes in structure and composition of plant community creates heterogeneity on the landscape, which can in-turn support a diverse system of fauna (Ostfeld et al. 1997; Fox & Fox 2000; Fuhlendorf et al. 2006; Hovick et al. 2015; Ricketts & Sandercock 2016).

Present land management promotes uniform moderate utilization of grassland ecosystems which can create homogenous plant communities (Briske et al. 2003, 2008; Fuhlendorf et al. 2009; 2012). Although uniform moderate grazing can be beneficial regarding ground cover and soil disturbance, it fails to create heterogeneity of plant communities within a landscape (Fuhlendorf & Engle 2001, 2004) and of habitat structure essential for niche species at extreme ends of the habitat structure gradient (Fuhlendorf et al. 2006, 2009, 2010; Ricketts & Sandercock 2016). Decoupling of fire and grazing has produced homogenous systems in many grassland ecosystems, but in the Northern Great Plains (NGP) has also instigated the dominance of non-native grasses, such as Kentucky bluegrass (*Poa pratensis*; hereafter bluegrass) and smooth brome (*Bromus inermis*) (Dillemuth et al. 2009; Murphy & Grant 2005; Toledo et al. 2014). Dominance of non-native grasses has a compounding effect on homogeneity in the NGP, by inhibiting native plant diversity through production of thick basal litter and thatch layers which limits access to nutrients, water and sunlight, creating novel ecosystems (Toledo et al. 2014; DeKeyser et al. 2015; Printz & Hendrickson 2015). A possible solution to restoring heterogeneity in this novel grassland ecosystem is the restoration of pyric-herbivory in the form of patch-burn grazing (Fuhlendorf & Engle 2001; Fuhlendorf et al. 2009; 2012).

Patch-burn grazing mimics the disturbance pattern of pyric-herbivory by creating discrete burned patches within a pasture that vary spatially and temporally, establishing patches of recently burned, unburned and transitional areas within a landscape (Fuhlendorf & Engle 2001). This generates spatial and temporal changes on a landscape produces a shifting mosaic of plant communities (Fuhlendorf & Engle 2004), thereby creating a wide variety of habitat structure and increased biodiversity (Fuhlendorf et al. 2009; Ricketts & Sandercock 2016). At present, much patch-burn grazing related work has been conducted primarily in the southern tallgrass prairie (Coppedge et al. 1998; Fuhlendorf & Engle 2004; Fuhlendorf et al. 2006, 2010; Vinton et al. 1993), a system that is dominated by warm-season (C4) grasses (Howe 1994). Conversely, relatively little is known how patch-burn grazing effects plant communities in the northern mixed-grass prairie (Vermeire et al. 2004; Dornbusch et al. 2020), which consists primarily of cool-season (C3) grasses mixed with a warm-season grass component. However, currently much of this ecosystem is dominated by non-native cool-season grasses (bluegrass and smooth brome) (Murphy & Grant 2005; Toledo et al. 2014). To better understand what impacts patch-burn grazing (PBG) may have on plant communities in this ecosystem, we conducted a study to compare two PBG systems, varying in size and season of fire, to a conventional season-long grazing system (SLG).

Previous PBG studies in this region have shown promising results in influencing plant community dynamics (Dornbusch et al. 2020), but a greater body of work is needed to identify what effects PBG will have on plant communities and by what mechanisms. We hypothesized that grazing systems would produce differences in plant community composition and metrics (diversity, richness, and dissimilarity). We expected this would be driven by native plant species (specifically native grasses) and forbs being positively affected by PBG (Dornbusch et al. 2020; Fuhlendorf & Engle 2004). Because the use of fire has been shown to have negative effects on bluegrass (Engle & Bultsma 1984; Kral et al. 2018) and smooth brome (Bahm et al. 2011), we suspected PBG would have a greater negative impact on these non-native grasses than SLG. Because these differences can be driven by the dynamics of time-since-fire within PBG (Fuhlendorf & Engle 2004), we quantified the effects of PBG and time-since-fire on: 1) plant community composition; 2) community metrics; 3) composition of species groups and dominate non-native grasses and; 4) cover of bare ground, basal litter, and standing dead litter. Our results will provide a better understanding of how reintroduction of pyric-herbivory, in the form of PBG, effects plant communities in the northern mixed-grass prairie.

## Methods

### *Study Area*

This study was conducted at the North Dakota State University, Central Grassland Research Extension Center (CGREC) in south-central North Dakota (lat. 46°46’N, long. 99°28’W) situated in the Missouri Coteau ecoregion of the northern mixed-grass prairie of the Great Plains. The Coteau is characterized by irregular, rolling plains and depressional wetlands (USDA-SCD 1981). The climate is characterized as temperate and has an average annual precipitation of 49.5 centimeters and temperature of 4.6° C (1991-2016, NOAA-NCEI 2021). Precipitation is summarized by month for each study year in Figure1.1.

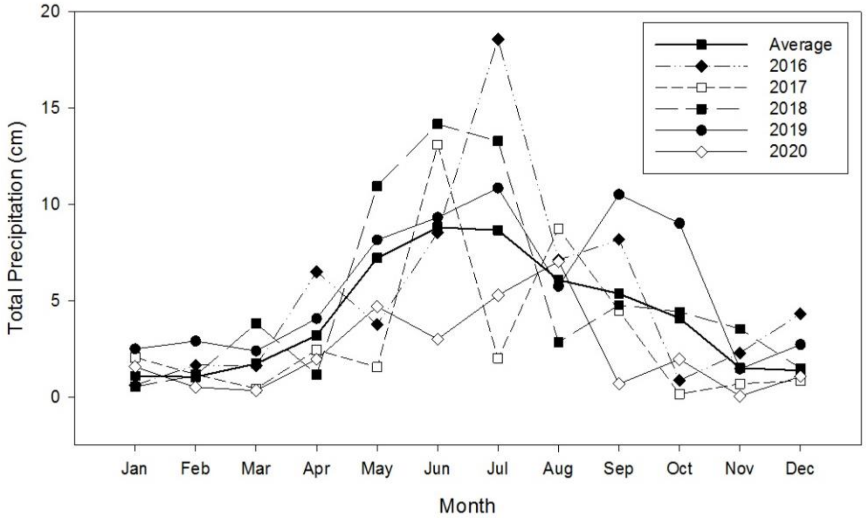

**Figure 1.1. Total monthly precipitation near Streeter, ND, USA from 2016 through 2020.** Weather data acquired at the Streeter 7 NW, ND USC00328415 station (46.7154$^{o}$N, -99.4475$^{o}$W) and retrieved from the National Environmental Satellite, Data, and Information Service of the National Oceanic and Atmospheric Administration (NOAA 2021). Average precipitation represents data from 1991-2016.

Vegetation of this area is characteristic of a northern mixed-grass prairie invaded by non-native cool-season grasses, such as Kentucky bluegrass (*Poa pratensis*) and smooth brome (*Bromus inermis*) (Limb et al. 2018). Much of the native grass community is dominated by cool-season grasses such as green needlegrass (*Nasella viridula*), needle and thread (*Hesperostipa comata*), and western wheatgrass (*Pascopyrum smithii*). The dominant woody species in this area is western snowberry (*Symphoricarpos occidentalis*). The forb community is diverse with common species including the goldenrod species (*Solidago* & *Oligoneuron spp.*), western ragweed (*Ambrosia psilostachya*), white heath aster (*Symphyotrichum ericoides*), and common yarrow (*Achillia millifolium*). Plant nomenclature follows the most current names listed by the USDA-NRCS plants database (USDA-NRCS 2021).

### *Treatment Structure*

Three treatments were applied to twelve 48 to 65 ha  pastures (experimental units) in the study area, with four pastures (replications) for each of the following treatments: (1) season-long grazing (SLG), (2) patch-burn grazing 16 ha (PB40) with early-growing season prescribed fires (late April to mid-May) applied to one of four 16 ha patches (40 ac or one-fourth of the pasture), and (3) patch-burn grazing 8 ha (PB20) with early-growing season fire being applied to 8 ha (20 ac or one-eighth of the pasture) of a 16 ha patch and a late-growing season fire (August to late-September) applied to the remaining 8 ha of the patch, with a 4-year fire return interval per patch. All treatments were grazed with Angus cross-bred cow/calf pairs from mid-May to mid-Oct at a full stocking rate to achieve an average 40-50 percent degree of disappearance across the pasture. The stocking rates for all treatments were 2.26-2.31 Animal Unit Months/ha.

Patch-burn grazing treatments (PBG) were structured as a management technique to mimic a pyric-herbivory disturbance regime (Fuhlendorf & Engle 2001), while our season-long grazing treatment was intended to replicate conventional cow/calf grazing management. Fires were randomly applied to patches that accumulated the most standing crop biomass in the previous growing season and that had not been previously burned. Prescribed fires were conducted using a ring-fire technique, with stripping head fires across patches, to make fires as uniformed as possible within patches. Because prescribed fires were applied when fuel moisture was sufficient to sustain a fire, we were only able to implement late-growing season fires to PB20 pastures in 2017 and half of our pastures in 2018, with 2020 burns being fully implemented after data collection.

### *Data Collection*

Sampling was standardized among treatments by artificially dividing all pastures into four 16 ha sampling units (patches) in all treatments, with sampling patches corresponding to burn patches in PBG treatments. Sampling occurred between mid-July and early-August of each year to test for differences between treatments over time and within each year. Two permanent 60 meters (m) transects were established randomly in each patch within the loamy ecological sites (Sedivec et al. 2021). Vegetation sampling was conducted by estimating canopy cover of plant species within 0.5 x 0.5 m frames at 2 m intervals along each transect (31 frames per transect) (Limb et al. 2018). We recorded canopy cover of plant species, standing dead litter and basal cover of bare ground, basal litter, rocks, and fecal pat using a modified Daubenmire cover class (1 = Trace – 1%, 2 = 1-2%, 3 = 2-5%, 4 = 5-10%, 5 = 10-20%, 6 = 20-30%, 7 = 30-40%, 8 = 40-50%, 9 = 50-60%, 10 = 60-70%, 11 = 70-80%, 12 = 80-90%, 13 = 90-95%, 14 = 95-97%, 15 = 97-98%, 16 = 99-100%; Daubenmire 1959). Cover classes were converted to percent cover midpoints (i.e., cover class 6 = 25%) for statistical analysis.

### *Data Analysis*

We primarily assessed within year treatment effects for each study year to compare vegetation data of similar climatic conditions. We also compared time-since-fire (TSF) intervals using data from the PB40 in 2020 after a full sequence of intervals (0-, 1-, 2-, &, 3-years TSF) were established within pastures. We did not include PB20 in our TSF calculations due to a lack of full implementation of fire within patches. We utilized nonmetric multidimensional scaling (NMS) in PC Ord 7.0 to determine the effect treatments had on community composition within each year using Sorenson (Bray-Curtis) distance measurement in autopilot mode based off average species cover within pastures (*n* = 4) (McCune & Mefford 2018). We tested for within year differences between treatments and across year differences within each treatment using permutational multivariate analysis of variance (PerMANOVA) by means of Sorenson (Bray-Curtis) distance and post-hoc Tukey tests in PC Ord 7.0 (Anderson 2001; McCune & Mefford 2018). The same NMS analysis was used to determine what effect TSF had on community composition using average patch species cover. However, we wanted to evaluate how similar different TSF communities were to SLG, so we used multi response permutation procedure test (MRPP) using Sorenson (Bray-Curtis) distance and post-hoc Tukey tests in PC Ord 7.0 (McCune & Mefford 2018). We constructed a bi-plot overlay to determine the linear relationships of percent composition of certain plant groups, dominate species, and basal litter cover to our NMS. We also overlayed 'hilltop plots' of basal litter and bare ground cover, which represent the non-linear relationship between these variables to community composition, to better understand how they, as an environmental variables, can effect pasture community composition (Nelson et al. 2015).

We then determined mean species richness, Shannon-Wiener diversity, and Sorenson (Bray-Curtis) dissimilarity of patches communities within each pasture for every study year. Because changes in these plant community metrics are caused by the dynamics of species composition, we also evaluated relative cover, as index of percent composition, of plant species groups (non-native grass species, native grass species, and forbs) and of dominant non-native grasses (bluegrass and smooth brome). We also assessed differences in bare ground, basal litter, and standing dead litter cover between treatments. To test for differences between treatments within each year, we used one-way analysis of variance (ANOVA) and post-hoc Tukey tests in IBM-SPSS Statistics software package (Version 27; IBM 2020). Relationships with TSF were established using linear regression in IBM-SPSS Statistics software package (Version 27; IBM 2020). Significance of tests was determined for *P* values at $\alpha = 0.05$.

## Results

We recorded 159 plant species during the duration of the study. We found there was no significant difference between PB40 and PB20 treatments in any community or species metrics ($P \geq 0.05$). Using within year comparisons, we determined that community composition of treatments in 2017, the first year of the study, were not different ($P = 0.234$). However, we did a find a significant difference in community composition in 2018 ($P = 0.045$) and increased in significance in subsequent years [2019 ($P = 0.017$); 2020 ($P = 0.012$)]. Pairwise comparisons within each year show that composition of PBG treatments were different from SLG ($P \leq 0.05$). Additionally, we determined community composition of each treatment did not vary significantly over time ($P \geq 0.05$). NMS analysis of community composition of treatments in all years was useful (stress = 0.098) and resulted in a 3-dimensional solution, with NMS axis 1 explained 75.6% of the variability, axis 2 explained 9.3%, and axis 3 explained 8.5% (cumulatively 93.4%).

