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Using the Past and the Present to Understand Fire Ecology in Sagebrush Habitats of the Gunnison Sage-Grouse

by

Petar Zdravko Simic

APPROVED BY

____
Jonathan Coop, Thesis Advisor

____
Jonathan Coop, Program Director

____
Melanie Armstrong, Dean, School of Environment
And Sustainability

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USING THE PAST AND PRESENT TO UNDERSTAND FIRE ECOLOGY IN SAGEBRUSH HABITATS OF THE GUNNISON SAGE-GROUSE

by

Petar Zdravko Simic (B.A.)

Thesis

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Abstract

The historical role of fire in shaping sagebrush ecosystems remains poorly understood, yet is important for informing the management and conservation of sagebrush landscapes and obligate species such as the threatened Gunnison sage-grouse (GUSG; *Centrocercus minimus*). To gain insight into the historical role of fire in sagebrush landscapes of the Upper Gunnison Basin (UGB), we reconstructed the historical (1424-2001) frequency of low-severity fire from tree-ring fire-scars at sagebrush-forest ecotones (10 sites, 111 trees), and conducted surveys of plant composition and structure at 100 sagebrush sites with and without recent (2001-2020) fire. Tree-ring fire-scars revealed a history of repeated (mean fire return interval of 18.2 to 79.7 years) low-severity fire at sagebrush-forest ecotones until ca. 1900, followed by over a century that was fire-free. Fires occurred synchronously at two or more sites on average every 23.6 years. Recent burns exhibited strong reductions in sagebrush (from an average of 36.5% to 5.7% cover) and concomitant increases in herbaceous cover (from 40.1% to 55.1%) relative to unburned sites. These shifts diminished with time since fire, but persisted for at least two decades. Together, these results indicate that portions of the sagebrush landscape of the UGB, including occupied GUSG habitat, were historically characterized by repeated fire and vegetation mosaics including patches dominated by grasses and forbs. These findings suggest that prescribed fire could be used to maintain and restore the important ecological process of fire, but also highlight the need for additional research on how such conditions might affect GUSG populations in the context of contemporary conditions.

Keywords: *Artemisia tridentata*, Gunnison Sage-Grouse, *Centrocercus minimus*, Fire Regimes, Fire History, Tree-Ring Fire Scars, Fire Effects, Prescribed Fire, Ecological Restoration, *Bromus tectorum*

Introduction

Sagebrush (*Artemisia* spp.) steppe landscapes are important and widespread across western North America, providing habitat for a range of obligate and generalist species and supporting essential ecosystem services. There is increasing concern about the susceptibility of sagebrush landscapes to undesirable ecosystem shifts caused by anthropogenic processes including land use, non-native species introductions, altered fire regimes, and climate change (Boyd, 2022; Bradley, 2010; Chambers et al., 2017; Knick et al., 2003; Knick & Rotenberry, 1997). In particular, recent wildfire activity in some sagebrush landscapes is catalyzing persistent conversion toward vegetation dominated by non-native annual grasses (Balch et al., 2013; Pilliod et al., 2017). However, the extent to which contemporary sagebrush fire regimes differ from historical norms remains poorly understood, in large part because little is known about the historical and pre-historical role of fire in sagebrush landscapes (Bukowski & Baker, 2013a). In some areas, fire frequency has increased recently in association with the expansion of highly flammable, non-native annual grasses (Baker, 2006; Knick & Connelly, 2011; Pilliod et al., 2017). However, other lines of evidence suggest that fires may not be occurring as frequently as they were prior to Euro-American settlement, due to the removal of Indigenous peoples, reduction of continuous fine fuels associated with livestock grazing, and modern, direct fire suppression (Davies et al., 2010; Kimmerer & Lake, 2001; Strand et al., 2014; Wrobleski & Kauffman, 2003).

Altered vegetation composition, structure, and landscape patterns associated with fire regimes shifts may reduce the capacity of sagebrush habitats to support obligate species, including the Gunnison sage-grouse (GUSG; *Centrocercus minimus*). Long-term declines of the greater sage-grouse (GRSG) have been linked to chronic effects of wildfire within the Great Basin (Coates et al., 2016), which is cause for concern for future effects of wildfire on the GUSG. The GUSG was first listed as a new species in 2000 and was listed as threatened under the federal Endangered Species Act in 2014 (USFWS, 2014; Young et al., 2000). The GUSG has experienced range-wide declines over the past century (Oyler-McCance et al., 2001; Schroeder et al., 2004) and currently occupies <10% of its former range (GSRSC, 2005; Schroeder et al., 2004). Causes for this decline have been linked to habitat fragmentation and degradation associated with mining, agriculture, livestock grazing, and energy development (Connelly et al., 2004; Green et al., 2017; Monroe et al., 2017). The largest and most stable population persists in the Upper Gunnison Basin (UGB; Fig. 1) of western Colorado, which currently supports 85% of the GUSG's global population (USFWS, 2014). However, populations in the UGB are also documented to have declined dramatically over the last century (Oyler-McCance et al., 2001) and have continued to decrease in recent decades to an all-time low (Coates et al., in review; Nicholson, 2019).

The extent to which vegetation change in the UGB over the last century may be influencing GUSG population declines is not well understood, in part because these dynamics are complex and poorly documented (Connelly & Braun, 1997). However, grass-fire cycles and conifer expansion are changes in vegetation within the Great Basin that have been linked to the long-term decline of the GRSG (Ricca & Coates, 2020). Notes from early expeditions mention areas of abundant grass in the UGB (map of UGB by Primus & Pelletier, 2016) and also mention areas where there was little to no forage for their horses and places where their wagons became stuck in dense sagebrush (Bradford, 2004; Mumey & Schiel, 1955). Euro-American settlement in the UGB was initiated in the late 1870s, and was associated with extensive cattle and sheep grazing, the removal of nomadic Utes and other Indigenous people, and the development of roads, railroads, and irrigated valley-bottom agriculture (Vandenbusche, 1980). These patterns parallel similar abrupt shifts in land use that occurred across much of interior western North America (Miller et al., 2011). Cattle grazing has continued across large portions of the sagebrush ecosystems of the UGB. As has been widely documented across other vegetation types (Brown et al., 2019; Davies et al., 2010), such changes are likely to have reduced the abundance and continuity of fine, grassy fuels and thus the frequency of fire, which would have been further constrained by modern fire suppression beginning in the mid-20th century. A turn-of-the century field survey of the UGB describes both Indigenous burning and numerous large-scale fires being ignited by miners, timber men, sheepherders, and campers (Smith, 1904). Fires in the Rocky Mountains today are started by a combination of human and lightning ignitions (NIFC, 2022). Most ignitions are subject to rapid suppression, though small areas have been treated with prescribed fire in the UGB (B. Stevens, personal communication, July 18, 2021). Consequently, we would expect that decreasing fire activity may have favored shifts from more patchy and grass-dominated communities toward greater dominance by woody shrubs, albeit depending on the differences between historical and contemporary fire activity (Mata-González et al., 2018).

While late-seral stage sagebrush forms a critical seasonal habitat for the GUSG, a broader range of vegetation types is needed to meet annual GUSG habitat requirements, which vary seasonally (Connelly et al., 2011; Fedy et al., 2012; Knick & Connelly, 2011; Miller et al., 2011). Sage-grouse prefer tall and dense shrub habitats for nesting, winter shelter and food, and for cover from depredation throughout the year. Patches of open or low-shrub habitats are utilized for leks and brood rearing (Apa, 2021). Sage-grouse have also been shown to move from sagebrush-dominated communities to more mesic mountain shrub-dominated communities when sagebrush vegetation understories desiccate (Fischer et al., 1996; Gibson et al., 2016). Finally, forb-rich, grassy habitat and sagebrush understories provide abundant, high-protein invertebrate food sources during the summer (Connelly et al., 1998; Hagen et al., 2007; Kirol et al., 2012). Whereas large continuous fires may lead to the extirpation of local populations (Pederson et al., 2003), patchy and relatively small fires may create a mosaic of varying post-fire seral stages, including early post-fire, herbaceous vegetation, subsequent shifts toward increasing cover, height, and age of sagebrush, and late-seral, unburned patches (Klebenow, 1973). Such historical conditions could theoretically support all GUSG habitat requirements, though their optimal proportional abundance is uncertain (Pederson et al., 2003).

The historical fire regime and attendant vegetation patterns across sagebrush landscapes within the GUSG range are not well understood. Bukowski and Baker (2013b) compiled historical General Land Office survey (GLO) data collected from 1872-1892, around the time of widespread Euro-American settlement, to reconstruct historical fire regimes within GUSG habitat. They inferred that these landscapes consisted of large, contiguous expanses of mature sagebrush with historical fire rotations on the order of hundreds of years (178-357 years in Wyoming big sagebrush and 90-143 years in mountain big sagebrush). However, GLO-based reconstructions have since been shown to be largely unreliable for reconstructing fire history (Fule et al., 2014). The dataset Bukowski and Baker created for their analysis was made up of surveyor vegetation descriptions of section lines where fires were inferred from vegetation data. The inferred historical fire boundaries were characterized by blocks confined by section lines, showing the variation of vegetation descriptions among surveyors. Additionally, scattered sagebrush was not considered as a fire indicator in their study, excluding the presence of patchy fires, which are common in sagebrush landscapes (Bukowski & Baker, 2013b). Even if surveyors reconstructed the historical fire regimes accurately, the fire frequency from the onset of widespread Euro-American settlement may differ from that of the historical frequency pre-Euro-American settlement.

As an alternate approach to characterizing historical fire regimes and infer their effects on vegetation, tree-ring fire scars provide multi-century estimates of the frequency, seasonality, and extent of fire. However, this approach has not been widely used to understand fire in sagebrush systems, as fire scars are rare to non-existent in sagebrush (Mensing et al., 2006), posing what would appear to be significant challenges to reconstructing fire histories of sagebrush ecosystems. However, tree-ring fire scars at forest ecotones have been used to make inferences about fire regimes of adjoining non-forest vegetation types, such as grasslands (Dewar et al., 2021) and could be used to understand the historical occurrence of fire in sagebrush landscapes. Fire scars in forest stands adjacent to sagebrush could be expected to record fires that were stand-replacing or patchy in sagebrush, given that most spreading fires are lethal for individual sagebrush plants (Beck et al., 2009; Miller & Eddleman, 2001). We would expect that fire-scarred trees at sagebrush-forest ecotones would thus also support inferences that portions of the adjacent sagebrush landscape were at times characterized by fire effects that included reduced woody cover and increased herbaceous cover. Fire has been shown to decrease woody cover and increase herbaceous cover in sagebrush landscapes of the Great Basin (Beck et al., 2009; Beck et al., 2012). However, no work has been done assessing fire effects in sagebrush habitats of the UGB.

The purpose of this study was to improve our understanding of the potential historical role of fire in shaping sagebrush ecosystems across sagebrush landscapes of the UGB, including historically- and currently-occupied GUSG habitat. We employ two complementary methodologies to ascertain the historical frequency of fire and characterize contemporary effects of such fires; together, these approaches are intended to shed light on likely patterns of historical vegetation composition and structure within sagebrush communities, as follows. First, we use tree-ring fire scars from sagebrush-forest ecotones to reconstruct historical fire frequency and seasonality, providing estimates of fire return intervals for at least a portion of the adjoining sagebrush landscape of the UGB. Second, to infer the extent and duration of historical fire effects on sagebrush plant communities, we sampled vegetation in a series of recent burns and adjacent unburned sites in comparable sagebrush habitats. In particular, we contrast the relative cover and height of sagebrush vs. herbaceous vegetation. Given concerns about fire-induced expansion of non-native, annual grasses and other invasive plant species, we also quantify differences in the abundances of these species in burned vs. unburned sagebrush. Taken together, our approaches are intended to yield new insight into historical processes and patterns and how they may differ from those of today in GUSG habitat within the Upper Gunnison Basin.

Methods

Study Area

Our study area spans sagebrush and forest margins in the Upper Gunnison Basin (UGB; Fig. 1), a large (ca. 845-km^2), high-elevation river basin in central Colorado, west of the Continental Divide and east of the Colorado Plateau. Sagebrush vegetation in the UGB is characterized by a cold, dry climate with a mean annual temperature of 3.1° C and an average annual precipitation of 27 cm (Aldridge et al., 2012). The UGB was chosen as our study area because it harbors the largest and most stable population of GUSG (USFWS, 2014).

Sagebrush-steppe is common across the UGB, with big sagebrush (*Artemisia tridentata*) being the dominant species. Intermixed with the sagebrush community were snowberry (*Symphoricarpos rotundifolia*), wild rose (*Rosa woodsii*), sticky-leaved rabbitbrush (*Chrysothamnus viscidiflorus*), and antelope bitterbrush (*Purshia tridentata*). Piñon (*Pinus edulis*)-juniper (*Juniperus scopulorum*) forests are rare in the UGB, with the sagebrush-steppe typically abutting directly against aspen (*Populus tremuloides*) or spruce (*Picea* spp.) forests at higher elevations (Johnston et al., 2001). Ponderosa pine (*Pinus ponderosa*) and Douglas-fir (*Pseudotsuga menziesii*) are also uncommon in the UGB, but are sometimes found at sagebrush ecotones (Johnston et al., 2001).

The UGB has a long history of human occupancy with the Utes being the primary occupants prior to Euro-American settlement (Stiger, 2008; Vandenbusche, 1980). The Utes were nomadic hunter-gatherers, following large game migrations into the UGB during the summer (Marsh, 1982). Little is known about the historical use of fire by Indigenous people in the UGB with some narratives describing that fire was used to corral game and regenerate grass (T. Knight Sr., personal communication, August 14, 2020) and other narratives explain that fire was not used at all (R. Lopez-Whiteskunk, personal communication, October 24, 2020). Around the time Gunnison became an incorporated city in 1880, the Utes were removed from the UGB and an economy was created dependent on mining, intensive livestock grazing, and the construction of a transcontinental railroad.

Fire history field and lab methods

Our first objective was to reconstruct historical fire regimes from tree-ring fire scar sites across the UGB. Fire scars occurring on trees at the sagebrush-forest ecotone (Fig. A in Appendix) represent the fire history of at least some portions of the adjacent sagebrush vegetation. In 2020, we established 10 fire history sites within areas mapped as currently occupied or historical GUSG habitat (Fig. 1). Sites were stratified broadly across the sagebrush margins of the UGB in order to ensure that inferences were representative of historical fire regimes across the entire basin. Sites contained at least 10 fire-scarred trees (including snags, stumps, logs, and live trees) within an area of ≤ 1 ha. Sampling at least 10 fire-scarred trees ensured a sufficient sample size to have repeated observations of individual fire years, reducing the chance of misidentifying single tree-injuries such as lightning.

