


RESEARCH ARTICLE

Disturbance type influences plant community resilience and resistance to *Bromus tectorum* invasion in the sagebrush steppe

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Abstract

Question: How does type of disturbance alter plant community composition when an invasive species with high intrinsic population growth rate is present? The sagebrush steppe is a cold semi-arid steppe dominated by the native shrub *Artemisia tridentata* Nutt., native bunchgrasses, and has been invaded by the non-native winter annual *Bromus tectorum* L.

Location: Sagebrush steppe, Montana, USA.

Methods: We assessed the effect of fire and soil disturbance, due to bulldozing to create a firebreak, on the resilience of plant communities and their resistance to invasion by *B. tectorum*. Plant species richness and species composition were monitored for 3 years at two sites post-fire and firebreak construction.

Results: Burned plant communities were resilient and had similar native grass cover and native species richness compared with the unburned sites after 3 years. Soil disturbance from firebreak construction resulted in species composition that was distinct and had lower native grass cover. Type of disturbance also affected the community's resistance to *B. tectorum*. *Bromus tectorum* cover was similar in burned and unburned areas, but increased up to three times and remained high where soil disturbance occurred, suggesting a shift to an alternative state.

Conclusion: In this northern portion of the sagebrush steppe, communities with native plant cover were resilient to fire but not soil disturbance, which facilitated *B. tectorum* increase and a transition to an alternative state. In areas of high native plant cover, management tactics should avoid soil disturbance.

KEYWORDS

alternative state, *Artemisia tridentata* subsp. *vaseyana*, cheatgrass, *Festuca idahoensis*, firebreak, plant invasion, *Pseudoroegneria spicata*, wildfire

1 | INTRODUCTION

Many plant communities are resilient to the particular disturbance regimes under which they evolved (e.g. Chambers et al., 2014; Keeley, Pausas, Rundel, Bond, & Bradstock, 2011). Resilience confers the ability of plant communities to regain their structure, processes and functioning following disturbance (Brooks et al., 2016; Chambers

et al., 2014). Additionally, a plant community can resist invasion of non-native plant species by preventing the species invasions or by limiting an invasive species to low relative abundance through complex networks of biotic interactions (Brooks et al., 2016). Major changes in the magnitude and frequency of disturbances can push a plant community beyond resilience and resistance thresholds, potentially transforming it to an altered or novel stable state (e.g.

Davies et al., 2012; Hobbs et al., 2006; Scheffer, Carpenter, Foley, Folke, & Walker, 2001). For example, increased fire frequency in plant communities that are not adapted to fire, or historically experienced infrequent fire, can reduce the resilience of the community and precipitate transitions to a novel state (D'Antonio & Vitousek, 1992; Keeley & Brennan, 2012). Likewise, disturbances have been shown to reduce plant community resistance to invasion, possibly through increased resource availability or altered habitat suitability (Chambers et al., 2014). Furthermore, the effect of disturbance on the resilience of a plant community and its resistance to invasion may interact. The alteration of disturbance regimes either through type of disturbance or frequency of disturbance can reduce resilience, resulting in longer recovery time and decreased resistance to invasion that leads to greater dominance by non-native plants, and a more rapid shift to an alternative state. Finally, a plant community's resilience is affected by the traits of its species, especially if species have traits conducive to rapid population growth or, alternatively, recover slowly following disturbance (Oliver et al., 2015). Understanding how plant communities respond to disturbance, especially when the plant community has been altered by the presence of an invasive species, is important for managing ecosystems to mitigate against undesirable changes (Hobbs & Huenneke, 1992; Keeley, 2006; Standish et al., 2014).

The sagebrush biome covers a broad geographic area of the western United States and is defined by the presence of shrubs in the genus *Artemisia* L., subgenus *Tridentatae*. The biome includes communities of sagebrush steppe and Great Basin sagebrush (Welch, 2005; West, 1983a,b). The sagebrush biome has been altered in the last 170 years by anthropogenic disturbance, increased fire frequency and invasive species (Germino, Chambers, & Brown, 2016). Within the sagebrush biome, the resilience of plant communities to disturbance varies by climate conditions, type and magnitude of the disturbance, and traits of the species in the community (Chambers et al., 2014). For example, in eastern Washington, sagebrush steppe plant communities exhibited differing resilience to disturbance because of climate conditions at different elevations and traits of species in plant communities (Davies et al., 2012). At a sagebrush steppe site in southern Idaho, fire and physical disturbance (soil disturbance around roads and facilities/developments) had different effects on plant communities, and plant diversity returned to undisturbed levels in plots disturbed by fire but not by physical disturbance; highlighting a difference in resilience to fire and soil disturbance (Lavin, Brummer, Quire, Maxwell, & Rew, 2013).

