PLANT COMMUNITY RESPONSES TO BISON REINTRODUCTION WITHIN MONTANA’S NORTHERN GREAT PLAINS

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Presented to
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Wildlife and Fisheries Biology.

by
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ABSTRACT

In western North America, the rapid loss of native grazers, abiotic disturbance processes (e.g., fire), and human-driven land conversion or degradation have resulted in steadily declining biodiversity and rangeland health. Keystone species restoration and their potential to increase rangeland health are common justifications for bison (Bison bison L.) reintroduction projects throughout North America’s Great Plains. Similarly, many other conservation groups also justify the removal of livestock from traditionally cattle-grazed rangelands by citing potential increases in rangeland health or community dynamics following years of heavy use by cattle. Our objective was to assess how ten-years of bison reintroduction and livestock removal influence plant community dynamics in the mixed-grass prairie compared to cattle-grazed rangeland. We compared our treatments to each other, and to a predicted historic climax plant community (HCPC) by collecting plant species incidence, abundance, height, and bare ground data at 10 different sampling sites across each of our treatments, all within a common ecological site. We found that bison exhibited mixed keystone effects ten-years post-reintroduction. In support of their keystone role, we observed higher species richness and compositional heterogeneity (β-diversity) in our bison-grazed treatment than either our cattle-grazed ($p = 0.01$ and $p = 0.03$ respectively) or livestock removal ($p = 0.007$ and $p = 0.002$ respectively) treatments. We also found that bison reintroduction outperformed cattle-grazing or livestock removal in moving plant communities toward a predicted HCPC-state, being not significantly different in forb composition (bootstrap resampling, $p < 0.0001$, nboot = 1,000) and abundance (LSM, $t = 1.80$, $p = 1.80$, $df = 19$), bare ground
cover (t = -0.36, \( p = 0.73, \ df = 4 \)), and abundance of grasses and sedges (t = -1.73, \( p = 0.12, \ df = 19 \)). Bison reintroduction areas were also lower in noxious weed abundance compared to cattle-grazed (t = 1.80, \( p = 0.042, \ df = 27 \)) and livestock removal (t = 2.88, \( p = 0.0039, \ df = 27 \)). Bison may show some of their predicted keystone effects after ten-years, and we suggest that their reintroduction may be a useful to restoring and conserving the Northern Great Plains mixed-grass prairie ecosystem.
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CHAPTER ONE

PLANT COMMUNITY RESPONSES TO BISON REINTRODUCTION ON THE NORTHERN GREAT PLAINS, USA: A TEST OF THE KEYSTONE SPECIES CONCEPT

ABSTRACT

Keystone species restoration, or the restoration of species whose effect on an ecosystem is much greater than their abundance, is a central justification for many wildlife reintroduction projects globally. However, the extent to which they act as keystone species following reintroduction is little studied. Following restoration, plains bison (*Bison bison* L.) have been identified as a keystone species in the tallgrass prairie ecoregion, but we know of no research that has been done to document similar effects in the mixed-grass prairie where extensive restoration efforts are ongoing. This study addresses whether Northern Great Plains (NGP) mixed-grass prairie plant communities exhibit traits consistent with five central keystone effects documented by bison in the tallgrass prairie. Specifically, we collected species composition, diversity, abundance, bare ground cover, and standing plant height data in treatments where cattle (*Bos taurus* L.) continuously grazed, cattle were removed for 10 years, and bison have been introduced and resident for 10 years. We observed mixed support for bison acting as keystone species in this system. In support of the keystone role of bison, we observed higher species richness and compositional heterogeneity (β-diversity) in the bison-grazed treatment than either the cattle-grazed (*p = 0.01* and *p = 0.03* respectively) or livestock removal (*p = 0.007* and *p = 0.002* respectively) treatments. However, bison grazing also resulted in lower forb abundance (*3.4%; p = 0.02*), and comparable bare ground and plant
height heterogeneity compared to cattle-grazed sites, contradicting reported keystone effects in other systems. Our results suggest that after 10 years of being restored, bison only partially fulfill their role as keystone species in the mixed-grass prairie, and we encourage continued long-term data collection to evaluate the longer-term influence of B. bison on plant communities in the mixed-grass prairie of the NGP.

INTRODUCTION

The restoration of keystone species, or those species who influence ecosystems more than their abundance would suggest (Paine, 1969), has been posited as essential for the maintenance and management of heightened biodiversity and ecosystem function (Mills et al. 1993). The keystone species concept has been expanded and employed by several studies to explore how best to recognize and categorize various keystone species: keystone predators, prey, plants, links, or modifiers (Mills et al., 1993; Power et al., 1996). Herbivores operating as keystone species are typically labelled keystone modifier species; defined as a species whose behaviors alter ecosystem structure and composition, such that removal of that species results in reduced overall biodiversity (Mills et al., 1993). These keystone (or foundational- see Soulé et al. (2003)) influences are thought to be a central theme guiding restoration and reintroduction projects to generate and sustain the habitat structure needed for high native species abundance and diversity (Conway, 1989). For example, restoration of the gray wolf (Canis lupus L.) to the Greater Yellowstone Ecosystem (GYE) is hypothesized to have increased biodiversity and improved habitat structure by reducing the browsing influence of wapiti (Cervus elaphus
L.) that would otherwise limit plant abundance and diversity (Ripple and Beschta, 2012). However, the reintroduction of large herbivores, namely those considered keystone modifiers, to restore ecosystem function has become a key rationale globally for many restoration projects attempting to increase biodiversity and ecosystem function (Seddon et al., 2014).

Although declining from nearly 60 million individuals to near extinction in the 19th century, the American plains bison is widely viewed by ecologists to be a keystone – or perhaps at least a foundation – species that historically had a major influence shaping North American grassland ecosystems (Knapp et al., 1999; Freese et al., 2007). Studies of remnant and restored B. bison populations have shown that they mostly influence ecosystems as a keystone modifier (Mills et al., 1993) through herding, grazing, rubbing, and wallowing behaviors that directly alter habitat structure and generate increased biodiversity across many arid and mesic grassland ecosystems (Collins, 1987; Fuhlendorf and Engle, 2001; Towne et al., 2005; Allred et al., 2012). For example, in mesic communities where woody encroachment potential is high, bison typically influence forest suppression through rubbing and horning behaviors (similar to elephants) on woody vegetation, thus directly altering habitat structure in those environments (Coppedge and Shaw, 1997). Bison patch-grazing and wallowing behaviors can also generate high levels of structural (i.e. plant height or growth habit) and compositional heterogeneity (i.e. species turnover or β-diversity), collectively viewed as increased grassland heterogeneity (Fuhlendorf and Engle, 2001; Toombs et al., 2010). Declines in grassland heterogeneity have been linked to declines in avian, amphibian, reptilian,
insect, and botanical diversity (Knapp et al., 1999; Koerner et al., 2014). In addition, bison grazing can increase heterogeneity in plant functional group richness (Knapp et al., 1999). These behaviors lower warm season (C4) grass dominance in tallgrass prairie plant communities, and thus act to generate a more equal proportion of cool season (C3) grass and forb to C4 grass abundances (Knapp et al., 1999). However, while numerous projects attempt to restore bison to the Great Plains of North America, to date evidence that bison are acting as keystone species has been limited to the tallgrass prairies of the mid-western United States (Knapp et al., 1999; Towne et al., 2005). Thus, we still have little understanding about whether the keystone effects of B. bison can be observed in other prairie ecotones, or how long post-reintroduction these effects become observable in prairie plant communities.

Our objective for this comparative study was to test whether the keystone role of bison as described in the tallgrass prairie ecosystem (Knapp et al., 1999; Fuhlendorf et al., 2010; Gates et al., 2010) can be applied to the mixed-grass prairies of the Northern Great Plains (NGP). To describe the extent to which restored bison could be acting as keystone species in mixed-grass prairies, we set out to evaluate support for four key plant community compositional and structural responses observed by Knapp et al. (1999) in their review of how bison can act as keystone species in tallgrass ecosystems. These hypothesized effects included: (H1) bison grazing results in lower overall abundance of C4 grasses compared to our cattle-grazed treatment, and bison grazing results in higher overall abundance of C3 grasses and forbs compared to our cattle-grazed treatment, (H2) bison grazing and disturbance generates higher overall species diversity and richness of
plants than does cattle disturbance or livestock removal, (H₃) greater species turnover occurs within bison grazed treatments than occurs within cattle-grazed or livestock removal treatments, and (H₄) heterogeneity in bare ground cover and average plant height is higher in bison-grazed treatments compared to cattle-grazed or livestock removal treatments. Accordingly, we designed this study to investigate the plant community responses that bison reintroduction, cattle removal, and cattle-grazing have on the mixed-grass prairie, and thus to compare how different grassland restoration or management strategies affect plant communities in the NGP.

METHODS

Study Area

Our study took place in the NGP region of the United States, in a portion of southern Phillips County, Montana (Figure 1.1). This area is part of a region of northeastern Montana known colloquially as the Missouri Breaks: a hilly, and formerly glaciated, part of the mixed-grass prairie (Manning, 2009). The Missouri Breaks region is a 1.4 million ha patchwork of public and private lands, with 23% of lands being privately held, 36% of lands publicly managed by the Bureau of Land Management (BLM), and the remaining 41% being publicly managed by the USFWS (Manning, 2009). This area is dominated by a mixture of short and tallgrass prairie species (e.g., *Pascopyrum smithii* (Rydb.) Á. Löve, *Schizachyrium scoparium* (Michx.) Nash, *Hesperostipa comata* (Trin. & Rupr.) Barkworth var. *comata*, etc.). The mixed-grass prairie, as a region, generally has a moderate, but highly variable climate (Savage, 2011)
as, for example, Phillips co. averaged 34 cm in total precipitation from 2000-2016, but only received a total of 29 cm in 2015; contrasting sharply with the 61 cm received in 2016.

The Taylor Grazing Act of 1934 allowed ranchers to lease public lands for grazing throughout the Great Plains (i.e., national grasslands, national wildlife refuges, bureau of land management lands), and in 1936 the first grazing leases were given out to graze within the Charles M. Russell National Wildlife Refuge (CMR) (Bill Haglan, USFWS, per. comm., February 2017). From 1915 to 1970 most of southern Phillips County was grazed similarly, most grazing being year-round, with unregulated grazing intensity (i.e. stocking rate), leading to a generally homogeneous distribution of extremely poor rangeland quality (high erosion, little vegetation cover, increased stream head cutting or channelization) (Bill Haglan, USFWS, per. comm. February 2017). Thus, we assumed all our treatments historically were subjected to loosely regulated year-round grazing pre-1970, but transitioned to seasonal (i.e., growing season only), moderate to light grazing intensity (i.e., 0.20 – 0.40 AUM/ha; Animal Unit Month; the amount of land needed to support one cow and one calf for one month) rest-rotation cattle management from 1970 to 2005 through combined regulation and oversight by federal and state agencies (Bill Haglan, USFWS, per. comm. February 2017; B.J. Rhodes, BLM, per. comm. October 2015).

*Bison-Grazed Treatment*
Our bison treatment plots were located within a 12,545-ha reintroduction area that is owned and managed by the American Prairie Reserve (APR; Figure 1). Specifically, we conducted our sampling in the 7,092-ha Telegraph and Box Elder creek drainages, referred to collectively as Box Elder, where cattle were removed in early 2004 (Michel Kohl, Utah State University, per. comm., February 2017). In October 2005, the APR reintroduced 16 bison to Box Elder, and the area has experienced year-round bison grazing with the bison population growing to roughly 600 animals (including juveniles and sub-adults) by 2015 (18.75% per year with an average 29 imported animals per year; (American Prairie Reserve, 2015)). Thus, bison have grazed Box Elder for ten years by the time of our sampling (Figure 1.1) during which bison grazing intensity has been maintained below a threshold of 0.39 AUM ha⁻¹.

Livestock Removal Treatment

We selected a 4,059-ha portion of the Charles M. Russell National Wildlife Refuge (CMR), where livestock were removed in 2004 as our livestock removal treatment. Since 1975, the refuge (managed by the U.S. Fish and Wildlife Service) has been expiring grazing leases, leading to some unique areas to the Northern Great Plains where grazing by large herbivores hasn’t occurred in up to 40 years. Specifically, we focused our sampling within an allotment named Telegraph Creek Pasture Five where cattle had been absent for 10-11 years. The allotted cattle grazing intensity data for the CMR (i.e. the AUM ha⁻¹ permitted for grazing) is unavailable to compare with our other
treatments, but the observed (or actual) grazing intensity from 1990 - 2004 averaged 0.16 AUM ha\(^{-1}\) (Std. Error = 10.00 AUM year\(^{-1}\), Range = 104 AUM year\(^{-1}\)).

_Cattle-Grazed Treatment_

Our cattle grazed (control) treatment was located within the 8,303-ha Fourchette Creek grazing allotment that is managed by the BLM. Cattle grazing on this allotment has been consistently managed via rest-rotation grazing since May 1, 1983 that allowed for up to 2,815 AUMs of grazing pressure during a grazing season that lasted from May 1st – October 30th of each year (B.J. Rhodes, BLM, per. comm., October 2015). Thus, grazing intensity in our cattle-grazed treatment area was maintained below a threshold of 0.33 AUM ha\(^{-1}\) from May 1st – October 30th during years 1983-2016 (B.J. Rhodes, BLM, per. comm., October 2015).

_Site Selection for Field Sampling_

In addition to selecting for areas with similar historical (i.e., pre-2005) grazing pressures, to ensure comparability in site condition and potential community productivity among our 3 treatments we selected sampling areas that were similar in terms of soil condition, slope, aspect, elevation, and other abiotic variables. To accomplish this, we utilized Ecological Site Description (ESD) data created by the U.S. Natural Resources Conservation Service (NRCS) that describe and outline areas with similar biotic and abiotic conditions (potential plant community, soil description, slope, elevation, etc.; https://esis.sc.egov.usda.gov). In addition, ESDs were developed as a tool to predict
forage production potential for each ecological site (Bestelmeyer and Brown, 2010). Given that we assumed vegetative community responses to grazing were likely to follow the Dynamic Equilibrium model, which predicts that the effects of disturbance are correlated positively with productivity (Huston, 1979; Yuan et al., 2016), we focused sampling in ESDs where plant community productivity, and thus grazing pressure, was likely highest. Therefore, our use of ESDs enabled us to effectively restrict sampling to areas with high levels of forage productivity and potential for grazing to impact vegetative communities, as well as areas with homogeneous environmental conditions (e.g. soil texture, slope, elevation, etc.). The most common ESD with high productivity occurring in all three treatments was Shallow Clay 11-14” (SC) capable of producing from 703-5,878 kg of grass and sedge forage per hectare (https://esis.sc.egov.usda.gov). We then randomly selected 10 sample points within SC polygons for each treatment in the study area.