PB40 and PB20 treatment communities are arranged in a linear relationship with community composition expanding along axes 1 and 2, diverging in composition from the SLG communities until 2019 (Figure 1.2a). Conversely, SLG communities are clustered together with a slight deviation in 2020 downwards along axis 2, with expansion and contraction of community composition happening from year-to-year (Figure 1.2a). Community composition of all treatments regressed in 2020, but PB40 and PB20 community compositions were still distinctly separate from SLG composition (Figure 1.2a). By overlaying a basal litter hilltop to our ordination, we found that plant communities in the bottom-left quarter of the ordination were associated with high amounts of basal litter (Figure 1.2b). This indicates that average community composition was highly influenced by basal litter. Using a bi-plot overlay, we determined that relative cover of plant groups, including bluegrass (POPR) and smooth brome (BRIN2), were strongly associated to axis 1 (Figure 1.2a). Relative cover of Non-native grasses (r = -0.984), and more specifically POPR (r = -0.801) and BRIN2 (r = -0.920), were negatively associated with axis 1. In contrast, forbs (r = 0.903), native species (r = 0.936), and more specifically native grasses (r = 0.826) were positively associated with axis 1 (Figure 1.2a).

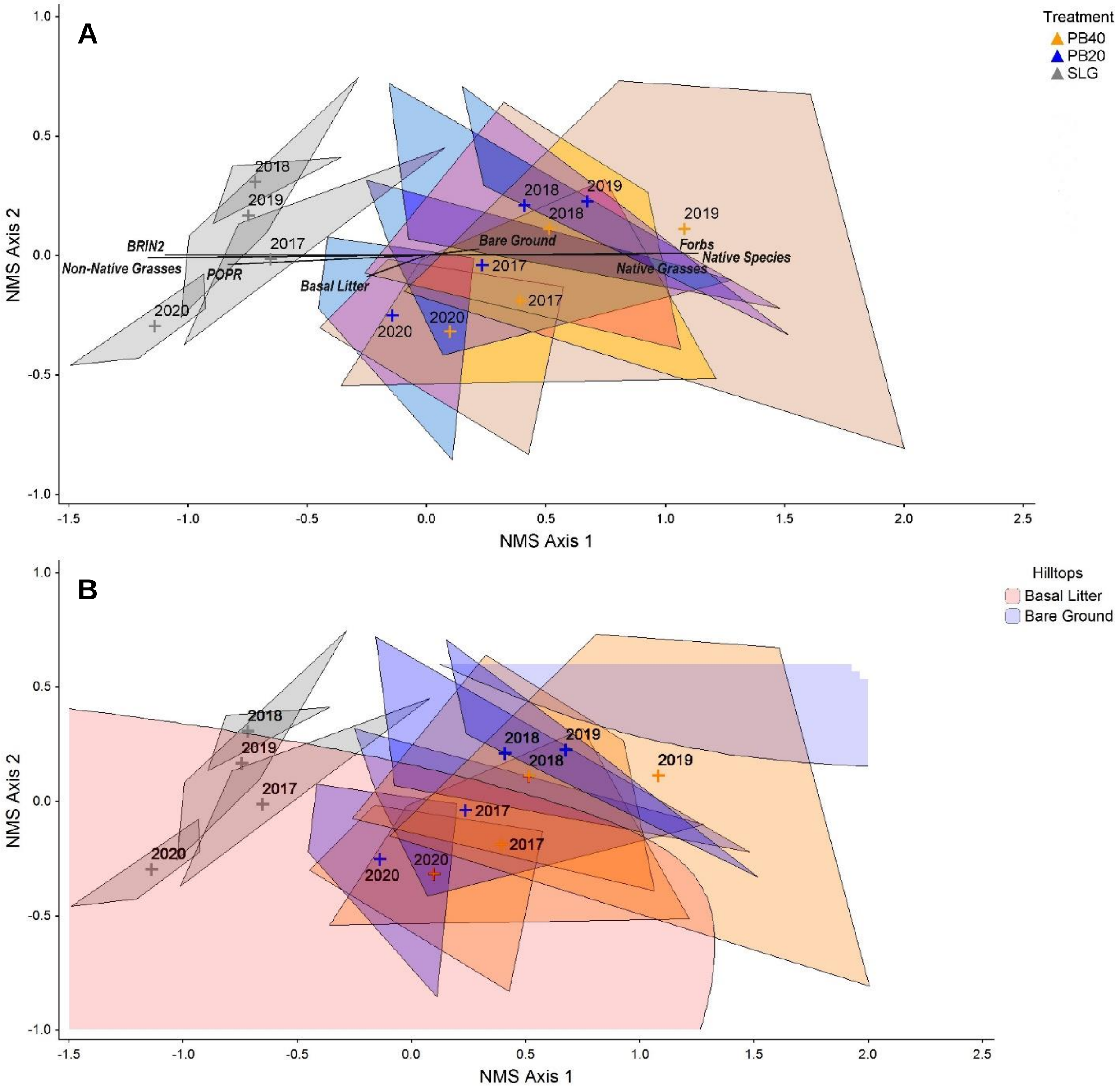

**Figure 1.2. NMS ordination of average pasture plant community composition of each treatment by year.** Plant community composition represented by convex hulls, using Sorenson (Bray-Curtis) distances, for season-long grazing (SLG), patch-burn grazing 20 ac (PB20), and patch-burn grazing 40 ac (PB40) treatments from 2017 through 2020 (*n* = 4). Greater separation of hulls suggests greater differences in community composition. Bi-plot overlay (A) represents the relationship of relative cover of plant groups and dominant non-native grasses (Kentucky bluegrass [POPR] and smooth brome [BRIN2]) and basal litter and bare ground cover to the NMS ordination. Basal litter hilltop overlay (B) represents the area of the ordination most associated with high amounts of basal litter and bare ground. Plant community data was collected at the North Dakota State University, Central Grasslands Research Extension Center near Streeter, ND from 2017-2020.

PB40 time-since-fire (TSF) NMS analysis resulted in a useful 2-dimensional ordination (stress = 0.112), with 82.6% of variability being explained by axis 1 and 8.7% being explained by axis 2 (cumulatively 91.2%). We determined there was a difference in composition with TSF and SLG patches ($P < 0.001$). Pairwise comparisons show TSF composition was only significantly different between patches of 1 year-since-fire and 3-years-since-fire ($P = 0.021$), with 2- and 3- years-since-fire and 0- and 1- years-since-fire patches being similar, with all burned patches being different from SLG patches ($P \leq 0.05$). Variability of composition decreased and became more similar to SLG with TSF, forming a linear pattern within our ordination (Figure 1.3). This suggests that, though 3 years-since-fire patches communities are significantly different from SLG, lack of focal disturbance causes as successional trajectory towards a community composition similar to SLG. Similar to overall community composition, bi-plot overlay shows POPR (r = -0.358), BRIN2 (r = -0.689), non-native grasses (r = -0.600), and basal litter (r = -0.745) had negative relationships to axis 1 while forbs (r = 0.646), native species (r = 0.592), native grasses (r = 0.608), and bare ground (r = 0.774) were all positively related (Figure 1.3). Meaning, positive movement along axis 1 in patch community composition was associated with increases in forbs, native species, native grasses, and bare ground, while negative movement along the axis was associated with increases in POPR, BRIN2, non-native grasses, and basal litter.

Diversity and richness were significantly different between PBG treatments and SLG in each year of the study ($P \leq 0.05$), with significance increasing from 2017 to 2020 (Table 1.1). PBG treatments did not react the same way with time, as PB40 diversity slightly increased from 2017 to 2020 while PB20 diversity slightly decreased (Table 1.1). This is likely due to the lack of full implementation of burning in PB20 pastures, resulting in some patches only being half burned, therefore decreasing the evenness of the community, and effecting Shannon's diversity. Although some PB20 patches were only half burned, relative difference of plant community metrics increased between the PBG treatments compared to SLG, with time. Richness of PBG treatments was higher than SLG in every year except PB40 richness in 2018 ($P = 0.125$) but increased with time (Table 1.1). Dissimilarity of patches became significantly different in 2019 ($P = 0.027$) and increased in significance in 2020 ($P = 0.002$). PB20 dissimilarity was different from SLG in 2019 and 2020, while PB40 was only different in 2020 (Table 1.1), with dissimilarity increasing relative to SLG in both PBG treatments. When comparing all TSF intervals, we did not find a significant relationship between TSF and diversity (r= 0.256, $P = 0.339$) and richness (r = 0.245, $P = 0.361$) (Figure 1.4). However, in a post-hoc analysis, we preformed regression analysis of 1- through 3-years-since-fire data and found significant negative relationships of diversity (r = -0.604, $P = 0.038$) and richness (r = -0.738, $P = 0.003$) with TSF, meaning, both diversity and richness decreased with TSF (Figure 1.4).

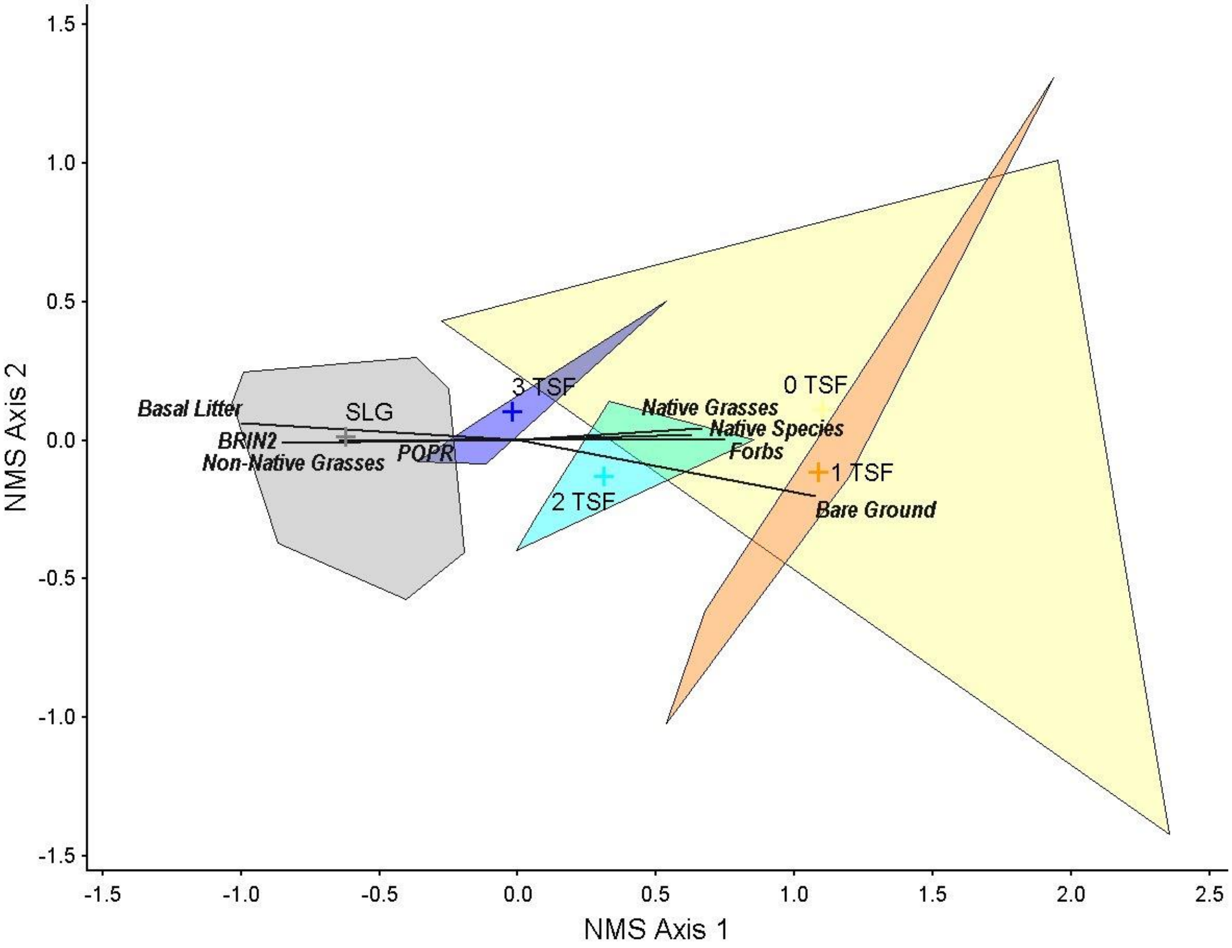

**Figure 1.3. NMS ordination of average patch plant community composition for each time-since-fire interval and season-long grazing.** Plant community composition is represented by convex hulls, using Sorenson (Bray-Curtis) distances, for each time-since-fire interval (TSF) (*n* = 4) and season-long grazing (SLG) (*n* = 16). Greater separation of hulls suggests greater differences in community composition. Bi-plot overlay represents the relationship of relative cover of plant groups and dominant non-native grasses (Kentucky bluegrass [POPR] and smooth brome [BRIN2]) and cover of basal litter and bare ground to the NMS ordination. Plant community data was collected at the North Dakota State University Central Grasslands Research Extension Center near Streeter, ND in 2020 within PB40 pastures.

