

Running Head: Reburns Reduce Sagebrush Diversity.

Title: Repeated Fires Reduce Plant Diversity in Low-Elevation Wyoming Big Sagebrush Ecosystems (1984-2014).

Authors:

Adam L. Mahood *

Department of Geography

University of Colorado Boulder

GUGG 110, 260 UCB

Boulder, CO 80309-0260

Jennifer K. Balch

Department of Geography

University of Colorado Boulder

GUGG 110, 260 UCB

Boulder, CO 80309-0260

*Corresponding author

Abstract

Sagebrush is one of the most imperiled ecosystems in Western North America, having lost about half of its original 62 million hectare extent. Annual grass invasions are known to be increasing wildfire occurrence and burned area, but the lasting effects (> five years post-fire) that the resulting reburns have on these plant communities are unclear. We created a fire history atlas from 31 years (1984 to 2014) of Landsat-derived fire data to sample along a fire frequency gradient (zero to three fires) in an area of northern Nevada that has experienced frequent fire in this time period. 32% of our study area (13,000 km²) burned in large fires (over 404 ha) at least once, 7% burned twice, and 2% burned three or more times. We collected plant abundance data at 28 plots (N=7 per fire frequency), with an average time-since-fire of 17 years. We examined fire's effect on plant diversity using species accumulation curves, alpha-diversity (Shannon's dominance, Pielou's evenness and number of species), and beta diversity (Whittaker, Simpson, and Z indexes). For composition, we used non-metric multidimensional scaling. We then used PERMANOVA models to examine how disturbance history, temperature, precipitation and aridity around the time of the fire affected subsequent community composition and diversity.

One fire fundamentally changed community composition and reduced species richness, and each subsequent fire reduced richness further. Alpha diversity decreased after one fire. Beta diversity declined after the third fire. Cover of exotics was 10% higher in all burned plots, and native cover was 20% lower than in unburned plots, regardless of frequency. PERMANOVA models showed fire frequency and antecedent precipitation as the strongest predictors of beta diversity, while time since fire and vapor pressure deficit for the year of the fire were the strongest predictors of community composition. Given that a single fire has such a marked effect on species composition, and repeated fires reduce richness and beta diversity, we suggest that in lower elevation big sagebrush systems fire should be minimized as much as possible, perhaps even prescribed fire. Restoration efforts should be focused on timing with wet years

on cooler, wetter sites.

Key Words: Bromus tectorum, cheatgrass, fire, sagebrush, fire frequency, repeated fire, biodiversity, community composition, Artemisia tridentata ssp. wyomingensis

Introduction

Wildfire activity has been increasing across the western U.S. since the 1980s (Westerling et al. 2006, Dennison et al. 2014, Westerling 2016, Balch et al. 2017), and this is leading to concern among land managers in the U.S. Great Basin (Miller et al. 2013, Integrated Rangeland Fire Management Strategy Actionable Science Plan Team 2016, Chambers et al. 2017). This trend will likely continue as rising temperatures and more frequent drought events increase the probability of fire (Krawchuk et al. 2009, Moritz et al. 2012, Liu et al. 2013), and as these climatic factors combine with increased human ignition pressure (Balch et al. 2017) and land use change (Bowman et al. 2011) to increase the length of the fire season (Wotton and Flannigan 1993, Jolly et al. 2015). This increased fire activity is one contributing factor to the loss of approximately half of the area of sagebrush (*Artemisia tridentata*) shrubland communities, which once occupied over 600,000 km² in the western US. Much of this land is now dominated by cheatgrass (*Bromus tectorum*) (Bradley and Mustard 2008), an introduced annual grass (Davies 2011). This in turn is initiating a positive feedback, wherein invading plants increase the probability of fire, and increased fire activity stimulates more annual grass invasion (D’Antonio and Vitousek 1992, Brooks et al. 2004, Balch et al. 2013). The result is a fire return interval that has decreased from a historical range of 100-342 years for intact sagebrush (Baker 2006, Bukowski and Baker 2013) to 78 years in invaded areas (Balch et al. 2013), to as low as 3-5 years in cheatgrass-dominated areas in the Snake River Plain (Whisenant 1990). This increase in fire activity results in more areas that are burned multiple times, and the lasting effect this has on plant communities’ biodiversity and composition is relatively unknown. There are relatively few studies on the impacts of fire after more than 5 years (but see Beck et al. 2009, Reed-Dustin et al. 2016), and fewer still that analyze the

impacts of repeated fires in the same location (Miller et al. 2013).

There are at least 40 vertebrate species of conservation concern associated with sagebrush habitats (Rowland et al. 2006), including the greater sage grouse (*Centrocercus urophasianus*). Greater sage grouse depends on sagebrush for its habitat and has been a management priority by land managers (Chambers et al. 2017). Optimal shrub cover for sage grouse is 15-25% with over 15% bunchgrasses and forbs (Beck et al. 2009). Fire is one of the top 2 threats to the greater sage grouse in the western part of its range (Brooks et al. 2015), and the loss of sagebrush due to wildfire has contributed strongly to its population declines over the past 30 years (Coates et al. 2016). Land management agencies have linked fire management with long-term conservation goals focused on sagebrush ecosystems and the greater sage grouse (Chambers et al. 2017).

There is emerging consensus among researchers and land managers that lower elevation Wyoming big sagebrush (*A. tridentata* ssp. *wyomingensis*) ecosystems are not resilient to fire (Chambers et al. 2014) and should be prevented from burning whenever possible, while higher elevation Mountain big sagebrush (*A. tridentata* ssp. *vaseyana*) ecosystems may still recover naturally (Hanna and Fulgham 2015) or with restoration by seeding (Knutson et al. 2014). Several authors have recommended attempting to reduce the size and frequency of wildfire, and stopping the use of prescribed fire (Whisenant 1990, Baker 2006, Lesica et al. 2007, Beck et al. 2009), while also reducing grazing (Shinneman and Baker 2009, Ellsworth and Kauffman 2013). Others have urged caution with the use of prescribed fire (Davies et al. 2009, Reed-Dustin et al. 2016, Shinneman and McIlroy 2016). There has been disagreement in the past about the historical fire return interval for Wyoming big sagebrush. It has been characterized as being every 35 – 100 years (Schmidt et al. 2002), every 100 – 240 years (Baker 2006), to every 171 – 342 years (Bukowski and Baker 2013). This discrepancy has important management implications, leading to disagreement as to which stressors or disturbances (e.g. grazing, fire) need to be increased or decreased in order to manage for

79 healthy sagebrush ecosystems. The lower estimations imply the system is fire-dependent and
80 requires frequent burning in order to persist, while the upper estimates suggest fire-sensitivity.
81 Wyoming big sagebrush assemblages are generally agreed to be an endangered ecosystem and
82 fire and the invasive plants that generally colonize afterwards are thought to be two major
83 drivers of declining biodiversity in this system (Davies et al. 2011). Cover of introduced
84 annual grass species have been mostly observed to be negatively related to species richness
85 and native diversity (Davies 2011, Gasch et al. 2013, Bansal and Sheley 2016), but over a 45
86 year period Anderson and Inouye (2001) found that while introduced annual grass cover was
87 negatively correlated with cover of native species, species richness was unrelated. While fire
88 is strongly correlated with annual grass cover in this system at regional scales (Balch et al.
89 2013), it has also been shown to be an unimportant predictor variable for both exotic cover
90 and species richness in eastern Washington (Mitchell et al. 2016).

