

LONG-TERM EFFECTS OF REPEATED FIRES ON THE DIVERSITY AND  
COMPOSITION OF GREAT BASIN SAGEBRUSH PLANT COMMUNITIES

by

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The final copy of this thesis has been examined by the signatories, and we find that both the content and the form meet acceptable presentation standards of scholarly work in the above mentioned discipline.

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Long-Term Effects of Repeated Fires on the Diversity and Composition of Great Basin Sagebrush  
Plant Communities

Thesis directed by Assistant Professor Jennifer Kakareka Balch

Sagebrush in the Great Basin is one of the most imperiled ecosystems in North America. Exotic plant invasions and wildfires have combined to convert these systems into those composed mostly of exotic annual grasses and forbs at a broad scale. While it is well documented that annual grass invasions are increasing wildfires, and that exotic annual grasses thrive after fire, the lasting effects that multiple fires have on plant communities are unclear. Namely, do multiple fires affect biodiversity and community composition in a cumulative fashion, or is one fire enough to initiate a lasting alternate state? We created a fire history atlas from 31 years satellite-derived fire data to design a stratified sampling scheme along a fire frequency gradient. We sampled 28 plots for plant community composition and soil characteristics. We examined fire's effect on species richness using species accumulation curves, and calculated alpha-diversity and 3 metrics of beta-diversity. We used non-metric multidimensional scaling to examine community clustering, and PERMANOVA models to examine how climate variable around the time of the fire affected community clustering and beta diversity.

Community clustering measures suggest that one fire pushes the system into an alternate state. Biodiversity measures indicated cumulative effects. There was no significant difference in alpha diversity per plot by fire frequency, but species accumulation show a clear step-wise progression of diversity decreasing as fire frequency increases. Beta diversity showed a significant decline after 3 fires. Non-metric multidimensional scaling showed most burned plots

clustering into the one community type dominated by cheatgrass, except three thrice-burned plots. When examining plots just by exotic and native cover, there was a clear threshold effect after one fire, with native shrubs dominating the unburned plots, and exotic annual grasses dominating the burned plots. While one burn might be enough to change the general community type, successive burns still continue to influence biodiversity.

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## CHAPTER I.

### 1. INTRODUCTION

Wildfire activity has been increasing across the western U.S. since the 1980s (Westerling et al. 2006, Dennison et al. 2014). This trend will likely continue as temperatures and drought events increase (Krawchuk et al. 2009, Moritz et al. 2012, Liu et al. 2013), and as the length of the fire season expands due to increased human ignitions (Balch et al. 2017), land use change (Bowman et al. 2011) and climate change (Wotton and Flannigan 1993, Jolly et al. 2015). This increased fire activity is having profound ecological effects in the Great Basin, where wildfire is converting vast areas (40,000 km<sup>2</sup>; Bradley and Mustard 2008) of *Artemisia tridentata* ssp. *wyomingensis* shrubland communities to grasslands dominated by cheatgrass (*Bromus tectorum*), an introduced annual grass. This in turn is initiating a positive feedback, wherein invading plants increase the probability of fire, and increased fire activity stimulates more annual grass invasion (D’Antonio and Vitousek 1992, Brooks et al. 2004, Balch et al. 2013). The result is a fire return interval that has decreased from a historical range of 100-342 years for intact sagebrush (Baker 2006, Bukowski and Baker 2013) to 78 years in invaded areas (Balch et al. 2013), to as low as 3-5 years in cheatgrass-dominated areas in the Snake River Plain (Whisenant 1990). But the lasting effect of this altered fire regime on plant communities’ biodiversity and composition is relatively unknown — there are relatively few studies that have looked at the impacts of fire after more than 5 years, and fewer still that analyze the impacts of multiple fires in this system (Miller et al. 2013).

There is conflicting evidence about how the persistence of this state of introduced annual grasses is related to fire history. Cheatgrass cover can increase initially after fire, then

decrease and stabilize above the pre-fire cover value (Reed-Dustin et al. 2016), but positive linear relationships between time since fire and cheatgrass cover have also been observed (Shinneman and Baker 2009), as well as areas where cheatgrass declined and was replaced by perennial grasses (West and Yorks 2002). At the community level, long-term measurements at two locations in Idaho (1923-1973, 1950-2006) revealed no clear relationship between community composition and fire, grazing regime, or precipitation (Bagchi et al. 2013). In contrast, Davies et al. (2012) analyzed plot data for an area that burned twice early in this millennium and found that in cases of multiple fires, cheatgrass can come to dominate areas with fire-intolerant natives post-fire, but in areas with pre-fire populations of fire-tolerant species (e.g. *Poa secunda*) native species can resist invasion and regenerate following fire.

Wyoming big sagebrush assemblages are generally agreed to be an endangered ecosystem (Davies et al. 2011), but the evidence of the impact that fire and other disturbances have on biodiversity is sparse and inconsistent. Cover of introduced annual grass species have been mostly observed to be negatively related to species richness and native diversity (Davies 2011, Gasch et al. 2013, Bansal and Sheley 2016), but over a 45 year period Anderson and Inouye (2001) found that while introduced annual grass cover was negatively correlated with cover of native species, species richness was unrelated. Less work has been done on fire, but the aforementioned results could reasonably be assumed to be analogous since fire is so strongly correlated with annual grass cover in this system. However, Mitchell et al. (2016) found fire to be unimportant as a predictor variable for either exotic cover or species richness.

Plant community composition within the *A. tridentata* ssp. *wyomingensis* system has been found to be correlated with soil texture, total C and total N (Davies et al. 2007). One of the primary mechanisms by which fire stimulates changes in community composition is

the fluctuation in available soil nutrients it causes (*sensu* Davis et al. 2000), and most of the evidence points to fire stimulating an initial pulse of nutrients, followed by a long-term decline, as the annual grasses that generally dominate after fire concentrate resources towards the surface and they are volatilized by fire or respired (Evans et al. 2001, Norton et al. 2004). Fire has been observed to stimulate a lasting (2 year) increase in inorganic N at the surface (Rau et al. 2008) and Jones et al. (2015) found no effect of repeated burning on soil C, which they were not expecting and attributed to low fire temperatures. Burned sites that are invaded by cheatgrass have significantly more total N than burned, uninvaded sites ten years after burning and subsequent conversion to an annual grass-dominated system (Gasch et al. 2013). The effect of cheatgrass invasion alone causes an initial increase in soil N, but a decrease in the N available to plants (Evans et al. 2001, Norton et al. 2004). Cheatgrass invasion may initially increase soil C pools, but over time it concentrates soil resources near the surface because of its comparatively shallow root system (Norton et al. 2004), and this combined with multiple fires has been hypothesized to lead to a long-term decrease in soil organic matter (Evans et al. 2001, Norton et al. 2004).

