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Ecosystem resilience is evident 17 years after fire in Wyoming big sagebrush ecosystems

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Abstract. Recent policy has focused on prevention of wildfire in the sagebrush steppe in an effort to protect habitat for the greater sage grouse (*Centrocercus urophasianus*). Historically, fire return intervals in Wyoming big sagebrush (*Artemisia tridentata* ssp. *wyomingensis*) ecosystems were 50–100 yr or more, but invasive species, climate change, and a legacy of intensive grazing practices have led to degraded rangeland condition, altered fire regimes and fire effects, and declines in sagebrush cover. Little is known about the long-term impacts of fire in this ecosystem in areas where grazing pressure has been removed, few invasive species exist, and fire return intervals are maintained. In this study, we quantified vegetation composition prior to prescribed burning, 1 year following fire, and 17 years after fire in a native-dominated Wyoming big sagebrush ecosystem at Hart Mountain National Antelope Refuge, Oregon, United States. Seventeen years following fire, the ecosystem was dominated by native herbaceous vegetation, with 8.3% cover of broad-leaved forbs and bunchgrasses in the understory, compared to just 3.8% cover of native herbaceous vegetation in unburned controls. Invasive annual grass cover ranged from 0.2% to 8.4% across all treatments and years ($P = 0.56$). One year following fire, the distance from a randomly located point and the nearest mature sagebrush was 16.6 m, but by 17 years after the fire, that distance had decreased to 2.5 m. Seventeen years after fires, shrub cover was 0.4–4% in burned plots compared to 13–24% in unburned controls. Collectively, these data demonstrate that good condition ungrazed Wyoming big sagebrush plant communities exhibited resilience following fire and maintained a native-dominated mosaic of shrubs, bunchgrasses, and forbs. Further, unburned control plots were dominated by woody vegetation and exhibited losses in herbaceous understory, possibly indicating that they are outside of their natural fire return interval. Our results illustrate that management of all habitat components, including natural disturbance and a mosaic of successional stages, is important for persistent resilience and that suppression of all fires in the sagebrush steppe may create long-term losses of heterogeneity in good condition Wyoming big sagebrush ecosystems.

Key words: *Artemisia tridentata; Centrocercus urophasianus;* cheatgrass; Great Basin; greater sage grouse; invasive grass; long-term fire effects; post-fire succession; prescribed fire; sagebrush steppe; Wyoming big sagebrush.

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Introduction

The sagebrush steppe is among the largest ecosystems in the North America, and is critically endangered due to the impacts of invasive species, land cover change, altered fire regimes, livestock grazing, and a changing climate (Noss et al. 1995, Knick 1999, Brooks et al. 2004, Chambers et al. 2014*a*). These threats often interact to modify ecosystem structure and function (Brooks and Pyke 2000, Davies et al. 2009). It is estimated that one-third of the presettlement sagebrush biome has already been converted to other land uses or has been highly degraded (McIver et al. 2010). The sagebrush steppe provides important habitat for many wildlife species, including the greater sage grouse (*Centrocercus urophasianus*, hereafter sage grouse), a species of conservation concern, and unprecedented cooperative research, management, and industry partnerships are currently underway throughout the western United States to address threats to these habitats and to the larger sagebrush biome (e.g., BLM National Greater Sage-Grouse Planning Strategy, Western Association of Fish and Wildlife Agencies Greater Sage-Grouse Comprehensive Conservation Strategy; Murphy et al. 2013, Chambers et al. 2014*a*, Brooks et al. 2015, Dahlgren et al. 2015).

Wyoming big sagebrush (*Artemisia tridentata* ssp. *wyomingensis*) is the most widespread and among the least resilient of sagebrush ecosystem plant associations due to its occurrence on the driest areas of the sagebrush steppe (Davies et al. 2006, Miller et al. 2013, Chambers et al. 2014*a*). In general, these low-elevation ecosystems are characterized by low soil moisture and warm soil temperature regimes (Miller et al. 2013) and have lower primary productivity and vegetative cover (Davies and Bates 2010) than higher elevation, more mesic mountain big sagebrush (*A. tridentata* ssp. *vaseyana*) ecosystems. While soil moisture and temperature regimes are dominant predictors of sagebrush type distribution, these relationships can vary based on elevation, slope, aspect, and soil characteristics (Chambers et al. 2014*b*). Wyoming big sagebrush communities are optimally a mosaic of native shrubs, perennial bunchgrasses, and annual and perennial forbs with litter, bare ground, and biological soil crusts in the interspace (West 1988, Davies et al. 2006, 2007*a*). Wildfire in Wyoming big sagebrush ecosystems is believed to have been historically infrequent, with at least 50–100 yr or longer between fire events (Wright and Bailey 1982, Baker 2006, Mensing et al. 2006, McIver et al. 2010, Bukowski and Baker 2013). Over the past century, the interacting influences of overgrazing and spread of invasive grasses have degraded large areas of the sagebrush steppe, resulting in losses of sagebrush cover, dominance by invasive grasses, and altered fire regimes in many areas (D'Antonio and Vitousek 1992, Brooks and Pyke 2000, Brooks et al. 2015).

