Post-fire vegetation response at the woodland–shrubland interface is mediated by the pre-fire community

ALEXANDRA K. URZA,[1,2,†] PETER J. WEISBERG,[1] JEANNE C. CHAMBERS,[3]
JESSICA M. DHAEMERS,[4] AND DAVID BOARD[3]

[1]*Department of Natural Resources and Environmental Science, University of Nevada-Reno, Reno, Nevada 89557 USA*
[2]*Program in Ecology, Evolution and Conservation Biology, University of Nevada-Reno, Reno, Nevada 89557 USA*
[3]*US Forest Service, Rocky Mountain Research Station, Reno, Nevada 89512 USA*
[4]*US Forest Service, Beaverhead-Deerlodge National Forest, Dillon, Montana 59725 USA*

Abstract.   Understanding the drivers of ecosystem responses to disturbance is essential for management aimed at maintaining or restoring ecosystem processes and services, especially where invasive species respond strongly to disturbance. In this study, we used repeat vegetation surveys from a network of prescribed fire treatments at the woodland–shrubland interface in the Shoshone Mountains, Nevada, USA, to investigate post-fire responses of the understory plant community. First, we characterized post-fire community trajectories for sites located along an elevational gradient, hypothesizing a positive relationship between elevation and resistance to invasion. Unburned understory communities and their responses to disturbance differed along the gradient. As hypothesized, lower elevations experienced greater species turnover and higher invasive annual grass (*Bromus tectorum*) cover after fire. Second, we characterized post-fire plant community trajectories for sites with varying levels of pre-fire pinyon and juniper cover, hypothesizing that pre-fire tree dominance and associated reductions in perennial understory species lead to less predictable post-fire trajectories. Among sites with low-to-moderate tree cover, burning largely eliminated differences in understory composition, suggesting that biotic legacies were sufficient to result in predictable trajectories. In contrast, sites with high pre-fire tree cover transitioned into an annual forb-dominated community with sparse vegetation cover, suggesting that the loss of the understory community initiated unpredictable and divergent post-fire trajectories. Because plant communities were still changing four years after fire, it is unclear whether the alternate trajectories in sites with high tree cover will result in the formation of alternate states, or whether community composition will eventually converge with other sites at the same elevation. Results indicate that careful evaluation of site characteristics can be used to predict treatment outcomes at the woodland–shrubland interface, and to guide the appropriate use of prescribed fire or other management practices.

Key words: annual invasive grass; biotic legacy; *Bromus tectorum;* ecological memory; environmental gradients; Great Basin; juniper; pinyon; prescribed fire; resilience; resistance; sagebrush ecosystems.

† **E-mail:** alexandra.urza@gmail.com

INTRODUCTION

Understanding the drivers of ecosystem responses to disturbance is essential for management aimed at maintaining or restoring ecosystem processes and services (Seastedt et al. 2008), particularly when disturbances are used as a management tool (Wisdom and Chambers 2009). The memory of past ecological states often interacts with abiotic filters to shape plant community responses to disturbance (Padisak 1992, Johnstone et al. 2016). Abiotic conditions constrain

post-disturbance plant community assembly by imposing filters on resource availability and species pools (Pickett et al. 2009), and topographic gradients of moisture and temperature have been shown to drive post-disturbance vegetation trajectories in deserts (Shryock et al. 2015), savannas (Smit et al. 2010), coastal heathlands (Vandvik et al. 2005), bogs (Benscoter and Vitt 2008), and subalpine and montane forests (Dynesius et al. 2009, Coop et al. 2010). However, differences in pre-disturbance biotic conditions can imprint long-lasting legacies of post-disturbance structure and function (Franklin 2000), initiating alternate and non-convergent trajectories even among communities with identical abiotic environments (Gunderson 2000).

Biotic legacies that persist within a disturbed area, such as surviving organisms, propagules, and residual structures, promote the stability of the pre-disturbance plant community (Franklin et al. 2000, Johnstone et al. 2016) and influence initial successional patterns (Turner et al. 1998, Bengtsson et al. 2003). Conversely, a weak ecological memory is generated where few biotic legacies persist through a disturbance, increasing the importance of stochastic dispersal-assembly processes (Myers and Harms 2009) and leading to alternate trajectories of community composition (Gunderson 2000). While biotic legacies comprising ecological memory (or lack thereof) have been credited with driving post-disturbance trajectories in many temperate forest (Seidl et al. 2014, Kemp et al. 2016, Urza and Sibold 2017) and wetland (Matthews and Endress 2010) plant communities, these concepts have been rarely applied to dryland ecosystems.

Plant invasions can influence the loss of biotic legacy and weaken ecological memory. Invasives that alter the composition of the pre-disturbance plant community may limit post-disturbance recovery of native communities (Schaefer 2011) and enhance their own persistence through reinforcing feedback processes. For example, invaders can alter disturbance regimes to favor their own persistence at the expense of native competitors (Brooks et al. 2004, Gaertner et al. 2014), such as through annual grass–fire cycles (D'Antonio and Vitousek 1992).

In sagebrush ecosystems of the Intermountain West, fire is the dominant broad-scale disturbance, although the effects of fire vary greatly across landscapes and among species. Many herbaceous plant species native to sagebrush ecosystems exhibit adaptations to fire, such as root sprouting or seed banking (Everett and Ward 1984, Koniak 1985, Miller et al. 2013). However, the dominant shrub species (*Artemisia* species, or sagebrush) lack re-sprouting capabilities, have poor dispersal ability (Young and Evans 1989), and often recover slowly after fire (Baker 2006, Lesica et al. 2007, Miller et al. 2013). *Bromus tectorum* (cheatgrass), a fire-adapted exotic annual grass species, has invaded vast portions of the Intermountain West, resulting in transformations of entire landscapes to annual grass dominance and altering the ecology of sagebrush ecosystems and their responses to fire (Balch et al. 2013, Germino et al. 2016). While many land-use practices facilitate *B. tectorum* invasion, it is mainly fire disturbance that ultimately leads to *B. tectorum* dominance (Pyke et al. 2016). In sagebrush ecosystems, elevational gradients of soil temperature and moisture directly affect the pre- and post-fire environment, influencing plant community trajectories (Davies et al. 2012) and the probability of annual grass invasion (Chambers et al. 2014*a, b*, 2016). After fire, warm and dry (low-elevation) sites have lower resistance to invasion by *B. tectorum* (Chambers et al. 2007, Condon et al. 2011, Taylor et al. 2014), slower recovery of sagebrush (Baker 2006), and lower rates of perennial herbaceous recruitment (Chambers et al. 2014*b*, 2016). Consequently, low-elevation sites are less resilient to fire (Chambers et al. 2014*a*).

In sagebrush ecosystems, native perennial herbaceous vegetation that persists after fire represents an important biotic legacy that promotes ecosystem resilience to disturbance (Chambers et al. 2014*a, b*). The progressive loss of fire-adapted, perennial herbaceous vegetation has been pervasive and is widely attributed to two, often interrelated processes: poor livestock management and expansion or infilling of woodlands. Pinyon–juniper woodland expansion and infilling in the western United States results from multiple interacting causes (Romme et al. 2009), including climate change (Miller and Wigand 1994), recovery from settlement-era tree harvesting that was associated with regional-scale production of charcoal for the mining industry (Young and Budy 1979, Ko et al. 2011, Lanner and Frazier 2011), slow reforestation following extensive 19th-century wildfires (e.g., Bauer and Weisberg 2009), poor

livestock management (Cottam and Stewart 1940, Miller and Wigand 1994), and fire exclusion (Miller and Rose 1999). Regardless of the underlying causes, increased tree cover often results in the loss of both sagebrush and associated native perennial herbaceous species from the understory (Roundy et al. 2014a), reducing regeneration from residual plants (Chambers et al. 2014b, Roundy et al. 2014a) and altering the composition of the soil seed bank (Allen and Nowak 2008, Bates et al. 2014b).

Cumulatively, these effects can reduce the ecological memory of native understory plant communities after fire. Sites with depleted understories, such as those with high pre-fire tree dominance, are expected to have post-fire trajectories that differ from sites previously dominated by shrubs and grasses. The result is often delayed recovery of native perennial understory vegetation (Condon et al. 2011, Roundy et al. 2014a), but the implications of delayed recovery are unclear. The empty ecological niche produced by the absence of perennial herbaceous vegetation, coupled with a release of soil resources (Rau et al. 2007, 2014, Roundy et al. 2014b), can facilitate post-fire invasion of annual grasses and forbs in climatically suitable areas (Bates et al. 2014a, b, Chambers et al. 2014b, Roundy et al. 2014a). Some have suggested that there is a threshold of pre-fire tree dominance beyond which the pre-fire plant community is unlikely to recover, and will instead enter an alternate state dominated by opportunistic natives or annual plants (Miller et al. 2005, 2013, Bates et al. 2014b, Roundy et al. 2014a).

Here, we used an experimental network of prescribed fire treatments in a Great Basin ecosystem co-dominated by sagebrush and pinyon and juniper to characterize understory community responses to fire for four years post-fire. Management efforts in the region are targeted at reducing tree cover to maintain shrub- and grass-dominated habitats and conserve sagebrush obligate species (Miller et al. 2013). Prescribed fire is one tool to achieve tree reduction objectives. The experimental design included replicate pairs of burned and control plots arranged along gradients of elevation and pre-fire tree cover, while controlling for potentially confounding factors such as topography, soil type, time period, and post-fire management. We used repeated measures of species composition and aerial cover to describe multivariate plant community trajectories and trends for key species and functional groups across abiotic and biotic gradients. We had two primary objectives. First, we characterized post-fire plant community trajectories for sites distributed along an elevational gradient to assess whether community responses to fire varied among ecological site types. We hypothesized that community trajectories would be similar among sites with similar abiotic conditions and that the low-elevation sites would exhibit the greatest turnover in species composition after burning. Second, we characterized post-fire plant community trajectories for mid-elevation sites with varying levels of pre-fire pinyon and juniper cover to assess whether pre-fire tree dominance influenced post-fire community structure. We hypothesized that sites with high pre-fire tree cover would experience greater compositional changes and higher variability among post-fire communities, due to heightened stochasticity where ecological memory was weakened by a reduced presence of perennial understory species before burning.

