



Fire and Grazing Influence Site Resistance to *Bromus tectorum* Through Their Effects on Shrub, Bunchgrass and Biocrust Communities in the Great Basin (USA)

Lea A. Condon^{1,2*}  and David A. Pyke²

¹Department of Botany and Plant Pathology, Oregon State University, 2082 Cordley Hall, Corvallis, Oregon 97333, USA; ²Present address: Forest and Rangeland Ecosystem Science Center, U.S. Geological Survey, Corvallis, Oregon 97331, USA

ABSTRACT

Shrubs, bunchgrasses and biological soil crusts (biocrusts) are believed to contribute to site resistance to plant invasions in the presence of cattle grazing. Although fire is a concomitant disturbance with grazing, little is known regarding their combined impacts on invasion resistance. We are the first to date to test the idea that biotic communities mediate the effects of disturbance on site resistance. We assessed cover of *Bromus tectorum*, shrubs, native bunchgrasses, lichens and mosses in 99 burned and unburned plots located on similar soils where fires occurred between 12 and 23 years before sampling. Structural equation modeling was used to test hypothesized relationships between environmental and disturbance characteristics, the biotic community and resistance to *B. tectorum*

cover. Characteristics of fire and grazing did not directly relate to cover of *B. tectorum*. Relationships were mediated through shrub, bunchgrass and biocrust communities. Increased site resistance following fire was associated with higher bunchgrass cover and recovery of bunchgrasses and mosses with time since fire. Evidence of grazing was more pronounced on burned sites and was positively correlated with the cover of *B. tectorum*, indicating an interaction between fire and grazing that decreases site resistance. Lichen cover showed a weak, negative relationship with cover of *B. tectorum*. Fire reduced near-term site resistance to *B. tectorum* on actively grazed rangelands. Independent of fire, grazing impacts resulted in reduced site resistance to *B. tectorum*, suggesting that grazing management that enhances plant and biocrust communities will also enhance site resistance.

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*Corresponding author; e-mail: lcondon@usgs.gov

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INTRODUCTION

Ecosystem responses to compound disturbances are of concern across biomes and continents as climate, land use, and fire interact (Westerling and others 2006). Shrub–steppe ecosystems (also known as temperate deserts and semi-deserts), where the primary land use is livestock grazing, make up 15% of Eurasia and 3% of North America (West 1983a). Grazing has likely reduced fire size in western Eurasia following millennia of livestock use with shifts in livestock types from grass-dependent to more browse-dependent animals as herbaceous vegetation has become limited (Breckle 1983; West 1983b). Unlike western Eurasia, the Great Basin of North America has only been grazed by livestock for less than 130 years. Over the last 80 years, increased livestock management in the Great Basin has led to improved herbaceous production and rangeland condition (Box 1990). Although these ecosystems have not and may never return to their pre-livestock-grazing condition, they do allow for the examination of impacts related to both fire and grazing on a system that is less altered by anthropogenic influences compared to similar ecosystems globally. When fire and grazing occur in the presence of invasive species, fire regimes can change and further promote invasive species (Rossiter and others 2003).

In Great Basin shrub–steppe ecosystems, fire and grazing are thought to regulate dominance of the exotic annual grass, *Bromus tectorum* L. (Pyke and others 2016), although they have rarely been examined simultaneously (Davies and others 2016). *Bromus tectorum* was introduced into the region from Eurasia in the late 1800 s and attained its current distribution by the 1930 s (Mack 1981). The invasion history of *B. tectorum* is long, as it is classified as an archaeophyte in Central Europe, having established there from its native steppe communities of southern Europe and the Middle East where it can dominate shrub–steppe ecosystems following excessive grazing (Terpó and others 1999; Kaczmarski 2000). Populations from Central Europe are known to exhibit reduced biomass and fewer inflorescences when situated with more native plant communities, particularly high cover of native bunchgrasses (Fenesi and others 2011). In the Great Basin, *B. tectorum* often creates a continuous fuel among perennial vegetation, where it dominates interspaces among vascular plants that were previously occupied by biological soil crusts (for example, lichens, mosses, and cyanobacteria on the soil surface), thus allowing fires to become more frequent than the time needed for many

native perennials to reach reproductive maturity (Brooks and others 2004). Bradley and others (2017) estimate *B. tectorum* is at 15% or greater cover on almost one-third of the Great Basin (210,000 km²) and that 10.7% of this area, over 22,000 km², burned between 2000 and 2014, demonstrating the extent of the grass–fire cycle in the region.