In recent years, research and management efforts surrounding habitat concerns for sage grouse have drawn greater attention to the sagebrush steppe, and to conservation and restoration objectives in Wyoming big sagebrush ecosystems, in particular (Wrobleski and Kauffman 2003, Murphy et al. 2013, Chambers et al. 2014*a*, Brooks et al. 2015, Dahlgren et al. 2015). It is well established that sage grouse require large expanses of sagebrush for cover, food, and nest and chick-rearing sites, as well as patches of open space with short-statured shrubs, access to riparian areas, and abundant forb and insect seasonal food sources (Crawford et al. 2004, Dahlgren et al. 2015). While there is some regional variability, the optimal density of shrubs during the nesting and brood rearing periods generally is between 15% and 25% canopy cover (Connelly et al. 2011), with ≥15% tall perennial bunchgrasses (≥18 cm) and forbs in the understory. During the winter, when sage grouse diets switch to exclusively sagebrush, higher density sagebrush stands are also commonly used (Gregg et al. 1994, Connelly et al. 2000, 2011). While fire is an important and natural ecosystem process in the sagebrush steppe, it has been shown to negatively impact sage grouse habitat, at least in the short term, by removing required woody cover (Fischer et al. 1996, Nelle et al. 2000), though it can also can result in increased native herbaceous vegetation and favor abundance of key sage grouse forage species (Wrobleski and Kauffman 2003, Chambers et al. 2007, Davies et al. 2007*b*). Post-fire increases in invasive grasses, particularly where there has been repeated human-caused fires (Davies et al. 2012), a site history of intensive livestock grazing (Knapp 1996, Shinneman and Baker 2009, Reisner et al. 2013), and/or presence of large amounts of invasive grass prior to fire (D'Antonio and Vitousek 1992, Mack and D'Antonio 1998, Bagchi et al. 2013) has often resulted in dominance of invasive grasses, particularly cheatgrass (*Bromus tectorum*).

Good condition (i.e., minimal invasive grasses and a robust native herbaceous understory) ecosystem patches of Wyoming big sagebrush are increasingly recognized as critical for sage grouse habitat as well as for the multitude of other goods and services provided by these ecosystems (Maczko et al. 2011). These areas likely have more post-fire resilience and resistance to invasive species (Wrobleski and Kauffman 2003, Davies et al. 2008, Chambers et al. 2014*b*) than that often described for the xeric end of the sagebrush steppe (Brooks et al. 2004, 2015). Remaining good condition Wyoming big sagebrush ecosystem patches are thus uniquely important as model ecosystems for understanding ecosystem processes, including the natural role of disturbance. Because Wyoming big sagebrush ecosystems are largely degraded (McIver et al. 2010) and fire return intervals are longer than most fire management records (Wright and Bailey 1982, Baker 1994, Bukowski and Baker 2013), most research in these ecosystems is limited to short-term fire effects (Miller et al. 2013), and information on the natural role of fire in good condition, uninvaded Wyoming big sagebrush beyond early succession is exceedingly limited. Further, the impacts of excluding fire in late-successional areas of Wyoming big sagebrush have not been well explored, as has been done for the more mesic mountain big sagebrush (*A. tridentata* ssp. *vaseyana*) plant association in similar condition (Davies et al. 2014). Few studies have examined post-fire succession in sites where domestic livestock were eliminated as a central part of the land management approach for ecosystem recovery. The overarching objective of this research was to compare burned and unburned vegetation composition 17 years after fire in Wyoming big sagebrush ecosystems, with emphasis on native and invasive species dynamics in historical fire and control (no fire on record; at least 50 yr) plots. We hypothesized that these ecosystems would show resilience to fire, as evidenced by (1) dominance of herbaceous native vegetation (forbs and perennial bunchgrasses), (2) no post-fire increases in invasive grass species (i.e., cheatgrass), (3) recovery of native shrubs, and (4) frequent occurrence of the forbs known to be important sage grouse foods (Wrobleski and Kauffman 2003).