Methods

Study area

The study was located in Underdown Canyon, in the Shoshone Mountains in Nye and Lander Counties, Nevada, USA. The climate of Underdown Canyon is typical of the Great Basin high desert and is characterized by cold winters and warm summers. Average annual precipitation in Underdown Canyon is 23 cm at the lower elevations and 50 cm at the upper elevations (Board et al. 2011) and typically experiences two peaks: one in January, in the form of snow, and another in May, in the form of rain (PRISM Climate Group 2016). The geology is dominated by welded and non-welded volcanic tuff, and soils are classified as coarse loamy mixed frigid typic haploxerolls (Rau et al. 2005). Tree assemblages in unburned portions of Underdown Canyon are dominated by single-leaf pinyon (*Pinus monophylla*), with lower abundance of Utah juniper (*Juniperus osteosperma*).

Study design and sampling

Underdown Canyon is a Joint Fire Sciences Program Demonstration Area and contains a network of experimental prescribed fire treatments.

The study utilized a before/after control/impact design, with three pairs of adjacent alluvial fans arranged along an elevational gradient (2073, 2225, and 2347 m) on a north-facing slope within the same watershed. One fan within each pair was burned (impact) by the USDA Forest Service in the spring of 2002, and the other remained unburned (control). Prior to burning, the mid-elevation fans were stratified into polygons representing tree cover categories: low (12% mean cover), moderate (38% mean cover), and high (74% mean cover; Reiner 2004). Only the mid-elevation alluvial fans contained sufficient variability in tree cover to include all three categories, and the low- and high-elevation fans included only the moderate tree cover category. Livestock were excluded for the duration of the study. Weather was variable over the study period, with years of drought and years of above-average precipitation.

Three sampling plots approximately 0.1 ha in size were located in each combination of control/burned, elevation group, and tree cover category, for a total of 30 plots (Appendix S1: Fig. S1). Data on understory species composition and cover were collected before burning in 2001 and after burning in 2003, 2004, and 2006 in quadrats systematically located along transect lines that were randomly stratified within plots. The 2001 data collection measured two diameters for all herbaceous species and shrubs within 50, 2-m^2 quadrats in each plot, which were then converted to percentage of area sampled to obtain aerial cover (Reiner 2004). In 2003, 2004, and 2006, 25–30, 0.25-m^2 quadrats were used to measure herbaceous cover in each plot; aerial cover was estimated by species using 13 cover categories (Daubenmire 1959), and the mid-point of each cover category was chosen to represent percent cover in each quadrat (Appendix S1: Table S1). In 2003, 2004, and 2006, shrub diameters (longest and perpendicular) and height were measured for all individuals in 15–30, 2-m^2 quadrats in each plot, and aerial cover was derived by converting to percentage of area sampled. No shrub data were collected on control plots in 2006.

Data analyses

Community types.—We identified distinct understory plant community types through a cluster analysis of species cover data for all plots across all years. We used the Bray–Curtis distance measure with Ward's hierarchical agglomerative method with the *vegdist* function in the "vegan" package (version 1.7.5) and the *hclust* function in the R base package version 3.1.2 (R Core Team 2015). Community types were characterized with an indicator species analysis using the "vegan" package, where the appropriate number of groups was identified by maximizing the number of statistically significant indicator species (Dufrene and Legendre 1997).

Community trajectories.—To compare multivariate patterns of community composition between plots, we performed non-metric multidimensional scaling (NMS) ordinations of species cover data for all plots across all years. NMS is an unconstrained ordination technique that uses rank order correlations to iteratively model observed ecological distances from a site dissimilarity matrix. Non-metric multidimensional scaling allows for non-parametric relationships, avoiding the assumption of linear or unimodal responses to environmental gradients, and so is well suited to non-normal or discontinuous species cover data (McCune and Grace 2002).

Percent cover was averaged by species within each plot. Unknown species and rare species (observed only once) were removed to reduce spurious influences on the ordination, and similar species with identification uncertainty were grouped by genus. For example, although multiple *Artemisia* species are known to exist at this site, they are difficult to distinguish in the seedling stage, so we combined these species for analysis. Wisconsin double standardization, which standardizes across both species and sites, was applied prior to ordination (Bray and Curtis 1957). We used Bray–Curtis distance metrics in the *metaMDS* function in the "vegan" package version 2.3-1 (Oksanen et al. 2015), which runs the NMS multiple times with random starting configurations to avoid convergence at local minima. In the ordination figures, interannual variability within all unburned (control) plots was shown using ellipses. Fire-induced shifts in species composition within burned plots were represented using arrows connecting each plot through time, as the Bray–Curtis distance metric is representative of beta diversity, or species turnover between sites (Ellingsen 2001).

Variability in community composition.—To assess the variability in community composition in

burned plots over time, we calculated Bray–Curtis dissimilarity metrics among plots within site groupings. We calculated dissimilarity among plots for each elevation and tree cover group for each year of the study. Additionally, we calculated dissimilarity for each of the community types identified from the cluster analysis.

Functional group cover.—Species were aggregated into six functional groups, which represented >99% of the total cover observed: perennial graminoids, annual graminoids, perennial forbs, annual forbs, non-sprouting perennial shrubs, and sprouting perennial shrubs. Percent cover was summed by functional group within each sampling quadrat, then averaged within each plot. We used the "lm" function in R to model functional group and total cover (log-transformed). Because the gradients of elevation and tree cover were not fully crossed in the experiment (i.e., only mid-elevation plots span a gradient of tree cover, and vice versa; Appendix S1: Fig. S1), we analyzed the effects of elevation and tree cover in separate models: Only moderate tree cover plots were used

to analyze the effect of elevation, and only mid-elevation plots were used to analyze the effect of tree cover. Control/burned ("Burn"), year, and treatment group (either elevation or tree cover), and all possible interactions were included as predictors in both models. As interactions between factors resulted in a large number of effect size estimates, we report only type 2 ANOVA statistics. We used a standard Bonferroni correction to adjust for multiple comparisons: Based on 14 hypothesis tests and a desired significance level of 0.05, our critical alpha level was 0.004.

RESULTS

Understory plant community types

Eight major plant community types were identified from the cluster analysis, using species composition data from all plots (Table 1; Appendix S1: Fig. S2). Four community types were comprised of unburned plots (pre-fire or controls), and four were comprised of burned plots (Appendix S1: Table S2). The four unburned community types

Table 1. Indicator species and dominant species for each community type.

Community type	Indicator understory species (indicator score)	Dominant understory species (mean % cover)
Big sagebrush/fescue shrubland	*Festuca idahoensis* (77), *Artemisia* (75), *Eriogonum umbellatum* (53), *Koeleria macrantha* (51)	*Artemisia* (21), *Festuca idahoensis* (6), *Chrysothamnus viscidiflorus* (2), *Lupinus argenteus* (2), *Symphoricarpos oreophilus* (2), *Elymus elymoides* (1)
Big sagebrush/bluegrass shrubland	*Poa secunda* (71)	*Poa secunda* (6), *Artemisia* (4), *Lupinus argenteus* (2), *Eriogonum microthecum* (<1), *Chrysothamnus viscidiflorus* (<1), *Arenaria aculeata* (<1)
Sparse perennial understory	*Ephedra viridis* (58)	*Poa secunda* (1), *Elymus elymoides* (1), *Artemisia* (1), *Ephedra viridis* (<1), *Lupinus argenteus* (<1), *Symphoricarpos oreophilus* (<1)
Big sagebrush-dominated	*Astragalus purshii* (59)	*Artemisia* (10), *Poa secunda* (1), *Lupinus argenteus* (1), *Chrysothamnus viscidiflorus* (1), *Eriogonum elatum* (1), *Elymus elymoides* (1)
Diverse mountain shrubland	*Penstemon watsonii* (90), *Symphoricarpos oreophilus* (85), *Phlox hoodii* (71), *Silene douglasii* (67), *Achnatherum hymenoides* (66), *Mentzelia albicaulis* (65), *Antennaria rosea* (63), *Carex* (60)	*Symphoricarpos oreophilus* (11), *Lupinus argenteus* (6), *Festuca idahoensis* (3), *Chrysothamnus viscidiflorus* (3), *Phlox hoodii* (2), *Leymus cinereus* (1)
Native perennial forbs and grasses	*Agoseris glauca* (69), *Arenaria aculeata* (60), *Pseudoroegneria spicata* (57), *Gayophytum racemosum* (45)	*Lupinus argenteus* (4), *Chrysothamnus viscidiflorus* (1), *Collinsia parviflora* (1), *Poa secunda* (1), *Eriogonum elatum* (1), *Eriogonum microthecum* (1)
Invaded forbs and grasses	*Bromus tectorum* (95), *Arenaria kingii* (85), *Arabis sparsiflora* (81), *Phlox longifolia* (80), *Chrysothamnus viscidiflorus* (69), *Eriastrum wilcoxii* (69), *Eriogonum elatum* (66), *Lappula occidentalis* (63)	*Chrysothamnus viscidiflorus* (7), *Lupinus argenteus* (3), *Bromus tectorum* (2), *Eriogonum elatum* (2), *Elymus elymoides* (1), *Poa secunda* (1)
Sparse annual forbs	*Microsteris gracilis* (82), *Collinsia parviflora* (66), *Astragalus oophorus* (66), *Lactuca serriola* (59), *Descurainia pinnata* (58)	*Collinsia parviflora* (1), *Symphoricarpos oreophilus* (1), *Microsteris gracilis* (1), *Elymus elymoides* (1), *Mentzelia albicaulis* (<1), *Eriogonum elatum* (<1)

Notes: Only significant indicator species ($P < 0.05$) are listed (up to eight per group). Top six dominant understory species are listed (based on mean % cover).

were (with abbreviated names) big sagebrush/fescue shrubland (sagebrush/fescue), big sagebrush/bluegrass shrubland (sagebrush/bluegrass), sparse perennial understory (sparse perennials), and big sagebrush-dominated (big sagebrush). The four burned community types were diverse mountain shrubland (diverse shrubland), native perennial forbs and grasses (native perennials), invaded forbs and grasses (invaded), and sparse annual forbs (sparse annuals). Plots with the same combination of site conditions (burned/unburned, elevation, and pre-fire tree cover) generally pertained to a single plant community type, suggesting low variability in species composition among replicate plots.