Vegetation Sampling and Assessment

Between June – August, 2015 and May – August, 2016 we established study plots and evaluated the vegetative community at 10 random sampling points within each of our treatments. We chose to sample 10 points based on a power analysis, where we utilized pilot data to generate reasonable estimates of: 1) the difference in mean response among our treatments, and 2) the variability among points within our treatments. We determined a statistical power estimate of $\geq 0.80$ with an alpha of 0.05 for 10 replicates within each treatment. To facilitate the ability for long-term, robust plant community data collection
beyond the timeline of our study, we chose to establish each of our study plots following a modified Whittaker plot design employed in many long-term ecological studies across the U.S. (Newell and Peet, 1998; Peet et al., 1998; Cavender-Bares et al., 2004; Fridley et al., 2005; Reilly et al., 2006; Carr et al., 2009). Specifically, at each point we established a 0.1 ha survey plot (20 m x 50 m), each consisting of ten individual 100 m² subplots (Figure 2.1; referred to hereafter as modules). We sampled modules 1-10 in each plot (Figure 2.1) for species incidence and directly used those data to estimate species richness for the entire plot. We restricted vegetation and bare ground cover sampling to modules 2, 3, 8, and 9 (Figure 2.1; hereafter referred as intensive modules). We estimated both the cover for each species encountered and bare ground cover for each intensive module (n = 4 per plot) on a scale from 1-9, to represent a range of percent cover values for each metric (trace, 0-1%, 1-2%, 2-5%, 5-10%, 10-25%, 25-50%, 50-75%, and 75-95% respectively; Figure 2.1). We estimated vegetation height variability across the whole 0.1 ha plot by recording standing vegetation heights (m) at each corner of a plot’s intensive modules (n = 9 per plot; Figure 2.1).

**Statistical Analysis**

We first evaluated support for each of our five hypotheses (i.e. H₁ – H₄) by applying one-way ANOVA techniques (when assumptions for normality could be met) to test for significant differences in each response variable (e.g. variance in bare ground cover) among our three treatments. We determined that treatment effects were statistically significant at an alpha of 0.05 for all statistical tests.
To test that C$_4$ grass, C$_3$ grass, and forb abundances differed among our three treatments (H$_1$), we transformed our cover class values to a midpoint percentage value (e.g., a species with 5-10% range was given a value of 7.5% for cover) for each species encountered in our four intensive modules at each plot (Peet et al., 1998). We then totaled, and averaged the abundances for each species across the plot aggregate, and organized them into their broader functional groups prior to analysis. Our C$_3$ grass abundance data was normally distributed and did not require transformation for ANOVA or pairwise tests. We log-transformed our non-normal C$_4$ grass abundances to meet normality assumptions for ANOVA and pairwise tests. If we detected a significant treatment effect, we used paired t-tests to further describe of the differences among our individual treatments. Our forb data was significantly non-normal regardless of transformation, and thus we used the non-parametric Wilcoxon test to detect differences among our treatments based on forb abundance. When significant differences were detected among our treatments we further tested these differences using Wilcoxon pairwise comparisons.

To test our hypothesis (H$_3$) that bison generated higher plant species diversity than cattle or livestock removal, we first calculated plot-level diversity values using our abundance (i.e., the recorded cover) data for species encountered, and calculated the Inverse Simpson’s (1 D$^{-1}$; where $D = 1/\sum_{i=1}^{s} p_i^2$) and Exponential Shannon’s ($e^H$; where $H = -\sum_{i=1}^{s} p_i \ln p_i$) index values for each plot. Plots were grouped by treatment, to yield one diversity value per plot ($n = 30$) for each index (Mittelbach, 2012; Gardener, 2014).
We then tested for significant differences in diversity among our three treatments using one-way ANOVA tests for each index.

To test the hypothesis that bison generated higher species richness (i.e. the total number of species found in an area) than cattle or livestock removal ($H_3$), we first utilized rarefaction to standardize species richness across treatments. This reduced potential influences of variability in species abundance values or sampling effort across samples in each treatment (Gotelli and Colwell, 2011; Chao et al., 2014). If we detected significant differences among our treatments based on ANOVA, we used Tukey-HSD pairwise comparisons to determine which pairs were significantly different from each other (Gardener, 2014).

We applied multivariate ordination to test our hypothesis that species turnover was highest in our bison treatment, and lower in cattle and livestock removal areas ($H_3$). Species turnover is a measure of the amount of compositional difference (or heterogeneity) between study sites, sample areas, or communities (Legendre et al., 2005; Arroyo- Rodríguez et al., 2013; Myers et al., 2013; Myers et al., 2015), and has been used to assess how management changes (e.g., fire or grazing) may directly affect compositional heterogeneity in plant communities (Reilly et al., 2006; Conradi et al., 2015). We were interested in the amount of variance in species composition among plots for each treatment, and thus we utilized group dispersion ordination techniques to visually compare species turnover between bison, cattle, and livestock removal treatments (Gardener, 2014). To accomplish this, we first generated a dissimilarity index
using species incidence data collected in each plot within the bison, cattle, and livestock removal treatments using Sørensen equation of dissimilarity:

\[ \beta_s = \frac{(b + c)}{(2a + b + c)} \]

where \( a \) equals the species shared between two sites, \( b \) is equal to the species unique to site 1, and \( c \) is equal to the number of species unique to site 2 (Anderson, 2006a; Gardener, 2014). We then used the multivariate dispersion function (betadisper) as part of the vegan package in R to generate an ordination of group dispersion using a principal coordinates analysis (PCoA) (Gardener, 2014; R Core Team, 2016). This multidimensional ordination visually shows the heterogeneity among plots within and across treatments, where each point in the ordination represents a \( \beta \)-diversity (species turnover) value for a plot. The further the distance that the point is from the center of the treatment (i.e., the center of each circle), the more different that sample point is from all the other samples in the whole treatment (i.e., the higher the variability) (Anderson, 2006a). Additionally, the bigger the circle, the more variable the treatment is in terms of species composition (Anderson, 2006a). Lastly, we used ANOVA to test for significant differences among treatments modelled in our multivariate ordination, and if we detected differences, we further tested \( \beta \)-diversity between pairs of treatments using the Tukey-HSD pairwise comparisons.

We tested our hypothesis that bison generated higher bare ground cover heterogeneity than cattle-grazed or cattle removed areas (H4) by comparing the coefficient of variation (CV) of bare ground between each of our three treatments (\( n = 5 \))
for bison; n = 10 for cattle, n = 10 for grazer removal). We calculated the median of our bare ground cover range values (e.g., 5-10% would be said to equal 7.5%), and then averaged these values to obtain the mean bare ground cover value at each plot (Figure 2.1). We then calculated the CV for mean bare ground cover for each treatment and performed an ANOVA to test for significant differences among our three treatments.

We evaluated whether differences in plant height heterogeneity occurred among sites by calculating the CV of our recorded plant height data, and comparing the average CV of plant height between treatments ($H_4$). We defined plant height heterogeneity as the amount of variation in the average plant height occurring across an area (i.e., each treatment for the purposes of this study). We first used the mean plant height per plot ($n = 30; n = 10$ per treatment) to calculate the CV for plant height across our three treatments. To maintain assumptions of normality, we transformed the CV plant height data on a log-scale. Where ANOVA suggested differences, we further explored differences between our treatments using LSD pairwise analyses.

RESULTS

Functional Group Abundance

We were unable to collect sufficient evidence to suggest that bison grazing decreases C$_4$ grass abundance ($H_1$; ANOVA, $F = 0.5, p = 0.5, df = 27, 2$), and increases C$_3$ season grass and forb abundance ($F = 1.9, p = 0.2, df = 27,2$) compared to cattle grazing. Contrary to our hypotheses, we detected 3.4% higher forb abundance in our cattle-grazed treatment compared to our bison-grazed treatment (Wilcoxon, $p = 0.02, df =$
Additionally, we did not observe any differences in C₃ grass abundance between bison and cattle treatments (Tukey-HSD, \( p = 0.12, df = 19 \)), but found that bison grazed treatment had significantly lower forb (Wilcoxon, \( p = 0.0191, df = 19 \)) and C₃ grass (Tukey-HSD, \( p = 0.005, df = 19 \)) abundance than was recorded in our livestock removal treatment.

Species Diversity and Richness

Contrary to our predictions, we did not observe significant differences in plant species diversity among our three treatments using either of our diversity indices (1/D: \( F = 0.3, p = 0.7, df = 27, 2 \); or \( e^H \): \( F = 0.8, p = 0.4, df = 27, 2 \)).

In line with our predictions, we collected evidence suggesting that bison-grazed treatments have higher species richness than sites where cattle-grazed or livestock were removed (\( F = 7.0, p = 0.003, df = 27, 2 \)). We found that our bison-grazed treatment had 57% higher species richness compared to our cattle treatment (Tukey-HSD, \( p = 0.009, df = 2 \)), and 56% higher richness compared to our livestock removal treatments (Tukey-HSD, \( p = 0.007, df = 2 \); Figure 4.1). We did not detect any difference in species richness between cattle-grazed and livestock removal treatments (Tukey-HSD, \( p = 0.9, df = 19 \)).

Species Turnover (\( \beta \)-diversity)

We collected sufficient evidence to suggest that bison grazed areas exhibited higher species turnover than would be observed in cattle or livestock removal sites (ANOVA, \( F = 7.7, p = 0.002, df = 27, 2 \)). We observed in our multivariate dispersion model that species turnover was 56% higher in our bison treatment than in our cattle-
grazed sites, and 59% higher than livestock removal treatment (Tukey-HSD, \( p = 0.03 \) and \( p = 0.002 \), \( df = 29 \); Figure 4.1). This variation in species turnover was also observed in our multivariate ordination, where the bison treatment circle was visibly much larger than our other two treatments, showing higher compositional heterogeneity within our bison treatment than within the others (Figure 5.1).

Bare Ground and Vegetation Height

We were unable to detect support for our hypothesis that our bison-grazed treatment had significantly higher bare ground cover than sites grazed by cattle (ANOVA, \( F = 1.8, p = 0.2, df = 22, 2 \)).

Although we detected differences in plant height heterogeneity among treatments (ANOVA, \( F = 7.7, p = 0.002, df = 27, 2 \)), we were unable to collect sufficient evidence to suggest that plant height heterogeneity was higher in sites grazed by bison than those that were cattle-grazed (LSD, \( p = 0.7, df = 19 \)). However, average plant height heterogeneity was 67% higher in the cattle-grazed treatment (LSD, \( p = 0.01, df = 19 \)), and 58% higher in the bison-grazed treatment (LSD, \( p = 0.03, df = 19 \)) compared to our cattle-removal treatment (Figure 6).

**DISCUSSION**

We observed mixed-support for bison acting as modifier keystone species in the NGP mixed-grass prairie ten years post-reintroduction, as we only found support for a subset (i.e., 2/5) of our hypotheses. Our results suggest that bison partially function as
modifier keystone species by increasing species richness and compositional heterogeneity (β-diversity) in mixed-grass prairie plant communities after converting from cattle to bison grazed rangeland. These observed increases in species richness and β-diversity follow what has been reported following bison restoration to tall and short grass prairie ecosystems (Knapp et al., 1999; Towne et al., 2005; Fuhlendorf et al., 2010). However, unlike other studies we did not observe functional group or habitat structural (i.e., bare ground or standing plant height) differences consistent with previous studies. Therefore, we were unable to find evidence that fully supports that bison are acting as keystone herbivores ten years after reintroduction in the NGP.

Very little is known about how long post-release the full effects of a large herbivore reintroduction become observable, and very little research has been done to parse out what direct ecological effect herbivore reintroductions have (Johnson and Cushman, 2007; Roberts et al., 2014). Our results both follow and counter previous observations of bison reintroduction in the tallgrass system: where three to ten years of bison grazing resulted in no significant differences with cattle-grazed areas in the dominance of C₄ grasses over C₃ grasses, but showed increased forb species richness and abundance (Knapp et al., 1999; Towne et al., 2005; Fuhlendorf et al., 2010). Similar studies looking at cattle grazing in the shortgrass steppe showed very little functional group differences between grazing treatments in less than 20 years, with functional group shifts not occurring for almost seventy years (Augustine et al., 2017). However, more productive ecotones like the mixed-grass prairie will likely show these shifts sooner than the arid shortgrass steppe (Huston, 1979), and this is likely reflected in the partial
transition observed in our study. Our study shows some evidence that bison may be acting to transition plant communities in our study area toward those expected from a keystone species effect (Knapp et al., 1999), but more time may be needed for NGP communities to exhibit the full influence of a bison reintroduction. Therefore, if conservation organizations justify reintroduction of bison based on the belief they will exhibit keystone impacts on grassland systems, it is critical that focused and sustained long-term monitoring are supported to test these hypothesized effects (Jachowski et al., 2016). More broadly, it is essential that bison reintroductions in other portions of the NGP similarly establish long-term monitoring strategies to further define the role that bison may play in the region’s ecosystems.

Although our bison reintroduction, cattle-grazed, and livestock removal treatments did not show predicted differences using broad functional groups (e.g., forbs), we suggest that future research utilize groupings based on more than just growth-habit alone to effectively parse out differences among treatments. Bison reintroduction is predicted to increase rangeland forb abundance and richness compared to cattle-grazed (Knapp et al., 1999), however we reported the contrary. Even so, when we took a finer-scale look at the forb composition of each treatment, we found that non-native (and often invasive) species constituted 32% and 46% of the total vegetation cover in our cattle-grazed and livestock removal treatments respectively. Our contradictory results regarding the effects of bison on forb abundance and composition may be partially explained by the disproportionate cover of non-native forbs in our other treatments. Studies attempting to reveal the interactions between wildlife and plant communities
often utilize broad-groupings of plants, however our study demonstrates that such basic views of plant communities and functional groups may lead to erroneous or conflicting interpretations of plant-wildlife interactions.