One roadblock to studying long-term fire effects on plant communities is that plots consistently sampled over long time periods are rare, and rarer still are networks of such plots that span a wide area. Without plots that have been monitored over a long time period, it is difficult to know the disturbance history of a place, as the completeness and accuracy of government fire records are often inconsistent (Short 2015). Now, Landsat records exceed 30 years of reliable data collection, and fire history has been documented for that period for fires above 500 acres for the entire western U.S. by the Monitoring Trends in Burn Severity project (MTBS; Eidenshink et al. 2007). This allows for sampling a wide region

and explicitly measuring the effect of different characteristics of fire and fire history on plant community composition and other ecosystem characteristics. A chronosequence approach such as this is appropriate in shorter-term (<100 years) studies in systems like those in the western U.S., which have low biodiversity and relatively predictable successional pathways within the timeframe of interest (Walker et al. 2010). The use of satellite-derived fire data for broad-scale studies has recently become more widespread for use in fire ecology research. Recent examples include research on twice-burned areas (Harvey et al. 2016) and conifer regeneration after one burn (Kemp et al. 2016) in Idaho, and on the interaction between pine beetle outbreaks and wildfire (Hart et al. 2015).

Here, we constructed an atlas of fire history for the Central Basin and Range Ecoregion and explicitly sampled the long-term effects of repeated fires on plant community composition and diversity. We constrained soil, ecological site type, elevation and climate and sampled blocks of plots stratified along a gradient of fire frequency. We expected plant diversity, species composition and soil nutrients to be a function of both fire frequency and time since fire. We also expected that increasing cheatgrass abundance would have a negative relationship with diversity. We hypothesized that (1) Species richness, alpha diversity (number of species in a sampling unit) and beta diversity (continuity or turnover of species between plots) would decrease with increasing fire frequency, and increase with time since fire; (2) Cheatgrass abundance would have a negative relationship with plant diversity, and no relationship with time since fire; (3) Community composition would change drastically after one fire, but then remain relatively similar after subsequent fires; (4) Soil N and C would increase after one fire and decline with subsequent fires, and would have a negative relationship with time since fire; and (5) Indicators of drought stress (high temperatures, vapor pressure deficit, precipitation)

at the time of the fire would exert a lasting influence over post-fire community composition and diversity.

## 2. METHODS

### 2.1. Study Area

We conducted the study in a 14,000 square kilometer region in northern Nevada (Figure 1). This was an attractive area within which to conduct the study because intensive agriculture is limited, there are few people, and it is mostly on public land. The region has hot, dry summers and cold, wet winters. Annual precipitation averages 293 mm, falling mostly from November to May. Mean temperatures range from 21.8 degrees Celsius in July to -1.4 degrees Celsius in December (PRISM Climate Group 2016). The region consists of mountain ranges that run north-south, and the sagebrush ecosystems generally lie on the lower slopes of the mountains; our sites ranged from 1272 to 1696 meters in elevation.

### 2.2. Site Selection

We used geospatial data representing each ecosystem state factor (*sensu* Amundson and Jenny 1997) to design a sampling scheme that constrained all factors except fire history. We used a United States Geological Survey (USGS) digital elevation model to extract elevation values within one standard deviation of the mean (1298 – 1921 m) in the study area. We used the LANDFIRE (Rollins 2009) biophysical setting layer to eliminate everything except big sagebrush shrubland. The LANDFIRE data has 62-68% classification accuracy for shrublands (Zhu et al. 2006). We used soil data from the Natural Resource Conservation Service to include only areas in the Loamy 8-10 precipitation zone (Soil Survey Staff, Natural Resources Conservation Service 2016). We used the Land Treatment Digital Library to exclude areas that had undergone extensive restoration activities (Pilliod and Welty 2013). Excluding private and military land, and areas more than 5 miles from a road eliminated impractical

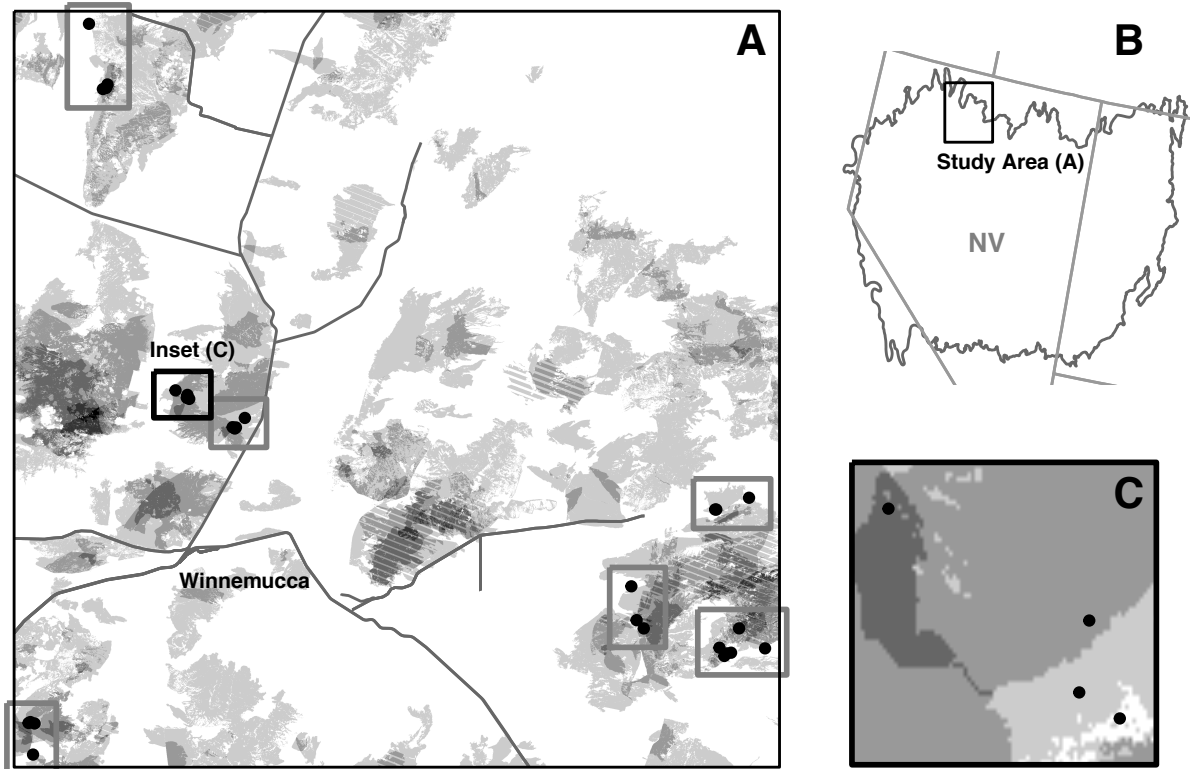


Figure 1: The extent of the study area is shown in (A). The striping from the scanner line correction failure from Landsat 7 is clearly visible and those areas were avoided in our sampling. Darker shading indicates higher fire frequency. The potential range is 0 to 5 fires, although areas with more than 3 fires were extremely rare (0.2% of total area). We sampled frequencies 0 to 3. The placement of the study area within the Central Basin and Range ecoregion is shown in (B). A detail of one of the study blocks is represented in (C).

plot locations and held human influence somewhat constant.

