
Through the Historical Lens: An Examination of Compositional Change in Yellowstone's Bunchgrass Communities, 1958–2002

Pamela G. Sikkink

College of Forestry and Conservation, University of Montana, Missoula, MT 59812

Paul B. Alaback

College of Forestry and Conservation, University of Montana, Missoula, MT 59812

Abstract

During the past 50 years, bunchgrass communities in and around Yellowstone National Park (YNP) have been affected by fluctuating climate, grazing pressure, and increased interactions with non-native species. The response of the communities to this environmental change has been recorded by a natural experiment that was initiated in 1958, when permanent plots were established inside and outside of big game exclosures in YNP. The monitoring records from these permanent plots show that the bunchgrass cover has been highly variable over five decades, and associated with changing environmental conditions. Compositionally, species within the bunchgrass communities changed frequently between 1958 and 2002, and species turnover was quite high. Even when individual species were present, their dominance varied significantly in the community. Between 1958 and 2002, the mean frequency of grass species decreased in both grazed (–11%) and ungrazed (–28%) areas. Drought-tolerant genera, such as *Opuntia*, *Phlox*, and *Sedum*, increased in both areas. Shrub dominance increased significantly in the absence of grazing, but diversity was not significantly different between ungrazed and grazed areas. Diversity and overall frequency of each lifeform was highest in the mid-1970s to early 1980s, but both decreased significantly at most sites by 2002. Using path analysis, the correlation of multiple environmental variables with community compositional change between sample periods was tested. Fluctuations in climatic factors correlated more significantly with species change than did variations in non-native species or wildlife populations. The most significant environmental factors were spring and summer precipitation and spring and winter temperatures.

Introduction

“To look backward in time is to refresh the eye, to restore it, and to render it more fit for its prime function of looking forward.”

—Margaret Fairless Barber, 1869–1901
(Andrews *et al.* 1996)

To the casual observer, the grassland landscape of Yellowstone National Park (YNP)'s northern big-game range looks almost unchanged after half a century of tourist visits and wildlife use in the park. The landscape gives the impression that its grassland communities are quite stable and resistant to environmental change (Figure 1). To determine whether these grasslands really are resistant to change, and for how long, however, requires an historical lens that focuses on individual community members and tracks their dynamics over time. Five decades of monitoring data from the Yellowstone winter range provides the historical lens needed to “look backward” at compositional changes in vegetation within this area and see whether the communities are truly

resistant to environmental change.

The historical perspective for this paper begins in the late 1950s, when several exclosures were constructed on YNP's northern range. The exclosures were created to allow for in-depth scientific studies and to provide demonstration areas for park personnel and visitors showing how grazing affects grass and shrub trends in the park (Edwards 1957). Transects established at the same time as these exclosures have constituted the main vegetation monitoring program in the park. Long-term monitoring data from the transects have been crucial to many scientific studies, especially those on the effects of elk grazing on vegetation (Houston 1982; Coughenour 1991; Barmore Jr. 2003) and the response of vegetation to fluctuations in temperature and precipitation (Coughenour *et al.* 1991). This study examines plant composition and species dynamics along these transects between 1958 and 2002.

The aim of this paper is to examine the development of bunchgrass communities on the northern



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Figure 1. Landscape showing Blacktail Ponds exclosures in 1962 (left) and 2005 (right).

range of YNP over the past 50 years, as well as the correlation of environmental factors with community change. By examining the compositional and structural changes that the communities have experienced in the past, we can get an indication of how future changes in climate and disturbance regimes may affect vegetation on the northern range of YNP, and what management strategies may be feasible for these particular grass and shrub communities.

Methods

In 1957, YNP personnel constructed eight exclosures in the park's northern big-game winter range that eliminated all big-game grazing within their fenced, two-ha (five-acre) boundaries (Edwards 1957). Inside each exclosure, they established between two and five permanent transects. Transects measured 33.3 m (100 ft) long and were marked at the beginning, middle, and end with metal stakes. Just outside the exclosures, complementary transects were established that remained open to big-game grazing year-round. In 1962, a second exclosure was constructed in close proximity to the 1957 exclosures. Each also had new transects established within its boundaries and transects with matching slopes and aspects on the outside.