At each fire history site, we used standard tree-ring fire history methods (Arno & Sneck, 1977; Dieterich & Swetnam, 1984; Swetnam et al., 1999) to collect samples from fire-scarred trees. We targeted at least one live tree and old remnant wood at each site to maximize the temporal extent of each chronology. We recorded species, location (using handheld Garmin eTrex 22x GPS unit), wood source (live tree, snag, stump, or log), and took photos of each sample. Cross-sections included the pith, all fire-scars, and the outermost ring (Fig. C in Appendix). Multiple samples were collected from each tree to account for variation in the tree rings widths and fire-scars locations.

Samples were processed in the lab using standard dendrochronological methods (Speer, 2010; Stokes & Smiley, 2008). This included mounting each sample onto plywood, flattening the samples with a band saw, and sanding with increasing grits of sandpaper (60-400 grit).

Fire history analysis

After processing, samples were cross-dated using locally developed chronologies from the UGB to determine the year and season (dormant, earlywood, or latewood) in which the fires occurred (Swetnam, 1999). Local ponderosa pine and Douglas-fir chronologies were accessed using the International Tree-Ring Database (ITRDB; National Centers for Environmental Information (NCEI), 2022). The codes of the chronologies used for this study were CO620, CO623, CO061, CO624, and CO627. Fire seasonality was determined based on intra-ring position of the fire-scars (Baisan & Swetnam, 1990). Fire scars in the dormant wood were assumed to have occurred in the spring, before the trees started growing (May or early June; Swetnam & Betancourt, 1998), early-earlywood likely indicates a fire occurring in June or July, middle-earlywood is likely July, late-earlywood is likely August, and latewood is likely September (Grissino-Mayer et al., 2004). For samples that we were not able to cross-date visually due to tree-ring suppression or old age, we measured the width of tree-rings using a measuring bench and the program COFECHA (Holmes, 1983) to find possible tree-ring dates, which we verified visually.

We utilized the Fire History Analysis and Exploration System (FHAES) software package to compile our findings and visualize synchronous fires and temporal shifts in fire regimes (version 2.0.2; Brewer et al., 2017). This software was also helpful in periodic quality control throughout the cross-dating process by allowing us to visualize plots that showed potential errors and anomalies in fire dates (Sutherland et al., 2015). The burnr fire history R package (version 0.5.0; Malevich et al., 2018) was utilized to find the mean, median, maximum, and minimum fire return intervals from each site as well as for the study area of the entire UGB. All analyses were conducted in R (version 4.1.2; R Core Team 2021). We compiled site-level fire chronologies and a study area composite fire chronology of the UGB. Together, these chronologies allowed us to make conclusions about the fire frequency of sagebrush and relative extent based on the synchronous fire events. We also determined seasonality percentages from each fire year and all fire years as well as the percentage of fires that occurred in drought years. All fire history data were provided to the North American Fire History Synthesis project database (Margolis et al., in review).

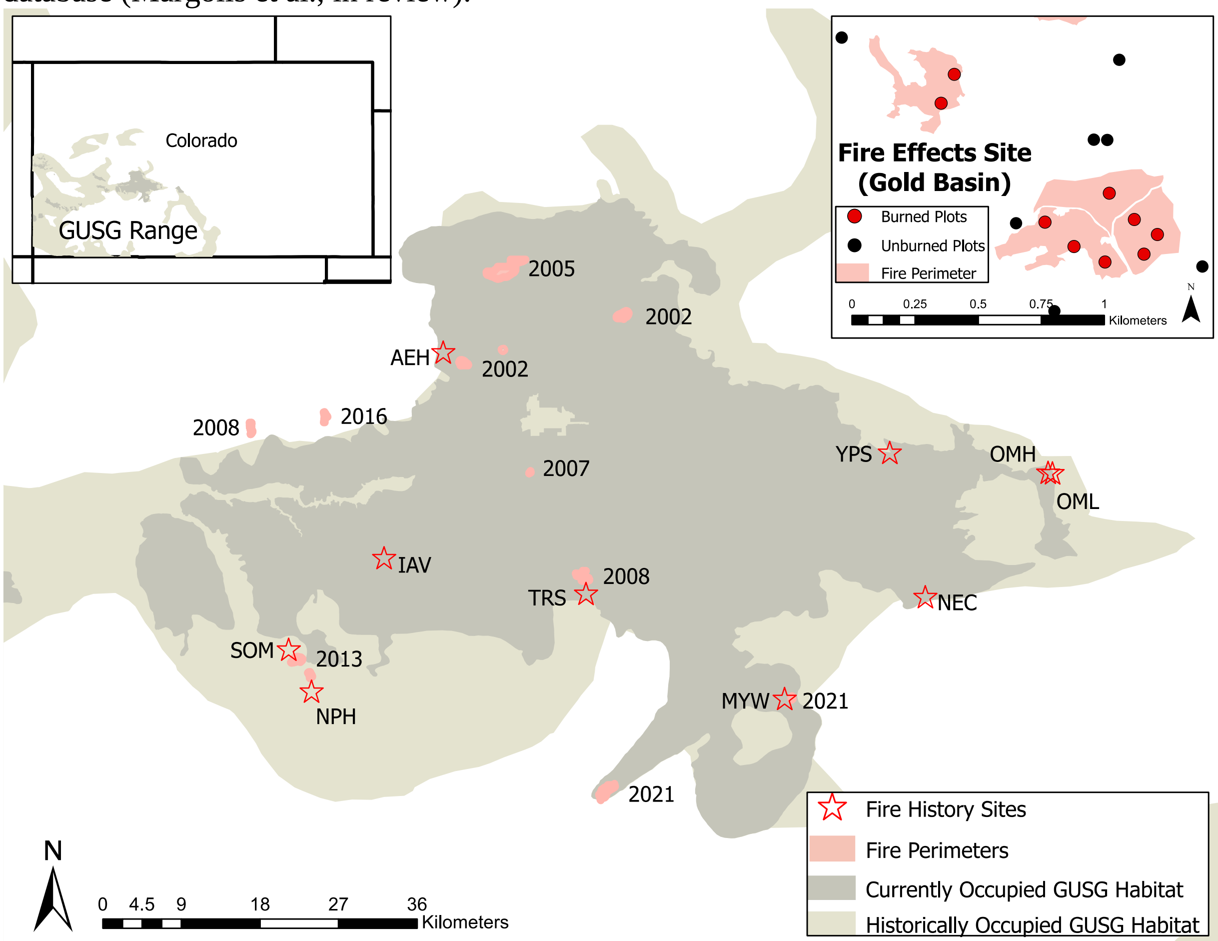

Figure 1. Map of the Upper Gunnison Basin showing fire history sites represented by the red stars labeled by three-letter site codes and sampled fires from our fire effects data represented by salmon-colored polygons labeled by the year the fire occurred. The fire polygons were enlarged for the sake of visibility and do not represent the actual size of the fire. Currently and historically occupied Gunnison sage-grouse habitat are represented by the darker and lighter shades of gray, respectively. Notice the fire history sites and fire effects sites proximity to each other as well as their location within Gunnison sage-grouse habitat. In the top right-hand corner is a map of the Gold Basin prescribed burned as an example of a fire effects site. Fire effects sites are represented by red dots for the burned sites and black dots for the unburned sites. Notice for every site sampled within the fire perimeter, an unburned site was sampled adjacent to the fire perimeter. The Gold Basin fire was within currently occupied Gunnison sage-grouse habitat. The inset map in the top left-hand corner shows currently and historically occupied Gunnison sage-grouse habitat.

Sagebrush fire effects field methods

To characterize fire effects on sagebrush vegetation in the UGB, we conducted vegetation surveys in 50 recently burned and 50 adjacent, unburned sagebrush sites (Fig. 1). Fire perimeter polygons were obtained from local US Forest Service (USFS) and Bureau of Land Management (BLM) offices, and included both prescribed burns and wildfires. Burned sites were sampled across 12 different fires occurring in eight different years between 2001 and 2021, (Table B in Appendix) facilitating a comparison of vegetation composition at varying temporal scales. We excluded from sampling any burns that were subject to intensive post-fire management including reseeding or planting of sagebrush. Sites were randomly distributed within fire perimeters and adjacent areas within 100-m of fire perimeters. For every burned site we sampled, an unburned site was sampled directly adjacent to the fire perimeter (Fig. 1). All sites were within occupied GUSG habitat or directly adjacent to occupied habitat and within the sagebrush steppe (Fig. 1).

To conduct the vegetation surveys, we used the BLM's nationally standardized Assessment, Inventory, and Monitoring (AIM) protocols (Toevs et al., 2011). These protocols include measures of plant cover and ground cover along line-point intercept (LPI) and continuous-line intercept (CLI) transects, and a survey of vascular plant species richness. At each site, we first established the plot center, where spatial coordinates were recorded using a handheld GPS unit. We next established three, 25-m transects (facing 0°, 120°, and 240°, respectively), beginning 5-m from plot center, creating a 30-m radius plot (2827 m^2 or 0.7 acres). For line-point intercept transects, a pin flag was dropped every 0.5-m along the transect line. All vascular plant species touching the pin flag were recorded, and the ground surface cover (bare soil, rock, or plant basal hit) was recorded. Maximum herbaceous and woody plant heights within a 15-cm radius from the transect tape were taken every 2.5-m. For continuous-line intercept transects, continuous shrub cover, by species, was recorded along the entire transect line, providing another estimate of shrub species cover. We began recording shrub cover where a threshold 50% cover over a 2-cm area was achieved; we stopped if there was a gap at least 5-cm long (Toevs et al., 2011). To provide a separate measure of richness, all plant species within the 30-m radius plot (including those not occurring on a transect) were recorded via a subsequent walking census that was continued until no new species had been observed for two minutes.

Vegetation data analysis

From the LPI transect data, we summed intercepts by species to calculate the total foliar cover of each species at each site. We also calculated total cover for each life form (woody, herbaceous, graminoid, and forb) as well as the absence of cover (bare ground), and total cover by native vs. non-native species. We averaged woody and herbaceous heights across each site. We ran paired t-tests to contrast key vegetation metrics including life form (percent woody, herbaceous, graminoid, and forb cover), total foliar cover, percent sagebrush cover, total native species cover and percent bare ground in burned and unburned sites. We ran Wilcoxon signed rank tests to contrast key vegetation metrics that were not normally distributed including average woody and herbaceous height and total non-native species cover. We then found averages for sagebrush cover for 0, 5, 10, 15, and 20 years after fire to make projections on how long it would take for these metrics to fully recover to the pre-fire state. We also constructed linear models to assess effects of time-since-fire on the community attributes mentioned above. In these models we only tested for effects on burned plots. Additionally, we ran Wilcoxon signed rank tests to contrast species-specific differences in cover using the 12 herbaceous species with the highest total percent cover.

From the CLI transect data, we summed intercepts by species to calculate the total foliar cover of each species at each site. We also calculated total woody and sagebrush cover. We ran paired t-tests to contrast woody cover and sagebrush cover between burned and unburned sites. We ran Wilcoxon signed rank tests to contrast species-specific differences in cover using the six woody species with the highest total percent cover.

Results

Fire history

We sampled ten tree-ring fire-scar sites at sagebrush-forest ecotones across the UGB. The number of trees sampled at a site ranged from 8 to 14 for a total of 111 trees (Table A in Appendix) from which a total of 177 tree-ring samples were collected. From those 111 trees, 7 were lodgepole pine (*Pinus contorta)*, 39 were ponderosa pine, and 65 were Douglas-fir. We were not able to date approximately 10% of our tree-ring samples due to suppressed ring growth or decay. Tree-ring dates ranged from 1362-2020 (Table A in Appendix) and fire dates ranged from 1424-2001 (Table 1). Fire intervals were calculated from a common period (1684-1892) when eight of the ten sites were recording and the remaining two sites started recording in the following decades. Mean fire intervals (MFI) varied among sites, ranging from 18.2 to 79.7 years for an average of 41.3 years, describing a history of repeated, low-severity fire at sagebrush-forest ecotones (Fig. 2; Fig. D in Appendix; Table 1). The tree-rings also revealed the abrupt cessation of repeated fire after 1892, followed by over a century that was fire-free. From the 47 historical fires the tree-rings revealed, 34.0% occurred in drought years. Two sites (NEC and NPH) recorded contemporary prescribed fire in 1999 and 2001 (Fig. 2).

Synchronous fire occurred at multiple sites separated by distances ranging from 0.5 to 70-km in 10 different fire years (1546-1879; Fig. K in Appendix; Fig. 2). From the 10 synchronous fires, 60.0% occurred during drought years. The MFI for synchronous fires during the common period (1684-1892) was 23.6 years. However, over the period when all ten sites were recording fire (1798-1892), the mean synchronous fire return interval was 13.5 (Fig. 2). Fire was also most frequent during this period, compared to any other century in our fire history. These estimates excluded synchronous fire years from two of our fire history sites (OML and OMH) due to their close proximity to each other.

Fires occurred in different seasons (Fig. B in Appendix), with 53% of the 220 dated fire scars occurring in the dormant wood, 17% in early earlywood, 11% in middle earlywood, 3% in late earlywood, and 1% in latewood. We could not determine the seasonality of 15% of fire scars due to decay or suppression. The period in which fire was most frequent (1798-1892; study area composite MFI of 6.3 years) included the greatest ratio (60%) of dormant fires (Fig. E in Appendix).

Table 1. The fire interval statistics for each fire history site as well as a composite of all ten-fire history sites across the Upper Gunnison Basin (1684-1892).

Site Name	Site Code	First Fire Scar Date	Last Fire Scar Date	Fires (#)	Fire Return Intervals (yrs)			
					Mean	Median	Min	Max
Antelope Hills	AEH	1685	1879	5	48.5	59.5	9	66
Iola Valley	IAV	1715	1834	2	23.8	23.8	23.8	23.8
Meyers West	MYW	1424	1868	4	63.4	39	3	162
Needle Creek	NEC	1529	2001	6	30.2	21	8	61
North Powderhorn	NPH	1514	1999	5	45.8	53	19	58
Old Monarch High	OMH	1798	1892	6	18.8	18	10	30
Old Monarch Low	OML	1759	1872	4	37.7	39	30	44
Sapinero Mesa	SOM	1690	1830	4	46.7	33	20	87
Timber Sale	TRS	1574	1879	5	18.2	19	7	28
Yellow Pine South	YPS	1633	1872	3	79.7	81	71	87
Study Area Composite		1424	2001	32	6.7	6	1	22

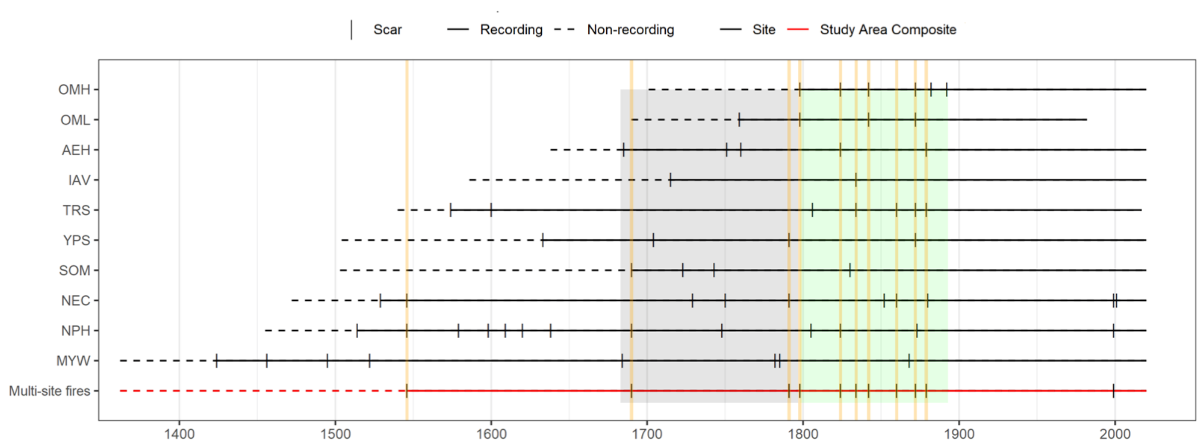

Figure 2. The study area composite fire chronologies for all fires at each site. The multi-site fire composite (red) represents all fires recorded in at least two sites, which are also highlighted in orange (1546, 1690, 1791, 1798, 1824, 1834, 1842, 1860, 1872, and 1879). Contemporary synchronous fires were excluded; since we know those were separate fires at separate sites. The grey/green-shaded square represents the common period used for analysis (1684-1892). The green portion of the square represents the portion of the common period where all sites were recording fire (1798-1892). The mean synchronous fire return interval for this period is 23.6 (excluding synchronous fire at OML and OMH because of their proximity to one another). Notice the year 1872 where four separate sites recorded fire events; some of these sites are separated by 70-km.