Stocking rate can have varying influence on rangeland community dynamics (Olff and Ritchie, 1998). We attempted to control for the effect of stocking rate on plant community composition and species abundances, but detailed records on the precise stocking rates (i.e. AUM/ha) that traditionally cattle-grazed lands have experienced is lacking or inconsistent between agencies (per. comm., BJ Rhodes, BLM, June 2016; per. comm., Randy Matchett, USFWS, August 2016). Bison reintroduction at the spatial scales used in this study (from ~3,000 to 12,500 ha over ten years) may not produce the effects expected from historic bison disturbance on vegetative communities. Kohl et al. (2013) suggested that the APR bison reintroduction area (3,555 ha at the time of their study) may not be large enough to facilitate our predicted historic ecological influence, and that continued access to areas >12,000 ha may both result in a return to historic disturbance patterns and vegetative community composition. Sanderson et al. (2008) suggest that bison reintroduction projects at scales > 200,000 ha are the most effective, and likely represent historic foraging behaviors, with a single bison foraging patch being >11,000 ha (Kohl et al., 2013). Additionally, while most non-bovine ungulate species in our study area (e.g. *Odocoileus virginianus* Zimmermann, *Odocoileus hemionus* Rafinesque, *Antilocapra americana* Ord.) are predominantly browsers, wapiti (*C. elaphus*) have been shown to be graminoid grazers, potentially amplifying the effect of bovine grazers on prairie plant communities (Keller, 2011). Therefore, we suggest that
future studies test along a gradient of grazing regimes at a variety of spatial scales post reintroduction, and integrate the potential additive effects of non-bovine grazers to further parse out differences between bison and cattle.

Our results suggest that livestock removal may contribute to declines in overall grassland biodiversity. The plant communities of the NGP have undoubtedly evolved in the presence of large grazers (Knapp et al., 1999), and large grazer exclusion or livestock removal in the tallgrass and shortgrass prairie is expected to result in lower annual forb cover compared to grazed sites (Fuhlendorf et al., 2001; Valone and Sauter, 2005; Manier and Hobbs, 2006). Our findings, however, are comparable with studies in the shortgrass prairie where livestock removal resulted in heightened forb abundance (Augustine et al., 2017), however our data suggests removal may additionally lead to landscape homogenization (evinced by lower species turnover compared to bison treatment). Increased rangeland homogenization (or lack of heterogeneity) can be commensurate with declines in grassland biodiversity, and the decline of wildlife species who require the influence of grazing to generate variability in plant community structure (standing biomass and bare ground cover) and composition (Fuhlendorf and Engle, 2001; Toombs et al., 2010). Thus, managers implementing grazer removal may both decrease habitat for many grassland plant and wildlife species who require structurally heterogeneous plant communities, and support lower biodiversity than sites grazed by either bison or cattle (Fuhlendorf and Engle, 2001).

Different ecological sites (or habitats) may respond slightly differently than our sites within the SC ESD, as it is hypothesized that grazing’s relationship to grassland
plant community composition varies along environmental gradients (e.g. soil, altitude, etc.) (Zemmrich et al., 2010). Discrepancies in habitat selection between bison and cattle may, in turn, result in stronger plant community responses in some ecological sites compared to others (Kohl et al., 2013). Since Our study only looked at a single ecological site (or ESD), limiting the reach of our conclusions to how these three options influence only a single documented rangeland community type, it is essential that more studies be conducted to parse out community-level effects of cattle-grazing, removal, and bison reintroduction, across a range of ecological sites.

CONCLUSIONS

Species introductions or reintroductions are often popularly advocated for based on possible keystone effects (Hansen et al., 2010; Newsome et al., 2015), but there have been comparatively few studies directly evaluating the influence that these species’ translocations have had on local ecosystems. Our study illustrates the need for further research on the existence and transferability of possible keystone species interactions when attempting to justify species reintroductions. Even where there is evidence that the ability to restore keystone effects could exist, such as gray wolf recovery in Yellowstone National Park, USA (Ripple and Beschta, 2012; Painter et al., 2015), corroborating evidence from other sites remains lacking, suggesting that the described keystone effects may be isolated to the GYE (Ford and Goheen, 2015). As translocation and reintroduction projects are rapidly gaining support as a means for achieving biodiversity restoration goals, it is essential for restoration ecologists and land managers to
continually evaluate and confirm the transferability of these processes across ecosystems (Hansen et al., 2010; Newsome et al., 2015). For bison restoration, there are many ecological, cultural, and aesthetic reasons for various groups to undertake a bison reintroduction project, however a major rationale for bison conservation and restoration is their ability to act as keystone species (Freese et al., 2007). If bison are to be reintroduced across the Great Plains based on expected keystone effects, it is imperative that managers utilize long-term, robust monitoring techniques to track their influence on rangeland plant communities.
Figure 1.1 Map (1) of our study area, located in Phillips County Montana, showing the extent of the Shallow Clay 11-14” ESD within our study area, as well as the spatial arrangement of our three treatments: (A) bison grazed, (B) cattle grazed, and (C) cattle removal. Plots are represented as filled circles. Inset map (2) shows the general location of our study area (Phillips County, Montana) within the Northern Great Plains region.
Figure 2.1  The spatial scale of an individual plot, consisting of ten 100 m$^2$ modules. Modules 2, 3, 8, and 9 are sampled as intensive modules (bold boxes). All other modules (i.e. 1, 4, 5, 6, 7, 10) were sampled as an aggregate, searching only for species not recorded in the intensive modules. The origin of the plot is marked with an open circle, and other long-term plot markers are represented by filled, black circles. Each bare ground cover measurement is denoted by an asterisk (*), and the individual sample points for plant height are marked as a cross (X).
Figure 3.1 (A) Inverse Simpson Diversity Index, (B) Exponential Shannon Diversity Index values, and (C) Rarefied species richness for each of our three treatments, with 95% confidence intervals for each and are represented as error bars. (D) Beta-diversity, or species turnover, is plotted as the distance of each plot from the overall centroid of the data for each treatment (see Figure 4.1), representing the overall variation in species composition for the respective sites (Significance is represented via pairwise notation; $\alpha = 0.05$).
Figure 4.1 Multivariate dispersion for species turnover ($\beta$-diversity) between bison, cattle, and cattle-removal treatments, showing both the difference in composition between each plot within each treatment (i.e. distance from the middle of each circle) and the difference among treatments (i.e. the distance from the center of the plot).
Figure 5.1 (A) Plant height and (B) bare ground heterogeneity measured using the coefficient of variation (CV), showing the amount of structural heterogeneity (i.e. plant height or open ground) that occurred within each treatment.
CHAPTER TWO

RANGELAND HEALTH IMPLICATIONS SURROUNDING BISON REINTRODUCTION, LIVESTOCK RETENTION, AND REMOVAL IN NORTHEASTERN MONTANA

ABSTRACT

Rangeland restoration projects are carried out by a multitude of agencies, private landowners, and NGOs, and progressing toward increased rangeland health is often a restoration goal. Common restoration techniques in the Northern Great Plains of North America include livestock removal, bison (*Bison bison* L.) reintroduction, and cattle (*Bos taurus* L.) retention. However, data concerning the efficacy of each of these approaches is limited, and restoration targets are often poorly defined. The objective of this study was to assess how each of these restoration techniques can influence progress toward restoration of historic climax plant communities (HCPCs), utilizing a combination of quantifiable rangeland health metrics (Pyke et al., 2002) and ecological site descriptions (Bestelmeyer and Brown, 2010). We compared managed communities to a predicted HCPC by collecting plant community composition and abundance data from bison reintroduction, livestock removal, and cattle-grazed areas in southern Phillips County, Montana. We found that bison reintroduction performed the best in moving plant communities toward a predicted HCPC-state, being not significantly different in forb composition (bootstrap resampling, \( p < 0.0001 \), nboot = 1,000) or abundance (LSM, \( t = 1.80, p = 1.80, df = 19 \)), bare ground cover (\( t = -0.36, p = 0.73, df = 4 \)), and abundance of grasses and sedges (\( t = -1.73, p = 0.12, df = 19 \)). Bison reintroduction areas were also lower in noxious weed abundance compared to cattle-grazed (\( t = 1.80, p = 0.042, df = 27 \))
and livestock removal (t = 2.88, p = 0.0039, df = 27). Cattle-grazed areas outperformed livestock removal, being not significantly different from the predicted HCPC in grass and sedge abundance (t = 0.82, p = 0.12, df = 19). Livestock removal showed higher litter abundance compared to our cattle retained (t = 4.25, p = 0.0001, df = 27) and bison reintroduction (t = 3.15, p = 0.002, df = 27) treatments, but performed the worst of all our treatments in being the most statistically different from the predicted HCPC. As managers increasingly try to define and quantify rangeland health, our results show that long-term monitoring of rangeland restoration projects is critical to understanding how various grazing management regimes affect rangeland health.

INTRODUCTION

Temperate grasslands or savannas have historically made up approximately 30% of the Earth’s landmass, but are currently considered among ecosystems that are the most threatened by conversion or degradation, with <50% remaining intact (Sala et al., 2000; Hoekstra et al., 2005). In western North America, the loss of native grazers, abiotic disturbance processes (e.g., fire), and human-driven land conversion or degradation have resulted in steadily declining rangeland health (Dreitz et al., 2017). Further, declining biodiversity in grassland ecosystems has been linked to increased susceptibility to disease, invasion by exotic species, and decreased productivity (Tilman et al., 1996; Tilman et al., 1997).

The imperilment of American prairie ecosystems, and subsequent declines in biodiversity and rangeland health, has been regarded as a biome crisis (Hoekstra et al.,
2005), and the conservation and restoration of grassland ecosystems (along with other imperiled ecosystems) has become a popular theme in rangeland ecology (Fuhlendorf and Engle, 2001; Briske et al., 2005; Havstad et al., 2007). Attempting to thwart this crisis, managers and agencies have developed quantitative indicators to track and measure progress toward rangeland health targets (Pyke et al., 2002). The publication titled *Interpreting the Indicators of Rangeland Health* was published by the U.S. Bureau of Land Management (BLM), Natural Resource Conservation Service (NRCS), the U.S. Geological Survey (USGS), and the Agricultural Research Service (ARS) to allow managers or landowners to assess various rangeland types, or ecological sites, by measuring seventeen predefined indicators of rangeland health (Pyke et al., 2002) – often referencing community structure or composition (Table 1). Soil and hydrological measurements make up nine of the seventeen (~53%) indicators, with the rest being related to vegetative composition, abundance, and structural measurements (eight of seventeen; ~47%). Additionally, of those seventeen measurements three of the indicators do not have a quantitative measurement (i.e. they are qualitative in nature), with two of the non-quantitative measurements being focused on soil or hydrological processes and one being focused on vegetation dynamics (Pyke et al., 2002). The publication by Pyke et al. (2002) shows rangeland managers or private landowners what rangeland health attributes to measure (e.g., invasive plant abundance, plant mortality, litter abundance, annual production, plant community composition and distribution, functional group abundance, and litter movement), but requires reference community data to set and track progress toward rangeland health objectives or targets.
A broad effort by U.S. federal agencies to consolidate ecological information for use in land management led to the development of an Ecological Site Database, cataloging all the registered ecological sites and reference communities throughout the American Great Plains and Rockies regions (Bestelmeyer and Brown, 2010). The Ecological Site Database and accompanying Ecological Site Descriptions (ESDs) were developed by the NRCS, BLM, and U.S. Forest Service to stratify grassland landscapes based on composition, structure, and dynamics, applied across all rangeland types and jurisdictions (Bestelmeyer and Brown, 2010). ESDs provide landowners, managers, or the public with complex and detailed information sheets for a specific geographic area, including information on soils, hydrological patterns, average range in elevation and slope - and perhaps most importantly to pastoralists and rangeland managers – vegetation community dynamics descriptions with some associated abundance data (Bestelmeyer and Brown, 2010). ESDs also contain data for an area’s predicted historic climax plant community (HCPC), or the plant community composition and abundance at some maximum successional state (Clements, 1936). ESDs are chiefly intended to aid in the management, restoration, and monitoring of ecological sites, and provide detailed information to researchers and managers about specific geographic areas to compile and monitor specific management or restoration objectives (Bestelmeyer and Brown, 2010). Thus, we propose that ESDs could be useful in obtaining reference community data for monitoring rangeland health (e.g. in combination with the seventeen indicators by Pyke et al. (2002)), and progress toward restoration targets.
In northeastern Montana, two competing grazer management tools are being used to try and increase rangeland health and meet restoration targets above traditionally cattle (Bos taurus L.) grazed lands: bison (Bison bison L.) reintroduction and livestock removal. The American plains bison evolved in North America roughly 16,000 years BP, with an estimated population of 30-60 million individuals ranging across southern, central, and northern North America (Lott, 2002; Shapiro et al., 2004; Roman, 2015). By 1889 the bison of Montana had been nearly extirpated from the wild, with only a handful (<30) remaining (Hornaday, 1889). As the American plains bison population was declining, pastoralists were rapidly replacing these native bovine ungulates with European cattle (B. taurus L.). A major rationale behind bison reintroduction is the restoration of key ecosystem interactions (Knapp et al., 1999), in hopes of restoring biodiversity through the redevelopment of predicted historic climax plant communities (Freese et al., 2007; Seddon et al., 2014). Today, cattle are the dominant grazers on the rangelands of northeastern Montana, with an estimated population of nearly 100,000,000 across North America (Kohl et al., 2013). Cattle grazing is a tool that managers can utilize to reach rangeland restoration or management targets, which generally are to move rangelands closer to predicted HCPCs (Fuhlendorf and Engle, 2001; Bestelmeyer and Brown, 2010; Toombs et al., 2010). However, in some portions of the NGP, livestock have been removed from historically grazed rangelands in an attempt to reach restoration targets (e.g., certain designated wilderness areas in the Charles M. Russell National Wildlife Refuge, Montana). Livestock removal, however, has mixed effects on biodiversity, community structure, and dominance depending on the system; and studies
reporting general long-term effects are limited (Augustine et al., 2017; Porensky et al., 2017). Thus, two different strategies are currently being employed in northeastern Montana, and very little is known about how effective these two competing strategies are at reaching the restoration targets specified by the seventeen indicators of rangeland health compared to rest-rotation cattle grazing.