Methods

Study area and experimental design

The study was conducted at Hart Mountain National Antelope Refuge (HMNAR) in south-central Oregon (Fig. 1). The 112,503-ha refuge is managed by the U.S. Fish and Wildlife Service for conservation and preservation of wildlife, including pronghorn antelope (*Antilocapra americana*) and greater sage grouse. Cattle grazing was discontinued on the site beginning in 1991 and all animals were removed by 1994. Feral horses (estimated 200–300 animals) were removed from the refuge in 1999, but trespass animals (reaching ~250 individuals) were documented on the refuge from 2005 to 2012 before complete removal. Much of the eastern side of the refuge lies at elevations from 1550 to 1615 m with level topography and is dominated by *Artemisia tridentata* ssp. *wyomingensis* communities. The ecological site description for this area (R023XY220OR—Clayey 10–12 PZ; Natural Resources Conservation Service; https://esis.sc.egov.usda.gov) suggests that the potential vegetation in a reference community is dominated by native grasses and forbs, with about 11% cover of native shrubs. Soils are a cobbly clay loam of the Ratto-Coglin complex, Ratto series (Soil Conservation Service). Mean annual (calendar year) precipitation at refuge headquarters for 1997–2014 was 302 mm. For the three sample years (1997, 1998, and 2014), annual precipitation was 304, 480, and 309 mm, respectively, and precipitation during the sample period and active growing season (1 May–31 July) was 57, 161, and 34 mm, respectively (PRISM Climate Group, Oregon State University, Corvallis, Oregon, USA).

Plant community response to fire was quantified in eight adjacent ~400-ha plots (Fig. 1). Plots were irregularly shaped to accommodate existing primitive roads, which were used as fire breaks during prescribed burns. Each plot was randomly assigned to be burned (N = 4; Lek, Skinny, Rock Creek, and Knoll) or control (N = 4; Rattlesnake, Flook, Hill, and Farout). Study plots had not previously burned for at least 50 yr (U.S. Fish and Wildlife Service, *unpublished data*). The plant association was described as *A. tridentata* ssp. *wyomingensis*/*Stipa thurberiana*, and plots were dominated by *A. tridentata wyomingensis*, with *Elymus elymoides* (bottlebrush squirreltail), *Poa sandbergii* (Sandberg's bluegrass), and many native forb species in the understory (Appendix S1). Cover of invasive cheatgrass averaged 1.4% (range 0.1–5.5%) before fires.

Prescribed fires were applied 23–28 September 1997 at the end of the natural fire season. Weather, fuels, and fire behavior data were

