Wildfire and Rehabilitation History Effects on *Artemisia tridentata* subsp. *wyomingensis* Communities Invaded by *Bromus tectorum*

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Abstract

Currently, ~50% of the sagebrush steppe in the Great Basin, USA, has been lost as a result of land use change, plant invasions, and altered fire regimes. The impact of such threats warrants rehabilitation treatments in order to maintain native plant communities; however, little research exists on the effects of rehabilitation treatment and fire history on native plant communities or sites with a history of rehabilitation across landscapes. We used a combination of field work and spatial analysis to examine the effect of fire history, rehabilitation history, and environmental variables on plant community assembly, *Bromus tectorum* invasion, and changes in fire regime characteristics. Environmental variables explained 41% of the variation in plant communities while fire and rehabilitation history explained 44% of the variation in plant cover. Native species richness increased with elevation, but nonnative species richness did not. *Bromus tectorum* cover and density were inhibited by diverse native bunchgrass communities. *Bromus tectorum* decreased as the number rehabilitation treatments or time since treatment increased which was attributed to native bunchgrass establishment success and population growth, respectively. Fire regimes were in part determined by site moisture with more xeric sites burning more overall and more frequently at shorter intervals in the last twenty years. The vegetation treatment history influenced the number of fires, fire return interval, and fire frequency. Sites that were aerially seeded prior to a fire had shorter fire turn intervals and more frequent fires in the last twenty years than drill seeded sites. The number of fires increased as aridity increased when they were aerially seeded, but aridity had no effect on the number of fires when drill seeded. When the most recent treatment was drill seeding, the fire return interval was greater, and frequency was lower than aerially seeded sites even when treatment history demonstrated

multiple aerial seeded treatments prior to drill seeding. Drill seeding with diverse bunchgrasses rather than monocultures of nonnative bunchgrasses further inhibited *B. tectorum* and resulted in fewer, less frequent fires with longer fire return intervals. To achieve the goal of minimizing the risk of fire in *A. tridentata* subsp. *wyomingensis* communities, managers should drill seed larger areas after a fire using a diverse assemblage of native grasses.

Acknowledgements

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Chapter 1: The effects of fire history, post-fire rehabilitation, and environmental factors on shrub steppe communities

Abstract

Currently, ~50% of the sagebrush steppe in the Great Basin, USA, has been lost to land use change, plant invasions, and altered fire regimes. These threats warrant potential rehabilitation treatments in order to maintain native plant communities; however, little research exists on the effects of rehabilitation treatments on native communities across landscapes. We examined plant communities in a landscape mosaic of fire and rehabilitation histories understand the impact of fire, rehabilitation, and the environment on plant community composition and diversity. Fire records from the Bureau of Land Management indicated sites had burned 0-6 times between 1955-2015. We found that sites that shared the same fire history and recent rehabilitation approach were somewhat similar in composition, but environmental characteristics, such as climate, elevation, and soil texture, explained about 41% of the variation in plant cover and density. Fire and rehabilitation history explained an additional 44% for plant cover, but only 12% for plant density. Time between the two most recent fires, as well as the number of treatments and time since last fire and rehabilitation treatment, were important for plant cover; time since first and most recent fire were important for predicting plant density. The total number of fires had an inconsistent effect on plant communities suggesting rehabilitation choices and the environment interact to shape plant communities after a fire. Native plant species richness and diversity generally increased with elevation, regardless of rehabilitation treatments, except when sites were aerially seeded after six fires. Nonnative species richness was unchanged with elevation and

represent a combination of species introduced by rehabilitation and invasive species. Drill seeding treatments are effective at low elevations sites to prevent domination by *Bromus tectorum*. The time that elapsed between fires, post-fire rehabilitation history, and climate were important indicators of the plant community that will establish after a fire and should be considered when evaluating the need for rehabilitation after a fire

Keywords

Post-fire rehabilitation, *Bromus tectorum*, *Artemisia tridentata* ssp. *wyomingensis*, *Poa secunda*, *Agropyron cristatum*, climate, elevation, plant communities.

Introduction

Globally, the number of days with dry, hot weather has increased in recent decades and is correlated with increases in wildfire number and size (Goetz et al. 2007, Jolly et al. 2015). Climate change models using the Keetch-Byram Drought Index suggest increased fire potential throughout South America, Australia, and the United States (Liu et al. 2010), but may be worse in northern latitudes (Krawchuk et al. 2009). Many regions in the western United States have already seen increases in fire size and number between 1984 and 2011 (Dennison et al. 2014) and fire frequency has increased across the Great Basin since the 1980s (Balch et al. 2013). Both fire frequency (Abatzoglou and Kolden 2011, Bradley et al. 2018) and the number of large wildfires (Barbero et al. 2015) in the western United States are predicted to increase with future climate change coupled with annual grass range expansion. Wildfire is a substantial threat to ecosystems in western rangelands and reducing

the “likelihood, size, and severity of rangeland fires” is a key goal of the Integrated Rangeland Fire Management Strategy (Jewell 2015b).

The sagebrush steppe is a common vegetation type in the Great Basin (Bradley and Mustard 2008). Historically, sagebrush steppe dominated 45 million hectares of the western United States (West 1999). For much of the twentieth century, sagebrush was thinned or completely removed and replaced with nonnative grasses to increase perennial grass forage for cattle grazing (Pellant and Lysne 2005). In addition, overgrazing has reduced diversity and allowed nonnative species to invade portions of these ecosystems (Blaisdell et al. 1982, Yens 1982). Approximately 50% of the sagebrush steppe has been replaced by agricultural land, towns, or other anthropogenic uses (Welch 2005). Since the 1980s, fire rotation has decreased in sagebrush steppe throughout the Great Basin and Snake River plain (Baker 2013) In the Snake River Plain fire rotation was historically 120-240 years, but is current 61-86 years (Baker 2013).

A significant contributing factor to increasing fire size across the western United States is alterations of fine fuel from invasive, annual grasses (Brooks et al. 2004). In the Great Basin, *Bromus tectorum* L. (cheatgrass, here after *Bromus*) has substantially altered fire regimes, leading to changes in fire size, frequency, and duration with 39 of the 50 largest fires from 2000-2009 starting in *Bromus* dominated ecosystems (Balch et al. 2013). *Bromus* recruits well after disturbance and fires (West and Hassan 1985, Peterson 2005), creates continuous, highly flammable fuels that aid the spread of fire (Brooks et al. 2004), and promotes further *Bromus* recruitment. Even low *Bromus* cover will increase the chance of adjacent native dominated communities burning in subsequent fires (Link et al. 2006). Additionally, some models suggest that climate change will increase the risk of *Bromus*

invasion in Idaho, Montana, and Wyoming (Bradley 2009). Thus, reducing *Bromus* cover and increasing ecosystem resistance to future invasion are important land management goals (Baker 2006, Chambers et al. 2014b, Chambers 2014, Jewell 2015a).

The Integrated Rangeland Fire Management Strategy and Secretarial Order 3336 indicated that post-fire rehabilitation plans should include the goal of reducing fine fuels from invasive, annual grasses (Jewell 2015a). The most common seeding methods include drill and aerial seeding, which are typically done in the fall or winter after the fire. Drill seeding creates a physical disturbance that could provide microsites for *Bromus* recruitment; the efficacy of aerial seeding has been called into question and lacks adequate examination of treatment effectiveness. In general, we know little about the effectiveness of these post-fire treatments on reducing annual plant invasions across landscapes, especially those with complex mosaics of fire, rehabilitation, and management history.

Climate plays a substantial role in determining plant species composition, productivity, and competitive interactions (Reever Morghan et al. 2007). Even small changes in the amount or seasonal timing of precipitation can alter plant communities in desert systems (Shreve 1942). found shifting precipitation regimes may favor cold-adapted species in the Sonoran Desert. Studies in the Great Basin Desert suggest plant communities at higher elevations with more mesic climates are more resistant to invasion and resilient to fire (Chambers et al. 2007, Chambers et al. 2014a). Maestas et al. (2016) suggested using a Soil Temperature and Moisture Regime (STMR) index as a proxy to predict potential restoration success in the sagebrush steppe.

Few studies have examined the impact post-fire rehabilitation or other vegetation treatments have had on shrub-steppe plant communities. Attempts to synthesize the effects

of fuels treatments on fire severity, fire behavior, and subsequent fuels in rangelands have been limited to a few small-scale experiments (Hudak et al. 2011, Martinson and Omi 2013). More recently, research using prescribed fire followed by rehabilitation on small scales or analyzing landscape level trends have resulted in insights but are hampered by limitations. For instance, wildfires in sagebrush steppe typically occur in the summer; however. research using prescribed fire are small scale and typically burned in early autumn (Seefeldt et al. 2007, Diamond et al. 2012, Bates and Davies 2014, Davies et al. 2016) or spring (Rau et al. 2008) when weather is cooler and more humid, which likely results in a lower intensity fire. Other research has focused on the effects of seed source (Brabec et al. 2015), environmental variables (Germino et al. 2018), or rehabilitation techniques (Ott et al. 2017) on *Artemisia* species. Recent research on post-fire rehabilitation on fuels and plant communities after wildfires at landscape scales have provided interesting insights (Wirth and Pyke 2011, Arkle et al. 2014, Knutson et al. 2014, Shriver et al. 2018) but are limited to sites that have only burned a single time since 1970 when much of the landscape has burned repeatedly

We examined the effects of fire history, post-fire rehabilitation, and environmental variables on *Artemisia tridentata* subsp. *wyomingensis* plant communities. We measured plant cover and density to determine the effects of repeated wildfire and rehabilitation type on plant communities along elevation and climatic gradients. We predicted that 1) fire and rehabilitation history would influence the dominant plant community, 2) fire and rehabilitation treatment history would be more influential than environmental variables in determining the dominant species in each plant community, 3) native species richness and diversity would increase with elevation regardless of fire or rehabilitation treatment history, and 4) nonnative species richness would decrease as elevation increased.

Methods

Site Description

The study area was located in southern Idaho, USA, in the Snake River Plain and Northern Basin and Range ecoregions (Figure 1) with sites located at elevations ranging from 770 - 1786 m. The 30-year (1981-2010) mean annual precipitation for study sites ranged from 22 - 36 cm, with mean annual temperatures ranging between lows of -2.3 - 3.5 °C and maximum temperatures of 14.5 - 18.8 °C (PRISM 2014). Precipitation in the region during the two study years was similar (18.27 cm in 2013-2014; 18.18 cm in 2014-2015), but the timing of rainfall events differed. In 2013-2014, most of the rain fell between January and May 2014 in a unimodal distribution. In 2014-2015, precipitation had a bimodal distribution with most rain falling from August 2014 – February 2015 with very little rain falling in spring until a second spike in rainfall in May 2015. Historically, the dominant vegetation type was Wyoming sagebrush steppe (*Artemisia tridentata* subsp. *wyomingensis* Beetle & Young, hereafter *Artemisia*) in various successional stages; since the mid twentieth century, much of the area has been dominated by both native and nonnative perennial bunchgrasses, as well as annual grasses, such as *Bromus*. The most common plant species across the study area included *Poa secunda* J. Presl (hereafter *Poa*), *Bromus tectorum* L. (hereafter *Bromus*), *Agropyron cristatum* (L.) Gaertn. (hereafter *Agropyron*), *Elymus elymoides* (Raf.) Swezey (hereafter *Elymus*), *Phlox aculeata* A. Nelson, and *Pseudoroegneria spicata* (Pursh) Á. Löve. (see full species list in Appendix A, Table 1.A1).

Data Collection

We collected geospatial datasets spanning 209,000 ha of sagebrush steppe on Bureau of Land Management (BLM) land (Figure 1). We compiled spatial data on rehabilitation treatments from four sources: the BLM National Operations Center (NOC) from Inside Idaho (http://inside.uidaho.edu); BLM field offices; Mountain Home Air Force Base; and the USGS Land Treatment Data Library (https://ltdl.wr.usgs.gov) (Table 1.A2). We obtained BLM fire perimeters from 1900-present from Inside Idaho (http://inside.uidaho.edu). Historic vegetation and general soil texture was obtained from SSURGO data on the Ecoclass Name attribute of the that included a general description of soil texture (Table 1.A2).

We created 2,000 random points throughout the study area (ArcGIS 10.1) and eliminated sites that were in water bodies, agricultural fields, and on private property. We extracted fire history and rehabilitation history at the remaining 1,200 points. We selected 68 sites stratified by the number of times burned since 1958 and most recent rehabilitation method. We chose treatment combinations based on the number of times burned (0, 1, 2, 3, 6) and whether they were untreated (N), drilled (D), or aerially (A) seeded after the most recent fire. We attempted to distribute the fire and rehabilitation treatment combinations (e.g.- 1N = untreated after one fire) across precipitation and elevation gradients (Figure 1.1); however, there was significant spatial autocorrelation (Moran's I, $Z = 10.65$, $P < 0.001$) suggesting sites with similar fire-treatment combinations were clustered within a region of the study area, particularly unburned sites and sites that burned six times.

We sampled plants at 68 sites each year in the summer of 2014 and 2015 with four to six sites for each fire-rehabilitation treatment combination. Fifty-six sites are characterized by mesic, aridic soils with low potential for resistance to *Bromus* and resilience to fire

(Maestas et al. 2016), five sites had moderate resistance and resilience, and seven sites had high resistance and resilience. Sites were sampled in 2014 and 2015 using three parallel 30 m line-point intercept transects spaced 30 m apart and all vegetation and ground cover data was recorded every 10 cm (Herrick et al. 2017). We calculated plant cover for herbaceous and woody species using the line point intercept data for each species by summing all vascular plant cover. Perennial herbaceous plant density was estimated using five- 1 m^2 quadrats. Annual plant species density was estimated using a Daubenmire quadrat (20x50 cm) placed within the 1 m^2 quadrat. Shrub species density was calculated using 2 m belt transects on each side of the 30 m transect. Species area curves suggested that the sampling effort was adequate to maximize species composition (data not shown).

Statistical Analysis

We used a partial Mantel test to determine whether plant cover and density collected in 2014 and 2015 were similar and could be pooled (McCune and Mefford 2016; MjM Software, Gleneden Beach , OR). A multiple response permutation procedure (MRPP) was used to test for homogeneity in plant communities based on plant cover and density. We used a Jaccard distance measure to deemphasize the impact of the ubiquitous species on the analysis of within-group homogeneity. We analyzed the within-group homogeneity for sites with similar numbers of fire and most recent post-fire rehabilitation treatment. In MRPP, the A-statistic determined if groups were more similar than expected by chance. When $A > 0$, groups were more homogenous; when $A < 0$, groups were more heterogeneous than expected by chance. We corrected p-values for multiple comparison tests using the Benjamini and Yekutieli False Discovery Rate (B-Y FDR) method (Narum 2006).

Nonmetric multidimensional scaling (NMS) was used to plot sites within the species space and determine the most important variables that correlated with each axis of the ordination (McCune and Mefford 2016; MjM Software, Gleneden Beach , OR). The NMS was run using the slow and thorough autopilot mode with a random starting location and Jaccard distance measure to increase agreement with the MRPP results. A Monte Carlo test was used to determine if the NMS solution extracted stronger axes than those expected by chance. There were 250 iterations for both the observed and randomized data. We deleted species found on fewer than 5% of the sites (McCune and Grace 2002), resulting in an analysis with 29 species for cover and 28 species for density. The secondary matrix had 24 variables, including the environmental characteristics, fire history, rehabilitation history and a categorical treatment variable (Table 1.A2).

Species richness and the inverse Simpson diversity index were calculated using density data (Morris et al. 2013). We used General Linear Models (GLM) to determine if there were significant differences in richness and diversity among sites that differed in the number of fires and recent post-fire rehabilitation seeding effort. Since unburned sites are not aerially seeded and drill seeding did not occur on sites with six fires, we analyzed those sites separately. Sites with 1-3 fires were kept in a single analysis that included fire number as a term in the analysis. A GLM was also used to analyze the effect of treatment and elevation on native and nonnative species richness.

Results

Fire and Rehabilitation

The partial Mantel test indicated communities were significantly similar in 2014 and 2015 for cover ($r = 0.60$, $p < 0.001$) and density ($r = 0.39$, $p < 0.001$); therefore, 2014 and 2015 data were pooled. In the MRPP, there was significant within group homogeneity of plant communities based on plant cover ($A = 0.19$, $p < 0.0001$). The average distance for each group ranged from 0.13-0.67 with 6 of the 13 treatments having a distance greater than 0.45, indicating considerable variation among sites within each treatment. The large polygon area in the NMS ordination represented the variability in plant composition within fire and treatment combination. (Figure 1.2). The B-Y FDR correction for multiple comparisons resulted in $\alpha = 0.0101$. This conservative interpretation indicated that few of the plant communities among fire and treatment groups were significantly different from each other (Appendix A, Table 1.A3). Unburned, unseeded (0N) sites were significantly different from all other treatments. The dominant vegetation in unburned, unseeded (0N) sites included *Poa*, *Artemisia*, and moss, with minimal *Bromus* cover (Table 1.1). Unburned, historically drilled sites (0D) were only different from sites aerially seeded after one or three fires (1A, 3A, respectively). The overlapping polygons in the NMS ordination reflect the similarity in plant communities among fire and rehabilitation groups (Figure 1.2 A,C,E). Since plant communities on burned sites were generally indistinguishable from each other regardless of the number of burns or treatment type, they were pooled together to assess patterns of the dominant species *Agropyron*, *Bromus*, and *Poa* (Table 1.1). The cover of *Poa* and *Artemisia* decreased with drill seeding and fire while *Bromus* and *Agropyron* increased (Table 1.1). A less conservative interpretation ($\alpha = 0.05$) suggested unburned, drill seeded (0D) sites were

significantly different from all treatments except sites drilled after the first and second fire (Table 1.A3). Plant cover at the unburned, drill seeded sites (0D) was dominated by *Poa* and followed by *Artemisia* and *Agropyron* (Table 1.1). Sites aerially seeded after one fire (1A) were also significantly different from sites aerially seeded after the sixth fire (6A) (Table 1.A3).

There was weak, but significant, within group similarity of plant communities based on plant density ($A = 0.07$, $p < 0.05$). Though statistically significant and common, values of $A < 0.1$ do not suggest ecologically meaningful similarity within groups. None of the fire-rehabilitation treatments were significantly different at $\alpha = 0.0101$; the seven of the 78 treatment comparisons that were significantly different at $\alpha = 0.05$ but did not indicate a consistent trend (Table 1.A4). The average distance for each group ranged from 0.27-0.66 with 8 of the 13 treatments having a distance greater than 0.31, indicating considerable variation among sites within each treatment. The substantial overlap in plant communities as measured by density is shown in the NMS ordination (Figure 1.2 B,D,F). These results suggest species composition as measured by density did not differ among plants communities of different treatments.

Environmental Variables

We had insufficient sample size to run an MRPP that analyzed fire number, treatment type, and elevation categories together. To test the effect of elevation and rehabilitation treatments on plant communities, we ran the MRPP with sites divided into elevation categories spanning 250 m elevation bands (low (770-1020m), medium low (1021-1270m), medium high (1271-1520m), and high (1521-1780m) and ran a second analysis using fire number and elevation together. We dropped drilled sites at low and high

elevations from the analysis because each had a sample size of one. This resulted in ten rehabilitation-elevation treatment combinations. The within-group agreement was strong for plant cover (A= 0.24, P < 0.0001) and density (A= 0.25, P < 0.0001) confirming better within group similarity. The average distance for each elevation-rehabilitation treatment grouping were smaller than fire-rehabilitation groups. The average group distance was greater than 0.45 for only one of ten elevation-rehabilitation categories for plant cover and four of ten treatments for plant density. Smaller average group distances indicated greater similarities in plant communities when grouped by rehabilitation treatment and elevation together than with fire and rehabilitation treatment.

The NMS ordination yielded a three-axis solution that explained most of the variation in plant cover among communities ($r^2 = 0.85$, $p = 0.004$, Table 1.2). The final stress and instability of the model was 11.75 and 0.00001, respectively. In general, communities measured by cover separated out by native perennial bunchgrasses, *Bromus*, and *Agropyron* (Figure 1.3A). The threshold for importance in contribution to each axis was set at ($r^2 \geq 0.1$). Axis one explained most of the variation ($r^2 = 0.41$) and was correlated with maximum and minimum temperature, precipitation, elevation, soil texture, and soil temperature and moisture regime (Table 1.2). Axis 2 explained a moderate amount of variation ($r^2 = 0.27$) and was weakly correlated with the number of rehabilitation treatments, number of aerial seedings, and time between the last two fires. Axis 3 explained the least amount of variation ($r^2 = 0.17$) and was correlated with soil temperature and moisture regime, historic site vegetation, time since last rehabilitation treatment, time since first aerial seeding, time since last aerial seeding, time since first fire, time since last fire, and time between last two fires.

The NMS ordination explained most of the variation in density among plant communities ($r^2 = 0.80$, $p = 0.004$, Table 1.3). The final stress for the NMS ordination with three axes was 10.85 with an instability of <0.0001. Patterns of species distribution in the ordination space was less clear for plant density. For density, communities mostly separated out by native species, *Bromus*, and *Agropyron* (Figure 1.3B). Similar to plant cover, axis one explained the most variation ($r^2 = 0.41$) and was correlated with the same six environmental variables as Axis 1 in the NMS of plant cover (Table 1.3). Axis 2 explained some variation ($r^2 = 0.27$) but did not significantly correlate with any variables. Axis 3 explained the least amount of variation ($r^2 = 0.12$) and was weakly correlated with minimum temperature, precipitation, elevation, soil temperature and moisture regime, time since first fire, and time since last fire.

There was considerable variation within groups based on the number of fires and rehabilitation types in the NMS for both cover and density. Since the groups were skewed along Axis 1 with climate, soil texture, and elevation (Figure 1.2). We reexamined the ordination by grouping sites using the four elevation categories used in the MRPP; however, the number of groups exceeded the maximum allowable for graphing the ordination. Therefore, we dropped fire number and grouped the sites by post-fire rehabilitation and elevation category, yielding twelve combinations (e.g.- drill seeding at low elevation), and the convex hulls within the ordination appeared smaller, suggesting stronger within group similarity when sites were grouped by elevation and rehabilitation treatment. Plant communities partially overlapped between 1021 m and 1520 m for all treatments for both plant cover and density (Figure 1.5A-F). Low and high elevation sites were generally distinct from the medium low and medium high elevation ranges, with the exception that

plant density at aerially seeded sites overlapped with the medium low and medium high elevation sites (Figure 1.5D). Drill seeded sites at low and high elevation had a sample size of one, meaning convex hulls could not be made; however, they were included in the NMS as single points (Figure 1.5E,F).

Species Richness and Diversity

There were significant effects of rehabilitation treatment, elevation, and their interaction on plant species richness, but the patterns varied by the number of fires (Table 1.4). For unburned sites and sites that burned 1-3 times, total species richness increased significantly with elevation (Figure 1.6A-D). Rehabilitation, the number of fires, and their interactions were not significant for sites that were unburned or burned 1-3 times. At sites that burned six times, the relationship between elevation and species richness differed by rehabilitation type (Figure 1.6E). After six fires, species richness increased with elevation on untreated sites; in contrast, species richness decreased with elevation on aerially seeded sites (Figure 1.6E). However, only one sample point for aerially seeded sites at the higher elevation suggests caution in interpretation.

The relationship between rehabilitation treatment, elevation, and the number of fires for Simpson's diversity were less clear. There was no significant effect of rehabilitation treatment or elevation on unburned sites (Table 1.5; Figure 1.7A). However, Simpson's diversity generally increased with elevation at sites that burned 1-3 times (Table 1.5; Figure 1.7B-D) with a few exceptions. Untreated sites after one fire had only a slight increase that may have been influenced by an outlier (Figure 1.7B). After the second fire, the Simpson diversity index at drilled and aerially seeded sites was nearly unchanged by elevation (Figure 1.7C). Simpson's diversity varied significantly among post-fire treatments on sites

that burned six times, where diversity for aerially seeded sites decreased with elevation, while untreated sites increased with elevation (Figure 1.7E).

There was a significant difference in native and nonnative species richness along the elevation gradient (Table 1.6). Native species richness increased with elevation (Figure 1.8). Despite a doubling in the number of native species at the highest elevations, nonnative species richness was largely unaffected by elevation (Figure 1.8). Fire and rehabilitation treatment type did not significantly affect native or nonnative species richness and did not interact with species type or elevation (Table 1.6).

Discussion

Fire and post-fire rehabilitation have the potential to homogenize plant communities. Indeed, the effects of fire and/or rehabilitation shifted community dominance away from *Artemisia* and *Poa* to communities dominated by *Poa*, *Agropyron*, and *Bromus*. *Artemisia tridentata* subsp. *wyomingensis* is not well-adapted to fire (Welch and Criddle 2003, Baker 2006, Cooper et al. 2007) and was often reduced by drilling treatments that started in the 1950s to plant *Agropyron* (Pellant and Lysne 2005, Gunnell et al. 2011). In addition, *Agropyron* tends to outcompete many native species (Marlette and Anderson 1986, Pendery and Provenza 1987, Welch and Criddle 2003, Pellant and Lysne 2005, Gunnell 2009). Although fire and seeding reduced *Poa*, *Poa* maintained dominance in the community.

At burned sites, *Poa* and *Agropyron* were retained while *Bromus* became established; all three species are known to be resilient to fire (Wright and Klemmedson 1965, Pehrson and Sowell 2011, Miller et al. 2013). *Bromus* has been present on Idaho rangelands since the 1920s (Yens 1982), directly inhibits native species (Booth et al. 2003,

Ogle et al. 2003), and alters fire regimes leading to a further loss of native species. *Poa* is competitive enough with *Bromus* (Goergen et al. 2011) that *Poa* can persist as *Bromus* cover increases after a fire. “Hycrest” crested wheatgrass, a common cultivar of *Agropyron* in this study area, is a better competitor against *Bromus* than some deep-rooted native perennial bunchgrasses (Aguirre and Johnson 1991), and *Agropyron desertorum*, formerly identified as a subspecies of *Agropyron cristatum*, can inhibit *Bromus* reproduction and growth (Yoder and Caldwell 2002). In some cases, the loss of many native forbs and grasses with repeated burning and the persistence of *Bromus*, *Poa*, and *Agropyron* often result in a less diverse community.

Bromus often increases in the years immediately following a fire (West and Hassan 1985, Bates and Davies 2014) and is reported to be a primary driver of fire regime change in the Great Basin (Link et al. 2006, Balch et al. 2013, Bradley et al. 2018). *Bromus* cover in our sites increased with more time between recent fires. Similarly, Bagchi et al. (2013) found that *Bromus* cover increased until reaching its peak cover for 8-10 years after a fire. These results suggest *Bromus* has a lag time before it dominates the landscape, which may be an opportune time to seed with native species. We found drill seeding inhibited *Bromus* below 1500 m and drill seeding after subsequent fires may maintain ecosystem resistance to *Bromus*. Sites that were drill seeded prior to the most recent fires were also less likely to be dominated by *Bromus*, even when there was no recent post-fire rehabilitation or the site was aerially seeded after the most recent fire. found post-fire rehabilitation after a single fire had inconsistent effects on *Bromus* cover, but a second rehabilitation treatment after a second fire that burned eight years later significantly decreased the relative cover of *Bromus*. Sites above 1500 m with no history of post-fire rehabilitation had highly diverse, native

communities even after fire, suggesting higher elevation sites may recover well on their own and not require seeding. Low diversity is common in sites dominated by *Agropyron* (Knutson et al. 2014, Williams et al. 2017), as native species have difficulty establishing in *Agropyron* stands (Pellant and Lysne 2005). Therefore, seeding unnecessarily with *Agropyron* may negatively impact native plant community diversity.

Many aerially seeded sites were drill seeded with *Agropyron* and *Poa* prior to the most recent fire (Pilliod and Welty 2013). Our results suggest that *Agropyron* may continue to remain dominant at higher elevations without multiple drilling; however, sites below 1500 m benefited from drill seeding even after 2-3 fires. Aerial and unseeded sites were more likely to be dominated by *Bromus* at lower elevations. Mature *Agropyron* can decrease *Bromus* cover, density, and biomass but will not exclude *Bromus* completely (Leffler et al. 2014, Davies and Johnson 2017). *Bromus* reduces *Agropyron* growth (Aguirre and Johnson 1991) and hinders *Agropyron* recruitment (Shown et al. 1969). Swanson et al. (2018) found vegetation in burned areas varied considerably but were more likely to be dominated by nonnative forbs and *Bromus*. Our research suggests a possible mechanism for this conversion in managed rangelands. Sites with a history of drill seeding maintained *Poa* and *Agropyron* dominance after one fire; however, several subsequent fires without drill seeding treatments resulted in a shift toward an ecosystem dominated by *Bromus* below 1500 m.

Environmental variables, such as climate and elevation, were primary influences on plant communities with rehabilitation treatments playing a secondary role. Plant communities within rehabilitation treatments were more similar when nested within elevation ranges than the number of fires. For instance, high elevation sites were dominated by native plant species, but when *Agropyron* species were used in drill seeding treatments

above 1500 m, *Agropyron* tended to dominate the community. Knutson et al. (2014) found sites drill seeded with *Agropyron* species only established and dominated sites above 1300 m, while *Bromus* was the dominant species at lower elevations. Higher elevation *Artemisia tridentata* subsp. *vaseyana* communities have greater plant cover, density, and biomass than drier, low elevation *Artemisia* communities (Davies and Bates 2010) likely increasing the competitive advantage for non-native species. Chambers et al. (2014b) described greater resistance to *Bromus* invasion in *A. tridentata* subsp. *vaseyana* than *A. tridentata* subsp. *wyomingensis* communities and contributed this resistance to greater access to moisture at high elevation.