91 Post-fire communities of introduced annual grasses are affected by both fire frequency and
92 time since fire. Cheatgrass cover can increase initially after fire, then stabilize above its
93 pre-fire cover after 2-5 years (Reed-Dustin et al. 2016), but positive linear relationships
94 between time since fire and cheatgrass cover have also been observed (Shinneman and Baker
95 2009), as well as areas where cheatgrass declined and was replaced by perennial grasses (West
96 and Yorks 2002, Hanna and Fulgham 2015). Pre-fire community composition might explain
97 the inconsistency in results. Cheatgrass can come to dominate areas with fire-intolerant
98 natives post-fire, but in areas with pre-fire populations of fire-tolerant species (e.g. *Poa*
99 *secunda*) these species can regenerate following fire (Davies et al. 2012, but see Bagchi et al.
100 2013).

101 Precipitation, temperature and aridity affect both fire occurrence and the subsequent recovery
102 of plant communities. Unlike most forested systems in the western US, burned area in
103 Great Basin sagebrush systems is best predicted by antecedent precipitation (Abatzoglou and
104 Kolden 2013, Pilliod et al. 2017). Precipitation also drives the invasion of cheatgrass into

lower elevation sagebrush systems (Chambers et al. 2007), which increases the probability of fire for several years due to the persistence of the litter it leaves behind (Pilliod et al. 2017). Cheatgrass invasion increases the continuity of fuels (Davies and Nafus 2013) and burned area (Balch et al. 2013), thereby reducing the number of unburned patches that provide the native seed sources critical for recolonizing burned areas. Unburned patches are essential for sagebrush regeneration as almost every species in this genus is a seed obligate and the seeds generally fall no more than 30 meters from the mother plant (Meyer 1994). Once established, a sagebrush seedling needs to be able to withstand drought conditions in the summer to survive and be recruited into the population (Meyer 1994).

Here, we explored how sagebrush community composition and diversity responded to increasing fire disturbance by constructing a fire history atlas and sampling plant communities that burned zero to three times between 1984 and 2014 in the Central Basin and Range ecoregion. We constrained soil, ecological site type, elevation and climate and sampled blocks of plots stratified along a gradient of 0-3 fires. Our first hypothesis was that community composition would change drastically between unburned and burned plots, but remain similar between burned plots of different fire frequencies. This was our expectation because in the Great Basin there are vast areas of sagebrush which are generally unburned in the last 30+ years, and burned areas are almost always completely dominated by cheatgrass, along with a handful of exotic forb species and a native grass, *Poa secunda*. These cheatgrass-dominated areas all appear very similar, regardless of fire frequency (Figure 1). But we suspected that there would be a signal on plant diversity after multiple fires, due to selective pressure against fire-intolerant plants. Thus our second hypothesis was that alpha diversity (Shannon-Weaver index, Pielou Evenness, and the number of species in a sampling unit), beta diversity (continuity or turnover of species between plots) and the extrapolated species richness (with plots pooled by fire frequency), would decrease with increasing fire frequency. Our third hypothesis was that cheatgrass abundance would have a negative relationship with plant diversity. Our fourth hypothesis was that temperature, vapor pressure deficit and precipitation around the

time of the fire would exert a lasting influence over post-fire community composition and diversity. This is based on evidence that the effects of introducing species at the beginning of secondary succession can be long-lasting (Veen et al. 2018), and in this system the assemblage of species that are able to successfully colonize an area after a fire depends on their abilities to compete for moisture and tolerate drought (Meyer 1994).

Methods

Study Area

We conducted the study in a 13,000 square kilometer region in northern Nevada (Figure 2). The region has hot, dry summers and cold, wet winters. Annual precipitation averages 293 mm, falling mostly from November to May. Mean temperatures range from 21.8 degrees Celsius in July to -1.4 degrees Celsius in December (PRISM Climate Group 2016). The region consists of mountain ranges that run north-south, and the sagebrush ecosystems generally lie on the lower slopes of the mountains; our sites ranged from 1272 to 1696 meters in elevation (median 1458, SD 99). From 1984 to 2014, 32% (4096 square kilometers) of the study area burned in large fires (over 500 acres) at least once, 7% burned twice, and 2% burned three or more times (Table S1).

Site Selection

We used a block sampling design, with each block containing one site from each of four fire frequencies (zero to three), and all fires occurring at least five years before the study. We used geospatial data representing ecosystem state factors (*sensu* Amundson and Jenny 1997) to design a sampling scheme that constrained all other factors. We used the LANDFIRE (Rollins 2009) biophysical setting layer to eliminate all vegetation types except big sagebrush shrubland. The LANDFIRE data has 62-68% classification accuracy for shrublands (Zhu et al. 2006). We used soil data from the Natural Resource Conservation Service to include only areas in the Loamy 8-10 precipitation zone (Soil Survey Staff, Natural Resources Conservation Service, United States Department of Agriculture (USDA) 2016). We chose this particular

zone simply because it was the most common type in our study area within the big sagebrush shrubland biophysical setting. We used the Land Treatment Digital Library to exclude areas that had undergone intensive restoration activities (Pilliod and Welty 2013). Excluding private and military land, and areas more than five miles from a road eliminated impractical plot locations and held human influence somewhat constant.

We accounted for additional, unknown disturbances such as grazing by using a block sampling design, and stratifying our statistical analyses by these blocks. Long-term grazing data were not available. Therefore, we assumed that plots within blocks were close enough together that they had experienced similar grazing pressure. Additionally, we visually assessed the impact of grazing on-site, aggregated what records we could for the allotments in our study (billed animal unit months (AUM) provided by the Bureau of Land Management), and normalized AUM by unit area and included these data in our statistical modeling.

Once we constrained the area to a consistent sampling space, we used Landsat-derived fire data to stratify the space along a fire frequency gradient. To generate fire history maps, we first extracted only the values two to four (low, medium and high severity) from each yearly burn severity mosaic from the Monitoring Trends in Burn Severity project (MTBS; Eidenshink et al. 2007), as these were the values where one can be reasonably certain that they actually burned. Unburned patches and post-fire green-up, which could be caused by a response to fire or an unburned patch, were excluded. To generate fire frequency maps, we reclassified each yearly layer to a binary grid, and summed all 31 layers. To avoid areas with less certain fire frequencies, we then converted the MTBS fire perimeter polygons to layers of fire frequency to extract only the grid cells where the frequency from the polygons matched the frequency from the reclassified raster grid. To generate last-year-burned maps, we reclassified each severity mosaic (values two to four) to the fire year, and calculated the maximum year for the entire time period for each pixel. To eliminate areas that had burned more recently than 2014, we masked pixels that burned in 2015 according to the MODIS

184 MCD64 burned area product (Giglio et al. 2009).

185 Kolden et al. (2015) have brought up several shortcomings for the use of the MTBS burn
186 severity mosaics, in particular inconsistent development of class thresholds and a lack of
187 empirical relationships between the classified values and ecological metrics. Because we only
188 used these data to get a more precise estimate of fire occurrence, (i.e. we used it to eliminate
189 areas of uncertainty) rather than using the severity data as an independent variable for
190 analysis, we thought it sufficient to use these data in this state. Another shortcoming that
191 should be noted is that there is no practical way for us to know what these sites looked like
192 before the earliest fires in the fire record. The fact that our unburned control plots were
193 all mature sagebrush is one piece of evidence suggesting these sites were mature sagebrush
194 pre-fire, but we cannot be 100% certain, and this is a shortcoming of all chronosequence
195 studies (Walker et al. 2010).