Recent fire effects in sagebrush vegetation.

Recent fire in sagebrush drove significant changes in vegetation composition and structure. Recent burns showed significant decreases in woody plant cover relative to unburned areas (site average of 17.5 vs. 33.5% (+/- 1 st. dev.) in burned and unburned sites, respectively; paired t-test P<0.001, 49 d.f.; Fig. 3a) and in particular, reductions in *Artemisia tridentata* spp. *wyomingensis* (sagebrush) cover (site average 5.7 vs. 26.5% (+/- 1 st. dev.) in burned and unburned sites, respectively; paired t-test P<0.001, 49 d.f.; Fig Fa in Appendix). Based on the rate of recovery from 0-20 years after fire, we projected that sagebrush cover would take about 45.0 years to fully recover to its pre-fire state. Recent burns also showed a significant increase in woody plant cover with time since fire (linear model P<0.001, 48 d.f.; Fig. 3b), and in particular, increases in sagebrush cover with time since fire (linear model P<0.001, 48 d.f.; Fig. Gb in Appendix). Conversely, recent burns showed significant increases in herbaceous plant cover relative to unburned areas (site average 55.1 vs. 40.1% (+/- 1 st.dev.) in burned and unburned sites, respectively; paired t-test P<0.001, 49 d.f.; Fig. 3c) and in particular, increases in graminoid cover (site average 46.3 vs. 31.4% (+/- 1 st.dev.) in burned and unburned sites, respectively; paired t-test P<0.001, 48 d.f.; Fig. Fc in Appendix). However, we found no clear relationship between time since fire and herbaceous plant cover (linear model P=0.52, 48 d.f.; Fig. 3d), graminoid cover (linear model P=0.80, 48 d.f.; Fig. Fd in Appendix), or forb cover (linear model P=0.12, 48 d.f.; Fig. Fb in Appendix). We also found that there was no significant difference in total plant cover (paired t-test P=0.81, 49 d.f.; Fig. Ha in Appendix), forb cover (paired t-test P=0.92, 49 d.f.; Fig. Fa in Appendix) or bare ground (paired t-test P=0.80, 49 d.f.; Fig. Ia in Appendix) between the burned and unburned sites. Recent burns also showed a significant increase in total foliar cover with time since fire (linear model P<0.01, 48 d.f.; Fig. Hb in Appendix).

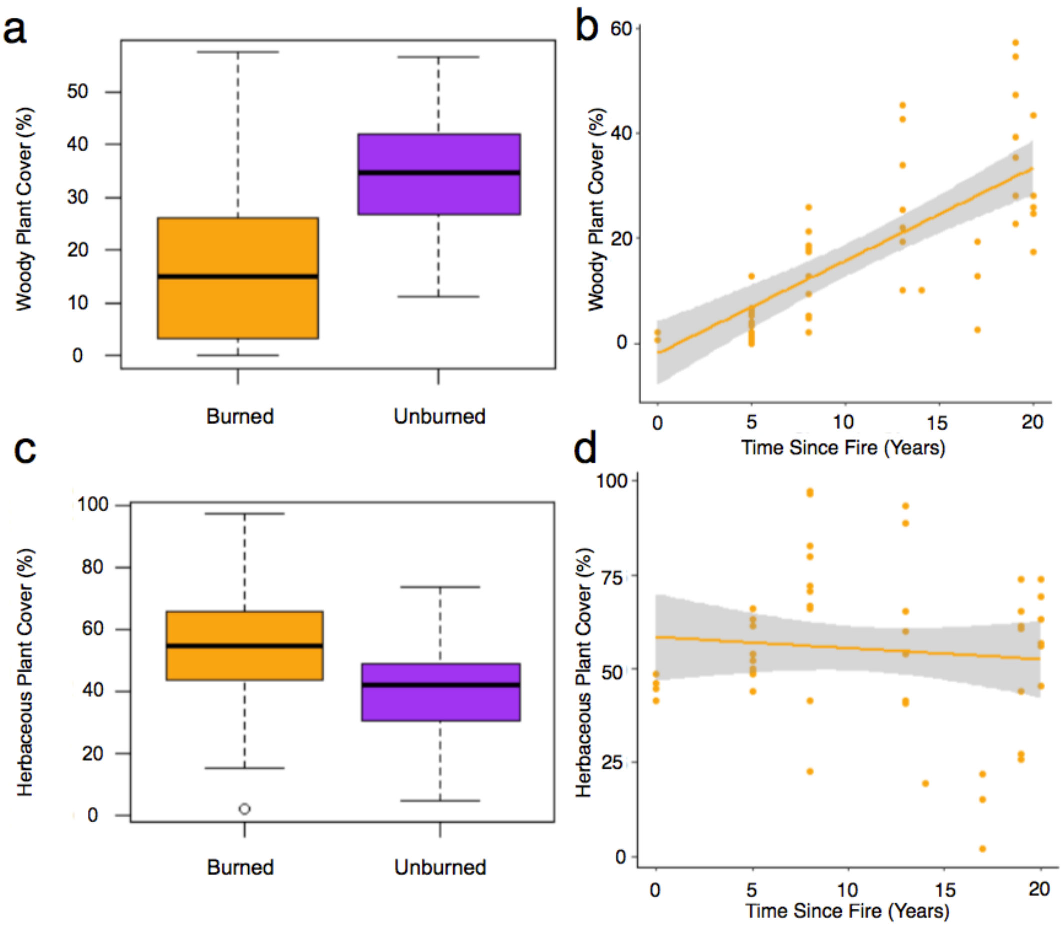

Figure 3. a) Boxplot comparing percent woody plant cover between all 50 burned and all 50 unburned sites. Boxplots show minimum, first quartile, median, third quartile, and maximum and includes outliers. Woody plant cover was significantly greater in the unburned sites compared to the burned sites (P<0.001). b) Linear model showing the change in percent woody plant cover with time since fire within all 50 burned sites. Woody plant cover showed a significant increase with time since fire (P<0.001). c) Boxplot comparing percent herbaceous plant cover between all 50 burned and all 50 unburned sites. Boxplots show minimum, first quartile, median, third quartile, and maximum and includes outliers. Conversely to woody plant cover, herbaceous plant cover was significantly greater in the burned sites compared to the unburned sites (P<0.001). d) Linear model showing the change in percent herbaceous plant cover with time since fire within all 50 burned sites. Herbaceous plant cover showed no significant relationship with time since fire (P=0.5).

Recent burns showed significant decreases in average woody plant height relative to unburned areas (site average 17.3 vs. 37.2 cm (+/- 1 st. dev.) in burned and unburned sites, respectively; Wilcoxon signed rank test P<0.001; Fig. 4a). Recent burns also showed a significant increase in average woody plant height with time since fire (linear model P<0.001, 48 d.f.; Fig. 4b). Conversely, recent burns showed significant increases in average herbaceous plant height relative to unburned areas (site average 28.2 vs. 24.7 cm (+/- 1 st.dev.) in burned and unburned sites, respectively; Wilcoxon signed rank test P<0.05; Fig. 4c) and significant decreases in average herbaceous plant height with time since fire (linear model P<0.05, 48 d.f.;

Fig. 4d). Based on the rate of recovery from 0-20 years after fire, we projected that woody plant height would take about 25.0 years to fully recover to its pre-fire state.

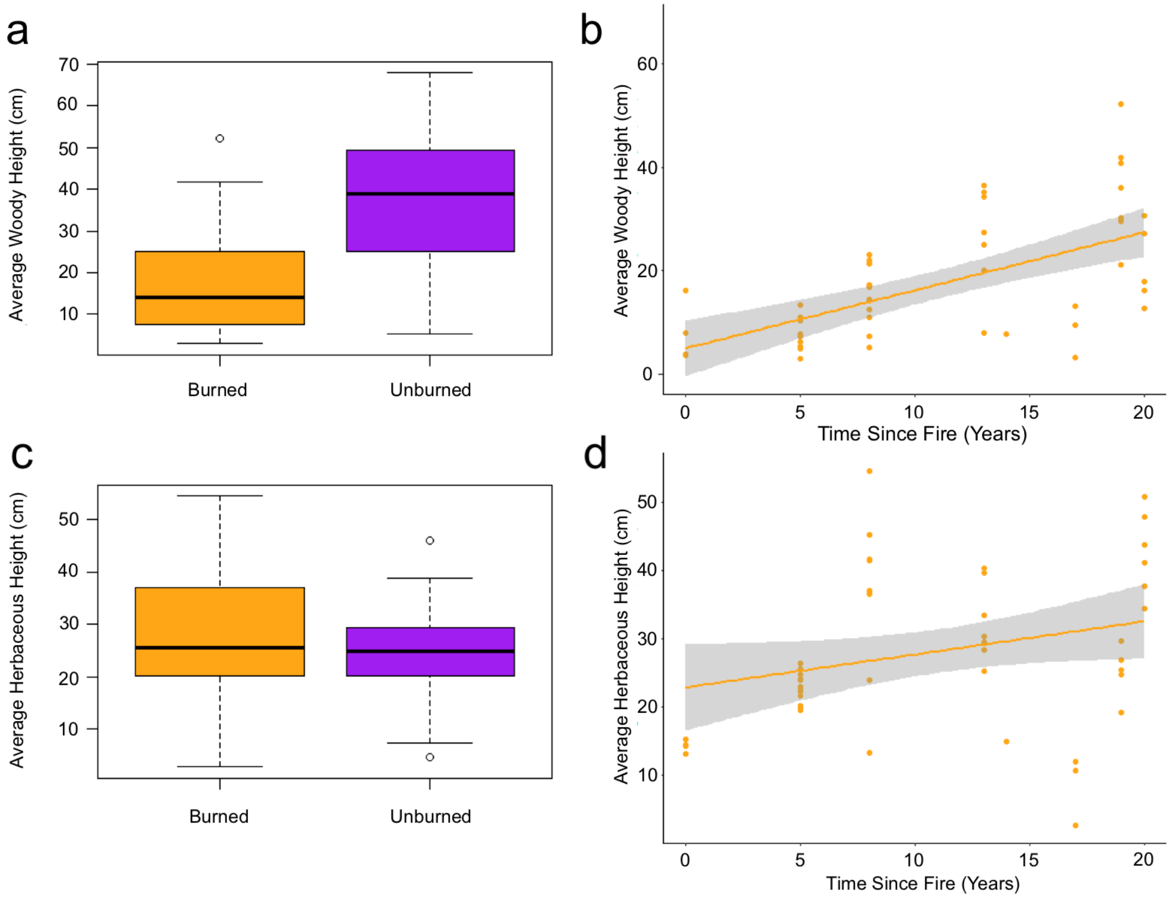

Figure 5. a) Boxplot comparing average woody plant height between all 50 burned and all 50 unburned sites. Boxplots show minimum, first quartile, median, third quartile, and maximum and includes outliers. Average woody plant height was significantly greater in the unburned sites compared to the burned sites ($P<0.001$). b) Linear model showing the change in average woody plant height with time since fire within all 50 burned sites. Average woody plant height showed a significant increase with time since fire ($P<0.001$). c) Boxplot comparing average herbaceous plant height between all 50 burned and all 50 unburned sites. Boxplots show minimum, first quartile, median, third quartile, and maximum and includes outliers. Conversely to average woody plant height, average herbaceous plant height was significantly greater in the burned sites compared to the unburned sites ($P<0.05$). d) Linear model showing the change in average herbaceous plant height with time since fire within all 50 burned sites. Average herbaceous plant height showed no significant relationship with time since fire ($P=0.06$).

From the 12 herbaceous species in which we compared cover between burned and unburned sites, the only plant species that had significantly higher cover in the burned sites compared to the unburned sites was crested wheatgrass *(Agropyron cristatum)* (site average 2.4 vs. 0.7% (+/- 1 st.dev.) in burned and unburned sites, respectively; Wilcoxon signed rank test $P<0.01$; Fig. 6). No herbaceous species showed significantly higher cover in the unburned sites (Fig. 6).

Our CLI data showed the same trend as our LPI data with a significantly greater amount of woody plant cover and sagebrush cover in the unburned sites compared to the burned sites. From the 6 woody species in which we compared cover between burned and unburned sites, the two plant species that had significantly higher cover in the burned sites compared to the unburned sites were yellow rabbitbrush *(Chrysothamnus viscidiflorus)* (site average 7.0 vs. 2.1% (+/- 1 st. dev.) in burned and unburned sites, respectively; Wilcoxon signed rank test $P<0.001$; Fig. 7) and roundleaf snowberry *(Symphoricarpos rotundifolius)* (site average 2.0 vs. 0.6% (+/- 1 st. dev.) in burned and unburned sites, respectively; Wilcoxon signed rank test $P<0.05$; Fig. 7). The following woody species had significantly higher cover in the unburned sites compared to the burned sites; black sagebrush *(Artemisia nova)* (site average 0.1 vs. 1.6% (+/- 1 st. dev.) in burned and unburned sites, respectively; Wilcoxon signed rank test $P<0.01$; Fig. 7), Wyoming big sagebrush *(Artemisia tridentata ssp. wyomingensis)* (site average 6.1 vs. 27.6% (+/- 1 st. dev.) in burned and unburned sites, respectively; Wilcoxon signed rank test $P<0.001$; Fig. 7), and antelope bitterbrush *(Purshia tridentata)* (site average 1.3 vs. 2.2% (+/- 1 st. dev.) in burned and unburned sites, respectively; Wilcoxon signed rank test $P<0.05$; Fig. 7). The only species that had no significant difference in cover between the burned sites and the unburned sites was spineless horsebrush *(Tetradymia canescens)* (Wilcoxon signed rank test $P=0.8$; Fig. 7). From our species richness data, we found no significant difference (paired t-test $P=0.6$) in species richness between the 50 burned sites and the 50 unburned sites.