The eight identified plant community types corresponded to different regions in the NMS ordination of species composition for all plots (Fig. 1). The NMS analysis showed that variation in species composition was best explained along two axes (105 sites, 92 species; final stress = 0.24;
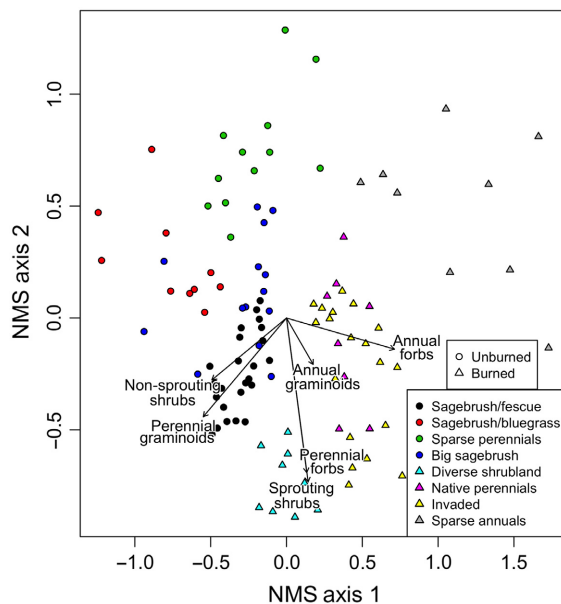

Fig. 1. Understory plant community composition for burned (triangles) and unburned (circles) plots, based on non-metric multidimensional scaling (NMS) ordination. Arrows indicate correlations between functional group cover and site NMS scores. Arrow length is proportional to the magnitude of the correlation. Point colors represent plant community types identified from hierarchical cluster analysis.

Appendix S1: Table S3). Axis 1 separated unburned from burned community types along a gradient of disturbance. Plots at the high end of Axis 1 had high annual forb cover ($r = 0.98$, $P = 0.001$), low non-sprouting shrub (*Artemisia*) cover ($r = -0.87$, $P = 0.001$), and low perennial graminoid cover ($r = -0.78$, $P = 0.001$). Axis 2 was related to a gradient of total vegetation cover. All functional groups were negatively correlated with Axis 2, and plots at the high end of the axis had low sprouting shrub cover ($r = -0.98$, $P = 0.001$), low perennial forb cover ($r = -0.98$, $P = 0.001$), and relatively sparse cover in all other functional groups.

Understory plant community composition along an elevational gradient

Unburned plots.—Species composition within the unburned plots (with moderate pre-fire tree cover) was well stratified by elevation, with each elevation group corresponding to a different plant community type (Table 1; Appendix S1: Table S4). The low-elevation plots corresponded to the "big sagebrush/bluegrass shrubland" community type, characterized by high cover of *Poa secunda*, *Artemisia*, and *Lupinus argenteus*. Mid-elevation plots were classified as "big sagebrush-dominated" understory communities, with *Artemisia* comprising the majority of vegetation cover with a minor component of sprouting shrubs. High-elevation plots were characterized as "big sagebrush/fescue shrubland" communities, with high cover of *Artemisia* and *Festuca idahoensis*, and an abundance of sprouting mountain shrubs such as *Chrysothamnus viscidiflorus* and *Symphoricarpos oreophilus*. All unburned plots shared several common species: *Artemisia*, *C. viscidiflorus*, *Elymus elymoides*, *P. secunda*, *L. argenteus*, *Phlox hoodii*, and *Arabis holboellii*. Among unburned plots at different elevations, the composition of the low-elevation plots was most distinctive, while the mid- and high-elevation plots had some overlap in NMS ordination space (ellipses in Fig. 2). Among-plot dissimilarity (Fig. 3a) and total understory cover (Appendix S1: Fig. S3) were positively related to elevation, and both were substantially greater at the highest elevation.

Community trajectories after burning.—After the burn treatment, all plots showed substantial turnover in species composition (trajectory arrows in Fig. 2). All elevation groups lost virtually all *Artemisia* cover as a result of burning,
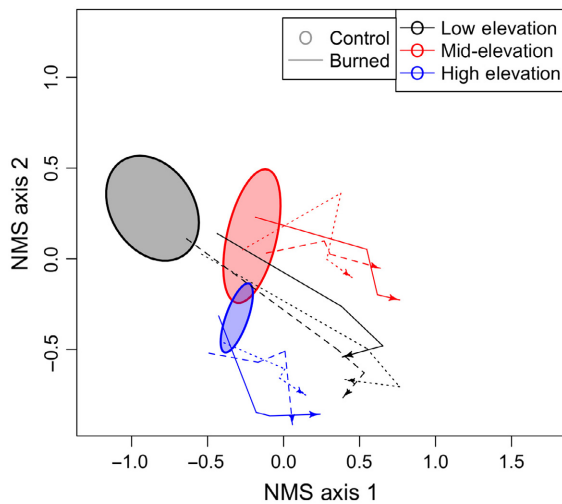
Fig. 2. Understory plant community composition of moderate tree cover plots for burned (arrows) and control (ellipses) plots along an elevational gradient, based on non-metric multidimensional scaling (NMS) ordination. Ellipses show the interquartile range for all control plots in 2001, 2003, and 2004 (N = 9). Arrows show the community trajectory of each burned plot through time, with a distinct line type for each plot (short-dash, long-dash, solids); arrowheads show plots in 2006, tails show plots in 2001 (pre-burn), and inflection points show plots in 2003 and 2004.

driving similar trajectories toward more positive values along Axis 1 (Fig. 2). All elevations showed slight increases in among-plot dissimilarity after burning (Fig. 3a), which persisted

through 2006. This increase was most marked for low- and middle-elevation plots, where plots were more similar before burning.

Low- and mid-elevation plots transitioned first to the "native perennial forbs and grasses" community type, with high cover of *L. argenteus* and several other perennial forbs and grasses as indicator species (Table 1). After two years post-burning, these plots transitioned to the "invaded forbs and grasses" community type, driven by the increase in *Bromus tectorum* and sprouting shrubs (Table 1; Appendix S1: Table S4). Both low- and mid-elevation plots had slightly decreased total cover of all functional groups combined in 2003 (one year after burning), followed by increases in subsequent years (Appendix S1: Fig. S3). By 2006, burned plots had regained pre-burn cover levels at the mid-elevation and exceeded pre-burn levels at the low elevation.

High-elevation plots transitioned into the "diverse mountain shrubland" community type after burning, characterized by high cover and richness of perennial grasses, forbs, and sprouting shrubs (Table 1; Appendix S1: Table S4). Total cover was reduced after burning (Appendix S1: Table S4), and control and burned plots showed small but persistent differences in all years (Appendix S1: Fig. S3). Overall, the high-elevation plots experienced the least turnover in species composition after burning, as seen in the relatively short trajectory arrows in Fig. 2.
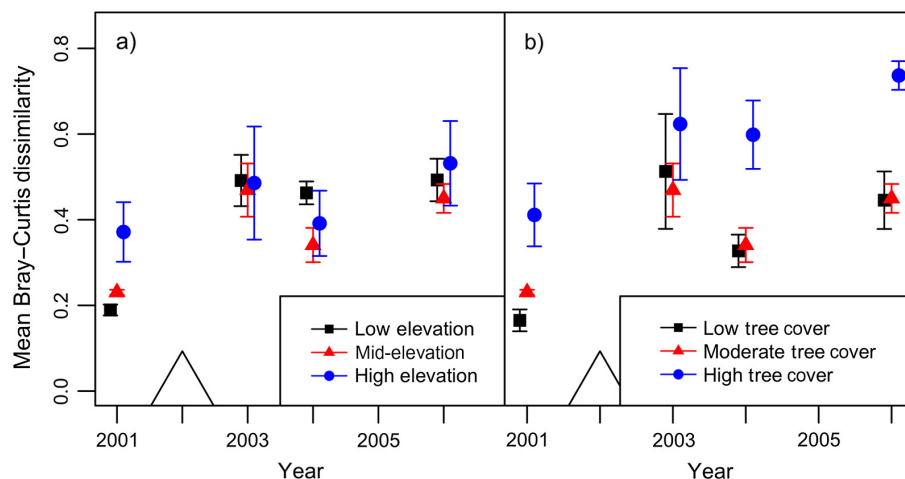

Fig. 3. Bray–Curtis dissimilarity among plots within elevation (a) and tree cover (b) groups. Only burned plots are included in the analysis. Data shown as mean ± 1 SE. Large triangle shows year of burn treatment.

Functional group responses to burning.—Perennial graminoid cover was not significantly affected by burning (Year × Burn: $P = 0.022$; Table 2) and was instead driven by high interannual variability in both control and burned plots (Fig. 4a). Perennial grass cover in burn and control plots differed among elevations and was greatest at high elevation (Year × Elevation: $P = 0.001$; Table 2), although there was not a consistent relationship between cover and elevation groups. Perennial grass cover was significantly lower for the burned plots (Burn: $P < 0.001$; Table 2), but this was the case both before and after treatment (Fig. 4a), suggesting that the difference was not due to burning.

Annual graminoid cover showed a distinctive burn response (Year × Burn: $P < 0.001$; Table 2), and the trajectories of control and burned sites diverged sharply after fire (Fig. 4b). Burned sites had large (though highly variable) increases in annual graminoid cover that were apparent in the final year of sampling, whereas control sites had no more than trace amounts in all years. Cover was inversely related to elevation (Elevation: $P < 0.001$; Table 2), as the greatest increases occurred at low elevation, and no annual graminoid cover was recorded at high elevation. *Bromus tectorum* was the only annual graminoid species recorded.

Perennial forb cover was also increased by burning (Year × Burn: $P = 0.002$; Table 2). Control and burned plots had similar perennial forb cover before burning in 2001, but cover increased on the burned plots through time and was greater than on control plots at all elevations by 2006 (Fig. 4c). This response varied by elevation, and the low-elevation burned plots had the largest apparent increase (Burn × Elevation: $P = 0.002$; Table 2).

Annual forb cover had a short-term positive response to burning (Year × Burn: $P < 0.001$; Table 2). At all elevations, annual forb cover peaked in 2004, though the magnitude of the peak, and the rate of decline to pre-burn levels, varied by elevation (Year × Elevation: $P < 0.001$; Table 2). At low and mid-elevations, annual forb cover began to increase in 2003 and was still elevated above pre-burn levels in 2006 (Fig. 4d). The high elevation showed a more short-lived flush of annual forbs, with increased cover only in 2004.

Non-sprouting perennial shrub cover was strongly negatively affected by burning (Year × Burn: $P < 0.001$; Table 2). At all elevations, cover was reduced to trace amounts immediately after burning, and minimal signs of recovery were evident by 2006 (Fig. 4e). Among control plots, there was a positive relationship between non-sprouting shrub cover and elevation, but this relationship was not reflected in burned plots. *Artemisia* (sagebrush) species were the only recorded non-sprouting shrubs.