**Table 1.1. Summary statistics of plant community metrics.** We reported average pasture Shannon's diversity, species richness, and Sorenson (Bray-Curtis) dissimilarity within season-long grazing (SLG), patch-burn grazing 20 ac (PB20), and patch-burn grazing 40 ac (PB40) treatments (n=4) from 2017 through 2020 at the North Dakota State University Central Grasslands Research Extension Center near Streeter, ND. If α = 0.05 was achieved by within year ANOVA, post-hoc Tukey's test was conducted. There were no differences between PBG treatments. P-values are reported for each within year ANOVA and subsequent post-hoc comparisons of PB40 and PB20 treatments relative to the SLG treatment.

| **Community Metrics** | | **Treatment** | | | **P-values** | | |
|---|---|---|---|---|---|---|---|
| | **Year** | **PB40** | **PB20** | **SLG** | **Within Year ANOVA** | **PB40 v. SLG** | **PB20 v. SLG** |
| **Diversity** | 2017 | 2.32 ± 0.06 | 2.57 ± 0.14 | 1.87 ± 0.14 | 0.008 | 0.066 | 0.007 |
| | 2018 | 2.35 ± 0.11 | 2.66 ± 0.13 | 1.85 ± 0.10 | 0.002 | 0.032 | 0.002 |
| | 2019 | 2.84 ± 0.13 | 2.79 ± 0.13 | 2.08 ± 0.15 | 0.006 | 0.008 | 0.012 |
| | 2020 | 2.45 ± 0.09 | 2.36 ± 0.10 | 1.60 ± 0.10 | <0.001 | <0.001 | 0.001 |
| **Richness** | 2017 | 46.69 ± 1.19 | 47.00 ± 2.15 | 32.06 ± 2.92 | 0.001 | 0.003 | 0.003 |
| | 2018 | 46.94 ± 4.53 | 51.00 ± 2.89 | 35.50 ± 3.43 | 0.039 | 0.125 | 0.037 |
| | 2019 | 53.81 ± 4.21 | 54.25 ± 1.43 | 39.06 ± 4.08 | 0.021 | 0.036 | 0.032 |
| | 2020 | 49.94 ± 1.26 | 48.63 ± 1.27 | 30.25 ± 2.11 | <0.001 | <0.001 | <0.001 |
| **Dissimilarity** | 2017 | 0.3424 ± 0.0189 | 0.3784 ± 0.0381 | 0.3052 ± 0.0310 | 0.284 | - | - |
| | 2018 | 0.3426 ± 0.0206 | 0.3635 ± 0.0358 | 0.2736 ± 0.0439 | 0.216 | - | - |
| | 2019 | 0.3724 ± 0.0232 | 0.4289 ± 0.0416 | 0.2806 ± 0.0281 | 0.027 | 0.160 | 0.023 |
| | 2020 | 0.3154 ± 0.0146 | 0.3768 ± 0.0308 | 0.1951 ± 0.0275 | 0.002 | 0.021 | 0.002 |

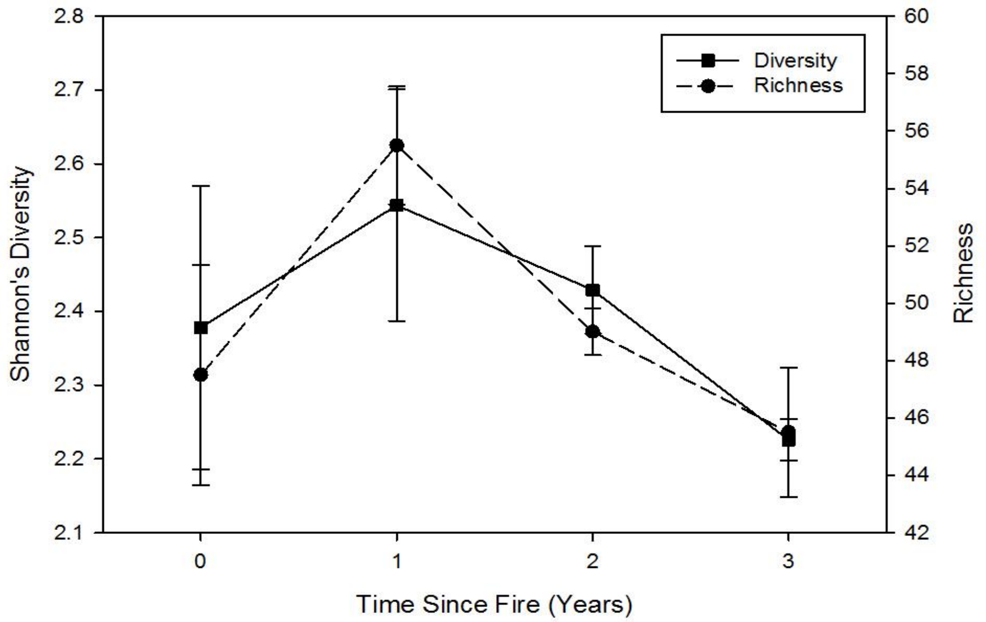

**Figure 1.4. Diversity and richness with time-since-fire.** Average diversity and richness of patches within the patch-burn grazing 40 ac treatment plotted as a function of time-since-fire (TSF) in 2020 at the North Dakota State University Central Grasslands Research Extension Center near Streeter, ND. Error bars represent standard error of mean. (Note: dual axis graph with Shannon's diversity represented on the left axis and species richness represented on the right axis)

We found relative cover of forbs was significantly higher in PBG treatments in all years ($P \leq 0.05$) and increased in significance with time (Table 1.2). There was no difference between treatments in non-native grasses ($P = 0.065$) or native grasses ($P = 0.295$) at the study initiation in 2017. However, native grasses relative cover was significantly higher in 2020 between PBG treatments and SLG ($P \leq 0.05$). From 2018 onwards, non-native grass relative cover became significantly different, with level of significance increasing in subsequent years between PBG treatments and SLG (Table 1.2). Non-native grasses consisted primarily of POPR and BRIN2, and both were affected by PBG treatments with time. Relative cover of BRIN2 was affected at the initiation of this study ($P = 0.013$), but level of significance increased with time between PBG and SLG (Table 1.2). POPR relative cover was not different between treatments at the start of this study ($P = 0.467$). Level of significance increased in the following years (Table 1.2) until

2020 where we found relative cover of POPR was different between PBG treatments and SLG ($P \leq 0.05$). TSF analysis revealed significant relationships with native grasses (r = -0.639, $P$ = 0.008), non-native grasses (r = 0.548, $P$ = 0.028) and BRIN2 (r = 0.604, $P$ = 0.013); but no relationship with forbs (r = -0.210, $P$ = 0.434) or POPR (r = 0.113, $P$ = 0.677) (Figure 1.5). However, when analyzing 1 to 3 years-since-fire data, we found significant relationships with forbs (r = -0.732, $P$ = 0.007) and POPR (r = 0.617, $P$ = 0.032), and stronger relationships in native grasses (r = -0.809, $P$ = 0.001), non-native grasses (r = 0.834, $P$ = 0.001), and BRIN2 (r = 0.616, $P$ = 0.033) (Figure 1.5).

Bare ground was different within each year of the study ($P \leq 0.05$). Bare ground was significantly higher in PB40 each year compared to SLG ($P \leq 0.05$) but was only higher in 2017 and 2020 of the PB20 ($P \leq 0.05$) (Table 1.3). Basal litter was the same in all treatments when the study was initiated ($P$ = 0.622). Basal litter became increasingly different from 2018 to 2020 in PB40 compared to SLG, while PB20 was different only in 2018 and 2020 (Table 1.3). Differences in the response of bare ground and basal litter between PBG treatments can likely be attributed to incomplete burns in PB20. Bare ground and basal litter both had a significant relationship with TSF. Bare ground cover decreased from 9.52% in 0 years-since-fire patches to 2.02% in 3 years-since-fire patches (r = -0.628, $P$ = 0.009) (Figure 1.6). Inversely, basal litter cover increased from 80.57% in 0 years-since-fire patches to 91.14% in 3 years-since-fire patches (r = 0.615, $P$ = 0.006) (Figure 1.6). Standing dead litter was not significantly different in any year ($P \geq 0.05$) (Table 3), nor was there a relationship with TSF (r = -0.222, $P$ = 0.408) (Figure 1.6).

**Table 1.2. Relative cover of species groups and dominate non-native grasses (Kentucky bluegrass and smooth brome)**. Average relative cover was reported within season-long grazing (SLG), patch-burn grazing 20 ac (PB20), and patch-burn grazing 40 ac (PB40) treatments (n=4) from 2017 through 2020 at the North Dakota State University Central Grasslands Research Extension Center near Streeter, ND. If α = 0.05 was achieved by within year ANOVA, post-hoc Tukey's test was conducted. There were no differences between PBG treatments. P-values are reported for each within year ANOVA and subsequent post-hoc comparisons of PB40 and PB20 treatments relative to the SLG treatment.

| **Species Groups** | | **Treatment** | | | ***P*-Values** | | |
|---|---|---|---|---|---|---|---|
| | **Year** | **PB40** | **PB20** | **SLG** | **Within Year ANOVA** | **PB40 v. SLG** | **PB20 v. SLG** |
| **Non-Native Grasses** | 2017 | 43.97 ± 6.62 | 48.26 ± 4.86 | 65.73 ± 6.18 | 0.065 | - | - |
| | 2018 | 45.83 ± 5.11 | 48.48 ± 5.16 | 72.50 ± 3.26 | 0.005 | 0.007 | 0.012 |
| | 2019 | 32.83 ± 5.09 | 35.33 ± 4.20 | 63.32 ± 5.41 | 0.003 | 0.005 | 0.008 |
| | 2020 | 50.46 ± 3.26 | 53.26 ± 3.17 | 77.01 ± 3.49 | 0.001 | 0.001 | 0.002 |
| | | | | | | | |
| **Native Grasses** | 2017 | 4.55 ± 1.45 | 5.54 ± 1.65 | 2.04 ± 1.46 | 0.295 | - | - |
| | 2018 | 5.03 ± 1.55 | 6.69 ± 1.22 | 2.23 ± 0.91 | 0.088 | - | - |
| | 2019 | 6.49 ± 2.05 | 7.59 ± 2.08 | 1.79 ± 0.85 | 0.095 | - | - |
| | 2020 | 5.62 ± 1.09 | 5.25 ± 1.29 | 1.01 ± 0.51 | 0.019 | 0.026 | 0.039 |
| | | | | | | | |
| **Forbs** | 2017 | 38.38 ± 3.09 | 34.13 ± 3.68 | 18.52 ± 1.12 | 0.002 | 0.002 | 0.009 |
| | 2018 | 40.16 ± 3.20 | 37.04 ± 4.30 | 17.24 ± 1.08 | 0.001 | 0.002 | 0.004 |
| | 2019 | 53.48 ± 3.31 | 49.37 ± 3.46 | 25.17 ± 3.58 | 0.001 | 0.001 | 0.002 |
| | 2020 | 35.35 ± 2.11 | 33.16 ± 3.22 | 13.49 ± 1.53 | <0.001 | <0.001 | 0.001 |
| **Dominate Non-Native Grasses** | | **Treatment** | | | **P-Values** | | |
| | **Year** | **PB40** | **PB20** | **SLG** | **Within Year ANOVA** | **PB40 v. SLG** | **PB20 v. SLG** |
| **Kentucky bluegrass *(Poa pratensis)*** | 2017 | 32.00 ± 5.33 | 33.30 ± 3.32 | 39.10 ± 3.50 | 0.467 | - | - |
| | 2018 | 32.48 ± 3.41 | 31.98 ± 2.58 | 40.40 ± 3.31 | 0.157 | - | - |
| | 2019 | 23.32 ± 3.74 | 21.90 ± 3.02 | 31.98 ± 3.60 | 0.139 | - | - |
| | 2020 | 35.83 ± 1.23 | 33.53 ± 2.74 | 42.96 ± 2.50 | 0.012 | 0.049 | 0.012 |
| | | | | | | | |
| **Smooth brome *(Bromus inermis)*** | 2017 | 10.74 ± 1.53 | 13.47 ± 3.28 | 24.61 ± 2.96 | 0.013 | 0.014 | 0.041 |
| | 2018 | 11.76 ± 2.44 | 15.36 ± 3.35 | 28.39 ± 1.39 | 0.003 | 0.003 | 0.013 |
| | 2019 | 7.79 ± 3.05 | 11.84 ± 2.00 | 29.12 ± 2.35 | <0.001 | <0.001 | 0.001 |
| | 2020 | 13.24 ± 2.71 | 17.16 ± 1.37 | 33.17 ± 2.20 | <0.001 | 0.001 | 0.003 |