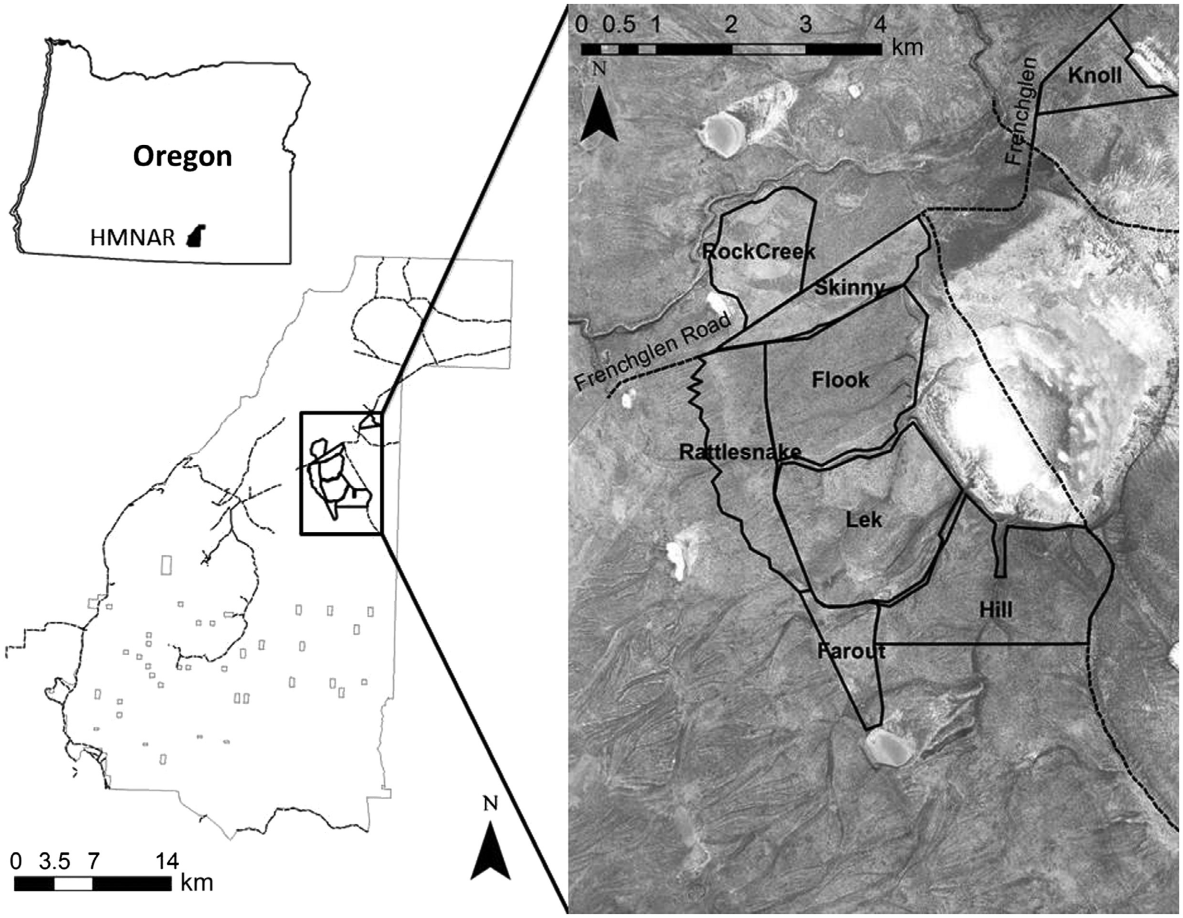

Fig. 1. Wyoming big sagebrush fire (Lek, Skinny, Rock Creek, and Knoll) and control (no fire in the 50-year fire record: Rattlesnake, Flook, Hill, and Farout) plots at Hart Mountain National Antelope Refuge, south-central Oregon, United States.

collected before, during, and after fires (see Wrobleski and Kauffman 2003). Fires burned in a mosaic pattern, leaving many unburned islands within the burn perimeter but completely consuming biomass in other patches. Overall, approximately 49% of the biomass within the burn perimeter was consumed by fire.

Community composition

To quantify the impacts of fire on plant community composition, all burn and control plots were sampled during the active growing season (May–June) before fire (1997; prefire), in the first post-fire year (1998; 1YPF), and 17 years following fire (2014; 17YPF). Percent cover of vegetation was measured along 10 randomly placed 20-m transects in each study plot and year. At 1YPF and 17YPF, transects were positioned within burned areas (i.e., excluding unburned islands) within treatment plots (burn plots), as well as in control plots.

*Shrubs.—*Each year (prefire, 1YPF, and 17YPF), percent cover of shrubs was measured with the line intercept technique (Canfield 1941). All shrubs intercepting the transect were also measured from the ground and classified into height classes as follows: short (<40 cm), medium (40–80 cm), and tall (>80 cm) because of the importance of tall and medium height shrubs for sage grouse nesting habitat (Gregg et al. 1994, Holloran et al. 2005, Connelly et al. 2011). To determine whether shrubs recolonized the burned areas, we measured the distance from a random location within the burn to the nearest mature sagebrush 1YPF

($N = 36$), permanently marked the point with a rebar post, and re-measured the distance 17YPF.

Herbaceous vegetation.—In all sample years, cover of all herbaceous species was measured within ten 20 × 50 cm microplots placed every 2 m along each of the ten 20-m transects in each plot (Daubenmire 1959). Cover of litter and bare ground was also quantified. Microplot data were averaged and scaled to give estimates of cover by species for each burn and control plot. Although there were some species for which we were interested in analyzing percent cover by species (i.e., cheatgrass), most were categorized into functional groups (deep-rooted perennial bunchgrasses, shallow-rooted perennial bunchgrasses, annual forbs, perennial forbs, key sage grouse forbs) for analysis. Nomenclature and native distribution follows the USDA Plants Database (USDA, NRCS 2016).

Analysis

Repeated-measures mixed model analyses were used to determine the effect of treatment (fire or control), time (prefire, 1YPF, and 17YPF), and the treatment × time interaction on each response variable (individual species or functional group cover). Plot was treated as the subject factor. Treatment, time, and their interaction were fixed factors. Post hoc multiple comparisons with a Tukey correction factor were performed following significant analyses to determine differences between time periods and determine whether there was a differential change over time between treatments (interaction term). Due to heteroscedasticity in the data, a nonparametric Mann–Whitney rank sum test was used to test the difference in distance from a random point to the nearest mature sagebrush at 1YPF and 17YPF time periods. Analyses were considered significant at $\alpha < 0.05$ and suggestive at $0.05 \leq \alpha < 0.10$. IBM SPSS version 23 (IBM SPSS, Chicago, Illinois, USA) was used for all analyses.

Results

Prescribed fires burned approximately 49% of the total area within burn plots, and just 21% of the total treatment area (burn and control plots combined, Fig. 1), creating a mosaic of mid-successional (17YPF) and late-successional (no fire on record) patches.

Bromus tectorum

Non-native *Bromus tectorum* was the only annual grass present in plots, averaging 0.2–8.4%, with no significant differences across sample years (mixed model, $P = 0.56$) or treatments (mixed model, $P = 0.07$). A suggestion of higher *B. tectorum* cover in burn plots was largely driven by increased cover at one of the burned plots (Lek) both before and after fires (Fig. 2).

