



Removal of perennial herbaceous species affects response of Cold Desert shrublands to fire

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Keywords

Annual invasive grasses; *Artemisia tridentata*; *Bromus tectorum*; Burning; Perennial native grasses; Plant functional groups; Resilience to disturbance; Shrubs; Species removals

Abbreviations

AIg = annual invasive grass; PNF = perennial native forb; PNG = perennial native grass.

Nomenclature

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Abstract

Questions: Two of the primary global change factors that threaten shrublands worldwide are loss of native perennial herbaceous species due to inappropriate livestock grazing and loss of native shrubs due to altered fire regimes. We asked: (1) how do the separate and interacting effects of removal of perennial herbaceous species and burning influence relative abundance of plant functional groups over longer time frames; and (2) how do interactions between perennial herbaceous species removal and burning differ along environmental gradients? We discuss implications of our findings for ecosystem resilience to these disturbances.

Location: Shoshone Mountain Range, Nevada and East Tintic Range, Utah, USA.

Methods: We used a factorial experiment to test effects of perennial herbaceous species removal (0%, 50% and 100%) and burning (burned and not burned) on plant functional group cover along elevation gradients within watersheds characterized by *Artemisia tridentata* Nutt. vegetation types. The experiment was conducted in two locations (Nevada and Utah) with sites located at low (1960 and 1710 m), mid (2190 and 2085 m) and high (2380 and 2274 m) elevations and was repeated in 2 yr. Percentage cover of native and exotic species and canopy area, density and size of the shrub *A. tridentata* were evaluated 12 and 13 yr after study implementation.

Results: Over a decade later, removal treatments resulted in highly significant decreases (40–62%) in perennial native grass and forb cover across site elevations. Burning decreased overall shrub and *A. tridentata* cover, but effects on perennial native grass cover differed among elevations. Removal had strong positive effects on *A. tridentata* seedling recruitment and resulted in progressive increases in density and canopy area following burning. *A. tridentata* canopy areas on burned plots with 0%, 50% and 100% removal were 0.19, 0.40 and 0.84 m², respectively. Annual invasive grass density also increased with degree of removal, and both density and cover decreased with elevation.

Conclusions: Our results show that loss of perennial herbaceous species, which can result from inappropriate livestock grazing, and loss of shrubs, which often results from fire, interact to affect key functional groups. The implications are that ecosystem resilience to disturbance in Cold Desert shrublands decreases when competition from perennial native grasses and forbs for available resources no longer prevents dominance by *A. tridentata* and other shrubs and/or annual invasive grasses. Managing livestock grazing to maintain or increase perennial herbaceous species, especially deep-rooted grasses, which contribute to resilience along elevation gradients, can help prevent threshold crossings to undesirable states and retain critical ecosystem services following disturbances such as wildfire.

Introduction

The separate and interacting effects of disturbances on plant species functional groups influence successional trajectories and consequently ecosystem response to subsequent disturbances. Human-caused disturbances that result in loss and degradation of key functional groups have negatively impacted functioning of a large variety of ecosystems worldwide (Ellison et al. 2005; Angelini et al. 2011). Such losses can reduce resilience, the capacity of ecosystems to reorganize and regain fundamental structure, processes and functioning (i.e. to recover) when altered by stressors or disturbances (Holling 1973; Allen et al. 2005). Few studies have evaluated how key functional groups interact with disturbance to affect other functional groups, invasion of exotic species and overall community composition and structure. Information on these effects is essential for management aimed at maintaining or restoring ecosystem resilience to disturbance.

In Cold Desert shrublands of the western USA altered disturbance regimes are resulting in changes in plant functional group composition that threaten plant communities and their associated animal species (Chambers et al. 2014a; Germino et al. 2016). Two of the primary disturbances causing changes in plant functional groups are inappropriate livestock grazing (heavy and repeated growing season or year-long) and wildfire. Inappropriate livestock grazing results in removal of perennial native grasses, such as *Pseudoroegneria spicata* (Pursh) Á. Löve and *Achnatherum thurberianum* (Piper) Barkworth, as well as other herbaceous species (Mueggler 1972; Reisner et al. 2013). Intensity of livestock use is directly and negatively associated with abundance and cover of native perennial grasses (Adler et al. 2005; Reisner et al. 2013). Livestock grazing generally has no direct effects on cover of dominant native shrubs, such as *Artemisia tridentata* and *Chrysothamnus* Nutt. spp., which are unpalatable to cattle, the primary grazers (Adler et al. 2005). In contrast, wildfire is the primary cause of removal of fire-intolerant shrubs such as *A. tridentata*. However, fire-tolerant native perennial grasses and forbs as well as root-sprouting shrubs typically regenerate following fire (Miller et al. 2013).