Long-term grazing data was difficult to obtain. However, we believe we adequately accounted for grazing intensity for this study by using a block sampling design, and stratifying our statistical analyses by these blocks. Plots within blocks were close enough together to reasonably assume they had experienced similar grazing pressure, visually assessing the impact of grazing on-site, aggregating what records we could for the allotments in our study (billed animal unit months (AUM) from 1992 - 2002, and 2012), and normalizing AUM by unit area and including it in our statistical modelling. Once we constrained the area to a consistent sampling space, we used Landsat-derived fire data to stratify the space along a fire frequency gradient. To generate fire history maps, we first extracted only the values 2-4 (low, medium and high severity) from each yearly burn severity mosaic from the Monitoring Trends in Burn Severity project (MTBS; Eidenshink et al. 2007), as these were the values where one can be reasonably certain that they actually burned. Other possible values are one and five. One includes unburned patches. Five indicates post-fire green-up, which could be caused by a response to fire or an unburned patch. To generate fire frequency maps, we reclassified each yearly layer to a binary grid, and summed all 31 layers. To avoid areas with less certain fire frequencies, we then converted the MTBS fire perimeter polygons to layers of fire frequency to extract only the grid cells where the frequency from the polygons matched the frequency from the reclassified raster grid. To generate last-year-burned maps, we reclassified each severity mosaic (values 2-4) to the fire year, and calculated the maximum year for the entire time period for each pixel.

We used the “out of the box” classified burn severity values from MTBS. Kolden et al. (2015) have brought up several shortcomings for the use of the MTBS burn severity mosaics,



in particular inconsistent development of class thresholds and a lack of empirical relationships between the classified values and ecological metrics. Because we only used these data to get a more precise estimate of fire occurrence, (i.e. we used it to eliminate areas of uncertainty) rather than using the severity data as an independent variable for analysis, we thought it sufficient to use these data in this state.

In order to isolate the effects of fire frequency while accounting for site characteristics like aspect and elevation, we used a block sampling design. We selected seven blocks in our sampling space in accessible areas where there was a range of fire frequencies and last years burned, and unburned areas for controls within relatively close proximity. Within each block, we created spatially balanced random points (Theobald et al. 2007) for each fire frequency, and sampled one plot for each fire history class within the block. At each block, we first sampled the unburned control plot to confirm that the area was indeed the correct vegetation type, and then sampled burned plots. After navigating to the predetermined coordinates for each plot we first confirmed the physical characteristics (soil type, lack of obvious restoration, lack of obvious overgrazing) were within the constraints of our sampling design. If a predetermined point was not suitable (e.g. soil was too rocky or sandy, an unburned control plot had obviously burned, or it was the wrong ecological site), we referred to georeferenced PDFs of our fire history atlas that we accessed with a simple application on a mobile device and located nearby areas within the site that were suitable. When a suitable area was found we used a random number generator to pick a random bearing and a random distance, and navigated to the new plot location.

We sampled 28 plots that fell along a gradient of fire frequency (0-3 fires; 7 plots per frequency) and a range of times since fire (4-31 years; mean = 17.6, std = 6.6; Figure 1).

Because most of the fire effects research in this system has been done within five years of a fire, we aimed to have the time since fire of all of the plots greater than or equal to 5 years. We encountered 53 plant species - 12 were introduced and 41 were native.

## **2.3. Field Sampling**

### **2.3.1. Plot Establishment**

We used GPS to navigate to predetermined plot locations. Upon arrival we hammered a permanent marker into the ground at the southwest corner of the plot. We recorded the slope, aspect, distance to the nearest *A. tridentata* individual or other shrub species, the topographic curvature of the site (convex, concave, flat), evidence of ecological restoration, grazing signs, and evidence of past fires. We then delineated the 50 x 50 meter plot, and placed pin flags at 9 randomly determined coordinates within the plot with a minimum spacing of 3 meters, which represented the SW corner of each subplot, and used engineering rulers to delineate each 1m<sup>2</sup> subplot. Pilliod and Arkle (2013) found this sampling density sufficient for this ecosystem, if supplemental methods are used to estimate disparate functional groups like trees and shrubs. Hence, we used the point-quarter method as a supplement to estimate shrub cover (see Pilliod & Arkle (2013) for detailed methods).

### **2.3.2. Vegetation**

To learn how fire frequency influences community composition and diversity, we measured the abundance and presence of all species. We identified and recorded occupancy data for every species within each subplot, and took a photograph from nadir with an Olympus Stylus TG-870 digital camera to be analyzed later for percent cover.

We used 'Samplepoint' software (Booth et al. 2006) to analyze the digital photographs

for percent cover. We prepared photographs for analysis by cropping them to the 1 m x 1 m area of the subplot. Then we used Samplepoint to overlay a regular grid of 100 points on each picture, and at each point identified whether it was litter, bare ground, rock, dung, or a plant. If it was a plant, we identified it to species with the aid of the occupancy data recorded at the plot. These data were then converted to percent cover. If we recorded a species as present within the subplot, but it was missed by the photographic analysis, we recorded it as 0.5% cover.

### **2.3.3. Soil**

To understand how fire frequency influences soil nutrients, we measured the concentration of soil N and C, and used the soil's bulk density to convert the concentration to an areal estimate. We collected two 10 cm deep soil cores with a punch auger at random locations in each subplot, and aggregated and homogenized them in a bucket (N = 18 per plot). The soil samples were sent to the Soil, Water and Forage Analytical Laboratory (SWFAL) and Oklahoma State University where they were analyzed for percent total N and C using a LECO TruSpec CN Analyzer (LECO Corp., St. Joseph, MI, USA). To estimate net N mineralization and nitrification, we weighed two 10 g subsamples of soil from each sample. These subsamples were mixed with 50ml of KCL, shaken vigorously for two minutes, then left to sit for 24 hours. Then the supernatant was poured through leached filter paper into a scintillation vial, which was labelled and put on ice. This was done for one subsample on the day of collection, and then for the second subsample 3 days later. Extractions were sent to SWFAL to be analyzed for  $\text{NH}_4$  and  $\text{NO}_3$  concentration using a Lachat® autoanalyzer. We calculated net mineralization and nitrification with the following equations:

Net mineralization =  $(\text{NH}_4 + \text{NO}_3 \text{ at time 3}) - (\text{NH}_4 + \text{NO}_3 \text{ at time 0})$

Net nitrification =  $(\text{NO}_3 \text{ at time 3}) - (\text{NO}_3 \text{ at time 0})$

One bulk density sample was collected for each plot at the southwest corner of a randomly selected subplot. We carefully inserted a 6 cm tall x 5 cm diameter metal cylinder into the ground until the top was just below the soil surface, scraped the soil off the top until it was perfectly flat and put a rubber cap on it. Then we dug a hole next to the cylinder several inches deeper than the bottom of the cylinder, carefully scooped the cylinder and the soil below it out of the ground and flipped it over, scraped the excess off until the other end of the cylinder was completely flat, and double bagged the sample in a Ziploc bag. The samples were weighed on the day of collection, and then dried at 105 degrees Celsius until the weight was stabilized and weighed. A few samples contained a significant volume of coarse rock fragments (>10g). In those cases, after the initial bulk density measurements were made, we removed and weighed the rocks and estimated their volume. We subtracted these weights and volumes from the raw measurements for an adjusted bulk density measurement.