Biotic communities can limit the magnitude of invasions by exotic species (Levine and others 2004). We use the Great Basin sagebrush steppe as a model to understand potential mechanisms that lead to ecosystem resistance to *B. tectorum* in temperate shrub–steppe ecosystems. The Great Basin sagebrush steppe is a comparable ecosystem to those of Eurasia, containing many similar life-forms (for example, perennial bunchgrasses, fire-intolerant shrubs, and biological soil crusts [lichens, mosses, and cyanobacteria on the soil surface hereafter called biocrusts]; Walter and Box 1983). Understanding the strength of interactions between biotic communities and site resistance to *B. tectorum* in the presence of disturbances such as fire and grazing is crucial to the management of sagebrush steppe ecosystems. Here we use “resistance” in the ecological sense as it is used by D’Antonio and others (2009) to mean the “ability of a community to withstand encroachment by nonnative species.”

Our goal in this study is to provide a comprehensive understanding of the role of the biotic community: shrubs, native bunchgrasses, and biocrusts in maintaining site resistance to *B. tectorum* in the presence of both fire and grazing across the region. We build upon two models of site resistance to *B. tectorum*, one in the presence of fire (Condon and others 2011) and one in the presence of grazing (Reisner and others 2013), linking these models with the findings of many studies on interactions between biotic, environmental and disturbance indicators (Table 1). Resistance in these models depended on cover of perennial vegetation, cover of biocrusts, or the distance among perennial plants. Expanding upon these models, we characterize fire and grazing with multiple factors that could be employed by land managers to predict and possibly facilitate site resistance (grazing animal stocking levels, fire severity, extent of fire, and time since fire). Additionally, we anticipated an interaction between fire and grazing, since cattle preferably use areas with light to moderate burn severity over unburned areas (Clark and others 2014). We expected that biocrusts would be more sensitive to disturbance, particularly grazing, compared to native bunchgrasses. In areas surrounding the Great Basin, results from surveys inside and

Table 1. Components of Hypotheses Represented by Initial Conceptual Model (Figure S1)