Perennial herbaceous species, especially deep-rooted grasses, and shrubs play key roles in ecosystem resilience or recovery following disturbances, such as inappropriate livestock grazing and wildfire, which result in elevated resource availability (Chambers et al. 2007, 2014a; Roundy et al. 2014). Perennial native grasses are highly competitive for available resources and are a strong indicator of resilience to disturbances that remove fire-intolerant shrubs (Davies 2008; Condon et al. 2011; Davies et al. 2012; Chambers et al. 2014b; Roundy et al. 2014). These grasses typically survive wildfires, regrow once conditions

are suitable, and stabilize hydrologic and biogeochemical processes if they are sufficiently abundant (Leffler & Ryel 2012; Miller et al. 2013). They also are highly effective competitors with widespread annual invasive grasses, such as *Bromus tectorum* L. and *Taeniatherum caput-medusae* (L.) Nevski (Chambers et al. 2007; Davies 2008; Blank & Morgan 2012). Perennial native shrubs also compete for resources and decreases in deep-rooted bunchgrasses, such as *P. spicata* and *A. thurberianum*, due to livestock grazing can result in increased density and cover of the dominant shrubs, *A. tridentata* subsp. (Cooper 1953; Harniss & Murray 1973; Burkhardt & Sanders 1992; Hanna & Fulgham 2015). Following wildfire and removal of *A. tridentata*, biomass and reproduction of *B. tectorum* often increases, especially if perennial native grasses have been depleted through livestock grazing (Chambers et al. 2007; Hoover & Germino 2012).

Resilience to disturbances such as inappropriate livestock grazing and wildfire and resistance to annual invasive grasses typically increase along elevation gradients in Cold Desert shrublands (Chambers et al. 2007, 2014a,b; Condon et al. 2011; Davies et al. 2012). More favourable environmental conditions for native plant establishment and growth and greater productivity due to higher precipitation and cooler temperatures equate to greater resilience at higher than lower elevations, which is indicated by a smaller change in plant functional group composition and more rapid recovery after disturbances and management treatments (Condon et al. 2011; Davies et al. 2012; Chambers et al. 2014a,b; Knutson et al. 2014). Less favourable environmental conditions for annual invasive grass establishment and growth due to colder soil temperatures coupled with increased competition due to more productive plant communities result in greater resistance to annual invasive grass at higher than lower elevations, which is indicated by lower density and cover of the invader (Chambers et al. 2007, 2014a,b, 2016; Condon et al. 2011; Brooks et al. 2016).

Understanding how loss of perennial herbaceous species, which can result from livestock grazing, and loss of shrubs, which often results from wildfire, influence plant functional groups and community composition and structure in Cold Desert shrublands requires a mechanistic approach that examines longer time frames and includes the environmental gradients that characterize these ecosystems. We used a factorial experiment to test the separate and interacting effects of removal of native perennial herbaceous species and burning on plant functional groups and plant communities along elevation gradients 12 and 13 yr after study implementation. Although removal of perennial herbaceous species is not an exact simulation of livestock grazing, the pervading effect of inappropriate livestock grazing is loss of perennial herbaceous vegetation

(Adler et al. 2005; Reisner et al. 2013, 2015). We asked two questions. (1) How do the separate and interacting effects of removal of perennial herbaceous species and burning influence relative abundance of plant functional groups over longer time frames? We predicted that decreases in perennial native grass and forb cover would result in increases in cover and density of both shrubs and annual invasive grasses, but in the absence of continued removals perennial native grasses and forbs would increase over time. We also predicted that burning would interact with removal and have long-term negative effects on shrub cover, but positive effects on other functional groups. (2) How do interactions between perennial herbaceous species removal and burning differ along environmental gradients? We predicted that long-term effects of removal and burning would be greatest at low elevation due to warmer and drier environmental conditions. We discuss implications of the effects of removal and burning on ecosystem resilience to disturbance and resistance to annual invasive grasses over the elevation gradient.

Methods

Study system

Our study was conducted in the states of Nevada and Utah in the western USA along elevation gradients within watersheds characterized by *A. tridentata* vegetation types (Chambers et al. 2007). In each state we selected three study sites dominated by native vegetation and in moderate to high ecological condition (i.e. >12% perennial native herbaceous cover, <25% shrubs and <2% annual invasive grass cover). In Nevada, sites were located in the Shoshone Mountain Range, on the Humboldt-Toiyabe National Forest at 39° N, 117° 30' W at low (1960 m), mid (2190 m), and high (2380 m) elevations in Underdown Canyon. In Utah study sites were located in the East Tintic Range on land administered by the Bureau of Land Management's Filmore Field Office at 40° N, 112° W at low (1710 m) and mid (2085 m) elevations in Black Rock Canyon and at high (2274 m) elevation in nearby Mill Canyon. All study sites were fenced to prevent livestock grazing prior to conducting the experiment and the fences were maintained over time.