We were also interested in how fire frequency affected the health of the biological soil crust. Soil aggregate stability (SAS) is a simple variable to measure that can serve as a proxy for biological soil crust health (Herrick et al. 2001). We measured SAS by carefully collecting two 6 mm diameter samples of the soil surface systematically at every subplot, and subjected the samples to a slake test (Herrick et al. 2001). For this test, we placed each sample on a small sieve, and submerged the sieve in water for 5 minutes. Then, the sample was dipped 5 times, and given a score from one to six based on how quickly and how completely it dissolved in water, one being completely dissolved within 30 seconds, six being >75% in tact after 5 minutes and 5 dips (see Herrick et al. (2001) for more details).

#### 2.3.4. Environmental Data

Aspect was converted to folded aspect (folded aspect =  $|180 - |\text{aspect} - 225||$ ; McCune and Keon 2002). This results in an approximation of heat load ranging from zero (northeast) to 180 (southwest). Elevation was extracted from 10m resolution digital elevation models. The study sites were situated among six grazing allotments. To account for grazing, we used billed animal unit month data acquired from the Bureau of Land Management from 1990 - 2002 for each allotment to calculate mean animal unit months, then divided by the area of the allotment to get animal unit months per acre. To learn how climate before, during and after the fire event affected the subsequent community composition and diversity, we extracted monthly maximum vapor pressure deficit, maximum temperature, and precipitation for the years before during and after the most recent fire at each plot. Maximum temperature and maximum vapor pressure deficit were averaged for the entire year before during and after, and precipitation was averaged for the two winters (November - May) prior and one after. We used monthly data provided by the PRISM climate group (PRISM Climate Group 2016) for all climate variables. Variables used in modeling are provided in table 1.

Table 1. Variables and their abbreviations.

Variable	Abbreviation	Source
<b>Fire</b>		
Time Since Fire	TSF	MTBS
Fire Frequency	FF	MTBS
<b>Climate</b>		
Maximum Vapor Pressure Deficit		
<i>Year of Fire</i>	vpdmax_during	GRIDMET
<i>Year before Fire</i>	vpdmax_before	GRIDMET
<i>Year after Fire</i>	vpdmax_after	GRIDMET
Maximum Temperature		
<i>Year of Fire</i>	tmax_during	GRIDMET
<i>Year before Fire</i>	tmax_before	GRIDMET
<i>Year after Fire</i>	tmax_after	GRIDMET
Precipitation		
<i>Nov - May; 2 Years Before Fire</i>	ppt_2pre	GRIDMET
<i>Nov - May; 1 Year Before Fire</i>	ppt_1pre	GRIDMET
<i>Nov - May; After Fire</i>	ppt_post	GRIDMET
<b>Other</b>		
Folded Aspect		Field Measurements
Elevation		USGS
Animal Unit Months per Acre	AUM_acre	BLM

## 2.4. Statistical Analysis

### 2.4.1. Species Richness, Alpha Diversity and Beta Diversity

We used plot-based species accumulation curves to assess how different fire history characteristics (frequency and time since fire) affected species richness. We used the sample-based rarefaction method (Chiarucci et al. 2008, Oksanen et al. 2016, R Core Team 2016). We used Tukey’s Honest Significant Differences test (hereafter, Tukey’s test) to see if different fire frequencies influenced alpha diversity, which is simply the number of species at each plot, and generalized linear mixed models (GLMMs) with the study block as a random effect to

assess the influence of time since fire and cheatgrass abundance on alpha diversity. There are several ways to quantify beta diversity, most of which are grouped into “measures of continuity” and “measures of gain and loss” (Koleff et al. 2003). We used the “Z” index and Whittaker’s original beta diversity index for continuity measures, and Simpson’s index for a measure of gain and loss. To see how beta diversity differed between fire frequencies, we modelled the homogeneity of dispersion of those matrices (Anderson et al. 2006), and ran pairwise permutation tests (Legendre et al. 2011) on these models with 9,999 permutations, stratified by the study blocks.

#### **2.4.2. Community Composition and Environmental Variables**

To analyze how fire frequency affects community composition, we used non-metric multidimensional scaling (NMDS). We ran a rank correlation test for fire history gradients against a matrix of relative cover of species per plot to determine the best hierarchical clustering method for creating a dissimilarity matrix. We used this index for NMDS to examine how those fire history characteristics affected the floristic composition. To assess which species and environmental variables had the most influence on community composition, we added those variables to the ordinations using the ‘envfit’ function from Vegan, with 9,999 permutations and stratified by the study block. Then we grouped species by their biogeographical origin (i.e. native or exotic), and used Tukey’s test to assess how fire frequency influenced native cover, exotic plant cover and cheatgrass abundance, and GLMMs to assess the influence of time since fire on those variables. Similarly, we used Tukey’s test and GLMMs to assess how fire history characteristics affected soil total N and C, mineralization, and soil aggregate stability.

### 2.4.3. PERMANOVA Modeling

To assess how pre- and post-fire climate, along with soil and other environmental variables (Table 1) affected post-fire community composition and diversity, we used permutational multivariate analysis of variance (PERMANOVA). PERMANOVA uses a dissimilarity matrix as the response variable, and columns from a separate data frame as the predictors. It makes the assumption that groups being modeled have homogeneous dispersions. If the test is run on groups with heterogeneous dispersions, it is vulnerable to type 1 error (Anderson and Walsh 2013). To account for this we built multivariate homogeneity of groups dispersions (MHGD) models on our community clustering and beta diversity matrices grouped by block, fire frequency, and burned vs unburned. We then ran ANOVAs and Tukey's test on each model, with p values below 0.05 considered to be an indication of heterogeneous dispersions. After removing variables with multi-collinearity, built PERMANOVA models with both community clustering and beta diversity matrices using an additive model-building process, with 9,999 permutations and stratifying the permutations by the study blocks, with the aim of producing parsimonious models.



### 3. RESULTS

#### 3.1 Species Richness, Alpha Diversity and Beta Diversity

Species accumulation curves showed a clear separation for time-since-fire and fire frequency, with a decline in plant diversity as fire frequency increases, and an increase in diversity as time-since-fire increases (Figure 2). Alpha diversity was higher in unburned plots, but the relationship was not significant ( $p > 0.05$ ) for fire frequency (Figure 4a). Cheatgrass abundance and time since fire did not have significant relationships with alpha diversity ( $p > 0.05$ ). Beta diversity for all three indexes followed a different pattern - similar levels for unburned through two fires, then a drop at three fires (Simpson's index is shown in Figure 4b). Fire frequencies 1 and 3 were significantly different ( $p < 0.05$ ) from each other for all three beta diversity indexes using the 'permutest' method, but none were significantly different when using Tukey's test.