Within the sagebrush biome, the introduced winter annual grass *Bromus tectorum* L. has invaded many disturbed plant communities, often associated with overgrazing, wildfire and herbicide treatment of other invasive species (Knapp, 1996; Mack, 2011; Reisner, Grace, Pyke, & Doescher, 2013; Skurski, Maxwell, & Rew, 2013). The presence of *B. tectorum*, which senesces early in the season and increases fine fuel loads, has been linked with more frequent and larger fires (Link, Keeler, Hill, & Hagen, 2006; Balch, Bradley, D'Antonio, & Gomez-Dans, 2013). *B. tectorum*-dominated sites are more likely to burn than sagebrush-dominated sites,

and most fires from 2000 to 2009 in the Great Basin started on *B. tectorum*-dominated sites (Balch et al., 2013). Increases in fire frequency and size, along with other disturbances such as overgrazing and soil disturbance (e.g. along roads and the common fire management practice of bulldozed firebreaks) have altered species composition in communities not resilient to these disturbances and reduced resistance to *B. tectorum* invasion, ultimately shifting many sagebrush biome communities to an altered or novel state dominated by annual grasses (Chambers et al., 2014).

Though the sagebrush biome has been affected by fire and *B. tectorum* invasion, both plant community resilience to disturbance and resistance to invasion are dependent on local variables such as climate, topography, available nitrogen, soil water and native vegetation cover (Brooks et al., 2016; Brummer et al., 2016; Condon, Weisberg, & Chambers, 2011; Davies et al., 2012; Seefeldt, Germino, & DiCristina, 2007; Taylor, Brummer, Rew, Lavin, & Maxwell, 2014). Plant communities at the warmest, low-elevation sites are dominated by obligate seeders and are less resilient to fire and less resistant to *B. tectorum* invasion compared to cooler and wetter, high-elevation sites, that tend to have more resprouting shrubs and bunchgrasses, and more available resources (Seefeldt et al., 2007; Davies et al., 2012; Chambers et al., 2014). In many of the less resilient areas with higher mean annual and summer temperatures and lower summer precipitation, *B. tectorum* dominates after fire. In contrast, in areas with lower mean annual temperatures and more early summer precipitation, the plant community is more resilient to disturbance and resistant to *B. tectorum* invasion, and thus *B. tectorum* plays a less transforming role (Chambers et al., 2014; Porensky & Blumenthal, 2016; Prevey & Seastedt, 2014; Taylor et al., 2014). Brummer et al. (2016) found that climate increased the transformative ability of *B. tectorum* when summers were dry (i.e. <10 mm precipitation in July and the associated driest quarter with a mean temperature of >15°C) and native grass cover was low. Such climate conditions are associated with communities where the main sagebrush species is *Artemisia tridentata* Nutt. subsp. *wyomingensis* Beetle & Young, and transformative *B. tectorum* invasion tends to be absent in other parts of the sagebrush biome that are dominated by *A. tridentata* subsp. *vaseyana* (Rydb.) Beetle (Brummer et al., 2016). However, this does not mean that *B. tectorum* is not present throughout the biome, but rather that there are some conditions where it is more likely to dominate and form monocultures.

To manage for ecosystems that are resilient to disturbance and resistant to plant invasions within the sagebrush biome, we need to understand the interaction of plant community resilience with resistance to *B. tectorum* invasion and how the interaction is affected by different types of disturbance which could lead to different plant community states or varying recovery times (Germino et al., 2016). The aim of this study was to assess the short-term resilience of plant communities and resistance to *B. tectorum* invasion when subjected to fire and intense soil disturbance in the northern cool and wet sagebrush biome. For 3 years (2013–2015) we monitored the recovery of plant communities that either burned, were unburned or were subject to soil disturbance during construction of a firebreak. We

asked how does: (1) the type of disturbance affect plant species richness and composition, and (2) the abundance of *B. tectorum*?

2 | METHODS

2.1 | Study sites

Research was conducted at two sites in the sagebrush steppe in southwestern Montana, USA. Plots were monitored in mid- to late Jun, from 2013 until 2015 in burned areas, unburned areas and areas where soil disturbance occurred (one site). The two sites, 15 km apart, were the Montana State University Red Bluff Research Ranch (45.593°N, 111.628°W; hereafter Red Bluff) and Preacher Creek in the Tobacco Root Mountains (45.595°N, 111.831°W; hereafter Preacher Creek), which is under the jurisdiction of the Bureau of Land Management. Both sites contain native perennial bunchgrasses, diverse forbs and shrubs, and *B. tectorum* is present throughout the region. On 7 Jul 2012, large portions of the area at Red Bluff burned in a human-caused fire called the Bear Trap 2 fire. At Preacher Creek, prescribed fire was conducted on 7 Apr 2013 on a southeast-facing slope and it burned an area of approximately 50 ha. Both fires were low to moderate in severity and resulted in mortality of *A. tridentata*, and burning of fine fuels and litter. *Bromus tectorum* was present at both sites prior to the fires.