Site resistance	
Abiotic factors	
HLE → + <i>Bromus</i>	↓ Increases in heat load result in reduced site resistance to <i>Bromus tectorum</i> L. (Chambers and others 2007; Condon and others 2011)
HLE → – grass cover	↓ Increases in heat load result in decreased productivity of bunchgrasses (Davies and others 2007) ¹
SPP → + bare ground	↓ Increased sand content is associated with increases in bare ground (BG) and <i>B. tectorum</i> establishment ¹
BG → + <i>Bromus</i>	↓ Safe sites in the form of bare ground (BG) increase establishment rates of <i>B. tectorum</i> (Fowler 1988) ¹
SPP → + <i>Bromus</i>	↓ Soils with deeper, coarser textures are associated with increased cover of <i>B. tectorum</i> (Stewart and Hull 1949) ¹
SPP → ± grass comp	↓ ↑ Increases in sand content are associated with different compositions of native bunchgrasses ¹
Grazing impacts	
Grazing → – biocrusts	↓ Grazing results in trampling of biocrusts and increases safe sites for establishment of <i>B. tectorum</i> (Ponzetti and others 2007) ¹
Grazing → ± <i>Bromus</i>	↓ ↑ Grazing results in a decrease in cover of <i>B. tectorum</i> by herbivory (Hempy-Mayer and Pyke 2009), an increase through propagule pressure via animal mediated seed dispersal (Schiffman 1997) or no direct effect in some areas ¹
Grazing → + gaps	↓ Increases in grazing intensity relate to positive increases in community gap structure (Condon and Pyke 2016) ¹
Grazing → – grass cover	↓ Cattle grazing decreases the cover of native bunchgrasses (Briske and Richards 1995) ¹
Grazing → ± grass comp	↓ ↑ Cattle grazing selects for a composition of native bunchgrasses that are more grazing-resistant (Briske and Richards 1995) ¹
Fire impacts	
Fire → – shrubs → + gaps	↓ By reducing understory species (shrubs, bunchgrasses, mosses, and lichens), fire increases gap community structure and temporarily increases safe sites for <i>B. tectorum</i> (Johansen and others 1984; Chambers and others 2007; Pyke and others 2015).
Fire → – grass cover → + gaps	Understory species recover with increasing time since fire and take longer to recover into fires of greater extent (Johansen and others 1984; Condon and Weisberg 2016)
Fire → – lichens/moss → + gaps	
Gaps → + <i>Bromus</i>	
Fire → + <i>Bromus</i>	↓ Fire may result in a direct increase in <i>B. tectorum</i> (Miller and others 2013)
Fire → + grass cover	↑ Fire may increase cover of native bunchgrasses after short-term reductions in cover (Cooper and others 2011)
Biotic interactions	
Grass cover → – <i>Bromus</i>	↑ Increased native bunchgrass cover results in fewer safe sites for establishment and reduced cover of <i>B. tectorum</i> (Chambers and others 2007; Condon and others 2011)
Shrubs → – <i>Bromus</i>	↑ Cover of <i>B. tectorum</i> is reduced in the presence of shrubs, mosses, and lichens (Serpe and others 2006, 2008; Reisner and others 2015)
Moss → – <i>Bromus</i>	
Lichen → – <i>Bromus</i>	
Moss → + grass cover	↑ The establishment, survival, nutrient status, and water relations of native bunchgrasses are influenced by mosses and lichens (Prasse and Bornkamm 2000; Harper and Belnap 2001)
Lichen → + grass cover	
Grass comp → ± gaps	↓ ↑ Native bunchgrass composition influences the community gap structure with different life-forms (James and others 2008) ¹
Bunchgrass → – gaps	↑ Increased cover of native bunchgrasses reduces the community gap structure (Herrick and others 2005) ¹
Gaps → + bare ground	↓ Increases in the community gap structure among perennial vegetation increases the number of safe sites for <i>B. tectorum</i> as well as the cover of <i>B. tectorum</i> as a result of increased resource availability (James and others 2008) ¹
Bare ground → + <i>Bromus</i>	
Gaps → + <i>Bromus</i>	
Interaction between fire and grazing	
Fire → + grazing	↓ Fire promotes grazing as cattle are more likely to use burned sites (Clark and others 2014)

HLE, heat load index; SPP, soil physical properties.

¹Demonstrated in Reisner and others 2013 and tested region-wide in this study.

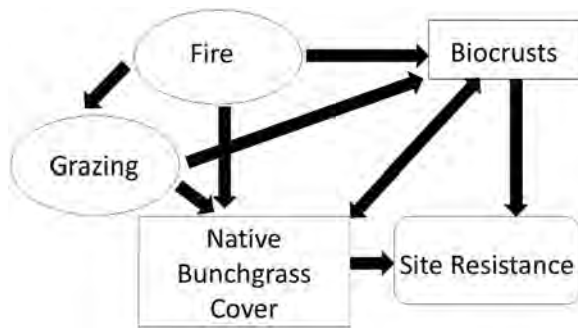


Figure 1. Meta-model representing the influence of biocrusts and native bunchgrass cover on site resistance (*Bromus tectorum* L. cover) in the presence of fire and grazing. Disturbance variables are presented in ovals. Biotic factors are presented in rectangles. Site resistance (*Bromus tectorum* L. cover) is presented in a rounded rectangle. Only the presence and not the strength of these relationships is hypothesized in the model.