Sprouting perennial shrub cover was positively affected by burning (Year × Burn: $P = 0.001$; Table 2), particularly at low elevation (Burn × Elevation: $P < 0.001$; Table 2). Low-elevation burned plots had sprouting shrub cover comparable to that of high elevation by 2006, despite a strong positive relationship between cover and

Table 2. Elevation effect on understory cover by functional group.

Response	Perennial graminoid cover	Annual graminoid cover	Perennial forb cover	Annual forb cover	Non-sprouting shrub cover	Sprouting shrub cover	Total cover
Predictor				*F (P)*			
Year	19.22 (**<0.001**)	9.67 (**<0.001**)	1.70 (0.179)	29.52 (**<0.001**)	14.39 (**<0.001**)	15.26 (**<0.001**)	21.96 (**<0.001**)
Burn	19.18 (**<0.001**)	17.86 (**<0.001**)	44.30 (**<0.001**)	199.14 (**<0.001**)	94.42 (**<0.001**)	77.60 (**<0.001**)	3.22 (0.080)
Elevation	41.31 (**<0.001**)	17.78 (**<0.001**)	10.86 (**<0.001**)	3.41 (0.041)	2.68 (0.080)	102.80 (**<0.001**)	59.41 (**<0.001**)
Year × Burn	3.53 (0.022)	11.42 (**<0.001**)	5.95 (**0.002**)	29.22 (**<0.001**)	20.55 (**<0.001**)	8.13 (**0.001**)	9.98 (**<0.001**)
Year × Elev	4.81 (**0.001**)	2.65 (0.027)	2.89 (0.018)	5.93 (**<0.001**)	0.27 (0.946)	0.59 (0.738)	3.85 (0.004)
Burn × Elev	0.39 (0.681)	5.58 (0.007)	6.91 (**0.002**)	0.81 (0.450)	0.85 (0.434)	54.75 (**<0.001**)	7.17 (**0.0021**)
Burn × Year × Elev	0.29 (0.944)	3.60 (0.005)	1.91 (0.098)	1.77 (0.125)	0.39 (0.814)	3.32 (0.019)	1.62 (0.187)
Adjusted R^2	0.7153	0.6671	0.6179	0.852	0.7498	0.8963	0.7964

Notes: Only moderate tree cover plots were included in the analysis. *F*-value and *P*-value calculated from type 2 ANOVA for a linear model predicting percent cover (log) for each functional group. All predictors are factors. Bolded where $P < 0.004$ (based on a Bonferroni correction for 14 tests at a desired significance value of 0.05). Burn = control (unburned) or burned.
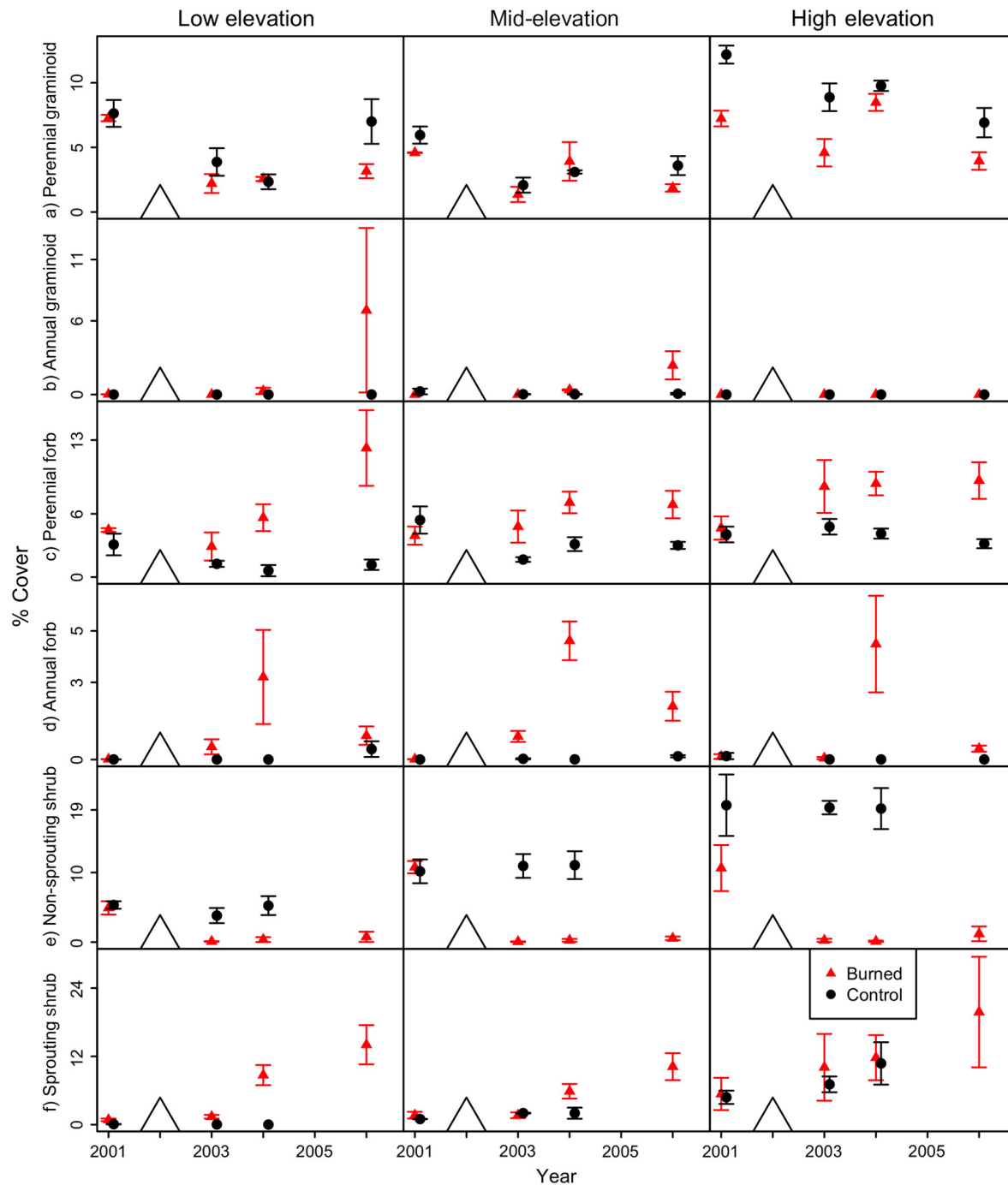
Fig. 4. Functional group cover for burned (red triangles) and control (black circles) plots along an elevational gradient. Only moderate tree cover plots are shown. Data are shown as mean ± 1 SE. No shrub control data were collected in 2006. Large triangle shows year of burn treatment.

elevation for the control sites (Fig. 4f). Post-fire sprouting shrub cover was dominated by *C. viscidiflorus* at low and mid-elevations and by *S. oreophilus* (with lower amounts of *C. viscidiflorus*) at high elevation.

Understory responses to burning along a gradient of pre-burn tree cover

Unburned plots.—Mid-elevation unburned plots were arranged along NMS Axis 2 based on tree cover (ellipses in Fig. 5), and each tree cover group corresponded to a different plant community type (Table 1; Appendix S1: Table S4). Low tree cover plots were characterized as "big sagebrush/fescue shrubland" communities, with high cover of *Artemisia* and *F. idahoensis*, as well as sprouting mountain shrubs such as *C. viscidiflorus* and *S. oreophilus*. Moderate tree cover plots were classified as "big sagebrush-dominated" understory communities, with *Artemisia* comprising the majority of vegetation cover with a minor
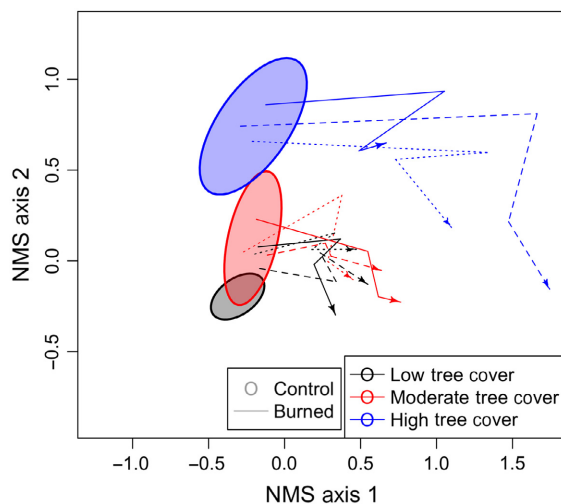

Fig. 5. Mid-elevation understory plant community composition for burned (arrows) and control (ellipses) plots along a gradient of pre-burn tree cover, based on non-metric multidimensional scaling (NMS) ordination. Ellipses show the interquartile range for all control plots in 2001, 2003, and 2004 (N = 9). Arrows show the community trajectory of each burned plot through time, with a distinct line type for each plot (short-dash, long-dash, solids); arrowheads show plots in 2006, tails show plots in 2001 (pre-burn), and inflection points show plots in 2003 and 2004.

component of sprouting shrubs. The high tree cover plots corresponded to the "sparse perennial understory" community type, characterized by lower total cover (Appendix S1: Fig. S4), a negligible shrub component (Appendix S1: Table S4), and a more diverse and variable assembly of uncommon annual forb species. The unburned "sparse perennial understory" community type clustered with the burned communities, rather than with the other unburned community types (Appendix S1: Fig. S2).

Among unburned plots with different levels of pre-fire tree cover, the high tree cover plots were the most distinct, while there was substantial overlap between low and moderate tree covers in NMS ordination space (ellipses in Fig. 5). High tree cover plots were distinguished from low and moderate plots by the absence of common perennial forb species such as *Eriogonum elatum* and *Eriogonum umbellatum*, and by the relative scarcity of *Artemisia, Agoseris glauca,* and *Crepis acuminata*. All unburned plots shared several common species, including *C. viscidiflorus*, *E. elymoides*, *P. secunda, L. argenteus*, and *P. hoodii*. Among-plot dissimilarity (Fig. 3b) was negatively related to tree cover and was substantially greater among unburned plots with high tree cover.

Community trajectories.—After the burn treatment, all plots experienced major changes in species composition (trajectory arrows in Fig. 5), and the changes were most pronounced in high tree cover plots. *Artemisia* cover was largely eliminated after burning in all plots, driving all trajectories toward more positive values along Axis 1.