Forbs

Annual forb species frequently encountered were predominantly small native species (Appendix S1) averaging 0.8% (range 0.1–3.0%) cover across all plots prior to fires. Fire increased annual forb cover in the first post-fire growing season to an average of 31% in burn plots, significantly higher than the 12% average cover in control plots for that year. Seventeen years after fire, cover of annual forbs averaged 2.4% cover across all plots, with no differences between treatments (post hoc multiple comparison, $P = 0.65$; Fig. 3A). There was a significant year effect, indicating that annual forb cover across both burn and control treatments was higher 1YPF than either pretreatment or 17YPF (mixed model, $P < 0.01$), and a significant year × treatment interaction (mixed model, $P < 0.01$), indicating that fire increased annual forb cover 1YPF, but this increase did not persist into the 17YPF period (Fig. 3A).

The most frequently encountered perennial forb species included *Astragalus* species (Fabaceae), *Crepis acuminata* and *C. modocensis* (Asteraceae), *Eriogonum* species (Polygonaeceae), and *Phlox longifolia* (Polymoniaceae; Appendix S1). There was a strong year effect on perennial forb cover (mixed model, $P < 0.01$) with much lower cover 17YPF than in either prefire or 1YPF (Fig. 3B). There was higher perennial forb cover in control plots than in burn plots, even prefire (mixed model, $P = 0.01$), but no evidence of a treatment × time interaction (mixed model, $P = 0.17$).

Forbs that have been shown to be important food species for sage grouse in this area were present in all burn and control plots, including *Agoseris* spp., *Antennaria* spp., *Astragalus* spp., *Crepis* spp., *Eriogonum* spp., *Lomatium* spp., *Microsteris* spp., *Phlox gracilis* Greene, *P. longifolia* Nutt., *Tragopogon* spp., and *Trifolium* spp. (Barnett and Crawford 1994, Drut et al. 1994, Gregg et al. 1994) Summed cover of all sage grouse

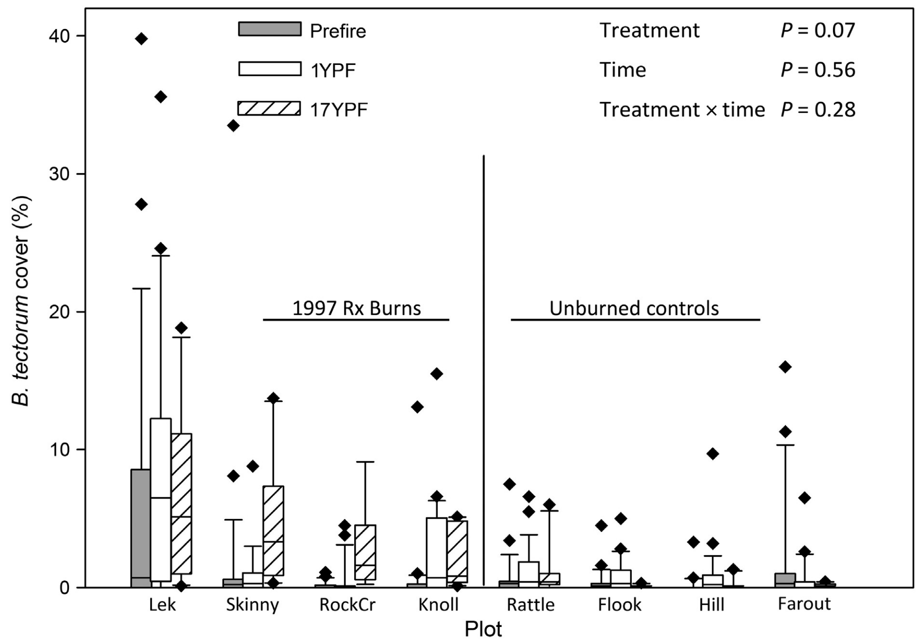

Fig. 2. Mean *Bromus tectorum* cover in prescribed fire and unburned control plots prefire (gray bars), 1 year post-fire (1YPF; white bars), and 17 years post-fire (17YPF; striped bars) in Wyoming big sagebrush ecosystems at Hart Mountain National Antelope Refuge, Oregon. Boxplots show the middle 50% of the distribution of the data around a median. Error bars show the top 25% of the distribution. Diamonds are outlier data points.

food species in treatment and control plots averaged 0.8% (range 0.4–1.8%) prefire, 5.1% (range 3.3–9.5%) at 1YPF, and 0.5% (range 0.1–0.7%) at 17YPF. There was a strong year effect (mixed model, $P < 0.01$) coincident with differences in annual precipitation, but there were no differences between burn and control plots (mixed model treatment effect; $P = 0.48$), or differences in changes in cover through time (mixed model treatment × year interaction; $P = 0.73$).