With the establishment of the exclosures and permanent transects, YNP began a long-term, natural experiment to demonstrate how grass and shrub communities were affected by grazing of fluctuating populations of wildlife in the park. The first descriptions of vegetation along the transects were done in 1958, by W. H. Kittams, NPS Regional Biologist from Omaha, and G. B. Denton of Montana State College, using a procedure established by K. W. Parker (Parker 1954). The procedure, known as the Parker Three-

Step method, was designed for long-term repeatability in vegetation sampling. It was also a fast, simple technique for sampling all transects established inside and outside the exclosures within a reasonable time frame. Along each line, vegetation or substrate encountered at each 0.33-m (1-ft) mark was recorded. Vegetation "hits" were identified to species and recorded as either overstory or understory in the canopy. Substrate hits were recorded as bare ground, rock, pavement, litter, or moss/lichen. All species and substrate hits were tallied separately. Each line had a total of 100 hits, so all species and substrate variables were given as a frequency of occurrence in each sample year. For almost five decades, transects were re-sampled at irregular intervals by different personnel using the same sampling protocol. The timing for each re-sampling was matched as closely as possible to the timing of historic samplings so that changes in species frequency over the monitoring period were not confused with seasonal physiologic changes. Photographs were taken of each line, as required by the sampling protocol, to visually capture vegetation structure and plant distribution that was not evident from the small-scale sampling. The most recent sampling analyzed for this study was completed in 2002 (Sikkink 2005).

The monitoring data were analyzed diagrammatically and statistically. The changes in species frequency from 1958 to 2002 were diagrammed using facies diagrams. Facies diagrams (with each species considered a facie) summarized overall changes in the community composition through time. They also visually depicted the changes in frequency of each grass, forb, and shrub species to scale and indicated the constancy of each species through time. Two transects from the Blacktail Ponds area were

selected to be diagrammed as case studies for this paper. They were chosen because they portrayed the common patterns of vegetation change inside and outside of exclosures, were re-sampled at the same times in history, and had complete photographic coverage for five decades.

Changes in community composition, diversity, and structure were analyzed using non-metric multidimensional scaling (NMS). NMS integrated all species at each sampling into a numeric value that represented the “community.” Community similarities over time, both within a single transect and between different transects, were compared using their relative positions within the NMS diagram. Similar compositions plotted close to each other in the NMS diagram; very different compositions plotted far apart. Ten transects, which were all that were sampled in 2002 using the Parker Three-Step method, were compared in the NMS ordinations. Both grazed and ungrazed transects were tested together in the ordination but diagrammed separately to contrast their change patterns. NMS was calculated within PCOrd V4.27 statistical software (McCune and Mefford 1999) using a Bray–Curtis distance measure and the autopilot function (step-down dimensionality starting in 6-D space, stability criterion=0.005, random number start). Each NMS analysis was run several times with random start numbers to ensure that the best configuration was achieved (i.e., to locate the solution with the least stress). Path analysis was used to test the strength of correlations between the changes in community composition and the environmental variables. Difference matrices were created that held differences in climatic, substrate, and origin variables between samples on the transect lines. These differences were tested for their correlations with the differences in positions of the plant “communities” (i.e., points) in species space of the NMS at each sample interval. In each path model, the changes in community composition were represented by changes in the NMS axes (designated y-variables). The covariance of each y-variable was tested against the absolute changes in environmental variables (x-variables). The x-variables included the frequency of bare soil, rock, and litter; average air temperature by season (FallTave, WinTave, SprTave, SumTave); precipitation by season (FallPrec, WinPrec, SprPrec, SumPrec); and species origin (native or non-native). Tests were run within LISREL 8.54 statistical software (Jöreskog and Sörbom 2003) using maximum likelihood estimations, 250 iterations, and a 0.000001 convergence criterion. The climate values were as-

signed to transect locations using a technique developed by Jolly et al. (2004), which interpolated values from nearby climate stations to specific sites on the landscape by adjusting for climatic variations caused by a site’s unique elevation, slope, and aspect.

Results

Over five decades, 69 species from 22 families were recorded along the 10 transects examined for this study. Seventy-three samplings were done. For all samplings inside and outside the exclosures, grass and sedge were encountered an average of 70% of the time along a line, shrubs 13%, and forbs 27%. Drought-tolerant species, such as cactus (*Opuntia polyacantha*), phlox (*Phlox hoodii*), and sedum (*Sedum lanceolatum* and *Sedum stenopetalum*) all increased in frequency between 1958 or 1962 and 2002. Cactus increased from 0.0 to 2.95 mean hits; members of the phlox family increased from a mean of 4.5 to 6.2; and mean hits of *Crassulaceae* increased from 1.06 to 1.33. None of the increases between 1958 and 2002 were significant, however, with a two-sample t-test ($p>0.05$). The average richness for all samples was 9.75 species.