The post-fire trajectories of low and moderate tree cover plots were overlapping and indistinguishable (Fig. 5), and both transitioned to the "native perennial forbs and grasses" community type immediately after burning, with high cover of *L. argenteus* and several other perennial forbs and grasses as indicator species (Table 1). At two years post-burning, these plots transitioned to the "invaded forbs and grasses" community type, driven by the arrival of *B. tectorum* (2.3% mean cover) and the increased presence of sprouting shrubs (8.2% mean cover; Table 1; Appendix S1: Table S4). A single low tree cover plot transitioned directly to the "invaded forbs and grasses" community type after burning. Both low and moderate tree cover plots had decreased total cover one year after burning

(Appendix S1: Fig. S4). Whereas moderate tree cover plots regained pre-burn cover levels by 2006, total cover remained decreased at low tree cover plots. Low and moderate tree cover plots maintained similar among-plot dissimilarity in all post-burn years (Fig. 3b).

High tree cover sites, in contrast, occupied their own area in ordination space (Fig. 5), indicating a distinct vegetation response with much greater species turnover (i.e., longer trajectory arrows) after burning. Burned high tree cover plots corresponded to the "sparse annual forbs" community type, a ruderal understory assemblage characterized by consistently low total cover (Appendix S1: Fig. S4) and a dominant presence of annual forbs such as *Collinsia parviflora*, *Microsteris gracilis*, and *Mentzelia albicaulis* (Table 1). Among-plot dissimilarity increased for high tree cover plots after burning and was continuing to increase at the time of last sampling (Fig. 3b).

Functional group responses to burning.—Perennial graminoid cover was inversely related to pre-burn tree cover (Tree Cover: $P < 0.001$; Table 3), particularly among the control plots. Perennial graminoid cover was not strongly affected by burning (Year $\times$ Burn: $P = 0.028$; Table 3), and control and burned plots had parallel trajectories over time (Fig. 6a). Perennial graminoid cover showed a strong signal of interannual variability (Year: $P < 0.001$; Table 3), with reduced cover in 2003, increased cover in 2004, and little to no change in 2006 (Fig. 6a).

Statistically significant differences between control and burned plots (Burn: $P < 0.001$; Table 3) were present both before and after treatment and thus cannot be inferred to result from burning.

Annual graminoid cover had a strong positive response to burning (Year $\times$ Burn: $P < 0.001$; Table 3) and showed a pattern of gradual increase in burned plots in all tree cover categories (Fig. 6b). This pattern was especially evident in the low tree cover plots (Burn $\times$ Tree: $P < 0.001$; Table 3), where mean annual graminoid cover doubled at each measurement. Control plots recorded no more than trace amounts of annual graminoid cover in all years. *Bromus tectorum* was the only annual graminoid species.

There was a strong inverse relationship between perennial forb cover and pre-burn tree cover (Tree cover: $P < 0.001$; Table 3; Fig. 6c). Perennial forb cover was positively affected by burning, and the nature of the response varied by pre-burn tree cover (Burn $\times$ Year $\times$ Tree: $P < 0.001$; Table 3). Burned plots had similar (or slightly lower) cover than the controls before burning. After burning, perennial forb cover was higher than in the controls (Fig. 6c). Immediate post-fire response was most pronounced at low tree cover, where perennial forb cover in burned plots was double that of the controls two years after fire.

Annual forb cover had a short-term positive response to burning (Year $\times$ Burn: $P < 0.001$; Table 3). Cover was low in all control plots, increased dramatically for two years after

Table 3. Tree cover effect on understory cover by functional group.

Response	Perennial graminoid cover	Annual graminoid cover	Perennial forb cover	Annual forb cover	Non-sprouting shrub cover	Sprouting shrub cover	Total cover
Predictor				F (P)			
Year	10.05 (**<0.001**)	9.72 (**<0.001**)	22.23 (**<0.001**)	63.48 (**<0.001**)	19.93 (**<0.001**)	0.44 (0.727)	17.89 (**<0.001**)
Burn	14.94 (**<0.001**)	50.63 (**<0.001**)	1.00 (0.322)	310.25 (**<0.001**)	63.63 (**<0.001**)	0.34 (0.566)	3.34 (0.075)
Tree cover	15.44 (**<0.001**)	8.70 (**<0.001**)	274.69 (**<0.001**)	3.74 (0.031)	65.17 (**<0.001**)	26.48 (**<0.001**)	173.40 (**<0.001**)
Year $\times$ Burn	3.31 (0.028)	12.93 (**<0.001**)	13.87 (**<0.001**)	43.44 (**<0.001**)	28.85 (**<0.001**)	0.17 (0.845)	13.46 (**<0.001**)
Year $\times$ Tree	1.05 (0.408)	1.29 (0.281)	10.11 (**<0.001**)	1.63 (0.159)	0.99 (0.445)	0.79 (0.581)	3.02 (0.015)
Burn $\times$ Tree	1.33 (0.275)	8.95 (**<0.001**)	14.98 (**<0.001**)	1.04 (0.360)	13.26 (**<0.001**)	0.16 (0.854)	3.28 (0.047)
Burn $\times$ Year $\times$ Tree	0.95 (0.466)	1.37 (0.248)	11.38 (**<0.001**)	1.85 (0.109)	0.98 (0.431)	0.27 (0.898)	5.30 (**0.001**)
Adjusted R^2	0.5221	0.6740	0.9180	0.8999	0.8461	0.404	0.8814

Notes: Only mid-elevation plots were included in the analysis. F-value and P-value calculated from type 2 ANOVA for a linear model predicting percent cover (log) for each functional group. All predictors are factors. Bolded where $P < 0.004$ (based on a Bonferroni correction for 14 tests at a desired significance value of 0.05). Burn = control (unburned) or burned.
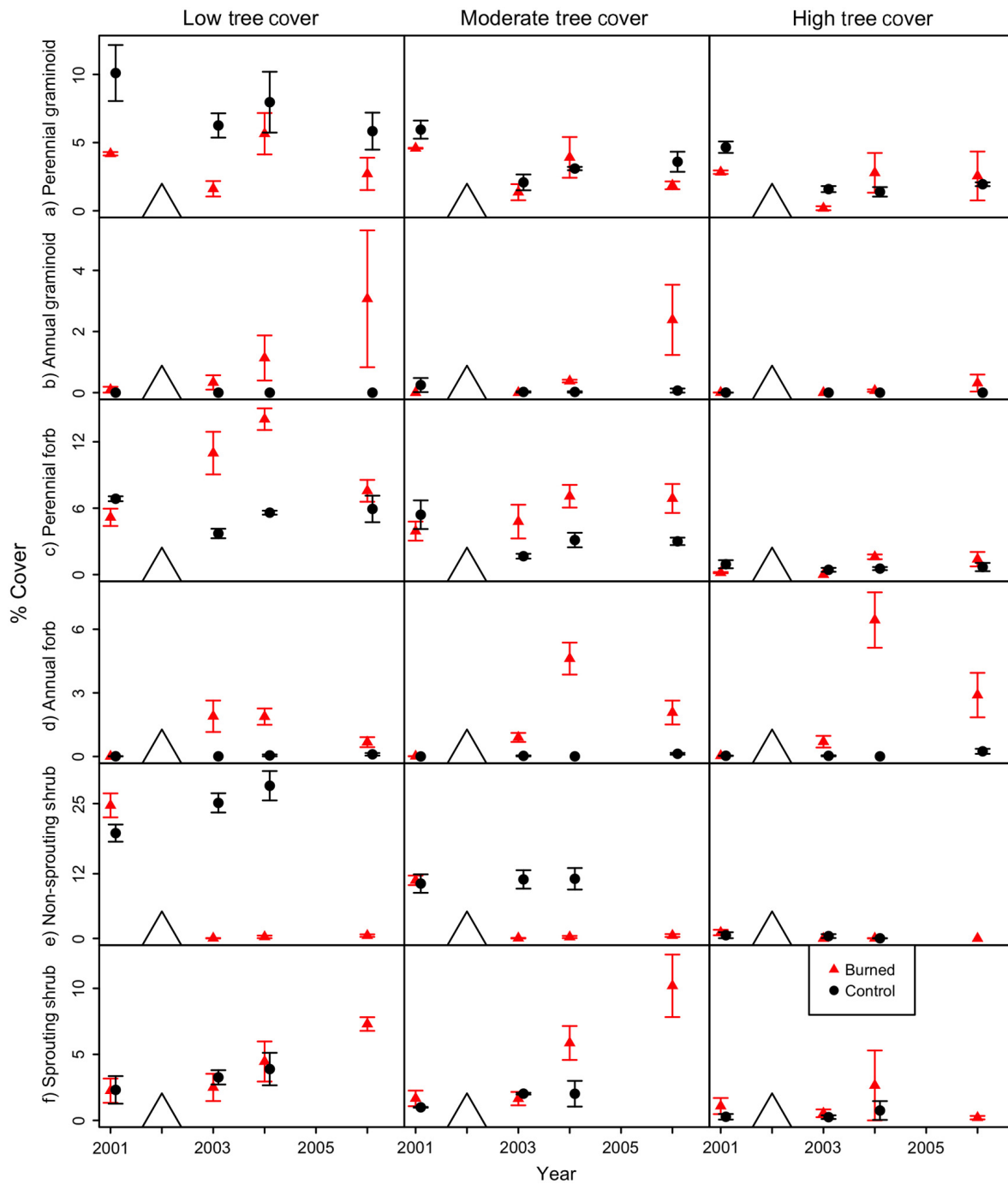
Fig. 6. Functional group cover for burned (red triangles) and control (black circles) plots along a gradient of pre-burn tree cover. Only mid-elevation plots are shown. Data shown as mean ± 1 SE. No shrub control data were collected in 2006. Large triangle shows year of burn treatment.

burning, and declined toward pre-burn levels after four years (Fig. 6d).

Non-sprouting shrub cover was negatively affected by burning (Year × Burn: $P < 0.001$; Table 3) and was reduced to trace amounts after burning at all levels of pre-burn tree cover (Fig. 6e). At low and mid-tree cover plots, non-sprouting shrubs had only begun to recover by 2006 (2% and 5% of pre-burn cover, respectively), and no recovery was detected in high tree cover plots. Among unburned plots, non-sprouting shrub cover (i.e., *Artemisia* species) was inversely related to pre-burn tree cover (Burn × Tree: $P < 0.001$; Table 3) and ranged from nearly zero for high tree cover to approximately 25% at low tree cover (Fig. 6e).

In our analysis, sprouting shrub cover was not significantly affected by burning (Year × Burn: $P = 0.845$; Table 3). However, our graph of cover indicates an increase over time in burned plots (Fig. 6f). Missing data for control plots in 2006 and high variability may have made the effect of burning difficult to detect statistically. Sprouting shrub cover varied by pre-burn tree cover (Tree cover: $P < 0.001$; Table 3), and high tree cover plots had substantially lower cover than low or moderate tree cover plots.