The vegetation type at the Red Bluff site was classified as *Festuca idahoensis* Elmer–*Agropyron spicatum* (*A. spicatum* was an older name for *Pseudoroegneria spicata* (Pursh) Á. Löve), *Artemisia tridentata*–*Agropyron spicatum* or *Artemisia tridentata*–*Festuca idahoensis*, depending on the amount of *A. tridentata* cover (Mueggler & Stewart 1979). *Pseudoroegneria spicata* and *Festuca idahoensis* are both bunchgrasses. Red Bluff soils were of the Nuley Rock Outcrop complex and are sandy loam from 0–10 cm and sandy clay loam from 10–30 cm (USDA 2016). The dominant habitat type at the Preacher Creek was *Artemisia tridentata*–*Festuca idahoensis* (Mueggler & Stewart 1979). Soils at Preacher Creek were of the Branham Rock Outcrop complex and consist of coarse sandy loam from 0–10 cm and gravelly coarse sandy loam from 10–30 cm (USDA 2016). Both sites had the same subspecies of *A. tridentata*, subspecies *vaseyana*. Climate varies slightly between sites: Red Bluff is slightly warmer, drier and lower in elevation (mean annual temperature 6.4°C, mean annual precipitation 400 mm, ~1,600 m a.s.l.) compared with Preacher Creek (mean annual temperature 5.2°C, mean annual precipitation 450 mm, ~1,770 m a.s.l.) based on PRISM and WorldClim data at a 0.5-km resolution (Hijmans, Cameron, Parra, Jones, & Jarvis, 2005; PRISM Climate Group 2004). During the period of monitoring both temperature and precipitation were slightly above the 108-year averages (Larson, Lehnhoff, & Rew, 2017; online resource).

2.2 | Monitoring design

At Red Bluff, a firebreak consisting of a strip (~5-m wide and 4-km long) of bare soil to control the fire was bulldozed, creating an interface between the burned and unburned areas. The experimental

design at Red Bluff consisted of four blocks randomly placed along the firebreak. Potential locations for blocks were selected based on having a shallow east-facing slope that consisted of open vegetation with no trees. Random start locations were selected within the potential locations along the burned and unburned interface, based on criteria that a 100-m long transect could be placed. Each block consisted of three parallel 50-m transects, one each in burned and unburned areas, and one in the firebreak between them. There were five 100-m² (10 m × 10 m) plots nested within each burned and unburned transect, and within each plot we estimated plant species cover within three 1-m² quadrats placed systematically along the plot diagonal. The firebreak transects also had five 100-m² (5 m × 20 m; to fit within the width of the firebreak) plots, and plant cover estimates were taken within three 1-m² quadrats placed systematically along the centre of the transect. The experimental design at Preacher Creek was similar except there was no firebreak. We selected four burned areas and then paired them with adjacent unburned areas (four blocks), and five plots were placed along the 50-m transects and plant cover estimates were made in three 1-m² quadrats across the diagonal of the 10 × 10 plot. Thus, at each site we had four transects (blocks) × five (100 m²) plots × three (1 m²) quadrats per treatment ($n = 60$).

At both sites, we recorded the presence and visually estimated the percentage cover of all plant species based on proportion of vegetation cover in each 1-m² quadrat in 2013, 2014 and 2015 during the third week of June, corresponding to peak biomass. All plant species were identified based on the nomenclature in Lesica, Lavin, and Stickney (2012). Native status, life span and growth form for each species was determined based on the PLANTS database (NRCS, 2015).

2.3 | Statistical analysis

2.3.1 | Analysis of species richness

To assess resilience based on species richness in burned, unburned and firebreak treatments through time, we calculated the total number of species that occurred in each 1-m² quadrat by summing the number of species recorded in a quadrat. We fit a GLMM of species richness using the Poisson distribution in response to disturbance (i.e. burned, unburned, firebreak), year, site and their interaction, to determine if overall species richness varied. To account for repeated measure of the same quadrats, the unique identity of each quadrat (a combination of transect number, 100-m² plot number and 1-m² quadrat number) was added as a random effect. Additionally, to better test our hypotheses, block and plot identity were also added separately as random effects to the models to control for the grouping of the three 1-m² quadrats within plots, the five 100-m² plots and the grouping of the transects with different treatments (Davies & Gray, 2015). We examined site and year, and site and disturbance interactions on richness to determine if site was more appropriately included as a random factor or as a fixed effect; a fixed effect was more appropriate because

of strong interactions among site and year. Therefore, the full model of species richness was fit in response to disturbance type, year, site and all interactions. Type III ANOVA was conducted to determine if predictor variables affected species richness using the ANOVA function in the 'car' package (Fox & Weisberg, 2011). Based on the ANOVA results we then conducted post-hoc multiple comparisons based on the Tukey method using the 'lsmeans' package (Lenth, 2016). Additionally, we assessed differences in the number of native forbs, grasses, and shrubs, annuals, biennials and perennials, and the ratio of native species to non-native species in quadrats. Generalized linear mixed-effects models were fit using 'lme4' package, and all statistical analysis was performed using R statistical environment (Bates, Maechler, Bolker, & Walker, 2015; R Foundation for Statistical Computing, Vienna, Austria).