196 We selected seven blocks in our sampling space in accessible areas where there was a range
197 of fire frequencies and unburned areas for controls within close proximity (0.5 - 10 km).
198 Within each block, we created spatially balanced random points (Theobald et al. 2007)
199 for each fire frequency, and sampled one plot for each fire history class within the block.
200 At each block, we first sampled the unburned control plot to confirm that the area was
201 indeed the correct vegetation type, and then sampled burned plots. After navigating to the
202 predetermined coordinates for each plot we first confirmed the physical characteristics (soil
203 type, lack of obvious restoration, lack of obvious overgrazing) were within the constraints of
204 our sampling design. If a predetermined point was not suitable (e.g. soil was too rocky or
205 sandy, an unburned control plot had obviously burned, or it was the wrong ecological site
206 type), we referred to georeferenced PDFs of our fire history atlas that we accessed with a
207 simple application (Avenza Maps <https://www.avenzamaps.com/>) on a mobile device and
208 located nearby areas within the site that were suitable. When a suitable area was found
209 we used a random number generator to pick a random bearing and a random distance, and

navigated to the new plot location.

We sampled 28 plots that fell along a gradient of fire frequency (zero to three fires; N = seven plots per frequency) and a range of times since fire (4-31 years; mean = 17.6, std = 6.6; Figure 2). Because most of the fire effects research in this system has been done within five years of a fire, we aimed to have the time since fire of all of the plots greater than or equal to 5 years. We encountered 53 plant species - 12 were introduced and 41 were native (Table S2).

Plot Establishment

We used GPS to navigate to predetermined plot locations. Upon arrival we established a permanent marker at the southwest corner of the plot. We recorded the slope, aspect, distance to the nearest *A. tridentata* individual or other shrub species, the topographic curvature of the site (convex, concave, flat), evidence of ecological restoration, grazing signs, and evidence of past fires. We then delineated a 50 x 50 meter plot, and placed pin flags at 9 randomly determined 1m² subplots within the plot with a minimum spacing of 3 meters. Pilliod and Arkle (2013) found this sampling density sufficient for this ecosystem, if supplemental methods are used to estimate disparate functional groups like trees and shrubs. Hence, we used the point-quarter method as a supplement to estimate shrub cover (see Pilliod & Arkle (2013) for detailed methods).

Vegetation Sampling

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

We used ‘Samplepoint’ software (Booth et al. 2006) to analyze the digital photographs for percent cover. We prepared photographs for analysis by cropping them to the 1 m x 1 m area of the subplot. Then we used Samplepoint to overlay a regular grid of 100 points on

each picture, and at each point identified whether it was litter, bare ground, rock, dung, or a plant. If it was a plant, we identified it to species with the aid of the occupancy data recorded at the plot. These data were then converted to percent cover. If we recorded a species as present within the subplot, but it was missed by the photographic analysis, we recorded it as 0.5% cover.

Environmental Data

Aspect was converted to folded aspect (folded aspect = $|180 - |\text{aspect} - 225||$; McCune and Keon 2002). This results in an approximation of heat load ranging from zero (northeast) to 180 (southwest). Elevation was extracted from 10m resolution digital elevation models. The study sites were situated among six grazing allotments. To learn how climate before, during and after the fire event affected the subsequent community composition and diversity, we extracted monthly maximum vapor pressure deficit, maximum temperature, and precipitation for the years before during and after the most recent fire at each plot. Maximum temperature and maximum vapor pressure deficit were averaged for the entire year before during and after, and precipitation was averaged for the two winters (November - May) prior and one after. We used monthly data provided by the PRISM climate group (PRISM Climate Group 2016) for all climate variables. Variables used in modeling are provided in Table 1. We also sampled soil C and N (see Mahood (2017) for detailed methods).

Statistical Analysis

Community Composition and Environmental Variables

To analyze how fire frequency affects community composition, we used non-metric multidimensional scaling (NMDS). We ran a rank correlation test for fire history gradients against a matrix of relative cover of species per plot to determine the best hierarchical clustering method for creating a dissimilarity matrix. We used this index for NMDS to examine how those fire history characteristics affected the floristic composition. To assess which species and environmental variables had the most influence on community composition, we added those

variables to the ordinations using the ‘envfit’ function from Vegan, with 9,999 permutations and stratified by the study block. Then we grouped species by their biogeographical origin (i.e. native or exotic), and used Tukey’s test to assess how fire frequency influenced native cover, exotic plant cover and cheatgrass abundance.

Species Richness, Alpha Diversity and Beta Diversity

We created species accumulation curves grouped by fire frequency to assess how fire frequency affected species richness. This is different from alpha diversity in that the species accumulation curve is estimating number of species across all of the sites within each group with each added plot, as opposed to simply calculating a diversity index for each plot. We used the sample-based rarefaction method (Chiarucci et al. 2008, Oksanen et al. 2016, R Core Team 2016). We used Tukey’s Honest Significant Differences test (hereafter, Tukey’s test) to see if different fire frequencies influenced alpha diversity (Shannon-weaver, Pielou evenness, and number of species per plot). There are several ways to quantify beta diversity, most of which are grouped into “measures of continuity” and “measures of gain and loss” (Koleff et al. 2003). We used the “Z” index and Whittaker’s original beta diversity index for continuity measures, and Simpson’s index (based on G. Gaylord Simpson’s asymmetric index (Simpson 1943) and modified by Lennon et al. (2001), not to be confused with Edward H. Simpson’s Index (1949)) for a measure of gain and loss. To see how beta diversity differed between fire frequencies, we modeled the homogeneity of dispersion of those matrices (Anderson et al. 2006), and ran pairwise permutation tests (Legendre et al. 2011) on these models with 9,999 permutations, stratified by the study blocks. To assess the influence of cheatgrass abundance on alpha and beta diversity, we used linear mixed models (Pinheiro et al. 2017) with the study block as a random effect. We included elevation as a fixed effect in addition to cheatgrass due to its strong correlation with temperature and moisture availability, and ecosystem resistance and resilience (Chambers et al. 2014). We ensured that predictors had no multicollinearity using a variable inflation factor test (Fox and Weisberg 2011), and used the partial coefficient of

determination (Jaeger et al. 2016) to determine the cheatgrass component of the model. To aid visualization, we removed the partial effects of elevation from the dependent variables (Hohenstein and Kliegl 2018).

Modeling Which Fire and Climate Variables Drive Post-fire Composition and Diversity

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

Code Availability

Data and code to reproduce the analysis are available at https://www.github.com/admahood/ff_study.