#### 3.2 Community Composition

The rank index test showed the Kulczynski index to have the most consistent high scores across gradients of fire history and soil characteristics, so we used this index for our hierarchical clustering and NDMS analyses. NMDS (Non-metric fit,  $R^2 = 0.992$ , Linear fit,  $R^2 = 0.972$ ) showed 7 unburned plots clustered around high abundances of *A. tridentata*, and 18 burned plots clustered around *B. tectorum* (Figure 3). Two thrice-burned plots were dominated by exotic annual forbs (*Sisymbrium altissimum* and *Erodium cicutarium*) and one was dominated by the native perennial grass *Poa secunda*. The ordination showed a clear separation between burned and unburned plots, but neither fire frequency or time since fire were significantly correlated with the ordination. Four environmental variables were found

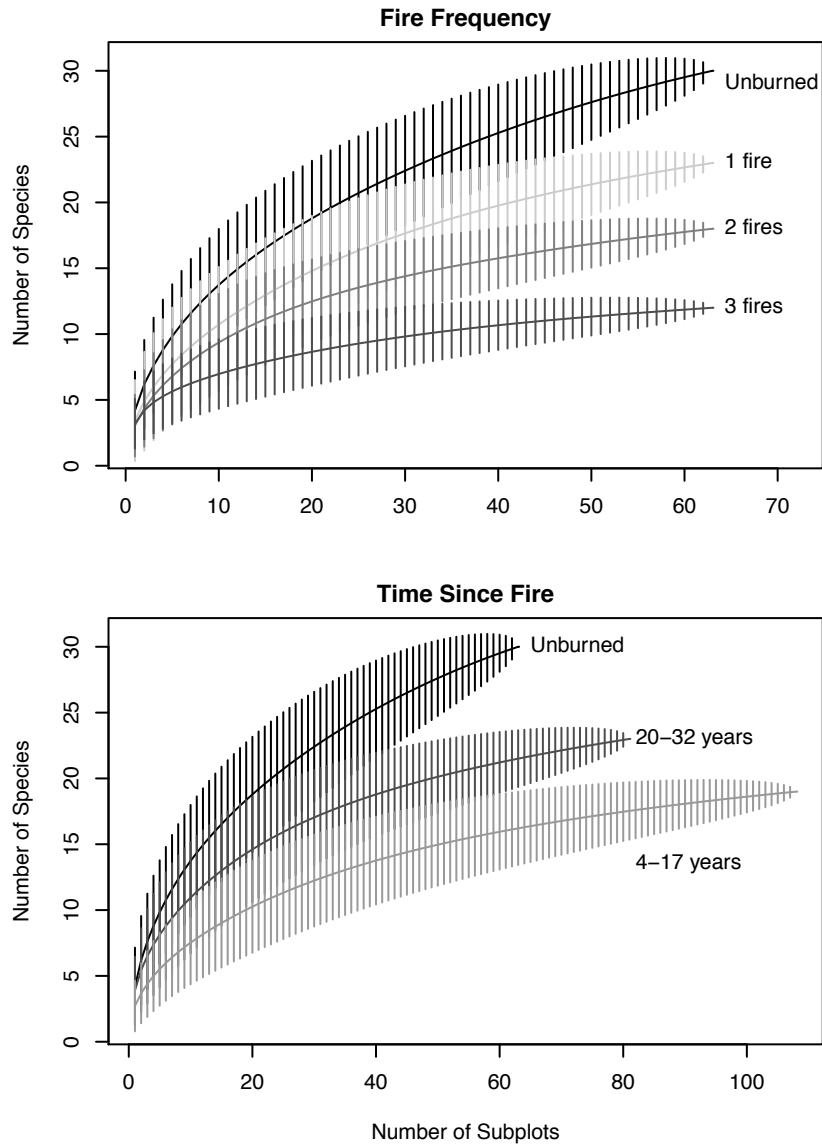


Figure 2: Species accumulation curves for fire frequency and time since fire. Vertical lines are error bars.

to be significantly correlated with the ordination space: Soil total C and N, elevation and folded aspect. This suggests that unburned plots are correlated with higher soil total C and N, higher elevations, and cooler aspects.

For the Tukey's tests of exotic versus native cover, there was a significant shift from zero to one fire ( $p < 0.05$ ) for both exotic and native cover, then no significant changes with subsequent fires (Figure 4c-d). Time since fire was unrelated to both exotic and native cover, as well as cheatgrass abundance. We divided the mean cover estimates into native and exotic life form groups (annual and perennial graminoids and forbs, and shrubs), and saw a dramatic decrease in native shrub cover after one fire, coupled with a dramatic increase in annual grass cover, that is thereafter relatively stable with subsequent fires (Figure 5).

### **3.3. Soil Nutrients**

We found no statistically significant relationships ( $p > 0.05$  for all comparisons) between fire frequency or time since fire and soil C, N, N mineralization. However, we did see a common pattern for these soil nutrients, where after one fire the resource increased, but by the third fire the resource was eventually near or below the unburned level. Soil physical characteristics (bulk density, aggregate stability) showed no clear pattern or significant differences.

### **3.4 PERMANOVA Modeling**

ANOVAs and Tukey Honest Significant Differences tests ran on MHGD models showed no significant heterogeneity in groups dispersions for both beta diversity and hierarchical clustering ( $p > 0.05$  for all models). This allowed us to be confident that the PERMANOVA models we ran subsequently did not violate their assumptions and the results would be robust.