Case study: Blacktail 58 C2T2 (ungrazed area)

When YNP’s natural experiment began in 1958, grass was encountered more frequently (23%) than shrubs (15%) along the case-study line in the Blacktail exclosure. Four grass species, three types of shrubs, and one forb (*Lupinus sericeus*) were identified. By 2002, the frequency of shrubs had increased significantly (Figure 2). Shrub and grass species were almost equally present along the line, and two added species of grass were more dominant than the four original grasses and sedge species. Between 1958 and 2002, both total vegetation and community richness fluctuated significantly along the line (Figure 3). Total vegetation hits fluctuated from about 20% to 85% (Figure 3). Richness varied from four species in 1986 to 11 species in 1974. On almost all transects, richness was highest between the mid-1970s and early 1980. The frequency of individual species varied within all of the lifeforms. Focal perennial bunchgrasses were not present along the line in some years (i.e., *P. spicata* in 1986; *F. idahoensis* in 1994), but were abundant in others (see 1981 in Figure 3). On the case study line, the bunchgrasses varied as much in time and space as annual and biennial forbs and grasses (Figure 3). Only *L. sericeus* was encountered in every sampling on the case-study transect, and its frequency varied from 1 to 10%.



Figure 2. Transect B58-C2T2 within the Blacktail exclosure in 1958 (left) and 2002 (right).

Case study: Blacktail MC1T1 (grazed area)

In the area open to grazing, the case-study line looked very similar in 1958 and 2002 (Figure 4). Both samplings had the same number of species, little or no shrub cover, and significant bare ground. Differences in composition were subtle, especially in the dominant grasses. *Koeleria macrantha* was the dominant grass in 1958; *Poa* spp. and *P. spicata* were co-dominant in 2002 (Figure 5).

In the intervening years between 1958 and 2002, however, the long-term monitoring records showed major differences in diversity, composition, and structure (Figure 5). Richness ranged from six species in 1967 to 13 in 1981. Grazed areas generally had higher richness than ungrazed areas, although the mean differences in richness between the grazed and ungrazed sites were not significant (9.7 and 9.8, respectively; $p > 0.1$). As in the exclosures, richness was greatest between 1974 and 1981. Grazed areas had fewer vegetation hits and more bare ground during each sampling than the exclosures did. Total vegetation hits were less than 50%. The amount of bare ground and lack of vegetation did not correlate with years of high bison or elk counts in the park (R. Wallen, pers. comm.; P. White, pers. comm.). Individual species varied in their frequency between

years, but the differences were not as extreme as in the exclosures (Figure 5). More species spanned the entire monitoring interval, which resulted in the appearance of a more stable community. Forbs, in particular, appeared more constant. Shrubs, especially *A. tridentata*, were infrequent in all years. However, comparison of 1958 and 2002 photographs showed that shrubs did increase in local patches adjacent to the line (Figure 4).

Community comparisons

Ungrazed and grazed communities had different change patterns. The ungrazed communities followed pathways from the grass-dominant portion of the ordination to the shrub-dominated portion through time (Figure 6). All samplings moved from the upper portion of Figure 6 to the lower left corner, where *A. tridentata* composed a high percentage of the community. The direction and amount of movement of the samples in species space between 1958 and 2002 indicated major changes in composition over the 50 years (Figure 6). The 1958 and 2002 samples were widely separated in species space for most transects and, therefore, not very similar in composition. Alternately, the grazed transects showed no clear change patterns in the NMS. As a group,