outside of livestock exclosures have demonstrated differences in biocrust abundance (Kleiner and Harper 1972) and community composition (Ponzetti and McCune 2001), indicating that some biocrusts are sensitive to livestock presence. In contrast, biocrust community composition following fire was similar to unburned sites when *B. tectorum* cover was low (less than 12% and one-third the cover of perennial grasses) (Bowker and others 2004). Similarly, cover of native bunchgrasses is reduced and composition is altered following sustained grazing by cattle (Briske and Richards 1995), and this in turn may increase the spatial distances among perennial grasses (Reisner and others 2013). Cover of bunchgrasses is temporarily reduced, but often increases following fire (Cooper and others 2011). Grasses located under shrubs will likely die because of the increased temperature of the burning woody fuel (Boyd and others 2015) and thus may increase gaps among perennial plants. We expected to observe interactions between biocrusts and native bunchgrasses since biocrusts have been shown to facilitate the establishment, survival, nutrient status, and water relations of native bunchgrasses (Prasse and Bornkamm 2000; Harper and Belnap 2001). These relationships are conceptually presented in a meta-model (Figure 1).

Hypothesized relationships between fire and grazing on impacts to lichens, mosses, shrubs, and native bunchgrasses (cover and composition) are presented using a system-level approach due to the large number of potential interconnections among biotic, environmental, and disturbance indicators (Table 1, Appendix 1 Figure S1). At the regional scale, we expected sites to vary in their inherent

resistance to invasion by *B. tectorum* based on the environmental tolerances of *B. tectorum* (Chambers and others 2007; Condon and others 2011; Chambers and others 2014). Our area of inference is the northern Great Basin with a wider range of annual precipitation than considered by previous models (Condon and others 2011; Reisner and others 2013). In sum, we hypothesized that single fires lead to temporary declines in site resistance, but that decreases in grazing intensity by livestock, either before or after the fire, would lead to increases in site resistance, mediated through increases in the cover of native bunchgrasses and biological soil crusts and through reductions in the distances among perennial plants.

MATERIALS AND METHODS

Area of Inference and Study Sites

The area of inference consists of big sagebrush (subspecies of *Artemisia tridentata*, family Asteraceae) ecosystems on loamy-textured surface soils, managed by the Bureau of Land Management (BLM) within southeastern Oregon, southwestern to southcentral Idaho, northern Nevada, and western Utah. Wyoming big sagebrush and mountain big sagebrush subspecies of sagebrush (*A. t. ssp. wyomingensis* Beetle and Young and *A. t. ssp. vaseyana* (Rydb.) Beetle) were lumped in this study. Common native perennial bunchgrasses encountered include *Achnatherum hymenoides* (Roem. and Schult.) Barkworth, *Elymus elymoides* (Raf.) Swezy, *Poa secunda* J. Presl, and *Pseudoroegneria spicata* (Pursch) Á. Löve. The region spans a gradient of increasing productivity from south to north and from lower to higher elevations, covering seven Major Land Resource Areas (similar to ecoregions; USDA NRCS 2006, Figure 2). Annual average precipitation across the region ranged between 158 and 419 mm (West 1983c), while the sites that we sampled ranged from 127 to 556 mm of precipitation during the first three years following fires. Landscapes represented in our sample have likely experienced regular grazing for nearly 100 years. Since the 1970s, some grazing allotments have changed from season-long or continuous year-round livestock grazing to deferred or rest-rotation grazing systems to provide annual changes in grazing seasons and periods of rest (no grazing) (Howery and others 2009).

Fifteen fire locations included in this study were a subset from Knutson and others (2014). Each location was within a single grazing allotment or pasture within an allotment (Figure 2) and con-