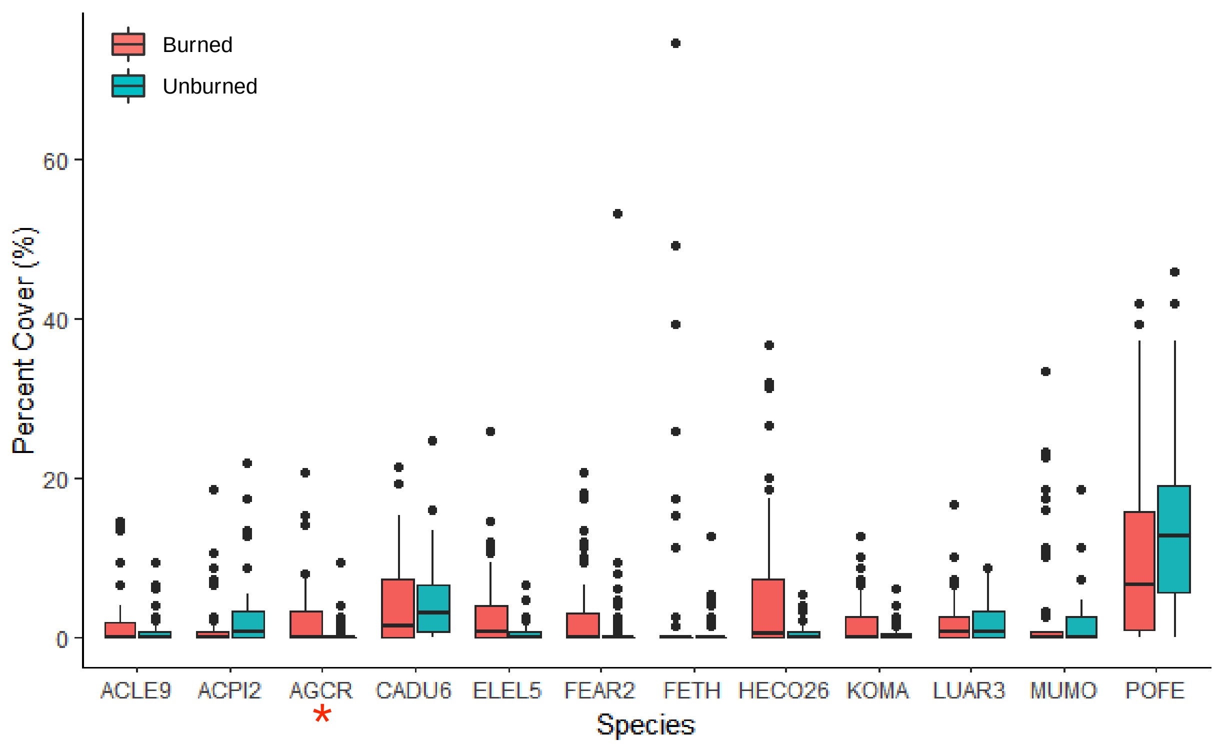

Figure 6. Boxplots of the 12 herbaceous species with the greatest total cover, comparing cover between the 50 burned sites with the 50 unburned sites. Boxplots show minimum, first quartile, median, third quartile, and maximum and includes outliers. The cover data came from our line-point intercept data. We chose the top 12 species because the rest of the herbaceous species had such low cover, a relationship between burned and unburned was not discernable. The plant codes correspond with the following species: ACLE9 *(Achnatherum lettermanii)*, ACPI2 *(Achnatherum pinetorum)*, AGCR *(Agropyron cristatum)*, CADU6 *(Carex duriuscula)*, ELEL5

(Elymus elymoides), FEAR2 *(Festuca arizonica)*, FETH *(Festuca thurberi)*, HECO26 *(Hesperostipa comata)*, KOMA *(Koeleria macrantha)*, LUAR3 *(Lupinus argenteus)*, MUMO *(Muhlenbergia montana)*, and POFE *(Poa fendleriana)*.

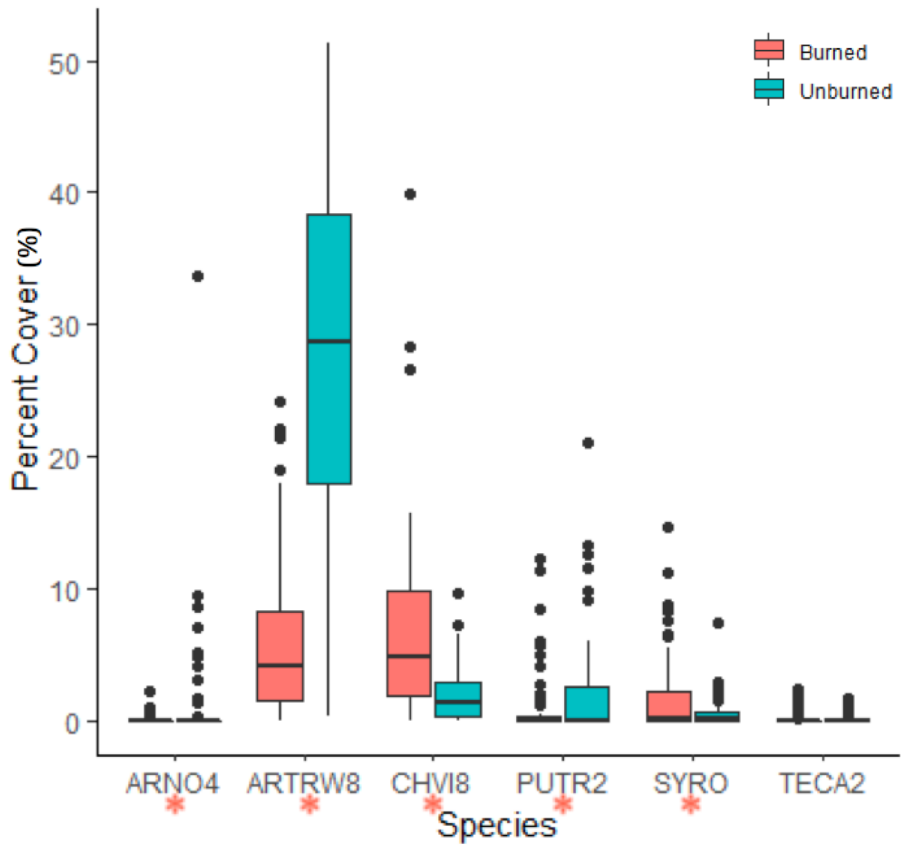

Figure 7. Boxplots of the 6 woody species with the greatest total cover, comparing cover between the 50 burned sites with the 50 unburned sites. Boxplots show minimum, first quartile, median, third quartile, and maximum and includes outliers. The cover data came from our continuous-line intercept data. We chose the top 6 species because the rest of the woody species had such low cover, a relationship between burned and unburned was not discernable. Species with a significant ($P<0.05$) difference in cover between burned and unburned are indicated by the red stars under the species codes. The plant codes correspond with the following species: ARNO4 *(Artemisia nova)*, ARTRW8 *(Artemisia tridentata* ssp. *Wyomingensis)*, CHVI8 *(Chrysothamnus viscidiflorus)*, PUTR2 *(Purshia tridentata)*, SYRO *(Symphoricarpos rotundifolius)*, and TECA2 *(Tetradymia canescens)*.

We found that both native plant cover (site average 27.6 vs. 17.5% (+/- 1 st. dev.) in burned and unburned sites, respectively; paired t-test $P<0.001$, 49 d.f.) and non-native plant cover (site average 2.6 vs. 0.8% (+/- 1 st. dev.) in burned and unburned sites, respectively; Wilcoxon signed rank test $P<0.01$) were significantly higher in the burned sites compared to the unburned sites (Fig. 8). We recorded 5 non-native plant species from the 109 species found in our plots across the 100 sites. Those species were cheatgrass (*Bromus tectorum)* (found at three of 100 sites), crested wheatgrass (*Agropyron cristatum)* (found at 33 of 100 sites), narrowleaf plantain *(Plantago lanceolata)* (found at one of 100 sites), common dandelion (*Taraxacum* *officinale*) (found at two of 100 sites), and yellow salsify (*Tragopogon dubius*) (found at eight of 100 sites). From the three sites in which cheatgrass was present, two of those sites were unburned. From the five non-native species found in our plots, only crested wheatgrass had a significantly higher cover (site average 2.4 vs. 0.7% (+/- 1 st. dev.) in burned and unburned sites, respectively; Wilcoxon signed rank test *P*<0.01; Fig. Ja in Appendix) in the burned sites compared to the unburned sites, accounting for the significance of higher non-native plant cover in the burned sites. The other four species showed no significant relationship between burned and unburned sites. Our linear models showed no significant relationship between cover and time since fire for native plant cover (linear model *P*=0.9; Fig. 8b), non-native plant cover (linear model *P*=0.3; Fig. 8d), or any of the five non-native species (linear model *P*>0.05; Fig. Jb in Appendix). Native plant cover showed a greater degree of significance compared to non-native plant cover and crested wheatgrass cover in relationship to fire (Fig. 8; Fig. Jb in Appendix).

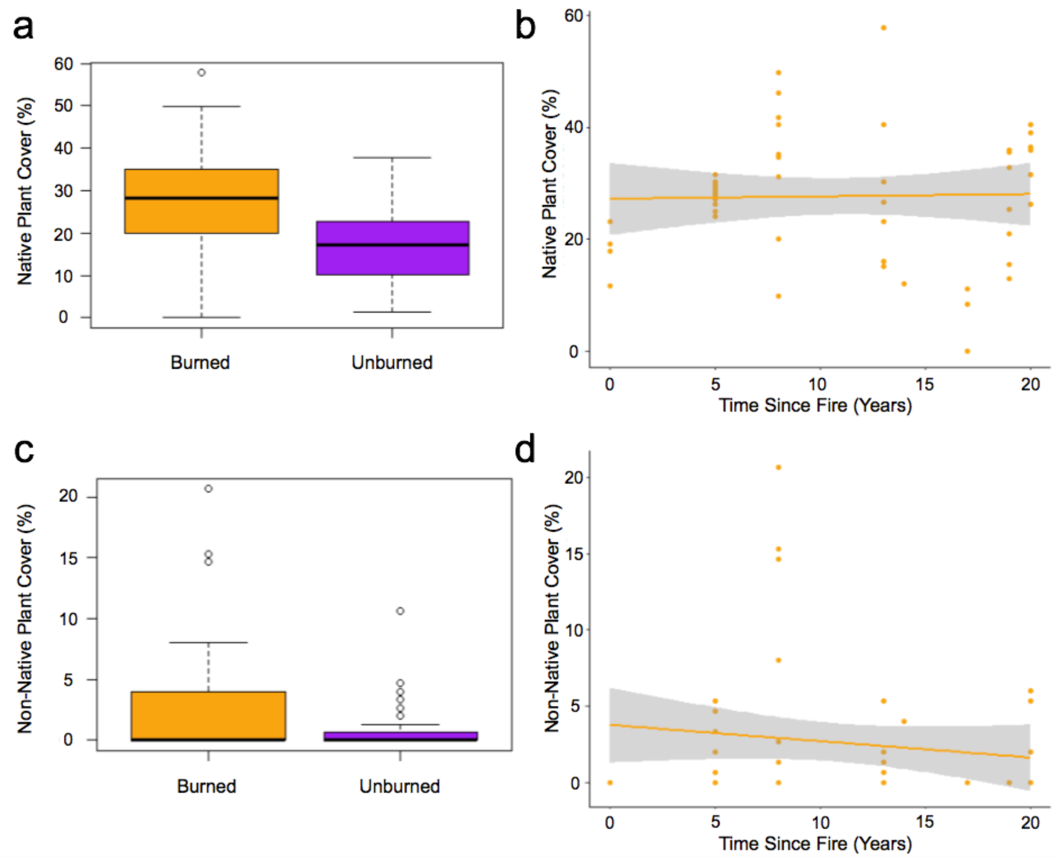

Figure 8. a) Boxplot comparing percent native plant cover (woody and herbaceous) between all 50 pairs of burned and unburned sites. Boxplots show minimum, first quartile, median, third quartile, and maximum and includes outliers. Native plant cover was significantly greater in the burned sites compared to the unburned sites (*P*<0.001). b) Linear model showing the change in percent native plant cover with time since fire within all 50 burned sites. Native plant cover showed no significant relationship with time since fire (*P*=0.9). c) Boxplot comparing percent non-native plant cover between all 50 burned and all 50 unburned sites. Boxplots show minimum, first quartile, median, third quartile, and maximum and includes outliers. Non-native plant cover was significantly greater in the burned sites compared to the unburned sites (*P*<0.01). d) Linear model showing the change in percent non-native plant cover with time since fire within

all 50 burned sites. Non-native plant cover showed no significant relationship with time since fire (*P*=0.3).

Discussion

To better understand the fire ecology of sagebrush landscapes within the Gunnison sage-grouse range, we used tree-ring fire scars from sagebrush-forest ecotones to reconstruct historical fire frequency and seasonality, providing estimates of fire return intervals for at least a portion of the adjoining sagebrush landscape of the UGB. In addition, we conducted vegetation surveys in recently burned sites and adjacent unburned sites in comparable sagebrush habitats, and put these findings together to assess how historical sagebrush landscapes of the UGB may differ from those of today. Our study found a range of mean fire return intervals (MFI) from 18.2-79.7 years from our ten fire history sites across the UGB for an average of 41.3 years. Fires occurring at multiple fire history sites occurred on average every 23.6 years. Fire, including synchronous fire was most frequent during the 19th century, prior to Euro-American settlement. The majority of fires (53%) occurred in early summer. Modern fires reduced sagebrush cover and increased herbaceous cover. This shift diminishes over time but persists for at least two decades after fire. From the five non-native plant species found in our plots, only crested wheatgrass cover was higher in the burned sites compared to the unburned sites. Cheatgrass was found at three of our 100 sites and two of those were unburned sites. We did not find a relationship between fire and cheatgrass cover in the UGB, however our surveys were conducted upslope from trails and roadsides where cheatgrass has invaded in the UGB. With the historical frequency of fire and the effects of fire on sagebrush landscapes, our findings suggest that the sagebrush landscapes of the UGB were characterized by a patchy mosaic of various post-fire seral stages.

1. *Historical fire regimes of the UGB*

Our results suggest that fire was more frequent in the UGB than previously described (Bukowski & Baker, 2013b) or assumed by land managers (B. Stevens, personal communication, July 18, 2021). We found that there was a history of repeated fire in the UGB (average MFI of 41.3 years) for over 500 years, followed by an abrupt collapse in fire regimes circa 1900 beginning a century that was fire free in the upper Gunnison sagebrush steppe. Our estimate of the historical fire frequency is likely a conservative one because of the limitation of fire-scarred trees and forest types that support low-severity fire.