2.3.2 | Analysis of β -diversity

To further assess resilience to disturbance, we analysed differences in β -diversity in response to disturbance type and years since disturbance. We used differences in species composition from the unburned sites, and changes of species composition in time to qualify differences in resilience to disturbance.

First, we calculated and compared relative species abundance by year and treatment using the sum of frequency in 1-m² quadrats as the measure of abundance. To compare species composition in quadrats we then used the species' cover in 1-m² quadrats to calculate dissimilarity among each quadrat using the Bray-Curtis index. We evaluated whether there were significant differences in plant species composition among years and disturbance, and set the grouping (strata) to the unique identity of quadrats, in the permutational multivariate ANOVA algorithm 'adonis'. We used NMDS with two dimensions for ordination of each 1-m² quadrat, and then used the ordination to calculate trajectories of change in species composition. Mean centroids and the ellipses were calculated based on the score for 1-m² quadrats; ellipse size was 1 SD around the mean. To assess how species' cover of the most common species was associated with differences among quadrats in the ordination, we used the score of the first two NMDS axes to predict site differences associated with cover. The analysis was implemented using the 'env.fit' algorithm in 'vegan'.

2.3.3 | Analysis of cover data

We assessed percentage cover of bare ground, *B. tectorum*, native grass species combined (*F. idahoensis*, *Koeleria macrantha*, *P. spicatum*, *Pascopyron smithii*, *Poa secunda*, *Stipa comata*, *S. nelsonii* and *S. viridula*) and of the dominant grasses *Pseudoerigeron spicata* and *Festuca idahoensis* individually over 3 years in 1-m² quadrats to determine if differences in disturbance and time affected cover. All mixed-effects models had a Gaussian distribution, and we assessed for overdispersion of the best models. All models were fit using 'lmer' in R package 'lme4' and type III ANOVA was conducted using 'lmerTest' (Bates et al., 2015). Random effects were unique identity for each quadrat, plot, block (see above) and site. Site was included as a random effect because we found

no important interactions among site and year, or site and disturbance. To make comparisons of mean cover differences for both years and treatments we conducted post-hoc Tukey HSD tests, and calculated 95% CI for the means for each interaction of disturbance and year at both the sites using the lsmeans R package (Lenth, 2016).

3 | RESULTS

3.1 | Plant species richness

The number of plant species varied across years in response to the type of disturbance (Figure 1, Table 1). The patterns of plant species richness also varied between the sites and among years (Figure 1, Table 1). The year after the fire at Red Bluff the firebreak, where soil disturbance occurred, had the lowest richness (7.6 species/m²) and had 2.8 ± 0.7 fewer species than the unburned plots ($df = 158.02$, $t = -4.1$, $p = .002$). Three years after the fire in 2015, richness in the firebreak remained the lowest (Figure 1a); there were 3.8 ± 0.66 fewer species in the firebreak compared to unburned quadrats ($df = 135.8$, $t = -5.6$, $p < .0001$) and 2.7 ± 0.66 fewer species compared to the burned quadrats ($df = 135.8$, $t = 4.1$, $p = .002$; Figure 1a). There was no difference in richness among the unburned and burned quadrats the year after the fire, and richness remained similar through 2015 (SE = 0.61, $df = 134.4$, $t = -1.675$, $p = .76$; Figure 1a). At Red Bluff the proportions of functional group (annual, biennial, perennial) and native vs non-native richness did not alter among the disturbances and years (Appendix S1: Figure S1).

At Preacher Creek, maximum plant species richness occurred in 2014, in the second growing season after fire, in both burned and unburned quadrats, and richness varied among years ($\chi^2 = 68$, $df = 2$, $p < .001$) but not between burned and unburned quadrats (Figure 1b; SE = 0.5, $df = 60$, $t = 0.46$, $p = .89$). The large differences in richness from 2014 to 2015 were due to a decline in forbs that were both annual and perennial (Figure 1b, Appendix S1: Figure S1). Additionally, the percentage of total richness accounted for by perennial species varied by year and increased from 80% in 2013 to 88% in 2015 (Appendix S1: Figure S1). In unburned quadrats at Preacher Creek there were more species of shrub present than at Red Bluff, but across sites there was similar richness of grass and forb species (Figure 1).

3.2 | Changes in plant species composition

Type of disturbance, year, site and their interactions all affected plant community composition (Table 2, Figure 2). In 2013, the first full growing season after the fire, the plant communities in the burned and unburned quadrats at Red Bluff, and the burned quadrats at Preacher Creek were similar but differed from those in firebreak quadrats at Red Bluff and the unburned quadrats at Preacher Creek (Figure 2). The differences in species composition remained over the 3 years of monitoring. Disturbance type (fire and firebreak) explained 12% of the variation in species composition; more than the difference between sites (7%) and more than that of year (2%) or