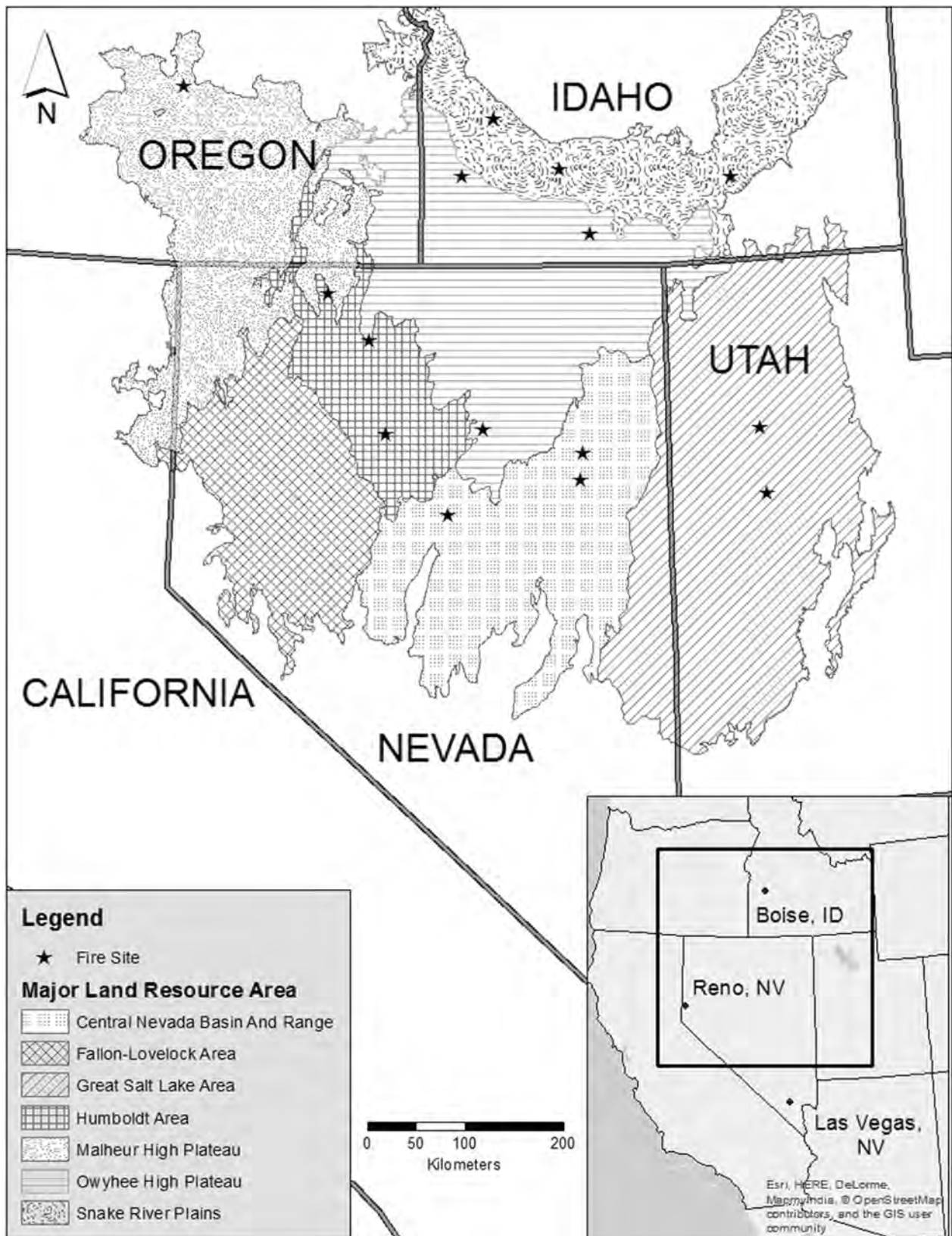


Figure 2. The locations of the fifteen fires surveyed relative to the major land resource areas across the Great Basin, USA.