Results

Community Composition Fundamentally Changed After One Fire

The rank index test showed the Kulczynski index to have the most consistent high scores across gradients of fire history characteristics, so we used this index for our hierarchical

clustering and NDMS analyses. NMDS (Non-metric fit, $R^2 = 0.992$, Linear fit, $R^2 = 0.972$) showed 7 unburned plots clustered around high abundances of *A. tridentata*, and 18 burned plots clustered around *B. tectorum* (Figure 3). Two thrice-burned plots were dominated by exotic annual forbs (*Sisymbrium altissimum* and *Erodium cicutarium*) and one was dominated by the native perennial grass *P. secunda* (these are the three thrice-burned plots outside of the “burned” ellipse). The ordination showed a clear separation between burned and unburned plots, but fire frequency was not significantly correlated with the ordination, nor were any environmental variables.

For the Tukey’s tests of exotic versus native cover, there were differences between unburned and burned plots ($p < 0.05$) for both exotic (increased by 10%) and native cover (decreased by 20%), and no differences among the burned plots. (Figure 4a-b). After dividing the mean cover estimates into native and exotic life form groups (annual and perennial graminoids and forbs, and shrubs), we saw lower native shrub cover for burned plots fire (24% to 3%), coupled with higher annual grass cover (4% to 14%; Figure 5).

Plant Biodiversity Decreased with Each Successive Fire

We found a decline in plant diversity at sites that had burned more frequently. Species richness estimates declined as fire frequency increased (Figure 6, Table S3). The number of species and the Shannon-weaver index were higher in unburned plots, but the differences were not significant, and Pielou evenness was not different between frequencies (Figure 4c-e). All three indexes of Beta diversity followed very similar patterns, so we only report on Whittaker’s index here. It was not different between zero and two fires, and lower for thrice-burned plots (Figure 4f), meaning that there is less dissimilarity within the group of thrice-burned plots, and more dissimilarity within the other groupings.

Alpha Diversity and Evenness Decreased with Cheatgrass Abundance

Cheatgrass abundance had a negative relationship with Shannon-weaver diversity ($p < 0.05$, partial $R^2 = 0.65$) and Pielou evenness ($p < 0.05$, partial $R^2 = 0.51$), a weak negative

relationship with the number of species ($p < 0.05$, partial $R^2 = 0.24$), and no relationship to beta diversity ($p > 0.5$, partial $R^2 = 0.08$; Figure 7, Table 2). Elevation was important in all models except Pielou evenness (Table 2).

Different Climate and Fire Variables Predict Post-Fire Composition and Diversity

PERMANOVA models showed that fire history and environmental factors influenced community composition and beta diversity differently. ANOVAs and Tukey's tests on MHGD models showed no heterogeneity in groups dispersions for both beta diversity and hierarchical clustering ($p > 0.05$ for all models). Community composition after fire was most affected by fire frequency, time since fire, maximum vapor pressure deficit of the year of the fire, and the interaction between fire frequency and time since fire (Table 3, $R^2 = 0.55$). The relatively low amounts of variation accounted for by the individual variables indicates these are subtle effects. Beta diversity on the other hand was influenced most by winter precipitation one and two years prior to the fire, fire frequency, and the interaction between winter precipitation one year prior and max temperature for the year after the fire (Table 4, $R^2 = 0.62$). Here, the effect was more pronounced, as more variation accounted for by the three most statistically significant variables (fire frequency and precipitation one and two winters prior to the fire).

Discussion

The purpose of this study is to assess how Wyoming big sagebrush plant communities respond to being burned repeatedly before returning to their prior condition. The combination of a 32-year fire history atlas and the use of the RRQRR (Theobald et al. 2007) to randomly stratify the sampling blocks over a large area provides broad-scale statistical inference for the lower elevation (<1500 m) portion of the Wyoming big sagebrush ecosystem. These lower elevation sites generally experience higher temperatures and lower soil moisture, and it is well documented that they have lower resilience after wildfires (Chambers et al. 2014). We did not detect recovery of Wyoming big sagebrush at our sites, and also found that while the cover of *Bromus tectorum* does not change with successive fires, the number of species in the

species pool does decrease, and that biodiversity decreases with cover of *B. tectorum*. The results of this study may seem to conflict with other recent studies documenting Wyoming big sagebrush recovery in the Great Basin (Ellsworth et al. 2016, e.g. Shinneman and McIlroy 2016). But all of the studies we are aware of showing sagebrush recovery were conducted at cooler, wetter sites, where Wyoming big sagebrush is more resilient after fire (Chambers et al. 2014).

Coupling the 30+ year fire history atlas created here with intensive field sampling offers a unique opportunity to explore plant diversity and composition changes in areas that have relatively high fire frequencies, such as grass-dominated or grass-invaded areas (Balch et al. 2013). As annual grass invasions and their alterations to fire regimes are a global phenomenon (D’Antonio and Vitousek 1992, Brooks et al. 2004), this type of study design will be useful for understanding the consequences of changing fire regimes in other regions. Additionally, new algorithms are being developed that will lead to more accurate and precise fire data products (e.g. Hawbaker et al. 2015), leading to more nuanced fire history atlases, and thus more precise sampling stratifications – especially now that burn severity information can be easily incorporated (Eidenshink et al. 2007).

Community Composition Fundamentally Changes After One Fire

In lower elevation *A. tridendata* ssp. *wyomingensis* systems, our results show that one fire can convert this shrub-dominated system to one composed mainly of introduced annual grasses and forbs, and we demonstrate that this new state can persist for decades with little sign of recovery to its prior condition. While almost all of our burned plots were dominated by cheatgrass, several thrice-burned plots were dominated by *P. secunda* or exotic annual forbs (see figure 3, where there are 3 plots that are outside the confidence envelope containing all other burned plots). This corroborates previous work showing that fire can push cheatgrass-invaded grassland and shrubland communities into those dominated by cheatgrass, *P. secunda*, and exotic forbs, while uninvaded sites, or sites that are invaded but still have

significant bunchgrass communities, can persist in a state of native bunchgrasses and forbs (Davies et al. 2012, Reisner et al. 2013, Condon and Pyke 2018). Other studies have found that topography can be a mediating factor, with native bunchgrasses more likely to persist on steeper, more north-facing slopes in the face of invasion and disturbance (Rodhouse et al. 2014, Reed-Dustin et al. 2016). One hypothesis that we were not able to test in this study is that increasing fire frequency may select for more fire-resilient plant functional traits. More research is needed to investigate the relationship between fire frequency and functional traits. While it has been demonstrated that *B. tectorum* establishes immediately post-fire and can persist in the shorter term (Davies et al. 2012, Hanna and Fulgham 2015), we show that this novel grass state can persist for long periods (i.e. > 17 years), corroborating recent work (Reed-Dustin et al. 2016). If there was recovery our study design would have enabled us to detect it, as Wyoming big sagebrush has been found to recover from disturbance in as little as nine (Wambolt et al. 2001) to 20 years (Shinneman and McIlroy 2016) following fire, and our fire history atlas goes back 32 years.