Chambers et al. (2014b) suggested using the soil temperature and moisture regimes to evaluate the likelihood of rehabilitation success, where there is greater resistance to invasion and resilience to fire in cooler, more mesic regions. In addition, Maestas et al. (2016) and Miller et al. (2013) indicated climate and prior vegetation determined plant community composition and suggested using soil temperature and moisture regimes, as well as ecological site descriptions, to make decisions on appropriate rehabilitation. Our current work confirms that climate is important, but using elevation, temperature, or precipitation data may suffice at local scales for land managers.

Species richness and diversity generally increased along the elevation gradient in our study. Greater diversity has been seen in higher elevation *A. tridentata* ssp. *vaseyana* communities (Davies and Bates 2010); similarly, our study found an increase in diversity with elevation in *A. tridentata* subsp. *wyomingensis* communities. Moody and Meentemeyer (2001) found greater species richness in California chaparral ecosystems on sites with limited soil moisture, but we found that sites with greater precipitation had greater species

richness and higher diversity. There are two likely reasons for the discrepancy between our study and Moody and Meentemeyer (2001). First, the increase in species diversity was due to an increase in native species as sites became more mesic. Most native plants species in this study area were perennial and require time to mature before they reproduce. More time since a fire and fewer fires would allow perennial native plants to establish and disperse. In arid climates, even small increases in precipitation can affect plant establishment and survivorship (Angert et al. 2007, Angert et al. 2009, Angert et al. 2010). In our study, invasive species composition changed along the environmental, but the number of species did not change. Second, in addition to greater access to moisture, higher elevation sites suffered fewer fires and less disturbance from post-fire rehabilitation. The conditions at these sites correspond to the intermediate disturbance hypothesis, which predicts the greatest diversity and evenness at intermediate rates of disturbances (Roxburgh et al. 2004, Svennson et al. 2007).

Native species richness increased with elevation while nonnative species richness did not. Others have found greater species diversity at higher elevations in a variety of different ecosystems (Moody and Meentemeyer 2001, Davies and Bates 2010, Chambers et al. 2014b). The increase in native species richness is likely the result of differences in the post-fire rehabilitation and fire history. Bunchgrasses and forbs native to *A. tridentata* subsp. *wyomingensis* communities did not evolve with frequent fire (Wright and Klemmedson 1965, West and Hassan 1985, Welch and Criddle 2003). When sites are drill seeded, few species were used in the seed mix, several of which may be nonnative, decreasing native plant species richness. Further, *Agropyron* was used in many of the seed mixes in this study area, a nonnative species which outcompetes native species and lowers the likelihood of

native bunchgrass establishment (Knutson et al. 2014). Since there were fewer fires, less rehabilitation, and fewer sites with *Agropyron* at elevations above 1300 m, native species were able to recruit and flourish there after a fire.

Several results from this study may assist land management. More post-fire rehabilitation at low elevations in historically *Artemisia tridentata* ssp. *wyomingensis* sites, particularly drill seeding, will decreased the likelihood that *Bromus* would dominate the plant community. Though some *Bromus* is likely on established bunchgrass sites, precluding rehabilitation after two or three fires allows *Bromus* to begin to convert the site into an annual grassland especially at low elevations. This suggests drill seeding is still beneficial past the third fire. The number of times a site burned was relatively unimportant in determining plant community composition after the first fire removed *Artemisia* and shifted the plant community to a grassland. Time since rehabilitation treatment was more important to plant community composition, as indicated in the NMS ordination. Land managers may consider drill seeding former *Artemisia tridentata* ssp. *wyomingensis* communities that have not been seeded for extended periods regardless of the number of fires. Though recent work suggests the use of a soil temperature and moisture regime indicates the likelihood of rehabilitation success at very coarse scales, PRISM climate data correlated strongly to the plant communities within *A. tridentata* subsp. *wyomingensis* ecological sites. Thus, at local scales, using PRISM 30-year mean precipitation or average maximum temperature complements the soil temperature and moisture regime framework and may be adequate to predict rehabilitation success within a plant community.

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Tables

Table 1.1 Percent cover for dominant species and functional groups among treatments indicated as significantly different by the MRPP. Burned sites since 1950 include all three rehabilitation treatments pooled together.

Cover Type	Unburned, Untreated	Unburned, Drilled	Burned
Poa secunda	33	26	18
Other native bunchgrasses	3	3	3
Artemisia tridentata subsp. *wyomingensis*	24	11	0
Agropyron cristatum	0	11	21
All Forbs	0.7	0.3	1.5
Bromus tectorum	6	2	21

Table 1.2 Correlation coefficients for predictor variables and each axis in the NMS ordination for plant cover. The symbol in parenthesis indicate whether the variable had a positive (+) or inverse relationship with the axis. Bold values are $r^2 \geq 0.1$.

Predictor Variable	**Axis 1** r^2		**Axis 2** r^2		**Axis 3** r^2	
Environment Variables						
Temperature Maximum, Mean (T+)	**0.445**	(+)	0.041	(+)	0.009	(-)
Temperature Minimum, Mean (T-)	**0.352**	(+)	0.027	(+)	0.012	(+)
Precipitation (P)	**0.333**	(-)	0.027	(-)	0.063	(+)
Elevation (E)	**0.412**	(-)	0.038	(-)	0.01	(+)
Soil Texture (ST)	**0.344**	(+)	0.002	(+)	0.005	(-)
Soil Temperature Moisture Regime (STMR)	**0.273**	(+)	0.001	(+)	**0.109**	(-)
Ecological Site Vegetation (ESV)	0.064	(+)	0.001	(+)	**0.11**	(-)
Rehabilitation History						
Number of All RebahilitationTreatments (Tn)	0.002	(+)	**0.15**	(-)	0.052	(+)
Rehabiltation Treatment, Most Recent Type (R)	0.084	(+)	0	(+)	0.042	(-)
Last Rehabilitation Treatment, Time Since (tLT)	0.036	(+)	0.07	(+)	**0.248**	(-)
Aerial Seeding, Number of (An)	0.03	(-)	**0.108**	(-)	0.049	(+)
First Aerial Seeding, Time Since (t1A)	0.072	(+)	0.036	(+)	**0.145**	(-)
Last Aerial Seeding, Time Since (tLA)	0.071	(+)	0.068	(+)	**0.12**	(-)
Drill Seeding, Number of (Dn)	0.091	(+)	0.096	(-)	0.012	(-)
First Drill Seeding, Time Since (t1D)	0.025	(-)	0.053	(+)	0.038	(-)
Last Drill Seeding, Time Since (tLD)	0.013	(-)	0.085	(+)	0.064	(-)
Fire History						
Fire, Number of (F)	0.04	(+)	0.088	(-)	0.07	(+)
First Fire, Time Since (t1F)	0.029	(+)	0.003	(+)	**0.141**	(-)
Last Fire, Time Since (tLF)	0	(+)	0.058	(+)	**0.371**	(-)
Time Between Last Two Fires (t2RF)	0.021	(-)	**0.143**	(+)	**0.165**	(-)

Table 1.3 Correlation coefficients for predictor variables and each axis in the NMS ordination for plant density. The symbol in parenthesis indicate whether the variable had a positive (+) or inverse relationship with the axis. Bold values are $r^2 \geq 0.1$.

Predictor Variable	**Axis 1** r^2	**Axis 2** r^2	**Axis 3** r^2
Environment Variables			
Temperature Maximum, Mean (T+)	**0.52** (+)	0.05 (+)	0.09 (-)
Temperature Minimum, Mean (T-)	**0.40** (+)	0.05 (+)	**0.18** (-)
Precipitation (P)	**0.33** (-)	0.01 (-)	**0.12** (+)
Elevation (E)	**0.48** (-)	0.07 (-)	**0.11** (+)
Soil Texture (ST)	**0.29** (+)	0.01 (-)	0.00 (-)
Soil Temperature Moisture Regime (STMR)	**0.21** (+)	0.01 (-)	**0.14** (-)
Ecological Site Vegetation (ESV)	0.03 (+)	0.03 (-)	0.09 (-)
Rehabilitation History			
Total Number of All Treatments (Tn)	0.01 (-)	0.00 (-)	0.08 (-)
Rehabilitation Treatment, Most Recent Type (R)	0.02 (+)	0.02 (-)	0.00 (+)
Last Rehabilitation Treatment, Time Since (tLT)	0.03 (+)	0.01 (-)	0.07 (+)
Aerial Seeding (An)	0.04 (-)	0.00 (-)	0.04 (-)
First Aerial Seeding, Time Since (t1A)	0.05 (+)	0.00 (-)	0.03 (+)
Last Aerial Seeding, Time Since (tLA)	0.06 (+)	0.00 (-)	0.03 (+)
Drill Seeding, Number of (Dn)	0.02 (+)	0.00 (-)	0.06 (-)
First Drill Seeding, Time Since (t1D)	0.01 (-)	0.05 (+)	0.08 (+)
Last Drill Seeding, Time Since (tLD)	0.00 (-)	0.01 (+)	0.09 (+)
Fire History			
Fire, Number of (F)	0.03 (+)	0.01 (+)	0.09 (-)
First Fire, Time Since (t1F)	0.00 (+)	0.01 (+)	**0.14** (+)
Last Fire, Time Since (tLF)	0.00 (+)	0.00 (-)	**0.11** (+)
Time Between Last Two Fires (t2RF)	0.00 (+)	0.00 (-)	0.02 (+)

Table 1.4 General linear model for species richness responses to rehabilitation treatment, elevation, and number of fires. Rehab = rehabilitation; Elev = elevation; Fire = number of fires.

Source	*df*	MS	*F*	*P*
Unburned				
Rehabilitation	1	1.51827	0.48332	0.51
Elevation	1	64.60003	20.56448	**< 0.003**
Rehab x Elev	1	0.63517	0.20220	0.67
Error	7	3.14134		
1-3 Fires				
Fire	2	3.57560	0.48269	0.62
Rehabilitation	2	10.23251	1.38135	0.27
Elevation	1	134.57793	18.16745	**<0.001**
Fire x Elev	2	4.41533	0.59605	0.56
Fire x Rehab	4	3.48254	0.47013	0.76
Rehab x Elev	2	12.90219	1.74174	0.19
Fire x Rehab x Elev	4	2.73554	0.36929	0.83
Error	28	7.40764		
6 Fires				
Rehabilitation	1	25.70865	10.55927	**0.017**
Elevation	1	13.53777	5.56035	0.056
Rehab x Elev	1	29.78249	12.23252	**0.013**
Error	6	2.43470		

Table 1.5 General linear model for the Simpson's diversity index responses to rehabilitation treatment, elevation, and number of fires. Rehab = rehabilitation; Elev = elevation.

Source	*df*	MS	*F*	*P*
Unburned				
Rehabilitation	1	0.02580	3.74576	0.094
Elevation	1	0.01516	2.20003	0.182
Rehab x Elev	1	0.02525	3.66526	0.097
Error	7	0.00689		
1-3 Fires				
Fire	2	0.02124	0.73757	0.487
Rehabilitation	2	0.00821	0.28515	0.754
Elevation	1	0.47177	16.38662	**<0.001**
Fire x Elev	2	0.01996	0.69319	0.508
Fire x Rehab	4	0.05551	1.92815	0.133
Rehab x Elev	2	0.01627	0.56512	0.575
Fire x Rehab x Elev	4	0.05176	1.79771	0.157
Error	28	0.02879		
6 Fires				
Rehabilitation	1	0.11247	6.12165	**0.048**
Elevation	1	0.02690	1.46390	0.272
Rehab x Elev	1	0.08255	4.49309	0.078
Error	6	0.01837		

Table 1.6 General linear model for native versus nonnative species richness along the elevation gradient among sites that varied in fire number and recent post-fire rehabilitation. Species = Native vs Nonnative species; Treat = Fire-Rehabilitation treamtent; Elev = elevation.

Source	***df***	**MS**	***F***	***P***
Native-Nonnative Species	1	73.518	33.156	**< 0.001**
Elevation	1	85.778	38.685	**< 0.001**
Fire-Rehabilitation Treatment	12	2.655	1.198	0.30
Species x Elevation	1	98.103	44.243	**< 0.001**
Treat x Species	12	2.459	1.109	0.36
Treat x Elev	12	2.958	1.334	0.22
Species x Elev x Treat	12	2.368	1.068	0.40
Error	82	2.217		

Figures

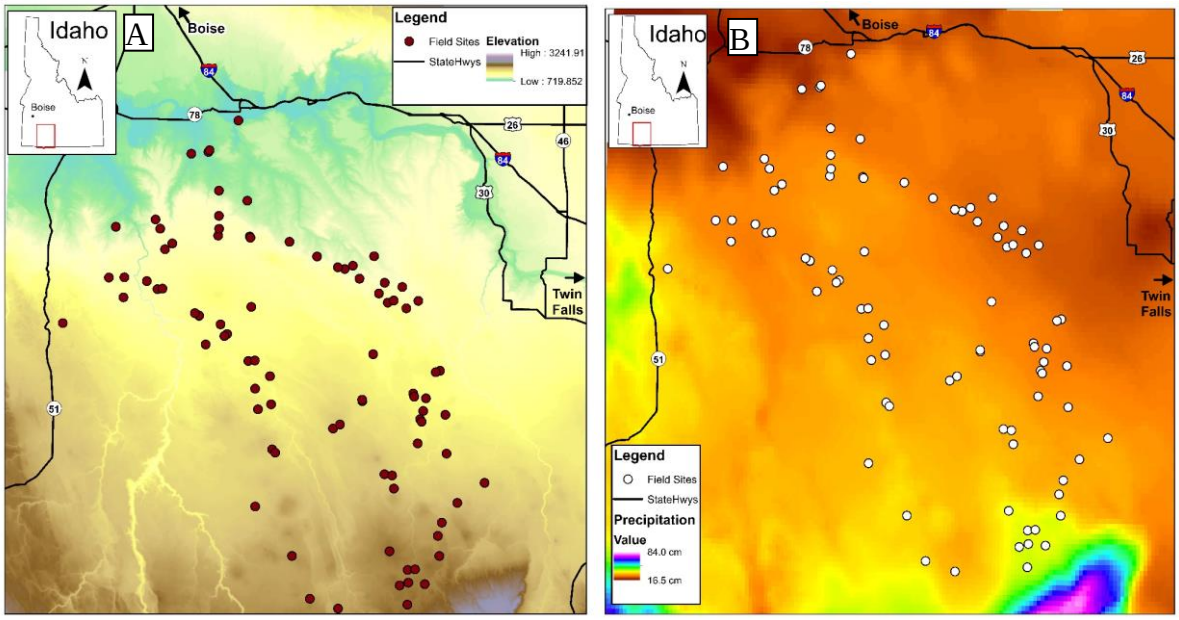

Figure 1.1 Sites were distributed along elevation (A) and precipitation (B) gradients within the study area.

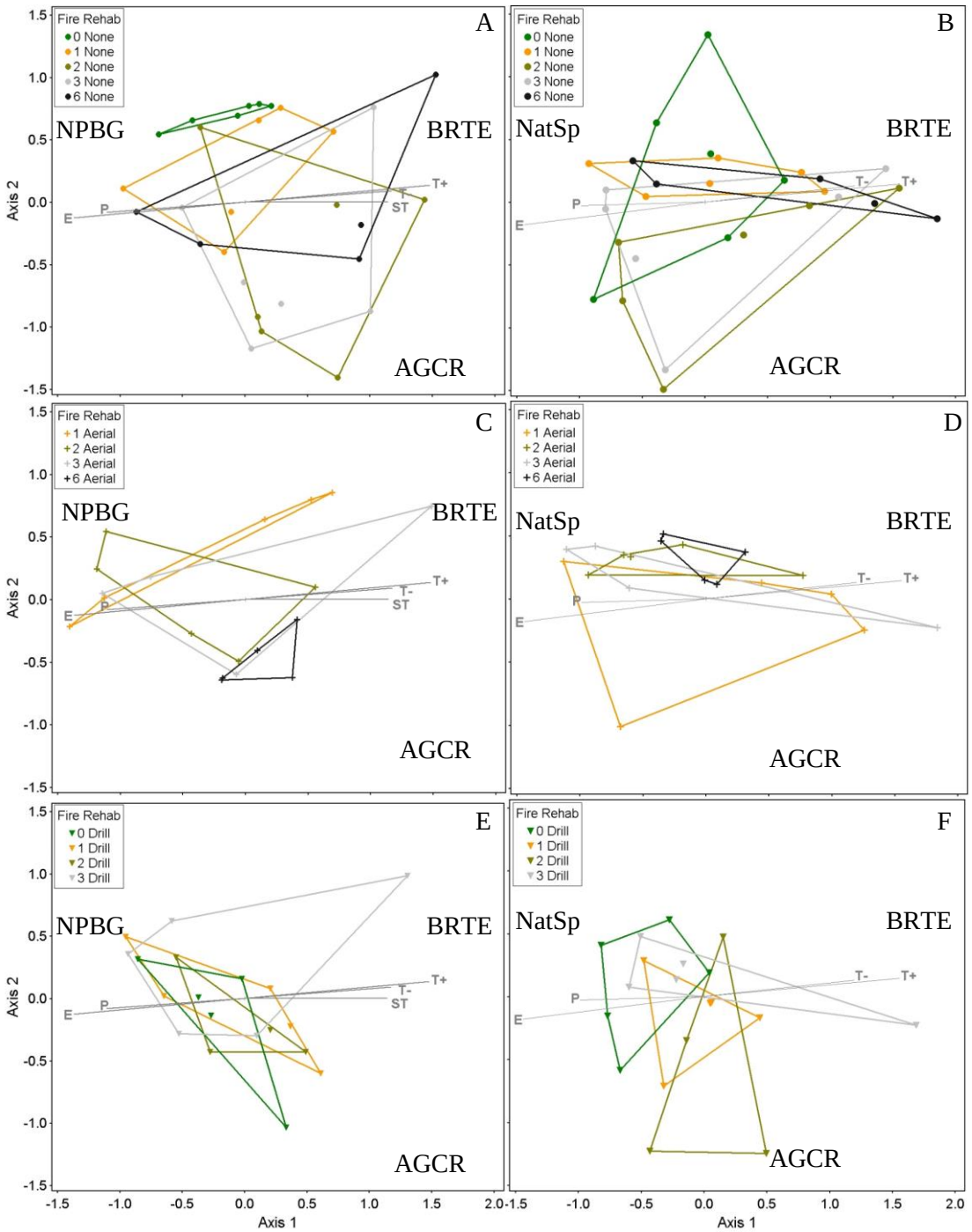

Figure 1.2 NMS ordination based on plant cover (A, C, E) and density (B, D, F) grouped by the number of fires (0, 1, 2, 3, 6) and the type of rehabilitation seeding done after the most recent fire (none, aerial, or drill). Each point represents the plant community for an individual site. Joint biplot of variables represents axis correlations ($r2 \geq 0.3$) for maximum (T+) and minimum (T-) temperature, precipitation (P), elevation (E) and soil texture (ST). Letters in gray indicate the dominant vegetation in each quadrant: native perennial bunchgrass (NPBG), Bromus (BRTE), Agropyron cristatum (AGCR), or native forbs and grasses (NatSp).

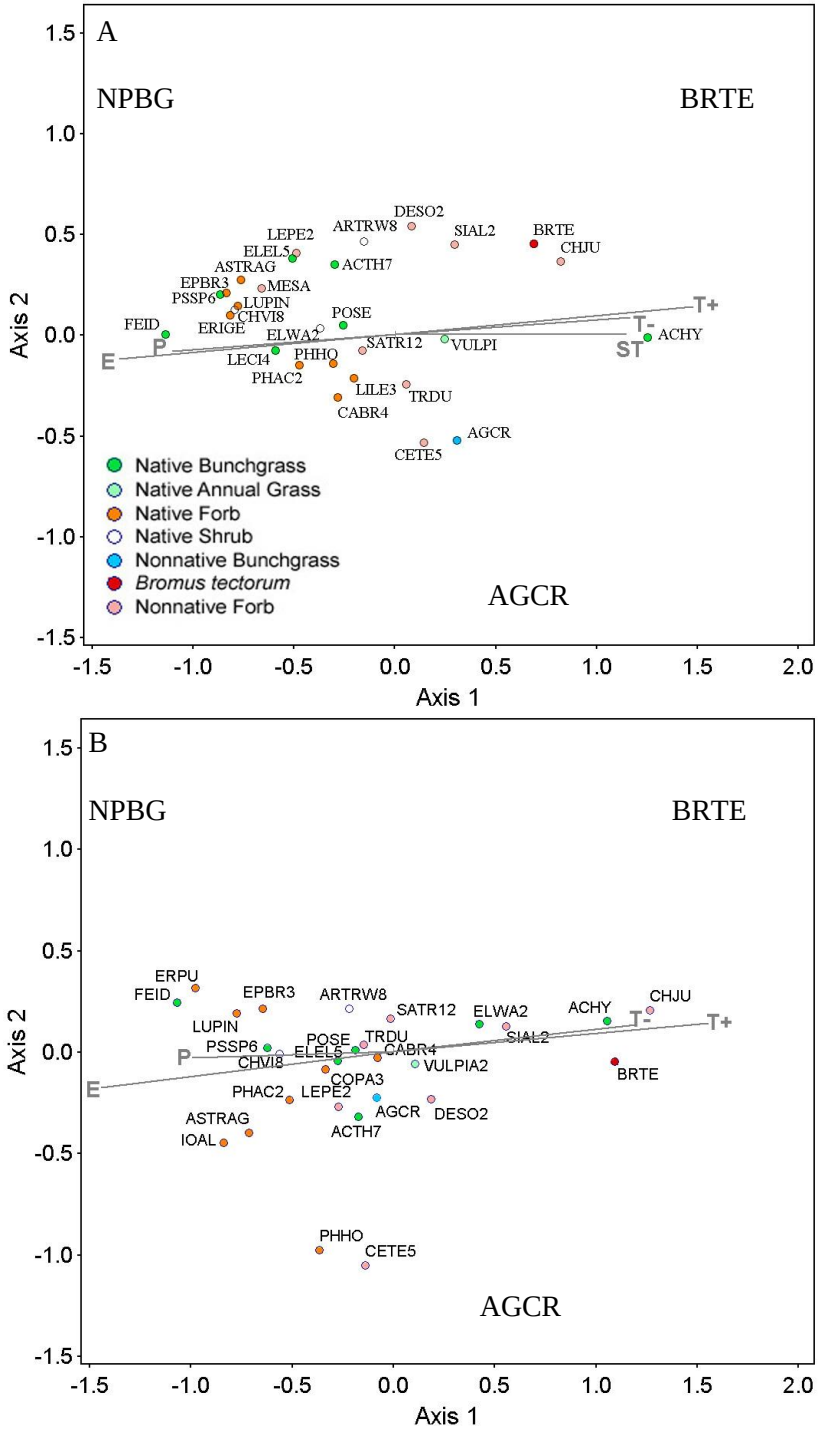

Figure 1.3 The species distribution for the NMS ordination for cover (A) and density (B). Letters in gray indicate the dominant vegetation in each quadrant: native perennial bunchgrass (NPBG), *Bromus* (BRTE), *Agropyron cristatum* (AGCR), or native forbs and grasses (NatSp). Environmental variables include: maximum (T+) and minimum (T-) temperature, precipitation (P), and elevation (E). Each point represents a plant species (see Table 1.A4for species codes). Joint biplot of variables represents axis correlations ($r^2 \geq 0.3$) for maximum (T+) and minimum (T-) temperature, precipitation (P), elevation (E) and soil texture (ST).

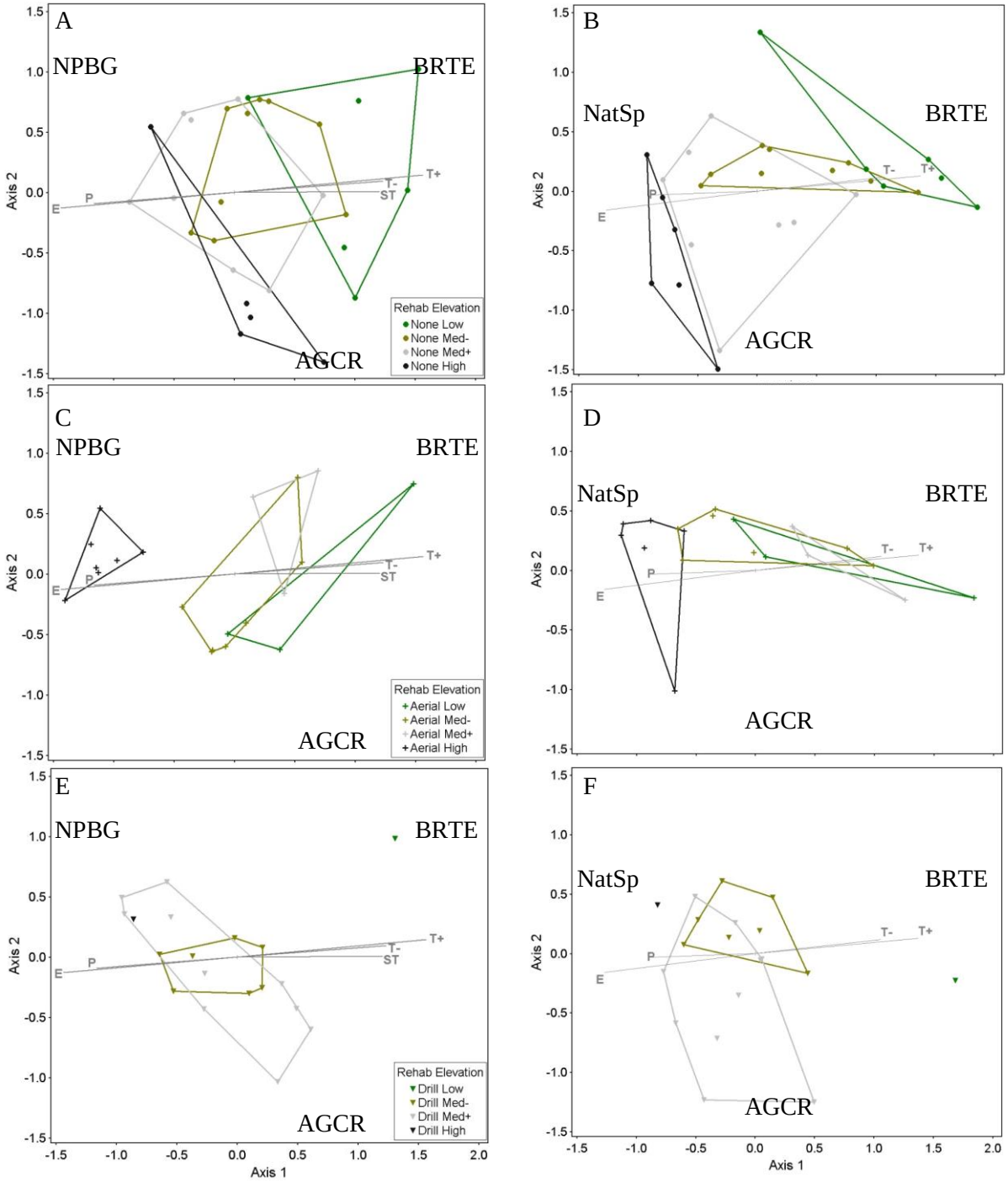

Figure 1.5 NMS ordination with sites grouped by most recent post-fire rehabilitation action and elevation for plant cover (A, C, E) and density (B, D, F). Letters in gray indicate the dominant vegetation in each quadrant: native perennial bunchgrass (NPBG), *Bromus* (BRTE), *Agropyron cristatum* (AGCR), or native forbs and grasses (NatSp). Each point represents the plant community for an individual site. Joint biplot of variables represents axis correlations ($r^2 \geq 0.3$) for maximum (T+) and minimum (T-) temperature, precipitation (P), elevation (E) and soil texture (ST).