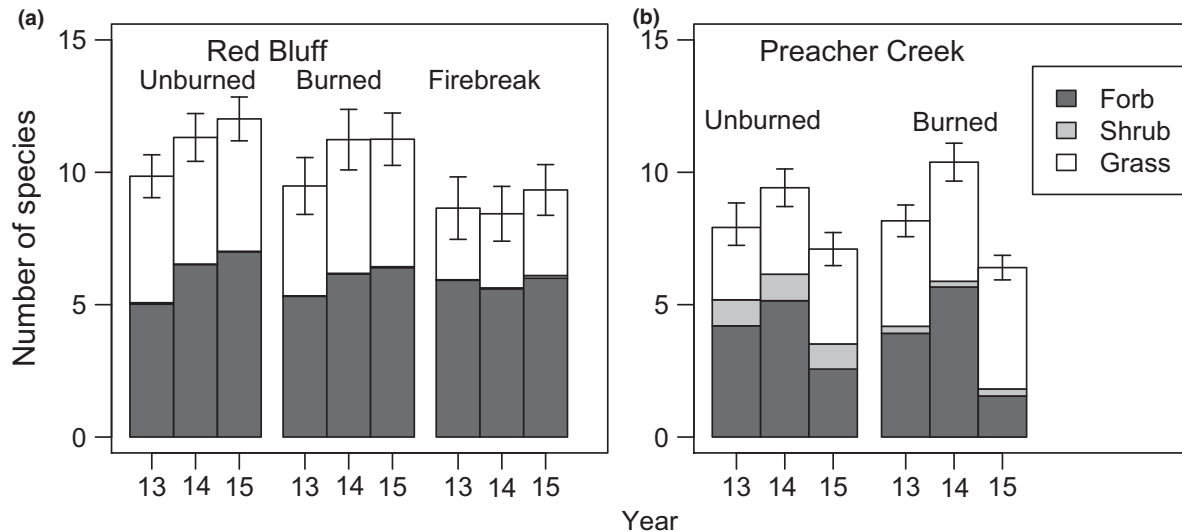


FIGURE 1 Number of plant species recorded at Red Bluff (a) and at Preacher Creek (b) in the years 2013 (13), 2014 (14) and 2015 (15). Mean plant species richness of forbs, grasses and shrubs are grouped by unburned, burned and firebreak quadrats (1 m²). Error bars indicate the upper and lower bounds of the 95% CI of the means

TABLE 1 Type III ANOVA table of plant species richness in 1-m² quadrats in response to year, type of disturbance, site and their interactions. The GLMM had a Poisson distribution and log link and *p*-values are based on Wald χ^2 tests

	χ^2 value	df	<i>p</i>
Year	59.3	2	<.001
Disturbance	3.1	2	.21
Site	0.72	1	.40
Year × disturbance	10.1	4	.03
Year × site	38.8	2	<.001
Disturbance × site	1.1	1	.30
Year × disturbance × site	1.7	2	.43

the interaction of year and disturbance (2%; Table 2). The interaction of disturbance and site explained 3% of variation in composition.

At Red Bluff, *P. spicatum* was most the abundant species across all disturbances and years, and the same non-native species were among the ten most frequent species (i.e. *B. tectorum*, *Alyssum desertorum*, *Tragopogon dubius*) across years and disturbances (Appendix S2: Table S1). At Preacher Creek, *P. spicatum* and *F. idahoensis* were the most frequent native grasses and the only non-native species that was one of the ten most abundant species in either burned or unburned quadrats was *B. tectorum*. The largest difference in species abundance at Preacher Creek between the burned and unburned quadrats was the cover and frequency of *A. tridentata*. While it was recorded in 53 of 60 quadrats in the unburned area, it was recorded in only 15 of 60 quadrats in the burned area in 2015 (Appendix S2: Table S1). *A. tridentata* cover was associated with the difference among burned and unburned sites at Preacher creek (Figure 2; $p < .001$, $R^2 = .38$) while *B. tectorum* cover was associated with the difference between the firebreak and the unburned and burned sites (Figure 2; $p < .001$, $R^2 = .48$).

3.3 | Changes in cover after disturbance

At both sites the amount of bare ground decreased rapidly as vegetation recovered after fire and soil disturbance (Figure 3a). The largest amount of bare ground was in 2013, the first full growing season after the fire in the firebreak; there was 30% more bare ground in the firebreak compared to the burned quadrats (SE = 3.6, $df = 225$, $t = -8.202$, $p < .0001$) and 49% more than in the unburned quadrats (SE = 3.6, $df = 229$, $t = 13.897$, $p < .0001$; Figure 3a). As the vegetation recovered post-fire, percentage bare ground decreased to levels similar to those observed in the unburned quadrats (10% of cover; firebreak 2015 – unburned 2015 = -0.39, SE = 3.4, $df = 199.75$, $t = -0.114$, $p = 1.0$; burned 2015 – unburned 2015 = 3.6, SE = 2.6, $df = 93.6$, $t = 1.4$, $p = .90$; Figure 3a).