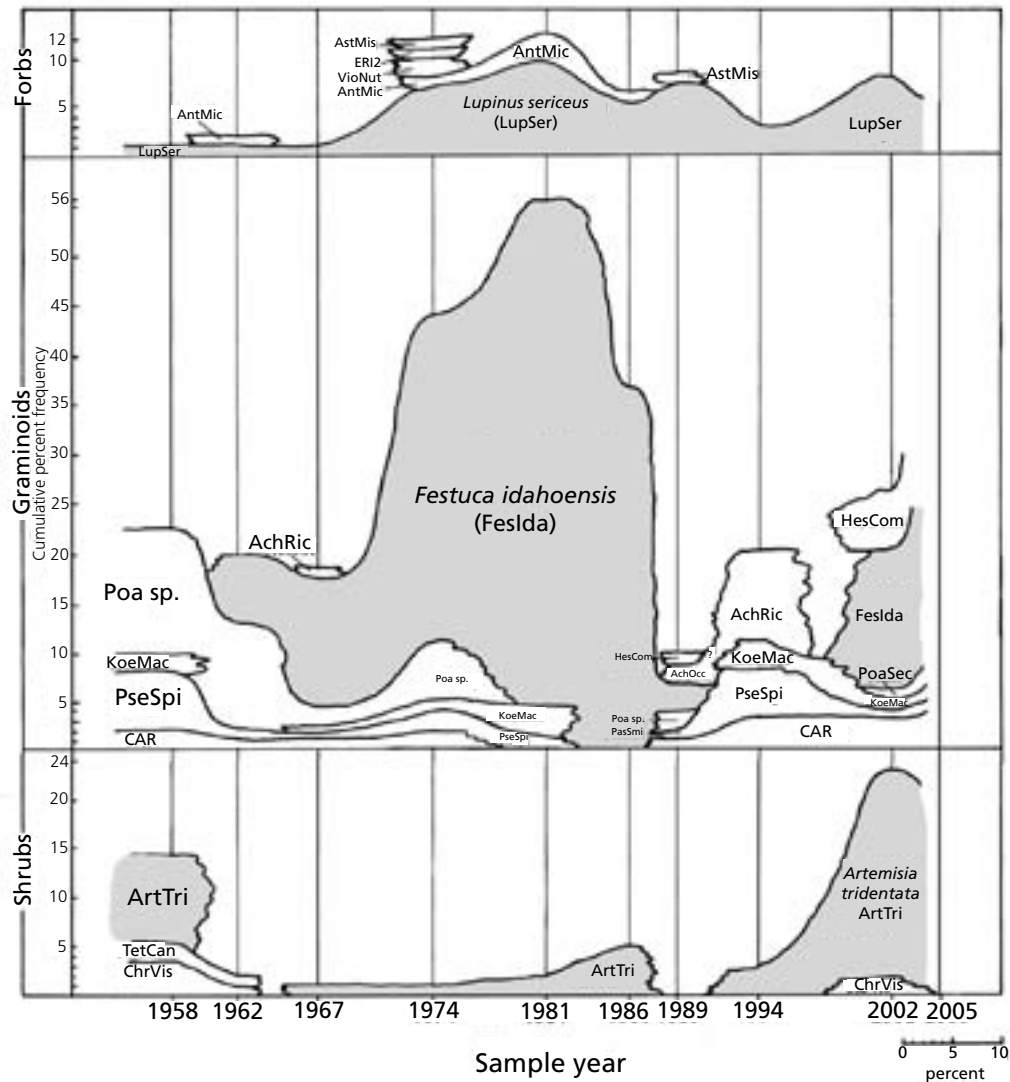


Figure 3. Facies diagram for B58-C2T2, inside the Blacktail (1958) enclosure (ungrazed area), Yellowstone National Park. Sample years are at vertical lines. Intervals between samples were manually interpolated. Percent cumulative frequency is diagrammed to scale by lifeform. Species abbreviations are listed in Appendix A.

they did not have strong directional trends toward any single part of the ordination diagram, nor were shrubs any more dominant in 2002 than in 1958. Two of the sample areas oscillated around a point in species space where *F. idahoensis* was the dominant grass (I and L, Figure 7). Two changed significantly over time from *P. spicata* and/or *K. macrantha* communities to *Poa* spp. or *Hesperostipa comata* communities, and each followed opposite change pathways through time (C and F, Figure 7).

Correlations of community change with environmental variables

The fluctuations of “community” positions

within the NMS over time correlated significantly with changes in several substrate and climatic variables between samplings. The most significant variables were frequency of bare soil and litter, spring and summer precipitation, and spring and winter temperatures; all had t-values greater than ± 0.35 and were significant at $p < 0.05$. Of these variables, only spring precipitation and winter temperature were positively correlated with point movements in species space (Figure 8). Bare soil and litter were negatively correlated with plant composition changes, and were probably not independent of the climate variables in the analysis. Non-native species were insignificant to community change in this analysis.