Study sites were semi-arid with most precipitation arriving from Nov through May as snow or snow mixed with rain. Mean annual precipitation for the study period (2001–2013) increased over the elevation gradients in Nevada and Utah, respectively: low (202 and 301 mm), mid (321 and 445 mm) and high (459 and 521 mm). Mean annual temperatures ranged from about 9.2–7.5 °C and decreased with increasing elevation. Soils on all sites were loams to sandy-loams (Chambers et al. 2007). Herbaceous cover was generally dominated by perennial native

grasses on the Nevada and Utah sites, and herbaceous cover values increased with increasing elevation in both states (Table 1). Native forb covers were higher in Nevada on low elevation sites, but higher in Utah on mid and high elevation sites. In Nevada and Utah sites at each elevation had the same *A. tridentata* subspecies and several common herbaceous species. Annual invasive grasses were comprised solely of *B. tectorum*.

Experimental design

Our experiment examined effects of herbaceous species removal and burning for three site types (low elevation, mid elevation and high elevation) in each of the two locations (Nevada and Utah) (Appendix S1). The experiment used a factorial, split-plot design that crossed the two treatments at each of the site types: herbaceous perennial species removal (0%, 50% and 100%) and burning (burned and not burned). The experiment was repeated in 2 yr and treatments were randomly assigned to subplots within each of the site types. There were three replicates of each treatment combination per site, and individual subplots (3.0-m diameter) were located around a focal *A. tridentata* shrub and separated by 2 m or more. Total number of subplots was 216 (2 locations [states] × 3 site types × 3 removals × 2 burnings × 2 yr × 3 replicates).

To test for effects of removal, treatments were applied in the spring of each treatment year (2001 and 2002) during active vegetation growth (mid- to late May). Herbaceous vegetation was removed by spraying with glyphosate (Roundup; Monsanto, St. Louis, MO, US), a nonspecific herbicide that has no residual activity in soil, at a dosage of 170.5 ml Roundup/4.5 L water. The 50% removal treatment involved hand spraying every other plant in the subplot while carefully shrouding non-target individuals. The 100% removal treatment was accomplished by spraying all herbaceous vegetation in the subplot.

To test for effects of burning, treatments were applied in 2001 and 2002 in early to mid-Oct for Nevada and early Nov for Utah by USDA Forest Service and Bureau of Land Management fire management personnel. A burn barrel 3.4 m in diameter was placed around the subplot to be burned, 4.5 kg of clean and weed-free dry straw was added for consistent fuel loading, and the subplot was lit with a drip torch (Chambers et al. 2007).

We evaluated response of the vegetation community in 2014, 12 and 13 yr after treatments were applied. Each subplot was divided into four uniform quarters using cardinal directions and two 0.25-m² quadrats were placed within each quarter. Aerial cover was estimated ocularly and density was counted for all plant species within quadrats. Also, height, longest diameter and diameter perpendicular to the longest diameter were measured for each

Table 1. Representative perennial native species and percentage cover (mean \pm SE) for each functional group in low, mid and high elevations sites in Nevada and Utah.

Site	Representative Species	Annual Invasive Grasses	Annual Native Forbs	Perennial Native Grasses	Perennial Introduced Grasses	Perennial Native Forbs	Shrubs
Nevada							
Low	<i>A. tridentata wyomingensis</i> (s), <i>Hesperostipa comata</i> (g), <i>Poa secunda</i> (g), <i>Linanthus pungens</i> (f), <i>Cryptantha flavocalata</i> (f)	0.53 \pm 0.08	1.4 \pm 0.34	8.4 \pm 1.0	0 \pm 0	4.0 \pm 0.85	16.4 \pm 4.4
Mid	<i>A. tridentata vaseyana</i> (s), <i>Chrysothamnus viscidiflorus</i> (s), <i>Poa secunda</i> (g), <i>Hesperostipa comata</i> (g), <i>Lupinus argenteus</i> (f)	0.17 \pm 0.06	2.1 \pm 0.30	9.6 \pm 1.5	0 \pm 0	2.2 \pm 0.45	17.8 \pm 3.6
High	<i>A. tridentata vaseyana</i> (s), <i>Symporocarpus oreophilis</i> (rs), <i>Festuca idahoensis</i> (g), <i>Pascopyrum smithii</i> (g), <i>Lupinus argenteus</i> (f)	0 \pm 0	0.31 \pm 0.08	25.3 \pm 2.0	0 \pm 0	2.8 \pm 0.83	15.0 \pm 3.0
Utah							
Low	<i>A. tridentata wyomingensis</i> (s), <i>Pseudoroegneria spicata</i> (g), <i>Poa secunda</i> (g), <i>Astragalus</i> spp. (f)	0.83 \pm 0.09	0 \pm 0	13.7 \pm 1.42	0 \pm 0	0.08 \pm 0.04	9.1 \pm 2.5
Mid	<i>A. tridentata vaseyana</i> (s), <i>Purshia tridentata</i> (s), <i>Poa fendleriana</i> (g), <i>Pseudoroegneria spicata</i> (g), <i>Petroradia pumila</i> (f)	0.22 \pm 0.07	0 \pm 0	12.4 \pm 1.38	0 \pm 0	7.4 \pm 1.3	23.6 \pm 4.2
High	<i>A. tridentata vaseyana</i> (s), <i>Symporocarpus oreophilis</i> (rs), <i>Leucopoa kingii</i> (g), <i>Poa fendleriana</i> (g), <i>Penstemon</i> spp. (f), <i>Helianthus multiflorus</i> (f)	0 \pm 0	0.14 \pm 0.06	20.8 \pm 1.8	0 \pm 0	31.3 \pm 2.4	16.22 \pm 2.3