Native bunchgrasses

Native bunchgrasses included deep-rooted *Achnatherum hymenoides, Achnatherum thurberianum, Elymus elymoides*, *Elymus lanceolatus*, *Hesperostipa comata, Leymus cinereus,* and *Pseudoroegneria spicata* as well as shallow-rooted *Poa secunda.* There were no non-native perennial grasses. Total deep-rooted bunchgrass cover averaged 5.6% (range 3.5–7.2%) before fires. Fire reduced deep-rooted bunchgrass cover 1YPF to 4.0%, compared to 6.3% in unburned control plots (mixed model multiple comparison, $P = 0.03$). Seventeen years following fires, deep-rooted bunchgrass cover in burned plots was 4.8% while in control plots it had decreased to 1.3% cover (mixed model treatment × time effect: $P < 0.01$; Fig. 4). *P. secunda*, the only shallow-rooted bunchgrass species, averaged 3.9% cover (range 1.5–6.5%) and we saw no evidence that this species was impacted by fire treatments (mixed model treatment effect, $P = 0.59$), was variable through time (mixed model year effect, $P = 0.70$), or that treatments had different trajectories through time (mixed model treatment × time, $P = 0.35$).

Shrubs

Shrub cover was dominated by *Artemisia tridentata* ssp. *wyomingensis* Beetle & Young, with occasional occurrences of *Artemisia arbuscula* Nutt., *Ericameria nauseosa* (Pall. ex Pursh) G.L. Nesom & Baird, *Chrysothamnus viscidiflorus* (Hook.) Nutt., and *Tetradymia* species. Total shrub cover in all plots averaged 26.0% cover before prescribed fires (Fig. 5). Post-fire transects were intentionally placed in areas where biomass was completely consumed; thus, shrub cover following fires was <1% in all burned plots, and 29.6% in unburned control plots 1YPF. 17YPF, shrub cover in burned plots averaged 2.3%, with 17.9% cover in unburned control plots. There

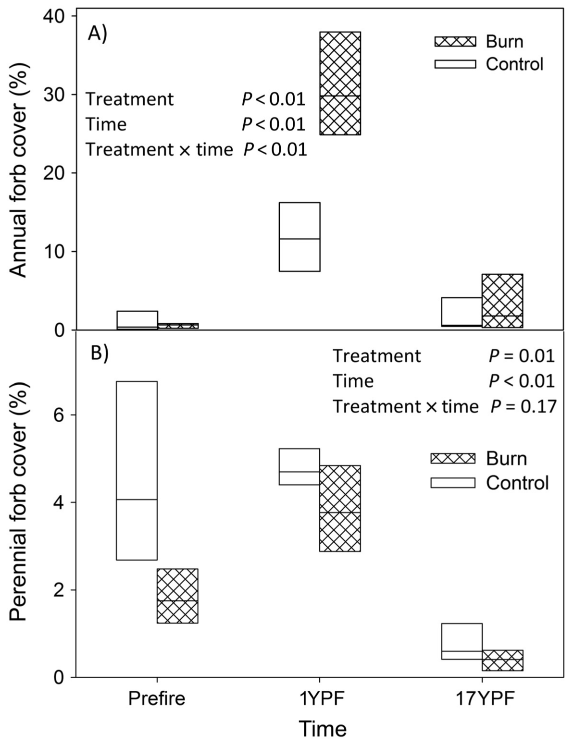

Fig. 3. Annual (A) and perennial (B) forb cover in prescribed fire (striped) and unburned control (white) plots prefire, 1 year post-fire (1YPF), and 17 years post-fire (17YPF) in Wyoming big sagebrush ecosystems at Hart Mountain National Antelope Refuge, Oregon. Boxplots show the middle 50% of the distribution of the data around a median.

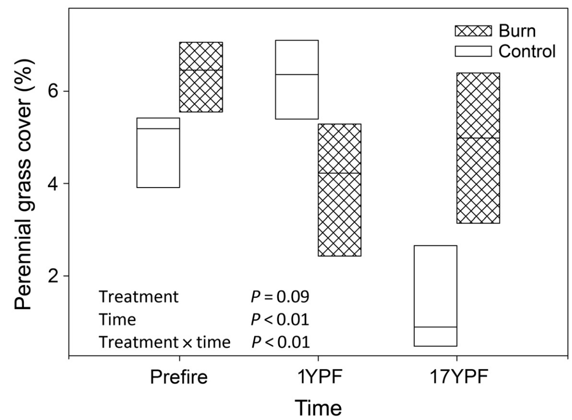

Fig. 4. Deep-rooted perennial bunchgrass cover in prescribed fire (striped) and unburned control (white) plots prefire, 1 year post-fire (1YPF), and 17 years post-fire (17YPF) in Wyoming big sagebrush ecosystems at Hart Mountain National Antelope Refuge, Oregon. Boxplots show the middle 50% of the distribution of the data around a median.

was a significant year × treatment interaction effect (mixed model, $P < 0.01$), indicating that fire treatments altered the trajectory of shrub cover through time (Fig. 5).