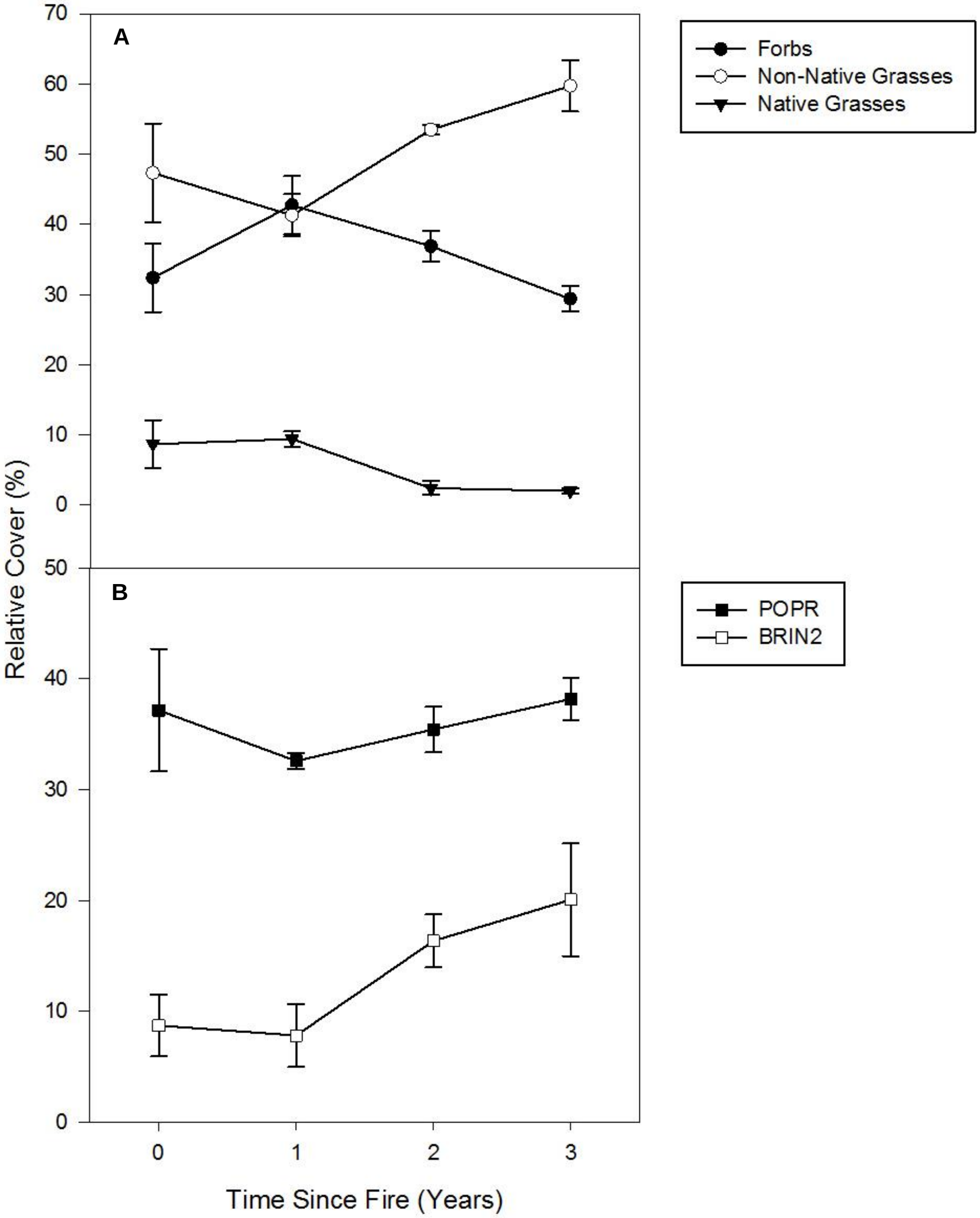

**Figure 1.5. Relative cover of species groups and dominate non-native grasses with time-since-fire.** Relative cover of species groups (A) and dominate non-native grasses (Kentucky bluegrass [POPR] and smooth brome [BRIN2] ) (B) as a function of time-since-fire (TSF) within the patch-burn grazing 40 ac treatment in 2020 at the North Dakota State University Central Grasslands Research Extension Center near Streeter, ND. Error bars represent standard error of mean. (Note: Change in scale between graphs)

**Table 1.3. Bare ground, basal litter, and standing dead cover.** Average cover of bare ground, basal litter, and standing dead within season-long grazing (SLG), patch-burn grazing 20 ac (PB20), and patch-burn grazing 40 ac (PB40) treatments from 2017 through 2020 at the North Dakota State University Central Grasslands Research Extension Center near Streeter, ND. If α = 0.05 was achieved by within year ANOVA, post-hoc Tukey's test was conducted. There were no differences between PBG treatments. P-values are reported for each within year ANOVA and subsequent post-hoc comparisons of PB40 and PB20 treatments relative to the SLG treatment.

| **Cover Type** | | **Treatment** | | | **P-values** | | |
|---|---|---|---|---|---|---|---|
| | **Year** | **PB40** | **PB20** | **SLG** | **Within Year ANOVA** | **PB40 v. SLG** | **PB20 v. SLG** |
| **Bare Ground** | 2017 | 2.50 ± 0.04 | 2.52 ± 0.04 | 0.74 ± 0.18 | <0.001 | <0.001 | <0.001 |
| | 2018 | 3.19 ± 0.60 | 1.71 ± 0.33 | 0.36 ± 0.18 | 0.003 | 0.002 | 0.102 |
| | 2019 | 9.56 ± 2.05 | 5.73 ± 0.86 | 3.62 ± 1.00 | 0.043 | 0.037 | 0.561 |
| | 2020 | 5.31 ± 0.18 | 4.95 ± 0.49 | 0.76 ± 0.15 | <0.001 | <0.001 | <0.001 |
| | | | | | | | |
| **Basal Litter** | 2017 | 90.98 ± 1.02 | 91.20 ± 0.35 | 85.22 ± 8.24 | 0.622 | - | - |
| | 2018 | 76.53 ± 1.95 | 76.28 ± 1.20 | 82.21 ± 0.95 | 0.028 | 0.049 | 0.040 |
| | 2019 | 69.55 ± 0.71 | 76.73 ± 2.99 | 83.65 ± 2.16 | 0.004 | 0.003 | 0.114 |
| | 2020 | 86.90 ± 0.45 | 85.80 ± 0.57 | 92.81 ± 0.97 | <0.001 | <0.001 | <0.001 |
| | | | | | | | |
| **Standing Dead** | 2017 | 4.37 ± 0.63 | 4.45 ± 1.02 | 6.73 ± 1.66 | 0.324 | - | - |
| | 2018 | 1.49 ± 0.14 | 1.71 ± 0.09 | 1.80 ± 0.10 | 0.185 | - | - |
| | 2019 | 1.60 ± 0.14 | 1.95 ± 0.18 | 3.24 ± 0.78 | 0.081 | - | - |
| | 2020 | 1.25 ± 0.17 | 1.69 ± 0.55 | 2.23 ± 0.61 | 0.399 | - | - |

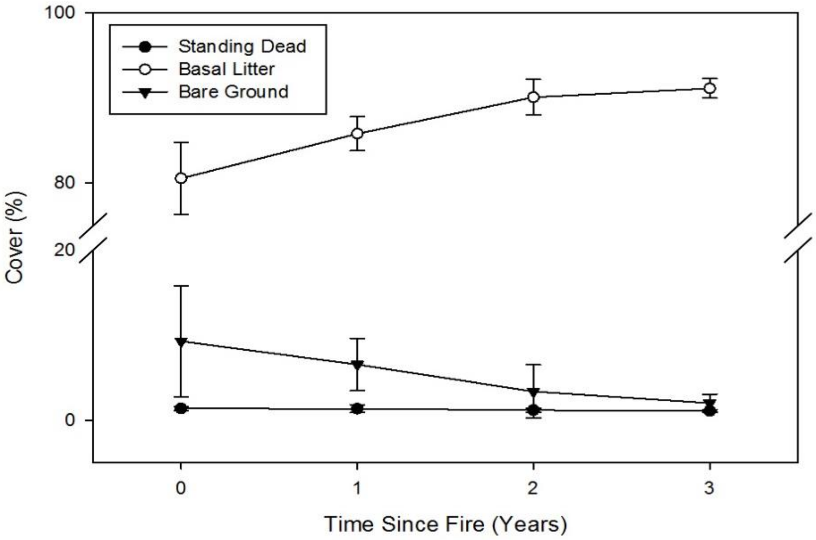

**Figure 1.6. Bare ground, basal litter, and standing dead cover with time-since-fire.** Average percent cover of basal litter, bare ground and standing dead as a function of time-since-fire (TSF) within the patch-burn grazing 40 ac treatment in 2020 at the North Dakota State University Central Grasslands Research Extension Center near Streeter, ND. Error bars represent standard error of mean. (Note: Change in scale between graphs)

## Discussion

Current land management in the NGP deviates from historic disturbance regimes and contributes to biodiversity declines and invasion of non-native grasses, creating novel ecosystems (Hobbs et al. 2009; Toledo et al. 2014; DeKeyser et al. 2015). Restoring heterogeneity-based disturbances in these grasslands can facilitate biodiversity conservation and decrease non-native grass expansion (Kelly et al. 2015; Dornbusch et al. 2020). We applied patch-burn grazing at two scales to pastures with novel plant community assemblages that were excluded from fire since at least the late 1970s. Though year-to-year variations in precipitation likely resulted in overall changes of plant communities in all treatments, PBG treatments caused changes in plant community composition, and increased plant diversity and richness while inhibiting non-native grasses, when compared to SLG.

Shifts in PBG plant community compositions were largely driven by relative declines in non-native grasses (predominantly bluegrass and smooth brome) coupled with relative increases of native grasses and forbs, which is consistent with previous studies conducted in the NGP (Dornbusch et al. 2020) and Southern Great Plains (Coppedge et al. 1998; Fuhlendorf & Engle 2004). The underlining mechanism resulting in these shifts can likely be attributed to changes in basal litter and bare ground following burning and focal grazing. Native plant communities in the NGP are restricted by increased basal litter and thatch layers associated with exotic grass invasion (Toledo et al. 2014, Limb et al. 2018). Increased basal litter accumulation can also decrease nutrient deposition, water infiltration, and sunlight, inhibiting native plant growth (Knapp & Seastedt 1986; Burke et al. 1998; Johnson et al. 2020) by creating a physical barrier between seeds of native plants and mineral soil, affecting seedling establishment (Fowler 1988; Printz & Hendrickson 2015). Burning and grazing these landscapes can ease these inhibitory effects by reducing amount of basal litter and thatch (Dornbusch et al. 2020). This in-turn increases the amount of bare ground available for establishment and expansion of forbs (Collins 1987; Adamidis et al. 2019; Johnson et al. 2020) and native grasses (Aguilera & Lauenroth 1993; Fowler 1988), altering species composition. We reduced basal litter and increased bare ground following burning, but changes were modest and less than in other systems (Fuhlendorf & Engle 2004; Archibald et al. 2005; Ansley et al. 2006). It is likely that continued focal disturbance of fire and grazing will reduce basal litter and increase bare ground.

One of the biggest factors determining the amount basal litter, bare ground, and therefore species composition of patches within PBG pastures was time-since-fire (TSF). Succession drives plant community composition as time progresses from a focal disturbance, such as fire and grazing (Gibson & Hulbert 1987; Coppedge et al. 1998). Community composition resembles pre-fire composition after approximately 3-5 years since disturbance, in tall and mixed-grass prairies (Fuhlendorf & Engle 2004). Progressively burning patches creates a mosaic of patches in differing TSF and therefore differing composition within a pasture. Community composition of recently burned patches was more variable than patches with a TSF of 2-3 years due to increases in forb abundance and decreases in grass abundance (Coppedge et al. 1998; Engle et al. 1998; Dornbusch et al. 2020). Though most grass species on our study sites were primarily cool-season grasses, which do not normally response well to early-season fire (Vermeire et al. 2011), native and non-native grasses did not respond similarly to burning, as non-native grasses decreased in abundance while native grasses increased. Because non-native grasses dominate this system, native grasses were likely able to capitalize on the temporary reduction of non-native grasses caused by direct mortality and reductions in basal litter caused by fire and grazing (Hendrickson & Lund 2010; Kral et al. 2018; Dornbusch et al. 2020), resulting in increased propagation and abundance of native grasses (Smart et al. 2013; Russell et al. 2015). As TSF progressed, the relationship between non-native grasses and forbs was inversely related with native grasses responding similarly to forbs. This resulted in less variable patch communities after 2-3 years, causing dissimilarity of patch communities within a pasture (Fuhlendorf & Engle 2004). It is likely this dissimilarity, combined with increased native grass abundance, contributed to changes in community composition at the pasture-level. Therefore, when establishing heterogeneous ecosystems through pyric-herbivory, a mosaic landscape of patch types differing in TSF is needed to increase biodiversity of the grassland ecosystems, as opposed to uniformly burning or grazing pastures resulting in a homogenous ecosystem (Fuhlendorf & Engle 2001, 2004).

Species diversity and richness of PBG treatments increased relative to the homogenous disturbance regime of the SLG treatment with time during this study. This is similar to other work conducted in NGP invaded by non-native grasses, such as bluegrass and smooth brome, (Dornbusch et al. 2020) and in the Southern Great Plains (Collins 1987), as added and interactive disturbances can increase species diversity and richness in grassland ecosystems (Collins & Barber 1985; Hartnett et al. 1996; Collins & Calabrese 2012; Briggler et al. 2017). Due to the dominance of non-native grasses and lack of bare ground in 2020, PBG did not exert an overall increase in diversity and richness from 2017 to 2020 but was able to inhibit non-native grass expansion and maintain diversity. However, diversity in the SLG continued to decrease due to increased dominance of non-native grasses. This relative increase of PBG diversity was likely a result of higher abundance of forbs and native grasses, and a relative increase in species richness.

In bare ground limited grassland ecosystems, establishment of forb species can increase due to natural disturbances which can in-turn increase species richness (Collins 1987; Coppedge et al. 1998; Dornbusch et al. 2020). Establishment of new forb species can be affected by fire frequency as annual fires have been shown to negatively impact establishment of new species but can still increase forb density (Biondini et al. 1989). By having a four-year fire return interval, this likely allowed new forbs to establish in the successive growing season post-fire, resulting in species richness being highest one year-since-fire. Although richness decreased with TSF, some newly established forb species were likely able to persist within PBG pastures (Collins 1987). The combination of newly established forb species along with increases in the abundance of forbs and native grasses was likely able to influence diversity of PBG treatments enough in 2020 to keep it from decreasing as much as it did in the SLG.

Since establishment of new species likely did not occur the same year of the burn, richness, and therefore diversity, were highest in one year-since-fire patches, but subsequently decreased with TSF. In the NGP, plant communities that are burned in the early-growing season can take approximately one year to resemble similar pre-fire diversity (Kral et al. 2018), but due to increased focal disturbance, patch-burn grazing can increase richness and diversity more than just burning (Collins 1987; Briggler et al. 2017). This would support the model predicted by Collins and Barber (1985) by where a combination of disturbances has a greater positive influence on richness and diversity than just a single disturbance in native grassland ecosystems. Because patches are effectively rested after fire, due to a lack of grazing, this caused diversity and richness to decrease with TSF (Gibson & Hulbert 1987). Due to the dynamics of TSF and this ecosystem being dominated by non-native grasses and thick thatch layers, PBG treatments only caused relative increases diversity and richness. We believe that continued burning and grazing will have a greater effect on diversity and richness over time as thatch layers, basal litter, and non-native grasses continue to decrease due to focal disturbance resulting in increased native species diversity and richness in this novel ecosystem (Toledo et al. 2014; Kral et al. 2018; Dornbusch et al. 2020).