Our research attempted to describe how these three management tools may affect some quantifiable indicators of rangeland health within mixed-grass prairies of the Northern Great Plains. Specifically, our objective was to compare rangeland plant community successional patterns (i.e., state-transition models) among our three treatments, as well as to the predicted climax plant community defined by the shallow clay 11-14” (SC) ESD, using quantifiable indicators outlined by Pyke et al. (2002). To meet our research objective, we tested the following hypotheses that we developed by applying 5 of the 17 indicators of rangeland health (Pyke et al., 2002) within a single ESD reference community: 

$H_1$: bison reintroduction sites are more closely related (i.e. more similar) to the SC ESD HCPC than livestock removal or cattle-grazed sites; 

$H_2$: bison reintroduction or livestock removal leads to heightened abundances of desirable perennial bunchgrasses, heightened litter abundance, and lower overall abundance of invasive exotic weed species (i.e. noxious weeds) compared to cattle-grazed sites, and results in each measure not being statistically different from the SC ESD HCPC; 

$H_3$: bison reintroduction or livestock removal sites have similar average functional group abundances and bare ground cover to the HCPC compared to cattle grazed sites.
METHODS

Study Area

Our study took place in the Northern Great Plains (NGP) region of the United States, in a portion of southern Phillips County, Montana (Figure 1.2). This area is part of a region of northeastern Montana known colloquially as the Missouri Breaks: a hilly, and formerly glaciated, part of the mixed-grass prairie (Manning, 2009). The Missouri Breaks region is a 1.4 million ha patchwork of public and private lands, with 23% of lands being privately held, 36% of lands publicly managed by the Bureau of Land Management (BLM), and the remaining 41% being publicly managed by the USFWS (Manning, 2009). This area is dominated by a mixture of short and tallgrass prairie species (e.g. Pascopyrum smithii (Rydb.) Á. Löve, Schizachyrium scoparium (Michx.) Nash, Hesperostipa comata (Trin. & Rupe.) Barkworth var. comata, etc.). The mixed-grass prairie, as a region, generally has a moderate, but highly variable climate (Savage, 2011) as, for example, Phillips co. averaged 34 cm in total precipitation from 2000-2016, but only received a total of 29 cm in 2015; contrasting sharply with the 61 cm received in 2016.

The Taylor Grazing Act of 1934 allowed ranchers to lease public lands for grazing throughout the Great Plains (i.e. national grasslands, national wildlife refuges, bureau of land management lands), and in 1936 the first grazing leases were given out to graze within the Charles M. Russell National Wildlife Refuge (CMR) (Bill Haglan, USFWS, per. comm., February 2017). From 1915 to 1970 most of southern Phillips County was grazed similarly, most grazing being year-round, with unregulated grazing
intensity (i.e. stocking rate), leading to a generally homogeneous distribution of extremely poor rangeland quality (high erosion, little vegetation cover, increased stream head cutting/channelization) across all southern Phillips co. (Bill Haglan, USFWS, per. comm. February 2017). Thus, we assumed all our treatments historically were subjected to loosely regulated year-round grazing pre-1970, but transitioned to seasonal (i.e. growing season only), moderate to light grazing intensity (i.e. 0.20 – 0.40 AUM/ha; Animal Unit Month; the amount of land needed to support one cow and one calf for one month) rest-rotation cattle management from 1970 to 2005 through combined regulation and oversight by federal and state agencies (Bill Haglan, USFWS, per. comm. February 2017; B.J. Rhodes, BLM, per. comm. October 2015).

Bison-Grazed Treatment

Our bison treatment plots were located within a 12,545-ha reintroduction area that is owned and managed by the American Prairie Reserve (APR; Figure 1.2). Specifically, we conducted our sampling in the 7,092-ha Telegraph and Box Elder creek drainages, referred to collectively as Box Elder, where cattle were removed in early 2004 (Michel Kohl, Utah State University, per. comm., February 2017), and bison were reintroduced in October of 2005. In 2005, the APR reintroduced 16 bison, and Box Elder has experienced year-round bison grazing with the bison population growing to roughly 600 animals (including juveniles and sub-adults) by 2015 (18.75% per year with an average 29 imported animals per year) (American Prairie Reserve, 2015). Thus, bison have
grazed Box Elder for ten years by the time of our sampling (Figure 1.2) during which bison grazing intensity has been maintained below a threshold of 0.39 AUM ha\(^{-1}\).

*Livestock Removal Treatment*

We selected a 4,059-ha portion of the CMR, where livestock were removed in 2004, as our livestock removal treatment. We focused our sampling within an allotment named Telegraph Creek Pasture Five where cattle had been absent for 10-11 years. The allotted cattle grazing intensity data for the CMR (i.e. the AUM/ha permitted for grazing) is unavailable to compare with our other treatments, but the observed (or actual) grazing intensity from 1990 - 2004 averaged 0.16 AUM ha\(^{-1}\) (Std. Error = 10.00 AUM year\(^{-1}\), Range = 104 AUM year\(^{-1}\)).

*Cattle-Grazed Treatment*

Our cattle grazed (control) treatment was located within the 8,303-ha Fourchette Creek grazing allotment that is managed by the BLM. Cattle grazing on this allotment has been consistently managed via rest-rotation grazing since May 1, 1983 that allowed for up to 2,815 AUMs of grazing pressure during a grazing season that lasted from May 1st – October 30th of each year (B.J. Rhodes, BLM, per. comm., October 2015). Thus, grazing intensity in our cattle-grazed treatment area was maintained below a threshold of 0.33 AUM ha\(^{-1}\) from May 1st – October 30th during years 1983-2016 (B.J. Rhodes, BLM, per. comm., October 2015).
Site Selection for Field Sampling

Testing the ability of our three treatments to move rangelands closer to the HCPC for a single ESD enabled us to simultaneously select areas with predicted similarity in soil condition, slope, aspect, elevation, and other abiotic variables. We utilized ESD data created by the NRCS that describe and outline areas with similar biotic and abiotic conditions (potential plant community, soil description, slope, elevation, etc.; https://esis.sc.egov.usda.gov). In addition, ESDs were developed as a tool to predict forage production potential for each ecological site (Bestelmeyer and Brown, 2010). Given that we assumed vegetative community responses to grazing were likely to follow the Dynamic Equilibrium model, which predicts that the effects of disturbance are correlated positively with productivity (Huston, 1979; Yuan et al., 2016), we focused sampling in ESDs where plant community productivity, and thus grazing pressure, was likely highest. Therefore, our use of ESDs enabled us to effectively restrict sampling to areas with high levels of forage productivity and potential for grazing to impact vegetative communities, as well as areas with homogeneous environmental conditions (e.g. soil texture, slope, elevation, etc.). The most common ESD with high productivity occurring in all three treatments was Shallow Clay 11-14” (SC) capable of producing from 703-5,878 kg of grass and sedge forage per hectare (https://esis.sc.egov.usda.gov). We then randomly selected 10 sample points within SC polygons for each treatment in the study area.
Vegetation Sampling and Design

Between June – August, 2015 and May – August, 2016 we established study plots and evaluated the vegetative community at 10 randomly sampled points within the SC ESD for each of our three treatment areas (n=30). We chose to sample 10 points based on a power analysis, where we utilized pilot data to generate reasonable estimates of: 1) the difference in mean response among our treatments, and 2) the variability among points within our treatments. We determined a statistical power estimate of $\geq 0.80$ with an alpha of 0.05 for 10 replicates within each treatment. At each point, we established a 0.1 ha (20 m x 50 m) modified Whittaker plot (Peet et al., 1998). Each plot consisted of ten individual 100 m$^2$ subplots (Figure 2.2; referred to hereafter as modules) that were sampled for species incidence. We restricted vegetation cover sampling to modules 2, 3, 8, and 9 (Figure 2.2; hereafter referred as intensive modules), where we estimated the cover for each species encountered on a scale from 1-9, representing: trace, 0-1%, 1-2%, 2-5%, 5-10%, 10-25%, 25-50%, 50-75%, and 75-95% respectively (Figure 2.2). Litter cover was evaluated using visual estimation, and a single percent-cover value (e.g. 45%) was recorded for each plot (n = 10 per treatment; n = 30 overall). Bare ground was evaluated by visual estimation, and each module received a cover value on a scale from 1-9 (i.e. the same as vegetation cover). We then averaged bare ground cover across all modules to obtain a single mean cover value per plot (n=5 for bison and n=10 in other treatments; n = 25 total).
Assessing treatment functional group abundance and overall composition divergence from HCPC

We used two separate approaches to assess how plant functional group abundances and composition compared between the HCPC reported in the SC ESD and each of our three treatments. We first utilized hierarchal cluster analysis techniques to visually analyze how compositionally different bison grazing, livestock removal, and cattle grazing were from the targeted HCPC composition ($H_1$) (Gardener, 2014). We used the climax community data presented in the SC ESD (Appendix A) to generate a species incidence and abundance list for the HCPC. The SC ESD listed different categorical cover value ranges than we used in our study (e.g., 0-5%, 1-5%, etc.), so we overcame this by converting them to cover classes used in our data collection (e.g., 0-T, 0-5%, and 1-5% reported in the ESD became 0-1%, 1-2%, and 2-5% categorical cover ranges respectively). To generate workable abundance values, we transformed our categorical cover classes to a mid-point percentage value (e.g. 1-2% would be transformed to 1.5%) (Newell and Peet, 1998). We used the average abundances of each species per plot to construct a table containing each average species abundance recorded per site aggregated by one of three functional group categories, following groupings listed in the SC ESD: forbs, shrubs/subshrubs, or grasses/sedges. We used our species abundance by site and functional group table to generate a dissimilarity matrix using the “correlation” dissimilarity equation used in the “pvclust” command in the program R v.3.3.2:
\[ C_d = 1 - \frac{\sum(x_{ij} - \bar{x}_j)(x_{ik} - \bar{x}_k)}{\sqrt{\sum(x_{ij} - \bar{x}_j)^2} \sqrt{\sum(x_{ik} - \bar{x}_k)^2}} \]  

where \( x_{ij} \) and \( x_{ik} \) are the species abundances at sites \( j \) and \( k \), and \( C_d \) is the level of dissimilarity between the two sites (Suzuki and Shimodaira, 2006; Gardener, 2014; R Core Team, 2016). We used the resulting dissimilarity matrix to perform a hierarchical clustering analysis in the program R v.3.3.2, and calculated \( p \)-values for each clustering using bootstrap resampling at 1000 bootstrap replicates (R Core Team, 2016). We visually assessed the results of our hierarchical clustering by generating a dendrogram to illustrate the relative relatedness of each site to the climax community.

We further analyzed how our sites compared based on functional group abundance by calculating the difference between each treatment and the HCPC. The general mathematical methodology is represented as:

\[ D_f = x_{ij} - y_i \]  

showing the difference in abundance of a functional group \( i \) at each plot \( j \) within each treatment \( x \) from the average abundance of the HCPC \( y \) for a functional group \( i \). Each difference was then run through a LSM t-test to detect whether the functional group abundances in each treatment were statistically different from the HCPC.

*Evaluating how treatments affect perennial bunchgrass, noxious weed, litter, and bare ground abundances*
We assessed the influence of bison, cattle, and livestock removal on plant and bare ground abundances by first transforming our data to midpoint percentage values for native perennial bunchgrasses, noxious weeds, and bare ground cover. Litter cover was collected as a direct percentage (e.g., 45%), and thus did not require transformation. We summed our species-level data for all species falling within each group (e.g., all species of perennial bunchgrass were merged together), then calculated the mean abundance of each group per plot. We then log-transformed our data to meet normality assumptions needed for further parametric statistical testing. We conducted a one-way ANOVA to determine whether bison, cattle, or livestock removal have any effect on litter, bare ground, perennial bunchgrass, and noxious weed cover. When we detected significant effects between our three treatments, we further explored the relationship of these effects by constructing and testing pairwise LSM contrasts between our treatments. We employed pairwise LSM contrasts to detect differences among each of our treatments and the HCPC. Significance for all tests was declared at $\alpha = 0.05$.

RESULTS

Hierarchical Clustering

We did not find extensive visual support for our hypothesis that bison reintroduction sites had overall functional group compositions more closely related to the HCPC of the SC ESD than livestock removal or cattle-grazed sites (Figure 3.2). Bison reintroduction forb composition and abundance was significantly grouped with both livestock removal and cattle-grazed sites (bootstrap resampling, $p = 0.04$, $au = 0.96$, $bp =$
0.99; Figure 3.2), and with the HCPC (\( p < 0.0001, \ au = 1.0, \ bp = 1.0; \) Figure 3.2).

However, our cattle-grazed and livestock removal sites were significantly more related to each other than to our bison reintroduction sites (\( p = 0.02, \ au = 0.98, \ bp = 0.93 \)). Bison reintroduction sites were approximately 40% related in forb species composition and abundance to our other two treatments, and were 80% related to the HCPC (Figure 3.2). Livestock removal and cattle-grazed sites were significantly grouped in their forb composition and abundance (\( p = 0.02, \ au = 0.98, \ bp = 0.93 \)), and were approximately 60% and 80% dissimilar from the bison reintroduction sites and HCPC respectively (Figure 3.2). Bison reintroduction, livestock removal, and cattle-grazed sites were all significantly grouped in their shrub and subshrub composition and abundance (\( p = 0.01, \ au = 0.99, \ bp = 0.88 \)), and all were approximately 20 – 30% related to the HCPC (Figure 3.2). Similarly, our bison reintroduction, livestock removal, and cattle-grazed sites were significantly grouped with each other in terms of grass and sedge composition and abundance (\( p = 0.01, \ au = 0.98, \ bp = 0.74 \)), and were all approximately 15 – 20% related to the HCPC (Figure 3.2).

* Differences in perennial bunchgrass, noxious weed, and litter abundance

We were unable to find support for our hypothesis that bison reintroduction or livestock removal increased the abundance of perennial bunchgrasses (\( F = 0.09, \ p = 0.90, \ df = 27, 2 \)) compared to cattle grazing. We observed that all our three treatments had lower perennial bunchgrass abundance compared to the HCPC, with both bison reintroduction (\( t = -5.38, \ p = 0.0004, \ df = 9 \)) and livestock removal being 6% lower (\( t = -
5.50, \( p = 0.0004, df = 9 \), and cattle grazing being 5% lower (\( t = -4.18, p = 0.0024, df = 9 \)) than the HCPC (Figure 4.2).

We found sufficient evidence to support our hypothesis that bison reintroduction, livestock removal, and cattle-grazed sites differed in noxious weed abundances (\( F = 4.23, p = 0.025, df = 27, 2 \)). We found that the bison reintroduction treatment had lower noxious weed abundances than our cattle-grazed (LSM, \( t = 1.80, p = 0.042, df = 27 \)) and livestock removal (\( t = 2.88, p = 0.0039, df = 27 \)) treatments (Figure 5.2). Specifically, we found that our cattle-grazed and livestock removal treatments contained 83% higher and 88% higher noxious weed abundances than our bison reintroduction treatment, respectively (Figure 5.2). Livestock removal and cattle-grazed treatments were not significantly different in noxious weed abundances (\( t = 1.08, p = 0.29, df = 27 \)).