PERMANOVA models showed that fire history and environmental factors influenced

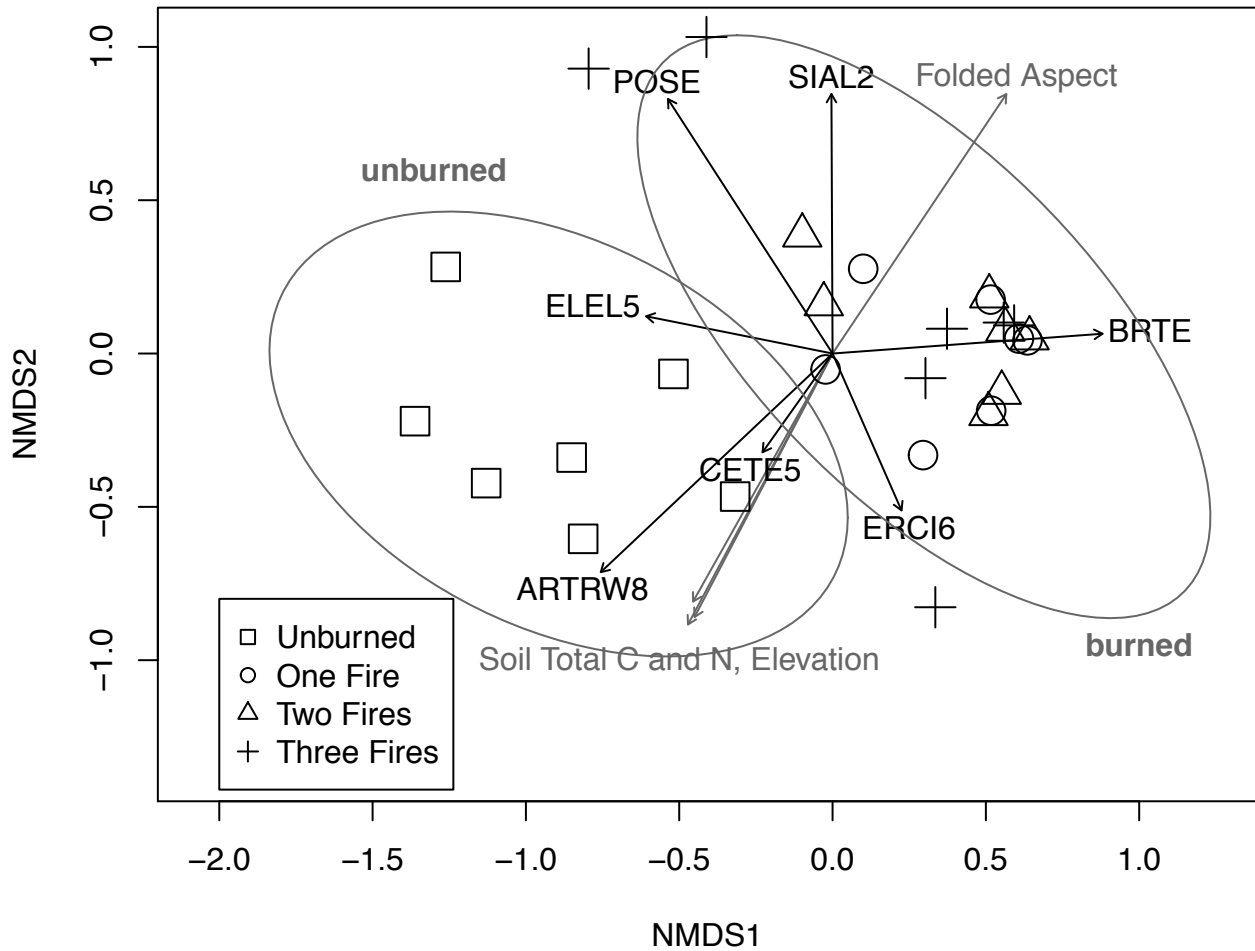


Figure 3: Ordination plot of non-metric multidimensional scaling conducted on plant community data using Kulczynski hierarchical clustering. Ellipses represent the 95% confidence interval around plots grouped by fire frequency. Species (black) and environmental variables (grey) significantly ( $p < 0.05$ ) influencing the ordination are shown, with arrows scaled by the strength of the correlation. Species are listed by their USDA plant codes. ARTRW8 is *Artemisia tridentata* ssp. *wyomingensis*; POSE is *Poa secunda*; ELEL5 is *Elymus elymoides*; SIAL2 is *Sisymbrium altissimum*; BRTE is *Bromus tectorum*; CETE5 is *Ceratocephalum testiculatum*; ERCI6 is *Erodium cicutarium*.

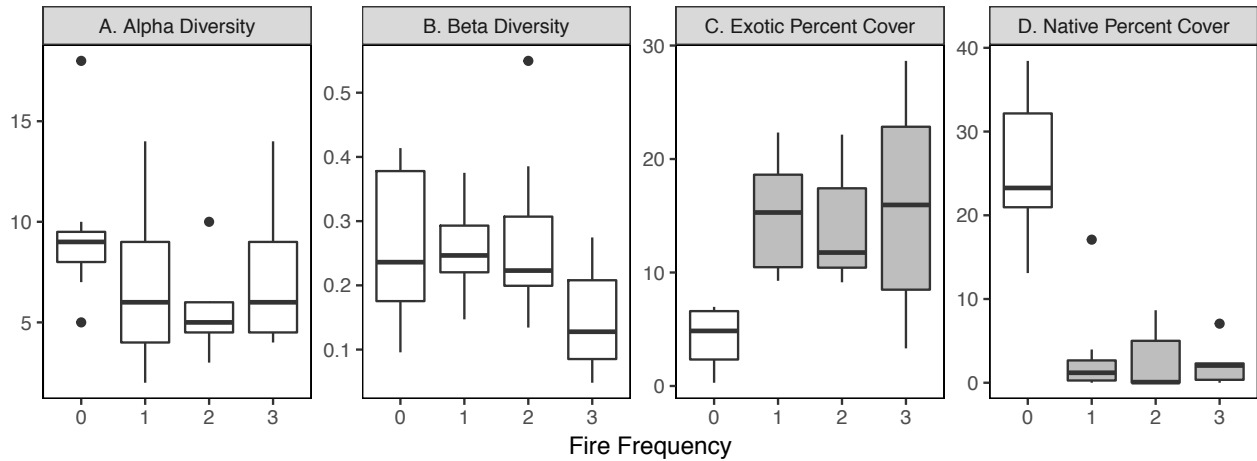


Figure 4: Alpha Diversity (number of species per plot), Beta Diversity (Simpson's index - the values are a unitless index of dissimilarity), and native and exotic plant cover, all grouped by fire frequency. Shading indicates significantly different groups as determined by Tukey's test. All three beta diversity indices exhibited a very similar pattern, so only one is shown.