The NGP rangelands invaded by bluegrass and smooth brome are novel ecosystems that provide unique challenges to land managers and conservationists (Toledo et al. 2014; DeKeyser et al. 2015; Printz & Hendrickson 2015). These grasses are highly competitive with native grasses as they are grazing-tolerant and begin growing earlier in the growing season but can be susceptible to fire (Toledo et al. 2014). Burning in the early-growing season (Hendrickson & Lund 2010; Kral et al. 2018), and annual and biennial fires (Smart et al. 2013) can reduced non-native grass cover. In this study, we found that PBG did not necessarily decrease non-native grass composition, but rather decreased it's rate of expansion compared to SLG. Of the two dominant non-native grasses, smooth brome was the most strongly impacted by PBG. Unlike bluegrass, smooth brome is more sensitive to defoliating events such as fire and grazing (Murphy

& Grant 2005). Bahm et al. (2011) found that smooth brome cover was consistently lower on burned sites than untreated sites in each year of the study up to three years post-fire after a single application of fire, while bluegrass varied from year-to-year. While bluegrass was significantly higher in the SLG by the end of our study, PBG did not appear to cause an overall decrease in its composition. This is similar to other work done in this novel ecosystem, as bluegrass expansion continued to increase with SLG while being inhibited by PBG (Dornbusch et al. 2020). This suggests that bluegrass dominance is continuing to increase in the NGP (DeKeyser et al. 2015).

Dominant non-native grasses were affected by TSF as composition increased successively with each TSF interval one-year post-fire. Bluegrass and smooth brome abundance increased with TSF due to a lack of defoliating events and returns to similar non-defoliated conditions after three years (Smart et al. 2013). Increases in bluegrass abundance with TSF is also dependent on season of burn, as dormant and late-growing season fires can have a greater affect than early-growing season fires (Kral et al. 2018). It should also be noted that in 2019, our study site received abnormally high amounts of late growing season precipitation, leading to highly productive growing season. It is likely that the increase in residual plant litter from the previous growing season was a strong mechanism for the increase in bluegrass in the 2020 growing season. The resulting basal litter accumulation would give bluegrass a competitive advantage over other plant species, causing an increase in its percent composition (Toledo et al. 2014; Printz & Hendrickson 2015). Though PBG did have a negative impact on both dominant non-native grasses compared to SLG, continued research is needed to determine whether further implementation of PBG can reduce composition of bluegrass.

Pyric-herbivory has been shown to have dynamic effects within plant communities of the southern tall grass prairie (Collins 1987; Coppedge et al. 1998; Fuhlendorf & Engle 2004), which can result in highly biodiverse ecosystems (Fuhlendorf et al. 2006, 2009, 2010; Ricketts & Sandercock 2016; Scasta et al. 2016) but has not been studied to the same extent in the northern mixed-grass prairie (Dornbusch et al. 2020). This is further compounded by the development of novel ecosystems dominated by non-native grasses creating unique challenges for land managers whose objectives are to restore and conserve biodiversity in this ecosystem (Toledo et al. 2014; Printz & Hendrickson 2015). Completely disrupting the positive feedbacks that increase dominance of these plant species and fully restoring these ecosystems is highly unlikely (Hobbs et al. 2009; Toledo et al. 2014), but PBG has shown promise in disrupting these positive feedbacks enough to limit non-native grass expansion and increase native species abundance (Dornbusch et al. 2020). Because novel ecosystems are highly resilient to changes, dramatic results may not be immediate. Continued implementation of PBG may result in a further increase of native species abundance and possibly an overall decrease in the abundance of non-native grasses. Further research is needed to determine the long-term effects of continued implementation of PBG in this novel ecosystem and to establish whether an ecological threshold has been crossed, in which PBG can only maintain dominance of non-native grasses versus actual declines.

## Implications

Initial results from this long-term study suggest that re-establishing pyric-herbivory can conserve biodiversity, inhibiting non-native grass expansion in the novel ecosystems of northern mixed-grass prairie. A longer timespan is needed to determine what cumulative effects multiple applications of fire may have on plant communities in this system. Repeated focal disturbance could cause a reduction of thick thatch layers resulting in dramatic changes in the native plant community (Toledo et al. 2014). It is possible that this system has reached an ecological threshold by which pyric-herbivory can only limit bluegrass and smooth brome dominance (Dornbusch et al. 2020). If this is the case, additional management techniques such as herbicide application may be needed to cross this threshold, though it would likely only result in further reduction of these grasses and not eradication (Ansley et al. 2010; Ereth et al. 2017). Full restoration to a native grassland is likely unobtainable as non-native species will always persist in these grasslands (Murphy & Grant 2005; Grant et al. 2020). Therefore, reasonable management goals in this system should be to reduce non-native grass abundance as much as possible, while increasing native species abundance and diversity (Toledo et al. 2014). Nonetheless, this study concludes that even in a novel grassland ecosystem, re-establishing pyric-herbivory in the form of PBG can cause dynamic changes in plant communities which can result in highly biodiversity ecosystem and can therefore serve as a viable conservation-based land management technique in the northern mixed-grass prairie.

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# CHAPTER 2: DYNAMICS OF SMALL MAMMAL COMMUNITIES IN RESPONSE TO PYRIC-HERBIVORY IN THE NORTHERN MIXED-GRASS PRAIRIE

## Abstract

Heterogeneity is vital to supporting biodiversity in ecosystems. Historically, heterogeneity in the Great Plains resulted from a combination of inherent and disturbance-based heterogeneity, caused by pyric-herbivory. This produced landscapes with variable habitat within which a variety of wildlife species could occupy. Present land management promotes uniform use of rangelands and reduction of the use of fire which has resulted in the reduction of heterogeneous vegetation and biodiversity. We reintegrated pyric-herbivory using patch-burn grazing, which is designed to mimic the dynamic spatial and temporal disturbance patterns of pyric-herbivory, to re-establish heterogeneity and potentially increase biodiversity of our grasslands. In our study, we compared how small mammal communities were affected by two patch-burn grazing treatments (PBG), differing in size and season of fire, to a traditional season-long grazing system (SLG). Our first PBG treatment consisted of 16 ha patches burned in the early-growing season (PB40). Similarly, our second PBG treatment consisted of 16 ha patches, but with 8 ha burned in the early-growing season and 8 ha burned in the late-growing season (PB20). We sampled small mammal communities over the course of four years to determine composition and abundance, to make comparisons between treatments and time-since-fire. We found the PB40 differed from the SLG communities at the conclusion of our study ($P \leq 0.10$), but PB20 did not ($P \geq 0.10$). Differences in community composition were likely driven by dissimilarity of patch communities within PB40 pastures as a result of a successional gradient of vegetation caused by time-since-fire. Additionally, we found that snowpack was a primary influencer of abundance in this study. By creating a mosaic of heterogeneous vegetation, PBG

was able to increase diversity of small mammal communities. As such, PBG can serve as an effective conservation-based land management system to restore pyric-herbivory in rangeland ecosystems and thereby increase biodiversity in the northern mixed-grass prairie.

## Introduction

Heterogeneity is essential to a biodiverse ecosystem (Ostfeld et al. 1997; Fox & Fox 2000). The combination of inherent heterogeneity, caused by abiotic factors such as soil, climate, topography, and nutrient availability, and disturbance-driven heterogeneity create heterogenous habitat structure (Fuhlendorf et al. 2017). The resulting heterogenous habitat structure, primarily driven by the structure of vegetation, can support a variety of wildlife species at extreme ends of the habitat structure gradient (Fox & Fox 2000; Fuhlendorf & Engle 2001). In the Great Plains, the interaction between grazing and fire, otherwise known as pyric-herbivory, was one of the primary sources of disturbance-driven heterogeneity (Fuhlendorf et al. 2009). Problematically, in much of the Great Plains, this interactive disturbance has been removed in rangelands in favor of continuous season-long grazing, resulting in a lack of heterogeneity in these rangelands (Fuhlendorf et al. 2012).

Pyric-herbivory creates a shifting mosaic of plant communities due to the temporal and spatial interactions of fire and grazing (Fuhlendorf et al. 2009). This occurs when large herbivores, such as bison or cattle, preferentially graze recently burned areas due to the new plant growth being more palatable and nutritious than mature and senescent plant material (Knapp et al. 1999; Vermeire et al. 2004; Allred et al. 2011). This allows patches that had been burned and grazed in previous growing seasons to recover from this focal disturbance (Fuhlendorf et al. 2009; Allred et al. 2011; Gates et al. 2017). These patches begin accumulating dead plant material due to a lack of grazing, which leads to increased fuel loads and probability that this patch will burn again, repeating the cycle of this fire-grazing interaction (Fuhlendorf & Engle 2004; Fuhlendorf et al. 2009). This produces varying plant community composition and structure through space and time on a landscape, which has been found to sustain diverse wildlife communities (Fox 1990; Fuhlendorf et al. 2006, 2010; Ricketts & Sandercock 2016). Because present land management has mostly removed this interaction from the landscape, creating more homogenous ecosystems, there has been an effort to develop land management strategies to reintegrate pyric-herbivory into grassland ecosystems (Fuhlendorf et al. 2012). One such strategy is a patch-burn grazing system (Fuhlendorf & Engle 2001, 2004).

Patch-burn grazing was developed to mimic pyric-herbivory in fire-prone ecosystems (Fuhlendorf & Engle 2001). This grazing treatment establishes discrete patches that can vary or be uniform in size and shape within a continuously grazed pasture. These patches are sequentially burned by random or systematically over the span of multiple years. After all patches in a pasture are burned, fire is reapplied to these patches after a set amount of time. The amount of time between fire applications is known as a fire return interval. The fire return interval, number of patches, and size of patches established for a pasture depends upon land management goals and the time a patch takes to recover from fire and grazing (Fuhlendorf & Engle 2001). Because this grazing system produces a rotational pattern of highly disturbed patches within a matrix of recovering and low disturbance patches, it creates a shifting mosaic of plant communities that very in structure and composition through time and space within a pasture (Fuhlendorf & Engle 2001; 2004). This shifting mosaic provides a wide variety of habitat for wildlife species, more specifically, small mammal species (Fuhlendorf et al. 2010; Ricketts & Sandercock 2016) which are sensitive to changes in vegetative structure due to their short-lived and high fecundity life histories (Grant & Birney 1979; Reed et al. 2007; Alford et al. 2012).

Small mammals fill an important niche within grassland ecosystems. They are a major food source for mesocarnivores, such as coyotes (Brillhart & Kaufman 1995), and many raptor species, where prairie voles (*Microtus pennsylvanicus*) can make up to 41% of an owl's diet (Huebschman et al. 2000). It has also been found that small mammals can influence plant community composition (Reed et al. 2004; Maron et al. 2012), increase plant species richness while also mediating the effects of increased soil Nitrogen on plant species richness (Poe et al. 2019), and increase water infiltration of soils (Laundre 1993). Deer mice (*Peromyscus maniculatus*), the most abundant small mammal in North America, has a diverse diet but is primarily a granivore (animal whose diet consists primarily of seeds) that prefers to consume large-seeded native plants while avoiding small-seeded exotics, such as smooth brome (*Bromus inermis*) (Everett et al. 1978; Witmer & Moulton 2012). This has been found to limit re-establishment of native plant species in some cases (Everett & Monsen 1990). Another common small mammal species, the meadow vole (*Microtus pennsylvanicus*), can have a diet, in prairie systems, that has almost no Kentucky bluegrass (*Poa pratensis*), except for in the winter, and consists mostly of big bluestem (*Andropogon gerardii*) (Lindroth & Batzli 1984). As such, increases in these small mammal species could be problematic, as much of the Northern Great Plains is dominated by smooth brome and Kentucky bluegrass, non-native grasses, which has compounded the effects of homogeny of brought on by uniformed disturbance, decreasing biodiversity (Toledo et al. 2014). Therefore, increases in the abundance of these small mammal species could result in increases in of these non-native grasses, which already dominate this ecosystem.

In fire-prone ecosystems, small mammals have adapted their behavior time to the changes brought on by disturbances, such as fire and grazing. These disturbances can alter vegetive structure, both spatially and temporally, which can cause small mammal species to react differently depending on habitat needs (Ricketts & Sandercock 2016). Generalist species, such as the deer mouse, adapt well to fire and grazing conditions because of their ability to occupy various habitat types (Reed et al. 2007; Witmer & Moulton 2012). In fact, deer mice have been found to respond favorably to fire and grazing, initially increasing in abundance after fire but decrease in abundance as time-since-fire increases (Fuhlendorf et al. 2010; Burke et al. 2020). Conversely, vole species (*Microtus spp*.) are very habitat sensitive, requiring litter layers (dead plant material) and vegetative cover (Burke et al. 2020; Ricketts & Sandercock 2016). Because of this, vole abundance initially decreases after fire, but increases with time-since-fire as litter and vegetative cover re-accumulating with time (Fuhlendorf et al. 2010; Ricketts & Sandercock 2016). Other small mammals like the hispid pocket mice (*Chaetodipus hispidus*) and the thirteen-lined ground squirrel (*Ictidomys tridecemlineatus*) prefer areas that are transitioning from disturbed to recovered areas (Fuhlendorf et al. 2010; Ricketts & Sandercock 2016; Scasta et al. 2016). In previous studies, patch-burn grazing treatments were found to create habitat heterogeneity suitable to supporting diverse small mammal communities (Fuhlendorf et al. 2010; Ricketts & Sandercock 2016). Because small mammals are an integral part of the grassland ecosystem, it’s important we study the effects of different grazing management systems on their community structures.

The objective of this study is to determine what effect pyric-herbivory in the form of patch-burn grazing has on small mammal communities using three treatments: two patch-burn grazing treatments that vary in size and season of fire and a conventional season-long grazing treatment. We hypothesis that the patch-burn grazing treatments will create a shifting mosaic of plant communities that will support a diverse small mammal community, while the season-long grazing treatment will promote even grazing pressure, creating a uniform vegetation structure, and decreased small mammal diversity.