s, Shrub; rs, root-sprouting shrub; g, grass; f, forb.

A. tridentata plant rooted in each subplot. These measurements were used to calculate individual *A. tridentata* volumes in m³, rooted density and canopy area in m² for the entire subplot.

Statistical analyses

The analyses evaluated the response to herbaceous species removal and burning for the three site types (elevations). A randomized complete block design was used in which the two locations (states) were treated as separate blocks. A split-plot, three-way mixed effects model was conducted in which site type was a whole plot factor and removal and burning treatments were split-plots within each site type. Site type, burning, removal and their interactions were treated as fixed effects; location, year of treatment and their interactions were treated as random effects. Random effects were used to account for temporal and spatial correlation (blocking) between experimental units and were not tested to maintain a broad inference space (Newman et al. 1997; Pinheiro & Bates 2006). Appropriate distributions and link functions were specified for each data type to meet assumptions about distribution of residuals in the model fitting procedures. Differences among means for significant fixed effects were evaluated with least squares means using the Tukey-Kramer adjustment at $P \leq 0.05$.

Variables analysed to evaluate treatment responses were percentage cover of perennial native grasses (PNG), perennial native forbs (PNF) and shrubs, and percentage cover and density of annual invasive grasses (AIG) and annual native forbs (ANF). Treatment response of the shrub, *A. tridentata*, was evaluated using canopy area, density and volume (size) data. All analyses were performed using Proc GLIMMIX in SAS v 9.1.2 (SAS Institute, Cary, NC, US). Detailed model results are in Appendix S2. Significant main effects and their interactions are included in the figures and significant pair-wise comparisons are provided in the results.

Results

Removal had highly significant effects on PNG cover, but the influence of removal varied among site elevations (Fig. 1; site type \times removal = $P < 0.003$). Pair-wise comparisons showed that the highest covers occurred on high elevation sites with no removal, followed by high, mid and low elevation plots with no or 50% removal (all $P \leq 0.05$). The 100% removal treatment resulted in the lowest covers in all site elevations (all $P \leq 0.03$), reducing PNG cover by 62%, 40% and 45% in high, mid and low elevation sites, respectively. Removal was the only significant treatment effect for PNF cover (Fig. 1). The 100% removal treatment had lower PNF cover than either 50% removal ($P \leq 0.01$)