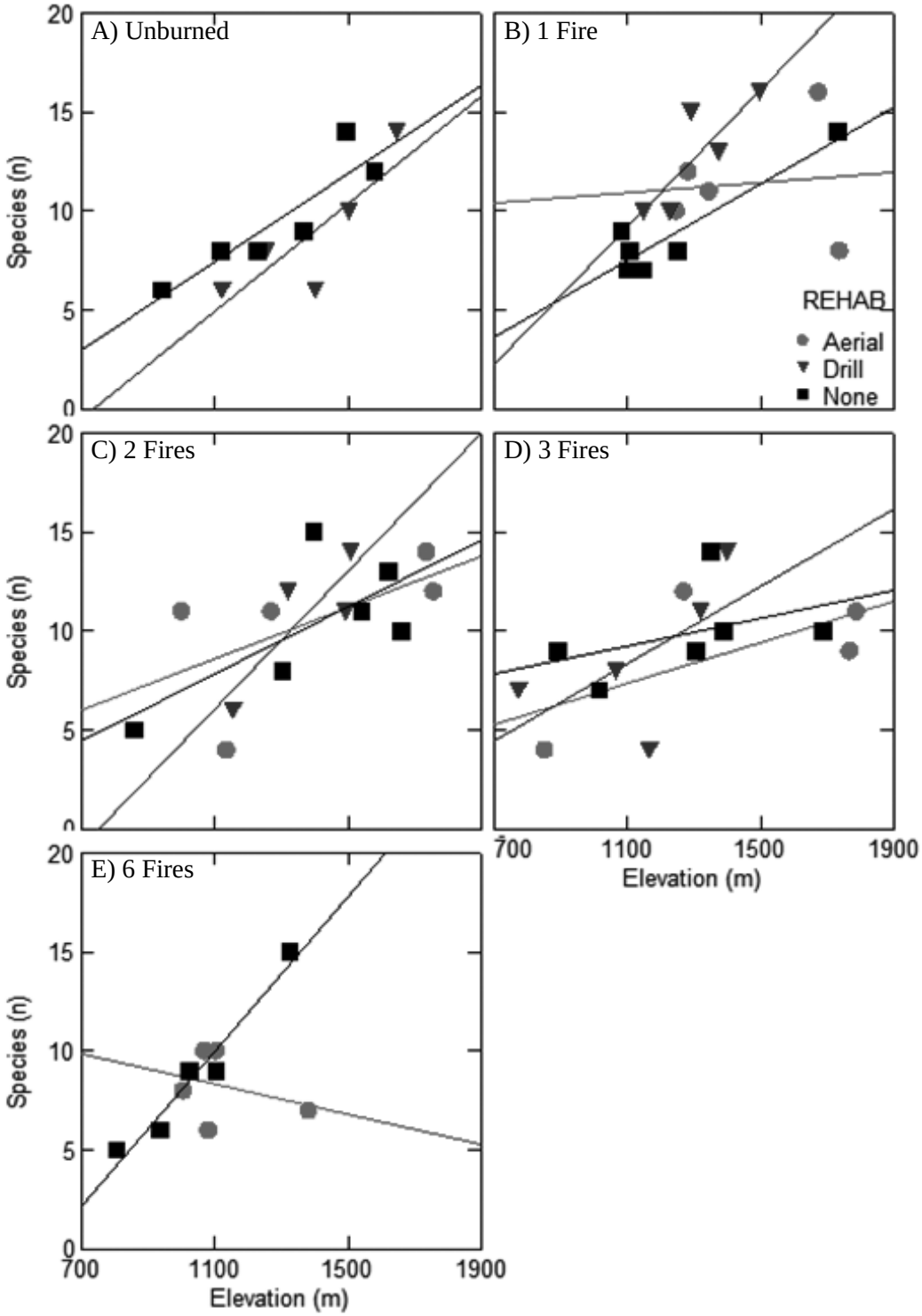

Figure 1.6 Scatterplot of total species richness along the elevation gradient for sites that burned 0-6 times under different rehabilitation treatments (none, aerial or drill seeded) after the most recent fire.

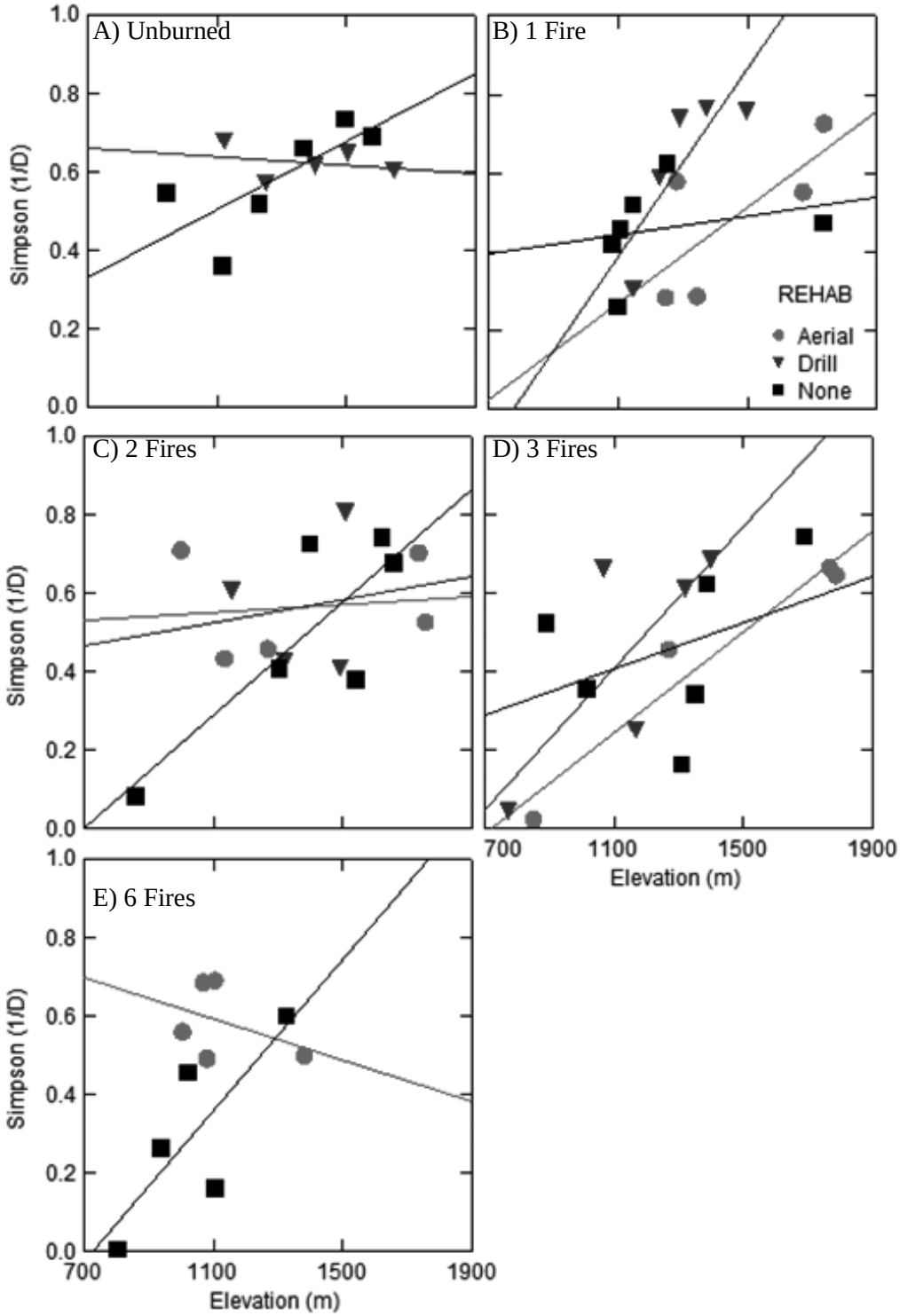

Figure 1.7 Scatterplot of species diversity (Simpson's Index) along the elevation gradient for sites that burned 0-6 times under different rehabilitation treatments (none, aerial or drill seeded) after the most recent fire.

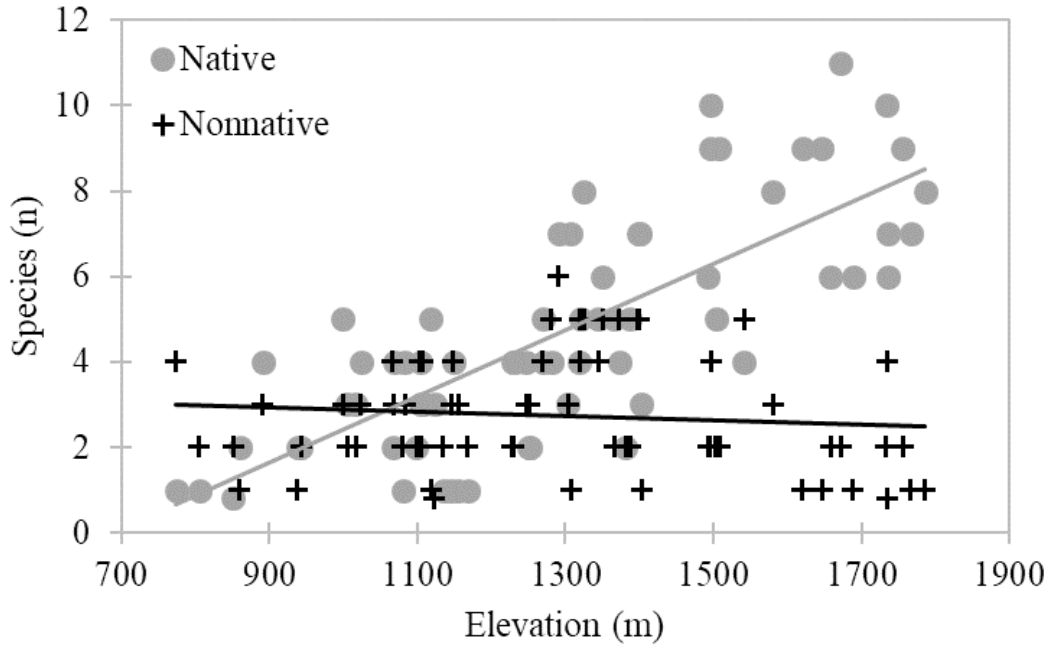

Figure 1.8 Native (O; gray) and nonnative (+; black) plant species richness along the elevation gradient.

Chapter 2: The effect of species, environment, fire history, and post-fire treatments on *Bromus tectorum*

Abstract

Annual grasses have led to considerable changes in fire regimes throughout the western United States. In the Great Basin, *Bromus tectorum* (hereafter *Bromus*) has contributed to increased fire size and frequency leading to the loss of native plant communities, including the sagebrush steppe. A key goal of post-fire rehabilitation is to reduce fine, continuous fuels caused by *Bromus* and other annual grasses, but little is known about the effectiveness of rehabilitation on *Bromus* reduction across landscapes. We analyzed the effect of 84 environment, rehabilitation, fire history, and plant species variables on *Bromus* cover and density in *Artemisia tridentata* subsp. *wyomingensis* steppe communities. *Bromus* cover and density had nonlinear responses to all predictor variables. *Bromus* cover and density were greatest at low and mid-elevation sites, decreasing as elevation increased above 1400 m. *Bromus* cover generally decreased as *Elymus elymoides* and native deep-rooted bunchgrass cover or *Poa secunda* density increased. *Bromus* cover was undetectable when native deep-rooted bunchgrass cover reached 40%, but *Bromus* maintained low density even with high native bunchgrass cover and *Poa secunda* density. *Bromus* cover decreased slightly as the number of rehabilitation treatments or time since rehabilitation increased. *Bromus* density decreased as *Achnatherum thurberianum* or native perennial deep-rooted bunchgrass cover increased. *Bromus* density also decreased as *Poa secunda* density or time since last rehabilitation treatment increased. Evidence suggests that

post-fire rehabilitation treatments that use a diverse mixture of native bunchgrass species can be an effective means of controlling *Bromus* after a fire.

Keywords

Poa secunda, *Agropyron cristatum*, *Elymus elymoides*, *Achnatherum thurberianum*, nonparametric multiplicative regression, invasions, rehabilitation

Introduction

Invasive species often exert strong negative effects on native plants and animals while altering community productivity, nutrient cycles, and fire regimes (Pyšek et al. 2012). Annual grasses are particularly effective in reducing native plant diversity and abundance by inhibiting native species fecundity (Pyšek et al. 2012). Annual grasses have altered nutrient cycling and fire regimes throughout the world (D'Antonio and Vitousek 1992), and the continuous, fine fuels created by annual grasses increase both the probability of ignition and the likelihood fires will spread (Brooks et al. 2004). In the western United States, annual grasses have altered fire regimes resulting in more frequent and larger fires than occurred historically (Brooks et al. 2004, Keeley et al. 2005, Klos et al. 2015). In the Great Basin, the annual grass, *Bromus tectorum* L. (hereafter *Bromus*), creates dense, continuous fuel beds that reduce fire return intervals, broadens fire extent, and increases the likelihood of a fire spreading into adjacent, non-invaded vegetation (Balch et al. 2013, Davies and Nafus 2013).

Bromus is a cool-season, annual grass that germinates in fall and/or early spring. *Bromus* was introduced from Eurasia multiple times in the late 1800s and early 1900s (Mack

1981, Novak and Mack 2016), and the species appears to have multiple ecotypes in the western United States (Merrill et al. 2012). *Bromus* is found primarily where the mean annual low temperature is above 0 °C but can be found on sites where the annual mean average low temperature is above -10 °C (Brooks et al. 2016). The *Bromus* precipitation niche centers around 500 mm, but it can be found at more xeric and mesic sites (Brooks et al. 2016). In the western United States, *Bromus* is found between 500-2500 m elevation but is most prevalent between 1300-1700 m (Bradley and Mustard 2006). *Bromus* is disturbance-adapted and is typically found near roads, utility corridors, and agricultural fields (Bradley and Mustard 2006).

Bromus alters ecosystem structure and function in several ways. In the sagebrush steppe, most native plant species are dormant in the winter and early spring while *Bromus* is active. This difference in phenology allows *Bromus* to access resources, particularly soil moisture, while many native perennial plants are still inactive (Mack and Pyke 1983). Once established, *Bromus* invasion is facilitated by altered nutrient cycles (Melgoza et al. 1990, Ogle et al. 2003, Sperry et al. 2006) and fire regimes, including increased fire ignition probability (Link et al. 2006), and creating a highly flammable, continuous fuel bed that promotes rapid spread of fire across the landscape (West and Hassan 1985, Davies et al. 2009). *Artemisia tridentata* Nutt. (big sagebrush) steppe habitats adapted to fires on multi-decadal or century scale now contend with more frequent fires that remove or reduce *A. tridentata* and other native plants (West and Hassan 1985, Baker 2013). These changes in native vegetation result in habitat loss for sagebrush obligate species and other wildlife (Welch and Criddle 2003, Coates and Delehanty 2010). Models based on future climate suggest the range of *Bromus* will expand northward in latitude and upward in elevation

(Bradley 2009, 2010). Managing *Bromus* cover and increasing ecosystem resistance to invasion is, therefore, an important goal of post-fire rehabilitation in the Great Basin (Baker 2006). The Secretarial Order 3336 identified *Bromus* reduction and control a necessary goal of future vegetation and rehabilitation treatments (Jewell 2015b).

Small-scale studies have suggested that perennial bunchgrasses may promote ecosystem resistance to invasion by *Bromus*. Chambers et al. (2014b) suggested a minimum of 20% perennial herbaceous cover could maintain *Bromus* cover at 25-35% and has been used as a management guideline. *Agropyron cristatum* (L.) (crested wheatgrass) and *A. desertorum* (Fisch. Ex Link) Schult. (desert wheatgrass) are Eurasian bunchgrasses that suppress the growth and reproduction of *Bromus* and are resilient to fire (Svejcar 1990). The native bunchgrass, *Elymus elymoides* (Raf.) Swezey (bottlebrush squirreltail, here after *Elymus*), can recruit in *Bromus*-dominated communities (Arredondo et al. 1998), facilitates sagebrush recruitment (Booth et al. 2003), and is somewhat resistant to fire (Wright and Klemmedson 1965, Jirik and Bunting 1994). *Poa secunda* J. Presl (Sandberg bluegrass, here after *Poa*) is an early-season, native, shallow-rooted bunchgrass that can suppress *Bromus* productivity in the spring and may evolve earlier phenology in response to invasion (Link et al. 1990, Goergen et al. 2011). Fire has been found to reduce *Poa* biomass but have no effect on *Poa* density or productivity (West and Hassan 1985, Davies et al. 2009).

Post-fire Emergency Stabilization and Rehabilitation (ESR) plans often include seeding to reduce fine, continuous fuels caused by annual grasses. The most common seed application methods in the sagebrush steppe are drill and aerial seeding. Drill seeding uses tractors to plow the soil and drop seed simultaneously. Aerial seeding uses helicopters or planes to drop seed from the air without disturbing the soil. In the 1950s to 2010, drill

seedings after fire, and those used to increase forage production, frequently used nonnative *Agropyron* species (Pellant and Lysne 2005, Gunnell et al. 2011). In recent decades, native species are being seeded more frequently (Knutson et al. 2014). *Elymus*, *Poa*, and *Agropyron* species are often added to post-fire rangeland seed mixes, but only limited published research exists on the effectiveness of such post-fire treatments on *Bromus* (Knutson et al. 2014, Taylor et al. 2014).

Though greenhouse pot studies and small-scale field experiments can yield some information on the effect of single species on *Bromus*, our understanding is incomplete without field studies that examine the relationship between *Bromus* and bunchgrasses across landscape gradients. To date, no research has examined the effect of bunchgrass species on *Bromus* at a landscape scale to determine the relative importance of rehabilitation, fire history, environmental, and species interactions on suppressing *Bromus*. To address this gap in knowledge, we asked two questions. First, what species, rehabilitation treatment, fire history, and environmental variables best predict *Bromus* cover and density? Since total herbaceous cover has been noted as potentially important in controlling *Bromus* cover, we added plant functional groups to ask a second question: Does using total functional group cover better predict *Bromus* cover and density?

Materials and Methods

Study Area and Design

The research was conducted at 67 sites across 209,000 ha of historically *Artemisia tridentata* subsp. *wyomingensis* Beetle and Young (Wyoming big sagebrush) plant communities in southern Idaho (Figure 2.1). The most common plant species were *Poa*

secunda J. Presl (Sandberg's bluegrass), *Agropyron cristatum* (L.) Gaertn (crested wheatgrass), and *Bromus* L. (cheatgrass or downy brome). Other native bunchgrasses included *Pseudoroegneria spicata* (Pursh) Á. Löve (bluebunch wheatgrass), *Achnatherum thurberianum* (Piper) Barkworth (Thurber's needlegrass, hereafter *Achnatherum*), and *Elymus elymoides* (Raf.) Swezey (squirreltail, hereafter *Elymus*). Native perennial forbs were present in small amounts, ranging 0%-5% percent cover per site; the most common species were *Phlox aculeata* A. Nelson (sagebrush phlox) and *Phlox hoodii* Richardson (spiny phlox). Nonnative annual and biennial forb cover ranged from 0%-22% cover per site; the most common nonnative forb species were *Sisymbrium altissimum* L. (tumble mustard), *Salsola tragus* L. (Russian thistle), and *Ceratocephala testiculata* (Crantz) Roth (bur buttercup). *Artemisia tridentata* subsp. *wyomingensis* was found on unburned sites and on a few sites that burned only once since 1958. A complete list of species used in the analysis and the number of sites where each species was found is included in Table 2.1.

We randomly selected 67 sites stratified by the number of fires (unburned and 1, 2, 3, or 6 fires; (BLM 2015) and the most recent post-fire rehabilitation treatment (drill seeded, aerially seeded, or untreated (Pilliod and Welty 2013, NOC 2014). Fire, treatment history, elevation, and climate data were extracted from geospatial layers (Table 2.2). We then calculated several additional variables, including time between treatments and fires, year of first fire, and year of first treatment. Elevation ranged from 780-1790m (USGS 2012) and modeled climate data indicated the average thirty-year, annual precipitation (1981-2010) varied from 22-36.4cm among sites (PRISM 2014). Soil descriptions from SSURGO data (Soil Survey 2016) indicated most sites had loamy or sandy loam soils with three sites having sandy soils and five sites with clay soils. The first recorded fire for these sites ranged

from 1958 to 2012 with 32 sites burning for the first time between 1970-1989 (BLM 2015). This area has seen an increase in fire frequency with many sites burning multiple times, including up to three times in the last 10 years and up to six times since 1970. The most recent fire for the majority of sites occurred in the last 16 years. For sites with two or more fires, the time between the two most recent burns ranged between 1-34 years. All sites had a history of cattle grazing and active grazing permits during the time of sampling. Several sites had suspended grazing after the 2012 Kinyon Road Fire while vegetation recovered or rehabilitation treatments established.

We sampled herbaceous and woody plant canopy cover and density by species at each site in 2014 and 2015. Each site was 180 m^2 with three parallel 30 m transects separated by 30 m. Plant cover was collected along each transect using line-point intercept with points taken at 10 cm intervals. We estimated herbaceous plant density by counting all individuals of each species within five-1 m^2 quadrats spaced 6 m apart along each transect (15 quadrats total per site). *Bromus* density was estimated using Daubenmire (20 x 50cm) quadrats spaced 6 m apart along each transect (15 quadrats total per site). Shrub density was calculated based on three 30 m long 2 m wide belt transects at each site. A partial Mantel test (McCune and Grace 2002) showed there was no difference in species cover or density among sample years (cover, $r = 0.60$, $p < 0.001$; density $r = 0.39$, $p < 0.001$), so the species data were pooled across 2014 and 2015.

Data Analysis

We used a multiple response permutation procedure (MRPP) in PC ORD v7.04 to test for differences in *Bromus* cover and density across types of recent post-fire treatments, total fire number, and elevation using the Sorenson distance measure (McCune and Mefford

2016; MjM Software, Gleneden Beach , OR). The MRPP reports an effect size (A) and the probability that groups are different (P). When A = 1, groups are identical; A = 0 group similarity is the same as random chance (McCune and Grace 2002). Ecological communities are commonly A < 0.1 and A > 0.3 is uncommon (McCune and Grace 2002). We analyzed the data with MRPP in two ways. First, we used the most recent post-fire rehabilitation treatment nested within the number of fires as the grouping variable. Second, other analyses (not shown) suggested groups of rehabilitation types nested within elevation groups had strong within-group homogeneity; thus, we also ran the MRPP using a rehabilitation-elevation categorical variable as the grouping variable. Elevation was divided into four 250 m elevation bands: low (770-1020m), medium low (1021-1270 m), medium high (1271-1520m), and high (1521-1780m). Multiple comparisons tested for significant differences between groups and p values were adjusted for multiple comparisons (Moran 2003). A Principle Components Analysis and ordination was then conducted to visualize and interpret the relationships indicated by the MRPP.

We used a Nonparametric Multiplicative Regression (NPMR) in HyperNiche 2.3 (McCune and Mefford 2009) to determine which environmental, management history, fire history, and species variables predicted *Bromus* cover and density. The NPMR analyzes how predictor variables interact in nonlinear and multiplicative ways to alter the dependent variable (McCune 2006). We used a quantitative local mean Gaussian weighting model. Model fit was assessed using cross-validated R^2 (xR^2). Cross-validated R^2 is calculated using a ‘‘leave-one-out’’ cross-validation and does not require withholding data for validation purposes. To control over fitting, the model improvement criteria was set at a data-to-predictor ratio of 10 and a minimum of a 3% improvement was required to increase

the number of variables in a model by an additional variable. The bootstrap resampling aids in detecting overfitting by randomly generating data sets from your original data and compares the stability of a model to the resampled data. Our bootstrap resampling generated one thousand other data sets providing an average fit (± standard error) between the final model and resampled datasets.

Unlike traditional regression, NPMR does not fit coefficients in an equation. Instead, NPMR reports tolerances — the standard deviations used in the Gaussian smoothing. High tolerance values, relative to the range of the predictor, indicate a greater distance among points targeted for estimation. The average neighborhood size and sensitivity are reported for each model. Neighborhood size is the average number of sample units contributing to the estimate of occupancy at each point on the modeled surface. Sensitivity indicates the relative importance of each quantitative predictor in the model. A sensitivity of 1 indicates that, on average, a 5% change in value of a predictor will cause the response variable to change by 5%. A sensitivity of 0 suggests a predictor has no effect on the response variable.

We used 80 variables in the predictor matrix to determine their effect on *Bromus* cover and density. The predictor variables included percent cover and density of other plant species sampled (Table 2.1) and abiotic variables, which included fire and treatment history, climatic variables, elevation, and more (Table 2.2). We used the predictor variables to analyze the response of *Bromus* cover and density to plant species and the environment using an NPMR analyses for each response variable. We evaluated the models with the 100 greatest xR^2 values and two to three models were selected based on the predictor variables that appeared most frequently. The sensitivity of the predictor variables was analyzed and the model with the greatest sensitivity was selected as the model to discuss.

We then reanalyzed *Bromus* cover and density by adding the cover and density of five plant functional groups: total native perennial bunchgrass cover including *Poa*, native deep-rooted perennial bunchgrass cover (this excludes *Poa*), native herbaceous cover (which included forb and grasses), nonnative herbaceous cover (excluded *Bromus*, but included forbs and grasses), and native woody plants. This expanded the number of predictor variables to 90. This was done to determine if herbaceous functional group cover was a better predictor of *Bromus* cover and density than single species cover as suggested by Chambers et al. (2014b). We then chose the model to discuss based on the criteria above.

Results

Bromus cover and density was similar to random chance when sites were grouped by similar histories in fire number and recent treatment type (A= -0.03, P= 0.78). Grouping sites within a 250 m elevation range by recent post-fire rehabilitation treatments resulted in significant within-group homogeneity in *Bromus* cover and density in the overall analysis (A= 0.15, P< 0.001). Treatments at high elevations were generally distinct from lower elevation sites. Aerially seeded sites above 1500 m were significantly different from aerially seeded sites at low (A=0.283, p=0.028), moderately low (A=0.209, p=0.013), or moderately high (A=0.325, p=0.019) elevations, but aerially seed sites below 1520m were not significantly different from each other (Figure 2.2A). Untreated sites at high elevations were also relatively homogenous and distinct from untreated sites at low (A=0.271, p=0.001), moderately low (A=0.279, p<0.001), or moderately high (A=0.166, p=0.005) elevations (Figure 2.2B). Comparisons of drilled sites along the elevation gradient were not possible due to small sample sizes at low (n=2) and high elevations (n=1).

When we compared sites across treatments along the elevation gradient, in general, *Bromus* cover and density at the same elevation were not distinct when different treatments were used. For example, *Bromus* cover and density at sites between 1271-1520 m were similar when drill seeded sites were compared to unseeded sites (A<0.004, p=0.348) and aerially seeded sites were compared to unseeded sites (A=0.079, p=0.130). There were some treatments comparisons that were nearly significant (e.g. aerially and drill seeded sites between 1271-1520 m, p=0.053), but their effects sizes were not large (A=0.065). Comparing treatments across elevations showed some distinctions. Aerial seeded sites at high elevations were distinct from untreated sites at low (A=0.304, p=0.003), moderately low (A=0.340, p=0.001), or moderately high (A=0.166, p<0.006) elevations, but aerial seeded sites were not statistically different when compared to untreated sites in the same elevation range (A=-0.069, p=0.79; Figure 2.3). Aerial seeded sites at high elevations were also distinct from drill seeded sites at moderately low (A=0.181, p=0.030) and moderately high elevations (A=0.171, p=0.016; Figure 2.3). Drill seeded sites at moderately high elevations were significantly different from untreated sites at low (A=0.068, p=0.039), moderately low (A=0.061, p=0.039), or high elevations (A=0.104, p<0.048, Figure 2.3), but the small effect sizes indicate this may not be ecologically significant.

Species Analysis

The NPMR model that best described *Bromus* cover included elevation, *Elymus* cover, the number of rehabilitation treatments, and *Poa* density (Table 2.3). Increasing *Poa* density decreased *Bromus* cover at all elevations (Figure 2.4A). Between 1200 and 1400 m, *Bromus* cover increased with increasing *Elymus* cover until *Elymus* cover exceeded 6% (Figure 2.4B). Above 6% *Elymus* cover, *Bromus* cover rapidly decreased to zero as *Elymus*

cover approached 12% at 1200-1400 m in elevation (Figure 2.4B). When *Elymus* cover was below 3%, increasing *Poa* density resulted in a decrease in *Bromus* cover (Figure 2.4C). The rate of decrease (slope) in *Bromus* cover as *Poa* density increased slowed to some extent as *Elymus* increased in cover between 3 and 6% (Figure 2.4C). Instead of *Poa* and *Elymus* having a synergistic effect on decreasing *Bromus* cover as might be expected, increasing *Poa* density when *Elymus* cover was at or above 6% resulted in no steeper change in the decrease in *Bromus* cover (Figure 2.4C). The increase in *Elymus* cover appeared to have a greater impact on *Bromus* cover than *Poa* density.

Increasing the number of rehabilitation treatments generally resulted in lower *Bromus* cover (Figure 2.5A-C). *Elymus* cover was greatest on sites that had four or fewer rehabilitation treatments (Figure 2.5A). When *Elymus* cover was low or not present, increasing the number of rehabilitation treatments decreased *Bromus* cover; however, when *Elymus* cover was 2% to 4%, *Bromus* cover increased slightly (Figure 2.5A). Above 4% *Elymus* cover, increasing the number of rehabilitation treatments did not alter *Bromus* cover (Figure 2.5A). *Bromus* cover decreased to near 0% when *Elymus* cover was 10% (Figure 2.5A). The effect of increasing rehabilitation treatments differed along the elevation gradient (Figure 2.5B). At sites below 1000 m, increasing the number of rehabilitation treatments led to slight increases in *Bromus* cover, but above 1000 m increasing the number treatments resulted in decreased *Bromus* cover (Figure 2.5B). *Poa* density worked synergistically with the number of rehabilitation treatments resulting in a larger decrease in *Bromus* cover together than increasing either independently (Figure 2.5C).

The model that best predicted changes in *Bromus* density included elevation, *Achnatherum* cover, and *Poa* density (Table 2.3). *Bromus* density decreased from 800 to

1000 m, increased from 1000 and 1300 m, and decreased above 1300 m (Figure 2.6A). Increasing *Poa* density slightly decreased *Bromus* density at all elevations above 1000 m, with the most noticeable decrease between 1000 and 1200 m (Figure 2.6A). Between 1300 and 1500 m, where *Achnatherum* cover was greatest, *Bromus* density increased when *Achnatherum* cover was 0 - 1.5%; however, *Bromus* density decreased substantially when *Achnatherum* cover exceeded 1.5% (Figure 2.6B). A similar trend was seen when *Poa* density and *Achnatherum* cover interacted (Figure 2.7A). When *Achnatherum* was low or not present, increasing *Poa* density led to decreased *Bromus* density (Figure 2.7A), but when *Achnatherum* cover exceeded 1.5%, increased *Poa* density increased *Bromus* density (Figure 2.7B).