We collected sufficient evidence to support our hypothesis that all three treatments had differing abundance of litter cover (\( F = 9.73, p = 0.0007, df = 27, 2 \)). Our livestock removal treatment contained 31% and 23% higher litter cover compared to our cattle-grazed (LSM, \( t = 4.25, p = 0.0001, df = 27 \); Figure 6.2) and bison reintroduction (\( t = 3.15, p = 0.002, df = 27 \)) treatments, respectively, and did not statistically differ from the HCPC (\( t = -0.63, p = 0.54, df = 9 \)). We were not able to find evidence that our bison reintroduction treatment had higher litter cover compared to our cattle-grazed treatment (\( t = -1.10, p = 0.14, df = 27 \)). Furthermore, both the cattle-grazed (\( t = 8.41, p < 0.0001, df = 9 \)) and bison reintroduction (\( t = 3.14, p = 0.011, df = 9 \)) treatments had significantly lower litter cover than is predicted to occur in the HCPC.
Native Functional Group Abundance and Bare Ground Cover Comparison with HCPC

We were unable to collect sufficient evidence to suggest that bison reintroduction or livestock removal resulted in communities that were completely similar in overall native functional group abundances compared to the reported HCPC in the SC ESD (Figure 7.2). However, we did observe that native forb abundances (LSM, \( t = 1.80, p = 0.10, df = 19 \)) along with native grass and sedge abundances (\( t = -1.73, p = 0.12, df = 19 \)) within our bison reintroduction treatment did not differ from those expected in the HCPC (Figure 7.2). We observed that the mean native shrub and subshrub abundance in our bison reintroduction treatment was approximately 12% higher than would be expected by the HCPC (\( t = 3.64, p = 0.0054, df = 19 \)). We observed that our cattle-grazed treatment contained native grass and sedge abundances not significantly different from the expected HCPC (\( t = 0.82, p = 0.12, df = 19 \)), but had 4% higher mean native forb abundance (\( t = 3.01, p = 0.015, df = 19 \)) and 12% higher mean native shrub and subshrub abundance compared to the HCPC (\( t = 5.00, p = 0.0007, df = 19 \); Figure 7.2). Our livestock removal treatment contained approximately 7% higher native forb abundance (\( t = 3.01, p = 0.015, df = 19 \)), 14% higher native grass and sedge abundances (\( t = 3.54, p = 0.0064, df = 19 \)), and 24% higher shrub and subshrub abundances compared to those expected from the HCPC (\( t = 5.84, p < 0.001, df = 19 \); Figure 7.2).

Although we did not detect differences among our treatments (\( F = 0.80, p = 0.46, df = 22, 2 \)), we collected sufficient evidence to suggest that bare ground cover in our bison reintroduction treatment did not significantly differ from the HCPC reported within the SC ESD (LSM, \( t = -0.36, p = 0.73, df = 4 \)). Both our cattle-grazed (\( t = -2.47, p = \))
and livestock removal (t = -2.33, p = 0.045, df = 9) treatments had 6-7% lower bare ground cover than expected within the HCPC (Figure 8.2).

DISCUSSION

Compared to cattle grazing or removal, our findings suggest that bison restoration increased three of the five measured indicators of rangeland health closer to the historic climax plant community in one ESD. Our finding that bison reintroduction outperformed both our cattle-grazed and our livestock removal treatments with respect to forb and bare ground cover in being similar to the expected HCPC follows what would be expected after the reintroduction of a native species – where the reintroduction leads to historic disturbance regimes well suited to the historic species compositions (Mills et al., 1993; Knapp et al., 1999; Painter et al., 2015). However, ten years following the reintroduction we did not observe a complete community structural and compositional (i.e. biotic and abiotic components) shift toward what would be expected within the historic climax community. Thus, our mixed results follow bison reintroduction studies performed in the tallgrass prairie, where bison and cattle showed slight divergence in community composition and structure, with a major divergence in native forb cover (Knapp et al., 1999; Towne et al., 2005).

Many of the differences between our bison reintroduction treatment and others, may be due to hypothesized foundational (or keystone) effects of bison on North American prairie ecosystems (Knapp et al., 1999). For example, bison commonly exhibit wallowing behaviors that generate large depressions of bare ground throughout the
prairie, which generate high grassland heterogeneity and biodiversity (Knapp et al., 1999; Truett et al., 2001; Freese et al., 2007; Miller et al., 2014). We observed that bison reintroduction areas had bare ground cover that was comparable to the expected historic community, and directly observed many large depressions of exposed ground certainly created by the wallowing behaviors in bison. Bison reintroduction areas also had lower noxious weed cover than our other treatments, which could be due to competitive exclusion generated by the high abundance of native forbs, potentially generated by keystone forage selectivity (Tilman et al., 1996; Knapp et al., 1999). We directly observed bison foraging on many prominent noxious weed species, namely yellow-sweet clover (*Melilotus officinalis* L.), alfalfa (*Medicago sativa* L.), and crested wheatgrass (*Agropyron cristatum* L.), suggesting that such foraging events (especially when mixed with fire) could further directly suppress annual or perennial noxious weeds in favor of increased similarity to the HCPC (Allred et al., 2011). Contrastingly, our cattle-grazed treatment had markedly higher noxious weed cover, but our observations may be related to the amount of human travel throughout cattle-grazed areas for management activities (e.g. moving cattle, checking tanks, monitoring forage consumption, etc.) (Mack and Lonsdale, 2001), or to the historic promotion of these species by planting or reseeding by ranchers or agency officials (Bahm et al., 2011). While the effect sizes we report are significantly large between our treatments, the difference in total cover is relatively small (e.g., our bison treatment with <1% versus our cattle treatment with ~3.5% noxious weed cover). However, if the goal of a restoration project is to lower (or eliminate) the overall
abundance of noxious weeds, then any reduction in noxious weed cover due to treatment effects is significant and meaningful in meeting restoration goals.

Cattle are non-native species to North America, and have many recognized behavioral and habitat selection differences with *B. bison* that could explain their lower performance in moving litter and bare ground cover closer to a HCPC (Plumb and Dodd, 1993; Kohl et al., 2013). The goal of rest-rotation cattle grazing techniques is to take as much palatable forage from the landscape, while attempting to maintain a certain amount of standing plant matter (residual cover) (Fuhlendorf and Engle, 2001). Rest-rotation cattle grazing, then, may reduce the amount of litter compared to our other treatments, due to the higher grazing intensity of the technique, and the time that cattle spend foraging compared to bison (Kohl et al., 2013). Behavioral dissimilarity with *B. bison* is likely the best descriptor for the lack of bare ground cover between cattle and the HCPC (Truett et al., 2001; Freese et al., 2007), although low bare ground cover is typically regarded to be a result of low-grazing pressure (Hart et al., 1988). Interestingly however, the grass and sedge cover in both our bison and cattle treatments were statistically equal to the HCPC, supporting mixed evidence that both management techniques could possibly be used to meet some restoration objectives (Allred et al., 2011) (Figures 3.2 and 7.2).

In general, livestock removal seems to be the least effective restoration tool at moving grassland plant communities toward goals aimed at restoring historic climax plant communities. The development of Great Plains plant communities was historically moderated by disturbances like grazing and fire (Fuhlendorf et al., 2006; Allred et al.,
2011; Koerner et al., 2014). Litter cover, for example, was much higher in our livestock removal treatment than our other two, supporting claims that the disturbance generated by both large grazers (and fire) work to regulate decomposition and nutrient cycling in temperate grasslands (Knapp et al., 1999; Anderson, 2006b). However, livestock removal did not significantly differ with the HCPC in litter cover, supporting claims that the short-term removal of large grazers may facilitate some limited increases in that category of rangeland health (Augustine et al., 2017). Overall, our finding that livestock removal did not result in much movement of plant communities toward HCPC conditions follows many studies that confirm grazing as a necessary disturbance agent in the maintenance of desirable rangeland plant communities (Augustine et al., 2017).

The climax community concept, and the repeatability of successional patterns within a single ecosystem has been historically controversial, but is still used to both describe plant community dynamics and direct management in rangeland ecosystems. Currently, most rangeland successional patterns are depicted using state-transition models, showing all major pathways (and associated mechanisms driving movement along each pathway) leading communities toward or away from some historic climax plant community (Briske et al., 2005). However, debate both for and against such static views on community dynamics have been occurring since the climax community concept was put forth by Clements (1936), with much of the opposition citing Gleason (1927) as holding a more palatable view (White, 1979). Additionally, with the threat of climate change, rangeland restoration projects will need to re-examine the utility of using state-transition models relying on Clementsian successional theory when communities are
predicted to experience shifts resulting from novel climate patterns. Therefore, we suggest that restoration ecologists, managers, and landowners begin to discuss the viability of restoration projects, and test the efficacy of using climate model predicted climax communities versus historical climax community data to set restoration targets.

Our results suggest that utilizing rangeland health indicators as quantitative measures in assessing progress toward restoration targets (e.g., HCPCs) may be useful in parsing out potential differences among restoration treatments at meeting the same goals. However, we also suggest that different ecological sites may respond slightly differently than our sites within the SC ESD, as it is hypothesized that grazing’s relationship to grassland plant community composition varies along environmental gradients (e.g. soil, altitude, etc.) (Zemmrich et al., 2010). In addition, different grazing regimes (e.g. stocking density, grazing time, etc.) may also exhibit different plant community responses (Hart et al., 1988; Fuhlendorn and Engle, 2001). Therefore, we recommend that future research attempt to address not only how each ESD is responding to each of our three treatments in the rangeland health indicator framework, but the effect of different grazing regimes on reaching a plant community’s climax state.

Overall, our study illustrates the value of using both quantitative measures of rangeland health and reference community data to evaluate rangeland restoration strategies. Without such quantitative assessments, assessing rangeland health can be dangerously subjective. Here we have outlined a novel approach to assess rangeland health by collecting quantitative criterion within the rangeland health indicator framework (Pyke et al., 2002), and comparing data to reference communities developed
using ecological site descriptions (Bestelmeyer and Brown, 2010). Further, consistent long-term monitoring of rangeland health, at a variety of spatial scales and treatments as discussed above, should be accomplished to honestly measure progress toward a restoration target.

**IMPLICATIONS**

As the grasslands of central North America continue to decline, and are consistently threatened by conversion or degradation, the restoration and conservation of rangelands is becoming ever-more important (Hoekstra et al., 2005; Seddon et al., 2014). Our research shows that bison reintroduction may be a viable way for rangeland managers to increase rangeland health, but more research is needed on the long-term effects of bison reintroduction on rangeland plant communities. We provide a novel approach in utilizing the rangeland health indicator framework (Pyke et al., 2002) to quantitatively track the progress of restoration projects in reaching a predicted historic climax plant community as defined by an area’s ecological site description (Bestelmeyer and Brown, 2010). We observed a strong performance by bison reintroduction in reaching our restoration targets within a single ESD, but each ESD has its own HCPC, and further research should parse out potential differences among restoration treatments at meeting the same goals. If the grasslands of central North America are to be conserved, and a potential biome crisis averted (Hoekstra et al., 2005), it is critical that land managers regularly monitor rangelands using quantitative measures to track progress.
toward a defined restoration target. If rangeland health is not quantitatively assessed and measured against a reference community, then evaluating *health* is entirely subjective.
Table 1.2 The seventeen indicators of rangeland health and the quantitative measurement for each from Pyke and others (2002). Each indicator we quantitatively measured in this study are shown in bold as well as the restoration or management target (i.e. the historic climax plant community; HCPC) for the ecological site description (ESD) labelled Shallow Clay 11-14” (SC) (obtained via: https://esis.sc.egov.usda.gov/)

<table>
<thead>
<tr>
<th>Indicator</th>
<th>Quantitative Measurement</th>
<th>SC ESD Target</th>
</tr>
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<tbody>
<tr>
<td>1. Rills</td>
<td>N/A</td>
<td>-</td>
</tr>
<tr>
<td>2. Water flow pattern</td>
<td>Percent basal cover</td>
<td>-</td>
</tr>
<tr>
<td>3. Pedestals or terracettes</td>
<td>Standard deviation of pin heights</td>
<td>-</td>
</tr>
<tr>
<td><strong>4. Bare ground</strong></td>
<td><strong>Percent bare ground</strong></td>
<td><strong>15-30%</strong></td>
</tr>
<tr>
<td>5. Gullies</td>
<td>Width-to-depth ratio and side slope angle</td>
<td>-</td>
</tr>
<tr>
<td>6. Wind-scoured, blowout, or depositional areas</td>
<td>N/A</td>
<td>-</td>
</tr>
<tr>
<td>7. Litter movement</td>
<td>Interspace vs. ground layer litter cover (proportion)</td>
<td>-</td>
</tr>
<tr>
<td>8. Soil surface erosion resistance</td>
<td>Average soil surface stability</td>
<td>-</td>
</tr>
<tr>
<td>9. Soil surface loss or degradation</td>
<td>Average soil subsurface stability</td>
<td>-</td>
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</tbody>
</table>
| **10. Plant community composition/distribution relative to infiltration and runoff** | Percent composition | 70 – 90% grasses and sedges: 10-20% represented by perennial sod-forming grasses [e.g. western wheatgrass (*Pascopyrum smithii*), plains reedgrass (*Calamagrostis montanensis*), 40-60% perennial bunchgrasses [e.g. bluebunch wheatgrass (*Pseudoroegneria spicata*), green needlegrass (*Nassella viridula*), plains muhly (*Muhlenbergia*..........)
cuspidata), etc., 3-7% sedges [e.g. threadleaf sedge (*Carex filifolia*),
5-15% shrubs and subshrubs [e.g. Wyoming big sagebrush (*Artemisia tridentata ssp. wyomingensis*), winterfat (*Krascheninnikovia lanata*), prairie rose (*Rosa acicularis*), etc.], and 1-5% forbs [e.g. purple prairiecover (*Dalea purpurea*), scarlet globemallow (*Sphaeralcea coccinea*), prairie thermopsis (*Thermopsis rhombifolia*), etc.]
<table>
<thead>
<tr>
<th>11. Compaction layer</th>
<th>Ratio of penetration resistance in the upper 15 cm between the sampling and reference area</th>
<th>-</th>
</tr>
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<tbody>
<tr>
<td>12. Functional or structural group composition</td>
<td>Percent composition by functional or structural group, and group richness</td>
<td>Dominated by grasses and sedges (40-60% canopy cover), followed by forbs (5-10%), and shrubs/subshrubs being the least-dominant (1-5%) functional/structural group. Forbs, however, represent the group with the highest richness, followed closely by grasses/sedges and forbs respectively.</td>
</tr>
<tr>
<td></td>
<td>Description</td>
<td>Measurement</td>
</tr>
<tr>
<td>---</td>
<td>------------------------------------------------------------------------------</td>
<td>--------------------------------------------</td>
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<tr>
<td>13.</td>
<td>Plant mortality or decadence</td>
<td>Proportion of live-to-dead canopy cover</td>
</tr>
<tr>
<td>14.</td>
<td><strong>Litter cover</strong></td>
<td>Percent litter cover</td>
</tr>
<tr>
<td>15.</td>
<td>Annual production</td>
<td>Total annual production</td>
</tr>
<tr>
<td>16.</td>
<td><strong>Invasive exotic plant (noxious weed) cover</strong></td>
<td>Percent cover of invasive-exotic species</td>
</tr>
<tr>
<td>17.</td>
<td>Reproductive capability of perennial plants</td>
<td>N/A</td>
</tr>
</tbody>
</table>
Figure 1.2  Map (1) of our study area, located in Phillips County Montana, showing the extent of the Shallow Clay 11-14” ESD within our study area, as well as the spatial arrangement of our three treatments: (A) bison grazed, (B) cattle grazed, and (C) cattle removal. Plots are represented as filled circles. Inset map (2) shows the general location of our study area (Phillips County, Montana) within the Northern Great Plains region.
Figure 2.2  The spatial scale of an individual plot, consisting of ten 100 m² modules. Modules 2, 3, 8, and 9 are sampled as intensive modules (bold boxes). All other modules (i.e. 1, 4, 5, 6, 7, 10) were sampled as an aggregate, searching only for species not recorded in the intensive modules. The origin of the plot is marked with an open circle, and other long-term plot markers are represented by filled, black circles.
Figure 3.2  Results of a hierarchical clustering analysis portrayed as a dendrogram, showing the similarity of each treatment (B = Bison, Re = Removal, Ca = Cattle) to the historic climax plant community (HCPC) per functional group. Approximate unbiased (au) p-values (displayed as 1-P * 100) and bootstrap estimates (bp) are displayed above each grouping. Cluster significance was considered at $\alpha = 0.05$, and bootstrapping was performed with 1000 replications. Height represents the amount of dissimilarity between clusters, as determined following the “correlation” dissimilarity index in the “pvclust”
command in the statistical software R v.3.3.2. Boxes are placed around significant groupings ($p \leq 0.05$) below 1.0 height.