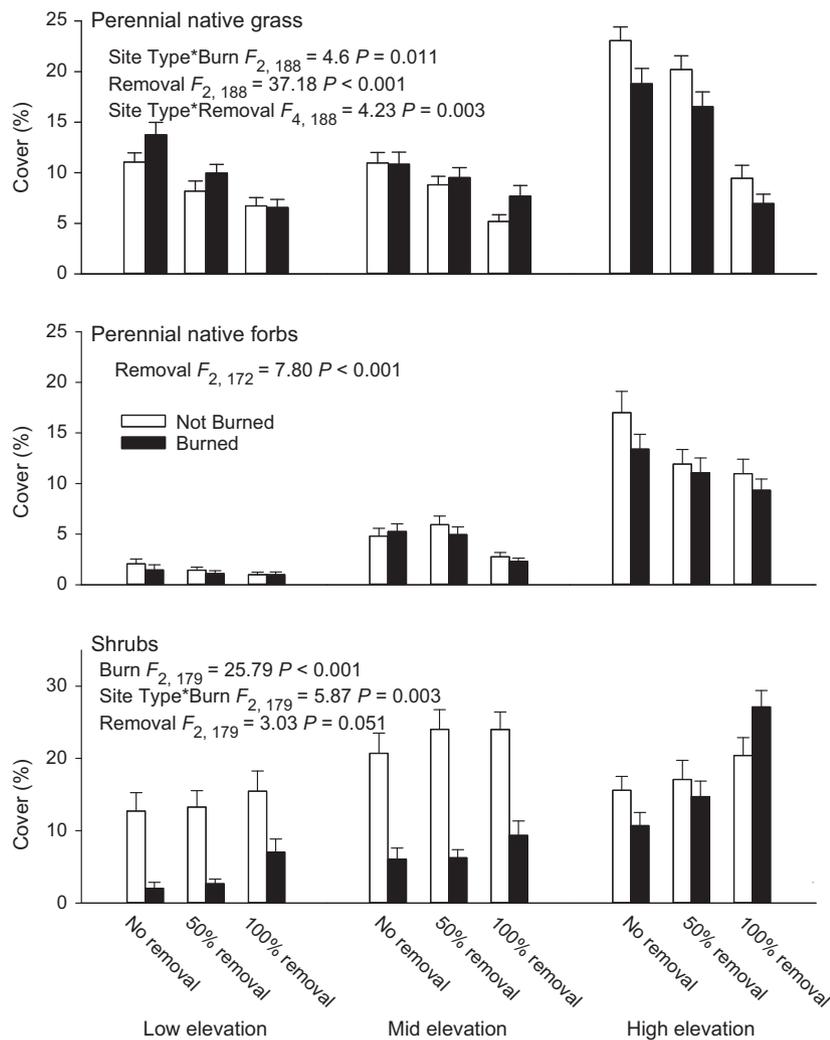


Fig. 1. Percentage cover (mean \pm SE) of perennial native grasses, forbs and shrubs in low, mid and high elevation sites treated in 2001 and 2002 by herbaceous species removal (no, 50% and 100%) and burning (not burned and burned).

or 0% removal ($P \leq 0.001$). The 50% and 100% removal treatments reduced PNF cover by 17% and 40%, respectively, across site types. Removal had a marginally significant effect on shrub cover (Fig. 1; $P < 0.51$), where 100% removal resulted in a 175% increase in shrub cover across site types.

The effect of burning on PNG cover differed among site elevations (Fig. 1; site type \times burn = $P < 0.011$). Burning resulting in a 17% and 12% increase in PNG cover on the low and mid elevation sites, respectively, but a 20% decrease in PNG cover on the high elevation site. The effect of burning on shrub cover also differed among site elevations (Fig. 1; site type \times burn = $P < 0.003$). As expected, burning had a negative effect on shrub cover in all site elevations (all $P \leq 0.04$) due to dominance of the fire-intolerant shrub, *A. tridentata*. However, shrub cover was greater on burned plots in high elevation sites (17%) than on

burned plots in mid (7%) or low (4%) elevation sites (both $P \leq 0.01$), and was higher on burned plots in mid elevation sites than burned plots in low elevation sites ($P \leq 0.001$).

Canopy area, density and average plant size of *A. tridentata* were affected by herbaceous species removal and burning, but again there were strong differences among site elevations (Fig. 2). Herbaceous species removal had no effect on *A. tridentata* canopy area in the not burned treatment, but resulted in progressively greater canopy area in the burned treatment – 100% > 50% > 0% due to progressive increases in seedling recruitment (burn \times removal = $P < 0.001$; all $P \leq 0.001$). Overall canopy area across site elevations in the burned treatment was 0.84, 0.40, and 0.19 m² for 100%, 50% and 0% removal, respectively. Density of *A. tridentata* exhibited a similar progressive response to removal with the largest densities