Functional Group Analysis

Adding plant cover and density for five plant functional groups (Table 2.1) to the analysis resulted in a five variable predictor model for *Bromus* cover (Table 2.4), which included the predictors elevation, native perennial bunchgrass cover, *Elymus* density, time since last treatment, and *Vulpia* cover. Hyperniche 2.0 is unable to conduct a bootstrap analysis with models consisting of more than four variables. Since our model had five variables, we removed the least sensitive variable (*Vulpia* cover) from the bootstrap analysis (Table 2.4). *Vulpia* was retained in the overall model and graphing for two reasons. First, removing *Vulpia* entirely could result in overfitting *Bromus* cover's response to the other predictor variables. Second, despite *Bromus* having a relatively low sensitivity to the low cover of *Vulpia* in our study area, *Vulpia* cover was present in the 100 models with the greatest xR^2 values. The consistent presence of *Vulpia* cover in the predictive models of *Bromus* cover warranted further exploration.

As in previous models, *Bromus* cover decreased between 800 and 1000 m, increased between 1000 and 1200 m, and decreased above 1300 m (Figure 2.8A). The time since the last rehabilitation treatment influenced *Bromus* cover along the elevation gradient. Below 1000 m, *Bromus* cover decreased slightly over time since rehabilitation, while cover increased with time between 1000 and 1200 m elevation. Time since rehabilitation had little effect on *Bromus* cover above 1200 m (Figure 2.8A). *Bromus* cover generally decreased as *Elymus* density, native perennial bunchgrass cover, and *Vulpia* cover increased (Table 2.4, Figure 2.8B-D). *Bromus* cover was unaffected by *Elymus* density below 1200 m, but from 1200 – 1400 m, *Bromus* cover decreased as *Elymus* density increased (Figure 2.8B). Increasing native, deep-rooted perennial bunchgrass cover decreased *Bromus* cover at all elevations, reducing *Bromus* cover to nearly zero when native deep-rooted bunchgrass cover reached 50% between 1300 and 1400 m (Figure 2.8C). *Bromus* cover decreased as *Vulpia* increased at elevations below 1200 m, but *Bromus* cover was unaffected by the low *Vulpia* cover between 1200 - 1500 m (Figure 2.8D). At 1600 m, *Bromus* cover increased as *Vulpia* cover increased (Figure 2.8D).

Bromus cover decreased more in response to increases in native deep-rooted bunchgrass than *Elymus* or *Vulpia* (Table 2.4; Figure 2.9A,B). As native deep-rooted bunchgrass increased, increasing *Elymus* density had no measurable effect on *Bromus* cover (Figure 2.9A). Where native deep-rooted bunchgrass were absent, *Bromus* cover was lower in places where *Vulpia* cover was greater, but a lack of *Vulpia* cover when native deep-rooted bunchgrass cover was high limited our analysis (Figure 2.9B). Though *Bromus* cover increased when *Vulpia* or *Elymus* were present individually, *Vulpia* cover and *Elymus*

density worked synergistically decreasing *Bromus* cover to a lower level than when either native species was present alone (Figure 2.9C).

Bromus cover responded differently to the time since last rehabilitation treatment when coupled with native grasses (Figure 2.10). *Bromus* cover increased slightly as time since last treatment increased in the presence of native deep-rooted bunchgrass (Figure 2.10A). *Bromus* cover increased as time passed when *Elymus* density was low (0-3 plants m^{-2}), but when *Elymus* density was >5 plants m^{-2}, *Bromus* cover decreased as time since treatment increased (Figure 2.10B). *Bromus* cover increased as time since rehabilitation increased in the presence of *Vulpia* species; however, where *Vulpia* species were present, *Bromus* cover was lower (Figure 2.10C).

Bromus density when four plant functional groups were added was best described by elevation, *Achnatherum* cover, and time since last rehabilitation treatment (Table 2.4). *Bromus* density decreased with elevation as found in previous analyses (Figure 2.11A). *Bromus* density decreased as time since treatment increased at our lowest elevation sites (<800m) and increased with time at 1000 – 1200 m, but *Bromus* density changed little over time above 1200 m (Figure 2.11A). *Bromus* density increased as time passed in the absence of *Achnatherum* (Figure 2.11B), but *Bromus* density decreased with time when *Achnatherum* cover was ≥1% (Figure 2.11C). *Bromus* density decreased in response to increased *Achnatherum* at 800 m, while between 1400 and 1600 m increased *Achnatherum* cover led to an initial *Bromus* density increase, followed by a decrease in *Bromus* density when *Achnatherum* cover exceeded 1.5% (Figure 2.11D).

Discussion

This study took place along a 1000 m gradient in what was historically dominated by *Artemisia tridentata* subsp. *wyomingensis*. Our work compliments previous work showing elevation was a key factor influencing *Bromus* presence (Bradley and Mustard 2006, Chambers et al. 2014b, Knutson et al. 2014). Climate and elevation are highly correlated with warmer, drier sites at low elevation and cooler, more mesic sites at high elevations. Temperature influences *Bromus* establishment (Bradford and Lauenroth 2006), population growth (Compagnoni and Adler 2014) and seedling establishment and competitiveness against *Pseudoroegneria spicata* and *Agropyron cristatum* X *A. desertorum*, a hybrid used in post-fire rehabilitation (Aguirre and Johnson 1991). Our study design did not allow us to separate the effect of climate from elevation; however, we presume the elevational effects are partially explained by climatic controls on *Bromus*.

Bromus was highly sensitive to changes in elevation. Most studies show *Bromus* had a linear decrease as elevation increased (Chambers et al. 2007, Chambers et al. 2014b, Knutson et al. 2014), but such studies lack the replication along a continuous gradient needed to capture nonlinear responses. Bradley and Mustard (2006) found *Bromus* presence along an elevation gradient was greatest at 1300-1600 m and tapered off at lower and higher elevations. Our results showed a similar peak in *Bromus* between 1200 and 1600 m. *Bromus* was most prevalent at 780-1000 m and was likely influenced anthropogenic features in the landscape. In our study area, farms, roads, and utility easements were more prevalent below 1000 m. Bradley and Mustard (2006) showed the probability of *Bromus* presences was greater within 6 km of agriculture, 3 km of transmission lines, and 0.5 km of roads.

The type of rehabilitation treatment implemented had little effect on *Bromus* on sites at similar elevations in part because the response of *Bromus* was highly variable. When we compared sites with similar treatments across our elevation gradient, within treatment groups became distinct from one another. This result possibly explains why other research did not find differences among treatments when conducting experiments at a single elevation range (Brooks et al. 2010, Chambers et al. 2014b). Chambers et al. (2014b) found considerable variation in *Bromus* response to mechanical and prescription fire treatments in Great Basin *Artemisia tridentata* subsp. *wyomingensis* shrub systems when they used a narrow elevation range. Wirth and Pyke (2011) found establishment of seeded species differed at discreet low and high elevation sites when aerial seeding was used, but plant establishment was not different among elevations when sites were drill seeded. We found the consistency of a seeding treatment at inhibiting *Bromus* invasion was elevation dependent. For example, there was considerably less variation in *Bromus* response above 1500 m for all treatments. Poor establishment of seeded species after fires prior to the most recent burn likely contributed to greater *Bromus* cover and density at lower elevations.

Poa likely inhibited *Bromus*, but *Poa* alone was not sufficient to control *Bromus*. *Poa*'*s* plasticity has also been shown to allow it to persist in sites with *Bromus* (Phillips and Leger 2015). *Poa* can complete its annual growth and reproduction prior to *Bromus* (Link et al. 1990), allowing it to reduce *Bromus* biomass (Goergen et al. 2011), but *Poa* alone never eliminated *Bromus*. At landscape scales, heterogeneity in abiotic and biotic conditions can alter which species holds the competitive advantage (Burke et al. 1999). For instance, soil type can affect *Poa* and *Bromus* cover (Morris et al. 2011). Spring grazing can decrease *Bromus* biomass while enhancing *Poa* seed production (Diamond et al. 2012).

Though *Poa* inhibited *Bromus*, *Bromus* was more sensitive to *Achnatherum* and *Elymus*. *Bromus* responded similarly to *Achnatherum* and *Elymus* and suggested thresholds of native species cover needed before native grasses suppress *Bromus*. Established perennial bunchgrass can effectively suppress *Bromus* (Blank and Morgan 2012, Davies and Johnson 2017), but disturbance from land management actions, such as drill seeding, can favor invasive species establishment (Bradley and Mustard 2006, Keeley 2006, Merriam et al. 2006). It is likely that disturbance from drill seeding caused an initial increase in *Bromus*, but once *Elymus* and *Achnatherum* established and recruited into the community, *Bromus* decreased. This is reinforced by the interaction between time since last treatment and both *Elymus* and *Achnatherum*. *Bromus* decreased as time since last treatment increased with both native bunchgrass species; therefore, it may take decades for native bunchgrass to establish and recruit well after rehabilitation. Increasing seeding rates during rehabilitation can increase native species cover after three years (Thompson et al. 2006) and could reduce the time it takes to reach the thresholds needed to inhibit *Bromus*.

As competition from other species increases, *Bromus* was predicted to decrease, but that was not always the case. An interaction between *Poa* and *Elymus* led to increased *Bromus* cover as *Poa* density increased and *Elymus* cover was low. When *Elymus* cover was greater than 5%, increasing *Poa* density had no effect on *Bromus* cover. The possible mechanism for this is complex. *Poa* is relatively unaffected by fire after June (Wright and Klemmedson 1965, Bates et al. 2009), when most fires in this system occur. If drill seeding occurs after fire, it can damage surviving *Poa* plants (Ott et al. 2016). Drill seeding may decrease *Poa* cover and biomass without affecting *Poa* density (Davies et al. 2009), making the surviving, damaged plants less vigorous and poorer competitors. The clearing and

disturbance caused by fire and drill seeding may initially favor *Bromus* until *Elymus* reached the threshold to inhibit *Bromus*.

Many of our sites burned within the last 2-15 years, some having burned up to three times in the last 15 years. Frequent fire can reduce the basal cover of *Elymus* (Wright and Klemmedson 1965, West and Hassan 1985) and *Achnatherum* (Wright and Klemmedson 1965) and cause high mortality in large, establish *Achnatherum* (Wright and Klemmedson 1965), thus making it difficult for *Elymus* and *Achnatherum* to reach the thresholds needed to inhibit *Bromus*. Short fire return intervals would constantly set the system back suggesting rehabilitation goals should include minimizing frequent fire risk.

Having a diverse deep-rooted, native bunchgrass community is key to controlling *Bromus*. The combined cover of *Elymus* and *Achnatherum* were generally low while native bunchgrass cover was high, suggesting there were one or more additional native bunchgrass species contributing to the bunchgrass diversity. Reisner et al. (2013) suggested *Achnatherum* was an indicator of increased plant diversity and we suggest *Elymus* is likewise an indicator of greater bunchgrass diversity. Depending on elevation and soil conditions, the other species that could have contributed to bunchgrass diversity may have included *Achnatherum hymenoides*, *Elymus wawawensis*, *Pseudoregina spicata*, and/or *Festuca idahoensis*. Several studies have shown inverse relationships between perennial cover and *Bromus*, but many studies lump perennial species together into functional groups without addressing the effect of perennial species diversity on *Bromus* (West and Hassan 1985, Akinsoji 1988, Davies et al. 2012, Chambers et al. 2014b). Bunchgrass diversity, rather than perennial cover *per se*, may be more important in controlling *Bromus* in arid sagebrush steppe systems.

Bunchgrass species effectiveness at suppressing *Bromus* is likely age and size dependent. Seedlings of *Pseudoregina spicata* and *Festuca idahoensis* are not competitive against *Bromus*, especially with elevated nitrogen levels (Vasquez et al. 2017), which is possible after a fire (Rau et al. 2008). However, once established, mature *Pseudoregina spicata* can be more competitive with *Bromus* than *Poa* (Mangla et al. 2011). Bunchgrasses require time to mature after a fire and evidence suggests sites with older rehabilitation seeding treatments are less invaded than more recently seeded sites (Pyke et al. 2013). One way to promote denser native bunchgrass assemblages with greater cover sooner, would be to increase seeding rates (Thompson et al. 2006) and species diversity. Diverse bunchgrass communities would build a system more resilient to fire because different bunchgrasses are susceptible to fire in different months (Wright and Klemmedson 1965) and allow more bunchgrass species to occupy different niches along elevational gradients. In the face of increasing fire with climate change (Krawchuk et al. 2009, Littell et al. 2009, Liu et al. 2010), building public lands that are resilient to fire is an important concern for managing public lands (Wisdom and Chambers 2009, Hurteau et al. 2014, Jewell 2015a).

Increasing species diversity in seed mixes would also benefit by including native annual species. *Vulpia* cover was rather limited in our study area, but it did have an impact on *Bromus* cover. *Vulpia octoflora* is an early successional species (Akinsoji 1988), and using it in seed mixes may help control *Bromus* in the years immediately following rehabilitation while native bunchgrasses are establishing.

Agropyron was a predictor in less than 1% of the top 400 models of *Bromus* response at landscape scales and was only present when native, deep-rooted bunchgrasses were also a predictor. *Agropyron cristatum*, *A. desertorum*, and/or *A. fragile* were present in 70% of our

sites and have been used rehabilitation treatments in our study system for half a century (Pilliod and Welty 2013, NOC 2014). Some sites had a history of all three species planted in successive treatments (Pilliod and Welty 2013, NOC 2014). Those species have also been used in rangelands throughout the Great Basin after sagebrush removal and post-fire rehabilitation (Gunnell et al. 2011); *A. cristatum* and *A. desertorum* in particular have been promoted as inhibiting *Bromus* growth, reproduction, or establishment in several small scale studies (Svejcar 1990, Yoder and Caldwell 2002, Davies and Johnson 2017). Two years post-rehabilitation, the hybrid cultivar of *A. cristatum* and *A. desertorum* grown in monoculture was equally as effective as a grass assembly that also include three native species at inhibiting *Bromus* establishment (Leffler et al. 2014). At landscape scales and over longer time periods, however, the nonnative *Agropyron* species do not appear to have a consistent, measurable effect on *Bromus tectorum*. Heterogeneity in rehabilitation history, fire history, and environmental variables lead to patchy plant establishment that may not be reflected in small-scale research. For instance, soil differences could alter the competitive interactions between *A. cristatum* and *Bromus*. *Agropyron cristatum* has an affinity for silty soils (Williams et al. 2017) and is inhibited by soil salinity (Rollins et al. 1968). Sites where *Agropyron* species did not inhibit *Bromus* cover may be on less favorable soil conditions for *Agropyron*. Although *Agropyron* species may slightly inhibit *Bromus* across landscapes, other bunchgrasses are needed for there to be a significant effect at landscape scales. The lack of *Agropyron* effect on *Bromus* is especially noteworthy since *A. cristatum*, *A. desertorum*, and the hybrid of those species used more recently, outcompete many native perennial bunchgrass forming virtual monocultures and inhibit *Artemisia* species recruitment (Marlette and Anderson 1986, Gunnell et al. 2010, Hulet et al. 2010, Nafus et al. 2015).

Using nonnative *Agropyron* species in seed mixes would inhibit the bunchgrass diversity our research suggests would lead to inhabitation of *Bromus*.

Bromus cover decreased as the number of rehabilitation treatments increased. A greater number of rehabilitation treatments likely means there was more drill seeding, which has been shown to reduce *Bromus* density (Jessop and Anderson 2007) and biomass (Taylor et al. 2014). In addition, multiple treatments may have also increased the successful establishment of native seeded species, which we found to be competitive with *Bromus*. Historical sagebrush removal treatments and early post-fire rehabilitation treatments used low diversity seed mixes (Pilliod and Welty 2013), but our results and recent management recommendations stress the need for diversity and the use of native species (Thompson et al. 2006, BLM 2007).

Bromus depended on the time since the last rehabilitation treatment, but it took decades to detect a measurable effect. Most research is conducted over a short period of time, but our results join a growing body of work that demonstrates analyzing data over decades can shed light on ecological relationships in the Great Basin. Arkle et al. (2014) found rehabilitation treatments were unlikely to reduce *Bromus* dominance 20 years after a fire, while research conducted in 90 year-old abandoned agricultural fields found *Bromus* did not dominate in fields with high *Elymus* and *Poa* cover (Morris et al. 2011). Our work bridges these two studies by showing a decrease in *Bromus* cover over a 60-year period and expands upon them by including other variables, such as the number of rehabilitation treatments.

Bromus responded to increased numbers of rehabilitation treatments differently along the elevation gradient. *Bromus* was common between 1200 and 1600 m; there,

increasing the number of rehabilitation treatments decreased *Bromus* cover. Aerial and drill seeding can increase plant establishment of desirable species at low elevations (Wirth and Pyke 2011), but rehabilitation is often more effective at higher elevation sites (Knutson et al. 2014). At the lowest elevation sites in our study area, *Bromus* cover increased slightly as more rehabilitation treatments were applied. *Bromus* establishment is favored by frequent fire (D'Antonio and Vitousek 1992, Bradford and Lauenroth 2006), disturbances from land management actions (Keeley 2006, Merriam et al. 2006), and close proximity to agricultural fields, powerline easements, and roads (Bradley and Mustard 2006) — all of which were more prevalent at the lowest elevation sites. Disturbance or the choice to use low diversity seed mixes at low elevations may have negated the effect of more treatments.

Bromus responded differently to time since the last rehabilitation treatment along the elevation gradient. Though *Bromus* increased with time since the last treatment below 1300 m, *Bromus* decreased over time since the last treatment above 1300 m, which may be explained by the use of different species seeded at different elevations. Above 1300 m, *Elymus* and *Achnatherum* were common and both contributed to decreases in *Bromus*. As time since rehabilitation increases, so would bunchgrass cover and density causing a decrease in *Bromus* over time (Blank and Morgan 2012, Davies and Johnson 2017). Differences in soil conditions (Morris et al. 2011) or grazing practices (West and Yorks 2002) along the elevation gradient may have also contributed to which species held the competitive advantage in the community favoring *Bromus* at lower elevations.

Conclusion

Bromus tectorum is one of the highest management concerns in the western US due to the impacts on fire regimes and native plant communities. In efforts to understand its distribution across landscapes, we examined the effects of climate, rehabilitation, and plant communities on *Bromus*. *Bromus* distributions were highly correlated with elevation where *Bromus* decreased with elevation, presumably due to lower temperatures and increased precipitation favoring native species. The information we found will benefit land managers trying to control fine fuels created by *Bromus* in the Great Basin as one of their post-fire rehabilitation management goals.

We found that individual species had negative effects on *Bromus*; however, a combination of several bunchgrass species allows for multiple niches to be filled and increasing the chance of controlling *Bromus*. Thus, increasing the seeding rate and diversity of native, deep-rooted perennial bunchgrasses used in drill seeding after a fire may be more effective at controlling *Bromus*. Increasing seeding rates of native species will allow native bunchgrasses to reach the thresholds necessary for inhibiting *Bromus* more quickly and give *Bromus* less time to establish after a fire. Increasing native bunchgrass diversity will also make public lands more resilient to future fire, if species are selected that differ in when and how they are susceptible to fire. When determining whether to drill seed after a fire, the susceptibility of surviving perennial plant species should be taken into consideration, as drill seeding may damage existing plants and lead to detrimental increases in *Bromus*.

Nonnative *Agropyron* species have been seeded extensively in the Great Basin both prior and after wildfire. Interestingly, *Agropyron* species had little effect on *Bromus* and is thought to be competitive with native species. We suggest caution when using nonnative

Agropyron species in post-fire rehabilitation and suggest managers consider using a diverse mix of native, deep-rooted perennial bunchgrass species.

Caution should be used when trying to extrapolate the effectiveness of any particular treatment (aerial, drill, or unseeded) at different elevations. The effectiveness of a treatment seems dependent on elevation, previous rehabilitation actions, and likely the number of fires sites have experienced. At high elevations, seeded species established well. At low elevations, more rehabilitation treatments were linked to increased *Bromus*, but this may reflect of poor establishment of seeded species. Establishment of seeded species could be aided by greater seeding diversity and seeding rates. Increasing seeding diversity by including species that recruit well in various climatic conditions would increase the likelihood of some recruitment success. In addition, it may be necessary to extend the post-fire rehabilitation monitoring beyond 2-3 years and giving land managers the opportunity to conduct a second year of seeding if recruitment is poor.

It should be noted that since *Bromus* has several ecotypes, the ability of native bunchgrasses to inhibit *Bromus* may depend on the *Bromus* ecotype and the native perennial bunchgrasses used. Understanding the role of differing *Bromus* ecotypes on the response to native deep-rooted bunchgrasses will be an important avenue of future research and could assist land managers in controlling *Bromus* throughout the Great Basin.

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Tables

Table 2.1 The species and the number of sites each species was found. The cover and density of each species was used in the predictor matrix for the nonparametric multiplicative regression analyses. Symbols indicate the functional group each species was assigned in the analysis that included the cover and density of: (*) all native bunchgrass cover, (†) deep-rooted native bunchgrasses (cover and density), (‡) total native herbaceous, (**) native woody, and (††) nonnative herbaceous forbs.

Functional Group	Species	Sites (n)
Native perennial bunchgrass‡	*Poa secunda* J. Presl *	66
	Elymus elymoides (Raf.) Swezey *†	33
	Pseudoroegneria spicata (Pursh) Á. Löve *†	20
	Achnatherum thurberianum (Piper) Barkworth *†	14
	Festuca idahoensis Elmer *†	7
	Elymus wawawaiensis J. Carlson & Barkworth *†	6
	Achnatherum hymenoides (Roem. & Schult.) Barkworth *†	4
	Leymus cinereus (Scribn. & Merr.) Á. Löve *†	4
Native forbs‡	*Phlox aculeata* A. Nelson	33
	Phlox hoodii Richardson	17
	Astragalus species L.	9
	Erigeron species L.	8
	Lupinus species L.	8
	Calochortus bruneaunis A. Nelson & J.F. Macbr.	6
	Epilobium brachycarpum C. Presl	5
	Linum lewisii Pursh	5
Native annual grass‡	*Vulpia* species C.C. Gmel.	11
Native shrubs**	*Artemisia tridentata* Nutt. subsp. *wyomingensis* Beetle & Young	23
	Chrysothamnus viscidiflorus (Hook.) Nutt.	19
Nonnative perennial bunchgrass	*Agropyron cristatum* (L.) Gaertn	47
Nonnative forb††	*Salsola tragus* L.	32
	Ceratocephala testiculata (Crantz) Roth	22
	Tragopogon dubius Scop.	17
	Descurainia sophia (L.) Webb ex Prantl	16
	Chondrilla juncea L.	13
	Lepidium perfoliatum L.	6
	Medicago sativa L.	5
Nonnative annual grass	*Bromus tectorum* L.	56

Table 2.2 Geospatial data extracted from shapefiles and raster data set at each sites location and used in in the predictor matrix for both of the nonparametric multiplicative regression analyses.

Category	Attribute	Source
Climate[1]	Mean annual precipitation Mean annual high temperature Mean annual low temperature	Parameter-elevation Relationships on Independent Slopes Model (http://prism.oregonstate.edu/)
Elevation[2]	DEM elevation (continuous) Elevation (250 m category)	USDA NRCS GeoSpatial Gateway (https://gdg.sc.egov.usda.gov/)
Soils	Soil temperature and moisture regime	https://map.sagegrouseinitiative.com
	Soil texture[3] Ecological site vegetation	NRCS Geospatial Gateway, SSURGO shapefile (https://gdg.sc.egov.usda.gov/)
Rehabilitation Treatment[4]	Total number Time since most recent First treatment year Number of drill seedings Time since most recently drilled Time since first drill seeding Year first drill seeded Number of aerial seedings Time since most recent aerial seeded Time since first aerially seeded Year first aerially seeded	Rehabilitation shapefiles from multiple sources: Jarbidge and Bruneau Field Office, BLM, Idaho National Operations Center, BLM, downloaded from Inside Idaho Mountain Home Air Force Base, DOD Land Treatment Digital Library, USGS
Fire History	First fire year Time since most recent fire Time between two most recent fires Time since first fire	All fire data was extracted or derived from shapefiles found on Inside Idaho Historic fire perimeters, BLM Current year fire perimeters, BLM
Categorical Synthetic Variables	Fire number and last treatment Fire number and elevation category Last treatment and elevation category	Authors combined data from sources above

1- 30 year means, 1981-2010.

2- DEM will be verified using GPS elevation data collected in the field during the 2015 season.

3- Soil texture was based on the Ecoclass Name attribute of the that included a general description of soil texture such as loam, sand, sandy loam, stony, and clay.

4- Treatments verified using data from BLM field offices.

Table 2.3 Nonparametric Multiplicative Regression (NPMR) results for *Bromus* cover and density for the species level analysis. The predictor variables that composed the best-fit models include elevation (Elev), *Elymus elymoides* cover (ELEL5_C), number of rehabilitation treatments (Rehab n), *Poa secunda* density (POSE_D), and *Achnatherum thurberianum* cover (ACTH7_C).

Response Variable[A]	xR^{2B}	Bootstrap xR^2 (SE)	Avg. Size[C]	Predictor	Sensitivity	Tolerance	
Bromus Cover**	0.64	0.77 (<0.001)	3.42	Elev	0.77	50.59	(5%)
				ELEL5_C	0.08	1.61	(15%)
				Rehab (n)	0.07	2.10	(35%)
				POSE_D	0.06	53.42	(35%)
Bromus Density*	0.63	0.72 (<0.001)	3.97	Elev	0.66	50.59	(5%)
				ACTH7_C	0.20	0.36	(5%)
				POSE_D	0.04	76.32	(50%)

A- Significance values *, $P < 0.04$; **, $P < 0.01$
B- xR^2 = Cross-validated R^2.
C- Avg. Size = Average neighborhood size.

Table 2.4 Nonparametric Multiplicative Regression (NPMR) models for *Bromus* cover and density for the community level functional group analysis. The predictor variables that composed the best-fit models include elevation (Elev), native deep-rooted bunchgrass cover (NPBG_C), *Elymus elymoides* density (ELEL5_D), time since last post-fire rehabilitations (tLT), *Vulpia* species cover (VULPI_C), and *Achnatherum thurberianum* cover (ACTH7_C).

Response Variable	xR^2	Bootstrap xR^2 (SE)	Avg. Size	Predictor	Sensitivity	Tolerance	
Bromus Cover**	0.67	0.79 (<0.001)[D]	3.57	Elev	0.75	50.59	(5%)
				NPBG_C	0.05	10.98	(25%)
				ELEL5_D	0.04	2.14	(35%)
				tLT	0.04	38.35	(65%)
				VULPI_C	0.02	0.35	(30%)
Bromus Density*	0.64	0.68 (±0.001)	4.95	Elev	0.65	50.59	(5%)
				ACTH7_C	0.23	0.36	(5%)
				tLT	0.03	35.40	(60%)

A- Significance values *, $P < 0.02$; **, $P < 0.01$
B- xR^2 = Cross-validated R^2.
C- Avg. Size = Average neighborhood size.
D- Hyperniche can only perform bootstrap analysis on models with 4 or fewer predictor variables. *Vulpia* species cover was removed from the bootstrap analysis.

Figures

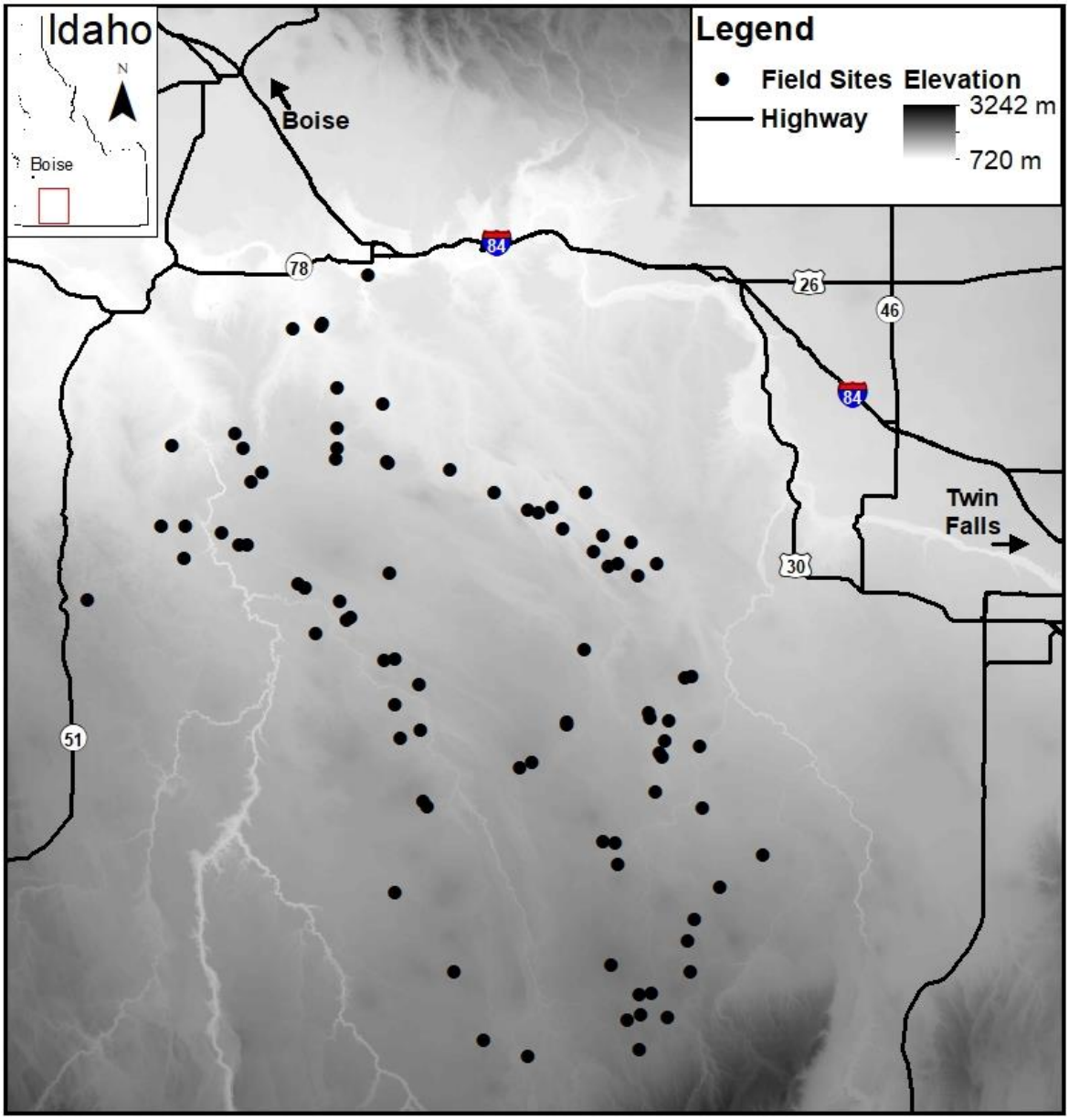

Figure 2.1 Study sites (circles) along the elevational gradient in southern Idaho, USA.