Other studies have estimated fire return intervals of 12-25 years at productive sagebrush sites (Burkhardt & Tisdale, 1976; Gruell et al., 1994; Houston, 1973; Miller & Rose, 1999), which is similar to our estimates in the UGB. However, our estimates may contradict more recent findings such as those of Bukowski and Baker (2013b) who found a fire rotation of 178-357 years in Wyoming big sagebrush and 90-143 years in mountain big sagebrush within the UGB. Bukowski and Baker (2013b) used descriptions of vegetation from General Land Office (GLO) survey data from the late 1800s to assess the extent of various post-fire seral stages in which they used to reconstruct the historical fire frequency in sagebrush landscapes across the UGB. However, there are challenges that GLO data pose when being used to reconstruct fire history. This data relies on surveyor's descriptions of the landscape, which were used to make assumptions on how recently the area burned based on the descriptions of vegetation. Descriptions of vegetation fail to describe fire's tendency to burn in a patchy way within sagebrush landscapes (Bukowski & Baker, 2013b). Additionally, the descriptions were made from 1872-1892, after Euro-American settlement and around the time of the cessation of fire in the UGB (Vandenbusche, 1980). Their management recommendations are widespread fire suppression to support stands of large, continuous sagebrush (Bukowski & Baker, 2013b). Contrarily, our findings of multi-decadal fire frequency in the UGB are from tree-ring fire scars, which are direct evidence of fire occurrence and have been shown to provide a reliable estimate of fire frequency (Dewar et al., 2020; Farris et al., 2010) and may suggest the importance of utilizing lines of evidence besides historical records to characterize historical fire regimes.

All 10 of our fire history sites are separated by currently or historically occupied GUSG habitat (Fig. 1) made up of sagebrush communities. Fires that occurred synchronously at two or more of these sites (MFI of synchronous fire is 23.6 years) is consistent with the sagebrush separating those sites burning as well (Dewar et al., 2020). Some of these sites that burned synchronously were separated by 70-km. It is unknown to what extent the sagebrush landscapes between our fire history sites are carrying synchronous fires rather than individual fire events occurring at our fire history sites. However, the synchronous fires not only occurred during the same year but also during the same or similar seasonality at multiple fire history sites (Fig. K in Appendix). Additionally, 60.0% of synchronous fires were associated with drought years where we might expect to see widespread fire events (Swetnam & Baisan, 1996). The majority of fires in the UGB (53%) occurred in the late spring or early summer. This is during a period in the UGB where the winds are very strong (Arno, 1980). A majority of historical fires occurring during the windy season is consistent with fires at ecotones spreading to adjacent sagebrush since sagebrush can carry fire well during strong winds (Britton et al., 1981).

Our fire history findings are consistent with Indigenous burning practices, as only 34.0% of fires were associated with drought years and the majority of fires occurred in the late spring before lightning season begins in mid-summer. Our findings were also consistent with historical records of Utes starting fires. A newspaper article from 1948 referenced a fire started by Utes in 1879 (Leckenby, 1948), which is consistent with our fire history findings, in which two fire history sites recorded fire the same year (Fig. Kb in Appendix). This article also mentions, “the quantity of timber and *grazing land* burned over, I cannot give it in acres, but it is immense” (Leckenby, 1948). The reference to grazing land being burned likely refers to sagebrush burning. The 1879 fire was started in May, which is consistent with the early season (dormant and middle earlywood) fires we observed in the tree-ring fire scars (Fig. Kb in Appendix). Additionally, the shift in fire regimes we observed circa 1900 correlated with Euro-American settlement, which occurred in the 1870s and 1880s in the UGB (Vandenbusche, 1980). This shift was likely due to the introduction of livestock grazing, which removed the fine fuels that characterize low-severity fire regimes (Allen, 2007; Swetnam et al., 2016; Touchan et al., 1996). The removal of the Ute people from the UGB may have also played a role, however the extent to which the Utes maintained this historical fire regime prior to Euro-American settlement is unknown.

2. *Modern fire effects on sagebrush of the UGB*

Recent wildfires and prescribed fire in sagebrush habitats of the UGB have shifted vegetation composition and structure in ways that are very likely to resemble historical fire effects, including reductions in woody plant cover and height, and increases in herbaceous plant cover and height. More specifically, fire reduced Wyoming big sagebrush cover and increased graminoid cover. Fire did not affect the plant productivity in sagebrush landscapes (no difference in bare ground or total foliar cover between burned and unburned sites), therefore the increase in graminoid cover did not come at the expense of total plant cover, which has important effects such as soil moisture retention, water infiltration, and wildlife habitat (Connelly et al., 2000; Crawford et al., 2004; Davies et al., 2006; Deutsch et al., 2010; Russel et al., 2001). There was no relationship between fire and forb cover, however other studies have found that fire increases forb cover (Baker, 2009; Beck et al., 2012; Nelle et al., 2000).

The effects of fire on sagebrush vegetation composition and structure diminished over time but persisted for at least 20 years after fire. Woody plant cover increased with time since fire. The average woody plant cover 20 years after fire (32.0%) was about the same as the average woody plant cover of the unburned sites (33.5%). However, sagebrush cover (11.4%) was still lower 20 years after fire compared to the unburned sites (26.5%), which we projected would take about 45.0 years to fully recover to its pre-fire state showing that woody plant composition and structure would require about 45.0 years for full recovery to the pre-fire state. Other woody species such as rabbitbrush and snowberry are successional pioneers and establish before sagebrush after a fire. Average herbaceous cover and herbaceous height 20 years after fire (55.6% and 28.7 cm, respectively) was still greater compared to that of the unburned sites (40.1% and 22.3 cm, respectively) indicating that sagebrush landscapes require over 20 years for a full recovery to its pre-fire state. Additionally, herbaceous plant cover and average herbaceous plant height did not change with time since fire, indicating that fire had a more lasting effect on herbaceous vegetation structure compared to woody vegetation. Interestingly, the increase in average herbaceous plant height with time since fire was nearly significant (P=0.05). Since average plant height was greater in the burned sites compared to the unburned sites, this shows that fire has an increasing effect on herbaceous plant height beyond that of post-fire recovery to the pre-fire state.

The potential effect of fire on invasive annual grasses is a topic of substantial research and concern in sagebrush ecosystems (Balch et al., 2013) including within the UGB (Boyte et al., 2016; Bradley et al., 2017; D'Antonio & Vitousek, 1992; Vitousek et al., 1996). In the Great Basin and Wyoming, cheatgrass has invaded across large sagebrush landscapes, diminishing sage-grouse habitat by preventing the recovery of native grasses and shrubs and increasing fire frequency (Crawford et al., 2004; Davies et al., 2012; Knapp, 1996; Lockyer et al., 2015; Taylor et al., 2014). Cheatgrass can become more dominant following fire, permanently converting sagebrush communities to annual non-native grasslands, which lack the perennial grasses, forbs, and shrub cover that sage-grouse need (Boyte et al., 2016; Miller & Eddlemen, 2001) and creating a cheatgrass-fire cycle (Balch et al., 2013). While we found that recent fires were associated with increases in non-native plant cover, recent fire also increased native plant cover. We found little non-native plant cover in general with an average of 2.6% cover in burned sites and 0.8% in unburned sites. There were only five non-native plant species from the 109 species we found across our 100 sites. We found no relationship between cheatgrass cover and recent fire in the UGB. Cheatgrass was hardly present in our study area and was only found at three of our 100 sites, two of which were unburned. However, the fires, which we sampled, were typically at higher elevations and upslope from trails and roadsides where cheatgrass has invaded in the UGB. We would expect the presence of cheatgrass in the UGB to worsen with increasingly warming and drying conditions moving the range of cheatgrass upslope from roadsides to higher elevations. Thus post-fire cheatgrass presence should be heavily monitored and aggressively treated to prevent invasions like in the Great Basin (Boyte et al., 2016; Bradley, 2009; Connelly et al., 2000). From the five non-native species found at our sites, only crested wheatgrass had a greater percentage of cover in the burned sites compared to the unburned sites.

This was from a single site, which had an unusually high amount of crested wheatgrass. The crested wheatgrass cover is what accounts for the greater non-native plant cover in the burned sites compared to the unburned sites. However, crested wheatgrass was seeded in the UGB historically to improve rangeland and is now considered a naturalized perennial grass rather than an exotic, non-native species.

3. *Fire history and fire effects implications on GUSG habitat*

The shifts in sagebrush vegetation structure and composition created by fire satisfy some of the various habitat requirements of the GUSG. Taller grass helps meet GUSG habitat requirements by supporting an invertebrate food source while simultaneously providing hiding and nesting cover from predators. Within the GUSG rangewide conservation plan (2005), grass height is listed as an understory vegetation structural characteristic guideline for GUSG breeding and summer-fall habitats. Previous GRSG studies have shown that grass taller than 18.0-cm has a positive correlation with nesting success (Coggins, 1998; Delong et al., 1995; Gregg et al., 1994; Sveum et al., 1998) and vegetation characteristic guidelines for the GUSG suggest grass height of at least 18.0-cm for breeding and summer-fall habitat (Connelly et al., 2000; GSRSC, 2005). We found that average herbaceous plant height in the burned sites was 28.1 cm. Forbs are a critical food source for GUSG during the summer (Drut et al., 1994) and have important effects on brood rearing and chick survival (Coggins, 1998; Drut et al., 1994; Peterson, 1970). Previous studies have shown that fire can enhance the protein content and nutrient quality of forbs and extend the length of the growing season for forbs (McDowell, 2000; Wrobleski, 1999). We found that fire did not diminish GUSG habitat quality by decreasing forb cover. Forb cover at both burned and unburned sites (8.8% and 8.7%, respectively) narrowly met the GUSG rangewide conservation plan (2005) guidelines for GUSG breeding (5-40%) or summer-fall habitat (5-35%). Forb cover varies from year to year based on precipitation and drought (Apa, 2004). With 2020 being an exceptionally dry year, we would expect that forb cover was generally lower than years with average precipitation.

Given the historical frequency of fire in the UGB, portions of the sagebrush landscape were likely characterized by a patchy mosaic of recent burns (Fig. 9). Due to discontinuous fuels, fire tends to burn patchy in sagebrush (e.g., Fig. 9), leaving unburned islands (Knick et al., 2008; Miller & Eddlemen, 2001). Because GUSG have a wide range of habitat requirements (Knick & Connelly, 2011; Miller et al., 2011), a patchy mosaic of post-fire seral stages may have met all the habitat requirements of the GUSG in a relatively small area (Pederson et al., 2003. Grass-dominated patches (most recently burned) provide GUSG with an invertebrate food source and cover for hiding and brood rearing (Kirol et al., 2012; Knick & Connelly, 2011; Miller et al., 2011), where patches of moderate sagebrush cover (5-25%; less recently burned) provide habitat for brood rearing, nesting, and breeding (Connelly et al., 2000; GSRSC, 2005), and patches of dense sagebrush cover (30-40%; unburned) would provide habitat for day use by males during the breeding season and habitat for wintering (Connelly et al., 2000; GRSRSC, 2005). We found that the average sagebrush cover within burned sites (6.1%) is within the rangewide conservation plan (2005) vegetation characteristic guidelines for summer-fall habitat where sagebrush cover within unburned sites (27.6%) is at the lower end of the guidelines for wintering habitat but exceeds the guidelines for breeding and summer-fall habitat. Previous studies within the Great Basin have reported that GRSG are initially attracted to recent burns during the summer, likely due to the abundance of forbs and invertebrates (Klebenow & Beall, 1977; Martin, 1990). Additionally, recent burns with adjacent sagebrush have been used as leks by GRSG (Miller &

Eddlemen, 2001). Today, sagebrush landscapes of the UGB are largely composed of large, continuous, mature sagebrush. This may pose challenges for the GUSG in finding habitat that meets their numerous requirements (Pederson et al., 2003).

When fire was most frequent in the UGB (1700s and 1800s), we would expect that the GUSG likely occupied a greater portion of the UGB and their population numbers were likely higher and more stable. However, we do not have any data pre-1950's to understand the long-term trends in population numbers of the GUSG. The ecological influences thought to contribute to the decline of the GUSG (mining, hunting, agriculture, and livestock grazing) were introduced into the UGB with Euro-American settlement, thus we would expect the beginning of the decline of the GUSG to correspond with Euro-American settlement and the shift in fire regimes circa 1900 (GSRSC, 2005; Nicholson, 2019; Oyler-McCance et al., 2001). The extent to which the change in fire regimes contributed to the decline of the GUSG is unknown, however, our findings suggest that there was repeated fire in the UGB for centuries (MFI ranged from 18.2-79.7 years), which the GUSG lived through. While it is difficult to fully explain the recent decline of the GUSG due to the complexity and multifaceted changes in GUSG habitat over time (Connelly & Braun, 1997), our study suggests that in at least some portions of its range, the GUSG coexisted historically with frequent fire and possibly benefited from the vegetation mosaic created by historical fire.

Figure 9. A photo from a prescribed burn at Gold Basin that burned in 2013. Notice the patchy vegetation structure that makes up this landscape with patches of older sagebrush mixed in with graminoid-dominated patches. This is possibly what much of the Upper Gunnison Basin looked like historically. This patchy mosaic may also benefit the Gunnison sage-grouse by meeting all the bird's habitat requirements.

4. *Management implications and directions for future research*

The continued careful use of prescribed fire in sagebrush landscapes within the GUSG range may be beneficial in recreating historical conditions of a patchy mosaic of post-fire seral stages (Fig. 9; Miller & Eddlemen, 2001). Other studies within the Great Basin have found that wildfire leads to low survival of GRSG by creating habitat sinks (O'Neil et al., 2020), thus more research needs to be done to understand how fire influences GUSG habitat within the UGB. Sagebrush landscapes vary across the western United States from the Great Basin to the UGB in terms of climate, elevation, precipitation, sagebrush cover, raven predation, annual grass invasion, and land use, which may cause different mechanisms to be at play for the decline of different sage-grouse species. Because the life cycle of the GUSG varies seasonally, optimal management goals should be aimed at maintaining a balance of forbs, grasses, and shrubs at the community and landscape scale (Miller & Eddlemen, 2001). The restoration of fire as an ecological process may be beneficial for restoring GUSG habitat by creating this balance, however more research needs to be done to understand GUSG behavior and the habitat needs in order to make specific management recommendations (Miller & Eddlemen, 2001). Management goals should focus on creating and maintaining a healthy balance of ecological processes through prescribed fire rather than recreating fire regimes. Future studies should monitor treated areas to determine if GUSG will colonize these areas, assess the mosaic of burns in the UGB, and determine if the mechanisms at play for the decline of the GRSG are the same as the GUSG (raven predation and cheatgrass).