Biodiversity Decreases with Each Subsequent Fire

Here we show that over a three decade period repeated fires had long-lasting effects on community composition and biodiversity in Wyoming big sagebrush ecosystems. Species richness declined with increasing fire frequency, but measures of alpha and beta diversity decreased after one and three fires, respectively (Figure 4a-b). Species accumulation curves demonstrated that repeated fires are decreasing the overall pool of species from which an individual patch might draw from. So while there may not have been significant differences in alpha diversity as fire frequency increased, as the number of species each plot can draw from decreased, this signal manifested itself when beta diversity declined after three fires.

We found negative relationships between cheatgrass abundance and alpha and beta diversity, as we hypothesized, but no relationship between cheatgrass abundance and the number of fires. Establishment and dominance of cheatgrass after fire is well documented (Whisenant

1990, Balch et al. 2013), and the relationship between fire and species richness is clear from this work. This implies that once an area is invaded by cheatgrass, the competitive effects from its increased abundance combine with its effect on fire frequency to exclude species that either cannot compete for moisture or cannot survive fire. It should be noted that because we selected sites that had burned at least three times since 1984, we may have biased our results to be applicable to only those areas that are susceptible to initiating a grass-fire cycle.

Time Since Fire and Vapor Pressure Deficit Drive Community Composition

PERMANOVA models showed that fire history and climate variables affect diversity and community composition differently. Composition was found to be influenced by both fire frequency and time since fire, and high vapor pressure deficit the year of the fire. This suggests that drought stress exerts a significant influence on the particular plant species that will survive and persist after a fire, and this effect can still be detected decades after the fire burned. Shinneman and McIlroy (2016) also found that climatic variables around the time of the fire influence the eventual composition, namely winter precipitation the year after the fire was beneficial for sagebrush recovery, but winter precipitation 2 years later had a negative effect. Elevation and recovery have been shown to be positively related in this system (Knutson et al. 2014), and most of the studies showing fast recovery times were done at higher elevations and latitudes (Wambolt et al. 2001, Hanna and Fulgham 2015, Ellsworth et al. 2016), in areas with long-term grazing exclusion (Ellsworth et al. 2016), or on sites that were specifically selected because their topographic position was such that there was potential for sagebrush recovery (Shinneman and McIlroy 2016). Here, we found that on low elevation sites, even after an average of 17 years, post-fire sagebrush cover was very low (<6%; also see Reed-Dustin et al. 2016). These differences in recovery rates (i.e. 9-20 years at cooler sites vs no detectable recovery at hotter sites) could be due to a slowing down of recovery rates as the system loses resilience with increasing drought stress at hotter sites, while cooler sites have not yet experienced sufficient drought stress to hamper recovery (*sensu*

Leemput et al. 2017).

Fire Frequency and Antecedent Precipitation Drive Beta Diversity

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

Management Implications

This work adds to the existing body of literature that suggests that in low elevation (< 1700m) Wyoming big sagebrush systems wildfire should be minimized due to the negative effects of single and repeated fires on community composition and biodiversity. The reality is that wildfire can not be prevented, but fire suppression policies and practices could be crafted to maximize the number and size of unburned patches within burns to increase the

probability that Wyoming big sagebrush and other native seed-obligates recover post-fire. These results also imply that prescribed burning is a risky proposition with potentially disastrous consequences for biodiversity and ecosystem structure and function. However, we did not directly assess the influence of prescribed fires in this study. Prescribed fires typically are conducted at a cooler time of year outside of or at the shoulder of the fire season, and may have different ecological effects due to the phenological stage plants would be in at this different time of year, as well as the lower burn severity that would be expected due to cooler ambient air temperatures and higher soil moisture. At a cooler, wetter site where grazing has been excluded since 1994, Ellsworth et al. (2016) detected the recovery of sagebrush 17 years after prescribed fires were conducted in late September 1997, which is the natural end of the fire season at that location. Two other studies at higher latitudes concluded that prescribed burning to be an unwise action even at those wetter sites. Beck et al. (2009) studied an area in southeast Idaho that was burned in late August 1989 by prescribed fire 14 years post-fire for its utility in improving sage grouse habitat. They recommended against prescribed fires due to the lack of recovery of sagebrush. Wambolt et al. (2001) found minimal benefit to the herbaceous plant community at 13 sites that had burned in prescribed fires in Western Montana, with little shrub recovery 6-15 years after fire. Thus, there is conflicting evidence on the use of prescribed fires for management objectives even at cooler wetter sites, providing less optimism for the use of prescribed fires in the lower elevation portion of the Wyoming big sagebrush ecosystems studied here. Future research could focus on comparing low elevation Wyoming big sagebrush sites that have been burned in prescribed fires in the past paired with nearby areas that burned in wildfires, with particular emphasis on teasing out the effects of seasonality and burn severity.

Our results from PERMANOVA modeling suggest that the success of post-fire restoration efforts will depend not only on elevation and topographic conditions (Arkle et al. 2014), but also the climatic conditions that occur around the time of the fire. This could mean that in a very dry year less money is spent on restoration efforts on low elevation sites, focusing

instead on higher elevation sites and cooler aspects, and in wet years directing more funding towards those more vulnerable low elevation, southwest-facing sites.

Disagreement on the actual historical fire rotation limits our ability to determine if Wyoming big sagebrush is fire-sensitive or fire-resistant. However, this question may be irrelevant given the disruption and interaction between invasive annual grasses and fires. We demonstrate that when both fire and invasive annual grasses operate in conjunction, sagebrush is fire-sensitive. Moreover, we show that an alternate exotic grass state can persist for 17 years post-fire even with only a single burn. This makes the use of prescribed burning problematic, as the risk of a fire-prone grassland establishing after a fire likely outweighs the potential benefits of a prescribed fire. Our results are specific to lower elevation ($< 1700\text{m}$), dryer, hotter Wyoming big sagebrush sites, and it remains to be explored how sagebrush at higher elevations and latitudes responds to increasing fire frequency, and how it will respond under future climate change scenarios. However, if temperatures continue to rise as projected in this region (Garfin et al. 2014), those areas may also become susceptible to a strong grass-fire cycle. Overall, this effort demonstrates that sagebrush communities are vulnerable to repeated fires (Seipel et al. 2018), which should be taken into account in land management decisions (Chambers et al. 2017) that attempt to conserve or restore these valuable ecosystems, and the threatened species that they harbor.

Acknowledgements

We are grateful for the assistance of Nick Whittemore and Kathleen Weimer for their assistance in the field and in the lab. We thank Tom Veblen and Carson Farmer for comments on previous versions of the manuscript. We appreciated the constructive criticism from three anonymous reviewers which greatly improved the paper. Thanks to Max Joseph for help with the data analysis. We are also very grateful for the support of the Nevada Bureau of Land Management, and the Central Nevada Interagency Dispatch Center. This work was funded by the National Aeronautics and Space Administration Terrestrial Ecology Program

under Award NNX14AJ14G, and start-up funding from the Department of Geography at CU Boulder.