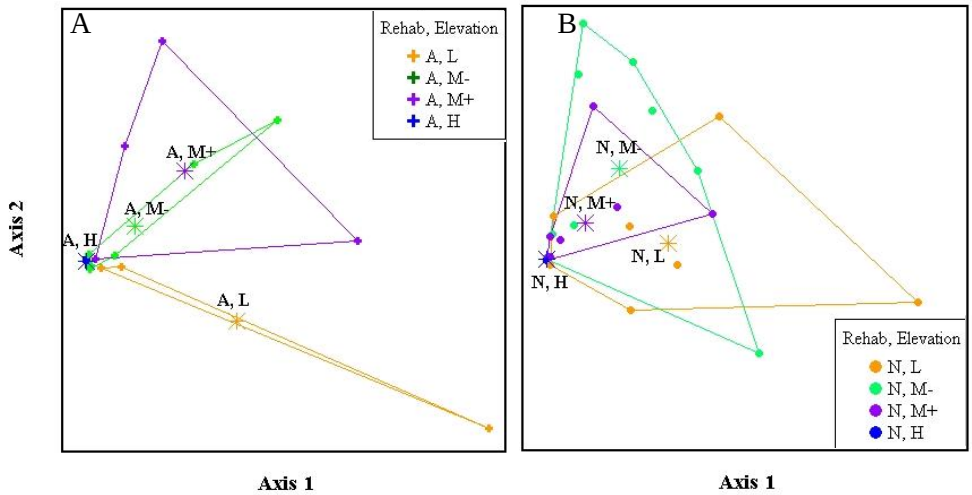

Figure 2.2 The Principle Components Analysis showing the response of *Bromus* cover to differences in elevation within aerial (A) and untreated sites (B). Sites were divided into four elevation ranges: low (L= 770-1020m, orange), medium low (M=, 1021-1270 m, green), medium high (M+= 1271-1520m, purple), and high (H= 1521-1780 m, blue). Centroids for each elevation are denoted with an astrik (*). *Bromus* cover increased from left to right on Axis 1. *Bromus* cover had a non-linear response to Axis 2 such that *Bromus* cover increased from the center of Axis 2 to the top or bottom

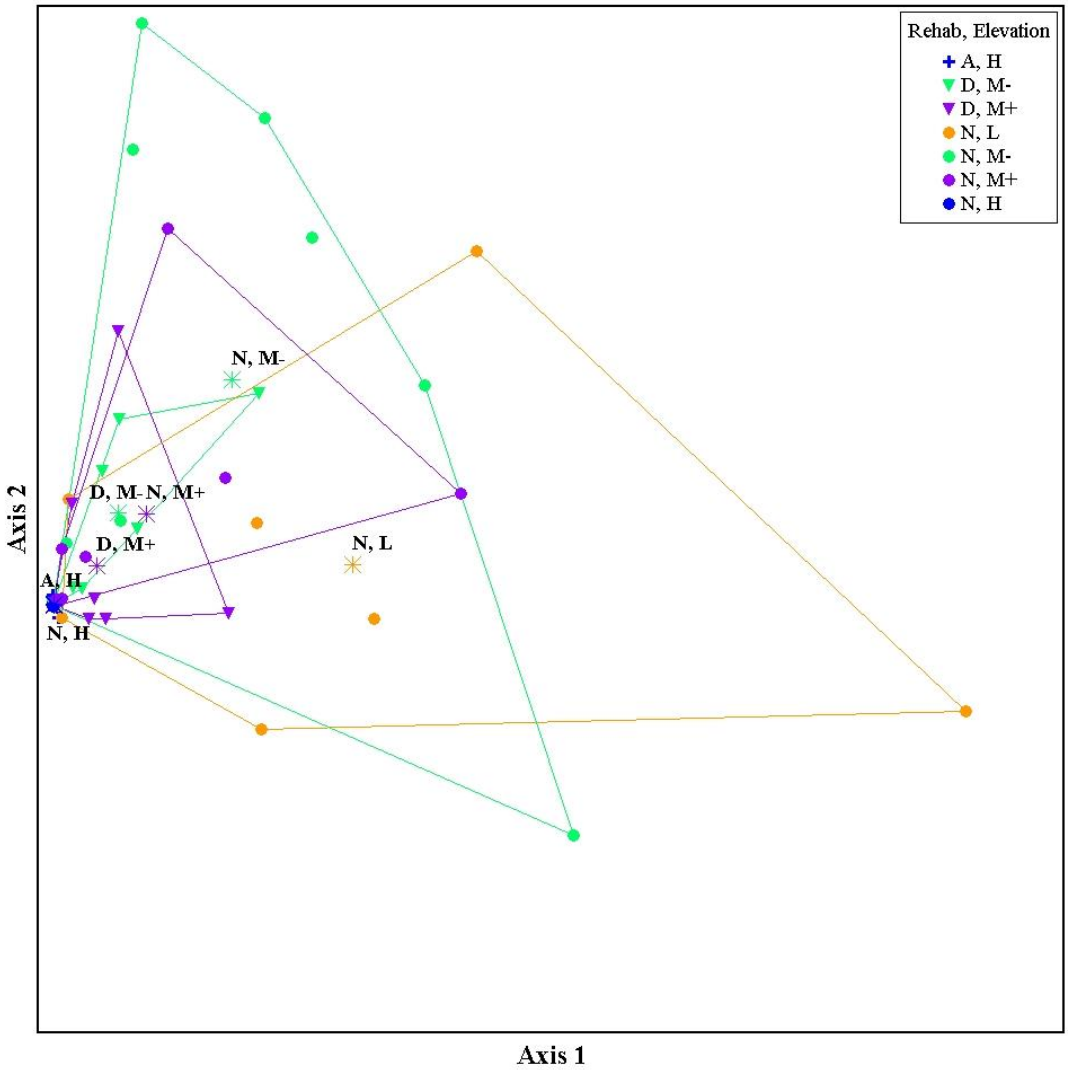

Figure 2.3 The Principle Components Analysis showing the response of *Bromus* cover to differences among sites that differed in both treatment (aerial,A; drill,D; untreated, N) and elevation ranges: low (L= 770-1020m, orange), medium low (M=, 1021-1270 m, green), medium high (M+= 1271-1520m, purple), and high (H= 1521-1780 m, blue). Centroids for each elevation are denoted with an astrik (*). *Bromus* cover increased from left to right on Axis 1. *Bromus* cover had a non-linear response to Axis 2 such that *Bromus* cover increased from the center of Axis 2 to the top or bottom.

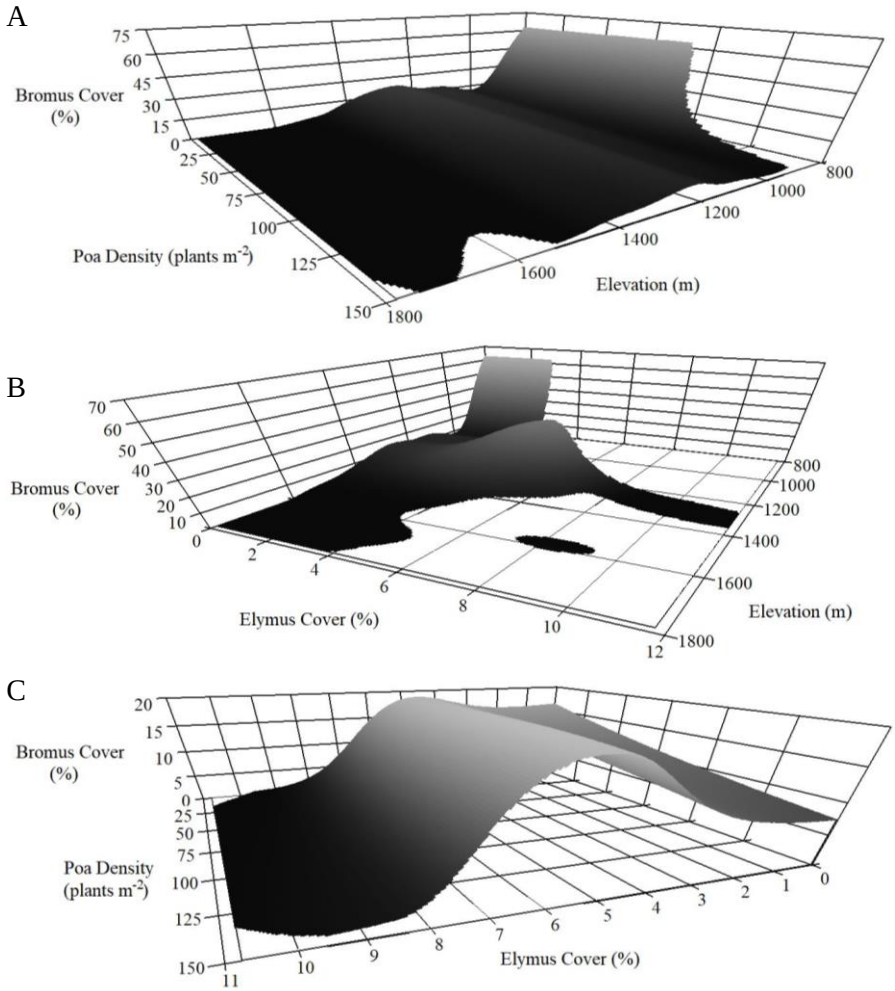

Figure 2.4 The Nonparametric Multiplicative Regression modeled relationship for *Bromus tectorum* cover in response to A) elevation and *Poa secunda* density, B) elevation and *Elymus elymoides* cover, and C) *Elymus* cover and *Poa* density when functional vegetation groups were not included in the analysis. Treatments include any vegetation or post-fire rehabilitation. Color scale ranges from near 0% *Bromus* cover (black) to maximum *Bromus* cover (gray). Unshaded areas in the predictor space represent areas where predictor variable data was insufficient to model the relationship.

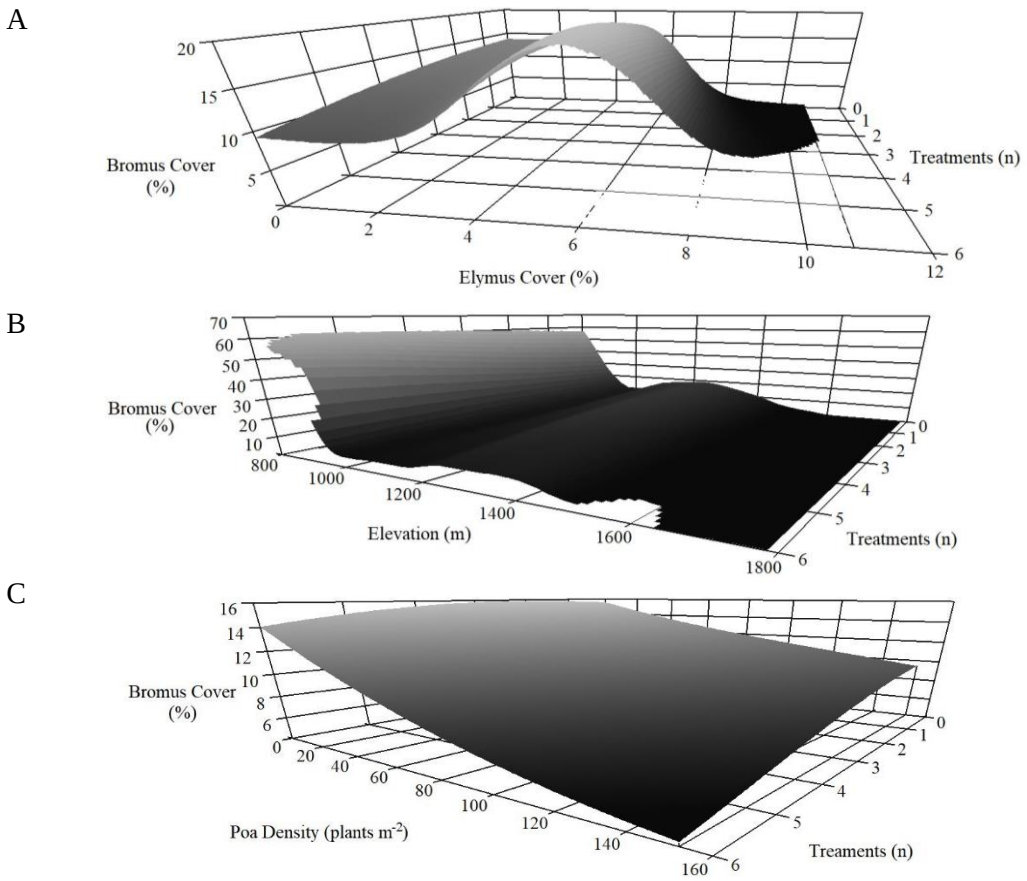

Figure 2.5 The Nonparametric Multiplicative Regression modeled relationship of *Bromus* cover in in response to *Elymus elymoides* cover and the number of rehabiliation treatments (A), elevation and the number of rehabilation treatments (B), and *Poa secunda* denisty and rehabiliation treaments (C) when functional vegetation groups were not included in the analysis. Color scale ranges from near 0% *Bromus* cover (black) to maximum *Bromus* cover (gray). Unshaded regions in the predictor space represent areas where there was insufficient data to model the relationships.

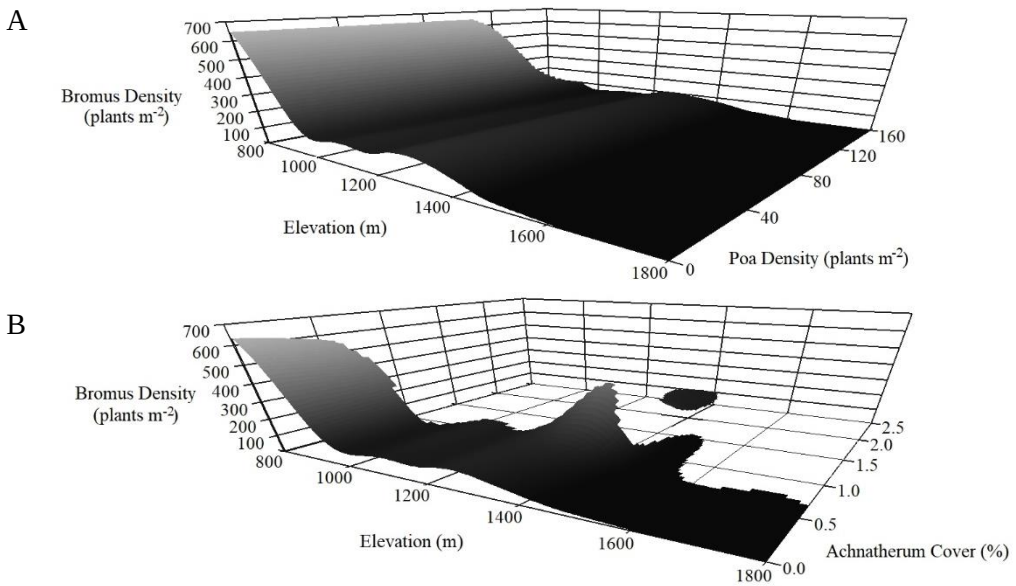

Figure 2.6 The Nonparametric Multiplicative Regression modeled relationship for *Bromus* density and in response to (A) elevation and *Poa secunda* density and (B) elevation and *Achnatherum thurberianum* cover. Color scale ranges from near 0% *Bromus* cover (black) to maximum *Bromus* cover (gray). Unshaded areas in the predictor space represent areas where there was insufficient predictor variable data to models the relationship.

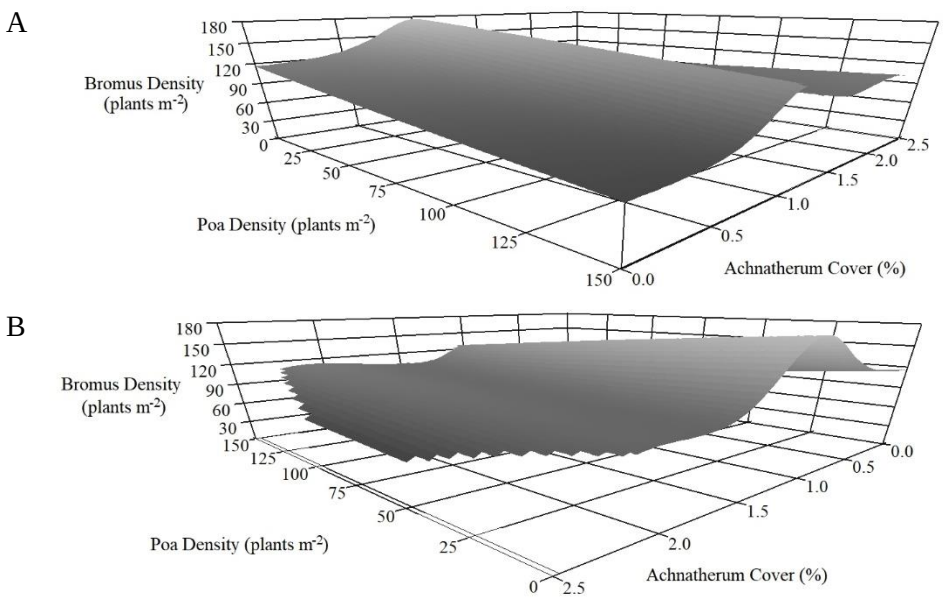

Figure 2.7 The Nonparametric Multiplicative Regression modeled relationship for *Bromus* density in response to *Poa secunda* density and *Achnatherum thurberianum* cover. Color scale ranges from near 0% *Bromus* cover (black) to maximum *Bromus* cover (gray). Unshaded areas in the predictor space represent areas where there was insufficient predictor variable data to models the relationship. Plots A and B are the same although shown from different vantage points to portray all patterns.

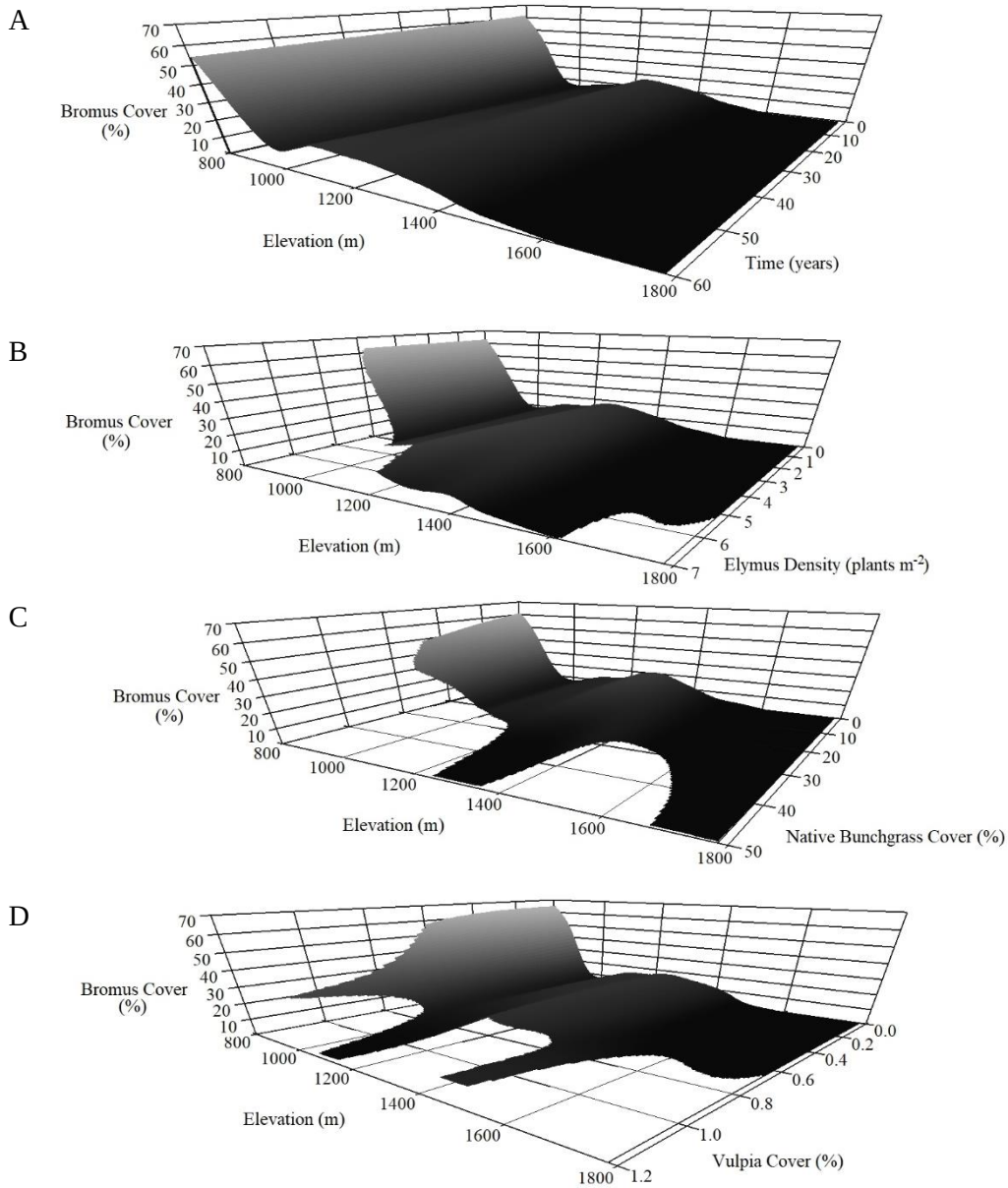

Figure 2.8 The Nonparametric Multiplicative Regression modeled relationship when plant functional groups were added to the analysis for *Bromus* cover in reponse to elevation and (A) time since the last rehabilitation treatment, (B) *Elymus elymoides* density, (C) native deep-rooted bunchgrasses, and (D) *Vulpia* species cover. Color scale ranges from near 0% *Bromus* cover (black) to maximum *Bromus* cover (gray). Unshaded areas in the predictor space represent areas where there was insufficient predictor variable data to models the relationship.

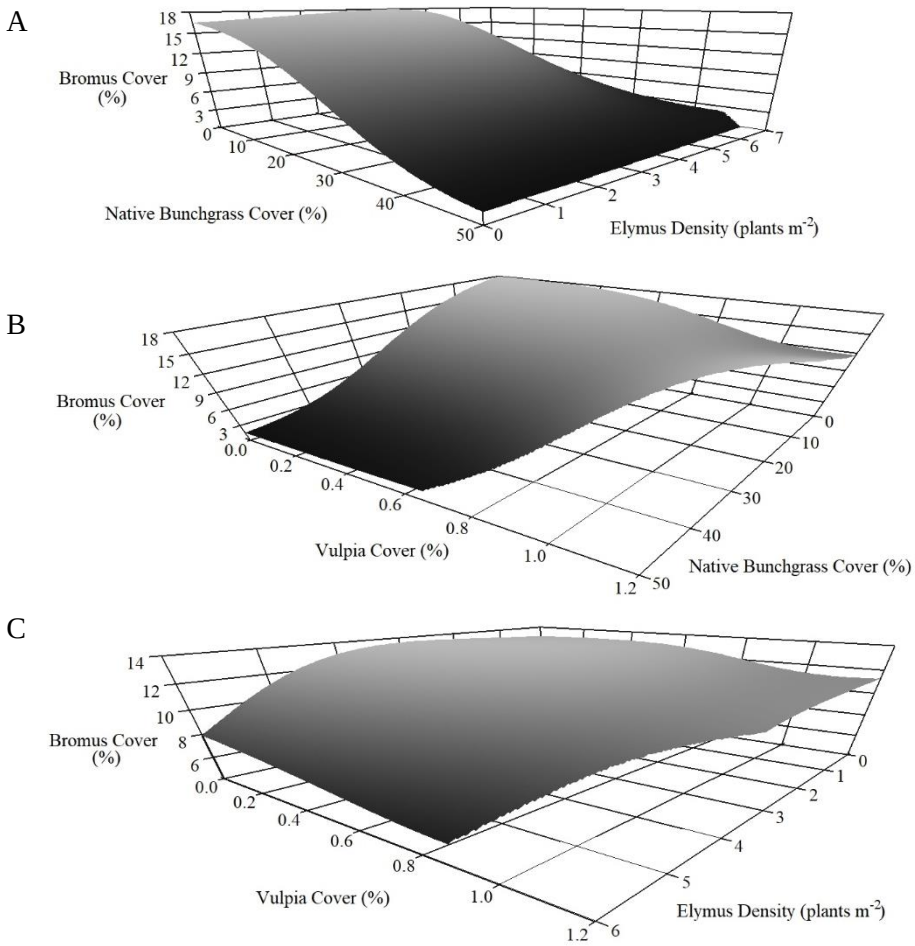

Figure 2.9 The nonparametric multiplicative regression modeled response when plant functional groups were added to the analysis of *Bromus* cover to (A) native, deep-rooted bunchgrass cover and *Elymus elymoides* density,(B) native deep-rooted bunchgrass cover and *Vulpia* species cover, and (C) *Elymus* density and *Vulpia* species cover. Color scale ranges from near 0% *Bromus* cover (black) to maximum *Bromus* cover (gray). Unshaded areas in the predictor space represent areas where there was insufficient predictor variable data to models the relationship.

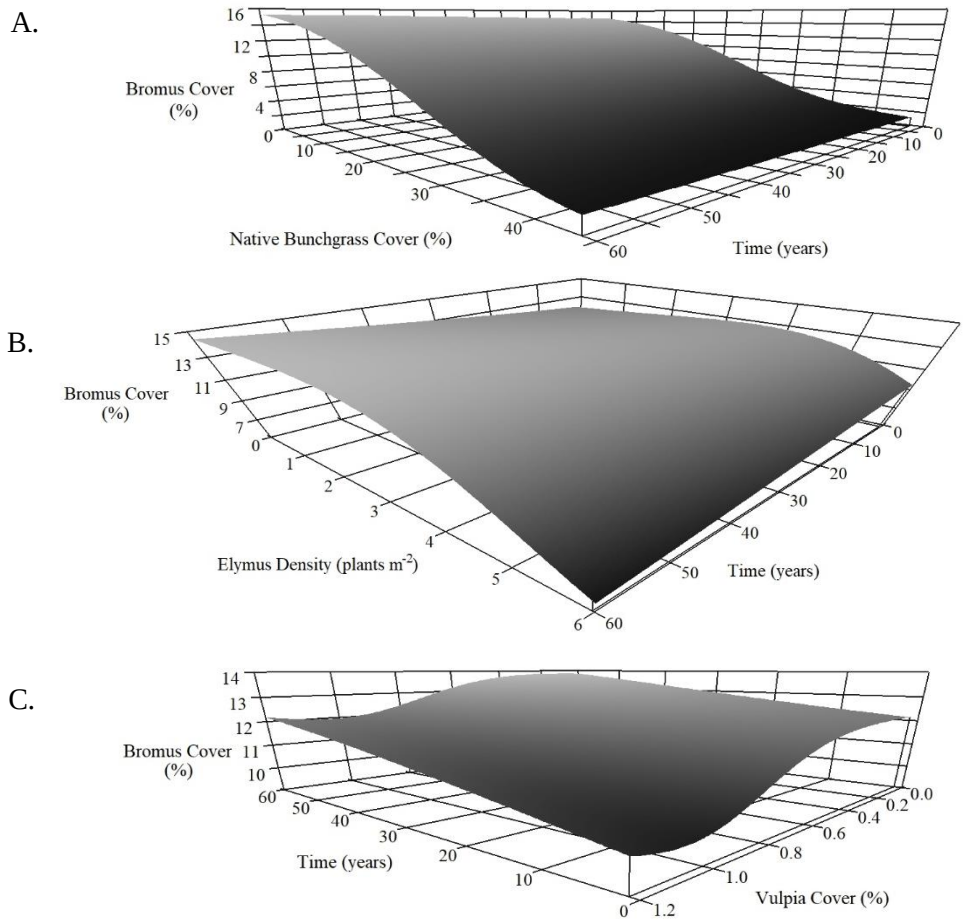

Figure 2.10 The Nonparametric Multiplicative Regression modeled relationship when plant functional groups were added to the analysis of *Bromus* cover in relationship to time since last rehabilitation treatments and (A) *Elymus elymoides density*, (B) native deep-rooted bunchgrass cover and (C) *Vulpia* species cover. Color scale ranges from near 0% *Bromus* cover (black) to maximum *Bromus* cover (gray). Unshaded areas in the predictor space represent areas where there was insufficient predictor variable data to models the relationship.