## Methods

### *Study Area*

This study was conducted at the North Dakota State University Central Grassland Research Extension Center (CGREC) in south-central North Dakota (lat. 46°46’N, long. 99°28’W). The CGREC is located in the Missouri Coteau ecoregion of the northern mixed-grass prairie of the Great Plains. The Coteau is characterized by irregular, rolling plains and depressional wetlands (USDA-SCD 1981). The climate is characterized as temperate and receives an average annual precipitation of 49.5 centimeters and temperature of 4.6° C (1991-2016, NOAA-NCEI 2021). Average winter snowpack, from October through April, from winter

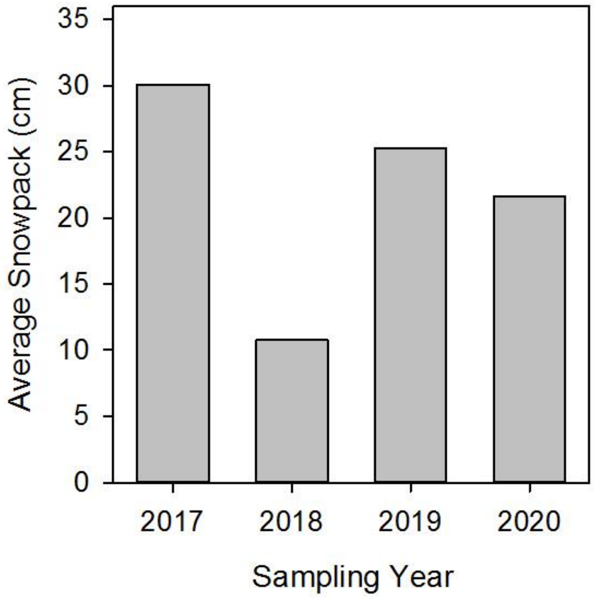

**Figure 2.1. Mean winter snowpack preceding each sampling year, from October through April, near Streeter, ND, USA using data from 2016 through 2020.** Weather data acquired at the Streeter 7 NW, ND US USC00328415 station (46.7154$^{o}$N, -99.4475$^{o}$W) and retrieved from the National Environmental Satellite, Data, and Information Service of the National Oceanic and Atmospheric Administration (NOAA 2021).

season preceding each sampling year of the study site are summarized in Figure 2.1 (2016-2020, NOAA-NCEI 2021). The vegetation of this area is typical of a northern mixed-grass prairie invaded by Kentucky bluegrass (*Poa pratensis*) and smooth brome (*Bromus inermis*) (Limb et al. 2018). Prominent native grasses include green needlegrass (*Nasella viridula*), needle and thread (*Hesperostipa comata*), western wheatgrass (*Pascopyrum smithii*), big bluestem (*Andropogon gerardii*), and little bluestem (*Schizachyrium scoparium*). Other key species in this area include western snowberry (*Symphoricarpos occidentalis*), goldenrods (*Solidago & Oligoneuron* spp.), white heath aster (*Symphyotrichum ericoides*), western ragweed (*Ambrosia psilostachya*), and common yarrow (*Achillea millefolium*).

### ***Treatment Structure***

Three treatments were applied to twelve pastures (experimental units) in the study area, with four pastures (replications) per treatment. Each pasture was approximately 48 to 65 ha and artificially sub-divided into four 16 ha patches. Two patch-burn grazing treatments (PBG) were applied: (1) patch-burn grazing 16 ha (PB40) treatment, with early-growing season prescribed fires (early to mid-May) being applied to one of four 16 ha patches (one-fourth of the pasture), and (2) patch-burn grazing 8 ha treatment (PB20) with early-growing season fire being applied to 8 ha (one-eighth of the pasture) of a 16 ha patch and a late-growing season fire (August to late-September) applied to the remaining 8 ha of the patch. These patch-burn grazing treatments are a management technique intended to mimic a historic disturbance regime of pyric-herbivory (Fuhlendorf & Engle 2001). Our third treatment was a season-long grazing treatment (SLG) intended to replicate a conventional cow/calf grazing management system. All treatments were grazed with Angus cross-bred cow/calf pairs from mid-May to mid-Oct at a moderate stocking rate to achieve approximately 40 to 50% degree of disappearance. The stocking rates for all treatments were 2.26-2.31 Animal Unit Months/ha. Because prescribed fires were applied when fuel moisture has decreased sufficiently enough to sustain a fire, we were only able to implement late-growing season fires to half of our PB20 pastures in 2018 and none in 2019.

### ***Small Mammal Sampling***

We sampled small mammals throughout June of each year, with each sampling period consisting of 25 days. Treatments were sampled concurrently to prevent biases associated with weather or time of day. Trapping occasions lasted two consecutive nights for each sampling site. Two sampling sites were randomly established in each patch. At each sampling site, we established 40x40 meter grids of 25 Sherman live-traps (7.6 x 8.9 x 22.9 cm), with traps spaced 10 meters apart. Traps were baited with a combination of rolled oats and peanut butter. We sampled one site randomly per pasture, per trapping occasion (12 sites / 1 per pasture). Two trapping occasions for a total of 100 trap-nights per patch (400 trap-nights per pasture) were used to sample small mammal patch communities. A "trap-night" being the number of traps used multiplied by the number of nightly trapping periods. Sampled individuals were marked with ear tags – Style 1005-3 from the National Band and Tag Company. We recorded species, sex, age, and other body measurements from sampled individuals.

### ***Statistical Analysis***

We used sampling data to generate an estimate of abundance with closed-capture Huggins models for each trapping site using Program MARK (version 9.0), based off the encounter history of each individual. To analyze the dynamics of small mammal communities between our treatments we utilized principal component analysis (PCA) based off the average pasture species composition of treatments within each year, based off the average estimated abundance of our top five most captured species in our study, in PC ORD 7.0 (*n* = 4) (McCune &

Mefford 2018). Using data from 2020, we also used this analysis to compare community dynamics of small mammal communities as a function of time-since-fire (TSF) in PB40 treatment patches (*n* = 4) and compared TSF communities to the SLG community patches (*n* = 16) based off our top six most captured species in 2020. We also overlayed ‘hilltop plots’ of basal litter and bare ground cover, which represent the non-linear relationship between these variables to community composition, to better understand how they, as an environmental variables, can effect community composition with TSF (Nelson et al. 2015). We tested for differences between years, treatments, treatments within year, and treatments across years with permutational multivariate analysis of variance (PerMANOVA) using Sorenson (Bray-Curtis) distance and post-hoc Tukey tests (Anderson 2001). To test for differences between TSF communities and their relationship to the SLG community, we used multi response permutation procedure test (MRPP) using Euclidean distance and post-hoc Tukey tests.

Mean dissimilarity of small mammal patch communities was determined for each pasture using Sorenson (Bray-Curtis) distance from which we found the mean for each treatment (*n* = 4). We determined the mean dissimilarity of each pasture based off six possible dissimilarity comparisons that could be made between small mammal patch communities. Mean abundance of treatments was calculated as the mean estimated abundance of sampling sites within a pasture (*n* = 4). We made comparisons of dissimilarity and abundance between treatments within each year using one-way analysis of variance (ANOVA) and post-hoc Tukey’s tests in IBM-SPSS Statistics software package (Version 27; IBM 2020). Correlation analysis was used to determine relationships between species and different types of dead plant material (litter), such as basal litter, standing dead litter, and bare ground, and between species and TSF using Pearson correlation coefficients in IBM-SPSS Statistics software package (Version 27; IBM 2020).

Vegetation data used in this analysis was collected from a study conducted concurrently to this study (M.C. Hamel, *unpublished data*). Data used to correlate species to plant litter was conducted using pasture data from all years, while species correlations to TSF were conducted using data from 2020 PB40 patches. Additionally, we used correlation analysis to determine what effect snowpack from the previous winter might have on the number of total captured individuals (all species) and deer mice (most abundant species) in each year using IBM-SPSS Statistics software package (Version 27; IBM 2020). Significance of all tests conducted was determined for $P$ values at $\alpha = 0.10$.

**Table 2.1. Total number of unique individuals captured.** Number of the unique individuals of 10 species (species abbreviations enclosed in parentheses) encountered from 2017 through 2020 at the North Dakota State University Central Grasslands Research Extension Center near Streeter, ND.

| **Species** | **Treatments** | | | |
|---|---|---|---|---|
| | **PB40** | **PB20** | **SLG** | **Species Totals** |
| **Deer mouse (PEMA)**<br>***Peromyscus maniculatus*** | 86 | 76 | 46 | 208 |
| **Prairie vole (MIOC)**<br>***Microtus ochrogaster*** | 9 | 6 | 19 | 34 |
| **Meadow vole (MIPE)**<br>***Microtus pennsylvanicus*** | 3 | 5 | 5 | 13 |
| **Thirteen-lined ground squirrel (ICTR)**<br>***Ictidomys tridecemlineatus*** | 6 | 10 | | 16 |
| **Richardson's ground squirrel (URRI)**<br>***Urocitellus richardsonii*** | 3 | 6 | 1 | 10 |
| **Meadow jumping mouse (ZAHU)**<br>***Zapus hudsonius*** | 2 | | 2 | 4 |
| **Northern pocket gopher (THTA)**<br>***Thomomys talpoides*** | 2 | | | 2 |
| **Least weasel (MUNI)**<br>***Mustela nivalis*** | | 1 | | 1 |
| **White-footed mouse (PELE)**<br>***Peromyscus leucopus*** | | 1 | | 1 |
| **Northern short-tailed shrew (BLBR)**<br>***Blarina brevicauda*** | 1 | | | 1 |
| **Treatment Totals:** | 112 | 105 | 73 | 290 |

## Results

From 2017 to 2020, we captured a total of 289 unique individuals made up of 10 species (Table 2.1). The PB40 had the most captured individuals with 114, followed by the PB20 at 103, and the SLG at 72 (Table 2.1). There were more than twice as many deer mice (*Peromyscus maniculatus*) captured than all other species combined and was most captured species in each treatment. The next most abundant species were prairie voles (*Microtus ochrogaster*), thirteen-lined ground squirrels (*Ictidomys tridecemlineatus*), meadow voles (*Microtus pennsylvanicus*), and Richardson's ground squirrel (*Urocitellus richardsonii*), respectively (Table 2.1).

Small mammal community composition varied by year ($P < 0.001$) and by treatment ($P = 0.014$). We also found differences over time within PB40 ($P = 0.033$) and SLG ($P = 0.038$) communities, but not the PB20 treatment ($P = 0.203$). There were no differences between treatment communities within any year except for in 2020 ($P = 0.092$). Pairwise comparisons of 2020 treatments show PB40 was different to SLG ($P = 0.032$), while PB20 was not different compared to SLG ($P = 0.191$) or PB40 ($P = 0.780$). PCA analysis produced an ordination accounting for 51.3% of the variation in the data. PCA axes 1 and 2 had eigenvalues of 1.29 and 1.28, respectively (Figure 2.2). Species most associated with axis 1 include Richardson's ground squirrels (URRI) ($r = 0.69$), meadow voles (MIPE) ($r = -0.53$), thirteen-lined ground squirrels (ICTR) ($r = -0.53$), and prairie voles (MIOC) ($r = 0.45$), while species most associated with axis 2 included deer mice (PEMA) ($r = 0.70$), ICTR ($r = 0.67$), MIOC ($r = -0.40$), and MIPE ($r = -0.36$). We also found axis 2 was positively associated with bare ground cover ($r = 0.53$). Generally, PBG treatment by year compositions shifted along axis 2, suggesting these communities were affected by changes in bare ground (Figure 2.2). Conversely, SLG composition varied by year along axis 1, except from 2019 to 2020 where all treatment compositions were negatively associated to axis 2, relative to their 2019 compositions (Figure 2.2). Further analysis of Bray-Curtis dissimilarity of patch communities within pastures shows treatments were not different until 2020, where PB40 had a significantly higher dissimilarity than PB20 and SLG ($P \leq 0.1$) (Figure 2.3).