Figure 4.2 The mean perennial bunchgrass cover (%) for our bison reintroduction, cattle-grazed, and livestock removal treatments. Also depicted is the expected mean perennial bunchgrass cover for the historic climax plant community reported within Montana’s Shallow Clay 11-14” Ecological Site Description. Error bars represent a 95% confidence interval of the mean ($\alpha = 0.05$).
Figure 5.2  The mean abundance of all invasive-exotic (i.e. noxious weed) species occurring in our bison-reintroduction, cattle-grazed, and livestock removal sites. Error bars represent a 95% confidence interval (α = 0.05). The historic climax plant community lacks invasive species (i.e. cover = 0%), and thus is not represented on this figure.
Figure 6.2  The mean litter cover (%) detected within our bison reintroduction, cattle-grazed, and livestock removal treatments.  Also depicted is the expected mean litter cover for the historic climax plant community reported within Montana’s Shallow Clay 11-14” Ecological Site Description.  Error bars represent a 95% confidence interval of the mean ($\alpha = 0.05$).
Figure 7.2 The mean abundance (Cover %) of forbs, grasses and sedges, and shrubs and subshrubs detected within our bison reintroduction, cattle-grazed, and livestock removal treatments. Also depicted is the expected mean forb, grass and sedge, and shrub and subshrub abundance within the historic climax plant community reported within Montana’s Shallow Clay 11-14” Ecological Site Description. Error bars represent a 95% confidence interval of the mean ($\alpha = 0.05$).
Figure 8.2 The log-mean bare ground cover (%) for our bison reintroduction, cattle-grazed, and livestock removal treatments. Also depicted is the expected log-mean bare ground cover for the historic climax plant community reported within Montana’s Shallow Clay 11-14” Ecological Site Description. Error bars represent a 95% confidence interval of the mean (α = 0.05).
APPENDICES
Appendix A

Ecological Site Description: Shallow Clay 11-14"

Ecological Site Description—Rangeland

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<thead>
<tr>
<th>MLRA: 58AC – Sedimentary Plains, Central</th>
<th>Shallow Clay (SwC), 11-14&quot; MAP</th>
</tr>
</thead>
</table>

1. **Physiographic features**: This ecological site can occur on nearly level to very steep uplands. It often occurs in complex with other ecological sites, particularly in rougher terrain. This site occurs on all slopes and exposures. Slight variations in plant community composition and production can result due to aspect. The amount of exposed rock outcrop tends to increase as slopes increase. Runoff and the potential for water erosion can be important features of this site.

   - **Landform**: sedimentary plain, hill, escarpment
   - **Elevation (feet)**: 2250 - 4500
   - **Slope (percent)**: 0-70
   - **Depth to Water Table (Inches)**: greater than 60
   - **Flooding**: none
   - **Ponding**: none
   - **Runoff Class**: medium to high
   - **Aspect**: all aspects, can be significant

2. **Soils**: These are clayey soils that are 10 to 20 inches deep to underlying beds of decomposed shale or nearly impervious clays. Few roots penetrate deeper than 20 inches. Available Water Holding Capacity to 20 inches is 2 to 4 inches.

3. **Associated sites**: Mainly Clayey, Clayey-Steep, and Shallow sites. Also Silty, Silty-Steep, Shale, Saline Upland, Clay Pan, Dense Clay, and shale outcrop.

4. **Similar sites**: Clayey, Shallow, Clayey-Steep.

   Clayey sites have similar textures, but differ mainly by being over 20 inches to rock, and having significantly more production. The plant community can be similar because of the restrictive layers of clayey textures. The Shallow site differs by having a different texture, and generally being over sandstone or loamy beds. The Clayey-Steep Site is over 20 inches deep to root restricting materials, as well as occurring on slopes over 15%.

   --SPLIT--
4. Similar sites: Clayey, Shallow, Clayey-Steep.

Clayey sites have similar textures, but differ mainly by being over 20 inches to rock, and having significantly more production. The plant community can be similar because of the restrictive layers of clayey textures. The Shallow site differs by having a different texture, and generally being over sandstone or loamy beds. The Clayey-Steep Site is over 20 inches deep to root restricting materials, as well as occurring on slopes over 15%.

5. Major Plant Community Types: The following are descriptions of several plant communities that may occupy this site:

Plant Community 1: Tall and Medium Grasses/ Forbs/ Shrubs: The physical aspect of this site in the Historical Climax (HPC) is that of a gentle to steep sloping grassland with scattered shrubs on steeper slopes. Approximately 70–75% of the annual production is from grasses and sedges, 5–10% from forbs, and 5–15% is from shrubs and half-shrubs. The canopy cover of shrubs is 1–6%.

Dominant species include bluebunch wheatgrass, green needlegrass, plains muhly, and western or thickspike wheatgrass. Short grasses such as Sandberg bluegrass and prairie junegrass are also present. There are abundant forbs (purple and white prairie clover, prairie coneflower, dotted gayfeather) which occur in smaller percentages. Shrubs such as Nuttall’s saltbush and winterfat are common. Rocky Mountain juniper may also occur on steeper slopes.

The occurrence, frequency, timing, and intensity of fire all have an important affect on this community. The Wyoming big sagebrush is susceptible to fire and will tend to decrease with fire. The Nuttall’s saltbush tends to be resistant to fire. Winterfat is very susceptible to burning, depending on the intensity. Some published reports indicate that spring burning may be least detrimental. Reports indicate further that fall burning has resulted in a 95 to 100 percent loss of winterfat in some situations.

This plant community is well adapted to the Northern Great Plains climatic conditions. The diversity in plant species and presence of tall, deep-rooted perennial grasses allows for drought tolerance. Plants on this site have strong, healthy root systems that allow production to increase significantly with favorable moisture conditions. Abundant plant
Ecological Site Description—Rangeland

MLRA: 58AC – Sedimentary Plains, Central
R058AC059MT

litter is available for soil building and moisture retention. Plant litter is properly distributed with very little movement off-site and natural plant mortality is very low. This plant community provides for soil stability and a functioning hydrologic cycle.

**Plant Community 2: Medium and Short Grasses/ Shrubs:** This community occurs from shifts in climate or other disturbances, such as grazing that tend to increase Wyoming big sagebrush. Dominant grasses include western or thickspike wheatgrass, Sandberg bluegrass, and prairie junegrass. Bluebunch wheatgrass, green needlegrass, and plains muhly will still be present but in smaller amounts. Palatable and nutritious forbs will be replaced by less desirable and more aggressive species, such as hairy goldenaster, silverleaf scurfpea, and scarlet globemallow. Sweet clover is a common invader on this ecological site.

Grass biomass production and litter become reduced on Community 2 as the taller grasses become less prevalent, increasing evaporation and reducing moisture retention. Additional open space in the community can result in undesirable invader species. This plant community provides for moderate soil stability.

**Plant Community 3: Shrubs and Half-shrubs/ Short Grasses:** This is a disturbance induced community, with dominant species including Wyoming big sagebrush, Sandberg bluegrass, prairie junegrass, blue grama, perennial forbs, and fringed sagewort. Remnant amounts of western or thickspike wheatgrass and needleandthread may be present. Tall grasses and palatable forbs will be mostly absent.

Plant Community 3 is much less productive than Plant Communities 1 or 2, and has lost many of the attributes of a healthy rangeland. The loss of deep perennial root systems reduces total available moisture for plant growth. Reduction of plant litter will result in higher surface soil temperatures and increased evaporation losses. Annual species are often aggressive and competitive with seedlings of perennial plants. This community can respond positively to improved grazing management but it will take additional inputs to move it towards a community similar in production and composition to that of Plant Community 1 or 2.

**Plant Community 4: Shrubs/ Half-shrubs/ Annual Grasses and Forbs/ Short Grasses:** This community is the result of continual adverse disturbances. Dominant species include Wyoming big sagebrush, fringed sagewort and broom snakeweed, and annuals such as cheatgrass, Japanese brome, and six-weeks fescue. Blue grama, Sandberg bluegrass, and prairie junegrass may be present in lesser amounts.

Plant community 4 has extremely reduced production of native plants (< 400 lbs./acre). The lack of litter and short plant heights result in higher soil temperatures, poor water infiltration rates, and increased evaporation, which gives short sod grasses and annual invaders a competitive advantage over the tall and medium grasses. This community has lost many of the attributes of a healthy rangeland, including good infiltration, minimal erosion and runoff, nutrient cycling and energy flow. Significant economic inputs and time would be required to move this plant community toward a higher successional stage and a more productive plant community.

5a. **Cover and structure (Historic Climax Plant Community)**

<table>
<thead>
<tr>
<th>COVER TYPE</th>
<th>BASAL COVER (%)</th>
<th>CANOPY COVER (%)</th>
<th>AVERAGE HEIGHT (INCHES)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Cryptogams</td>
<td>T-5</td>
<td>T-5</td>
<td>0.25 - 0.50</td>
</tr>
<tr>
<td>Grasses/ sedges</td>
<td>5-12</td>
<td>40-60</td>
<td>18</td>
</tr>
<tr>
<td>Forbs</td>
<td>1-4</td>
<td>6-10</td>
<td>6</td>
</tr>
<tr>
<td>Shrubs</td>
<td>1-5</td>
<td>1-5</td>
<td>6</td>
</tr>
<tr>
<td>Litter</td>
<td>40-60</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Coarse fragments</td>
<td>5-10</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Bare ground</td>
<td>15-30</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>
## Ecological Site Description—Rangeland