Figure 4. Transect MC1T1 outside the Blacktail enclosure in 1958 (left) and 2002 (right).

Discussion

Insights into the development of temperate grassland communities and the environmental stresses that affect each of them over time can only be obtained through an historical lens. An historical lens focused on the temperate grasslands of YNP reveals that its plant communities change continually within a grassland landscape that at a larger scale appears relatively unchanged with the passage of time.

The most obvious general change in the bunchgrass communities occurred within the exclosures. Between 1958 and 2002, shrub coverage increased dramatically. Most of the expansion occurred after the early 1990s, when a combination of factors, including exclusion of grazing, exclusion of fire, and drought prevailed in YNP. The YNP exclosures are not unique in their response to these environmental stresses. Similar increases in shrub cover were found in areas excluded from grazing or fire in southeastern Idaho by Anderson and Holte (1981), regionally by Briggs et al. (2005), and worldwide by Archer et al. (1995). In YNP, elimination of grazing and fire is not associated with changes in diversity in these communities. In other grassland communities, the effects of shrub encroachment and elimination of grazing on diversity have been mixed (Floyd et al. 2003; Landsberg et al. 2003; Metzger et al. 2005),

but in this study, diversity (richness) was the same in 1958 and 2002 in both the grazed and ungrazed areas. This supports previous work on diversity indices in YNP by Stohlgren et al. (1999), who found no significant differences among several measures of species diversity between grazed and ungrazed sites at a 1,000-m² plot scale. Interestingly, if 1958 and 2002 were the only monitoring points, then the communities would appear static. However, like shrub cover, diversity varied significantly in the intervening years. Both areas had their highest richness values in the mid-1970s to early 1980s, when annual precipitation was greater in the area. The differences in diversity between the grazed and ungrazed areas were not statistically significant.

From 1958 to 2002, the dynamic bunchgrass communities were affected by climatic fluctuation, changes in natural disturbance regimes, and invasion of native plants. These environmental stresses are also not unique to YNP. The composition and community dynamics of many temperate grasslands worldwide have been influenced by the timing and amount of precipitation (Fay et al. 2002), temperature fluctuations (Alward et al. 1999), the timing and intensity of disturbance (Fuhlendorf et al. 2001; Jacobs and Schloeder 2002), fire exclusion (Leach and Givnish 1996), and invasion of non-native

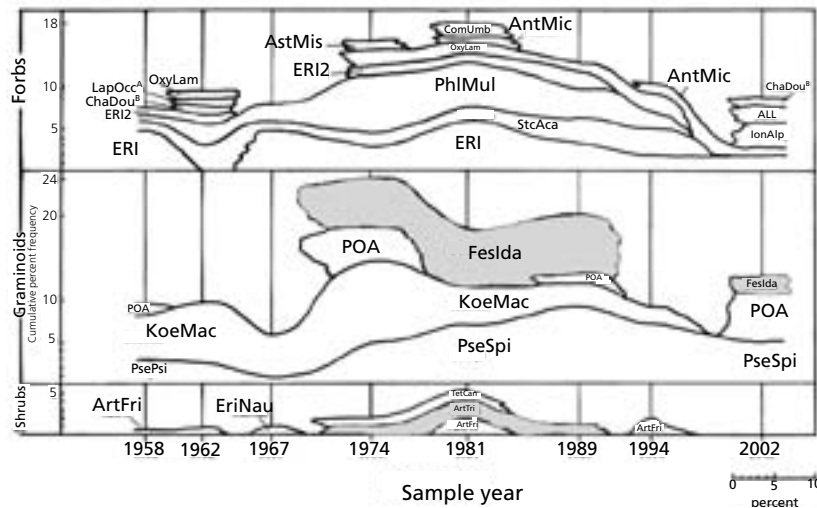


Figure 5 (top). Facies diagram for MC1T1, outside Blacktail enclosure (grazed area), Yellowstone National Park. Sample years are at vertical lines. Intervals between samples were manually interpolated. Percent cumulative frequency is diagrammed to scale by lifeform. A= annual; B= biennial. Species abbreviations are listed in Appendix A.