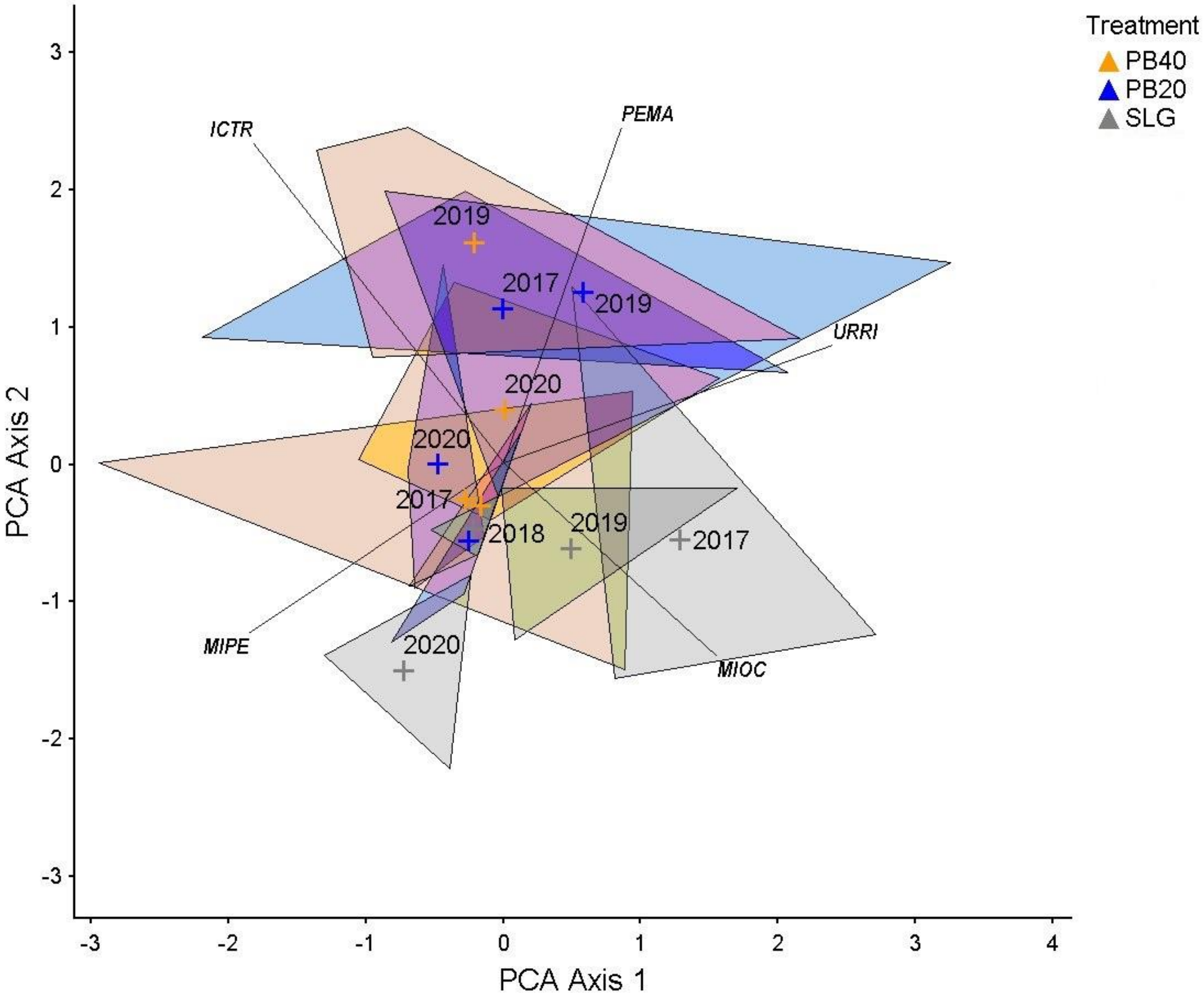

**Figure 2.2. PCA ordination of average pasture small mammal community composition.** Community composition is represented by convex hulls for each year by treatment of top five encounter species (represented by their species code). Treatments shown are: PB40, PB20, and SLG from 2017 through 2020 at the North Dakota State University Central Grasslands Research Extension Center near Streeter, ND. Greater separation of hulls suggests greater differences in community composition. (Note: 2018 label represents all year by treatment communities)

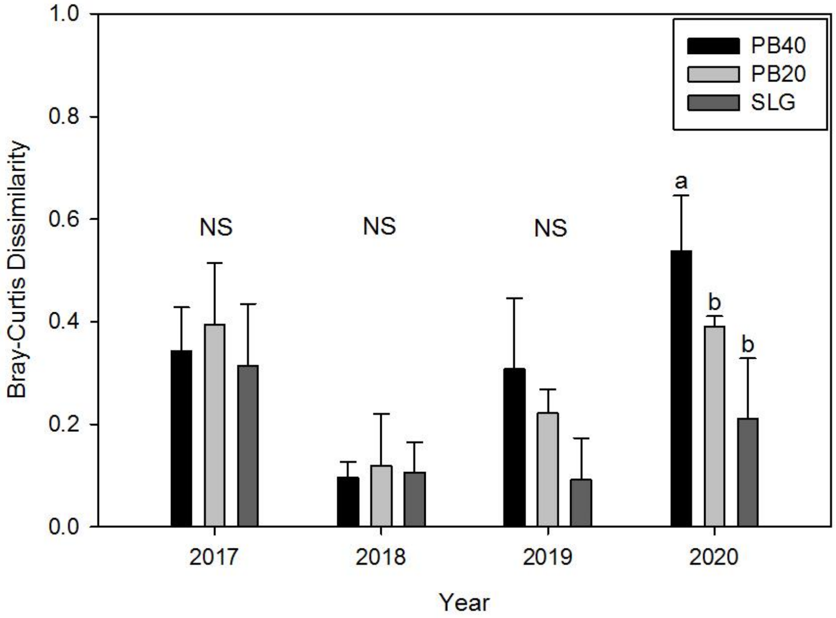

**Figure 2.3. Bray-Curtis dissimilarity of patch communities**. Average dissimilarity of patches within pastures by treatment from 2017 through 2020 at the North Dakota State University Central Grasslands Research Extension Center near Streeter, ND. Letters (a & b) represent statistical differences of treatments within each year ($p \leq 0.10$). Error bars represent standard error of the mean.

Time-since-fire did affect small community composition, which differed to the SLG treatment depending on time-since-fire (*P* = 0.023). Pairwise comparisons show the SLG community differed to the 0- and 2-year-since-fire communities (*P* = 0.009 & *P* = 0.040; respectively). Further, we found differences between 0- and 3-year-since-fire communities (*P* = 0.008) and 2- and 3-year-since-fire communities (*P* = 0.061). PCA analysis of time-since-fire communities yielded an ordination of which 51.3% of the variation in the data was explained (Figure 2.4). PCA axes 1 and 2 had eigenvalues of 1.78 and 1.30, respectively. Species most associated with axis 1 were MIOC (r = -0.91) and MIPE (r = -0.92). Species most associated with axis 2 were PEMA (r = 0.74), meadow jumping mouse (ZAHU) (r = -0.60), and URRI (r = 0.55). Furthermore, we found associations between axis 2 and basal litter (r = -0.42), and bare ground (r = 0.38). Using hilltop overlays (which show regions of an ordination that are most associated with a certain variable) we observed that time-since-fire communities of 0-, 1-, and 2-

years-since fire and PEMA, URRI, and ICTR were most associated with bare ground (Figure 2.5). Additionally, 3-years-since-fire and SLG communities and MIOC, MIPE, and ZAHU were more associated with basal litter (Figure 2.5).

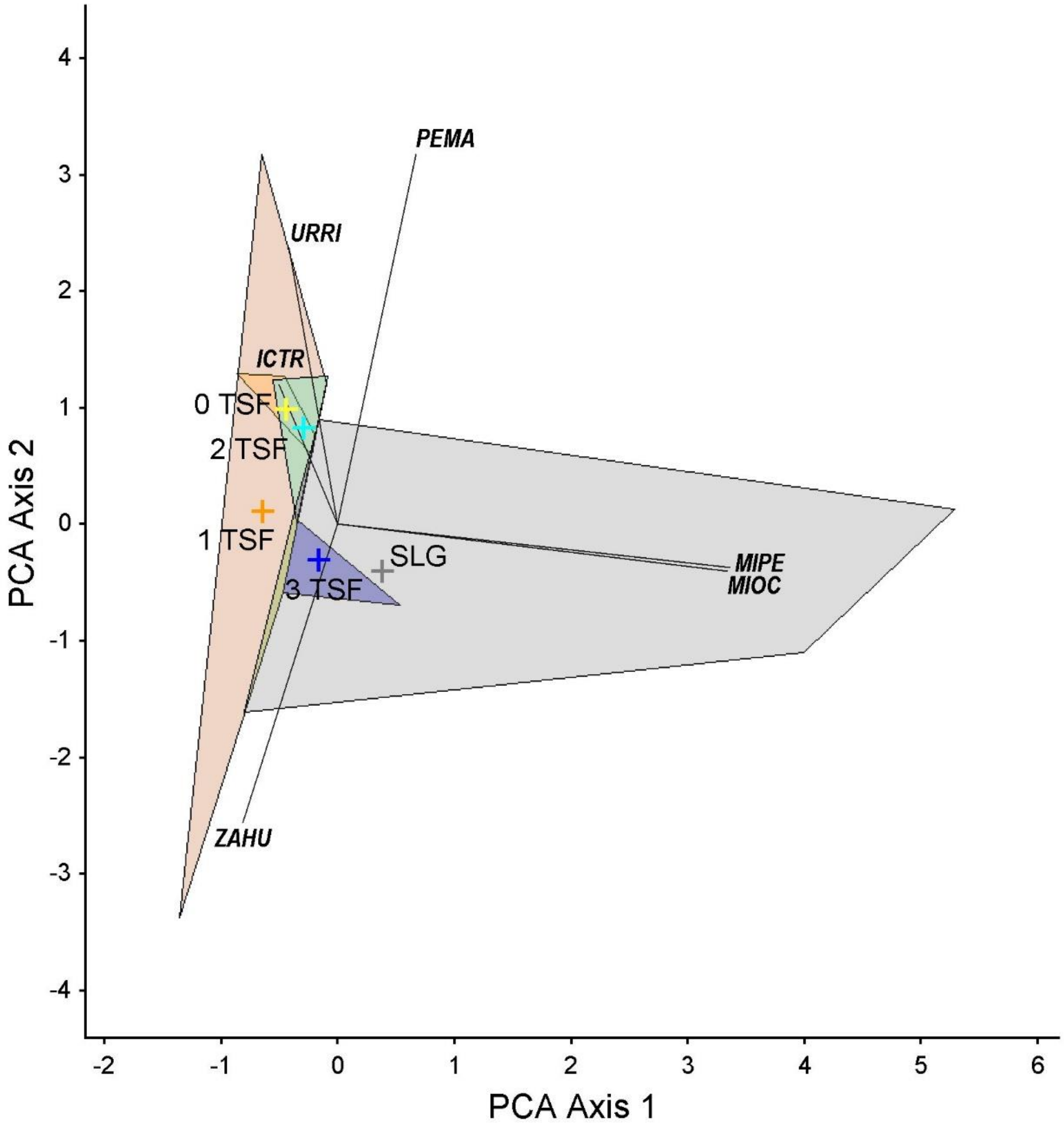

**Figure 2.4. PCA ordination of average patch small mammal community composition for each time-since-fire interval and season-long grazing.** Community composition of time-since-fire (TSF) and SLG community is represented by convex hulls of the top six encountered species (represented by their species code) in 2020 at the North Dakota State University Central Grasslands Research Extension Center near Streeter, ND. Greater separation of hulls suggests greater differences in community composition.

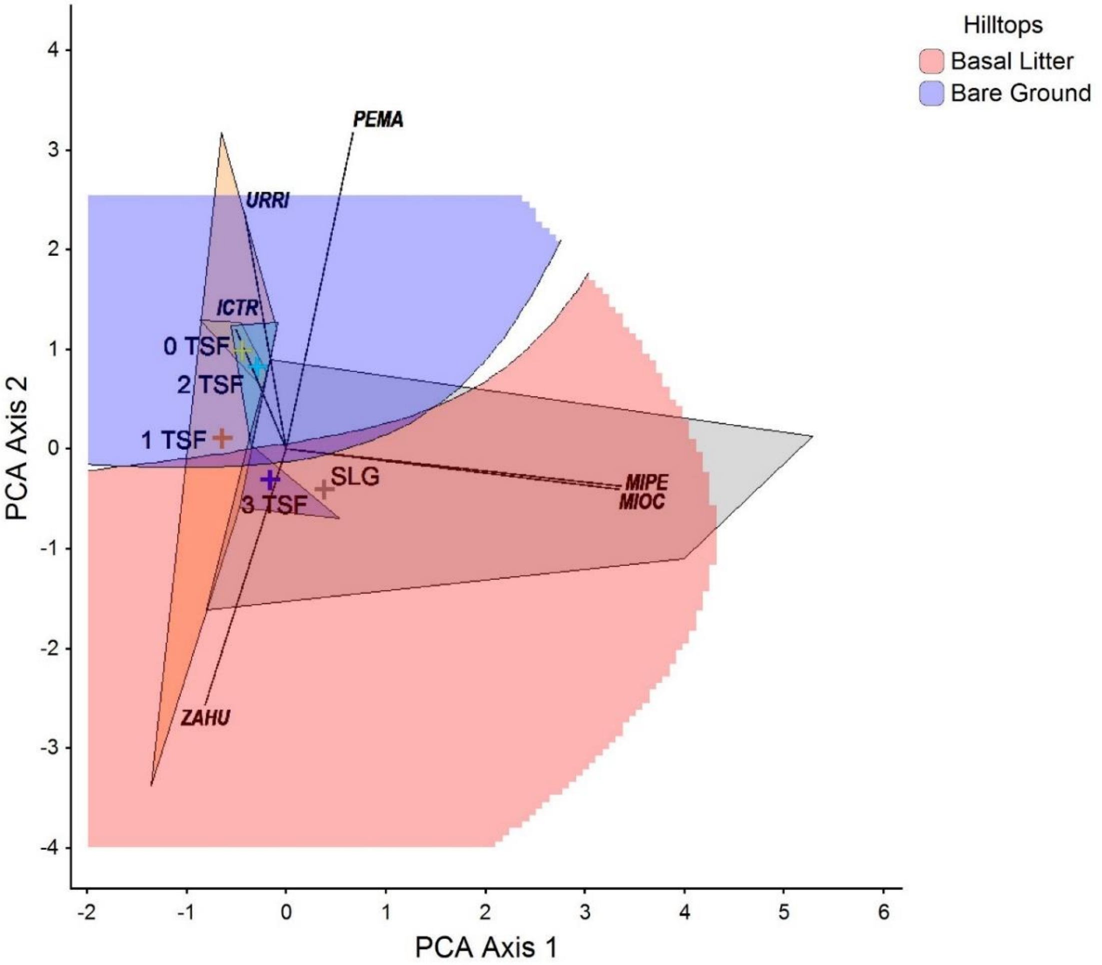

**Figure 2.5. PCA ordination of average patch small mammal community composition for each time-since-fire interval and season-long grazing with hilltop overlays.** PCA ordination of patch community composition for each time-since-fire (TSF) and SLG community represented of our top six encounter species (represented by their species code) with hilltop overlays depicting areas of the ordination most associated with that variable in 2020 at the North Dakota State University Central Grasslands Research Extension Center near Streeter, ND.