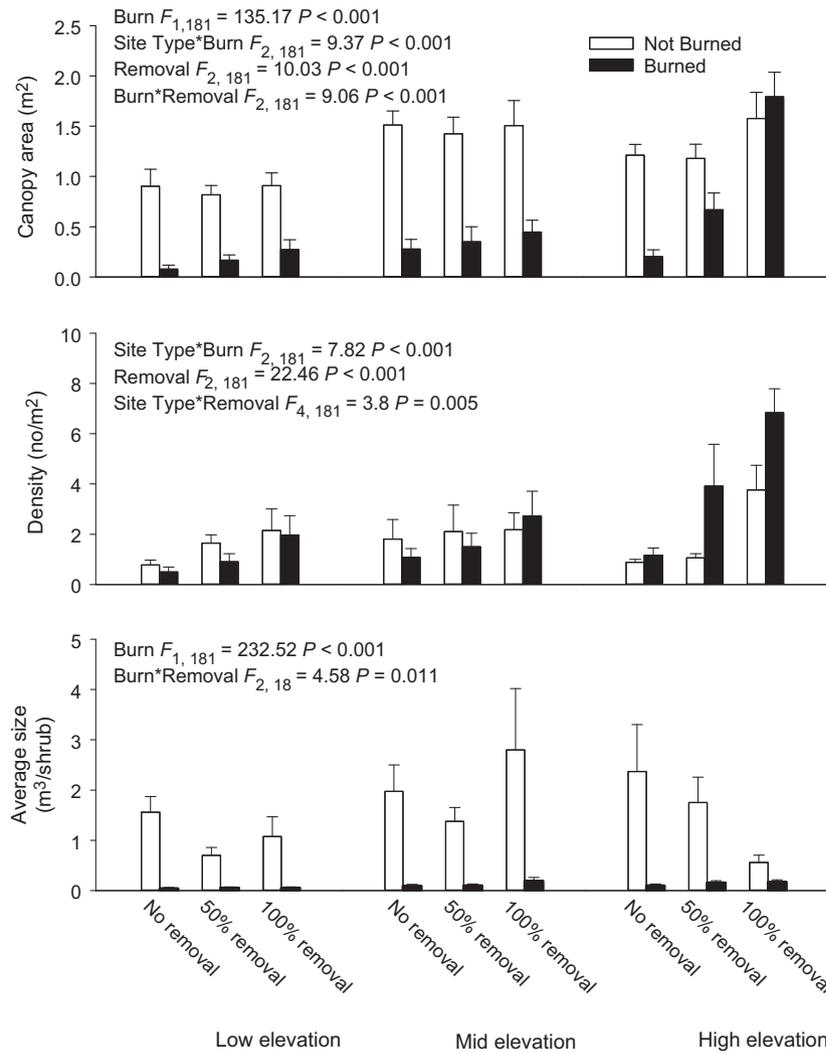


Fig. 2. *A. tridentata* shrub canopy area (mean \pm SE), plant density (mean \pm SE) and shrub size (mean \pm SE) in low, mid and high elevation sites treated in 2001 and 2002 by herbaceous species removal (no, 50% and 100% removal) and burning (not burned and burned).

occurring at high elevation sites in the 100% removal treatment (site type \times removal = $P \leq 0.005$; all $P \leq 0.001$). Also, *A. tridentata* size was smaller in the unburned treatment with 100% removal than with no removal ($P \leq 0.02$).

The effect of the burn treatment on canopy area of *A. tridentata* differed among site elevations (Fig. 2; site type \times burn = $P < 0.001$). As expected, overall canopy area of *A. tridentata* was lower in the burn than unburned treatment at all elevations (all $P \leq 0.001$). However, *A. tridentata* canopy area in burned sites in low (0.17 m²) and mid (0.36 m²) elevation sites was less than in high elevation sites (0.89 m²) (both $P \leq 0.012$), particularly in the 100% removal plots (1.79 m²). The response of *A. tridentata* density to burning also differed among site elevations (Fig. 2; site type \times burn = $P < 0.001$). Density was similar in burned and unburned plots at low and mid-elevations

(one to three individuals), but higher in burned plots at high elevation (as many as seven individuals; all $P \leq 0.001$). The burned treatment was characterized by seedlings and juvenile shrubs, and *A. tridentata* size was generally smaller in the burned than unburned treatment (all $P \leq 0.001$).

Annual native forbs were a minor community component, and cover values were low in this semi-arid ecosystem. Cover of ANF ranged from about 0.3–1.0% while densities ranged from about 5–75 plants·m⁻². Species identities differed among sites, and there were no significant treatment or elevation effects (Appendix S2).

Cover of AIG was comprised exclusively of *B. tectorum* and ranged from about 0.1–1.5% (Fig. 3). AIG cover was less on high elevation (0.09%) than low elevation (1.1%) sites ($P \leq 0.05$), and AIG density was less on high elevation (1 plant·m⁻²) than mid (21 plants·m⁻²)

and low elevation (36 plants·m⁻²) sites (both $P \leq 0.02$). Burning and removal had an interactive effect on AIG cover with no clear trend. However, AIG density was higher with 100% removal than 50% or 0% removal (both $P \leq 0.05$), especially on low elevation sites where densities were 52, 34 and 23 plants·m⁻² for 100%, 50% and 0% removal.

Discussion

The response of these Cold Desert shrublands to burning was strongly conditioned by removal of perennial herbaceous vegetation (PNG and PNF) and varied consistently along an elevational gradient associated with differences in resource availability. Removal prior to burning resulted in increased establishment of *A. tridentata*, particularly at higher elevations. Removal also resulted in higher densities of *B. tectorum*, but only in climatically suitable sites at mid and especially low elevation. These results have strong implications for resilience of Cold Desert shrublands to disturbance over the elevation gradients that characterize these ecosystems.

Effects of perennial herbaceous species removal and burning

Longer-term functional group cover was affected not only by the direct and interacting effects of perennial

herbaceous species removal and burning, but also by interactions of removal and burning with site elevation. Over a decade after treatment, complete removal of perennial herbaceous species reduced PNG and PNF cover by 40–60% across site elevations and burn treatments. As predicted, PNG and PNF cover increased over time in the absence of repeated removals. However, the increases in PNG and PNF in our study plots resulted from seedling recruitment and were likely higher than would be observed in areas where inappropriate livestock grazing causes loss of perennial herbaceous species and seed availability is lower.