Since fire does not currently appear to pose a risk of annual non-native grass invasion in the upslope sagebrush landscapes of the UGB, prescribed burns might be done with a relatively low-risk of converting GUSG habitat to an annual invasive monoculture through annual non-native establishment; however, such is not true for other areas of the UGB where cheatgrass is more established and spreading. Prescribed burns should avoid using roads as anchors and should not be conducted within low, downslope areas to avoid the post-fire invasion of cheatgrass. Areas with transmission lines, landfills, roadsides, and high presence of predators (ravens and coyotes) should be avoided as well. Prescribed fire should not be conducted in optimal nesting habitat (dense sagebrush cover) and currently occupied nesting habitat since GUSG have strong site fidelity. Previous threatened species habitat restoration studies have focused on unoccupied habitat between populations to increase species-wide genetic variation, which is a problem among threatened species (Hess & Fischer, 2001; Oyler-McCance et al., 2005) including GUSG because of their strong site fidelity. Fire could also be reintroduced along wet meadow sites to expand grassy vegetation and decrease sagebrush cover in areas where the water hydrology would support expansion of wet meadows and riparian habitat for broods.

The findings of this study describe the role of historical fire in ecological processes influencing the shrub-steppe habitat of a threatened species in decline. However, we can no longer simply use the past to guide contemporary land management given the extent of recent changes including climate, drought, and land use. Using the past to guide contemporary management needs to be coupled with contemporary research to understand how recent changes might influence the re-creation of historical conditions. The use of fire in the UGB must be done carefully and considerably. Future warming and drought conditions may change the effects of fire on sagebrush landscapes by increasing annual non-native grass prevalence, diminishing plant community resilience to disturbance such as fire (Boyte et al., 2016), reducing female sage-grouse nesting success (Coates, unpublished data), or confounding the effects of livestock grazing (Branson, 1985; Miller & Eddlemen, 2001; Tisdale, 1994). Resource assessments of site potential and ecological site health along with current wildlife use should be made before applying treatments of prescribed fire, ensuring the presence of perennial grasses and forbs and the absence of exotic species (Miller & Eddlemen, 2001). The past is a useful tool for contemporary management, however needs to be used with a keen eye for changes into the future.

Conclusion

Our study shows that there was a history of repeated, moderate frequency fire for over 500 years in the UGB. From the frequency of synchronous fires and from the seasonality of the fires, we estimate that these fires likely burned through sagebrush on average every 23.6 years. We also observed that modern fires influenced sagebrush vegetation and composition by reducing sagebrush cover and increasing native graminoid cover. These shifts diminished over time but persisted for at least 20 years after fire. Together, our findings suggest that the historical character of portions of the sagebrush landscape of the UGB and habitats of the GUSG included repeated fire and more abundant, patchy mosaics of various post-fire seral stages including dense sagebrush, forbs, and grasses. Consequently, our findings support the deliberate use of prescribed fire as a means to restore ecological processes and patterns. These findings also point toward important research questions on the effects of fire on GUSG habitat use, and future opportunities for research-management knowledge co-production that may benefit both ecosystem function and species conservation. Future research should focus on cheatgrass invasion in the UGB after fire, the prevalence of ravens and other factors that contribute to the decline of the GRSG, and GUSG use of burned areas.

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Appendix

Figure A. Sagebrush-forest ecotone at one of our fire history sites (Yellow Pine Ridge). Notice the proximity of fire-scarred ponderosa pine trees and sagebrush.

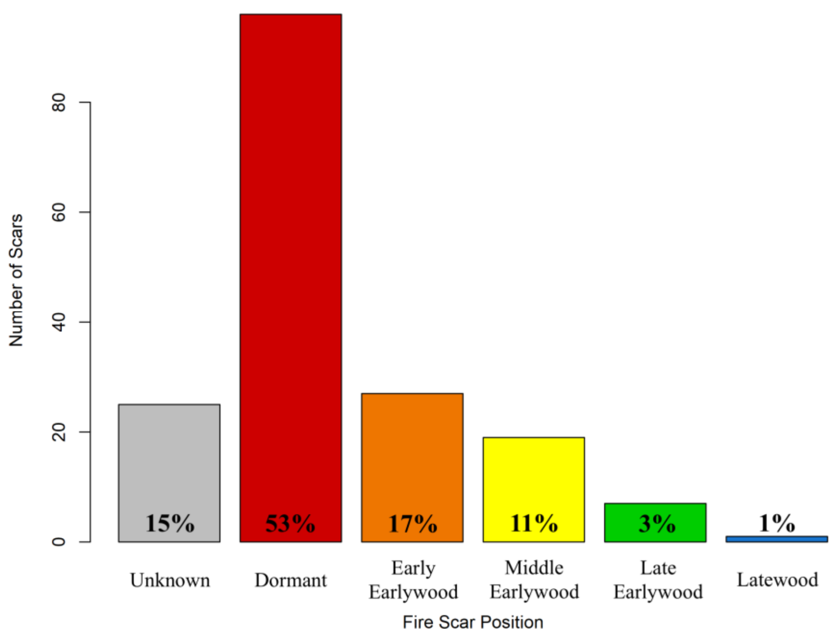

Figure B. Distribution of intra-ring fire-scar positions (seasonality) from ten tree-ring fire-scar sites at sagebrush-forest ecotones across the Upper Gunnison Basin (n=220). Dormant is likely a spring/early-summer fire, before the tree starts growing (May or June); early earlywood is likely

June or July; middle earlywood is likely July; late earlywood is likely August, and latewood is likely September. We could not identify the fire-scar position in 15% of fire-scars due to the level of decay of the tree-ring samples.

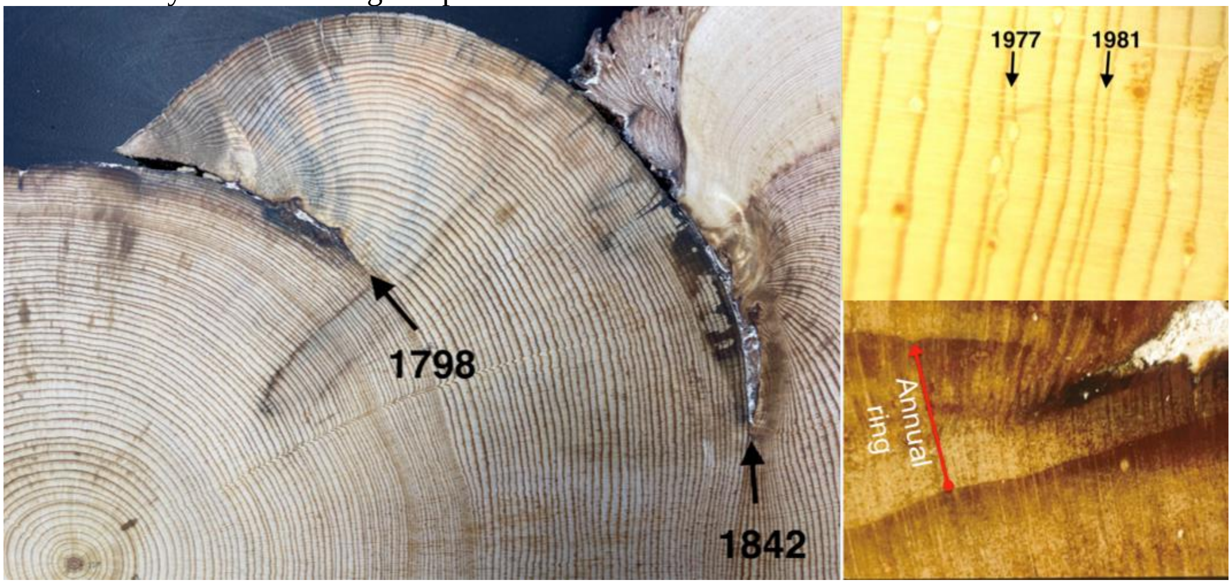

Figure C. On the left is a cross section taken from a living ponderosa pine tree collected from a sagebrush-forest ecotone near Old Monarch Pass, within currently occupied Gunnison sage-grouse habitat. Arrows point to tree-ring fire scars (1798 & 1842). Both of these fire years occurred at multiple sites. In the top right corner is a photo of narrow tree-rings at 1977 and 1981, a pattern widespread across the Upper Gunnison Basin. This pattern was used as a pattern to cross-date samples across the Upper Gunnison Basin. On the bottom right is a photo of the 1842 fire-scar under a microscope. This is a dormant-wood fire as the fire-scar is directly adjacent to the latewood of the tree-ring from the previous year.

Table A. Information of each of the 10 fire history sites including first and last tree-ring date, number of trees at each site, and elevation. Study area composite includes fire history information across all 10 fire history sites.

Site Name	Site Code	First Tree Ring Date	Last Tree Ring Date	Number of Trees	Elevation (m)
Antelope Hills	AEH	1635	2020	10	2875
Iola Valley	IAV	1586	2020	10	2652
Meyers West	MYW	1362	2020	12	2862
Needle Creek	NEC	1472	2020	13	2841
North Powderhorn	NPH	1455	2020	12	2728
Old Monarch High	OMH	1701	2020	12	3142
Old Monarch Low	OML	1696	1982	10	3004
Sapinero Mesa	SOM	1503	2020	10	2709
Timber Sale	TRS	1540	2017	14	2971
Yellow Pine South	YPS	1504	2020	8	2848
Study Area Composite		1362	2020	111	

Table B. Information of each of the 12 fires that were sampled including latitude and longitude, type of fire (prescribed or wildfire), fire start date (or year if date not known), whether it was seeded following the fire, size of fire (in acres), the agency that has ownership over the area burned or conducted the prescribed burn, and the purpose of the burn if it was prescribed.

Fire Name	Latitude	Longitude	Fire Type	Year/Date	Seeded?	Acerage	Agency	Primary Purpose
Flat Top	38.701139	-106.971355	Rx	11/15/07	Unknown	752	USFS	Big Game Winter Range in Non-Forested Areas
Almont	38.6540247	-106.84537	Wildfire	7/5/01	Unknown	182	USFS	N/A
Antelope Hills 1	38.6183984	-106.968873	Rx	4/10/02	No	12	BLM	Hazardous Fuels Reduction
Antelope Hills 2	38.604727	-107.0097586	Rx	3/15/01	No	89	BLM	Wildland Urban Fuels, Sage-Grouse
Hartman Rocks	38.4925165	-106.9408539	Wildfire	6/29/07	No	3.3	BLM	N/A
Rainbow Lake	38.5497986	-107.1519528	Rx	2016	Unknown	Unknown	USFS	Unknown
Red Creek	38.5385889	-107.2281898	Rx	5/16/08	No	43	BLM	Hazardous Fuels Reduction, Big Game
Gold Basin	38.386979	-106.8915723	Rx	3/23/12	No	14	BLM	Hazardous Fuels Reduction, Wildland Urban Fuels
Myer's Gulch	38.2599081	-106.6716063	Rx	2016	Unknown	Unknown	USFS	Unknown
Los Pinos	38.1643665	-106.8629267	Rx	2021	Unknown	258	USFS	Unknown
Goose Creek	38.2995745	-107.1807853	Rx	5/3/13	No	118	BLM	Hazardous Fuels Reduction, Wildland Urban Fuels
Indian Creek	38.2839551	-107.1671476	Rx	9/15/04	No	38	BLM	Wildland Urban Fuels, Wildland Urban Fuels

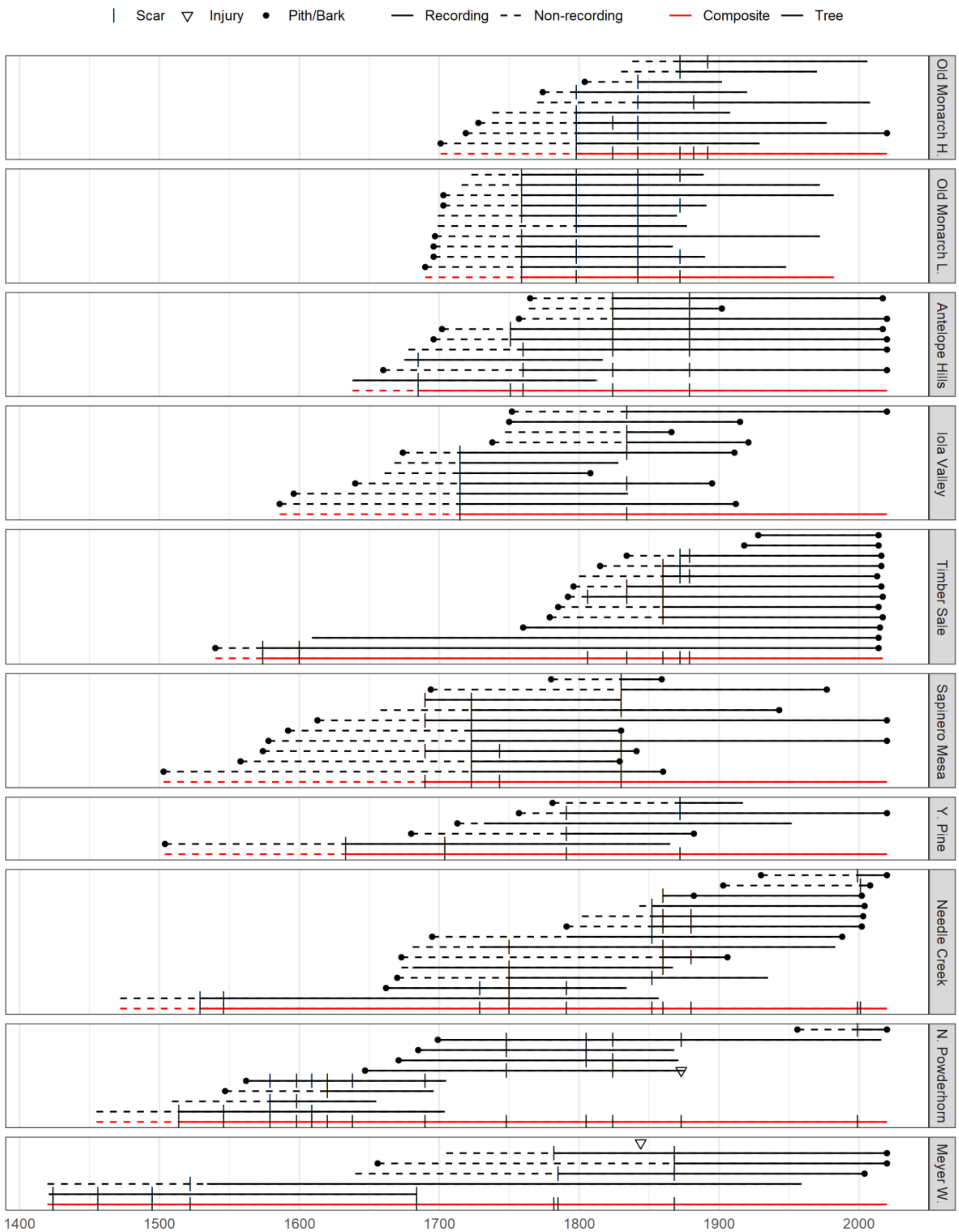

Figure D. The fire charts for ten tree-ring fire-scar sites at the forest/sagebrush ecotones across the Upper Gunnison Basin. Black horizontal lines represent individual trees and black vertical lines represent fire scars. Red horizontal lines represent the site composites, which include all recorded fires from all trees at that site. Black dots represent either a pith date or a bark date. Site names are on the right hand side of each chart and the years are on the bottom.