**Table 2.2. Correlations of small mammal species to three types of plant litter cover.** Average species abundance was correlated to standing dead litter, basal litter, and bare ground cover using data from 2017 through 2020 at the North Dakota State University Central Grasslands Research Extension Center near Streeter, ND.

| **Cover Type** | **Vole Species** (MIOC + MIPE) | | **Deer mouse** | | **Thirteen-lined ground squirrel** | | **Richardson's ground squirrel** | |
|---|---|---|---|---|---|---|---|---|
| | ***r*** | ***P*** | ***r*** | ***P*** | ***r*** | ***P*** | ***r*** | ***P*** |
| **Standing Dead Litter** | 0.41 | 0.002 | 0.36 | 0.007 | -0.12 | 0.203 | -0.02 | 0.437 |
| **Basal Litter** | 0.31 | 0.016 | 0.00 | 0.499 | -0.11 | 0.229 | 0.09 | 0.269 |
| **Bare ground** | -0.30 | 0.020 | 0.30 | 0.018 | 0.55 | <0.001 | 0.07 | 0.331 |

Correlations of species to types of plant litter cover present within this study yielded multiple significant relationships. We found positive correlations of voles species to standing dead and basal litter, and a negative correlation to bare ground (Table 2.2). Conversely, PEMA was positively correlated to bare ground, while also being positively correlated to standing dead litter (Table 2.2). Of the two ground squirrel species in this study (ICTR & URRI), we could only find one significant correlation, where ICTR was positively correlated to bare ground (Table 2.2).

Average abundance of small mammals was not different between treatments within any year ($P \geq 0.1$) (Figure 2.6a). However, we did find a strong correlation between average snowpack of the preceding winter before sampling of each year to total number of small mammal species captured (r = 0.982, *P* = 0.009) and to number of deer mice captured (r = 0.883, *P* = 0.058) (Figure 2.6b). Subsequently, we found a significant negative correlation between time-since-fire and average abundance (r = -0.47, *P* = 0.032) (Figure 2.6a). Additional time-since-fire analysis revealed an even stronger relationship when excluding 0-years-since-fire data (r = -0.58, *P* = 0.025) (Figure 2.7a). Further, analysis of deer mice abundance data indicated a significant negative relationship time-since-fire (r = -0.37, *P* = 0.078) (Figure 2.7b).

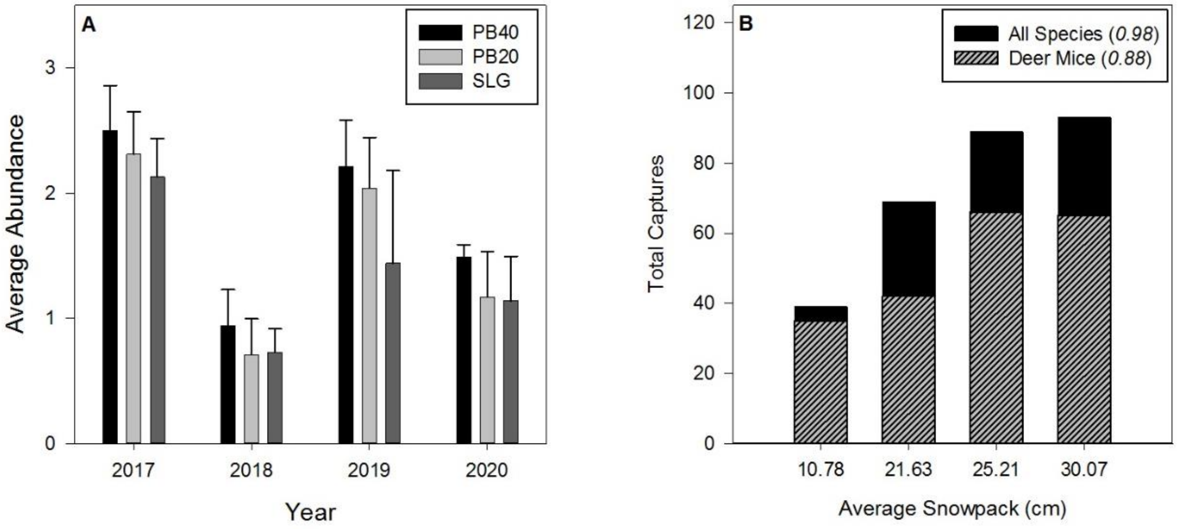

**Figure 2.6. Small mammal abundance and total captures correlated to average snowpack.** Mean abundance of small mammals represented by treatment and grouped by year (A) and total captures of all small mammal species and deer mice correlated to mean snowpack (Note: Pearson correlation coefficients of captures to snowpack reported in parentheses next to capture type in legend) (B). This data was collected from 2017 through 2020 at the North Dakota State University Central Grasslands Research Extension Center near Streeter, ND. Error bars represent standard error of the mean.

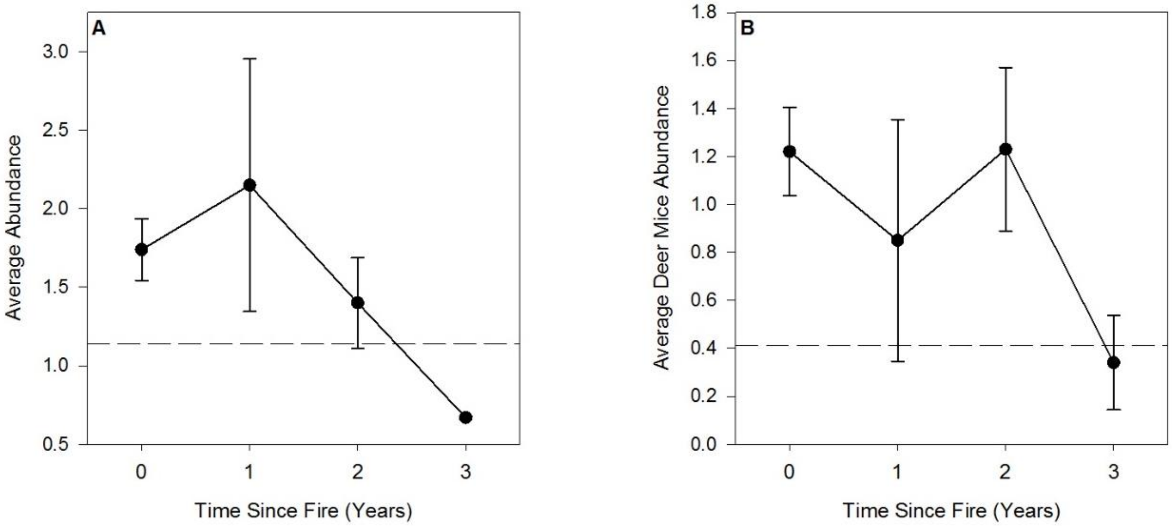

**Figure 2.7. Small mammal and deer mice (*Peromyscus maniculatus*) abundance with time-since-fire.** Mean abundance of small mammals correlated to time-since-fire (A) and mean abundance of deer mice correlated to time-since-fire (B) using data from the PB40 treatment, with dashed lines representing the SLG average. This was done using data from 2020 at the North Dakota State University Central Grasslands Research Extension Center near Streeter, ND. Error bars represent standard error of the mean.

# Discussion

Loss of biodiversity in the Great Plains is of critical concern. Conversion to cropland and urban areas in the Northern Great Plains has resulted in the reduction of native prairie by as much as 99.9% in some areas, resulting in loss of habitat (Samson & Knopf 1994). Within remnant prairies, loss of habitat this is further compounded by the dominance of non-native grasses, such as Kentucky bluegrass and smooth brome, which create homogenous plant community composition and structure for wildlife (Toledo et al. 2014; DeKeyser et al. 2015). We initially found that abundance of small mammals was not dependent on fire and grazing treatments but was affected by the previous winter snowpack. High amounts of snowpack create a larger subnivean zone (area within snowpack) which can insulate from harsh winter temperatures (Marchand 1982). In turn, changes in the subnivean zone can influence small mammal abundance by not providing protection against winter weather (Auerbach & Halfpenny 1991), an area in which to tunnel and forage (Happold 1998), and added cover to avoid predation by foxes (Green & Sanecki 2006) and coyotes (Gese et al. 1996). We did find that abundance of small mammals, and specifically deer mice, were negatively correlated by time-since-fire (TSF), as was the case in other studies (Briani et al. 2004; Fuhlendorf et al. 2010; Burke et al. 2020). However, by mimicking the dynamic disturbance regime of pyric-herbivory within the framework of PBG, we were able to produce a small mammal community that differed and more diverse than that of a homogenous disturbance regime of a season-long grazing system in the fourth year.

Consistent with previous work conducted in the tallgrass prairie of the Southern Great Plains, complete burning of patches within PB40 pastures was able to create heterogeneity of habitat resulting in a distinctly different small mammal community from that of SLG pastures

(Fuhlendorf et al. 2010; Ricketts & Sandercock 2016). Due to abnormally high amounts of precipitation in 2018 and 2019, some summer fires were not applied to patches within the PB20 pastures, which resulted in some patches being only half burned. This likely lead to communities of SLG and PB20 not being different, as unburned areas within PB20 pastures would effectively be receiving the same disturbance (grazing) as the SLG, resulting in similar communities. This is supported by our PCA analysis, as shifts in community composition were influenced primarily by the amount of bare ground, which can result from patch-burn grazing (Fuhlendorf & Engle 2004). Although PB20 did not elicit a significant change in community composition, it does appear its composition is shifting away from SLG composition. We believe that with time and full implementation of fire, PB20 communities will diverge from the SLG community.

Average species composition of pastures in this study was heavily influenced by average dissimilarity of patch communities within pastures. Greater dissimilarity of small mammal communities can occur because of greater heterogeneity of vegetative structure caused by disturbance within a landscape but can also be influenced by the net productivity of plant communities (Swan et al. 2020). Within a PBG system, heterogeneity of vegetative structure is produced at the patch-level as a product of plant community successional patterns associated with TSF (Ricketts & Sandercock 2016). This distinct difference in vegetative structure between patches allows species that can occupy a broad range of different habitats (generalist), like deer mice, and species that require specific habitat (specialist) such as vole species (*Microtus spp.*) to occur within the same landscape, separated into different patches. This also resulted in species, that were rarely encountered, such as the northern pocket gopher (*Thomomys talpoides*), least weasel (*Mustela nivalis*), white-footed mouse (*Peromyscus leucopus*), and the northern short-tailed shrew (*Blarina brevicauda*) being present within PBG pastures and not within the more homogenous habitats of SLG pastures. As a result, PBG was able to include communities found within the SLG but also those associated with post-fire successional patterns associated with TSF, thereby expanding the ecological niche (Briani et al. 2004; Rickets & Sandercock 2016).

Time-since-fire (TSF) is a crucial factor in determining the larger effects of fire on small mammal communities (Briani et al. 2004; Fuhlendorf et al. 2010; Ricketts & Sandercock 2016; Burke et al. 2020). This relationship of community composition to time-since-fire was evident within the PB40 treatment, as community composition differed with TSF, becoming more similar to the SLG community as TSF increased. Though the 1-year-since-fire community did not differ from SLG, this is likely due to high amounts of variation within the 1-year-since-fire community, as it was the most compositionally diverse TSF community. As TSF increased, patch community composition transitioned from being more associated with bare ground to being associated with basal litter. This is largely due to vegetative structure and plant community composition tends to recover or become similar to pre-fire/less disturbed conditions after approximately 2-3 years (Fuhlendorf & Engle 2004; Ricketts & Sandercock 2016). This similarly effects small mammal and bird communities, as species react to the changes in habitat associated with this successional pattern (Fuhlendorf et al. 2006, 2010; Hovick et al. 2015; Burke et al. 2020).

Species reacted as expected to differences in basal and standing dead plant material (litter) and bare ground in this study. Consistent with other studies, specialist species such as the prairie vole was positively associated with areas of high standing dead and basal litter, and negatively associated with bare ground; while the thirteen-lined ground squirrel was positively associated with areas of bare ground (Fuhlendorf et al. 2010; Ricketts & Sandercock 2016; Burke et al. 2020). As with previous studies, we found deer mice were more associated to areas of bare ground, but also found a positive association to standing dead litter, which deer mice are not commonly associated with (Kaufman et al. 1988; Clark et al. 1998; Matlack et al. 2001; Richardson 2010). Deer mice are a generalist species that can occupy a variety of habitats and so are not necessarily strongly related to any specific habitat type (Kaufman et al. 2000). As in the shortgrass prairies of Wyoming, deer mice were found to be more associated with areas of dense vegetation and shrub height and not bare ground (Thompson & Gese 2013), suggesting deer mice are not only affected by vegetation structure but also by vegetation type (Kaufman et al. 2000). By understanding the relationships of these species to different types of habitat, we can better understand the dynamics of communities within landscapes managed with PBG.

## Implications

The results presented from this study support the findings of a growing field of research, that PBG can create more diverse small mammal communities than that of homogenous disturbance practices by way of spatial and temporal changes in vegetative structure within a landscape (Fuhlendorf et al. 2010; Ricketts & Sandercock 2016). Full implementation of fire in patches and pastures within a PBG system is crucial to creating a more heterogeneous community composition. If fire is not fully applied, this will result in similar plant community structure and composition as the SLG, and therefore similar small mammal communities. However, homogenous vegetative structure can arise from uniform application of fire to landscapes, resulting in no successional gradient of plant communities necessary for diverse small mammal communities (Ricketts & Sandercock 2016; Burke et al. 2020). Therefore, when restoring pyric-herbivory to establish heterogeneity in rangelands, it is essentially that fire be applied to distinct patches sequentially within a landscape over time. This will result in a shifting mosaic of plant communities, varying in structure and composition, providing a variety of habitat for small mammals and other wildlife species increasing the biodiversity of out rangelands (Fuhlendorf & Engle 2001; Scasta et al. 2016).

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