Literature Cited

- Abatzoglou, J. T., and C. A. Kolden. 2013. Relationships between climate and macroscale area burned in the western United States. *International Journal of Wildland Fire* 22:1003–1020.
- Amundson, R., and H. Jenny. 1997. On a state factor model of ecosystems. *BioScience* 47:536–543.
- Anderson, J. E., and R. S. Inouye. 2001. Landscape-Scale Changes in Plant Species Abundance and Biodiversity of a Sagebrush Steppe over 45 Years. *Ecological Monographs* 71:531–556.
- Anderson, M. J., and D. C. I. Walsh. 2013. PERMANOVA , ANOSIM , and the Mantel test in the face of heterogeneous dispersions: What null hypothesis are you testing? *Ecological Monographs* 83:557–574.
- Anderson, M. J., K. E. Ellingsen, and B. H. McArdle. 2006. Multivariate dispersion as a measure of beta diversity. *Ecology Letters* 9:683–693.
- Arkle, R., D. Pilliod, S. Hanser, M. L. Brooks, J. C. Chambers, J. B. Grace, K. C. Knutson, D. A. Pyke, J. L. Welty, and T. A. Wirth. 2014. Quantifying restoration effectiveness using multi-scale habitat models: implications for sage-grouse in the Great Basin. *Ecosphere* 5:1–32.
- Bagchi, S., D. D. Briske, B. T. Bestelmeyer, and X. Ben Wu. 2013. Assessing resilience and state-transition models with historical records of cheatgrass *Bromus tectorum* invasion in North American sagebrush-steppe. *Journal of Applied Ecology* 50:1131–1141.
- Baker, W. L. 2006. Fire and restoration of sagebrush ecosystems. *Wildlife Society Bulletin* 34:177–185.
- Balch, J. K., B. A. Bradley, J. T. Abatzoglou, R. C. Nagy, E. J. Fusco, and A. L. Mahood. 2017. Human-started wildfires expand the fire niche across the United States. *Proceedings of the National Academy of Science*.
- Balch, J. K., B. A. Bradley, C. M. D’Antonio, and J. Gómez-Dans. 2013. Introduced annual grass increases regional fire activity across the arid western USA (1980-2009). *Global Change Biology* 19:173–183.
- Bansal, S., and R. L. Sheley. 2016. Annual grass invasion in sagebrush steppe: the relative importance of climate, soil properties and biotic interactions. *Oecologia* 181:543–557.
- Beck, J. L., J. W. Connelly, and K. P. Reese. 2009. Recovery of Greater Sage-Grouse habitat features in Wyoming big sagebrush following prescribed fire. *Restoration Ecology* 17:393–403.
- Booth, D. T., S. E. Cox, and R. D. Berryman. 2006. Point sampling digital imagery with

556 'Samplepoint'. Environmental Monitoring and Assessment 123:97–108.

557 Bowman, D. M. J. S., J. K. Balch, P. Artaxo, W. J. Bond, M. A. Cochrane, C. M. D'Antonio,
558 R. S. Defries, F. H. Johnston, J. E. Keeley, M. A. Krawchuk, C. A. Kull, M. Mack, M. A.
559 Moritz, S. J. Pyne, C. I. Roos, A. C. Scott, N. S. Sodhi, and T. W. Swetnam. 2011. The
560 human dimension of fire regimes on Earth. Journal of Biogeography 38:2223–2236.

561 Bradley, B. A., and J. F. Mustard. 2008. Comparison of phenology trends by land cover
562 class: A case study in the Great Basin, USA. Global Change Biology 14:334–346.

563 Brooks, M. L., C. M. D. Antonio, D. M. Richardson, J. B. Grace, J. E. Keeley, J. M.
564 DiTomaso, R. J. Hobbs, M. Pellant, and D. Pyke. 2004. Effects of Invasive Alien Plants on
565 Fire Regimes. BioScience 54:677–688.

566 Brooks, M. L., J. R. Matchett, D. J. Shinneman, and P. S. Coates. 2015. Fire Patterns in
567 the Range of the Greater Sage-Grouse , 1984 – 2013 — Implications for Conservation and
568 Management: U.S. Geological Survey Open-File Report 2015-1167. Page 66.

569 Bukowski, B., and W. L. Baker. 2013. Historical fire regimes, reconstructed from land-survey
570 data, led to complexity and fluctuation in sagebrush landscapes. Ecological Applications
571 23:546–564.

572 Chambers, J. C., J. L. Beck, J. B. Bradford, J. Bybee, S. Campbell, J. Carlson, T. J.
573 Christiansen, K. J. Clause, G. Collins, M. R. Crist, J. B. Dinkins, K. E. Doherty, F. Edwards,
574 S. Espinosa, K. A. Griffin, P. Griffin, J. R. Haas, S. E. Hanser, D. W. Havlina, K. F. Henke,
575 J. D. Hennig, L. A. Joyce, F. F. Kilkenny, S. M. Kulpa, L. L. Kurth, J. D. Maestas, M.
576 Manning, K. E. Mayer, B. A. Meador, C. McCarthy, M. Pellant, M. A. Perea, K. L. Prentice,
577 D. A. Pyke, L. A. Wiechman, and A. Wuenschel. 2017. Science Framework for Conservation
578 and Restoration of the Sagebrush Biome: Linking the Department of the Interior's Integrated
579 Rangeland Fire Management Strategy to Long-Term Strategic Conservation Actions . Part 1.
580 Science basis and applications. Gen. Te:213.

581 Chambers, J. C., B. A. Bradley, C. S. Brown, C. D'Antonio, M. J. Germino, J. B. Grace,
582 S. P. Hardegree, R. F. Miller, and D. A. Pyke. 2014. Resilience to stress and disturbance,
583 and resistance to *Bromus tectorum* L. invasion in cold desert shrublands of western North
584 America. Ecosystems 17:360–375.

585 Chambers, J. C., B. A. Roundy, R. R. Blank, S. E. Meyer, and A. Whittaker. 2007.
586 What makes Great Basin sagebrush ecosystems invisable by *Bromus tectorum*? Ecological
587 Monographs 77:117–145.

588 Chiarucci, A., G. Bacaro, D. Rocchini, and L. Fattorini. 2008. Discovering and rediscovering
589 the sample-based rarefaction formula in the ecological literature. Community Ecology 9:121–
590 123.

591 Coates, P. S., M. A. Ricca, B. G. Prochazka, M. L. Brooks, K. E. Doherty, T. Kroger,
592 E. J. Blomberg, C. A. Hagen, and M. L. Casazza. 2016. Wildfire, climate, and invasive
593 grass interactions negatively impact an indicator species by reshaping sagebrush ecosystems.

594 Proceedings of the National Academy of Sciences:201606898.

595 Condon, L. A., and D. A. Pyke. 2018. Fire and Grazing Influence Site Resistance to *Bromus*
596 *tectorum* Through Their Effects on Shrub, Bunchgrass and Biocrust Communities in the
597 Great Basin (USA). *Ecosystems* 21:1416–1431.

598 Davies, G. M., J. D. Bakker, E. Dettweiler-Robinson, P. W. Dunwiddie, S. A. Hall, J. Downs,
599 and J. Evans. 2012. Trajectories of change in sagebrush steppe vegetation communities in
600 relation to multiple wildfires. *Ecological Applications* 22:1562–1577.

601 Davies, K. W. 2011. Plant community diversity and native plant abundance decline with
602 increasing abundance of an exotic annual grass. *Oecologia* 167:481–491.