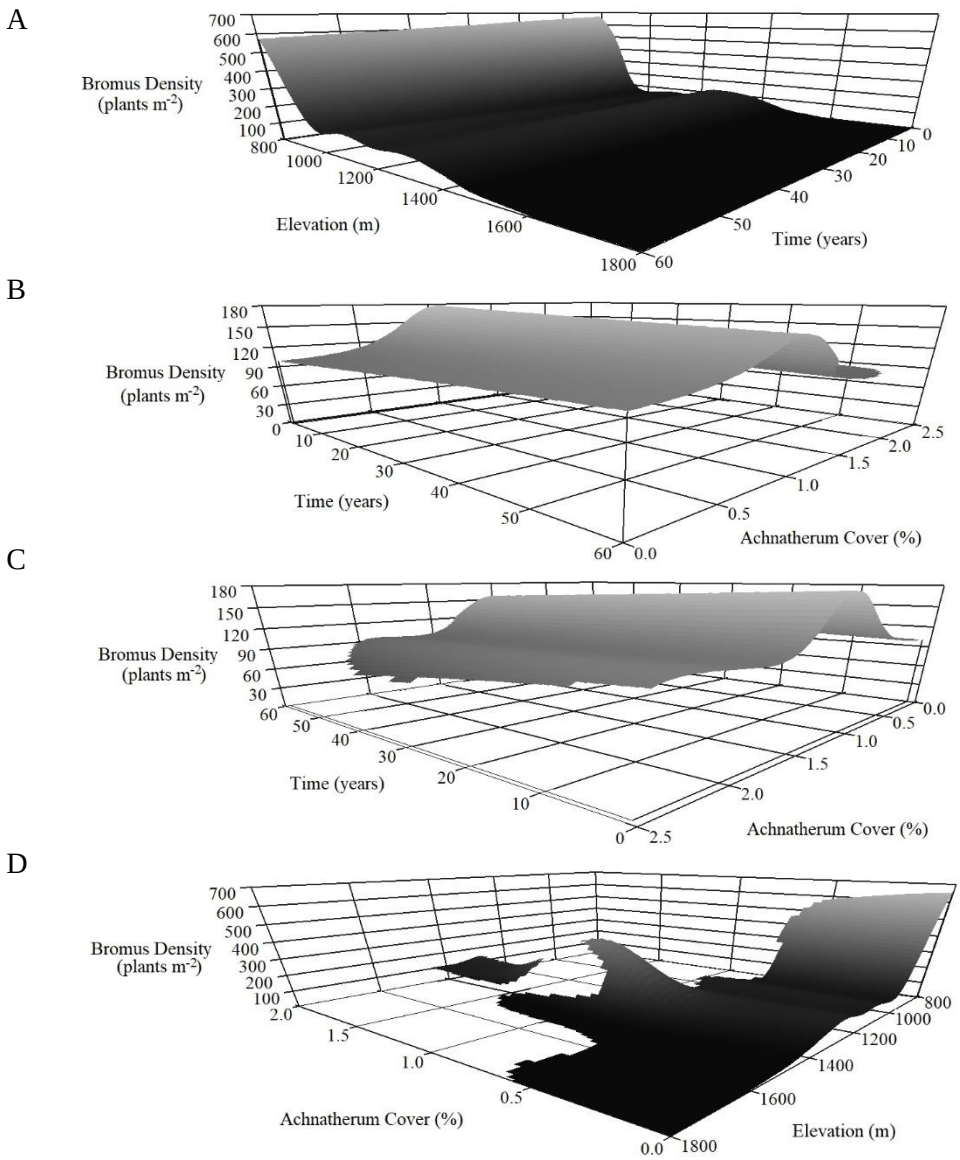

Figure 2.11 The nonparametric multiplicative regression modeled response when plant functional groups were added to the analysis of *Bromus* density to (A) elevation and time since last treatment, *Achnatherum thurberianum* cover and time since last treatment from two perspectives (B,C), and (D) *Achnatherum* cover and elevation. Color scale ranges from near 0% *Bromus* cover (black) to maximum *Bromus* cover (gray). Unshaded areas in the predictor space represent areas where there was insufficient predictor variable data to models the relationship.

Chapter 3: The Effect of Post-fire Rehabilitation and Climate on Fire Regimes in the Sagebrush Steppe

Abstract

Wildfire is an important driver of plant communities and alterations to historical fire regimes has led to shifts in plant communities and in some cases resulting in invasive plant dominance. Climate change, anthropogenic actions, and plant invasions themselves will further alter fire regimes in the future. We analyzed the effects of climate, post-fire rehabilitation history (aerial and drill seeding), and proximity to anthropogenic ignition sources on fire characteristics in *Artemisia tridentata* subsp. *wyomingensis* shrub steppe communities in the Great Basin, USA. A nonparametric multiplicative regression found climate, post-fire rehabilitation, time since first fire, and first year treated as the best predictors of fire regime characteristics. Arid sites had more fires than mesic sites. The mean fire return intervals were shorter in arid sites with the shortest fire return interval found on sites first treated between 1975 and 1995. Fires were more frequent on arid, low elevation sites than higher elevation sites. Sites with different recent post-fire rehabilitation treatments type had different fire regime characteristics. Aerially seeding sites after a fire resulted in more fires at greater frequency and shorter fire return intervals than drill seeded or untreated sites. Fire number and frequency decreased, while fire return interval increased, as precipitation increased for aerially seeded but not drill seeded sites. Biomass was used as a proxy for fuels composition and abundance and was not affected by rehabilitation treatments. Annual grass biomass was different among treatments and greater at lower elevations likely contributing to the greater fire number and frequency seen at lower

elevations. These results suggest that drill seeding could reduce the risk of frequent fire regardless of precipitation in *Artemisia tridentata* subsp. *wyomingensis* shrub steppe communities. If the goal of post-fire rehabilitation is to increase time between fires to allow the reestablishment of *Artemisia*, then drill seeding after a fire may be better than aerial seeding at achieving that goal.

Keywords

Agropyron cristatum, *Agropyron desertorum*, *Elymus wawawaiensis*, *Bromus tectorum*

Introduction

Fire regimes have considerably changed since the 1980s with increases in wildfire size and frequency (Goetz et al. 2007, Liu et al. 2010). Climate change has led to shorter winters, decreased snowfall, shifts in precipitation regimes, and longer and more extreme periods of drought, which have contributed to longer period of fire risk (Gedalof et al. 2005, Littell et al. 2009, Cleetus and Mulik 2014). Historic overgrazing and seed dispersal by cattle in arid lands and forests have contributed to annual grass invasions (Mack 1981, Keeley 2006), while athropogenic features, such as fuel breaks (Keeley 2006), roads, and ulitity lines (Bradley and Mustard 2006), act as dispersal corridors. Climate change has shifted native plant-to invasive-dominated communities, which can promote fire (Brooks et al. 2004, Liu and Wimberly 2016). Thus, the change in climate and increase in annual grass cover in the western United States make arid shrublands prone to fire, especially during periods of severe

weather, such as dry lightning and strong winds (Lutz et al. 2009). Complicated interactions among climate, fire, and vegetation provide uncertainty in projecting future fire activity in the region, and models predict continued changes in fire regimes throughout the western United States (Lutz et al. 2009).

In the Great Basin, USA, the fire regime of the sagebrush steppe ecosystem varies based on elevation and species of sagebrush. The fire rotation for 100,000 ha of more mesic, higher elevation *Artemisia tridentata* subsp. *vaseyana* communities was estimated to be 137-217 while the fire rotation of the more xeric, low elevation *Artemisia tridentata* subsp. *wyomingensis* 171-342 years (Bukowski and Baker 2013). Historical fires in *Artemisia tridentata* subsp. *wyomingensis* communities were larger, more continuous, stand-replacing fires than in *Artemisia tridentata* subsp. *vaseyana* communities (Bukowski and Baker 2013).

Shifts in climate have favored a range expansion of the winter annual grass, *Bromus tectorum* (cheatgrass), in the Great Basin and Intermountain West (Bradley 2009). As a consequence, *B. tectorum* has altered the historical fire regime in the Great Basin leading to profound changes in fire size, frequency, and duration (Balch et al. 2013). *Bromus tectorum* recruits well after disturbance and fires (West and Hassan 1985, Peterson 2003, Jessop and Anderson 2007) and creates continuous, highly flammable fuels that aid the spread of fire promoting further recruitment (Brooks et al. 2004). Even low *B. tectorum* cover will increase the chance of adjacent, non-invaded habitat burning in subsequent fires (Link et al. 2006). Models suggest that climate change will increase the risk of *B. tectorum* invasion in Idaho, Montana, and Wyoming (Bradley 2009), making a reduction in *B. tectorum* cover and

promoting plant communities resistant to *B. tectorum* an important goal of many fuel and post-fire rehabilitation treatments in the Great Basin (Baker 2006, Jewell 2015b).

After a wildfire, Emergency Stabilization and Rehabilitation (ESR) plans under the Bureau of Land Management in the sagebrush steppe often include seeding as a way to reduce fine fuels from annual grasses (Jewell 2015b). The primary goals of these treatments are to reduce the risk of soil erosion and reduce fine fuels from annual grasses in order to reduce chances of future fires (Jewell 2015a, b). The most common seed application methods are drill and aerial seeding. Drill seeding uses modified tractors to till the soil while simultaneously sowing seed. Tilling the soil may create microhabitats that promote recruitment of desirable species, but the disturbance may also enhance the recruitment of *B. tectorum* (Keeley 2006, Merriam et al. 2006). Aerial seeding from aircraft avoids soil disturbance but may drop seeds in unfavorable habitat and limit plant recruitment. Managers also combine aerial and drill seeding to enhance diversity and improve the likelihood of recruitment and increase plant diversity.

Few studies have examined the effects of post-fire rehabilitation treatment practices on fire regimes, but land management practices have been shown to contribute to *B. tectorum* invasion. For example, fuel breaks, green strips, and prescribed fires create disturbances that can increase *B. tectorum* (Bradford and Lauenroth 2006, Keeley 2006). Disturbance along roads and power line corridors provide both suitable habitat and a corridor for *B. tectorum* dispersal (Bradley and Mustard 2006). Studies also suggest that livestock grazing can facilitate *B. tectorum* invasion by transmitting seeds and clearing or damaging existing vegetation through preferential grazing (Ponzetti et al. 2007, Reisner et al. 2013). Increasing *B. tectorum* would lead to more frequent annual grass fires resulting in

further shifts in the fire regime. Little research has been conducted on the landscape effects of post-fire rehabilitation or fuels treatments in rangelands (Hudak et al. 2011, Martinson and Omi 2013), so it is unclear what effect such actions might have on invasive species, plant communities, and/or shifts in fire regime attributes.

We examined the geospatial relationships among fire history, post-fire rehabilitation treatments, and environmental characteristics to test the effect of aerial seeding, drill seeding, and combined treatments on fire regime variables. Fire regime variables included the number of fires between 1955-2015, the mean fire return interval between 1995-2014 (time between fires), and the fire frequency between 1995-2014 (number of fires per unit time) (Miller *et al.* 2013). Though the fire return interval and fire frequency are correlated, they provide two different aspects of fire regimes. The fire return interval indicates the time in which vegetation may establish and recruit successfully between fires. Fire frequency is used in fire modeling, which indicates the probability that a fire will occur. Our objectives were to understand how climate and post-fire rehabilitation treatments might affect the number of fires since 1950, as well as fire return intervals and fire frequency over the last 20 years. We hypothesized that treated sites would 1) have fewer fires, 2) have longer mean fire return intervals, and 3) less frequent fires.

Methods

Site Description

The study area was located in southern Idaho, USA, in the Snake River Plain (Figure 3.1). Annual precipitation within the study area ranges from 17 cm in the northwest to 70 cm in the southeast creating a strong precipitation gradient (Daly 2013). The thirty-year average

annual precipitation declined from an average of 25.36 cm in the period of 1951-1980 to 24.5 cm in the 1981-2010 period (Figure 3.2). Elevation in this region ranges from 750-1800 m with an increase in elevation southward. The dominant shrub was *Artemisia tridentata* subsp. *wyomingensis* Beetle and Young (Wyoming big sagebrush). The most common grass species were *Poa secunda* J. Presl (Sandberg bluegrass, hereafter *Poa*), *Agropyron cristatum* (L.) Gaertn (crested wheatgrass, hereafter *Agropyron*), and *Bromus tectorum* L. (cheatgrass or downy brome, hereafter *Bromus*). Other native bunchgrasses included *Pseudoroegneria spicata* (Pursh) Á. Löve (bluebunch wheatgrass), *Achnatherum thurberianum* (Piper) Barkworth (Thurber's needlegrass, hereafter *Achnatherum*), and *Elymus elymoides* (Raf.) Swezey (squirreltail, hereafter *Elymus*). *Poa* cover was >15% at 70% of our sites and was co-dominant with either *Agropyron* or *Bromus*. The historical fire rotation for *Artemisia tridentata* subsp. *wyomingensis* is estimated between 100 and 342 years, depending on the method used to estimate fire return (Baker 2006, Bukowski and Baker 2013). Most of the study area has burned at least once, while other areas have burned up to seven times, in the past 50 years (BLM 2015). Vegetation treatment data was acquired from the Land Treatment Digital Library (Pilliod and Welty 2013) and the Bureau of Land Management (NOC 2014, BLM 2019). Seeded species varied by treatment and year. Seeded species for drill seeding treatments prior to 2000 were primarily low diversity seed mixes dominated by nonnative *Agropyron* species. After 2000, native grasses and forbs began to be included in post-fire rehabilitation treatments. In our study area, aerial seeding was used primarily to seed shrubs species, though a small percentage of aerial treatments also include grasses and forbs when seeded on Wilderness Management Areas or rocky sites.

Data Extraction

We used ArcMap 10.3 software (ESRI) to generate 4000 random points across our study site with a minimum distance of 1 km. Points that fell on roads, highways, water, agriculture, and cities were eliminated. We then used LANDFIRE 2014 Environmental Site Potential Biophysical Settings (https://www.landfire.gov/bps.php) to remove all points that were not identified as "Wyoming Big Sagebrush-Wheatgrass" in the "Group Name" category. We then extracted polygon and raster data to the remaining 573 points (Figure 3.1) to create a table with 99 variables for each point (Table 3.1).

Field Collection

Dried herbaceous and woody biomass was used as a measure of available the amount of fuels (fuel load). Biomass was collected at 67 field sites along the elevational gradient (Figure 3.1). Sites were divided into those that had been drill seeded, aerially seeded, or unseeded after the most recent fire. Biomass was collected from six randomly placed 1 m^2 quadrats within a 180 m^2 location and separated into one of four functional groups: perennial bunchgrass, annual grass, forb, and shrubs.

Statistical Analysis

Using historic fire data from 1900 to present (BLM 2015), we determined that there were few fires in our study area prior to 1950. We defined fire number as the number of times a site burned in between 1950 and 2014. To determine how past vegetation management, fire history, and environmental conditions shaped the current fire regime characteristics, we defined fire return interval as the average number of years between fires

from 1994-2014. Fire frequency was determined by dividing the number of fires that burned on a site over the twenty-year period from 1994-2014 by 20 years.

We used a Nonparametric Multiplicative Regression (NPMR) in HyperNiche 2.3 (McCune and Mefford 2009) to determine how climate, management, and proximity to anthropogenic features (Table 3.1 predicted fire number, fire return interval, and fire frequency. The NPMR analyzes how explanatory variables interact in nonlinear and multiplicative ways to alter the dependent variable. We used a quantitative local mean Gaussian weighting model. We assessed model fit using cross-validated R^2 (xR^2). Cross-validated R^2 is calculated using a ‘‘leave-one-out’’ cross-validation and does not require withholding data for validation purposes. To control over fitting, the model improvement criteria was set at a data-to-predictor ratio of ten and a minimum of a 2% improvement was required to increase the number of variables in a model by an additional variable. Bootstrap resampling (each dataset resampled with replacement 100 times to generate 100 new datasets, each with n - 1 plots) was used to assess model stability against the inclusion of particular plots in a given analysis by providing an average fit (±SE) between the final model and 100 resampled datasets.

Unlike traditional regression, NPMR does not fit coefficients in an equation. Instead, NPMR reports tolerances — the standard deviations used in the Gaussian smoothing. High tolerance values, relative to the range of the predictor, indicate a greater distance among points targeted for estimation. In addition, we report the average neighborhood size and sensitivity for each model. Neighborhood size is the average number of sample units contributing to the estimate of occupancy at each point on the modeled surface. Sensitivity indicates the relative importance of each quantitative predictor in the model. A sensitivity of

1 indicates that, on average, the percent change in value of a predictor will result in a similar percent change in the estimate of the response variable, while a sensitivity of 0 indicates the predictor has no effect on the response variable. Since tolerance and sensitivity indicate by how much a dependent variable change in response to a predictor variable, they can only be calculated for continuous variables.

We used 99 explanatory variables to determine their effect on fire regime characteristics (fire number, fire return interval, and fire frequency) in response to fire and treatment history; monthly, seasonal, and annual climatic variables; and elevation (Table 3.1). We evaluated the models with the 100 greatest xR^2 values and two to three models were selected based on the predictor variables that appeared most frequently. The sensitivity of the predictor variables was analyzed and the model with the greatest sensitivity was selected as the model to discuss.

To understand if fuels composition (i.e., the types of fuels) and amount of each fuel type may be contributing to changes in fire regimes, we pooled biomass into four functional groups (perennial bunchgrass, annual grass, forb, and shrubs). We analyzed the composition of functional group biomass using a Multi-Response Permutation Procedure (MRPP), a multivariate approach that analyzes dependent variables (the biomass of four functional groups) and determines if there are differences based on categorical, independent variables. The MRPP looks for similarities among groups. If the values for one variable are orders of magnitude greater it can skew the analysis to be based primarily on that one variable. In our data, woody biomass was orders of magnitude greater than the biomass of the other three groups. To normalize the data, biomass was square root transformed and we used a Jaccard distance measure (Peck 2016). We used the MRPP to test for homogeneity in biomass

composition among sites with differ in post-fire rehabilitation strategies (aerial, drill, or untreated) and at four 250 m elevation ranges: low (770-1020m), medium low (1021-1270 m), medium high (1271-1520m), and high (1521-1780 m) (McCune and Mefford 2016; MjM Software, Gleneden Beach , OR). In MRPP, the A-statistic determined if within groups similarity is greater than expected by chance. When A > 0 groups are more homogenous; when A < 0 groups are more heterogeneous than expected by chance. The MRPP compares individual groups in a multiple comparison test but does not correct for multiple comparisons. We used the Benjamini and Yekutieli false discovery rate (FDR) method described by Narum (2006) to establish a threshold for significance in the multiple comparison test (α=0.0115). We used a Nonmetric Multidimensional Scaling ordination with a Jaccard distance matrix to visualize relationships among MRPP groups. Drill seeded sites at 770-1020 m and 1521-1780 m had only one representative site at each and were dropped from the analysis.

Though the MRPP detects differences in biomass composition among groups, it does not indicate whether any individual dependent variable changed along the elevation gradient. In other research we conducted in this study area, plant composition changed in cover and density along the elevation gradient. Thus, we used linear regressions to further elucidate patterns for functional group biomass along the elevation gradient.

Results

The NPMR model that best predicted the number of fires included the first year a site was burned, minimum spring vapor pressure deficit (VPD), total number of rehabilitation treatments, and most recent post-fire rehabilitation method (Table 3.2). The number of fires

was unaffected by vapor pressure deficit (VPD) for sites that first burned prior to 1990 (Figure 3.3A). For sites that burned for the first time after 1990, arid sites (greater spring VPD) tended to have more fires than more mesic sites. At sites that burned for the first time in 2014, the most arid sites burned 2.5 times on average while more mesic sites burned only once (Figure 3.3A). The number of fires increased with the number of rehabilitation treatments regardless of the first year a site burned (Figure 3.3B). Fire number increased with increasing treatments and was exacerbated by spring aridity; six treatments contributed to two fires at the most mesic sites and nearly four fires at more arid sites (Figure 3.3C).

The pre-fire rehabilitation treatment method had a significant effect on the modeled number of fires (Figure 3.4). Sites that burned only once and had no prior fire or vegetation treatment history to the first fire were identified as unburned, nontreated sites for pre-fire rehabilitation treatments. Unburned, nontreated sites that did not burn after 1950 have a fire number of 0 while unburned, nontreated sites that burned once since 1950 have a fire number of 1 (Figure 3.4). Sites that were drill seeded or aerial and drill seeded prior to the most recent fire tended to only burn twice; untreated sites burned three to four times and aerial seeded sites burned three to five times (Figure 3.4A). Increasing aridity resulted in increased fire number for sites that were aerially seeded or untreated prior to the most recent fire, but sites that were drill seeded, aerial and drill seeded, or had no prior history of vegetation treatments did not increase with aridity (Figure 3.4A). Fire number decreased as the year a site burned became more recent for aerially seeded treatments, but the number of fires for other pre-fire treatments were relatively unaffected by the year a site first burned (Figure 3.4B). Regardless of the number of historic treatments on a site, aerially seeded, sites burned more times than other treatments (Figure 3.4C). On sites with one treatment, if

the site was aerially seeded or left untreated after the penultimate fire, there was three fires at the site compared to two when drill seeded (Figure 3.4C). On sites with one treatment, drill seeded sites burned twice, while aerially seeded and untreated sites burned three times (Figure 3.4C).

The NPMR model that best predicted the fire return interval included four variables: the number of aerial seeding treatments, the first year a site was treated, the minimum spring VPD, and the pre-fire rehabilitation method (Table 3.2). When the number of aerial seeding treatments increased, the fire return interval decreased across all levels of spring VPD but was particularly reduced at high VPD (Figure 3.5A). On sites without aerial seeding treatments, fire return interval was shortest on sites that first burned between 1975 and 1990 (Figure 3.5B). Adding aerial seeding treatments resulted in decreased fire return intervals, particularly at sites first treated before 1970 (Figure 3.5B). The fire return interval was shorter when on more arid sites regardless of the first time a site was treated (Figure 3.5C). Sites first treated in 1975-1995 had the shortest fire return interval on the most arid sites, while the shortest fire return interval on the more mesic sites were when the site was treated between 1985-1995 (Figure 3.5C).

The type of pre-fire rehabilitation affected fire return intervals, and there is evidence of a legacy effect. Untreated sand burned sites had a fire return interval of 15-21 years; fire return intervals were lower on sites that were aerial seeded (Figure 3.6A). On sites with a history of one aerial seeding, sites that were aerially seeded after the penultimate fire had the shortest fire return intervals (Figure 3.6A). Drill seeding in addition to aerial seeding increased the fire return interval, although sites that were untreated and only drilled also had higher fire return intervals (Figure 3.6A). For aerial seeded sites, fire return interval

increased as the first treatment year became more recent; however, aerial and drill seeding decreased fire return intervals as first treatment year became more recent (Figure 3.6B). Fire return interval decreased as the minimum spring VPD increased on untreated or aerially seeded sites after the penultimate fire (Figure 3.6C). Fire return interval on drill only or aerial and drill seeding were unaffected by the increase in spring VPD (Figure 3.6C).

The NPMR model that best predicted fire frequency included four variables: the number of drill seeding treatments, spring precipitation, the number of aerial seeding treatments, and the pre-fire rehabilitation method (Table 3.2). Fire frequency decreased slightly as precipitation increased (Figure 3.7A, B). Fire frequency increased with the number aerial seeding treatments with the greatest increase at high precipitation from a frequency of 0.02 (once every 50 years) to 0.18 (once every 5.5 years, Figure 3.7A). Fire frequency increased slightly as the number of drill seeding treatments increased with the greatest increase in fire frequency at low spring precipitation (Figure 3.7B). Fire frequency did not change as the number of drill seeded treatments increased when aerial seeding treatments were 1 or fewer (Figure 3.7C). Fire frequency decreased with increasing drill seedings when a site had three aerial seeding treatments (Figure 3.7C).

Sites varied in fire frequency based on the post-fire rehabilitation used after the prior fire. Fire frequency increased with the number of aerial seeding treatments, but frequency was less when sites were drilled alone or in combination with aerial seeding treatments (Figure 3.8A). Fire frequency was greatest on sites that were aerially seeded after the penultimate fire regardless of whether there was one or two drill seeding treatments previously (Figure 3.8B). Fire frequency was similar on drill seeded or unburned and untreated sites prior to the most recent fire and was not affected by spring precipitation

(Figure 3.8C). Fire frequency was greater for aerial and drill seeded sites than sites with only drill seeding and showed a slight decrease as precipitation increased (Figure 3.8C). Variation in fire frequency for untreated and aerially seeded sites decreased as precipitation increased (Figure 3.8C). Fire frequency for aerially seeded sites decreased as precipitation increased (Figure 3.8C).

Recent rehabilitation types did not have significant within group similarity in biomass composition (A=0.016, p=0.13). Biomass components were significantly different along the elevational gradient (p=0.007) but within group homogeneity was low (A=0.058) suggesting a high degree of variability demonstrated by the NMS (Figure 3.9A). Analysis of biomass by treatment type within elevation improved within-group similarity and significance (A=0.109, p=0.004) but there was still considerable variation within treatment and elevation groups (Figure 3.9B).

The MRPP pairwise-comparisons showed biomass composition was significantly different between aerial seeded sites above 1521 m and four other groups (Figure 3.9B): sites below 1020 m that were aerially seeded (A=0.211, p<0.004) or left untreated (A=0.247, p<0.0002); and aerially seeded sites that were found between 1021-1270 m (A=0.096, p<0.01) or 1271-1520 m (A=0.194, p<0.003). The difference among treatment and elevation groups was primarily due to a significant difference in annual grass biomass (F=2.34, p=0.026), but bunchgrasses biomass approached significance (F=1.86, p=0.078). The biomass of forbs (F=1.29, p=0.264) and shrubs (F=1.45, p=0.189) did not differ among treatments grouped by elevation. Treatments above 1521m had little annual grass biomass and were dominated by bunchgrass and shrub biomass, while aerial treatments at other

elevations and untreated sites the lowest elevations had much less shrub and more annual grass biomass (Figure 3.10).

As elevation increased, shrub biomass increased (Figure 3.11A) and annual grass biomass decreased significantly (Figure 3.11B), but the strength of the relationship was weak. There was no significant relationship between elevation and forb biomass (Figure 3.11C) or perennial bunchgrass biomass (Figure 3.11D). The degree of variation and lack of strong relationships between plant biomass and elevation explain why the MRPP did not detect significant differences among the categorical elevation ranges.

Discussion

Two categories of variables consistently appeared as predictor variables of fire regime characteristics: treatments and site aridity. The best-fit model for each variable included pre-fire vegetation treatment and the number of one or more of following: total treatment, aerial seeding, or drill seeding. Our research adds to a growing body of work that examines what shapes post-fire communities in the sagebrush steppe (Miller et al. 2013).

Climate was a key predictor of fire regime characteristics and adequate rain after rehabilitation is key to the establishment of seeded species after rehabilitation. More arid locations (lower precipitation or greater vapor pressure deficit) were prone to more fires at greater frequency. In our study area, precipitation increased with elevation. Greater spring moisture had no effect on fire regime characteristics on sites that were recently drill seeded, but on aerially seeded sites, decreased aridity resulted in fewer fires, lower fire frequency, and increased time between fires. *Artemisia tridentata* subsp. *wyomingensis* communities have lower vegetation recovery from fire and are highly susceptible to fire, but sites with

greater precipitation, such as *A. tridentata* subsp. *vaseyana* communities, are more resilient to fire (Chambers 2014) and *A. tridentata* subsp. *wyomingensis* recovery may be faster with greater precipitation after a fire (Shinneman and McIlroy 2016). Our study suggests that precipitation gradients within *A. tridentata* subsp. *wyomingensis* are important in determining fire regimes. Spring moisture is important for native bunchgrass establishment (Hulet et al. 2010) suggesting rehabilitation on more arid sites may hinder when native grasses are used. *Bromus tectorum* can establish in arid environments (Brooks et al. 2016). Though the bulk of *B. tectorum* seed germinates in autumn (Mack and Pyke 1983), growth and reproduction occur during the spring months (Hulbert 1955, Peterson 2003, Dyer et al. 2012). *Bromus tectorum* is more effective at accessing and taking advantage of water than native bunchgrasses (Link et al. 1990, Melgoza et al. 1990, Aguirre and Johnson 1991, Booth et al. 2003). Though spring moisture is key to the establishment of native perennial bunchgrasses, the increase in spring moisture in recent decades may favor *B. tectorum* when present in a rehabilitated site, thus contributing to more fires at greater frequency.