Table 2. Variables Considered in Site Selection from Knutson and others 2014¹

Description	Units	Mean (S.D.)	Range
<i>Average precipitation</i> ¹ (PRISM 2010)			
Average precipitation is given for each of the three water years following the fire as modeled by PRISM	Mm	WY 1-256 (54) WY 2-274 (74) WY 3-300 (101)	WY 1-179-373 WY 2-168-437 WY 3-155-556
<i>Fire severity</i> ¹ (MTBS 2012)			
Fire severity was estimated with dNBR. Sites were selected to cover a range of fire severities. Plots were classified according to their dominant fire severity	N/A	N/A	Unburned—51 p Low severity—29 p Moderate severity—16 p High severity—3 p
<i>Season of fire</i> ¹ (MTBS 2012)			
Julian date of ignition	N/A	222 August 10 (24.5)	160-259 (June 9-Sept 16)
<i>Time since fire</i> ¹ (Pilliod and Welty 2013)			
The number of years between the fire and the 2012-13 sampling date	Years	16 (3.8)	12-23 (1990-2001)
<i>Total area burned</i> ¹ (Pilliod and Welty 2013)			
The area inside the fire perimeter measured in ArcMap	Hectares	6013.9 (10,269.3)	540.7-42,920.6
<i>Average and standard deviation in the gap among perennial plants</i> (field measured, Knutson and others 2014)			
Standard deviation of the average (avg) gap among perennial plants along the 50-m transects at each plot	Cm	Avg gap-230.1 (553.7) SD of avg gap-199.5 (297.8)	Average-36.3-5000 SD-0-1962
<i>Dung density</i> ¹ (unpublished data, archived at USGS SAGEMAP (http://sagemap.wr.usgs.gov/ESR_Chrono.aspx))			
Dung from cattle per meter squared counted in shrub belt transects.	#/m ²	5 (5)	0-25
<i>Distance from water</i> (derived from GIS with http://nhd.usgs.gov and 1-m resolution NAIP imagery)			
Mapped and measured with NAIP and National Hydrography Dataset	Meters	1915.1 (1294.2)	144.3-5802.8
<i>Active AUMs</i> (Rangeland Administration System http://www.blm.gov/ras/)			
Active AUMs as of September 15, 2015	AUMs	5320.7 (4555.9)	0-13,326
<i>Suspended AUMs</i> (Rangeland Administration System http://www.blm.gov/ras/)			
Suspended AUMs as of September 15, 2015	AUMs	1297.6 (2269.6)	0-7473
<i>Permitted AUMs</i>			
Permitted AUMs as of September 15, 2015 (estimated capacity)	AUMs	6618.2 (5858.8)	0-15,174

All listed variables were considered in analysis. Average values and (standard deviations) are shown. Headings are variables (sources of information).

AUMs, animal unit months; dNBR, differenced normalized burn ratio; MTBS, monitoring trends and burn severity database; p, plots; WY, water year.

¹Sites were selected to represent the range of values.

sisted of at least three plots each within: (1) a wildfire and not reseeded after the fire; and (2) an unburned area that surrounded the burned area, but on the same ecological site as burned plots (that is, land potential; USDA NRCS 2003). Plots were

randomly placed within similar soil map unit components within the fire and were verified in the field to insure the same ecological site. Fire locations were selected to cover a broad range of predictor variable values, which included average

precipitation for each of three years following the fire, elevation, fire severity, time since fire, season of ignition, total acres burned, and grazing intensity represented by cattle dung density (dung density), Table 2). We have described fire locations in regard to both cover of *B. tectorum* found in burned and unburned plots and site resistance as determined by soil temperature and moisture regimes (Chambers and others 2014, Table 3), demonstrating that these sites are within the range of *B. tectorum*. Further description of all locations can be found in Knutson and others 2014. Plots (total of 99 plots; one fire location had six unburned plots and three burned plots, and another fire had a total of six unburned plots and six burned plots) were circular with three, 50-m transects beginning 5 m from a central point and radiating from that point every 120° (Herrick and others 2005). Shrub density by species was counted in 2-m or 6-m (burned or unburned plots) by 50-m belt transects (Knutson and others 2014). In 2012 and 2013, we measured canopy cover of biocrusts (mosses and lichens) and vascular plant life-forms (shrubs, native bunchgrass, and annual grasses (exclusively *B. tectorum*)). Cover was estimated visually (to the nearest 1%) within 0.25-m² square quadrats located at 10-m intervals along each transect for a total of 15 quadrats per plot. Factors that we expected to affect site resistance to *B. tectorum* (quantified as cover of *B. tectorum*) were measured at scales that matched the scale of process. For example, grazing is measured at a coarse scale (dung density within belt

transects) and cover of biocrusts is measured at a fine scale (canopy cover in 0.25-m² square quadrats).