603 Davies, K. W., and A. M. Nafus. 2013. Exotic annual grass invasion alters fuel amounts,
604 continuity and moisture content. *International Journal of Wildland Fire* 22:353–358.

605 Davies, K. W., C. S. Boyd, J. L. Beck, J. D. Bates, T. J. Svejcar, and M. A. Gregg.
606 2011. Saving the sagebrush sea: An ecosystem conservation plan for big sagebrush plant
607 communities. *Biological Conservation* 144:2573–2584.

608 Davies, K. W., T. J. Svejcar, and J. D. Bates. 2009. Interaction of Historical and Nonhistorical
609 Disturbances Maintains Native Plant Communities. *Ecological Applications* 19:1536–1545.

610 Dennison, P. E., S. C. Brewer, J. D. Arnold, and M. A. Moritz. 2014. Large wildfire trends
611 in the western United States, 1984–2011. *Geophysical Research Letters*:2928–2933.

612 D’Antonio, C. M., and P. M. Vitousek. 1992. Biological invasions by exotic grasses, the
613 grass/fire cycle, and global change. *Annual Review of Ecological Systems* 23:63–87.

614 Eidenshink, J., B. Schwind, K. Brewer, Z.-l. Zhu, B. Quayle, and S. Howard. 2007. A Project
615 for Monitoring Trends in Burn Severity. *Fire Ecology* 3:3–21.

616 Ellsworth, L. M., and J. B. Kauffman. 2013. Seedbank responses to spring and fall prescribed
617 fire in mountain big sagebrush ecosystems of differing ecological condition at Lava Beds
618 National Monument, California. *Journal of Arid Environments* 96:1–8.

619 Ellsworth, L. M., D. W. Wroblewski, J. B. Kauffman, and S. A. Reis. 2016. Ecosystem
620 resilience is evident 17 years after fire in Wyoming big sagebrush ecosystems. *Ecosphere* 7.

621 Fox, J., and S. Weisberg. 2011. An R companion to applied regression. Second. Sage,
622 Thousand Oaks CA.

623 Garfin, G., G. Franco, H. Blanco, A. Comrie, P. Gonzalez, T. Piechota, R. Smyth, and R.
624 Waskom. 2014. Southwest: The Third National Climate Assessment. In J. M. Melillo, T. C.
625 Richmond, & G. W. Yohe (Eds.), *Climate Change Impacts in the United States: The Third*
626 *National Climate Assessment* (pp. 462–486). Pages 462–486.

627 Gasch, C. K., S. F. Enloe, P. D. Stahl, and S. E. Williams. 2013. An aboveground –
628 belowground assessment of ecosystem properties associated with exotic annual brome invasion.
629 *Biology and Fertility of Soils* 49:919–928.

630 Giglio, L., T. Loboda, D. P. Roy, B. Quayle, and C. O. Justice. 2009. An active-fire based

burned area mapping algorithm for the MODIS sensor. *Remote Sensing of Environment* 113:408–420.

Hanna, S. K., and K. O. Fulgham. 2015. Post-fire vegetation dynamics of a sagebrush steppe community change significantly over time. *California Agriculture* 69:36–42.

Hawbaker, T. J., S. Stitt, Y.-J. Beal, G. Schmidt, J. Falgout, B. Williams, and J. Takacs. 2015. Provisional burned area essential climate variable (BAECV) algorithm description. United States Geological Survey.

Hohenstein, S., and R. Kliegl. 2018. Remef: Remove partial effects.

Integrated Rangeland Fire Management Strategy Actionable Science Plan Team. 2016. The Integrated Rangeland Fire Management Strategy Actionable Science Plan. Page 128. U.S. Department of the Interior, Washington, DC.

Jaeger, B. C., L. J. Edwards, K. Das, and P. K. Sen. 2016. An R^2 statistic for fixed effects in the generalized linear mixed model. *Journal of Applied Statistics* 44:1086–1105.

Jolly, W. M., M. a. Cochrane, P. H. Freeborn, Z. A. Holden, T. J. Brown, G. J. Williamson, and D. M. J. S. Bowman. 2015. Climate-induced variations in global wildfire danger from 1979 to 2013. *Nature Communications* 6:7537.

Knutson, K. C., D. A. Pyke, T. A. Wirth, R. S. Arkle, D. S. Pilliod, M. L. Brooks, J. C. Chambers, and J. B. Grace. 2014. Long-term effects of seeding after wildfire on vegetation in Great Basin shrubland ecosystems. *Journal of Applied Ecology* 51:1414–1424.

Kolden, C. A., A. M. S. Smith, and J. T. Abatzoglou. 2015. Limitations and utilisation of Monitoring Trends in Burn Severity products for assessing wildfire severity in the USA. *International Journal of Wildland Fire* 24:1023–1028.

Koleff, P., K. J. Gaston, and J. J. Lennon. 2003. Measuring beta diversity for presence-absence data. *Journal of Animal Ecology* 72:367–382.

Krawchuk, M. A., M. A. Moritz, M. A. Parisien, J. Van Dorn, and K. Hayhoe. 2009. Global pyrogeography: The current and future distribution of wildfire. *PLoS ONE* 4.

Leemput, I. A. van de, V. Dakos, M. Scheffer, and E. H. van Nes. 2017. Slow Recovery from Local Disturbances as an Indicator for Loss of Ecosystem Resilience. *Ecosystems*:1–12.

Legendre, P., J. Oksanen, and C. J. F. ter Braak. 2011. Testing the significance of canonical axes in redundancy analysis. *Methods in Ecology and Evolution* 2:269–277.

Lennon, J. J., P. Koleff, J. Greenwood, and K. J. Gaston. 2001. The geographical structure of british bird distributions: Diversity, spatial turnover and scale. *Journal of Animal Ecology* 70:966–979.

Lesica, P., S. V. Cooper, and G. Kudray. 2007. Recovery of Big Sagebrush Following Fire in Southwest Montana. *Rangeland Ecology & Management* 60:261–269.

Liu, Y., S. L. Goodrick, and J. A. Stanturf. 2013. Future U.S. wildfire potential trends

projected using a dynamically downscaled climate change scenario. *Forest Ecology and Management* 294:120–135.

Mahood, A. L. 2017. Long-Term Effects of Repeated Fires on the Diversity and Composition of Great Basin Sagebrush Plant Communities. PhD thesis, University of Colorado Boulder.

McCune, B., and D. Keon. 2002. Equations for potential annual direct incident radiation and heat load. *Journal of Vegetation Science* 13:603–606.

Meyer, S. E. 1994. Germination and establishment ecology of big sagebrush: implications for community restoration. Pages 244–251 *in* Symposium on management, ecology, and restoration of Intermountain annual rangelands, boise, id, may 18-21, 1992.

Miller, R. F., J. C. Chambers, D. A. Pyke, F. B. Pierson, C. J. Williams, B. Fred, and C. A. Jason. 2013. A Review of Fire Effects on Vegetation and Soils in the Great Basin Region: Response and Ecological Site Characteristics. United States Department of Agriculture Forest Service:1–136.