The year following disturbance *B. tectorum* cover was 15% higher in the firebreak where soil disturbance occurred compared with the burned quadrats (SE = 3.3, $df = 91.5$, $t = -4.606$, $p < .001$) and 16% higher than the unburned quadrats (SE = 3.3, $df = 93.1$, $t = 4.848$, $p < .001$; Figure 3b). *B. tectorum* cover did not differ between burned and unburned quadrats (SE = 2.6, $df = 43.55$, $t = 0.329$, $p = 1$; Figure 3b). *Bromus tectorum* cover increased the most in the firebreak, and had more than doubled from 15% to 37% by 2015, 31% more than in the unburned (SE = 3.2, $df = 82.6$, $t = 9.6$, $p < .0001$) and 21% more than in the burned quadrats (SE = 3.2, $df = 82.6$, $t = -6.7$, $p < .0001$; Figure 3b). The cover of *B. tectorum* was also negatively associated with native grass cover ($r = -.36$, $t = -11.6$, $df = 883$, $p < .001$) and native forb cover ($r = -.16$, $t = -4.7$, $df = 883$, $p < .001$).

Native grass cover did not differ between unburned quadrats and burned quadrats across the three growing seasons (burned – unburned = 3.1, SE = 1.8, $df = 40.14$, $t = 1.696$, $p = .2190$; Figure 3c). In the firebreak, where considerable mortality of native grasses resulted from being scraped with a bulldozer, cover was lowest in the first growing season after fire but native grass cover increased

	df	Sums of Sq/	Mean Sq.	F-value	R ²	p
Year	2	6.3	3.2	12.6	.02	<.001
Disturbance	2	34.9	17.4	69.6	.12	<.001
Site	1	21.3	21.3	84.8	.07	<.001
Year × treatment	4	4.4	1.1	4.4	.02	<.001
Year × site	2	3.3	1.7	6.6	.01	<.001
Disturbance × site	1	10.2	10.2	40.5	.03	<.001
Year × site × disturbance	2	1.3	0.6	2.5	.004	<.001
Residuals	870	218.9	0.25		.728	

TABLE 2 Permutational ANOVA table of models of dissimilarity in species composition among years (2013–2015) in response to disturbance (unburned, burned, firebreak; latter at Red Bluff only) at different sites (Red Bluff and Preacher Creek) plus their interactions

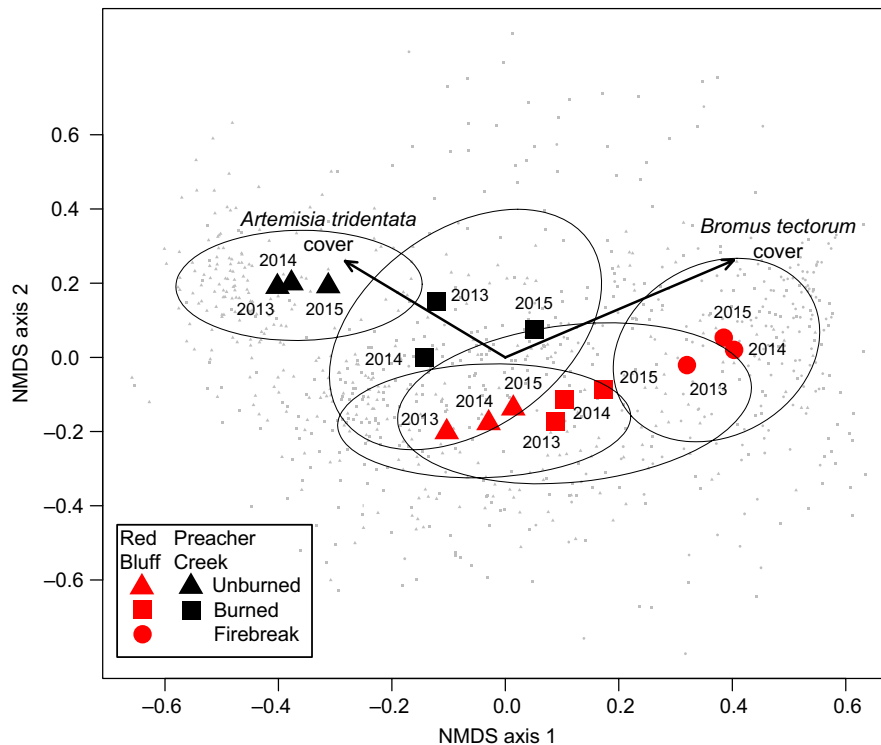


FIGURE 2 Variation in plant species composition in response to disturbance type: burned, unburned and soil disturbance (i.e. firebreak) at two sites, Red Bluff and Preacher Creek, from 2013 to 2015. The axes were calculated using NMDS and the dissimilarity index was Bray-Curtis. Ellipses represent the SD of the centroid for disturbance type and site averaged across years. The two vectors are fitted models of cover of *Artemisia tridentata* and *Bromus tectorum* cover in response to the two axes of the ordination. The two sites are indicated with different colours [Colour figure can be viewed at wileyonlinelibrary.com]

annually thereafter (Figure 1c). However, after 3 years native grass cover was still only 15%, 8.7% lower when compared to the unburned sites ($SE = 2.8$, $df = 197.2$, $t = -3.068$, $p = .06$) and 13% lower when compare to burned areas ($SE = 2.9$, $df = 197.2$, $t = 4.480$, $p < .001$).