Discussion

The results of our study show that abiotic and biotic gradients interact to influence short-term plant community responses to fire and, under some conditions, initiate alternate successional trajectories. In particular, pre-fire vegetation structure had a pronounced effect on post-fire plant responses, and sites with high tree cover had a profoundly different community trajectory after disturbance. Community composition was still changing rapidly four years after fire, and it remains unclear whether divergent trajectories will result in the formation of alternate states, or whether community composition will eventually converge among site groupings. In dryland landscapes where successional processes are typically slow (Pickett 1980), long-term studies are needed to ascertain the existence of alternate stable states.

The widespread use of prescribed fire as a management tool requires a thorough understanding of potential successional trajectories, particularly where invasive species respond to

disturbance and can initiate nonlinear and divergent pathways of plant community change (Brooks et al. 2004, Gaertner et al. 2014). Rather than examining vegetation responses to fire in the context of specific functional groups or species of interest (Young and Evans 1978, Lesica et al. 2007, Pyke et al. 2014, Roundy et al. 2014a), our multivariate approach considered all species within the plant community simultaneously. Post-fire compositional trajectories were similar within specific ranges along biotic and abiotic gradients (Fig. 7), suggesting that at the scale of this study, plant community responses to fire are more predictable than stochastic.

Post-fire community trajectories differ along elevation gradient

Unburned sites in Underdown Canyon with similar ecological conditions (i.e., tree cover) had understory communities stratified along an elevational gradient, clustering into common ecological site types. At the low elevation, the pinyon and juniper understory community was typical of a Wyoming big sagebrush site, characterized by high cover of the non-sprouting shrub *Artemisia tridentata* spp. *wyomingensis* and common perennial native grass *Poa secunda*. The mid-elevation understory community resembled a mountain big sagebrush assemblage, dominated by the non-sprouting shrub *Artemisia tridentata* spp. *vaseyana* and common native perennial species. The high-elevation community had a diverse mountain brush understory, with high total cover dominated by *Artemisia tridentata* spp. *vaseyana* and a varied assemblage of sprouting shrubs, perennial grasses, and perennial forbs.

After fire, sites at all elevations experienced substantial change in species composition and increased among-plot dissimilarity. Spatial heterogeneity of pre-fire vegetation and fire behavior creates mosaics of surviving individuals, propagules, and available resources (Pausas et al. 2004, Johnstone and Chapin 2006, Hollingsworth et al. 2013), and stochastic processes largely determine seed arrival (Egler 1954). All elevation groups lost sagebrush, gained cover of perennial forbs and sprouting shrubs, and experienced a pulse of annual forbs. At the highest elevation, burning led to the formation of a mountain shrub community, with rapid recovery of sprouting shrubs and a diverse collection of native perennial grasses
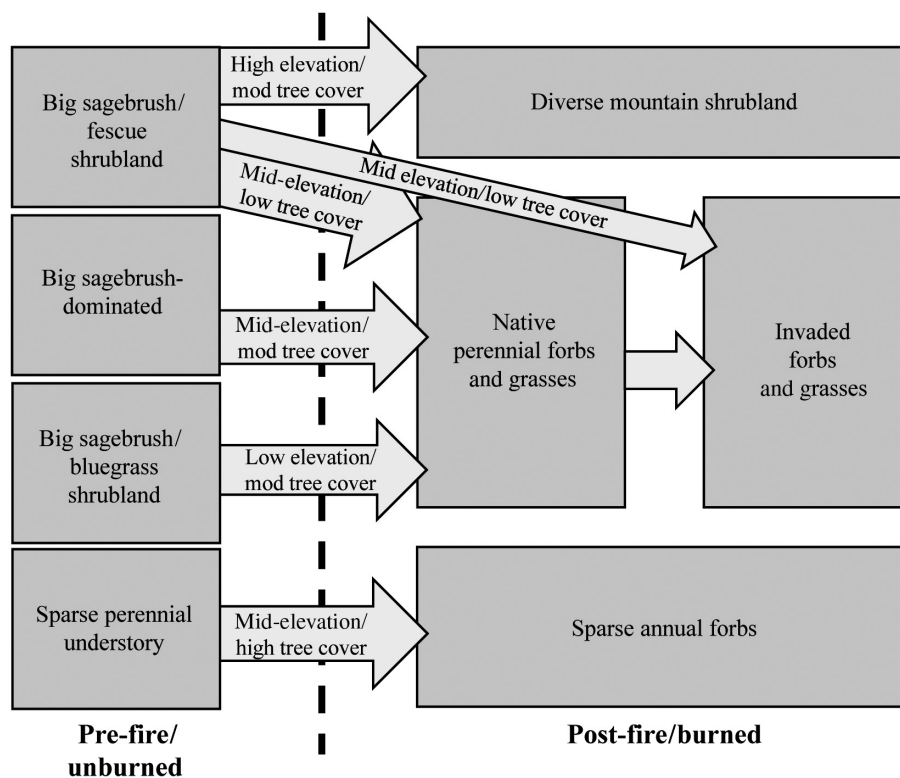
Fig. 7. Diagram of community trajectories resulting from burning. Distinct plant community types, identified from cluster and indicator species analysis, are shown in dark gray boxes. Site types transitioning among community types are shown in light gray arrows.

and forbs. Burning resulted in convergent pathways of understory composition at low and mid-elevations, where these sites transitioned first into an early-seral community of perennial forbs and grasses, then to an invaded community type with clear increases in *B. tectorum* and sprouting shrub cover. Sagebrush cover was eliminated in all plots by burning and began to recover four years after fire only in the high-elevation site. Post-fire sagebrush establishment rates are often higher on moister ecological sites with greater winter precipitation, where favorable weather for recruitment is more likely to coincide with the ephemeral period during which banked seeds are still viable (Baker 2006, Ziegenhagen and Miller 2009, Nelson et al. 2014).

As predicted, low-elevation sites experienced the greatest species turnover after burning, which was driven by major changes in several functional groups, including the increase in *B. tectorum*. The presence of *B. tectorum* is consistent with previous studies from the Inter-mountain West, which have shown that resistance to invasion is lower on warm, dry sites where establishment, growth, and reproduction are favored (Chambers et al. 2007, Condon et al. 2011, Leffler et al. 2013). Long-term trajectories are often uncertain for sites with post-fire *B. tectorum* invasion (Chambers et al. 2014b, Morris and Leger 2016). However, multiple studies show that *B. tectorum* cover is negatively related to native perennial grass cover (Anderson and Inouye 2001, Reisner et al. 2013, 2015, Chambers et al. 2014b). Although *B. tectorum* will likely always be a component of these communities, its relative abundance over time will likely depend on the capacity to maintain or increase native perennial herbaceous species (Reisner et al. 2013, Chambers et al. 2014b).

Disturbances provide opportunities for community reorganization by removing species and altering the availability of light, water, and

nutrients (Tilman 2004), but the underlying abiotic environmental context constrains the species pool that is available for colonization (Pickett et al. 2009). We saw distinct post-fire trajectories at each elevation (i.e., no overlap of trajectory arrows in Fig. 2), illustrating the importance of the abiotic environment on successional trajectories in pinyon and juniper woodlands. However, the existence of an invaded post-fire community type at the lower elevations suggests that, where resistance to invasion is limited, these ecosystems are susceptible to crossing ecological thresholds to alternative community states. Because the fine fuels produced by *B. tectorum* promote fire spread (Balch et al. 2013, Gaertner et al. 2014), invasion may result in grass–fire cycles that promote its continued dominance (D'Antonio and Vitousek 1992, Brooks et al. 2004).

Ecological memory of pre-burn tree cover affects post-fire community trajectory

At middle elevations, unburned sites had varying levels of pinyon and juniper cover, and as such contained a mosaic of understory plant communities. Mid-elevation sites with low tree cover belonged to the same community type as high-elevation sites with moderate tree cover (diverse mountain brush community). This is likely due partly to overlap in climatic suitability for dominant species but also demonstrates how overstory vegetation structure interacts with topoclimatic context to determine the resources available to understory vegetation (Tilman 1994). The understories of sites with moderate tree cover were compositionally similar to those with low tree cover, but had lower total cover and a greater dominance of sagebrush. Sites with high tree cover had understory communities with little resemblance to other plots of the same elevation group, and were characterized by much lower vegetation cover, a negligible shrub component, and a more prominent presence of annual forbs (Miller et al. 2000).

After burning, the pre-fire effects of tree cover on the understory species persisted, creating biotic legacies that shaped post-fire trajectories of community assembly (Padisak 1992). Sites with low and moderate tree cover were compositionally similar before burning and converged into the same community types after burning (Fig. 7). These sites transitioned into a native early-seral community of perennial forbs and grasses immediately after burning, and within two years, *B. tectorum* and sprouting shrub cover began to increase. Low tree cover sites experienced a stronger short-term pulse of perennial forbs, a weaker pulse of annual forbs, and a greater increase in *B. tectorum* cover than those with moderate tree cover. Overall, burning largely eliminated differences in understory vegetation for sites with low-to-moderate tree cover, suggesting that differences in the biotic legacies from the pre-fire community were insufficient to result in different successional trajectories.

Sites with high pre-fire tree cover, in contrast, had divergent trajectories after fire, transitioning into a community type dominated by annual forbs with persistently sparse vegetation cover. The delayed recovery of perennial species suggests that the pre-fire reduction of common understory species reduced the biotic legacy of the native understory community. The decrease in understory species, combined with the likelihood of increased perennial mortality near heavy fuels, indicates that propagule dispersal from adjacent areas is important for establishment in high tree cover sites (Bengtsson et al. 2003). Relatively low perennial cover may reduce future resistance to *B. tectorum* invasion in the high tree cover sites as the lack of native perennial species and a post-fire pulse of resources can create an empty niche that facilitates establishment and spread of invasive species (Shea and Chesson 2002, Schaefer 2011). However, four years after the burn treatment, *B. tectorum* was nearly absent in sites with higher pre-burn tree cover, perhaps due to limited dispersal to these areas at the time of sampling.