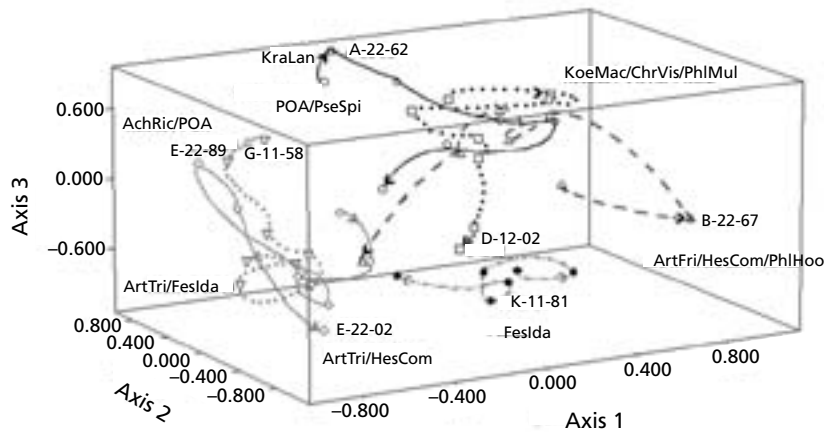


Figure 6 (middle). Plot movements in NMS ordination space for ungrazed plots of YNP using all species in community. The vectors connect consecutive sampling units and show directions (first and last arrows only), magnitudes, and compositional trends at each site over the monitoring period of each plot. A-22-YR = Gardiner 58 enclosure line C2T2; B-22-YR = Gardiner 62 enclosure line C2T2; D-12-YR = Blacktail 58 line C1T2; E-22-YR = Blacktail 62 line C2T2; G-11-YR = Lamar 58 line C1T1; K-11-YR = Junction Butte 62 line C1T1. (YR = year sampled.) Species abbreviations are listed in Appendix A. (Note: Grazed and ungrazed plots are processed together in NMS but plotted in separate diagrams to highlight differences.)

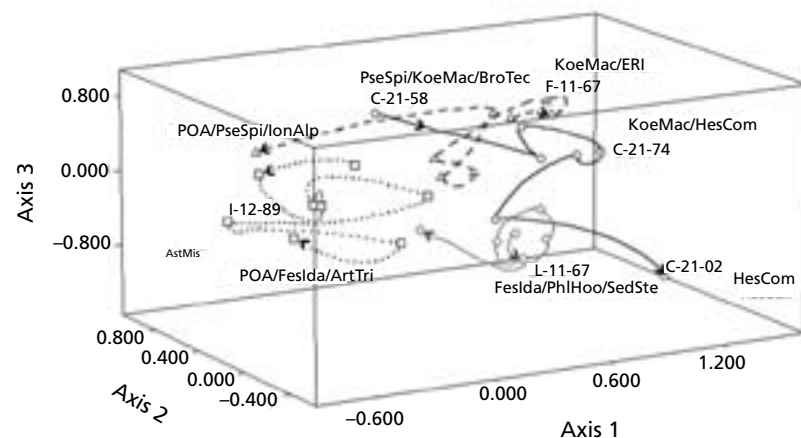


Figure 7 (bottom). Plot movements in NMS ordination space for grazed plots of YNP using all species in community. Vectors connect consecutive sampling units and show directions (first and last arrows only), magnitudes, and compositional trends at each site over the monitoring period of each plot. C-21-YR = line C2T1 outside Gardiner enclosure; F-11-YR = line C1T1 outside Blacktail enclosure; I-12-YR = outside Lamar enclosure; L-11-YR = outside Junction Butte enclosure. (YR = year sampled.) Species abbreviations are given in Appendix A. (Note: Grazed and ungrazed plots are processed together in NMS but plotted in separate diagrams to highlight differences.)

species (Abbott et al. 2000). The most important influence on the presence of individual species and species dominance at any point in time in YNP, however, appears to be climatic fluctuation. Inside and outside the exclosures, diversity as well as grass and forb species have responded in similar ways through time, indicating that climatic controls on specific species override grazing effects in determining species dominance within these particular communities. Both areas had years when certain species were abundant (i.e., *F. idahoensis* in 1974 and 1981, Figures 3 and 5) and other years when the same species were absent (i.e., *F. idahoensis* in 1958 and 1994). Shrub encroachment, although influential to community change within these grasslands, has also been related to climatic factors (Archer, Schimel, and Holland 1995). Even though the data do not show that shrubs have increased in grazed areas as much as in ungrazed ones, photographs of the transect lines do show shrub increases in both areas, which supports a climatic influence for encroachment. Path analysis indicates that the most important climatic factors for this time interval were mild spring and winter temperatures and increased moisture early in the growing season. Coughenour et al. (1991) found similar overriding climate controls on composition on the transect lines in YNP. Surprisingly, non-native species are not a significant influence on compositional change in the exclosures or their surrounding areas, although they have dramatically changed other grassland ecosystems (Hobbs 2001) and are a source of concern in other areas of the park (Yellowstone National Park 2005).