The medium (40–80 cm) and tall (>80 cm) sagebrush plants that have been shown to be particularly important for sage grouse nesting habitat (Gregg et al. 1994, Holloran et al. 2005, Connelly et al. 2011) made up 68% and 11%, respectively, of the total shrub cover across all plots prefire. All medium and tall shrubs were consumed by the fire, leaving none 1YPF. By 17YPF, medium height sagebrush averaged 59% of the total shrub cover in burned plots and unburned controls and that ratio was not significantly different between treatments (mixed model multiple comparison, $P = 0.22$). Sagebrush had not grown into the tall height class (0% of shrub cover) by 17YPF in any burned plot, and averaged 5% of the total shrub cover in unburned controls.

Despite the low shrub cover in burned areas 17YPF, we saw evidence that shrubs were recolonizing burned areas. 1YPF, the mean distance between a random point within the burn perimeter (beginning of shrub transects) and the nearest reproductive age sagebrush plant was 16.6 m. By

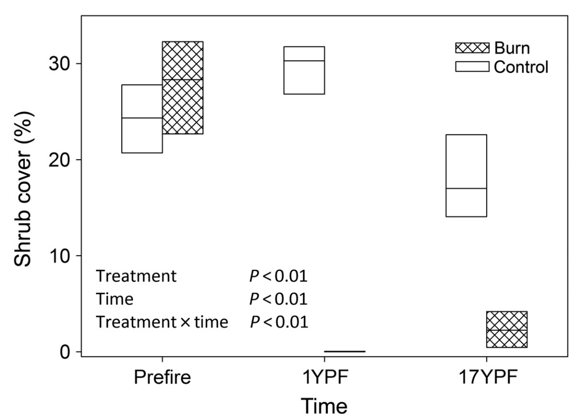

Fig. 5. Shrub cover in prescribed fire (striped) and unburned control (white) plots prefire, 1 year post-fire (1YPF), and 17 years post-fire (17YPF) in Wyoming big sagebrush ecosystems at Hart Mountain National Antelope Refuge, Oregon. Boxplots show the middle 50% of the distribution of the data around a median.

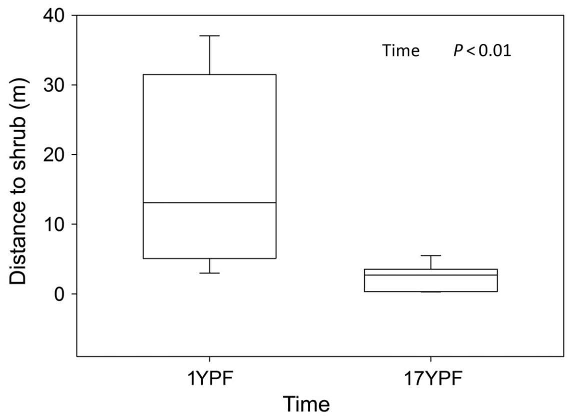

Fig. 6. Distance from a random point to the nearest mature sagebrush plant 1 year post-fire (1YPF) and 17 years post-fire (17YPF) in Wyoming big sagebrush ecosystems at Hart Mountain National Antelope Refuge, Oregon. Boxplots show the middle 50% of the distribution of the data around a median. Error bars show the top and bottom 25% of the distribution.

17YPF, this distance had decreased to 2.5 m (Mann–Whitney test, $P < 0.01$; Fig. 6).

Ground cover

Bare ground before treatments averaged 26.9% cover (range 20–33%). Fire increased bare ground 1YPF to 83.3% (range 81.8–85.1) compared to 48.6% (range 44.6–52.8%) in controls, and by 17YPF, there was more bare ground in unburned control plots (mean 65%, range 60–68%) than in burned plots (mean 54%, range 32–69%; mixed model year effect, $P < 0.01$; treatment effect, $P = 0.01$; year × treatment interaction, $P < 0.01$). Litter cover before treatments averaged 72% (range 63–80%). Fire decreased litter cover 1YPF to 16% compared to 52% in controls, but by 17YPF there was more litter in burned plots (mean 47%) than in unburned controls (mean 35%; year effect, $P < 0.01$; mixed model treatment effect, $P < 0.01$; year × treatment interaction, $P < 0.01$).

Discussion

Our results demonstrate a post-fire resilience that is not well documented in xeric Wyoming big sagebrush ecosystems. In contrast, recent research and policy has emphasized a trend toward post-fire dominance by exotic grass species and a resultant need for widespread suppression of fire in the sagebrush steppe (Knick 1999, Murphy et al. 2013). We believe that these differences in post-fire response may be due to the low invasive cover, lack of domestic livestock grazing, and native vegetation community composition in our study areas prior to fire, as has been similarly documented by Davies et al. (2008). Additionally, many studies have focused only on short-term patterns of ecosystem response to fire (Miller et al. 2013), rather than a temporal scale that more closely captures the slow rate of succession in Wyoming big sagebrush ecosystems (but see Morris and Leger 2016).