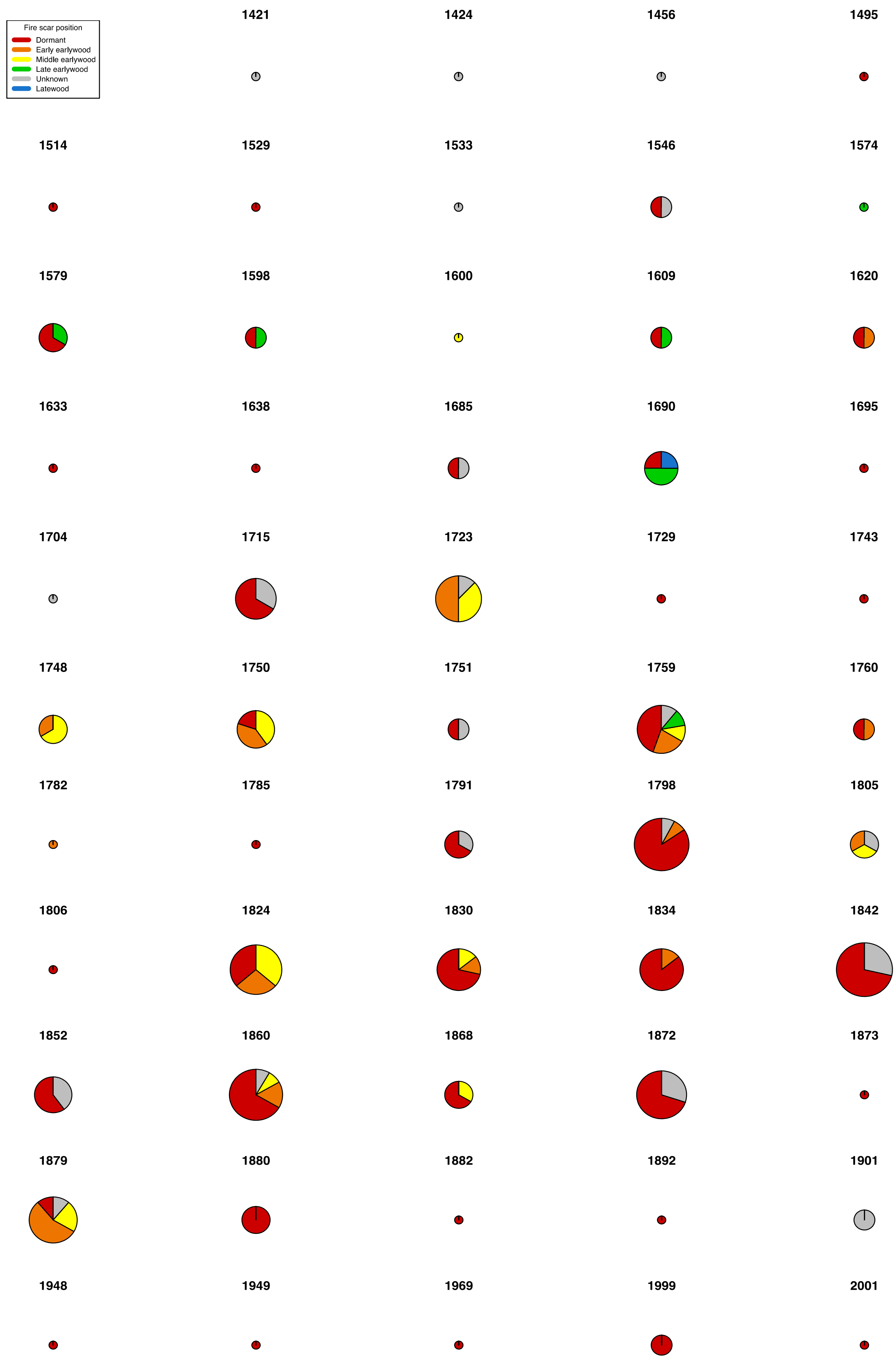

Figure E. Proportion of fire scar positions (season) by year for the Upper Gunnison Basin fire history study (n = 54 fire years, 1421 - 2001).

Table C. Checklist of plant species encountered in sample sites in the Upper Gunnison Basin. Latin names, common names, plant species symbols, and authors are provided following USDA plants. Average percent cover is given for both burned and unburned sites.

Latin Name	Common Name	Symbol	Author	Burned Average Percent Cover (%)	Unburned Average Percent Cover (%)
Achnatherum hymenoides	Indian ricegrass	ACHY	(Roem. & Schult.) Barkworth	0.04	0
Achnatherum lettermanii	Letterman's needlegrass	ACLE9	(Vasey) Barkworth	2.88	1.26
Achillea millefolium	common yarrow	ACMI2	L.	0.2	0.1
Achnatherum pinetorum	pine needlegrass	ACPI2	(M.E. Jones) Barkworth	1.98	3.76
Acacia rossei	yellowdine wattle	ACRO6	F. Muell.	0.02	0
Unknown	Unknown	AF02	Unknown	0.04	0
Unknown	Unknown	AF06	Unknown	0.04	0
Unknown	Unknown	AF09	Unknown	0	0.02
Unknown	Unknown	AF10	Unknown	0.02	0.04
Unknown	Unknown	AF11	Unknown	0.12	0
Agropyron cristatum	crested wheatgrass	AGCR	(L.) Gaertn.	3.66	1
Agoseris glauca	pale agoseris	AGGL	(Pursh) Raf.	0.04	0.08
Amelanchier utahensis	Utah serviceberry	AMUT	Koehne	0.22	0.06
Antennaria rosulata	Kaibab pussytoes	ANRO3	Rydb.	0.1	0.02
Antennaria	pussytoes	ANTEN	Gaertn.	0.98	1.12
Artemisia frigida	prairie sagewort	ARFR4	Willd.	0.26	0
Artemisia nova	black sagebrush	ARNO4	A. Nelson	0.1	2.14
Artemisia tridentata ssp. Vaseyana	mountain big sagebrush	ARTRV	Nutt. (Rydb.) Beetle	0.82	0
Artemisia tridentata ssp. wyomingensis	Wyoming big sagebrush	ARTRW8	Nutt. Beetle & Young	7.42	37.66
Astragalus convallarius	lesser rushy milkvetch	ASCO12	Greene	0.02	0.1
Astragalus shortianus	Short's milkvetch	ASSH3	Nutt.	0.04	0
Astragalus	milkvetch	ASTRA	L.	0.22	0.12
Balsamorhiza sagittata	arrowleaf balsamroot	BASA3	(Pursh) Nutt.	0	0.08
Arabis	rockcress	BOECH	L.	0.08	0.1
Bouteloua gracilis	blue grama	BOGR2	(Willd. ex Kunth) Lag. ex Griffiths	0.8	1.32
Arabis drummondii	Drummond's rockcress	BOST4	A. Gray	0.02	0.04
Bromus porteri	Porter brome	BRPO2	(J.M. Coult.) Nash	0	0.04
Bromus tectorum	cheatgrass	BRTE	L.	0.12	0.04
Castilleja angustifolia	northwestern Indian paintbrush	CACH7	(Nutt.) G. Don var. *dubia* A. Nelson	0.1	0.24
Carex duriuscula	needleleaf sedge	CADU6	C.A. Mey.	6.48	6.64
Carex geyeri	Geyer's sedge	CAGE2	Boott	0.54	0.3
Calochortus gunnisonii	Gunnison's mariposa lily	CAGU	S. Watson	0	0.02
Castilleja linariifolia	Wyoming Indian paintbrush	CALI4	Benth.	0.08	1
Carex	sedge	CAREX	L.	0	0.02
Carex rossii	Ross' sedge	CARO5	Boott	0.24	0.36
Ceanothus fendleri	Fendler's ceanothus	CEFE	A. Gray	0.02	0.18
Chenopodium album	lambsquarters	CHAL7	L.	0.02	0
Chrysothamnus depressus	longflower rabbitbrush	CHDE2	Nutt.	0.26	0.5
Chrysothamnus viscidiflorus	yellow rabbitbrush	CHVI8	(Hook.) Nutt.	10.66	4.4
Clematis hirsutissima	hairy clematis	CLHI	Pursh	0.02	0.16
Comandra umbellata	bastard toadflax	COUM	(L.) Nutt.	0.58	0.34
Crepis acuminata	tapertip hawksbeard	CRAC2	Nutt.	0.4	0.3
Crepis atribarba	slender hawksbeard	CRAT	A. Heller	0	0.08
Dasiphora fruticosa	shrubby cinquefoil	DAFR6	(L.) Rydb.	0.08	0.02
Elymus elymoides	squirreltail	ELEL5	(Raf.) Swezey	5.34	1.04
Elymus trachycaulus	slender wheatgrass	ELTR7	(Link) Gould ex Shinners	0.42	0.66
Eriogonum cernuum	nodding buckwheat	ERCE2	Nutt.	0.02	0.02
Erigeron concinnus	Navajo fleabane	ERCO27	(Hook. & Arn.) Torr. & A. Gray	0.38	0.32
Erigeron flagellaris	trailing fleabane	ERFL	A. Gray	0.02	0.02
Erigeron formosissimus	beautiful fleabane	ERGLV	Greene	0.5	0.28
Erigeron	fleabane	ERIGE	L.	0.02	0
Eriogonum racemosum	redroot buckwheat	ERRA3	Nutt.	0.56	0.18
Eriogonum umbellatum	sulphur-flower buckwheat	ERSU11	Torr. var. *majus* Hook.	0.06	0.3
Eriogonum umbellatum	sulphur-flower buckwheat	ERUM	Torr.	0.78	0.82
Festuca arizonica	Arizona fescue	FEAR2	Vasey	4.22	3.06
Festuca thurberi	Thurber's fescue	FETH	Vasey	7.12	1.08
Galium boreale	northern bedstraw	GABO2	L.	0	0.04
Gayophytum decipiens	deceptive groundsmoke	GADE2	F.H. Lewis & Szweykowski	0.84	0.28
Gayophytum ramosissimum	pinyon groundsmoke	GARA2	Torr. & A. Gray	0.02	0
Geranium	*geranium*	GERAN	L.	0	0.02
Geranium richardsonii	Richardson's geranium	GERI	Fisch. & Trautv.	0.1	0.02
Hesperostipa comata	needle and thread	HECO26	(Trin. & Rupr.) Barkworth	8.26	0.8
Heliomeris multiflora	showy goldeneye	HEMU3	Nutt.	0.08	0
Heterotheca villosa	hairy false goldenaster	HEVI4	(Pursh) Shinners	0.12	0
Equisetum hyemale	scouringrush horsetail	HIHYA	L. var. *affine* (Engelm.) A.A. Eaton	0.06	0.28
Hymenoxys richardsonii	pingue rubberweed	HYRI	(Hook.) Cockerell	0.14	0.06
Koeleria macrantha	prairie Junegrass	KOMA	(Ledeb.) Schult.	2.72	0.68
Lathyrus laetivirens	aspen pea	LALEL	Greene ex Rydb.	0.22	0.52
Lappula occidentalis	flatspine stickseed	LAOC3	(S. Watson) Greene	0.02	0
Lappula occidentalis	flatspine stickseed	LARE	(S. Watson) Greene var. *occidentalis*	0.02	0
Lilium	lily	LILIU	L.	0	0.02
Linanthus pungens	granite prickly phlox	LIPU11	(Torr.) J.M. Porter & L.A. Johnson	0.08	0.12
Ligusticum tenuifolium	Idaho licorice-root	LITE2	S. Watson	0.02	0
Lupinus	lupine	LUPIN	L.	2.9	2.84
Mahonia repens	creeping barberry	MARE11	(Lindl.) G. Don	0.04	0.14
Muhlenbergia	muhly	MUHLE	Schreb.	0	0.04
Muhlenbergia montana	mountain muhly	MUMO	(Nutt.) Hitchc.	5.42	2.52
Opuntia polyacantha	plains pricklypear	OPPO	Haw.	0.12	0.02
Cryptantha bakeri	Baker's cryptantha	ORBA4	(Greene) Payson	0.04	0
Orthocarpus luteus	yellow owl's-clover	ORLU2	Nutt.	0.06	0
Pascopyrum smithii	western wheatgrass	PASM	(Rydb.) Á. Löve	3.9	0.36

Latin Name	Common Name	Symbol	Author	Burned Average Percent Cover (%)	Unburned Average Percent Cover (%)
Penstemon caespitosus	mat penstemon	PECA4	Nutt. ex A. Gray	0.26	0.36
Penstemon rydbergii	Rydberg's penstemon	PERY	A. Nelson	0	0.06
Pediocactus simpsonii	mountain ball cactus	PESI	(Engelm.) Britton & Rose	0.02	0.04
Penstemon strictus	Rocky Mountain penstemon	PEST2	Benth.	0.02	0.02
Phlox hoodii	spiny phlox	PHHO	Richardson	0.32	0.18
Astragalus ceramicus	painted milkvetch	PHLO7	Sheldon var. *filifolius* (A. Gray) F.J. Herm.	0.02	0
Phlox multiflora	flowery phlox	PHMU3	A. Nelson	0.52	1.34
Plantago lanceolata	narrowleaf plantain	PLLA	L.	0	0.06
Poa fendleriana	muttongrass	POFE	(Steud.) Vasey	15.26	21.8
Poa secunda	Sandberg bluegrass	POSE	J. Presl	0.02	0
Potentilla	cinquefoil	POTEN	L.	1	0.4
Purshia tridentata	antelope bitterbrush	PUTR2	(Pursh) DC.	2.08	3.48
Rhus trilobata	skunkbush sumac	RHTR	Nutt.	0.04	0
Ribes leptanthum	trumpet gooseberry	RILE	A. Gray	0.04	0
Rosa woodsii	Woods' rose	ROWO	Lindl.	0.16	0.02
Senecio integerrimus	lambstongue ragwort	SEIN2	Nutt.	0.02	0
Sedum lanceolatum	spearleaf stonecrop	SELA	Torr.	0.04	0.1
Silene scouleri	simple campion	SISCH	Hook. ssp. *hallii* (S. Watson) C.L. Hitchc. & Maguire	0.08	0.04
Sphaeralcea coccinea	scarlet globemallow	SPCOC	(Nutt.) Rydb. ssp. *coccinea*	0.02	0
Wyethia amplexicaulis	mule-ears	WYAM	(Nutt.) Nutt.	0	0.1
Yucca harrimaniae	Spanish bayonet	YUHA	Trel.	0.06	0
Symphoricarpos rotundifolius	roundleaf snowberry	SYRO	A. Gray	3.66	1.42
Taraxacum officinale	common dandelion	TAOF	F.H. Wigg.	0.04	0
Tetradymia canescens	spineless horsebrush	TECA2	DC.	0.46	0.44