Burning resulted in a long-term decrease in shrub cover as predicted, but the magnitude of the effect decreased with site elevation. Greater cover of shrubs on high than mid and low elevation sites following burning can be attributed to a higher proportion of shrub species that root-sprout following fire, such as *Chrysothamnus viscidiflorus* (Hook.) Nutt. and *Symphoricarpos* spp. Duham (Table 1), and more favourable conditions for seedling establishment and growth on high elevation sites (Chambers et al. 2007, 2014a). Burning interacted with site type and although low and mid elevation sites had greater PNG in the burn treatment, high elevation sites had lower PNG. These results contrast partly with shorter-term studies that report increases in cover or density of perennial herbaceous species following wildfires and prescribed fires that reduce shrub cover (Stubbs & Pyke 2005; Blank et al. 2007;

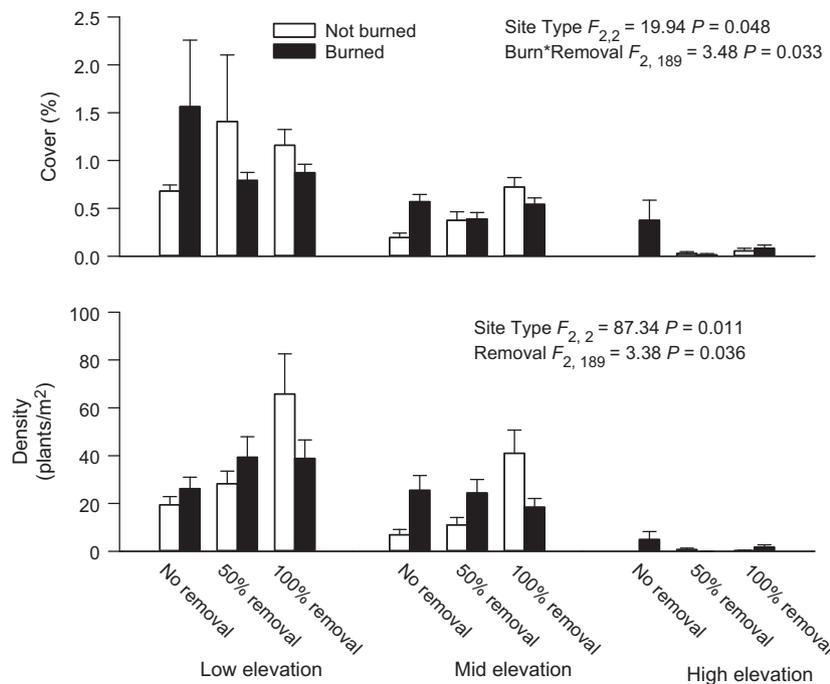


Fig. 3. Percentage cover (mean ± SE) and plant density (mean ± SE) of annual invasive grasses in low, mid and high elevation sites treated in 2001 and 2002 by herbaceous species removal (no, 50% and 100%) and burning (not burned and burned).

Chambers et al. 2007; Rau et al. 2008; Roundy et al. 2014).

The decrease in cover of PNG and PNF due to removal resulted in increases in cover or density of other functional groups, as predicted. This finding can be attributed to increased soil water and nitrate availability after removal of PNG and PNF and competitive release of the other functional groups (Blank et al. 2007; Chambers et al. 2007). Although burning also increased soil water and N availability, burning without removal had only minor initial effects on these soil resources due to rapid regrowth of perennial herbaceous species (Blank et al. 2007; Chambers et al. 2007).

Removal of PNG and PNF and burning had both separate and interacting effects on *A. tridentata* seedling recruitment across all site elevations. Removal had a strong positive effect on *A. tridentata* densities in burned and unburned treatments, and resulted in progressively increased canopy area in the burned treatment: 100% > 50% > 0%. Removal also resulted in a progressive increase in *A. tridentata* density and canopy area with elevation in the burned treatment. Establishment of all *A. tridentata* subspecies is limited by small, short-lived seeds (1–3 yr) with low dispersal distances (9–12 m), and by sufficient soil water resources in sequential years for both seed production and seedling establishment (Miller et al. 2011). Thus seedling establishment is generally greater on cooler and moister *A. tridentata* subsp. *vaseyana* sites at higher elevation than warmer and drier *A. tridentata* subsp. *wyomingensis* sites at lower elevation following wildfire (Knutson et al. 2014; Miller et al. 2013). Lower levels of resources, especially soil water (Chambers et al. 2007), likely resulted in lower levels of both recruitment and plant growth at low elevation in our study. Seed availability of *A. tridentata* was probably higher and seedling recruitment greater in our study than after large-scale wildfire.

Site elevation had the largest effect on AIG (*B. tectorum*); cover or density was less in high elevation than mid and low elevation sites. This is consistent with our previous work indicating that for the range of environmental conditions examined, establishment, growth and/or reproduction of *B. tectorum* are constrained in high elevation sites by low soil temperatures, and are relatively optimal in low elevation sites under moderate temperature and water availability (Chambers et al. 2007). On mid and low elevation sites, AIG density was higher with 100% removal of herbaceous species than 50% or 0% removal. Negative relationships are typically found between *B. tectorum* cover and PNG or PNG and PNF cover in *A. tridentata* subsp. *wyomingensis* shrublands, which occur at lower elevations (Anderson & Inouye 2001; West & Yorks 2002; Chambers et al. 2014b).