Consistent with our hypotheses, native herbaceous vegetation dominated the post-fire response. Perennial grass cover was low in the unburned controls, likely due in part to dense shrub cover prior to fires and drought conditions in the current (17YPF) and previous (16YPF) years' growing seasons (PRISM Climate Group). Similarly, while both overall forb cover and cover of those forbs that are important sage grouse foods (Gregg et al. 1994) did not differ between burn and control plots 17YPF, drought conditions during the growing season rather than any fire effect have likely contributed to decreased cover (Fig. 3). The plastic response observed by herbaceous native plants, particularly forbs, to interannual variability in precipitation in this climatically unpredictable environment demonstrates the resilience of the native herbaceous community.

Annual grass cover 17 years following fire remained low, though there is a suggestion of increased annual grass in burned plots across all sample years than in control plots (Fig. 2) and a trend toward post-fire increases. Additionally, the variability in cheatgrass response, as indicated by the magnitude of the outliers in Fig. 2, likely demonstrates the heterogeneity of disturbance effects. During this period of early post-fire recovery, it is likely that repeated or more continuous fires would increase the risk of further increases in early successional invasive species (Murphy et al. 2013). Because there are many unburned islands within the fire perimeter, a strong native component, and adequate seed sources, with more time since fire we expect increased dominance of native perennial herbaceous species (Morris and Leger 2016) in the absence of re-occurrence of fire and livestock grazing.

Within the study plots, sagebrush cover (20–33%) before fires was higher than the 7–18% shrub cover observed in similar communities (Wambolt and Gene 1986, Nelle et al. 2000, Davies and Svejcar 2008). A diminished herbaceous understory in unburned control plots is likely in part an effect of recent drought conditions and a legacy of domestic grazing (Anderson and Inouye 2001), but when coupled with dense sagebrush cover may also indicate that the vegetative community is currently outside the historical fire return interval. In similar Wyoming big sagebrush systems, Reisner et al. (2013) showed the importance of a strong native bunchgrass component in suppressing nonnative grass invasions. In our control plots, perennial native cover (bunchgrasses and forbs combined) averaged only 3.8% cover, and burn plots 17YPF averaged 8.3% cover, indicating that even modest levels of native bunchgrass cover, when accompanied by low invasive grass cover, may facilitate post-fire resilience when livestock are not present. With additional time since fire, we expect to see continued shifts toward increased perennial dominance in the herbaceous understory as longer lived plants outcompete early seral species, as has been seen with increasing time since disturbance in similar systems (Morris and Leger 2016), thus increasing ecological resilience of the system.

Shrub cover increased with time since fire during the first 17 years of post-fire succession. This is typical for sagebrush, as individual plants are killed by fire and require establishment by seed for shrub regeneration. Seeds are typically only dispersed a short distance from parent plants and remain viable only 4–6 yr (Whisenant 1990, Schlaepfer et al. 2014). We saw increases in sagebrush cover that closely followed the modeled expectations predicted by Watts and Wambolt (1996) and more rapid sagebrush recolonization and recovery than that seen in most previously published studies examined in a recent meta-analysis by Baker (2011). The mosaic pattern of the moderate intensity prescribed fires provided a high perimeter:area ratio and left many unburned sagebrush islands within the burn perimeter, providing ample sagebrush seed sources and facilitating re-establishment of shrubs into the burned area. Additionally, the few seedlings observed 1YPF turned into additional seed source islands in a matrix of herbaceous vegetation by 17YPF.

Recent efforts to protect dense stands of sagebrush as habitat for sage grouse have called for prevention and suppression of rangeland fires across the American West (i.e., Secretarial Order No. 3336). These policies were enacted to mitigate the impacts of the large-scale, invasive grass-driven wildfires (Murphy et al. 2013). However, we caution that these policies should be coupled with efforts toward increasing long-term ecosystem resilience in good condition sagebrush steppe by maintaining a balance of habitat components, which may include patches of early seral vegetation. Fire suppression alone will not restore sage grouse habitat, and may ultimately result in a degradation of the mosaic of plant communities and successional stages over the long term. Allowing some fire in resource management planning in areas where post-fire environments facilitate native species recovery may help create future ideal habitat for sagebrush steppe-associated wildlife species. This study provides information on post-fire sagebrush dynamics that has not been well documented—areas that have gone without fire, perhaps for too long, and are at risk of future type conversion due to a loss of herbaceous understory. We believe that the current paradigm of suppression of all fires in the sagebrush steppe is not universally appropriate and may create long-term losses of heterogeneity in some Wyoming big sagebrush ecosystems. The data presented here show that these xeric sagebrush steppe ecosystems exhibit greater post-fire resiliency than typically measured because they were (1) in relatively good ecological condition at the time of fire, (2) post-fire anthropogenic disturbances were minimal, and (3) there were many unburned islands within the fire perimeter that provided native seed sources following the fire. Further, these results show that there is often a mismatch between ecosystem processes (such as disturbance and succession) in these very slow-growing ecosystems and the temporal scale at which we plan and conduct both management and research.

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Supporting Information

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