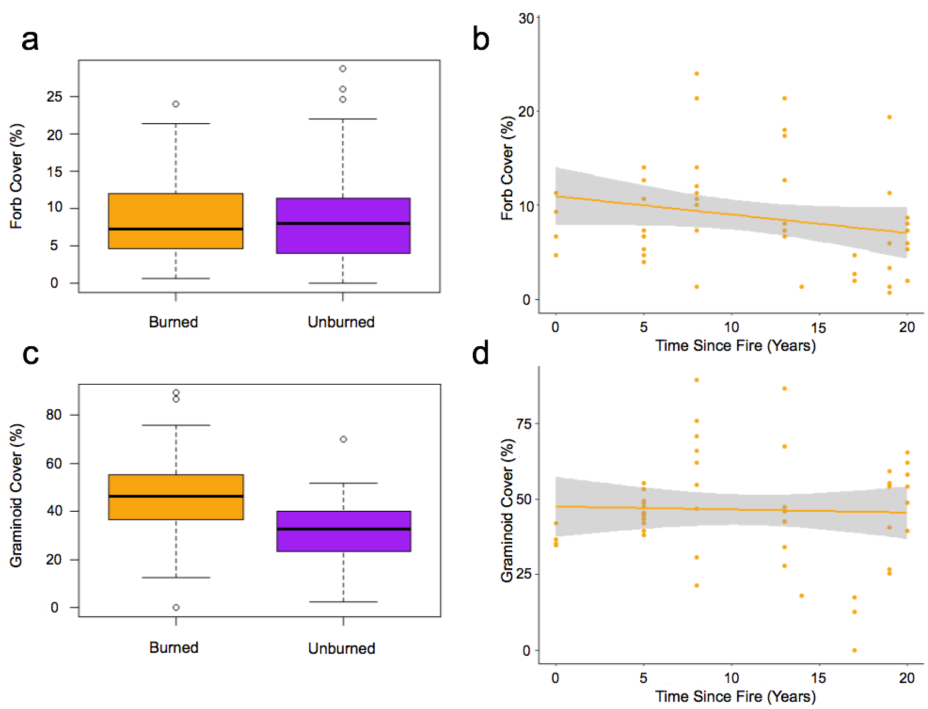

Figure F. a) Boxplot comparing percent forb cover between all 50 burned and all 50 unburned sites. Boxplots show minimum, first quartile, median, third quartile, and maximum and includes outliers. Forb cover showed no significant relationship with fire (P=0.92). b) Linear model showing the change in percent forb cover with time since fire within all 50 burned sites. Forb cover showed no significant relationship with time since fire (P=0.17). c) Boxplot comparing percent graminoid cover between all 50 burned and all 50 unburned sites. Boxplots show minimum, first quartile, median, third quartile, and maximum and includes outliers. Graminoid cover was significantly greater in the burned sites compared to the unburned sites (P<0.001). d) Linear model showing the change in percent graminoid cover with time since fire within all 50 burned sites. Graminoid cover showed no significant relationship with time since fire (P=0.8).

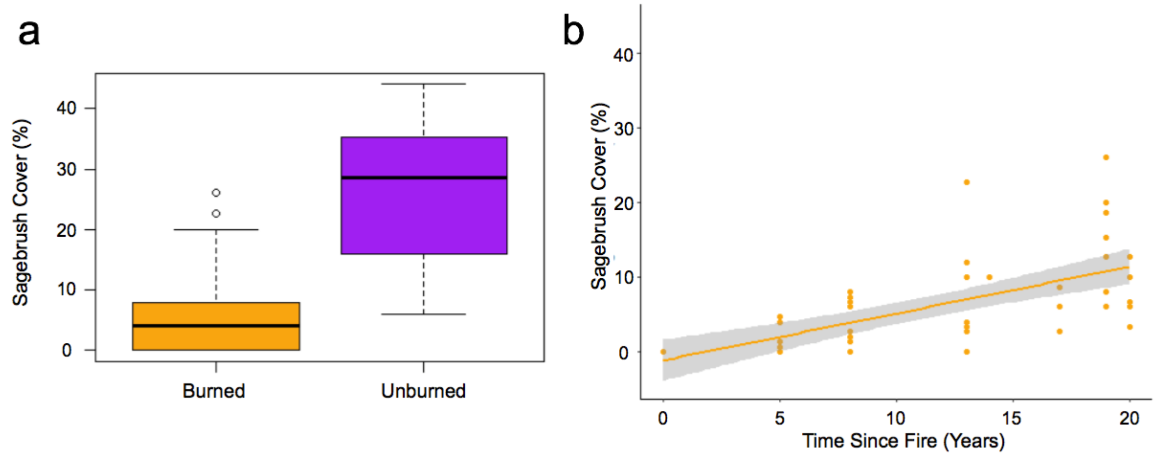

Figure G. a) Boxplot comparing percent *Artemisia tridentata* spp. *wyomingensis* (sagebrush) cover between all 50 burned and all 50 unburned sites. Boxplots show minimum, first quartile, median, third quartile, and maximum and includes outliers. Sagebrush cover was significantly greater in the unburned sites compared to the burned sites (*P*<0.001). b) Linear model showing the change in percent sagebrush cover with time since fire within all 50 burned sites. Sagebrush cover exhibited a significant increase with time since fire (*P*<0.001).

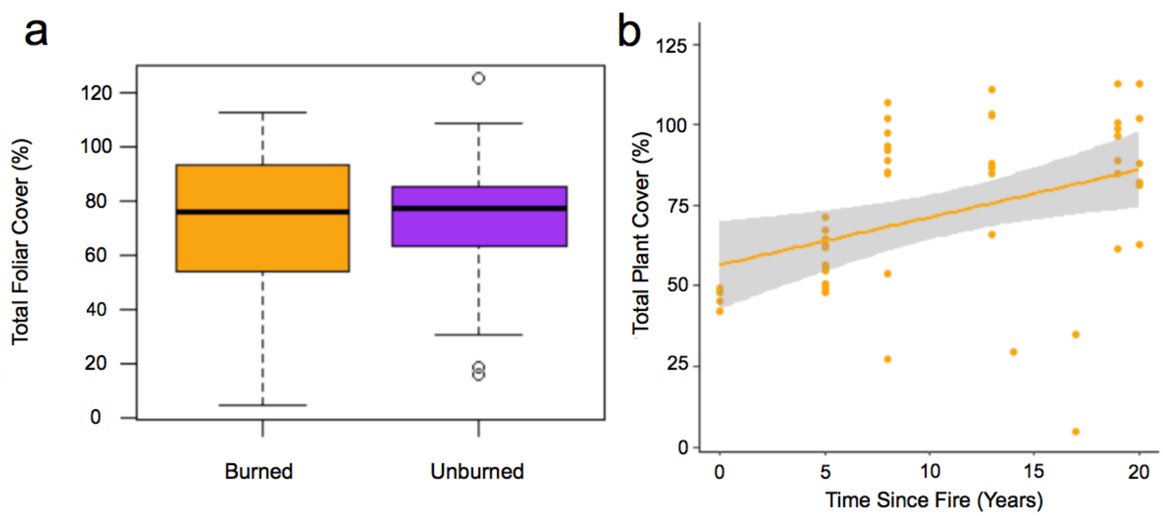

Figure H. a) Boxplot comparing percent total foliar cover between all 50 burned and all 50 unburned sites. Boxplots show minimum, first quartile, median, third quartile, and maximum and includes outliers. There was no significant difference in total foliar cover between burned and unburned sites (*P*=0.81). b) Linear model showing the change in percent total foliar cover with time since fire within all 50 burned sites. Total foliar cover increased with time since fire (*P*<0.001).

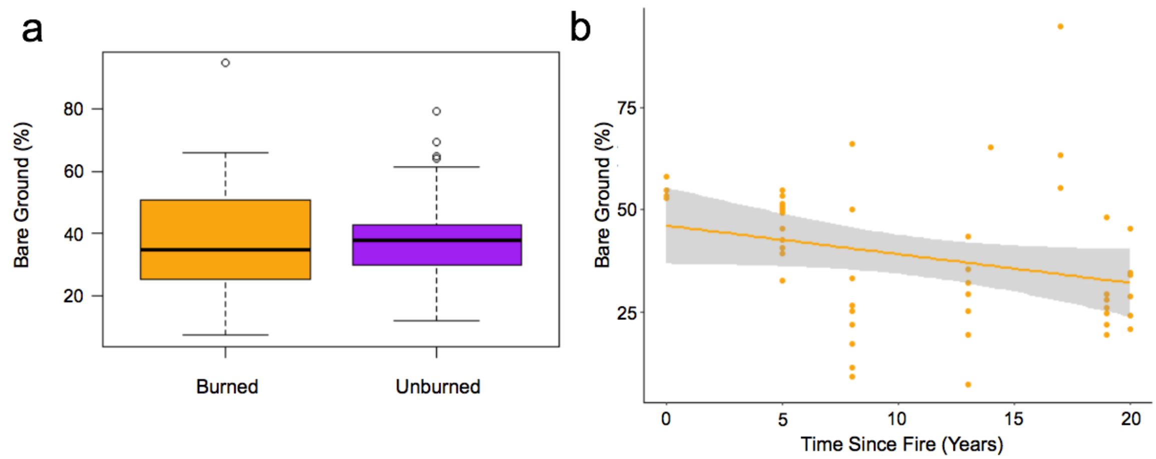

Figure I. a) Boxplot comparing percent bare ground between all 50 burned and all 50 unburned sites. Boxplots show minimum, first quartile, median, third quartile, and maximum and includes outliers. There was no significant difference in bare ground between burned and unburned sites (*P*=0.80). b) Linear model showing the change in percent bare ground with time since fire within all 50 burned sites. Bare ground exhibited no significant relationship with time since fire (*P*=0.06).

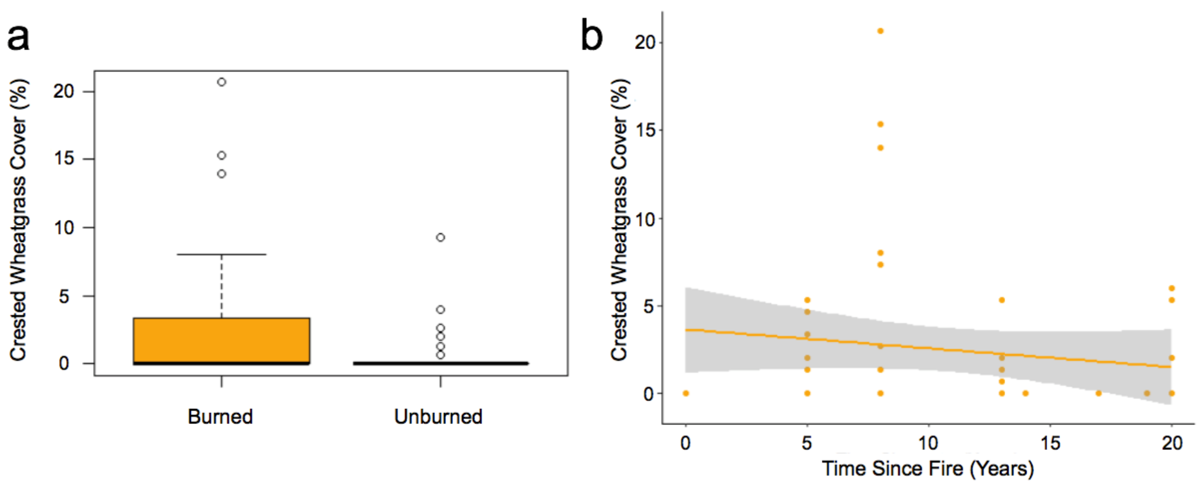

Figure J. a) Boxplot comparing percent *Agropyron cristatum* (crested wheatgrass) cover between all 50 burned and all 50 unburned sites. Boxplots show minimum, first quartile, median, third quartile, and maximum and includes outliers. There was a significantly greater amount of crested wheatgrass cover in the burned sites compared to the unburned sites (*P*<0.01). b) Linear model showing the change in percent crested wheatgrass cover with time since fire within all 50 burned sites. Crested wheatgrass cover exhibited no significant relationship with time since fire (*P*=0.27).

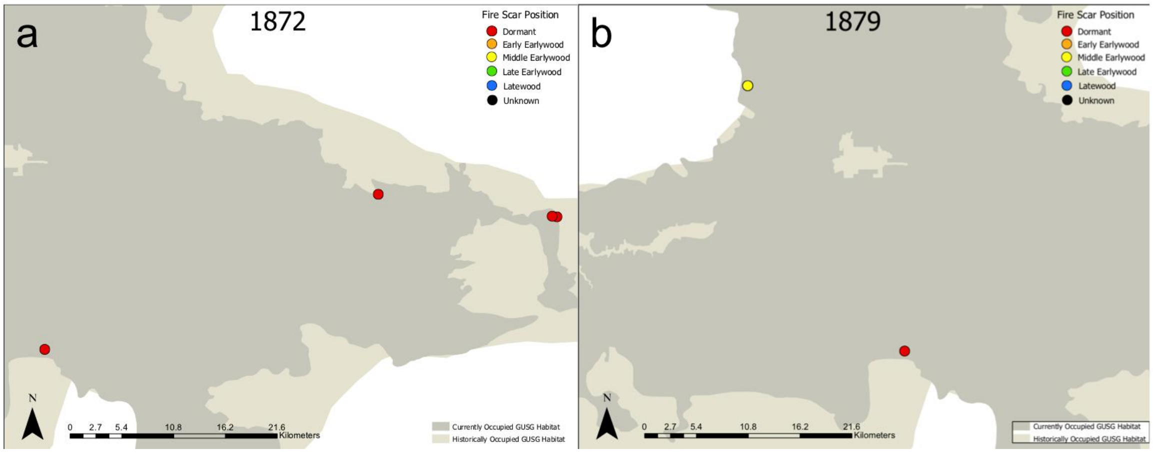

Figure K. a) Map of the Upper Gunnison Basin showing fire history sites that recorded fire in 1872. Seasonality is denoted by the colors in the upper right hand corner. Currently occupied Gunnison sage-grouse habitat is represented by the dark gray colored polygon and historically occupied habitat is represented by the light gray. In 1872, four of our fire history sites recorded fire and all four sites recorded spring fires (fire scars in dormant wood). Notice the Gunnison sage-grouse habitat between the fire history sites that likely burned in 1872. b) Map of the Upper Gunnison Basin showing fire history sites that recorded fire in 1879. In 1879, two of our fire history sites recorded fire, one site recorded fire only in the dormant wood (spring) and the other site recorded fire in the dormant wood and middle earlywood (mid-summer). Notice the Gunnison sage-grouse habitat between the fire history sites that likely burned in 1879.

Figure L. One of our fire effects sites, near Rainbow Lake that burned in 2016. The left side of the photo was burned and the right side was not. From the photo, we can see the difference in sagebrush cover in the burned vs. unburned areas.