Time was an important predictor variable for the number of fires and fire return interval. The species used in vegetation treatments changed over the time. Prior to 1970, *Agropyron desertorum* was frequently used alone or in seed mixes with 3 or fewer species (Hull and Klomp 1966, Pilliod and Welty 2013). In the 1970s, "Fairway wheatgrass," *Agropyron cristatum*, was seeded with *A. desertorum*, with the use of *A. cristatum* becoming increasingly dominate in the late 1970s and early 1980s (Pilliod and Welty 2013, NOC 2014). In the late 1980 and early 1990s, vegetation treatments included *A. cristatum* and *A. fragile* (Pilliod and Welty 2013, NOC 2014). Between 2000 and 2008 post-fire rehabilitation treatments included *E. wawawaiensis* and *A. fragile* (Pilliod and Welty 2013, NOC 2014).

We found that the numbers of fires did not differ along the climate or treatment number gradients on sites that first burned in prior to 1970, but on sites that burned for the first time after 2000, the number of fires double on more arid sites and tripled as treatment number increased. Other research has shown that older vegetation treatments are more likely to decrease invasive species when the seeded species established (Pyke et al. 2013). Mature bunchgrasses inhibit *B. tectorum* better than seedlings (Mangla et al. 2011, Reisner et al. 2013, Davies and Johnson 2017) and *A. desertorum* has also been identified as a species that inhibits *B. tectorum* growth and seed production (Yoder and Caldwell 2002, Davies and Johnson 2017) so it is possible that there is less *B. tectorum* present on the older seedings which would reduce the likelihood of fire. Since *E. wawawaiensis* is unpalatable to cattle and goats (Jones et al. 1994, Ganskopp et al. 1996, David et al. 1997) and more recent treatments are susceptible to *B. tectorum* invasion (Pyke et al. 2013, Davies and Johnson 2017), on sites seeded between 2000-2008 it is likely fine fuels accumulated from annual and perennial grasses resulting in more fires. Fire return intervals were shortest for sites first treated between 1975 and 1995 when *A. cristatum* was seeded at high rates with low diversity. *Bromus tectorum* can establish and survive in the presence of *A. cristatum* (Aguirre and Johnson 1991, Arredondo et al. 1998) and be co-dominant with *A. cristatum* and *Poa secunda* in this system (Bowman-Prideaux et al. In Prep). Communities with *B. tectorum* are more likely to have fire spread throughout the system (Link et al. 2006) burned more frequently than native vegetation (Balch et al. 2013). The presence of *B. tectorum* may be contributing shorter fire return intervals at sites seeded between 1975 and 1995.

The number of treatments showed a combination of expected and unexpected results. Sites with recent fires often get post-fire rehabilitation (Pilliod and Welty 2013), therefore

the number of treatments should increase as the number of fires increases. We found increasing the number of treatments on sites that first burned between 1965 and 1975 only increase the number of fires slightly while the increase in fire number increased from one to three on sites that burned for the first time between 2005-2014. The number of fires increased when the most recent rehabilitation was aerial or untreated, but fire number did not increase when the most recent treatment included drill seeding. Drill seeding also had longer fire return intervals and lower fire frequency in the last 20 years. This consistent effect on fire regimes suggests there is a consistent difference in fuels characteristics between the two rehabilitation treatments.

The choice of vegetation seeding technique influences the fuels composition and can affect the likelihood of successful plant establishment. Sites with aerial seeding prior to the most recent fire generally had more fires overall and, in the last 20 years, fire occurred at shorter return intervals and at greater frequency. Aerial seeding grass species results in only low levels of seeded species cover in forested systems (Hunter et al. 2006). In the sagebrush steppe, aerial seeding of nonnative perennial bunchgrass after one fire resulted in greater bunchgrass cover at high elevations without herbicide (Knutson et al. 2014) and possibly at low elevations when combine with herbicide application reduce annual grasses prior to seeding (Wirth and Pyke 2011). One drawback of aerial seeding is a high potential of low soil contact with the seed and results in low establishment of seeded species (BLM 2007). Great Basin native bunchgrass and forb recovery is not enhanced by aerial seeding after a fire (Bruce et al. 2007) and is inhibited when nonnative grasses, like *A. cristatum*, are included in the seed mix (Knutson et al. 2014). Aerial seeding does not increase *Artemisia*

tridentata cover or density after a fire (Ott et al. 2017) even after two decades (Knutson et al. 2014).

In our study area, the majority of post-fire aerial seed treatments only included *A. tridentata* seeded into existing fire resilient vegetation, such as *A. cristatum*, *A. fragile*, or *E. wawawaiensis* (Secar cultivar) (Pilliod and Welty 2013). The typical method of aerially seeding *A. tridentata* subsp. *wyomingensis* in the winter without drill seeding, which was typical in our study area, is unlikely to promote shrub establishment after a fire (Ott et al. 2017). When aerial seeding is combined with seeding into *A. cristatum* stands that are known to inhibit all *A. tridentata* subspecies (Newhall et al. 2011), *A. tridentata* subsp. *wyomingensis* will not establish. *Agropyron cristatum* inhibits native forbs and grasses leading to sites with low diversity or evenness (Marlette and Anderson 1986, Pellant and Lysne 2005, Gunnell 2009) even when native species initially establish at the same rate as *A. cristatum* (Nafus et al. 2015). This suggests sites where native forbs and grasses were aerially seeded may also fail to establish. The Secar cultivar of *E. wawawaiensis* is less palatable to cattle than other bunchgrasses used in post-fire rehabilitation (Jones et al. 1994, David et al. 1997) and avoided by goats (Ganskopp et al. 1996) increasing herbivore pressure on other native seeded species which is likely shifting the community to an unpalatable or invasive dominated system (Orrock and Witter 2010) where fuels accumulate over time and create continuous fuels that promote larger fires. Whether the aerial seeding is occurring in *A. cristatum* or *E. wawawaiensis* dominated communities in this study area, the long-term result is likely a low diversity grassland. Research in restored grasslands indicate that sites with poor seeded species establishment or low diversity were more susceptible to invasion by small seeded, winter annual species (Roscher et al. 2015), like *B. tectorum.*

Bromus tectorum likely contributed to our fire regime results. The number of fires and the frequency of fire was greatest below 1200 m. Annual grass biomass was greater at our low elevation sites and composed predominantly of *B. tectorum*. Aerial seeding treatments may lead to a localized increases in *B. tectorum* cover (Pyke et al. 2013), but the increase in *B. tectorum* cover is not seen at landscape scales (Knutson et al. 2014). Poor establishment of seeded species results in successful establishment and subsequent invasion of *B. tectorum* (Bradford and Lauenroth 2006, Condon et al. 2011), but modeling suggests even successful establishment of seeded species after a fire may be insufficient to limit the risk of *B. tectorum* invasion in *A. tridentata* subsp. *wyomingensis* ecological sites after a fire using current seeding strategies (Evers et al. 2013). Low levels of *B. tectorum* cover increases the probability of fire spreading (Link et al. 2006) and communities where *B. tectorum* is a dominant species have more frequent fires than other arid plant communities (Balch et al. 2013).

Drill seeding treatments mitigated the effect of aerial seeding treatments on fire regime characteristics. Seeds that are drill seeded have greater soil contact than when aerially seeded, which likely contributes to greater species establishment (BLM 2007). Drill seeding can increase native bunchgrass cover when nonnative grasses are not included in the seed mix (Wirth and Pyke 2011, Knutson et al. 2014) and decrease *B. tectorum* cover when seeded species establish successfully (Jessop and Anderson 2007, Pyke et al. 2013, Knutson et al. 2014), but drill seeding success is complicated. Seeding success is dependent on pre-fire plant communities and the climate during the year after fire and rehabilitation (Miller et al. 2013). Species composition and establishment are affected by soil composition and seeded species used (Williams et al. 2017) and species dominance shifts in response to

differences in soils and climates (Rollins et al. 1968, Bradford and Lauenroth 2006, Morris et al. 2011, Williams et al. 2017). Freezing and drought can limit the establishment of native grass and forb species used in rehabilitation (Svejcar et al. 2017). Native grasses have difficulty establishing when spring moisture is low (Hulet et al. 2010). Native bunchgrasses and forbs recruit well on flat sites and slopes with northern aspects, but *B. tectorum* can inhibit native plant establishment on southern aspects (Kulpa et al. 2012). The drill till depth influences the species that establish on a site (Ott et al. 2016). Increasing the seeding rate can promote the establishment of native herbaceous species (Thompson et al. 2006) and *A. tridentata* subsp. *wyomingensis* (Ott et al. 2017). Increasing native species diversity can limit resources for *B. tectorum* (Reisner et al. 2013) and build plant communities that are more resilient to the timing of fires (Wright and Klemmedson 1965).

Many factors may affect fire regimes, including average climate and interannual variation in climate (Miller et al. 2013, Pilliod et al. 2017), available fuels (Chambers et al. 2014b, Davies et al. 2014, Strand et al. 2014), historical fire management practices (Hudak et al. 2011, Martinson and Omi 2013), and interactions between climate, fuels, and management (Hurteau et al. 2014). There is lack of understanding how vegetation treatments affect fire regimes across arid landscapes (Davies et al. 2010, Hudak et al. 2011, Martinson and Omi 2013). Though some research has looked at treatments after one fire (Pyke et al. 2013, Knutson et al. 2014, Davies and Johnson 2017, Ott et al. 2017, Williams et al. 2017) our results included sites with fire and rehabilitation histories over >50 years. Our results suggest that spring moisture is an important determinant of fire regime, but the effect of spring moisture varies among rehabilitation techniques. Drill seeded sites had fewer fire fires over the 60-year study period and in recent years had longer fire return intervals and

less frequent burns than aerial seeded sites. This trend did not differ along the moisture gradient and fire regimes on recently drilled sites had similar fire regimes despite differences in moisture and time since first fire. Aerially seeded sites had more frequent fires and were dominated by *A. cristatum*, *E. wawawaiensis*, or *B. tectorum*. *Elymus wawawaiensis* and *B. tectorum* are unpalatable to many livestock and some senesced *A. cristatum* is typically left after cattle grazing resulting in an accumulation of fine fuels that likely contributed to frequent fires. If the goal is to minimize the number and frequency of fires (Jewell 2015a), more drill seeding may be necessary on sites historically dominated by *A. tridentata* subsp. *wyomingensis*. Aerial seeding treatments in our study area were generally seeded *A. tridentata* subsp. *wyomingensis* and occurred in established *Agropyron* seedings that are resilient to fire but likely outcompete and inhibit recruitment of *A. tridentata*. The on-the-ground conditions that lead to the choice to aerially seeded (e.g.- treatment legacy of seeded species) should be re-evaluated. Additional treatments, such reduction of *A. cristatum* and *E. wawawaiensis* or the inclusion of drill seeding, may better establish diverse communities that are more palatable to livestock and wildlife, more resilient to *B. tectorum* invasion, and less prone to fire.

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Tables

Table 3.1 Geospatial data extracted from shapefiles and rasters and used in in the predictor matrix for the nonparametric multiplicative regression analyses.

Predictor Variable	Note	Source
Aerial Treatments	Total Number	Rehabilitation shapefiles from multiple sources: • Jarbidge and Bruneau Field Office, BLM, Idaho (personal communication) • Mountain Home Air Force Base, DOD (personal communication) • National Operations Center, BLM (https//catalog.data.gov) • Land Treatment Digital Library, USGS (https://ltdl.wr.usgs.gov)
Drill Treatments	Total Number	
All Rehabilitation Treatments	Total Number Includes Drill and Aerial	
First Fire Year	First year a fire burned the site	
First Treatment Year	First year a vegetation treatment occurred	
First Vegetation Treatment	First treatment at the site, includes sagebrush removal and post-fire rehabilitation	
First Treatment Type	First type of post-fire rehabilitation treatment	
Pre-fire Vegetation Treatment	Effort prior to most recent fire	
Post-fire Vegetation Treatment	Effort After the Most Recent Fire	
Resistance and Resilience Rating	Based on Maestas et al. (2016)	Sage Grouse Initiative (https://map.sagegrouseinitiative.co
Distance to Nearest road	Within 5 km Radius, Calculated	USDA NRCS GeoSpatial Gateway (https://gdg.sc.egov.usda.gov)
Total Road Length	Within 5 km Radius, Calculated	
Total Area of Private Land	Within 5 km Radius, Calculated	
Elevation (10 m resolution)	Digital Elevation Model	
Maximum Temperature*	Monthly, Seasonal, Annual	Parameter-elevation Relationships on Independent Slopes Model (http://prism.oregonstate.edu/)
Minimum Temperature*	Monthly, Seasonal, Annual	
Maximum Vapor Pressure Deficit*	Monthly, Seasonal, Annual	
Minimum Vapor Pressure Deficit*	Monthly, Seasonal, Annual	
Precipitation	Monthly, Seasonal, Annual	

* - These variables include the 30-year average for each month, season, and the annual (16 variables in total).

Table 3.2 The NPMR best-fit models for each fire regime variable. The explanatory variables that compose the models include the first year a site was burned (1st Fire Year), 30 year mean minimum vapor pressure deficit from March-May (Spring VPD min), the pre-fire vegetation treatment prior the fire (Pre-fire Veg), the number of times a site was aerially seeded (Arial Seeding (n)), and 30 year mean spring precipitation from March – May (Spring Precip).

Response Variable	Eval xR^2	Model Fit xR^2 (±SE)	Avg Size	Predictor Variable	Sensitivity	Tolerance	
Fires (n)*	0.8	0.83 (±0.0)	31.2	1st Fire Year	0.09	9.45	(15%)
				Spring VPD min	0.05	0.26	(25%)
				Treatment (n)	0.05	1.5	(25%)
				Pre-fire Veg†	-	-	-
Fire Return Interval*	0.78	0.81 (±0.0)	43.32	Aerial Seeding (n)	0.22	0.5	(10%)
				1st Year Treated	0.15	10.35	(15%)
				Spring VPD min	0.02	0.46	(45%)
				Pre-fire Veg†	-	-	-
Fire Frequency*	0.76	0.77 (±0.0)	33.29	Drill Seeding (n)	0.07	0.75	(25%)
				Spring Precip	0.05	6.28	(25%)
				Aerial Seeding (n)	0.03	0.25	(5%)
				Pre-fire Veg†	-	-	-

Eval xR2 = The correlation from original model analysis.
Model Fit xR2 = Correlation based on the bootstrap analysis.
Avg. Size = The number of sample units contributing to the estimate of occupancy.
SE = Standard error.
* $p < 0.01$
† Categorical variable. Sensitivity and tolerance can only be calculated with continuous variables.

Figures

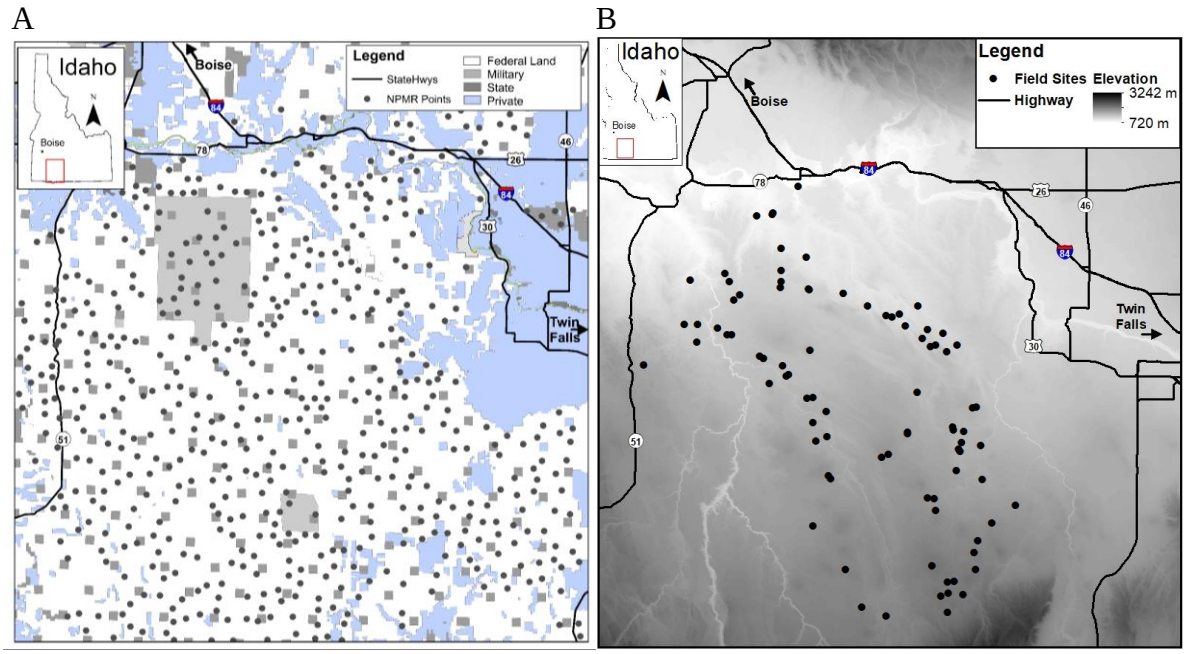


Figure 3.1 Climate, environment, and data on anthropogenic features as well as the location's fire and management history was extracted from GIS source or derived layers for 573 sites in southern Idaho, USA(A). Biomass was collected at 67 sites along the elevation gradient (B).

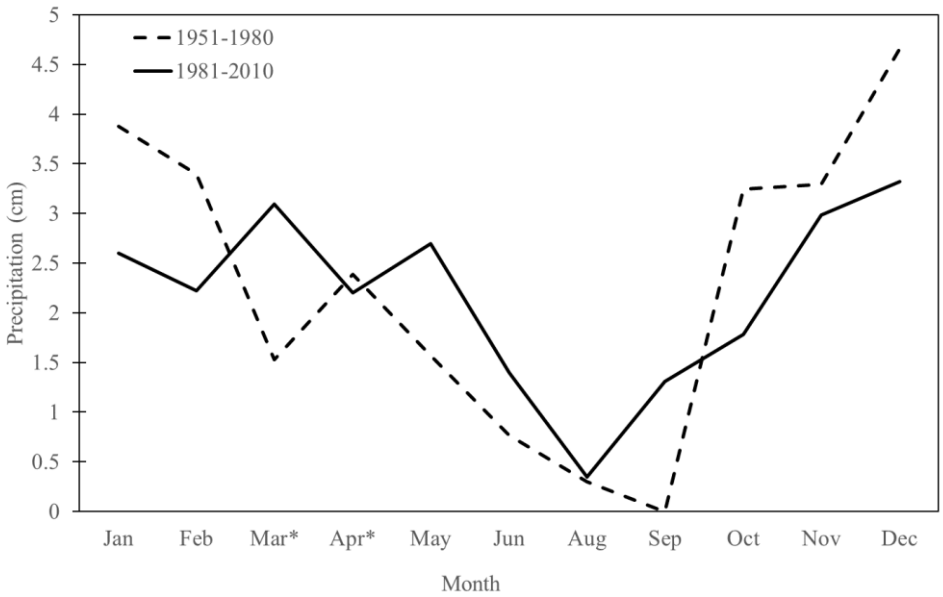


Figure 3.2 Thirty-year average monthly precipitation for Mountain Home, Idaho, northwest of the study area. Data is from PRISM models (http://prism.oregonstate.edu). Months used for spring vapor pressure deficit and precipitation are denoted (*).

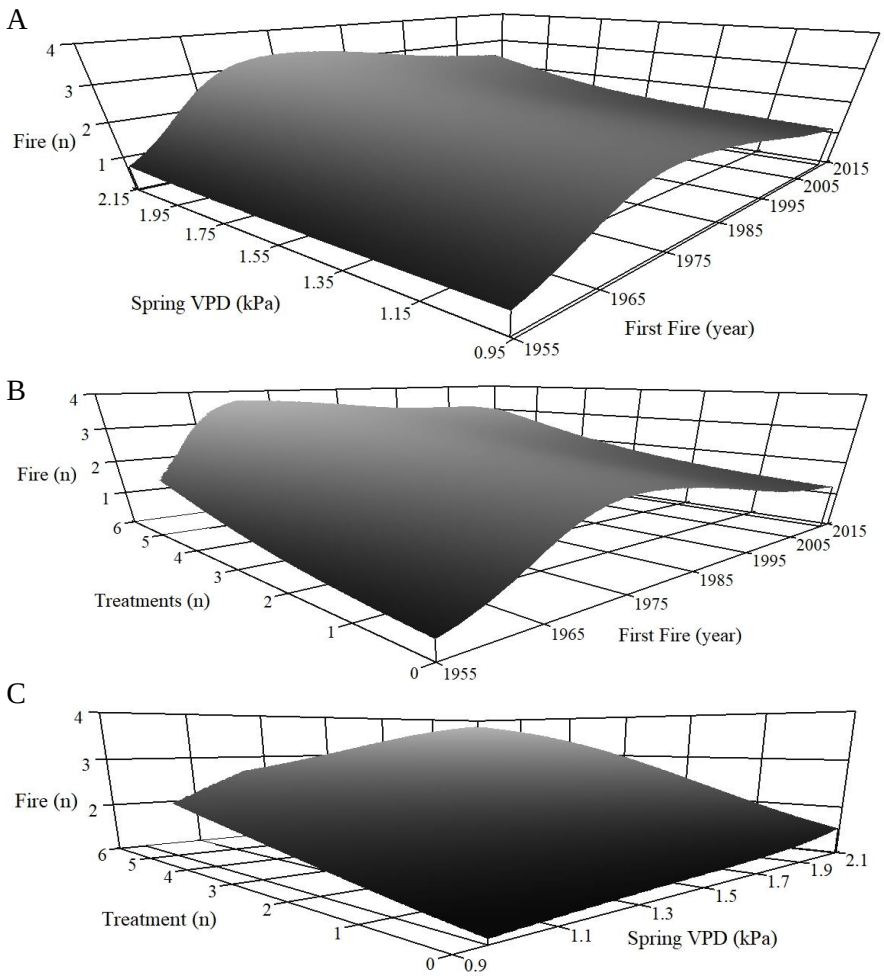


Figure 3.3 The Nonparametric Multiplicative Regression modeled relationship response of number of fires to (A) the first year the site experienced fire and the 30-year average minimum vapor pressure deficit in spring (spring VPD), (B) the first year the site experienced fire and the total number of treatments, and (C) the 30-year average minimum vapor pressure deficit in spring and the total number of treatments. Color scale ranges from 0 fires (black) to 4 fires (gray).

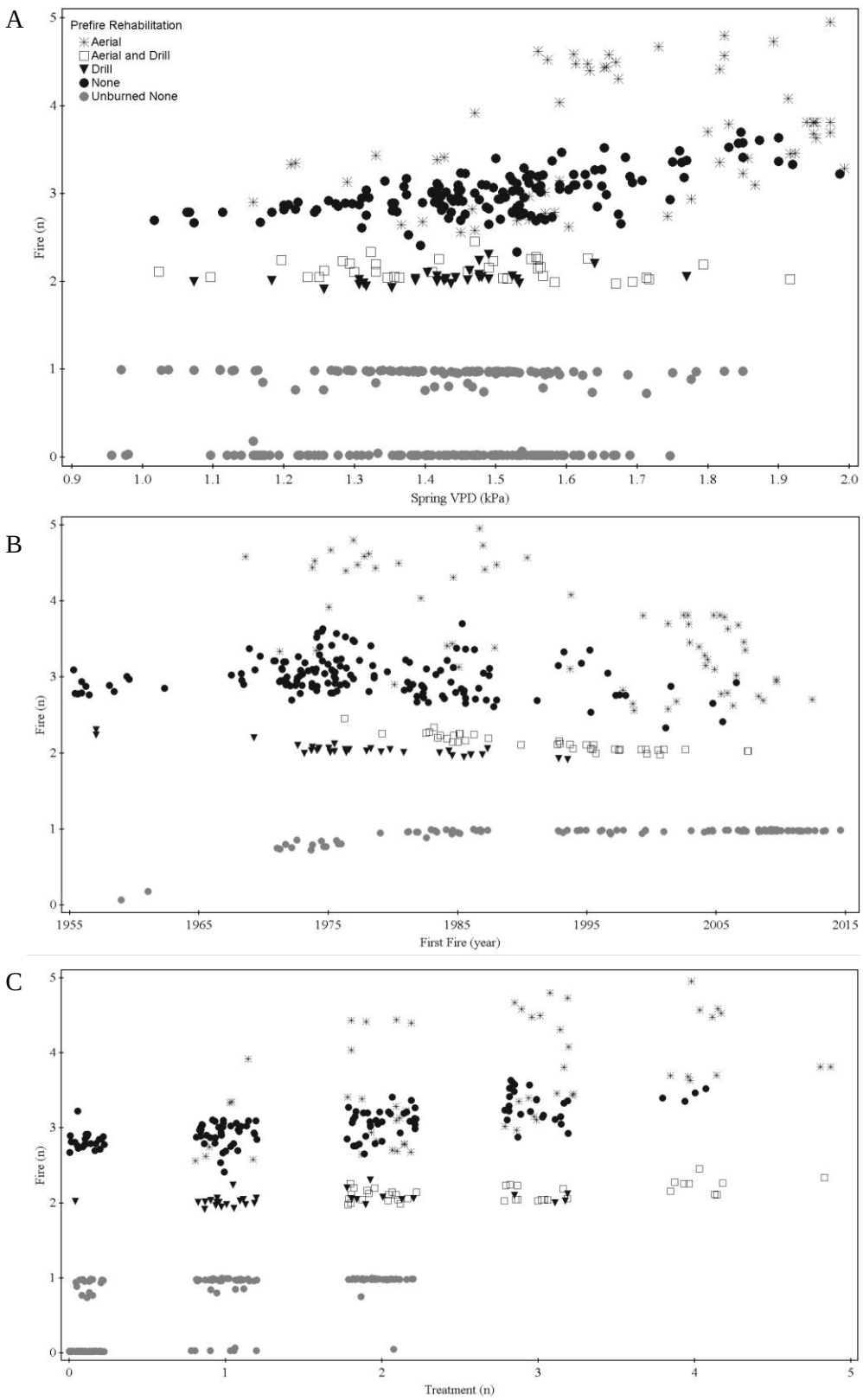


Figure 3.4 The modeled relationship between the number of fires grouped by the type of pre-fire rehabilitation treatment (none, aerial, or drill seeding) prior to the most recent fire along the gradient in (A) the minimum spring vapor pressure deficit (VPD), (B) the year the site first burned in a fire, and (C) the total number of rehabilitation treatments (both aerial and drill seeding). Five percent jittering along the y-axis (A,B) or x-axis (C) was used to see overlapping treatments.

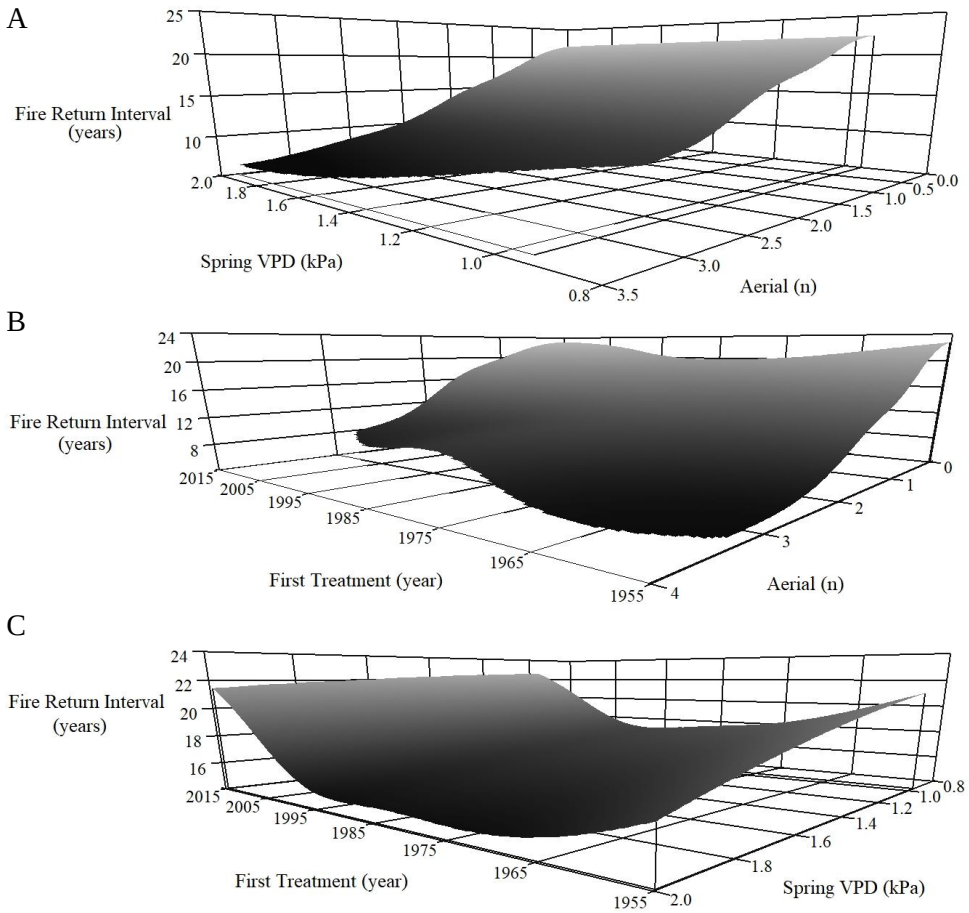


Figure 3.5 The Nonparametric Multiplicative Regression modeled relationship response of fire return interval (FRI) to (A) the number of aerial seeding treatments and the 30-year average minimum vapor pressure deficit in spring (spring VPD), (B) the first year a site had a rehabilitation treatment and the number of aerial seeding treatments, (C) the first year a site had a rehabilitation treatment and the spring VPD. Color scale ranges from shorter FRIs (black) to longer FRIs (gray). Unshaded areas in the predictor space represent areas where predictor variable data was insufficient to model the relationship.