In communities that are very responsive to climatic fluctuations, long-term management or restoration must plan for community change. These data suggest that global climate change, which for this region is predicted to result in increasingly prolonged droughts, will create profound challenges for conservation of grassland systems in Yellowstone. Continued monitoring of these exclosures will be

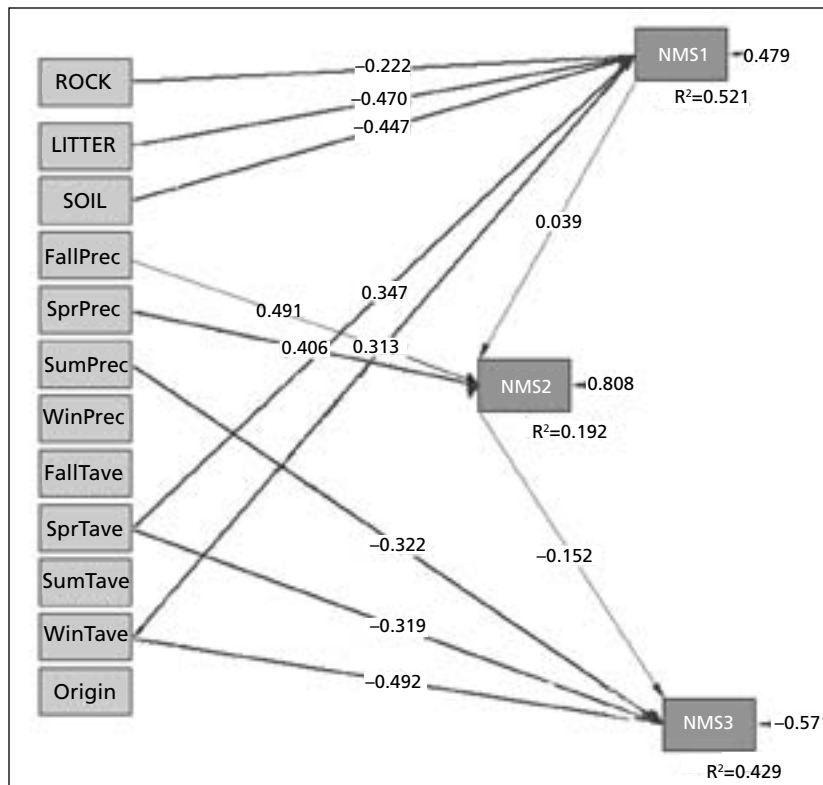


Figure 8. Path coefficients for transects in Yellowstone National Park. Only paths with significant t-values are shown. NMS = Non-metric multidimensional scaling position on axis 1, 2 or 3. FallPrec = Fall precipitation. FallTave = Fall average temperature. Origin = native or non-native species. Chi-square = 5.60, df = 11, p value = 0.89894, RMSEA = 0.000, n = 63.

critical to determine the resiliency of these systems to increased climate-induced stress and further exotic species invasions, as well as their ability to sustain large populations of ungulates.

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Appendix A. Species codes and characteristics.