### 5b. Major Plant Species Composition - Historical Climax Plant Community

<table>
<thead>
<tr>
<th>Common Name</th>
<th>Plant Symbol</th>
<th>Plant Group</th>
<th>Percent Comp.</th>
<th>Group Max. %</th>
<th>Mean Annual Precipitation (Inches)</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>11 (lbs./acre) 12 (lbs./acre) 13 (lbs./acre) 14 (lbs./acre)</td>
</tr>
<tr>
<td><strong>Grasses and Sedges</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Bluebunch wheatgrass</td>
<td>PSSW</td>
<td></td>
<td>2</td>
<td>30-60</td>
<td>630-610 700-800 770-980 840-1080</td>
</tr>
<tr>
<td>Western or Thickspike wheatgrass</td>
<td>PASM</td>
<td></td>
<td>14</td>
<td>5-15</td>
<td>45-135 50-150 55-165 60-180</td>
</tr>
<tr>
<td>Green needlegrass</td>
<td>BLIL</td>
<td></td>
<td>2</td>
<td>5-15</td>
<td>270-640 300-600 330-890 360-720</td>
</tr>
<tr>
<td>Needleleaf tifthead</td>
<td>HECOCB</td>
<td></td>
<td>10</td>
<td>0-5</td>
<td>0-45 0-50 0-55 0-60</td>
</tr>
<tr>
<td>Plains muhly</td>
<td>MUCO3</td>
<td></td>
<td>3</td>
<td>0-5</td>
<td>0-50 0-55 0-60</td>
</tr>
<tr>
<td>Threadleaf sedge</td>
<td>CAF1</td>
<td></td>
<td>12</td>
<td>0-5</td>
<td>0-10 0-100 0-110 0-120</td>
</tr>
<tr>
<td>Needleleaf sedge</td>
<td>CADUR</td>
<td></td>
<td>18</td>
<td>0-5</td>
<td>0-5 0-100 0-110 0-120</td>
</tr>
<tr>
<td>Blue grama</td>
<td>BDGR2</td>
<td></td>
<td>15</td>
<td>0-5</td>
<td>0-5 0-100 0-110 0-120</td>
</tr>
<tr>
<td>Prairie junegrass</td>
<td>KORJ</td>
<td></td>
<td>12</td>
<td>0-5</td>
<td>0-5 0-100 0-110 0-120</td>
</tr>
<tr>
<td>Sandberg bluegrass</td>
<td>POSE</td>
<td></td>
<td>12</td>
<td>0-5</td>
<td>0-5 0-100 0-110 0-120</td>
</tr>
<tr>
<td>Plains reedgrass</td>
<td>CAMO</td>
<td></td>
<td>18</td>
<td>0-5</td>
<td>0-5 0-100 0-110 0-120</td>
</tr>
<tr>
<td>Other native grasses</td>
<td>2GP</td>
<td></td>
<td>0-5</td>
<td></td>
<td></td>
</tr>
<tr>
<td><strong>Forbs</strong></td>
<td></td>
<td></td>
<td></td>
<td>1-5%</td>
<td>9-45 10-50 11-55 12-60</td>
</tr>
<tr>
<td>Purple prairieclover</td>
<td>DAPUS</td>
<td></td>
<td>21</td>
<td>1-5</td>
<td></td>
</tr>
<tr>
<td>White prairieclover</td>
<td>DACAT</td>
<td></td>
<td>21</td>
<td>1-5</td>
<td></td>
</tr>
<tr>
<td>Prairie coreflower</td>
<td>KACO3</td>
<td></td>
<td>23</td>
<td>1-5</td>
<td></td>
</tr>
<tr>
<td>Dotted gayfeather</td>
<td>LUPO</td>
<td></td>
<td>21</td>
<td>1-5</td>
<td></td>
</tr>
<tr>
<td>Scutia spp.</td>
<td>PSAR</td>
<td></td>
<td>23</td>
<td>1-5</td>
<td></td>
</tr>
<tr>
<td>Hairy goldenaster</td>
<td>HELV2</td>
<td></td>
<td>23</td>
<td>1-5</td>
<td></td>
</tr>
<tr>
<td>Scarlet globemallow</td>
<td>EPCO2</td>
<td></td>
<td>20</td>
<td>1-5</td>
<td></td>
</tr>
<tr>
<td>American vetch</td>
<td>VIAM</td>
<td></td>
<td>18</td>
<td>1-5</td>
<td></td>
</tr>
<tr>
<td>Milkvetch spp.</td>
<td>ASTRA</td>
<td></td>
<td>24</td>
<td>1-5</td>
<td></td>
</tr>
<tr>
<td>Hood’s phlox</td>
<td>PHRH2</td>
<td></td>
<td>28</td>
<td>1-5</td>
<td></td>
</tr>
<tr>
<td>Tufted milkvetch</td>
<td>ASSP6</td>
<td></td>
<td>24</td>
<td>1-5</td>
<td></td>
</tr>
<tr>
<td>Primrose spp.</td>
<td>OENOT</td>
<td></td>
<td>24</td>
<td>0-5</td>
<td></td>
</tr>
<tr>
<td>Backwheel spp.</td>
<td>EROG2</td>
<td></td>
<td>23</td>
<td>1-5</td>
<td></td>
</tr>
<tr>
<td>Western yarrow</td>
<td>ACM2</td>
<td></td>
<td>19</td>
<td>0-5</td>
<td></td>
</tr>
<tr>
<td>Biscuitroot spp.</td>
<td>LCMD1</td>
<td></td>
<td>24</td>
<td>0-5</td>
<td></td>
</tr>
<tr>
<td>Miners candy</td>
<td>CRAR</td>
<td></td>
<td>24</td>
<td>0-5</td>
<td></td>
</tr>
<tr>
<td>Penstemon spp.</td>
<td>PENST</td>
<td></td>
<td>28</td>
<td>0-5</td>
<td></td>
</tr>
<tr>
<td>Pussytoes spp.</td>
<td>ANTEI</td>
<td></td>
<td>20</td>
<td>0-5</td>
<td></td>
</tr>
<tr>
<td>Prairie thermopsis</td>
<td>THRPH</td>
<td></td>
<td>20</td>
<td>0-5</td>
<td></td>
</tr>
<tr>
<td>Other native forbs</td>
<td>ZFP</td>
<td></td>
<td>0-5</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Twogrooved poisonvetch**</td>
<td>ASUE2</td>
<td></td>
<td>24</td>
<td></td>
<td></td>
</tr>
<tr>
<td>White pent lacy **</td>
<td>OXSE</td>
<td></td>
<td>24</td>
<td>0-5</td>
<td>0-5 0-5 0-5 0-5</td>
</tr>
<tr>
<td>Larkspr spp. **</td>
<td>DELPH</td>
<td></td>
<td>24</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Death camas **</td>
<td>ZGAD</td>
<td></td>
<td>32</td>
<td></td>
<td></td>
</tr>
<tr>
<td><strong>Shrubs and Half-shrubs</strong></td>
<td></td>
<td></td>
<td>5-15%</td>
<td>45-135 56-150 55-165 60-180</td>
<td></td>
</tr>
<tr>
<td>Wyoming big sagebrush</td>
<td>ARTW8</td>
<td></td>
<td>37</td>
<td>1-5</td>
<td>9-45 10-50 11-55 12-60</td>
</tr>
<tr>
<td>Wintersel</td>
<td>KRLA2</td>
<td></td>
<td>35</td>
<td>1-5</td>
<td>0-90 0-100 0-110 0-120</td>
</tr>
<tr>
<td>Nutta’s saltbush</td>
<td>ATNU2</td>
<td></td>
<td>34</td>
<td>1-5</td>
<td>0-5 0-100 0-110 0-120</td>
</tr>
<tr>
<td>Silver sagebrush</td>
<td>ARCA13</td>
<td></td>
<td>36</td>
<td>0-5</td>
<td></td>
</tr>
<tr>
<td>Fringed sagewort</td>
<td>ARF4</td>
<td></td>
<td>38</td>
<td>0-5</td>
<td></td>
</tr>
<tr>
<td>Prairie rose</td>
<td>ROAR2</td>
<td></td>
<td>38</td>
<td>0-5</td>
<td></td>
</tr>
<tr>
<td>Green rabbitbrush</td>
<td>CHYB2</td>
<td></td>
<td>38</td>
<td>0-5</td>
<td></td>
</tr>
<tr>
<td>Rubber rabbitbrush</td>
<td>ERHAN5</td>
<td></td>
<td>36</td>
<td>0-5</td>
<td></td>
</tr>
<tr>
<td>Other native shrubs</td>
<td>ZSB</td>
<td></td>
<td>28</td>
<td>0-5</td>
<td></td>
</tr>
<tr>
<td>Broom snakeweed</td>
<td>GUS2A</td>
<td></td>
<td>37</td>
<td>0-5</td>
<td>0-5 0-5 0-5 0-5</td>
</tr>
<tr>
<td>Plains pricklypear</td>
<td>OIPPO</td>
<td></td>
<td>38</td>
<td>0-5</td>
<td></td>
</tr>
<tr>
<td><strong>Total Annual Production</strong></td>
<td></td>
<td></td>
<td>100%</td>
<td>900 1000 1100 1200</td>
<td></td>
</tr>
</tbody>
</table>

**This species tends to occur mainly in the higher precipitation areas of the RRU.**

** These plants are poisonous to some grazing animals, during at least some portion of their life cycle.
5c. Plant Communities and Transitional Pathways (diagram)

(1) Tall and Medium Grasses, Forbs, Shrubs
(Historic Climax Plant Community)
Bluebunch wheatgrass, green needlegrass,
western/ thickspike wheatgrass, purple prairie clover,
prairie coneflower, dotted gayfeather, Nutall's saltbush,
Wyoming big sagebrush, winterfat

(2) Medium and Short Grasses, Shrubs
Western or thickspike wheatgrass, Wyoming
big sagebrush, Sandberg bluegrass,
bluebunch wheatgrass, green needlegrass,
silverleaf scurvygrass, scarlet globemallow

(3) Shrubs and Half-shrubs, Short Grasses
Wyoming big sagebrush, Sandberg bluegrass,
blue grama, western thinskewspike wheatgrass,
fringed sagewort

(5) Shrubs, Half-shrubs, Annual Grasses and
Forbs, Short Grasses
Wyoming big sagebrush, fringed sagewort,
broom snakeweed, Japanese brome, weedy
forbs, blue grama

Smaller boxes within a larger box indicate that these communities will normally shift among themselves with slight variations in precipitation and other disturbances. Moving outside the larger box indicates the community has crossed a threshold (heavier line) and will require intensive treatment to return to Community 1 or 2. Dotted lines indicate a reduced probability for success. Yellow boxes indicate caution that the community may be in danger of crossing a threshold. Orange boxes represent communities that have crossed over thresholds from the HCPC and may be difficult to restore with grazing management alone. Red boxes represent communities that have severely shifted away from the HCPC and probably cannot be restored without mechanical inputs.

NOTE: Not all species present in the community are listed in this table. Species listed are representative of the plant functional groups that occur in the community.

PG = Prescribed Grazing: Use of a planned grazing strategy to balance animal forage demand with available forage resources. Timing, duration, and frequency of grazing are controlled and some type of grazing rotation is applied to allow for plant recovery following grazing.

NPG = Non-Prescribed Grazing: Grazing which has taken place that does not control the factors as listed above, or animal forage demand is higher than the available forage supply.

Fire: Prescribed fire or non-prescribed wildfire.
6. **Livestock Grazing Interpretations:** Managed livestock grazing is suitable on this site as it has the potential to produce a moderate amount of high quality forage. Forage production is somewhat limited by steep slopes and shallow soils, and the potential for runoff, which reduces the effectiveness of the precipitation received for plant growth. The steeper slopes may also limit livestock travel and result in poor grazing distribution, especially in areas away from water. Management objectives should include maintenance or improvement of the plant community. Shorter grazing periods and adequate re-growth after grazing are recommended for plant maintenance and recovery. Heavy stocking and season long use of this site can be detrimental and will alter the plant community composition and production over time.

Whenever Plant Community 2 (medium and short grasses) occurs, grazing management strategies need to be implemented to avoid further deterioration. This community is still stable, productive, and healthy provided it receives proper management. This community will respond fairly quickly to improved grazing management, including increased growing season rest of key forage plants. Grazing management alone can usually move this community back towards the potential community.

Plant Communities 3 and 4 have substantially reduced forage production, and a high percentage of aggressive, non-palatable species. Once these plant communities become established, it will be much more difficult to restore the site to a community that resembles the potential with grazing management alone. Additional growing season rest and some type of brush management is often necessary for re-establishment of the desired species and to restore the stability and health of the site.
6a. Guide to Safe Stocking Rates: The following charts provide guidance for determining an initial safe stocking rate. Animal Unit Month (AUM) figures are based on averages of forage production from data collected for this site over several years. The characteristic plant communities and production values listed may not accurately reflect the productivity of a specific piece of land. These tables should not be used without on-site information collected to determine the average forage productivity of the site. Adjustments to stocking rates for each range unit must be made based on topography, slope, distance to livestock water, and other factors which affect livestock grazing behavior.
## 6b. Stocking Rate Guide:

<table>
<thead>
<tr>
<th>Major Plant Community Dominant Plant Species</th>
<th>MAP</th>
<th>Total Production (pounds/ac)</th>
<th>Cattle</th>
<th>Sheep</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td></td>
<td>Forage Production</td>
<td>AUM/ac</td>
</tr>
<tr>
<td>1. Tall and Medium Grasses, Forbs, Shrubs (HCPC)</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Bluebunch wheatgrass, green needlegrass, western wheatgrass, purple prairie clover, dotted gayfeather, Nutall's saltbush, Wyoming big sagebrush, winterfat (S.I. &gt; 75%)</td>
<td>13-14'</td>
<td>1100-1200</td>
<td>925-1075+</td>
<td>.25-.29+</td>
</tr>
<tr>
<td></td>
<td>11-12'</td>
<td>900-1000</td>
<td>775-900+</td>
<td>.21-.25+</td>
</tr>
<tr>
<td>2. Medium &amp; Short Grasses, Shrubs</td>
<td>13-14'</td>
<td>605-1020</td>
<td>375-875</td>
<td>.10-.24</td>
</tr>
<tr>
<td>Western or thickspike wheatgrass, Wyoming big sagebrush, Sandberg bluegrass, bluebunch wheatgrass, green needlegrass, silverleaf scurfpea, scarlet globemallow (S.I. 40-75%)</td>
<td>11-12'</td>
<td>490-850</td>
<td>300-725</td>
<td>.08-.20</td>
</tr>
<tr>
<td>3. Shrubs &amp; Half-shrubs, Short Grasses</td>
<td>13-14'</td>
<td>440-840</td>
<td>225-500</td>
<td>.06-.14</td>
</tr>
<tr>
<td>Wyoming big sagebrush, Sandberg bluegrass, blue grama, western thickspike wheatgrass, fringed sagewort (S.I. 20-46%)</td>
<td>11-12'</td>
<td>360-700</td>
<td>175-425</td>
<td>.05-.12</td>
</tr>
<tr>
<td>4. Shrubs &amp; Half-Shrubs, Annual Grasses &amp; Forbs, Short Grasses</td>
<td>11-14'</td>
<td>180-480</td>
<td>50-175</td>
<td>.01-.05</td>
</tr>
</tbody>
</table>

Stocking rates are calculated from average forage production values using a 25% Harvest Efficiency factor for preferred and desirable plants, and 10% Harvest Efficiency for less desirable species. AUM calculations are based on 915 pounds per animal unit month (AUM) for a 1,000-pound cow with calf up to 4 months. No adjustments have been made for site grazability factors, such as steep slopes, site inaccessibility, or distance to drinking water.
Ecological Site Description—Rangeland

MLRA: 58AC – Sedimentary Plains, Central
R05BAC059MT

7. Wildlife Interpretations: Complex topography and vegetative structure, along with the tendency to occur in a mosaic with other ecological sites make this site an important component of wildlife habitat diversity. Big game species are particularly attracted to this site, where it occurs in rough topography, because of thermal cover and winter range values. South slopes tend to stay open in winter where important browse species such as winterfat and Nuttall’s saltbush are available. Rock outcrops and scattered Rocky Mountain junipers provide hunting perches for a variety of raptors. Golden eagles often hunt low to the ground along the steep sideshills characteristic of this site where they can surprise small mammals as they cruise over small drainages. Ferruginous hawks may nest on rock outcrops. Sites having steeper, rocky topography provide habitat for interesting songbird species such as rock wrens, canyon wrens and spotted towhees. Scattered junipers and pines host field sparrows and chipping sparrows. Springs and seeps may occur along toe slopes. These provide habitat for amphibians and many other wildlife species.