Native forb cover did not differ among disturbance type (Table 3, Figure 3d). There was significant interaction among year and treatment due to a 5.6% decrease in forb cover in burned sites over the 3-year period ($SE = 1.3$, $df = 584.94$, $t = 4.6$, $p < .001$), and a 6% increase in forb cover in the firebreak over the 3-year period ($SE = 1.9$, $df = 599$, $t = -3.4$, $p = .02$).

4 | DISCUSSION

Plant community resilience to disturbance and resistance to *B. tectorum* invasion were impacted by the type of disturbance. In this study, the plant communities were largely resilient to fire and resisted *B. tectorum* invasion, but where soil disturbance occurred from the creation

of a firebreak, plant community resilience to disturbance and resistance to invasion were lower. The creation of the firebreak resulted in mortality of much of the native grass that otherwise survived in the burned areas. Ample bare ground in the firebreak resulted in an increase in cover of *B. tectorum* to 37% and lower native grass cover compared to the burned and unburned areas. The burned areas were both resilient and resistant; average native grass cover was the same in burned and unburned areas, and *B. tectorum* did not increase above 15% of total cover. The richness and cover of native forbs and grasses were minimally affected by fire and were similar to unburned areas.

Our study, demonstrating plant community resilience to fire, contrasts with other studies conducted in warmer and drier portions of the sagebrush biome (see examples in Taylor et al., 2014). These studies reported a large increase in *B. tectorum* after fire, at the expense of native grasses. Differences in resilience across a biome are not unexpected, as other studies have shown that resilience of plant communities to fire in semi-arid areas varies by amount of native grass cover, forb cover, region and climate (Chambers et al., 2014). Given that native grass cover was >20% in the unburned areas at our sites, representative of the

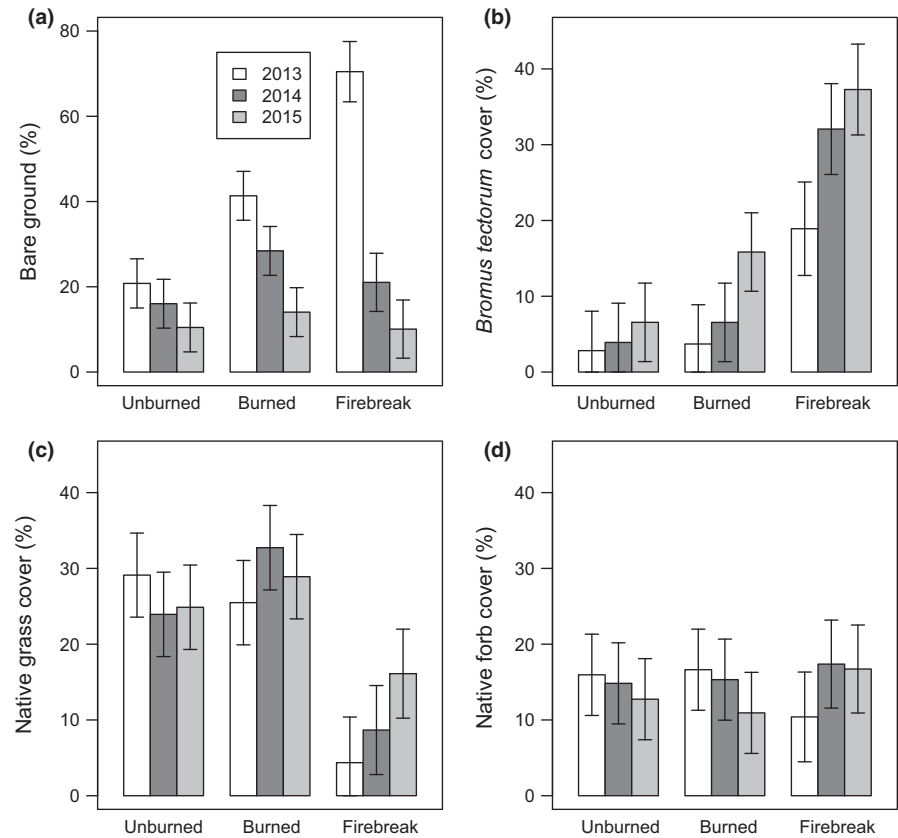


FIGURE 3 (a) Mean response of bare ground after fire, (b) mean response of *Bromus tectorum*, (c) native grass cover, (d) native forb cover (from one to three growing seasons after the fire) and by treatment (unburned, burned and firebreak). Error bars indicate the 95% CI of the mean

TABLE 3 Type III ANOVA table for bare ground, *Bromus tectorum*, native grass and native forb cover predicted by year (2013, 2014, 2015) since fire or soil disturbance (treatments: burned, unburned or firebreak) and their interaction. Mixed-effects models were fit and the Satterthwaite approximation was used for denominator *df*