Cover of ANF was generally low, densities were highly variable and there were no significant treatment effects (Appendix S2). ANF are often a major component of the seed banks in these ecosystems (Allen et al. 2008; Koniak & Everett 1982), and ANF have been observed to increase immediately after complete removal of vegetation (Boyd & Svejcar 2011) and after fire, but to decrease over time with increasing competition from PNG (Miller et al. 2013). Also, ANF cover likely differs over time as a function of weather, especially in low elevation sites (West & Yorks 2002). Generally high variability of ANF, low competitive ability with PNG and lower cover in the burned treatment indicate that ANF likely play a minor role in the longer-term vegetation dynamics of many *A. tridentata* shrublands.

Implications for ecosystem resilience

Results of this mechanistic study support prior research in these shrublands indicating that loss of PNG and PNF, which can result from inappropriate livestock grazing, and loss of *A. tridentata*, which can result from fire, interact to affect the relative abundance of functional groups over time and thus ecosystem resilience to disturbance (Cooper 1953; Harniss & Murray 1973; Burkhardt & Sanders 1992; Chambers et al. 2007, 2014a,b; Hanna & Fulgham 2015). Decreases in resilience or recovery potential following wildfire generally occur when competition from perennial native forbs and especially grasses for available resources no longer prevents dominance by *A. tridentata* and other shrubs and/or AIG. We show that following removal of herbaceous species and burning larger densities of seedlings and juveniles and thus higher canopy area of *A. tridentata* can result in strong intra- and interspecific competition and potential for near exclusion of perennial herbaceous species, especially in high elevation sites. Previous research shows that both biomass and reproductive effort of *P. spicata* decrease progressively as level of clipping (none, heavy, extreme) and competition from shrubs and other herbaceous species (none, partial, full) increase (Mueggler 1972). Negative relationships between shrubs and PNG cover are generally evident in *A. tridentata* shrublands as a function of grazing intensity (Adler et al. 2005), and have developed after moderate to heavy grazing (Cooper 1953) and during grazing release (Anderson & Inouye 2001) in *A. tridentata* subsp. *wyomingensis* shrublands. Similar relationships are observed over 30-yr periods after fire under moderate grazing in *A. tridentata* subsp. *vaseyana* shrublands (Harniss & Murray 1973; Hanna & Fulgham 2015).

We reaffirm that cover or density of AIG is less in high elevation than mid and especially low elevation sites, and increases with herbaceous species removal (see Chambers et al. 2007). High intensity grazing can increase AIG in low

elevation *A. tridentata* subsp. *wyomingensis* sites (Reisner et al. 2013). Also, grazing effects increase with heat and water stress in these ecosystems and can result in *B. tectorum* dominating the herbaceous vegetation and perennial native grasses occurring only under protective shrubs (Reisner et al. 2015).

Our results indicate that longer-term effects of fire interact with relative abundance of PNG and PNF at the time of burning, resistance to AIG and environmental conditions (temperature and moisture regimes as influenced by elevation). Regardless of elevation, the degree to which PNG and PNF recover following burning depends on their initial abundance over both short (Chambers et al. 2014b; Roundy et al. 2014) and, as we show in this study, longer time frames. Shrub cover in general increases in response to reductions in PNG and PNF, as we also document in this study. Higher woody fuel loads due to increases in shrub cover can result in increased fire severity and the potential for higher PNG and PNF mortality (Miller et al. 2013), especially when PNG occur primarily under the protective cover of shrubs (Reisner et al. 2015). Low cover of PNG and PNF following fire significantly increases the probability of increases in AIG density and cover in areas with low to moderate resistance to invasion (Chambers et al. 2007, 2014b; Davies 2008). Finally, as we show in this study, fire can interact with reductions in PNG and PNF cover to increase recruitment of *A. tridentata*. However, this increase is likely to be beneficial only where resistance to AIG is relatively high and *A. tridentata* does not rapidly dominate the area. Understanding these interactions can help managers to adapt grazing practices and determine appropriate fuels management treatments to maintain or increase resilience to wildfire in these ecosystems. Better quantifying the relative proportions of key perennial grasses and shrubs that contribute to resilience along environmental gradients can provide information needed to predict the outcomes of both disturbance and management treatments.

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Supporting Information

Additional Supporting Information may be found in the online version of this article:

Appendix S1. Schematic of experimental design.

Appendix S2. Detailed mixed model results: (A) perennial natives; (B) *A. tridentata* cover, density and size; (C) annual native forbs; (D) annual invasive grasses.