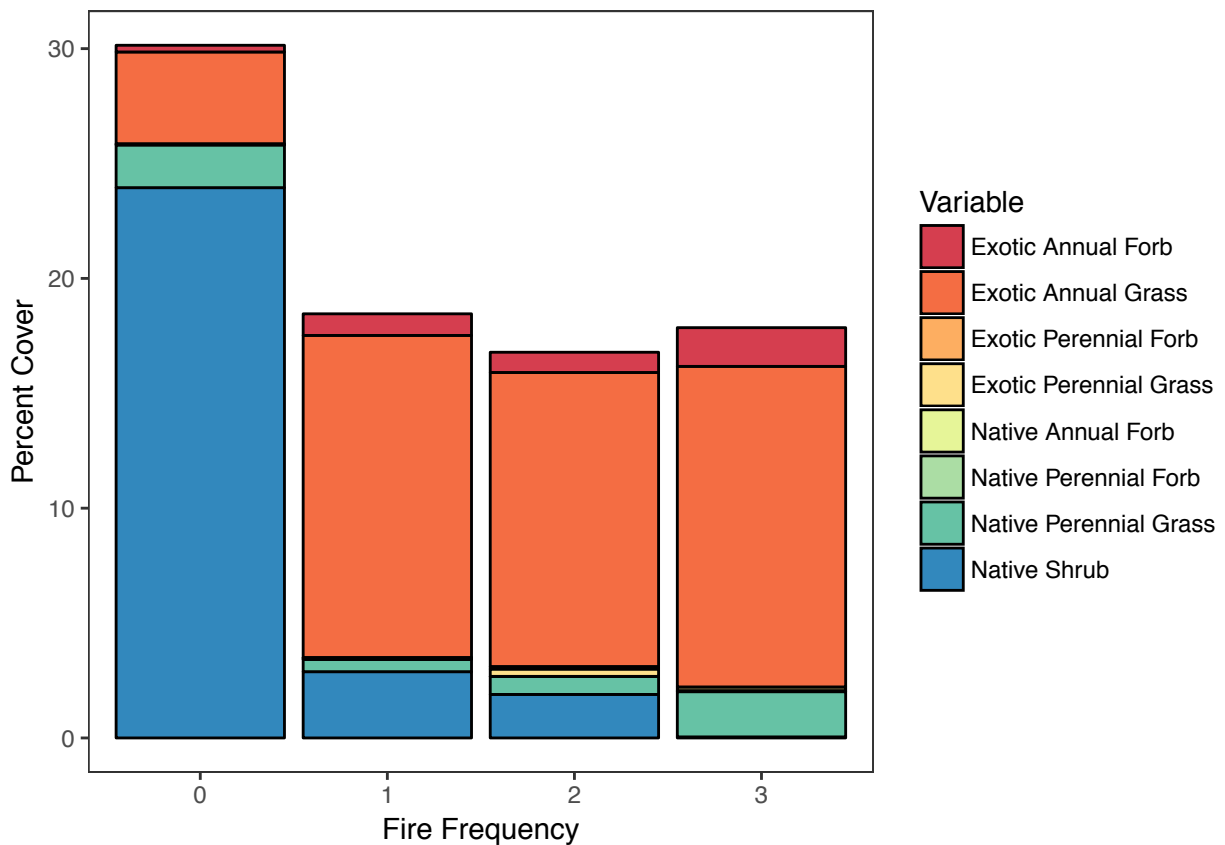


Figure 5: Percent cover of life forms, grouped by fire frequency. Of the two most dominant life forms, exotic annual grass is >99% cheatgrass, and native shrub is >99% Wyoming big sagebrush.

community clustering and beta diversity differently. Community clustering after fire was most significantly affected by fire frequency, time since fire, maximum vapor pressure deficit of the year of the fire, and the interaction between fire frequency and time since fire (Table 2,  $R^2 = 0.55$ ). The relatively low amounts of variation consumed by the individual variables indicates these are subtle effects. Beta diversity on the other hand was influenced most by winter precipitation one and two years prior to the fire, fire frequency, and the interaction between winter precipitation one year prior and max temperature for the year after the fire (Table 3,  $R^2 = 0.62$ ). Here, the effect was more pronounced, as more variation consumed by the most statistically significant variables (FF, ppt\_1pre and ppt\_2pre).

Table 2. PERMANOVA results for fire history and environmental factors influencing post-fire **community composition**.

Variable	Df	SumsOfSqs	MeanSqs	F.Model	R2	Pr(>F)
<b>TSF</b>	1	0.1457105	0.1457105	2.018883	0.0712998	<b>0.0089</b>
FF	1	0.2341868	0.2341868	3.244761	0.1145935	0.0521
<b>vpdmax_during</b>	1	0.2243206	0.2243206	3.108060	0.1097657	<b>0.0025</b>
tmax_during	1	0.0951676	0.0951676	1.318588	0.0465679	0.1460
tmax_pre	1	0.0776360	0.0776360	1.075680	0.0379892	0.1833
AUM_acre	1	0.2037624	0.2037624	2.823217	0.0997061	0.2162
<b>TSF:FF</b>	1	0.1245873	0.1245873	1.726212	0.0609637	<b>0.0388</b>
Residuals	13	0.9382597	0.0721738		0.4591141	
Total	20	2.0436309			1.0000000	

Table 3. PERMANOVA results for fire history and environmental factors influencing post-fire **beta diversity**.

Variable	Df	SumsOfSqs	MeanSqs	F.Model	R2	Pr(>F)
<b>FF</b>	1	0.2109555	0.2109555	2.4408035	0.0782962	<b>0.0065</b>
<b>ppt_1pre</b>	1	0.5235936	0.5235936	6.0580970	0.1943319	<b>0.0019</b>
tmax_after	1	0.1075021	0.1075021	1.2438242	0.0398994	0.0613
<b>ppt_2pre</b>	1	0.3992901	0.3992901	4.6198772	0.1481966	<b>0.0096</b>
TSF	1	0.1450149	0.1450149	1.6778551	0.0538223	0.2598
folded_aspect	1	0.1104566	0.1104566	1.2780078	0.0409960	0.4745
Elevation	1	0.0441504	0.0441504	0.5108301	0.0163864	0.9530
<b>ppt_1pre:tmax_after</b>	1	0.1162184	0.1162184	1.3446734	0.0431345	<b>0.0272</b>
Residuals	12	1.0371446	0.0864287		0.3849366	
Total	20	2.6943262			1.0000000	

## 4. DISCUSSION

### 4.1. Biodiversity and Community Composition

We hypothesized that biodiversity by any measure would decrease with increasing fire frequency, and increase with time since fire. Here we show that over a three-decade period repeated fires had long-lasting effects on community composition and biodiversity in Wyoming big sagebrush ecosystems. Species accumulation curves demonstrate how species richness declines with increasing fire frequency, but measures of alpha and beta diversity decrease after one and three fires, respectively (Figure 4a-b). The species accumulation curves demonstrate that repeated fires are decreasing the overall pool of species from which an individual patch might draw from. So while there may not be significant differences in alpha diversity as fire frequency increases, as the number of species each plot can draw from decreases, this signal shows up as a decrease in beta diversity after three fires, even with only 7 plots.

We found no relationship between cheatgrass abundance and alpha or beta diversity, contrary to our hypothesis. The positive relationship between cheatgrass and fire is obvious from our results and prior work (Whisenant 1990, Balch et al. 2013), and the relationship between fire and species richness is clear. This implies that effect of cheatgrass invasion on diversity may be an indirect byproduct of its effect on fire frequency. It is also possible that wet years see more species of annuals, dampening the signal that other studies may have detected in drier years. The summer of 2016 was preceded by a particularly wet winter (most of our study area experienced 50 – 150% higher than normal precipitation) which led to higher annual cover compared to drier years (e.g. we saw annual grass values more than double compared to 2013 measurements (Mahood et al. unpublished data)).

Here, we show that in *Artemisia tridentata* ssp. *wyomingensis* systems, one fire can



convert this shrub-dominated system to one composed mainly of introduced annual grasses and forbs, and this new state can persist for decades with little sign of recovery to its prior condition. Subsequent fires, however, are not inconsequential. Earlier work has suggested that Wyoming big sagebrush can recover from disturbance in as little as 9 years following fire (Wambolt et al. 2001), but recent work has shown that while individual plants can establish relatively quickly after fire (Shinneman and McIlroy (2016) found that the oldest individual in most stands established about 5 years after the most recent burn) and grow to maturity in about 20 years, it still takes over 100 years for the landscape to achieve its previous cover of sagebrush (Baker 2006, Bukowski and Baker 2013). Most of the studies showing quick recovery times were done at higher latitudes (Wambolt et al. 2001), or on sites that were specifically selected because there was potential for sagebrush recovery (Shinneman and McIlroy 2016). Here we found that on most sites, even after an average of 17 years, post-fire sagebrush cover was sometimes minimal, but mostly nonexistent (median = 0%, mean = 1.6%, standard deviation = 3.7%).