The combination of sharply diverging post-fire trajectories and persistently low perennial vegetation cover suggests that a recovery threshold may have been crossed for sites with high pre-fire tree cover (Beisner et al. 2003). Nonetheless, the possible threshold that we observed between pre-fire tree covers of 38% and 74% should be interpreted with caution and within the specific context of our study area. In our study, the effects of pre-fire tree cover were only tested for mid-elevation sites, and it is logical to assume an interaction between tree cover and elevation effects. We would expect that the recovery threshold would occur at higher levels of tree

cover as elevation increases, resources become more abundant, and the species pool contains more species adapted to fire (Johnson and Miller 2006). Additionally, it is possible that the relationship between tree cover and post-fire recovery does not exhibit a distinct threshold (Roundy et al. 2014a) and that a more continuous effect was missed by the discrete tree cover categories in our study design. Although the results of our study show that high tree cover sites can remain in an unproductive state with low vegetation cover for at least four years after burning, vegetation recovery in dryland ecosystems is a slow process (Koniak 1985, Baker 2006, Morris and Leger 2016). Long-term observations of plant community trajectories, gathered from continued monitoring efforts within controlled experiments, are necessary for fully understanding the effects of prescribed fire in dryland landscapes.

Management implications

The prescribed burning treatment resulted in a mixture of desired and undesired outcomes. Post-fire recovery varied by functional group, suggesting that the outcomes of prescribed fire interventions are highly dependent on the abiotic environment and pre-fire biotic legacies, specifically the residual vegetation and seed sources. In our study area, burning generally resulted in increased perennial forb cover, but did not have a strong effect on perennial grass cover. Burning also reduced shrub cover, especially non-sprouting sagebrush species. As post-fire reductions in sagebrush cover can persist for years to decades (Nelson et al. 2014), mechanical treatments may be a preferred management alternative where tree reduction objectives coincide with preserving sagebrush habitat (Arkle et al. 2014).

Importantly, the effects of burning were not homogenous across the landscape. Consistent with previous research (Chambers et al. 2007, 2014b, Davies et al. 2012), warm and dry low-elevation sites were less resistant to *B. tectorum* invasion after fire. To reduce the risk of invasion, the use of prescribed fire should be avoided in the drier portions of the landscape, and only more resilient higher-elevation sites with sufficient perennial herbaceous species to promote recovery should be considered for prescribed fire treatments (Chambers et al. 2014a, Miller et al. 2014). The increase in *B. tectorum* cover following prescribed fire or mechanical treatment is negatively related to native perennial grass cover, indicating that pre-treatment cover of perennial grass is a strong predictor of site resistance to invasion (Chambers et al. 2014b).

Post-fire plant community responses were also greatly dependent on pre-fire tree cover, and sites with high tree cover followed a post-fire trajectory that was independent of the other sites. Although high tree cover sites at mid-elevation did not show increased rates of *B. tectorum* invasion within four years of fire, the delayed recovery of perennial cover suggests prolonged exposure to erosional processes and an increased risk of future invasion, especially in a warming environment. High tree cover sites are generally low priority for meeting tree reduction objectives (Miller et al. 2013, 2014). If the decision is made to treat these sites, mechanical treatments are preferred over burning and biomass removal and seeding may be required to meet management objectives.

These results indicate that careful evaluation of site characteristics, including temperature and moisture regimes and pre-treatment vegetation composition, and potential treatment severity, as indicated by pinyon and juniper cover, can be used to predict treatment outcomes (Miller et al. 2014). Post-treatment monitoring can be used to evaluate successional trajectories and adapt management over time to maintain or increase landscape resilience.

LITERATURE CITED

Allen, E. A., and R. S. Nowak. 2008. Effect of pinyon-juniper tree cover on the soil seed bank. Rangeland Ecology & Management 61:63–73.

Anderson, J. E., and R. S. Inouye. 2001. Landscape-scale changes in plant species abundance and biodiversity of a sagebrush steppe over 45 years. Ecological Monographs 71:531–556.

Arkle, R. S., D. S. Pilliod, S. E. Hanser, M. L. Brooks, J. C. Chambers, J. B. Grace, K. C. Knutson, D. A. Pyke, J. L. Welty, and T. A. Wirth. 2014. Quantifying restoration effectiveness using multi-scale habitat models: implications for sage-grouse in the Great Basin. Ecosphere 5:1–32.

Baker, W. L. 2006. Fire and restoration of sagebrush ecosystems. Wildlife Society Bulletin 34:177–185.

Balch, J. K., B. A. Bradley, C. M. D'Antonio, and J. Gómez-Dans. 2013. Introduced annual grass increases regional fire activity across the arid western USA (1980-2009). Global Change Biology 19: 173–183.

Bates, J. D., R. O'Connor, and K. W. Davies. 2014a. Vegetation recovery and fuel reduction after seasonal burning of western juniper. Fire Ecology 10:27–48.

Bates, J. D., R. N. Sharp, and K. W. Davies. 2014b. Sagebrush steppe recovery after fire varies by development phase of *Juniperus occidentalis* woodland. International Journal of Wildland Fire 23: 117–130.

Bauer, J. M., and P. J. Weisberg. 2009. Fire history of central Nevada pinyon-juniper woodland. Canadian Journal of Forest Research 39:1589–1599.

Beisner, B. E., D. T. Haydon, and K. Cuddington. 2003. Alternative stable states in ecology. Frontiers in Ecology and the Environment 1:376–382.

Bengtsson, J., P. Angelstam, T. Elmqvist, U. Emanuelsson, M. Ihse, F. Moberg, and M. Nyström. 2003. Reserves, resilience and dynamic landscapes. Ambio 32:389–396.

Benscoter, B. W., and D. H. Vitt. 2008. Spatial patterns and temporal trajectories of the bog ground layer along a post-fire chronosequence. Ecosystems 11:1054–1064.

Board, D. I., J. C. Chambers, and J. G. Wright. 2011. Effects of spring prescribed fire in expanding pinyon-juniper woodlands on seedling establishment of sagebrush species. Natural Resources and Environmental Issues: 16:Article 20.

Bray, J. R., and J. T. Curtis. 1957. An ordination of the upland forest communities of southern Wisconsin. Ecological Monographs 27:325–349.

Brooks, M. L., C. M. D'Antonio, D. M. Richardson, J. B. Grace, J. E. Keeley, J. M. Ditomaso, R. J. Hobbs, M. Pellant, and D. Pyke. 2004. Effects of invasive alien plants on fire regimes. BioScience 54:677–688.

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

Chambers, J. C., M. J. Germino, J. Belnap, C. S. Brown, E. W. Schupp, and S. B. St. Clair. 2016. Plant community resistance to invasion by *Bromus* species: the roles of community attributes, Bromus interactions with plant communities, and Bromus traits. Pages 275–304 *in* M. J. Germino, J. C. Chambers, and C. S. Brown, editors. Exotic brome-grasses in arid and semiarid ecosystems of the western US: causes, consequences, and management implications. Springer, New York, New York, USA.

Chambers, J. C., R. F. Miller, D. I. Board, D. A. Pyke, B. A. Roundy, J. B. Grace, E. W. Schupp, and R. J. Tausch. 2014b. Resilience and resistance of sagebrush ecosystems: implications for state and transition models and management treatments. Rangeland Ecology and Management 67:440–454.

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

Condon, L., P. J. Weisberg, and J. C. Chambers. 2011. Abiotic and biotic influences on *Bromus tectorum* invasion and *Artemisia tridentata* recovery after fire. International Journal of Wildland Fire 20:597–604.

Coop, J. D., R. T. Massatti, and A. W. Schoettle. 2010. Subalpine vegetation pattern three decades after stand-replacing fire: effects of landscape context and topography on plant community composition, tree regeneration, and diversity. Journal of Vegetation Science 21:472–487.

Cottam, W. P., and G. Stewart. 1940. Plant succession as a result of grazing and of meadow desiccation by erosion since settlement in 1862. Journal of Forestry 38:613–626.

D'Antonio, C. M., and P. M. Vitousek. 1992. Biological invasions by exotic grasses, the grass/fire cycle, and global change. Annual Review of Ecology and Systematics 23:63–87.

Daubenmire, R. 1959. A canopy-coverage method of vegetational analysis. Northwest Science 33:43–64.

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

Dufrene, M., and P. Legendre. 1997. Species assemblages and indicator species: the need for a flexible asymmetrical approach. Ecological Monographs 67:345–366.

Dynesius, M., K. Hylander, and C. Nilsson. 2009. High resilience of bryophyte assemblages in streamside compared to upland forests. Ecology 90:1042–1054.

Egler, F. E. 1954. Vegetation science concepts I. Initial floristics composition, a factor in old-field vegetation development with 2 figs. Plant Ecology 4: 412–417.

Ellingsen, K. E. 2001. Biodiversity of a continental shelf soft-sediment macrobenthos community. Marine Ecology Progress Series 218:1–15.

Everett, R. L., and K. Ward. 1984. Early plant succession on pinyon-juniper controlled burns. Northwest Science 58:57–68.

Franklin, J. F. 2000. Messages from a mountain. Science 288:1183–1184.

Franklin, J. F., D. Lindenmayer, J. A. MacMahon, A. McKee, J. Magnuson, D. A. Perry, R. Waide, and D. Foster. 2000. Threads of continuity. Conservation in Practice 1:8–17.

Gaertner, M., R. Biggs, M. Te Beest, C. Hui, J. Molofsky, and D. M. Richardson. 2014. Invasive plants as drivers of regime shifts: identifying high-priority invaders that alter feedback relationships. Diversity and Distributions 20:733–744.

Germino, M. J., J. Belnap, J. M. Stark, E. B. Allen, and B. M. Rau. 2016. Ecosystem impacts of exotic annual invaders in the Genus Bromus. Pages 61–95 in M. J. Germino, J. C. Chambers, and C. S. Brown, editors. Exotic brome-grasses in arid and semiarid ecosystems of the western US: causes, consequences, and management implications. Springer, New York, New York, USA.

Gunderson, L. H. 2000. Ecological resilience–In theory and application. Annual Review of Ecology and Systematics 31:425–439.

Hollingsworth, T. N., J. F. Johnstone, E. L. Bernhardt, and F. S. Chapin. 2013. Fire severity filters regeneration traits to shape community assembly in Alaska's boreal forest. PLoS ONE 8:e56033.

Johnson, D. D., and R. F. Miller. 2006. Structure and development of expanding western juniper woodlands as influenced by two topographic variables. Forest Ecology and Management 229:7–15.

Johnstone, J. F., and F. S. Chapin. 2006. Effects of soil burn severity on post-fire tree recruitment in boreal forest. Ecosystems 9:14–31.

Johnstone, J. F., et al. 2016. Changing disturbance regimes, ecological memory, and forest resilience. Frontiers in Ecology and the Environment 14: 369–378.