Code	Genus/species	Common name	Lifecycle	Origin	Family
AchOcc	<i>Achnatherum occidentale</i> (<i>Stipa occidentalis</i> Thurb. ex S. Wats)	Western needlegrass	Perennial	Native	Poaceae
AchRic	<i>Achnatherum richardsonii</i> (<i>Stipa richardsonii</i> Link)	Spreading needlegrass	Perennial	Native	Poaceae
ALL	<i>Allium</i> spp.	Wild onion	Perennial	Native	Liliaceae
AntMic	<i>Antennaria microphylla</i>	Rosy pussytoes	Perennial	Native	Asteraceae
ArtFri	<i>Artemisia frigida</i>	Fringed sagewort	Perennial	Native	Asteraceae
ArtTri	<i>Artemisia tridentata</i>	Big sagebrush	Perennial	Native	Asteraceae
AstMis	<i>Astragalus miser</i> Dougl.	Weedy milkvetch	Perennial	Native	Fabaceae
BroTec	<i>Bromus tectorum</i>	Cheatgrass or downy brome	Annual	Introduced	Poaceae
CAR	<i>Carex</i> spp.	Sedge	Perennial	Native	Cyperaceae
ChaDou	<i>Chaenactis douglasii</i>	Dusty maiden	Biennial/ Perennial	Native	Asteraceae
ChrVis	<i>Chrysothamnus viscidiflorus</i>	Rabbitbrush	Perennial	Native	Asteraceae
ComUmb	<i>Comandra umbellata</i>	Pale bastard toadflax	Perennial	Native	Santalaceae
ERI	<i>Erigeron</i> spp.	Fleabane	Unknown	Undeter- mined	Asteraceae
ERI2	<i>Eriogonum</i> spp.	Wild buckwheat	Annual/ Perennial	Undeter- mined	Polygona- ceae
EriNau	<i>Ericameria</i> <i>nauseosus</i> (<i>Chrysothamnus</i> <i>nauseosus</i> (Pallas) Britton)	Gray rabbitbrush	Perennial	Native	Asteraceae
FesAlt	<i>Festuca altaica</i> (F. <i>scabrella</i> Torr. ex Hook.)	Rough fescue	Perennial	Native	Poaceae
FesIda	<i>Festuca idahoensis</i>	Idaho fescue	Perennial	Native	Poaceae
HesCom	<i>Hesperostipa comata</i> (<i>Stipa comata</i> Trin. & Rupr.)	Needle and thread	Perennial	Native	Poaceae
IonAlp	<i>Ionactis alpina</i> (<i>Aster scopulorum</i> Gray)	Crag aster/lava aster	Perennial	Native	Asteraceae
KoeMac	<i>Koeleria macrantha</i> (K. <i>cris- tata</i> auct. P.p. non Pers.)	Prairie Koeler's grass/junegrass	Perennial	Native	Poaceae
KraLan	<i>Krascheninnikovia lanata</i> (<i>Ceratoides lanata</i>)	Winterfat/white sage	Perennial	Native	Chenopodia- ceae
LapOcc	<i>Lappula occidentalis</i> (Lap- pula <i>redowskii</i> (Hornem.) E.	Flat-spine sheepburr	Annual	Native	Boragina- ceae
LupSer	<i>Lupinus sericeus</i>	Blue-bonnet lu- pine, silky lupine	Perennial	Native	Fabaceae
OxyLam	<i>Oxytropis lambertii</i>	Colorado loco purple	Perennial	Native	Fabaceae
PHL2	<i>Phlox</i> spp.	Phlox	Perennial	Undeter- mined	Polemoniace

Code	Genus/species	Common name	Lifecycle	Origin	Family
PhlHoo	<i>Phlox hoodii</i>	Hood's phlox	Perennial	Native	<i>Polemonia-ceae</i>
PhlMul	<i>Phlox multiflora</i>	Rocky mountain phlox	Perennial	Native	<i>Polemoniace</i>
POA	<i>Poa spp.</i>	Bluegrass	Annual/ Perennial	Undeter- mined	<i>Poaceae</i>
PoaSec	<i>Poa secunda</i> (<i>Poa sandbergii</i> Vasey)	Curly bluegrass	Perennial	Native	<i>Poaceae</i>
PasSmi	<i>Pascopyrum smithii</i> (<i>Agropyron smithii</i> Rydb.)	Western wheatgrass	Perennial	Native	<i>Poaceae</i>
PseSpi	<i>Pseudoroegneria spicata</i> (<i>Agropyron spicatum</i> Pursh)	Bluebunch wheatgrass	Perennial	Native	<i>Poaceae</i>
SteAca	<i>Stenotus acaulis</i> (<i>Haplopappus acaulis</i> (Nutt.) Gray)	Stemless mock goldenweed	Perennial	Native	<i>Asteraceae</i>
SedSte	<i>Sedum stenopetalum</i>	Worm-leaf stonecrop	Perennial	Native	<i>Crassulaceae</i>
TetCan	<i>Tetradymia canescens</i>	Gray horse-brush	Perennial	Native	<i>Asteraceae</i>
VioNut	<i>Viola nuttallii</i>	Nuttall's violet	Perennial	Native	<i>Violaceae</i>

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