NMDS ordinations show that while the relationship between fire frequency and species richness might be linear, its effect on the specific community composition is more complex, and probably depends on site-specific conditions at the time of the fire. While almost all of our burned plots were dominated by *B. tectorum*, several thrice-burned plots were dominated by *P. secunda* or exotic annual forbs. Previous work showed that fire can push cheatgrass-invaded grassland and shrubland communities into those dominated by *B. tectorum*, *P. secunda*, and exotic forbs, while uninvaded sites can persist in a state of native bunchgrasses and forbs (Davies et al. 2012). This work corroborates that conclusion and, because of our high time-since-fire values (17.6 years compared to 2 years for Davies et al (2012)), we also show

that these states can persist for long periods between disturbances, corroborating the work of Reed-Dustin et al. (2016), which indicated after an immediate post-fire increase, *B. tectorum* will stabilize and persist at an intermediate value.

Species richness, population growth rate, and rate of disturbance has been proposed as a tri-variate relationship, where species richness increases as the correlation between population growth rate and rate of disturbance increases (Huston 1979, White and Jentsch 2001). Community composition is a function of species with the particular survival strategies appropriate for the conditions on hand — ruderal, stress tolerating, or competitive strategies, which are related to stress intensity and disturbance intensity (Grime 1977). Wyoming big sagebrush has a stress-tolerating survival strategy – it endures long periods of water stress, and opportunistically reproduces in wet years, when the time is right (Meyer 1994). Stress-tolerating plants generally become dominant when the disturbance regime is infrequent, relative to their growth rate (Grime 1977). This is corroborated by research showing that higher fire frequencies favor resprouting plants, while low frequencies favor seed obligates like Wyoming big sagebrush (Pausas and Bradstock 2007). When cheatgrass invades, disturbance rates increase (Balch et al. 2013), increasing mortality for the native stress-tolerators. Cheatgrass can persist in this high-stress, high disturbance environment, because rather than devoting resources to tolerating stress, cheatgrass grows, sets seed, and dies during the short window of opportunity in the spring when the soil is moist (Booth et al. 2003), and the fire season starts after its life cycle is complete. So cheatgrass is in a low-stress environment while it is alive actively growing, and the subsequent high-stress, high-disturbance period only damages its neighbors – a realization of the “kill thy neighbor” hypothesis (Bond et al. 1995).

## 4.2. Soil Nutrients

We hypothesized that repeated fires would lead to long-term reductions in soil C and N, based on the results of prior work (Evans et al. 2001, Norton et al. 2004, Rau et al. 2008). While we did see these patterns, there were no significant differences or trends with fire frequency or time since fire. If there were, as has been hypothesized, positive feedbacks resulting from changes in nutrient uptake and input caused by plant invasions, it may be that (a) they take longer than 17 years to manifest, or (b) we needed a higher sample size to detect the trend. If those hypothesized mechanisms are not occurring, perhaps the actual mechanism by which these introduced grasses persist is primarily a combination of competition (Booth et al. 2003) and fire killing the propagules of fire-intolerant natives. We did, however, see a significant correlation between soil C and N, elevation and folded aspect and the NMDS ordinations, which seems to follow the burned vs unburned gradient. This could mean (a) that the plants in unburned shrub-dominated systems are inputting more soil nutrients in the soil, or (b) that higher, wetter sites that are also unlikely to burn are also able to store more soil nutrients.

## 4.3. PERMANOVA Modeling

PERMANOVA models showed that fire history and climate variables affect diversity and community composition differently. Composition was found to be influenced by both fire frequency and time since fire, and high vapor pressure deficit the year of the fire. This suggests that drought stress exerts a significant influence on the particular plant species that will survive and persist after a fire, and this effect can still be detected decades after the fire burned. This corroborates prior findings that cheatgrass, the most influential post-fire

species, is limited by soil moisture at lower elevation sites (Chambers et al. 2007), and has can decline in particularly dry years (West and Yorks 2002).

We found that Beta diversity was most heavily influenced by fire frequency, precipitation for the two wet seasons prior to the fire, and an interaction between antecedent precipitation and maximum temperature for the year after the fire. Antecedent precipitation has also been shown in other studies to be an important predictor of fire occurrence in this system (Abatzoglou and Kolden 2013, Balch et al. 2013). Since this is a fuel-limited system, high precipitation stimulates widespread high fine fuel loads and continuity (Davies and Nafus 2013), leading to higher fire probability, more homogeneously burning fires, and larger extents. This same process could also be the driving factor behind decreasing diversity. Following highly contiguous and extensive fires there would be fewer unburned patches as seed sources which are essential for the seed-obligate sagebrush to reestablish quickly (Shinneman and McIlroy 2016). In addition, Wyoming big sagebrush is an opportunist in reproduction, setting most of its seed in wet years (Meyer 1994). So, in the years that Wyoming big sagebrush is maximizing its expenditure on reproductive resources, increased horizontal fuel continuity (Davies and Nafus 2013) a) increases the probability of burning, and b) increases rates of competition for resources post-fire, during the short window in early spring when enough water is available in the soil for plants to uptake nutrients (Ryel et al. 2010, Schlaepfer et al. 2014). All of this results in a more homogeneous post-fire landscape populated mostly by fire-tolerant plants, and hence lower species turnover, adding to existing evidence for a correlation between “pyrodiversity” and biodiversity (Kelly and Brotons 2017).

#### **4.4. Implications**

We now have a reliable satellite fire record spanning over 30 years. For many systems the fire return interval is too long for a record of this length to be useful. But here, the fire return interval has decreased to the point where it matches the satellite record and can provide key insights on fire frequency in grass-dominated or grass invaded systems (Balch et al. 2013). Annual grass invasions and their alterations to fire regimes are a global phenomenon (D'Antonio and Vitousek 1992, Brooks et al. 2004), and this type of study design will be useful for many other systems that are experiencing or expect to see increases in fire activity. Additionally, new algorithms are being developed that will lead to more accurate and precise fire data products (e.g. Hawbaker et al. 2015), leading to more nuanced fire history atlases, and thus more precise sampling stratifications – especially now that burn severity information can be relatively simply incorporated (Eidenshink et al. 2007).

This work adds to the existing body of literature that suggests that Wyoming big sagebrush systems should probably be rested from disturbances, if not actively protected from them. Several authors have recommended taking measures to try and reduce the size and frequency of wildfire, and stop using prescribed fire in this system (Whisenant 1990, Baker 2006, Lesica et al. 2007), while also reducing grazing (Shinneman and Baker 2009, Ellsworth and Boone Kauffman 2013). Those that have not recommended against prescribed fire are still very cautious (Davies et al. 2009, Reed-Dustin et al. 2016, Shinneman and McIlroy 2016). The fire return interval experienced by Wyoming big sagebrush before European colonization has been characterized as being every 35 – 100 years (Schmidt et al. 2002), every 100 – 240 years (Baker 2006), to every 171 – 342 years (Bukowski and Baker 2013). This discrepancy has important management implications, leading to disagreement as to which stressors (e.g. grazing, fire) need to be increased or decreased in order to manage for healthy

sagebrush. The lower estimations imply the system is fire-dependent and requires frequent burning in order to persist. But if Wyoming big sagebrush was a fire-dependent system, fire would not be expected to cause the widespread, lasting declines in species richness we have observed. Furthermore, even if in the past that were true, today the risk of a fire-prone grassland establishing after a fire likely outweighs the potential benefits of a prescribed fire.

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