Kemp, K. B., P. E. Higuera, and P. Morgan. 2016. Fire legacies impact conifer regeneration across environmental gradients in the U.S. northern Rockies. Landscape Ecology 31:619–636.

Ko, D. W., A. D. Sparrow, and P. J. Weisberg. 2011. Land-use legacy of historical tree harvesting for charcoal production in a semi-arid woodland. Forest Ecology and Management 261:1283–1292.

Koniak, S. 1985. Succession in pinyon-juniper woodlands following wildfire in the Great Basin. Great Basin Naturalist 45:556–566.

Lanner, R. M., and P. Frazier. 2011. The historical stability of Nevada's pinyon-juniper forest. Phytologia 93:360–387.

Leffler, J. A., J. J. James, and T. A. Monaco. 2013. Temperature and functional traits influence differences in nitrogen uptake capacity between native and invasive grasses. Oecologia 171:51–60.

Lesica, P., S. V. Cooper, and G. Kudray. 2007. Recovery of big sagebrush following fire in southwest Montana. Rangeland Ecology & Management 60: 261–269.

Matthews, J. W., and A. G. Endress. 2010. Rate of succession in restored wetlands and the role of site context. Applied Vegetation Science 13:346–355.

McCune, B., and J. B. Grace. 2002. Analysis of ecological communities. MjM Software Design, Gleneden Beach, Oregon, USA.

Miller, R. F., J. D. Bates, T. J. Svejcar, F. B. Pierson, and L. E. Eddleman. 2005. Biology, ecology, and management of western juniper. Oregon State University, Agricultural Experiment Station, Technical Bulletin 152.

Miller, R. F., J. C. Chambers, and M. Pellant. 2014. A field guide for selecting the most appropriate treatment in sagebrush and piñon-juniper ecosystems in the Great Basin: evaluating resilience to disturbance and resistance to invasive annual grasses, and predicting vegetation response. United States Department of Agriculture, Forest Service, General Technical Report RMRS-GTR-322, Fort Collins, Colorado, USA.

Miller, R. F., J. C. Chambers, D. A. Pyke, F. B. Pierson, and J. C. Williams. 2013. A review of fire effects on vegetation and soils in the Great Basin region: response and ecological site characteristics. United States Department of Agriculture, Forest Service, General Technical Report RMRS-GTR-308, Fort Collins, Colorado, USA.

Miller, R. F., and J. A. Rose. 1999. Fire history and western juniper encroachment in sagebrush steppe. Journal of Range Management 52:550–559.

Miller, R. F., T. J. Svejcar, and J. A. Rose. 2000. Impacts of western juniper on plant community composition and structure. Journal of Range Management 53:574–585.

Miller, R. F., and P. E. Wigand. 1994. Holocene changes in semiarid pinyon-juniper woodlands. BioScience 44:465–474.

Morris, L. R., and E. A. Leger. 2016. Secondary succession in the sagebrush semi-desert 66 years after fire in the Great Basin, USA. Natural Areas Journal 36:187–193.

Myers, J. A., and K. E. Harms. 2009. Seed arrival, ecological filters, and plant species richness: a meta-analysis. Ecology Letters 12:1250–1260.

Nelson, Z. J., P. J. Weisberg, and S. G. Kitchen. 2014. Influence of climate and environment on post-fire recovery of mountain big sagebrush. International Journal of Wildland Fire 23:131–142.

Oksanen, J., F. G. Blanchet, R. Kindt, P. Legendre, P. R. Minchin, R. B. O'Hara, G. L. Simpson, P. Solymos, M. H. H. Stevens, and H. Wagner. 2015. Community Ecology Package. R package version 2.3-1.

Padisak, J. 1992. Seasonal succession of phytoplankton in a large shallow lake (Balaton, Hungary) – A dynamic approach to ecological memory, its possible role and mechanisms. Journal of Ecology 80:217–230.

Pausas, J. G., R. A. Bradstock, D. A. Keith, J. E. Keeley, and GCTE Fire Network. 2004. Plant functional traits in relation to fire in crown-fire ecosystems. Ecology 85:1085–1100.

Pickett, S. T. A. 1980. Non-equilibrium coexistence of plants. Bulletin of the Torrey Botanical Club 107:238–248.

Pickett, S. T. A., M. L. Cadenasso, and S. J. Meiners. 2009. Ever since Clements: from succession to vegetation dynamics and understanding to intervention. Applied Vegetation Science 12:9–21.

PRISM Climate Group. 2016. PRISM Gridded Climate Data. http://prism.oregonstate.edu

Pyke, D. A., J. C. Chambers, J. L. Beck, M. L. Brooks, and B. A. Mealor. 2016. Land uses, fire, and invasion: exotic annual Bromus and human dimensions. Pages 307–337 in M. J. Germino, J. C. Chambers, and C. S. Brown, editors. Exotic brome-grasses in arid and semiarid ecosystems of the western US: causes, consequences, and management implications. Springer, New York, New York, USA.

Pyke, D. A., S. E. Shaff, A. I. Lindgren, E. W. Schupp, P. S. Doescher, J. C. Chambers, J. S. Burnham, and M. M. Huso. 2014. Region-wide ecological responses of arid Wyoming big sagebrush communities to fuel treatments. Rangeland Ecology & Management 67:455–467.

R Core Team. 2015. R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria.

Rau, B. M., R. R. Blank, J. C. Chambers, and D. W. Johnson. 2007. Prescribed fire in a Great Basin sagebrush ecosystem: dynamics of soil extractable nitrogen and phosphorus. Journal of Arid Environments 71:362–375.

Rau, B. M., J. C. Chambers, R. R. Blank, and W. W. Miller. 2005. Hydrologic response of a central Nevada pinyon-juniper woodland to prescribed fire. Rangeland Ecology & Management 58:614–622.

Rau, B. M., J. C. Chambers, D. A. Pyke, B. A. Roundy, E. W. Schupp, P. Doescher, and T. G. Caldwell. 2014. Soil resources influence vegetation and response to fire and fire-surrogate treatments in sagebrush-steppe ecosystems. Rangeland Ecology & Management 67:506–521.

Reiner, A. L. 2004. Fuel load and understory community changes associated with varying elevation and pinyon-juniper dominance. Thesis. University of Nevada-Reno, Reno, Nevada, USA.

Reisner, M. D., P. S. Doescher, and D. A. Pyke. 2015. Stress-gradient hypothesis explains susceptibility to Bromus tectorum invasion and community stability in North America's semi-arid Artemisia tridentata wyomingensis ecosystems. Journal of Vegetation Science 26:1212–1224.

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

Romme, W. H., et al. 2009. Historical and modern disturbance regimes, stand structures, and landscape dynamics in piñon–juniper vegetation of the western United States. Rangeland Ecology & Management 62:203–222.

Roundy, B. A., R. F. Miller, R. J. Tausch, K. Young, A. Hulet, B. Rau, B. Jessop, J. C. Chambers, and D. Eggett. 2014a. Understory cover responses to piñon–juniper treatments across tree dominance gradients in the Great Basin. Rangeland Ecology & Management 67:482–494.

Roundy, B. A., K. Young, N. Cline, A. Hulet, R. F. Miller, R. J. Tausch, J. C. Chambers, and B. Rau. 2014b. Piñon-juniper reduction effects on soil temperature and water availability of the resource growth pool. Rangeland Ecology & Management 67:495–505.

Schaefer, V. H. 2011. Remembering our roots: a possible connection between loss of ecological memory, alien invasions and ecological restoration. Urban Ecosystems 14:35–44.

Seastedt, T. R., R. J. Hobbs, and K. N. Suding. 2008. Management of novel ecosystems: Are novel approaches required? Frontiers in Ecology and the Environment 6:547–553.

Seidl, R., W. Rammer, and T. A. Spies. 2014. Disturbance legacies increase the resilience of forest ecosystem structure, composition, and functioning. Ecological Applications 24:2063–2077.

Shea, K., and P. Chesson. 2002. Community ecology theory as a framework for biological invasions. Trends in Ecology and Evolution 17:170–176.

Shryock, D. F., T. C. Esque, and F. C. Chen. 2015. Topography and climate are more important

drivers of long-term, post-fire vegetation assembly than time-since-fire in the Sonoran Desert, US. Journal of Vegetation Science 26:1134–1147.

Smit, I. P. J., G. P. Asner, N. Govender, T. Kennedy-Bowdoin, D. E. Knapp, and J. Jacobson. 2010. Effects of fire on woody vegetation structure in African savanna. Ecological Applications 20:1865–1875.

Taylor, K., T. Brummer, L. J. Rew, M. Lavin, and B. D. Maxwell. 2014. *Bromus tectorum* response to fire varies with climate conditions. Ecosystems 17:960–973.

Tilman, D. 1994. Competition and biodiversity in spatially structured habitats. Ecology 75:2–16.

Tilman, D. 2004. Niche tradeoffs, neutrality, and community structure: a stochastic theory of resource competition, invasion, and community assembly. Proceedings of the National Academy of Sciences of the United States of America 101:10854–10861.

Turner, M. G., W. L. Baker, C. J. Peterson, and R. K. Peet. 1998. Factors influencing succession: lessons from large, infrequent natural disturbances. Ecosystems 1:511–523.

Urza, A. K., and J. S. Sibold. 2017. Climate and seed availability initiate alternate post-fire trajectories in a lower subalpine forest. Journal of Vegetation Science 28:43–56.

Vandvik, V., E. Heegaard, I. E. Måren, and P. A. Aarrestad. 2005. Managing heterogeneity: the importance of grazing and environmental variation on post-fire succession in heathlands. Journal of Applied Ecology 42:139–149.

Wisdom, M. J., and J. C. Chambers. 2009. A landscape approach for ecologically based management of Great Basin shrublands. Restoration Ecology 17: 740–749.

Young, J. A., and J. D. Budy. 1979. Historical use of Nevada's pinyon-juniper woodlands. Journal of Forest History 23:112–121.

Young, J. A., and R. A. Evans. 1978. Population dynamics after wildfires in sagebrush grasslands. Journal of Range Management 31:283–289.

Young, J. A., and R. A. Evans. 1989. Dispersal and germination of big sagebrush (*Artemisia tridentata*) seeds. Weed Science 37:201–206.

Ziegenhagen, L. L., and R. F. Miller. 2009. Postfire recovery of two shrubs in the interiors of large burns in the Intermountain West, USA. Western North American Naturalist 69:195–205.

SUPPORTING INFORMATION

Additional Supporting Information may be found online at: http://onlinelibrary.wiley.com/doi/10.1002/ecs2.1851/full