	Mean Sq	Num <i>df</i>	Den <i>df</i>	F-value	<i>p</i>
Bare ground					
Year	69726	2	609.88	305.0	<.001
Disturbance	6321	2	63.29	27.6	<.001
Year × disturbance	14026	4	609.42	61.3	<.001
<i>Bromus tectorum</i>					
Year	5361.5	2	39.5	40.1	<.001
Disturbance	8229.3	2	601.02	61.6	<.001
Year × disturbance	1402.2	4	600.79	10.5	<.001
Native grass					
Year	844.2	2	607.96	4.5	.01
Disturbance	7058.5	2	61.91	37.9	<.001
Year × disturbance	2046.3	4	607.2	11.0	<.001
Native forb					
Year	892.3	2	590.45	4.1	.016
Disturbance	10.8	2	60.71	0.0	.96
Year × disturbance	3100.2	4	590.12	7.8	<.001

plant community pre-fire, and the regional climate is cooler and wetter than areas to the south and west of our study sites, we expected resilience to fire (Taylor et al., 2014). The burned plant community closely resembled the unburned after 3 years, with the exception to the slower recovery of *A. tridentata*. Slow recovery of *A. tridentata* has been recorded but does not by itself indicate a lack of resilience (Ellsworth, Wroblewski, Kauffman, & Reis, 2016). When placed into the context of

resilience, the results for native grass cover are similar to studies that have shown native grasses are resilient to fire (Antos, McCune, & Bara, 1983; Link, Gee, Thiede, & Beedlow, 1990).

Vegetation response to fire is dependent on pre-fire species composition and their traits, and is also dependent on the state of the extant vegetation (Chambers, Roundy, Blank, Meyer, & Whittaker, 2007; Condon et al., 2011; Davies et al., 2012). *A. tridentata* is not

a fire-tolerant species (Baker, 2009), and after fire at our sites more area was available for colonization by native grasses, and this can explain the increase in grass cover after fire. Fire decreased *A. tridentata*, suggesting that a prescribed burn in an area dominated by the non-fire adapted *A. tridentata* could increase the dominance of *B. tectorum* if a sufficient cover of native grasses and forbs is not present. Intact communities of native plants with only a small component of invasive plants may recover quicker and more completely than pre-fire communities with higher proportions of invasive plants. Thus, there may be a threshold condition of the pre-fire community, perhaps <20% native grass cover, which predisposes it to post-fire novel states dominated by invasive annual grasses (Germino et al., 2016; Hobbs et al., 2006).

A large increase in *B. tectorum* occurred where major soil disturbance (i.e. the firebreak) caused mortality of nearly all vegetation, leading to the lack of resistance to *B. tectorum* invasion and showing that low native grass cover is a predictor of *B. tectorum* invasion. This is similar to other studies that have shown soil disturbance promotes invasion by annual species, and introduced species in general, including *B. tectorum* (Kotanen, 1997; Lavin et al., 2013). The burned areas were largely resistant to *B. tectorum* invasion, with only a slight increase of *B. tectorum* to a mean of 15% cover over 3 years. The increase to 15% cover is still considerably less than for other sites where *B. tectorum* positively responded to fire (e.g. 40–80% cover, see Munson et al., 2015; Reed-Dustin, Mata-González, & Rodhouse, 2016) and increased to 37% in the firebreak.

5 | CONCLUSIONS

In cooler and wetter portions of the sagebrush steppe, characterized by *A. tridentata* subsp. *vaseyana*, plant communities exhibited both resilience and resistance to *B. tectorum* invasion following fire, but not to physical soil disturbance. Lack of a positive *B. tectorum* response to fire at our sites is supported by the modelling predictions of Brummer et al. (2016), who showed that the transformative ability of *B. tectorum* is constrained by climate and cover of native grasses. The firebreak, where the soil was highly disturbed, had less native grass cover because of mortality caused by creation of the firebreak and *B. tectorum* more easily invaded. This indicates plant community response to fire in the sagebrush steppe is dependent on disturbance type and varies in response to the extant plant community (Chambers et al., 2016).

Overall our results suggest that within the sagebrush biome where native grass cover is considerable (>20%) the community is resilient to fire, with native grasses recovering rapidly and the plant community composition resembling pre-burn composition. The only exception is the shrub *A. tridentata*, which is slower to recover. Plant communities are largely not resilient to extensive soil disturbance, which may lead to lower resistance to *B. tectorum* invasion. Therefore, we recommend avoiding extensive soil disturbance that facilitates invasion and conducting post-fire monitoring to determine if management

practices such as re-seeding of desired species are needed to prevent a transition to an alternative undesirable vegetation state.

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SUPPORTING INFORMATION

Additional Supporting Information may be found online in the supporting information tab for this article.

APPENDIX S1 Richness, cover different traits and by sites.

APPENDIX S2 Relative species abundance data.

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