**Plant Community 1: Tall and Medium Grasses/Forbs/Shrubs (HCPC):** The diversity of forbs, half-shrubs and shrubs provides feeding substrate for a variety of pollinating insects, which are prey for many birds, reptiles and small mammals. Springs and seeps provide habitat for amphibians such as tiger salamanders. The short-horned lizard is a representative reptile. The diversity of plant species and life forms, in combination with topographic variation, provides high quality bird habitat. Lark sparrows, chipping sparrows, rock wrens and ferruginous hawks are examples of birds using this community. Sharp-tailed grouse and sage grouse may use this community for lek sites on ridge tops and fairly level topography. The predominance of grasses plus a diversity of forbs, shrubs and half-shrubs in this community favors grazers and mixed feeders such as bison, pronghorn and elk. Winter range value is often high for mule deer and pronghorn when topographic diversity provides south exposures and browse plants such as Nuttall’s saltbush and winterfat are available. Small mammal diversity may be fairly high. Example species include the kangaroo rat, deer mouse, olive-backed pocket mouse and desert cottontail.

**Plant Community 2: Medium and Short Grasses/Shrubs:** Pollinator insect species diversity may decline with the loss of some succulent, palatable forbs. Livestock trampling and grazing around springs and seeps degrades amphibian habitat. A reduction in litter cover and residual plant material during early spring decreases nesting habitat value for sage grouse and other ground-nesting birds. The potential increase in big sagebrush cover may benefit sage grouse nesting and winter habitat to some extent. Pronghorn and mule deer still find winter browse but overall nutrition value declines with the reduction in winterfat and Nuttall’s saltbush cover. Herbivorous small mammals, such as voles, may decline with the reduction in litter cover.

**Plant Community 3: Shrubs and Half-shrubs/Short Grasses:** Insect species diversity further declines with the simplification of the plant community, although some species, such as grasshoppers, may be very abundant during population highs. The general drying of the site following loss of litter cover and residual vegetation continues to degrade amphibian habitat. Sparse vegetation and increased bare ground may provide suitable habitat for a few nesting bird species (i.e. horned larks) but the lack of complex vegetative structure and residual cover makes this community poor habitat in general for most ground-nesting birds and relatively poor big game habitat. Pronghorn and mule deer may forage in this type throughout the year. However, nutritional levels for big game are greatly reduced and are available for a much shorter period as compared to the HCPC.

**Plant Community 4: Shrubs and Half-shrubs/Annual Grasses and Forbs/Short Grasses:** Insects may be very abundant during population highs (i.e. grasshoppers) but diversity is low, especially of pollinators. Amphibian habitat is very degraded; ephemeral pools evaporate rapidly and the soil surface is very dry and hot during summer. Ground nesting bird habitat value is poor because of the lack of litter cover and residual plant cover in early spring. Sage grouse and Brewer’s sparrows may be fairly abundant in the heavier sagebrush cover but probably suffer heavy losses while nesting on the poorly protected ground surface. Mountain plovers prefer to nest in this community type if a somewhat pebbly surface is present. Mule deer and pronghorn may utilize sagebrush and fringed sagewort during winter in this community.

8. Hydrology Data: The soils associated with this ecological site are generally in Hydrologic Soil Group D. The infiltration rates for these soils will normally be slow to very slow. The runoff potential for this site is moderate to high, depending on slope and ground coverhealth. Runoff curve numbers generally range from 79 to 94.
Ecological Site Description—Rangeland

MLRA: 58AC - Sedimentary Plains, Central
R058AC059MT

9. Site Documentation:
Authors: Original NRCS, 1983  Revised: MJR, REL, RSN, POH, 2003

Supporting Data for Site Development:
NRCS-Production & Composition Record for Native Grazing Lands (Range-417): 3
BLM-Soil & Vegetation Inventory Method (SVIM) Data: 6
NRCS-Range Condition Record (ECS-2): 10
NRCS-RangeSoil Correlation Observations & Soil 232 notes: 10
Ecological Site Reference: NRCS 417 No.: Sweetgrass County 506 & 516, Musselshell County 516

Field Offices where this site occurs within the state:
Big Sandy  Columbus  Harlowton  Roundup
Big Timber  Crow Agency  Joliet  Stanford
Billings  Fort Belknap  Lewistown  White Sulphur Springs
Chinook  Hardin  Malta  Winnett

Site Approval: This site has been reviewed and approved for use:

Loretta J. Metz  10/22/2004
State Rangeland Management Specialist  Date

USDA–NRCS–MT  9  October 2004
Ecological Site Description—Rangeland

MLRA: SWRC - Sedimentary Plains, Central
RO30AC08940T

Shallow Clay, 11-14" MAP
Sedimentary Plains, Central
Plant Community 1
HCPC
Sweetgrass County
Bluebunch wheatgrass, Green needlegrass

Shallow Clay, 11-14" MAP
Sedimentary Plains, Central
Plant Community 1
HCPC
Musselshell County

Shallow Clay, 11-14" MAP
Sedimentary Plains, Central
Plant Community 1
HCPC
Sweetgrass County
Ecological Site Description—Rangeland

Shallow Clay (SwC), 11-14" MAP

MLRA: 58AC – Sedimentary Plains, Central
R08AC050MT

Shallow Clay, 11-14" MAP
Sedimentary Plains, Central
Plant Community 1
HCPC
Sweetgrass County

Shallow Clay, 11-14" MAP
Sedimentary Plains, Central
Plant Community 1
Musselshell County
Bluebunch wheatgrass, Wyoming
big sagebrush

Shallow Clay, 11-14" MAP
Sedimentary Plains, Central
Plant Community 1
HCPC
Ecological Site Description—Rangeland

MLRA: 58AC = Sedimentary Plains, Central
R008AC099MT

Shallow Clay, 11-14” MAP
Sedimentary Plains, Central
Plant Community 2
Musselshell County

Shallow Clay, 11-14” MAP
Sedimentary Plains, Central
Plant Community 2
Musselshell County

Shallow Clay, 11-14” MAP
Sedimentary Plains, Central
Plant Community 2
Golden Valley County
Western wheatgrass, Nuttall’s saltbush, Wyoming big sagebrush
Ecological Site Description—Rangeland

MLRA: 588C - Sedimentary Plains, Central
R030AC189141

Shallow Clay, 11-14" MAP
Sedimentary Plains, Central
Plant Community 3
Musselshell County

Shallow Clay, 11-14" MAP
Sedimentary Plains, Central
Plant Community 3

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# Appendix B

## Glossary

<table>
<thead>
<tr>
<th>Term</th>
<th>Definition</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Abundance</strong></td>
<td>The amount of space occupied by one species or group relative to all other groups within a specific geographic area (e.g., species density); usually measured using cover, biomass, or number of individuals.</td>
</tr>
<tr>
<td><strong>Beta diversity</strong></td>
<td>The difference in species composition between two or more sites, usually depicting the number of shared versus the number of unique species to one site relative to all other sites.</td>
</tr>
<tr>
<td><strong>Climax Community</strong></td>
<td>The final stage of succession for a community, representing the highest order of productivity or composition for an area under specific disturbance and climatic pressures (Clements XXX).</td>
</tr>
<tr>
<td><strong>Community</strong></td>
<td>A collection of interdependent and co-occurring species occupying a single habitat.</td>
</tr>
<tr>
<td><strong>Compositional Heterogeneity</strong></td>
<td>See beta diversity.</td>
</tr>
</tbody>
</table>
### Cool Season Grass (C₃)
Grasses adapted to temperate, mesic habitats; requiring cooler, wetter climates to effectively and efficiently perform photosynthesis. Examples include western wheatgrass (*Pascopyrum smithii* (Rydb.) Á. Löve) and needle-and-thread grass (*Hesperostipa comata* (Trin. & Rupr.) Barkworth ssp. *comata*).

### Cover
The relative basal space occupied by an individual species or collective group of species (e.g., functional group).

### Dissimilarity Matrix
A matrix of numbers displaying the dissimilarity of one sample (or site) relative to all other samples (or sites).

### Diversity
The amount of variation in both species occurrence and evenness within a single site, sample, or treatment; usually measured using an index (e.g., Inverse Simpson’s Diversity Index).

### Forb
All non-woody wildflowers. Examples include common yarrow (*Achillea millefolium* L.) and prairie coneflower (*Ratibida columnifera* (Nutt.) Wooten & Standl.).
<table>
<thead>
<tr>
<th>Term</th>
<th>Definition</th>
</tr>
</thead>
<tbody>
<tr>
<td>Foundation Species</td>
<td>A species who has a large influence on ecosystems or ecological communities, but is also very abundant, or even relatively dominant, across the landscape.</td>
</tr>
<tr>
<td>Functional Group</td>
<td>The growth habit of an organism relative to other species, where all species within the same functional group share the same growth habit and functional characteristics within a single community or habitat-type.</td>
</tr>
<tr>
<td>Heterogeneity</td>
<td>Variation in vegetative abundance, composition, structure, species diversity, and abiotic disturbances (e.g., bare ground) across a multitude of spatial scales.</td>
</tr>
<tr>
<td>Keystone Species</td>
<td>A species whose influence on an ecosystem or ecological community is disproportionally larger than its abundance.</td>
</tr>
<tr>
<td>Module</td>
<td>One of many divisions that make up a single vegetation sampling plot (e.g., a quadrat).</td>
</tr>
<tr>
<td>Sedge</td>
<td>All non-grass, grass-likes. Examples include needle-leaf sedge (<em>Carex duriuscula</em> C.A. Mey) and threadleaf sedge (<em>Carex filifolia</em> Nutt.).</td>
</tr>
</tbody>
</table>
Shrub All large woody (usually non-palatable) vegetation. Examples include Wyoming big-sagebrush (*Artemisia tridentata* Nutt. ssp. *wyomingensis* Beetle and Young) and greasewood (*Sarcobatus vermiculatus* (Hook.) Torr.).

Species Composition All species relative to the total vegetative layer, across all growth habits, functional groups, or botanical families.

Species Richness The total number of species found in an area.

Species Turnover See beta diversity.

State-Transition Model An approach to describing plant communities along a successional trajectory of predicted “states” (i.e., relative to a predicted climax community), along with the transitional pathways between “states”. Usually depicted with the disturbance or management pressures that will push plant communities toward or away from desired successional “states” (e.g., prescribed grazing, fire, etc.).

Subshrub All woody vegetation with a (usually) smaller growth habit than shrubs. Examples include sagewort (*Artemisia frigida*...
Willd.s) and winterfat (*Krascheninnikovia lantana* (Pursh) A. Meeuse & Smit).

**Vegetative Structure**

The average stature (e.g., height) of the collective vegetation occurring in an area. Also, may be defined as the relative composition of functional groups occurring in an area (e.g., dominance of shrubs versus forbs versus grasses, etc.).

**Warm Season Grass (C\text{4})**

Grasses adapted to thrive in more arid regions relative to cool-season grasses, utilizing malate and other compounds to minimize water loss through transpiration and behaviors related to photosynthesis. Examples include blue grama (*Bouteloua gracilis* (Willd. ex Kunth) Lag. ex Griffiths) and plains muhly (*Muhlenbergia cuspidata* (Torr. ex Hook.) Rydb.).
## Appendix C

### Chapter 1 Summary Table

Table showing the relationship between our findings, and those described by Knapp et al. (1999) in the tallgrass prairie.

<table>
<thead>
<tr>
<th>Hypotheses</th>
<th>Knapp et al. (1999)</th>
<th>Our Study</th>
</tr>
</thead>
<tbody>
<tr>
<td>H₁</td>
<td>C₄ Grasses</td>
<td>Decreased (↓)</td>
</tr>
<tr>
<td></td>
<td>C₃ Grasses &amp; Forbs</td>
<td>Increased (↑)</td>
</tr>
<tr>
<td>H₂</td>
<td>Diversity</td>
<td>Increased (↑)</td>
</tr>
<tr>
<td>H₃</td>
<td>Richness</td>
<td>Increased (↑)</td>
</tr>
<tr>
<td>H₄</td>
<td>Heterogeneity</td>
<td>Increased (↑)</td>
</tr>
</tbody>
</table>
Table showing the overall relatedness of each treatment to our reference historic climax plant community (HCPC), which was reported in the Shallow Clay 11-14” ESD. Relatedness is reported using overlapping symbology, with overlapping symbols representing non-significant differences between a treatment and the HCPC. Arrows represent both general abundance (e.g., ↑ increase in abundance) and significant differences, with overlapping symbols representing non-significant differences.

<table>
<thead>
<tr>
<th>Predicted Relationships</th>
</tr>
</thead>
<tbody>
<tr>
<td>Hypotheses</td>
</tr>
<tr>
<td>H₁</td>
</tr>
<tr>
<td>Overall Composition</td>
</tr>
<tr>
<td>H₂</td>
</tr>
<tr>
<td>Perennial Bunchgrass Cover</td>
</tr>
<tr>
<td>Litter Cover</td>
</tr>
<tr>
<td>Noxious Weed Cover</td>
</tr>
<tr>
<td>H₃</td>
</tr>
<tr>
<td>Functional Group Abundance</td>
</tr>
<tr>
<td>Bare Ground</td>
</tr>
</tbody>
</table>
### Observed Relationships

<table>
<thead>
<tr>
<th>Hypotheses</th>
<th>Overall Composition</th>
<th>HCPC</th>
<th>Bison</th>
<th>Cattle</th>
<th>Removal</th>
</tr>
</thead>
<tbody>
<tr>
<td>H&lt;sub&gt;1&lt;/sub&gt;</td>
<td></td>
<td>+</td>
<td>+/-</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td>H&lt;sub&gt;2&lt;/sub&gt;</td>
<td>Perennial Bunchgrass Cover</td>
<td>↑</td>
<td>↓</td>
<td>↓</td>
<td>↓</td>
</tr>
<tr>
<td></td>
<td>Litter Cover</td>
<td>↑</td>
<td>↓</td>
<td>↓</td>
<td>↑</td>
</tr>
<tr>
<td></td>
<td>Noxious Weed Cover</td>
<td>N/A</td>
<td>↓</td>
<td>↑</td>
<td>↑</td>
</tr>
<tr>
<td>H&lt;sub&gt;3&lt;/sub&gt;</td>
<td>Functional Group Abundance</td>
<td>+</td>
<td>+/-</td>
<td>+/-</td>
<td>-</td>
</tr>
<tr>
<td></td>
<td>Forbs</td>
<td>+</td>
<td>+</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td></td>
<td>Grasses/Sedges</td>
<td>+</td>
<td>+</td>
<td>+</td>
<td>-</td>
</tr>
<tr>
<td></td>
<td>Shrubs/Subshrubs</td>
<td>+</td>
<td>-</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td></td>
<td>Bare Ground</td>
<td>+</td>
<td>+</td>
<td>-</td>
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REFERENCES