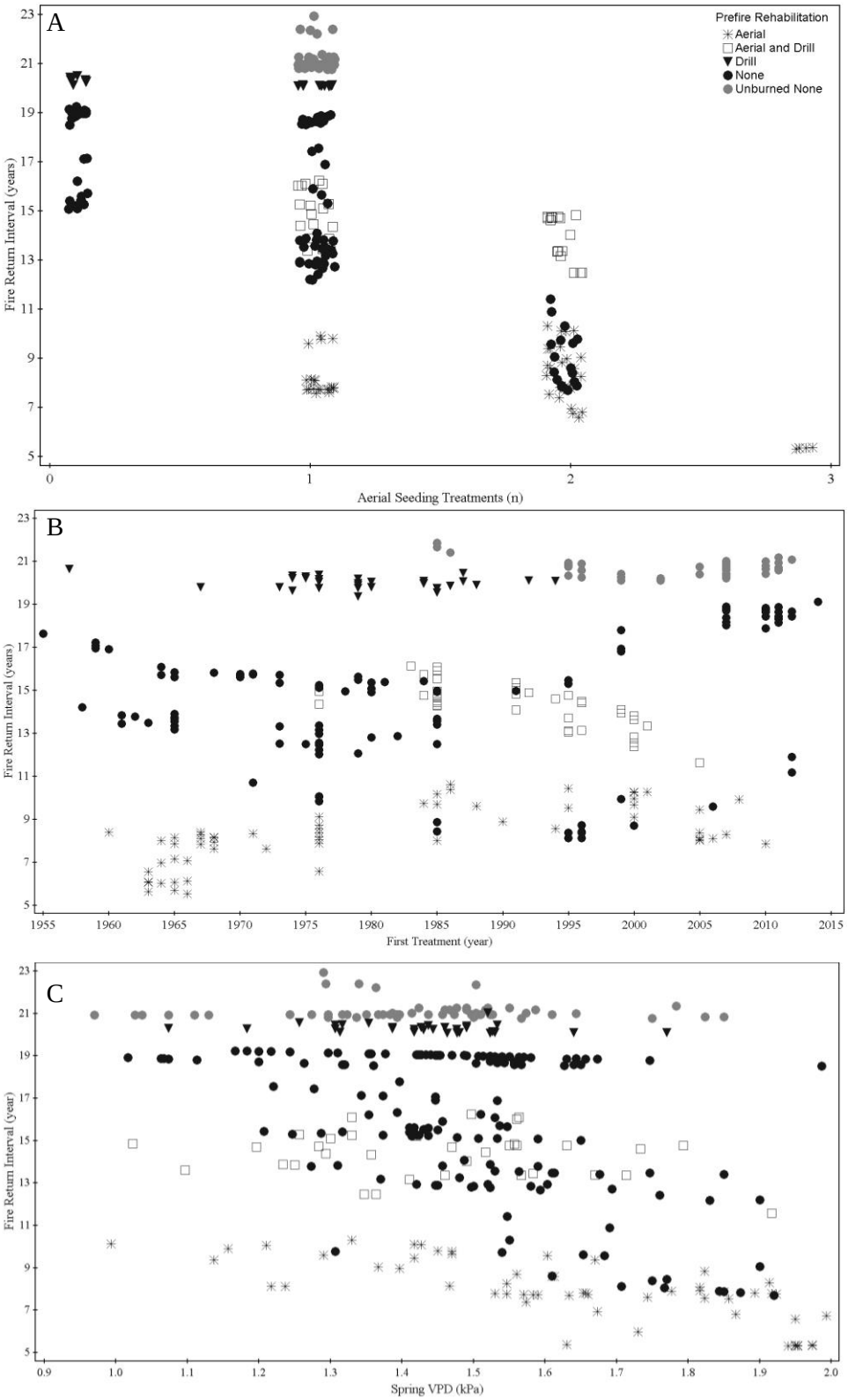


Figure 3.6 The modeled relationship between the fire return interval grouped by the type of pre-fire rehabilitation treatment (none, aerial or drill seeding) prior to the most recent fire along with (A) the number of aerial seeding treatments, (B) first treatment year, and (C) the 30 year average spring vapor pressure deficit. Figures include 5% jittering along the x-axis (A) or y-axis (B, C) was used to see overlapping treatments.

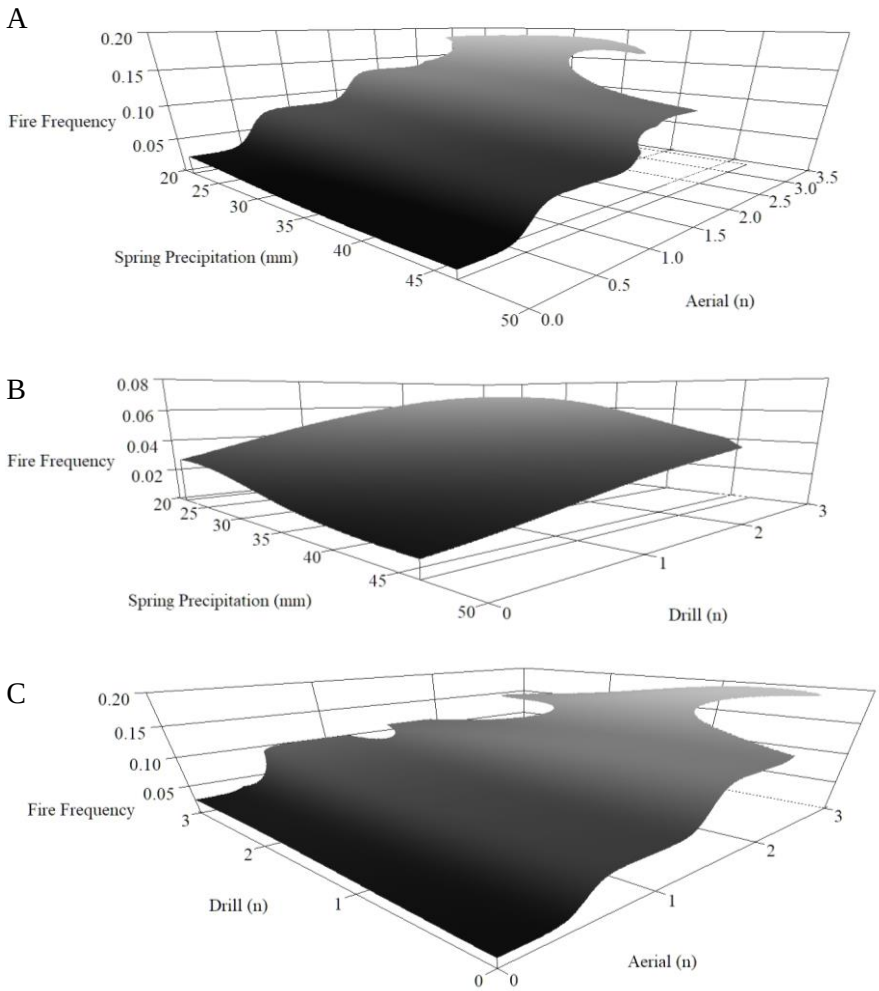
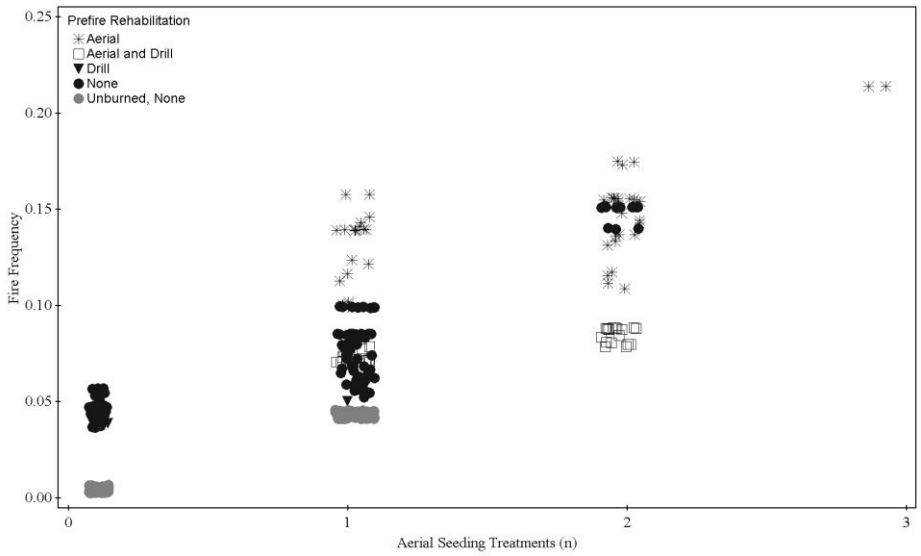
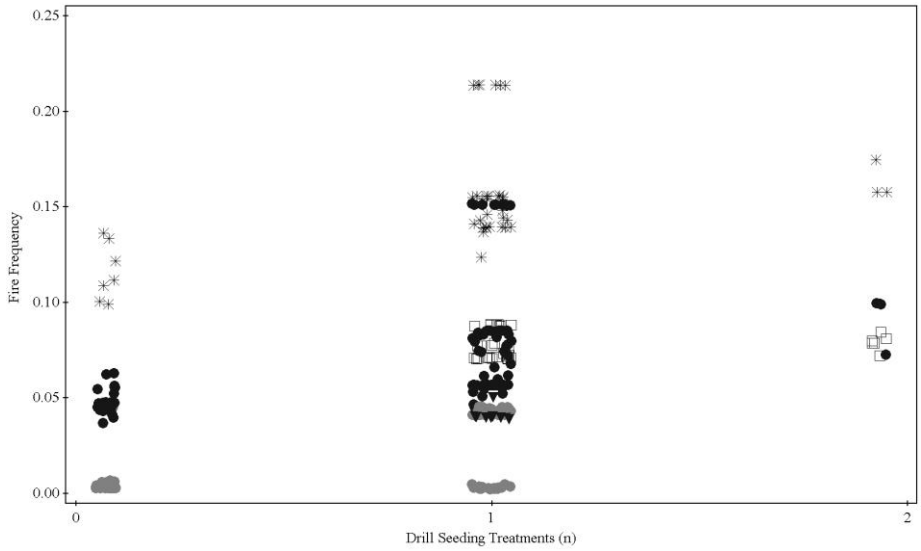


Figure 3.7 The Nonparametric Multiplicative Regression modeled relationship response of fire frequency to (A) the 30-year average spring precipitation and the number of aerial seeding treatments, (B) the 30-year average spring precipitation and the number of drill treatments, and (C) the number of drill seeding and the number of aerial seeding treatments. Color scale ranges from less frequent fires (black) to more frequent fires (gray). Unshaded areas in the predictor space represent areas where predictor variable data was insufficient to model the relationship.

A



B



C

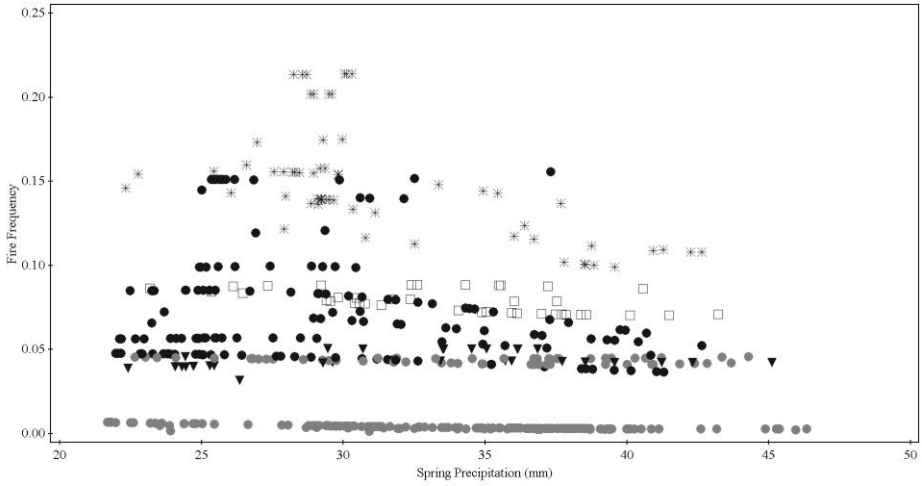


Figure 3.8 The modeled relationship between fire frequency grouped by the type of pre-fire rehabilitation treatment (none, aerial or drill seeding) prior to the most recent fire as the number of aerial (A) or drill seeding treatments (B) increased and along the gradient in spring precipitation (C) Figures include 5% jittering along the x-axis (A,B) or y-axis (C) was used to see overlapping treatments

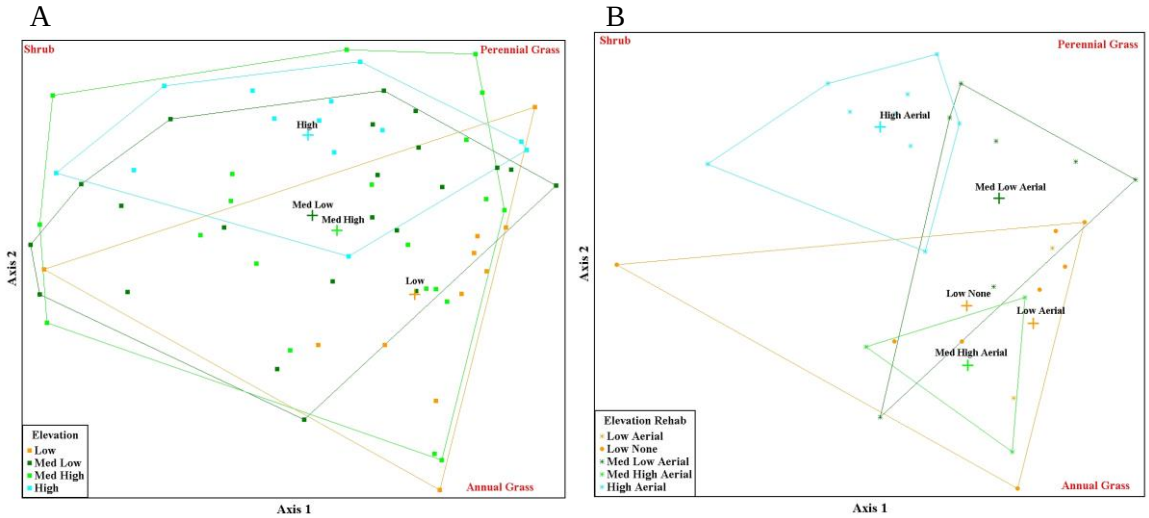


Figure 3.9 NMS ordination of the biomass grouped by elevation (A) and elevation and treatment types (B). Elevation ranges were low (770-1020m), medium low (1021-1270 m), medium high (1271-1520m), and high (1521-1780 m). Treatments shown include aerial seeding (Aerial) or unntreated sites (None). Centroids for each elevation are denoted (+). Plant functional groups (red) indicate where the biomass for each group was the greatest (e.g. Shrub biomass increased from right to left on Axis 1 and from bottom to top on Axis 2).

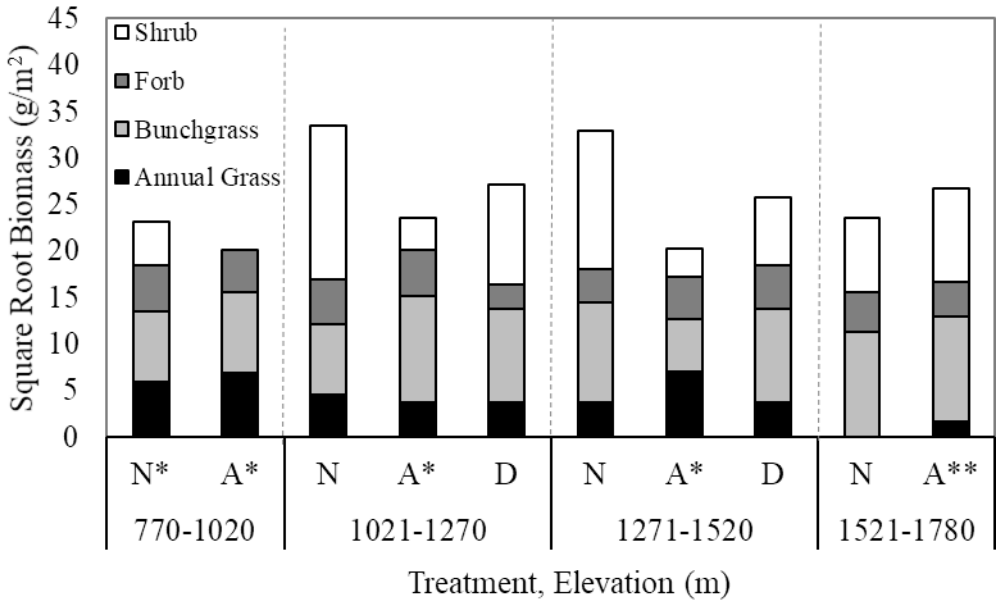


Figure 3.10 Mean biomass of each plant functional group for each treatment (Aerial, A; Drill, D; Untreated, N) along the elevation gradient: low (770-1020m), medium low (1021-1270 m), medium high (1271-1520m), and high (1521-1780 m). Drill seeded sites at low and high elevations had an n=1 and were dropped from the analysis. Aerial seeding treatments above 1521 m (**) were significantly different from four other treatment-elevation groups (*) in the multiple response permutation procedure.

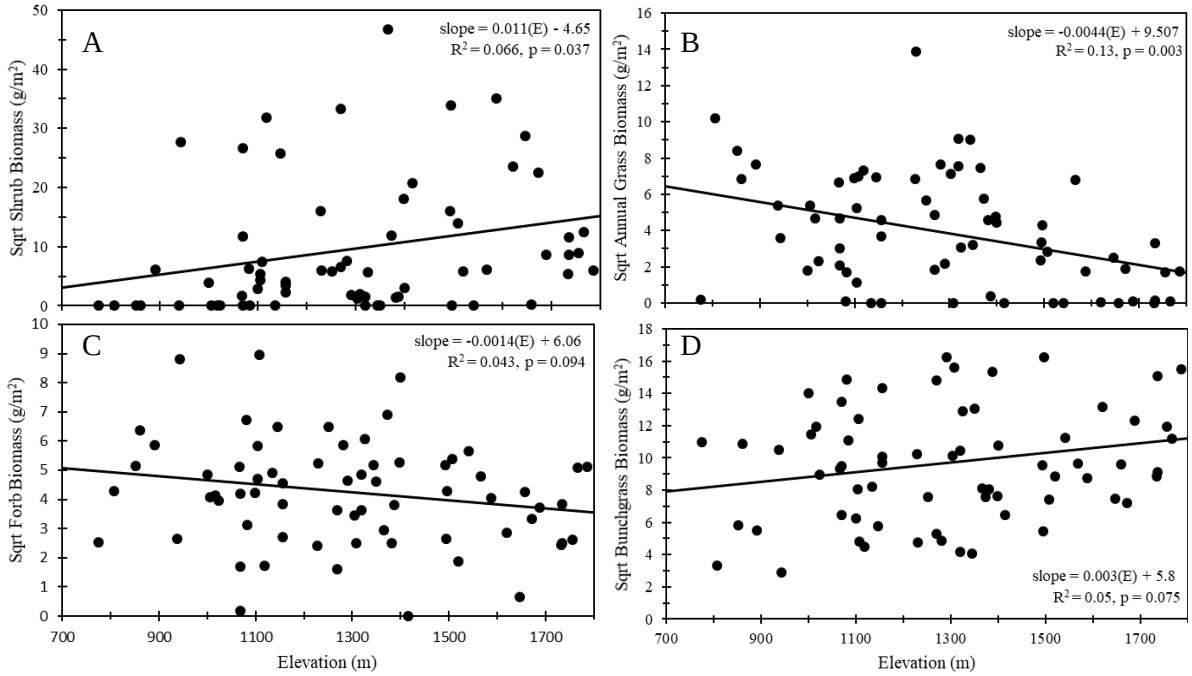


Figure 3.11 The relationship between elevation and biomass of each functional group analyzed: shrub (A), annual grass (B), forb (C) and perennial bunchgrass (D). Y-axis values are in the square root (sqrt) of the biomass collected. Lines show the linear regression slope where E is elevation. The strength of the relationship between biomass and elevation (R^2) provided.

Appendix A: Supplementary Information for Chapter 1

Table 1.A1 Species list for all species found across the two study years. Not all species were included in the primary matrix for the analysis. Bolded species symbol indicate nonnative species. Plant species codes from USDA Plants database (https://plants.usda.gov/)

Symbol	Species
ACHY	*Achnatherum hymenoides* (Roem. & Schult.) Barkworth
ACTH7	*Achnatherum thurberianum* (Piper) Barkworth
AGCR	*Agropyron cristatum* (L.) Gaertn.
AGDE2	*Agropyron desertorum* (Fisch. ex Link) Schult.
AGGL	*Agoseris glauca* (Pursh) Raf.
ALAC4	*Allium acuminatum* Hook.
ARAR8	*Artemisia arbuscula* Nutt.
ARMI	*Arabis microphylla* Nutt.
ARNO4	*Artemisia nova* A. Nelson
ARTRW8	*Artemisia tridentata Nutt. ssp. wyomingensis* Beetle & Young
ASNE6	*Astragalus newberryi* A. Gray
ASPU9	*Astragalus purshii* Douglas ex Hook.
ASSC4	*Astragalus scaphoides* (M.E. Jones) Rydb.
ATCA2	*Atriplex canescens (*Pursh) Nutt.
ATCO	*Atriplex confertifolia* (Torr. & Frém.) S. Watson
BAPR5	*Bassia prostrata* (L.) A.J. Scott
BASA3	*Balsamorhiza sagittata* (Pursh) Nutt.
BRTE	*Bromus tectorum* L.
CABR4	*Calochortus bruneaunis* A. Nelson & J.F. Macbr.
CAQU2	*Camassia quamash* (Pursh) Greene
CASTI2	*Castilleja spp.* Mutis ex L. f.
CETE5	*Ceratocephala testiculata* (Crantz) Roth
CHJU	*Chondrilla juncea* L.
CHVI8	*Chrysothamnus viscidiflorus* (Hook.) Nutt.
COPA3	*Collinsia parviflora* Lindl.
DEPI	*Descurainia pinnata* (Walter) Britton
DESO2	*Descurainia sophia* (L.) Webb ex Prantl
ELEL5	*Elymus elymoides* (Raf.) Swezey
ELMU3	*Elymus multisetus* M.E. Jones
EPBR3	*Epilobium brachycarpum* C. Presl
EPMI	*Epilobium minutum* Lindl. ex Lehm.
ERNA10	*Ericameria nauseosa* (Pall. ex Pursh) G.L. Nesom & Baird
ERNA5	*Erigeron nanus* Nutt.
ERPU2	*Erigeron pumilus* Nutt.
FEID	*Festuca idahoensis* Elmer

Table 1.A1 Species list (continued)

Symbol	Species (cont)
IOAL	*Ionactis alpina* (aka. *Aster scopulorum*) (Nutt.) Greene
KRLA	*Krascheninnikovia lanata* (Pursh) A. Meeuse & Smit
LASE	*Lactuca serriola* L.
LECI4	*Leymus cinereus* (Scribn. & Merr.) Á. Löve
LEPE2	*Lepidium perfoliatum* L.
LILE3	*Linum lewisii* Pursh
LIPU11	*Linanthus pungens* (Torr.) J.M. Porter & L.A. Johnson
LOMAT	*Lomatium* Raf.
LUNE	*Lupinus nevadensis* A. Heller
LUPIN	*Lupinus* spp. L.
MACA2	*Machaeranthera canescens* (Pursh) A. Gray
MESA	*Medicago sativa* L.
ORLU2	*Orthocarpus luteus* Nutt.
PESP	*Penstemon speciosus* Douglas ex Lindl.
PHAC2	*Phlox aculeata* A. Nelson
PHHO	*Phlox hoodii* Richardson
PHLO2	*Phlox longifolia* Nutt.
POSE	*Poa secunda* J. Presl
PSSP6	*Pseudoroegneria spicata* (Pursh) Á. Löve
SATR12	*Salsola tragus* L.
SIAL2	*Sisymbrium altissimum* L.
SOAR2	*Sonchus arvensis* L.
SPMU2	*Sphaeralcea munroana* (Douglas) Spach
STPI	*Stanleya pinnata* (Pursh) Britton
THIN6	*Thinopyrum intermedium* (Host) Barkworth & D.R. Dewey
TRDU	*Tragopogon dubius* Scop.
VULPI	*Vulpia* C.C. Gmel.
ZIVE	*Zigadenus venenosus* S. Watson

Table 1.A2 Variables included in the secondary matrix.

Data Type	Attribute	Source
PRISM[1]		
	Mean annual precipitation	http://prism.oregonstate.edu/
	Mean high temperature	
	Mean low temperature	
Soils		
	Soil temperature and moisture regime	Maestas et al. (2016)
	Ecological site vegetation	NRCS Geospatial Gateway, SSURGO shapefile (https://gdg.sc.egov.usda.gov/)
	Soil texture[2]	
Elevation		
	Elevation (ground truth)	Garmin 60X GPS, 3-4 m resolution
	Elevation categories (250 m interval)	
Rehabilitation Treatment		
	Most recent type of treatment	Jarbidge Field Office, BLM, Idaho
	Total number	Bruneau Field Office, BLM, Idaho
	Time since most first treatment	USGS Land Treatment Digital Library (https://ltdl.wr.usgs.gov/)
	Time since most recent treatment	
	Number of drill seedings	BLM National Operations Center Completed Treatments (http://insideidaho.org/)
	Time since most recently drilled	
	Time since first drill seeding	
	Number of aerial seedings	Mountain Home Airforce Base Natural Resources Specialist, Carl Rudeen (carl.rudeen.1@us.af.mil)
	Time since most recent aerial seeded	
	Time since first aerially seeded	
	Year of first treatment	
Fire History		
	Time since most recent fire	Historic Fires, BLM (http://insideidaho.org/)
	Time between two most recent fires	
	Fire number	
	Time since first fire	
	Year of first fire	

1- 30-year means

2- Soil texture was based on the Ecoclass Name attribute of the that included a general description of soil texture such as loam, sand, sandy loam, stony, and clay.

Table 1.A3 The plant cover MRPP multiple comparisons for comparing sites categorized by fire number (0, 1, 2, 3, 6) and recent post-fire rehabilitation treatments: aerial (A), drill (D), none (N). Comparisons marked by p-values with a * indicate significant differences after correcting for multiple tests using the Benjamini and Yekutieli False Discovery Rate (α = 0.0101). P-values in black are significant at α = 0.05.

	0D	0N	1A	1D	1N	2A	2D	2N	3A	3D	3N	6A	6N
0D													
0N	**0.003***												
1A	**0.005***	**0.003***											
1D	0.079	**0.001***	0.201										
1N	**0.015**	**0.004***	0.395	0.464									
2A	**0.041**	**0.001***	0.220	0.613	0.454								
2D	0.058	**0.001***	0.088	0.655	0.216	0.542							
2N	**0.019**	**0.001***	**0.046**	0.235	0.051	0.096	0.278						
3A	**0.006***	**0.002***	0.420	0.089	0.132	0.492	0.207	0.136					
3D	**0.020**	**0.001***	0.558	0.877	0.593	0.847	0.282	0.142	0.466				
3N	**0.027**	**0.001***	**0.047**	0.241	**0.035**	0.139	0.397	0.883	0.422	0.153			
6A	**0.014**	**0.001***	**0.003***	0.271	**0.024**	0.196	0.643	**0.037**	**0.014**	**0.028**	0.106		
6N	**0.033**	**0.002***	0.351	0.481	0.420	0.370	0.392	0.873	0.402	0.600	0.589	0.180	

Table 1.A4 The plant density MRPP multiple comparisons for comparing sites categorized by fire number (0, 1, 2, 3, 6) and recent post-fire rehabilitation treatments: aerial (A), drill (D), none (N). Bolded P-values are significant at α = 0.05. None of the treatments were significantly different when corrected for multiple comparisons using the Benjamini and Yekutieli False Discovery Rate (α = 0.0101).

	0D	0N	1A	1D	1N	2A	2D	2N	3A	3D	3N	6A	6N
0D													
0N	0.172												
1A	0.076	0.274											
1D	0.281	0.446	0.230										
1N	0.098	0.234	0.538	0.492									
2A	0.311	0.100	0.196	0.132	0.457								
2D	0.129	0.330	0.462	0.578	0.177	0.073							
2N	0.053	0.123	0.374	0.255	0.103	**0.045**	0.564						
3A	0.187	0.093	0.580	**0.026**	0.254	0.333	0.215	0.234					
3D	0.242	0.121	0.498	0.582	0.783	0.595	0.254	0.153	0.591				
3N	0.186	0.258	0.728	0.567	0.407	0.170	0.747	0.951	0.517	0.711			
6A	0.062	**0.031**	**0.045**	0.540	0.548	0.237	0.139	**0.028**	**0.023**	0.561	0.201		
6N	**0.023**	0.123	0.796	0.195	0.610	0.165	0.223	0.339	0.377	0.555	0.393	0.262	