Mitchell, R. M., J. D. Bakker, J. B. Vincent, and G. M. Davies. 2016. Relative importance of abiotic, biotic, and disturbance drivers of plant community structure in the sagebrush steppe. *Ecological Applications*:n/a–n/a.

Moritz, M. A., M.-A. Parisien, E. Batllori, M. A. Krawchuk, J. Van Dorn, D. J. Ganz, and K. Hayhoe. 2012. Climate change and disruptions to global fire activity. *Ecosphere* 3:49.

Oksanen, J., F. G. Blanchet, M. Friendly, R. Kindt, P. Legendre, D. McGlinn, P. R. Minchin, R. B. O’Hara, G. L. Simpson, P. Solymos, M. H. H. Stevens, E. Szoecs, and H. Wagner. 2016. *Vegan: Community ecology package*.

Pilliod, D. S., and R. S. Arkle. 2013. Performance of Quantitative Vegetation Sampling Methods Across Gradients of Cover in Great Basin Plant Communities. *Rangeland Ecology & Management* 66:634–647.

Pilliod, D. S., and J. L. Welty. 2013. Land Treatment Digital Library, <https://ltdl.wr.usgs.gov/>. Reston, VA.

Pilliod, D. S., J. L. Welty, and R. S. Arkle. 2017. Refining the cheatgrass-fire cycle in the Great Basin: Precipitation timing and fine fuel composition predict wildfire trends. *Ecology and Evolution*:1–26.

Pinheiro, J., D. Bates, S. DebRoy, D. Sarkar, and R Core Team. 2017. nlme: Linear and nonlinear mixed effects models.

PRISM Climate Group. 2016. PRISM Gridded Climate Data. Oregon State University.

R Core Team. 2016. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria.

Reed-Dustin, C. M., R. Mata-González, and T. J. Rodhouse. 2016. Long-Term Fire Effects on Native and Invasive Grasses in Protected Area Sagebrush Steppe. *Rangeland Ecology &*

Management 69:257–264.

Reisner, M. D., J. B. Grace, D. A. Pyke, and P. S. Doescher. 2013. Conditions favouring *Bromus tectorum* dominance of endangered sagebrush steppe ecosystems. *Journal of Applied Ecology* 50:1039–1049.

Rodhouse, T. J., K. M. Irvine, R. L. Sheley, B. S. Smith, S. Hoh, D. M. Esposito, and R. Mata-Gonzalez. 2014. Predicting foundation bunchgrass species abundances: sagebrush steppe. *Ecosphere* 108:1–16.

Rollins, M. G. 2009. LANDFIRE: a nationally consistent vegetation, wildland fire, and fuel assessment. *International Journal of Wildland Fire* 18:235–249.

Rowland, M. M., M. J. Wisdom, L. H. Suring, and C. W. Meinke. 2006. Greater sage-grouse as an umbrella species for sagebrush-associated vertebrates. *Biological Conservation* 129:323–335.

Ryel, R. J., A. J. Leffler, C. Ivans, M. S. Peek, and M. M. Caldwell. 2010. Functional differences in water-use patterns of contrasting life forms in Great Basin steppelands. *Vadose Zone Journal* 9:548.

Schlaepfer, D. R., W. K. Lauenroth, and J. B. Bradford. 2014. Natural Regeneration Processes in Big Sagebrush (*Artemisia tridentata*). *Rangeland Ecology & Management* 67:344–357.

Schmidt, K. M., J. P. Menakis, C. C. Hardy, W. J. Hann, and D. L. Bunnell. 2002. Development of course-scale spatial data for wildland fire and fuel management. Page 41 p. United States Department of Agriculture Forest Service.

Seipel, T., L. J. Rew, K. T. Taylor, B. D. Maxwell, and E. A. Lehnhoff. 2018. Disturbance type influences plant community resilience and resistance to *Bromus tectorum* invasion in the sagebrush steppe. *Applied Vegetation Science*:1–10.

Shinneman, D. J., and W. L. Baker. 2009. Environmental and climatic variables as potential drivers of post-fire cover of cheatgrass (*Bromus tectorum*) in seeded and unseeded semiarid ecosystems. *International Journal of Wildland Fire* 18:191–202.

Shinneman, D. J., and S. K. McIlroy. 2016. Identifying key climate and environmental factors affecting rates of post-fire big sagebrush (*Artemisia tridentata*) recovery in the northern Columbia Basin, USA. *International Journal of Wildland Fire* 25:933–945.

Simpson, E. H. 1949. Measurement of diversity. *Nature* 163.

Simpson, G. G. 1943. Mammals and the nature of continents. *American Journal of Science* 241:1–31.

Soil Survey Staff, Natural Resources Conservation Service, United States Department of Agriculture (USDA). 2016. Web Soil Survey.

Theobald, D. M., D. L. Stevens, D. White, N. S. Urquhart, A. R. Olsen, and J. B. Norman. 2007. Using GIS to Generate Spatially Balanced Random Survey Designs for Natural Resource

741 Applications. *Environmental Management* 40:134–146.

742 Veen, G. F., W. H. van der Putten, and T. M. Bezemer. 2018. Biodiversity-ecosystem
743 functioning relationships in a long-term non-weeded field experiment. *Ecology* 99:1836–1846.

744 Walker, L. R., D. A. Wardle, R. D. Bardgett, and B. D. Clarkson. 2010. The use of
745 chronosequences in studies of ecological succession and soil development. *Journal of Ecology*
746 98:725–736.

747 Wambolt, C. L., K. S. Walhof, and M. R. Frisina. 2001. Recovery of big sagebrush communities
748 after burning in south-western Montana. *Journal of environmental management* 61:243–252.

749 West, N. E., and T. P. Yorks. 2002. Vegetation responses following wildfire on grazed and
750 ungrazed sagebrush semi-desert. *Journal of Range Management* 55:171–181.

751 Westerling, A. L. 2016. Increasing western US forest wildfire activity: sensitivity to changes
752 in the timing of spring. *Philosophical Transactions of the Royal Society B: Biological Sciences*
753 371.

754 Westerling, A. L., H. G. Hidalgo, D. R. Cayan, and T. W. Swetnam. 2006. Warming and
755 earlier spring increase western U.S. forest wildfire activity. *Science* 313:940–943.

756 Whisenant, S. G. 1990. Changing fire frequencies on Idaho’s Snake River plains: ecological
757 and management implications. Pages 4–10 *in* E. D. McArthur, E. M. Romney, S. Smith,
758 and P. T. Tueller, editors. *Proceedings of the symposium on cheatgrass invasion, shrub*
759 *die-off, and other aspects of shrub biology and management*. Forest Service General Technical
760 Report INT-276.

761 Wotton, B. M., and M. D. Flannigan. 1993. Length of the fire season in a changing climate.
762 *The Forestry Chronicle* 69:187–192.

763 Zhu, Z., J. Vogelmann, D. Ohlen, J. Kost, X. Chen, and B. Tolk. 2006. Mapping existing
764 vegetation composition and structure for the LANDFIRE prototype project. Pages 197–215
765 *in* Gen. tech. rep. rmrs-gtr-175. fort collins: U.S. department of agriculture, forest service,
766 rocky mountain research station.