Characterization of Fire

For each fire, we included characteristics that are typically used to define fire regimes: severity, extent (area burned), and season of fire (Sugihara and others 2006, Table 1) and we added time since fire. Frequency of fire was not addressed because we selected sites that had burned only once since 1970 (Knutson and others 2014). Fire severity was represented by shrub cover lost to fire, which was more plot specific, compared to what was detected with remote sensing (Monitoring Trends in Burn Severity [MTBS] 2012). Fire extent was calculated in ArcMap 10.2 (ESRI 2013), and season of fire was reported from MTBS (2012, Table 1).

Characterization of Livestock Grazing

Characterizing cattle use on public lands is difficult in the Great Basin because monitoring data are often of different data types among allotments or management units (Veblen and others 2014). We examined several indicators of grazing intensity that were measured consistently and may relate to site resistance across the region. Using a piosphere approach, increasing distance to water, including springs, seeps, wells, and associated water troughs, was used as a proxy for declining grazing intensity (Andrew and Lange 1986; Landsburg and others

Table 3. Fire Names (Locations) and Fire Codes Summarized by Both Range in Cover of *Bromus tectorum* and Associated Resistance and Resilience Class Based on Soil Temperature and Moisture Regimes

Fire name, fire code	<i>Bromus tectorum</i> cover		Resistance and resilience class
	Burned plots	Unburned plots	
Castle Creek, F052	2–5 (3.0)	0–8 (4.0)	High
Pigtail Butte, F074	4–7 (5.7)	0 (0)	Low
RRMP, F116	3–11 (6.7)	13–19 (15.0)	Low
Wapi, F480	3–5 (4)	2–8 (4.3)	Low
Frenchie Flat, J194	11–15 (13.3)	2–10 (5.3)	Low
Junction, J458	13–15 (14)	5–15 (11.3)	Low
Trail Canyon, K909	14–15 (14.7)	3–10 (7)	Low
Butte, K267	10–15 (12.3)	0–2 (1.3)	Low
Cinder Butte, N567	7–9 (8)	6–14 (11)	Moderate
Eight Mile, Q161	15–16 (15.3)	10–14 (12)	Low
Keg Mountain, Q989	14–15 (14.7)	5–8 (6.3)	Low
Rabbit, X075	1–13 (6.3)	0 (0)	Low
Buffalo, X393	0–4 (2)	0–6 (1.7)	Low
King, X465	14–15 (14.3)	10–15 (13)	Low
East Slick, Z269	15–16 (15.3)	13–15 (14.3)	Low

Average cover on burned and unburned plots is shown in parentheses.

1997). Distance to the closest single water source was measured in ArcMap 10.2 (ESRI 2013) using a combination of 1-m resolution images from the National Agriculture Imagery Program and the National Hydrography Dataset (accessed February 10, 2016; <http://nhd.usgs.gov>, Table 1). A second measure of grazing intensity on site resistance was gap size (distance) among perennial vegetation (Reisner and others 2013; Condon and Pyke 2016). We used the standard deviation of the average gap size among perennial plants because this estimate of variance took into account site conditions and showed a stronger correlation with *B. tectorum* cover than average gap size. The standard deviation of the average gap size among perennial plants has a Pearson's correlation of 0.76 with the variable used by Reisner and others, percent of the line covered by gaps greater than 200 cm. A third measure, dung density, came from the Knutson and others (2014) dataset (sagemap.wr.usgs.gov/ESR_Chrono.aspx, Table 1).

We quantified current and historic grazing intensity with records provided by the BLM Rangeland Administration System (RAS 2015; <http://www.blm.gov/ras/>, accessed September 15, 2015). RAS data have recently been used to examine landscape-level cattle impacts on plant productivity and sage grouse population trends (Monroe and others 2017) and provides numbers of active use (synonymous with billed use, the amount of forage that livestock will likely use during the grazing period) and permitted use (maximum level of forage in the allotment that a livestock can use) in animal unit months (AUMs) per grazing allotment. AUMs are an estimate of the amount of forage needed to sustain a standard animal unit (for example, a 454-kg cow with a suckling calf for 1 month) onsite that can be translated into the number of animals the site can feed for a set time (Ruyle and Ogen 1993). RAS also reports the number of suspended AUMs, which is the number of AUMs removed from use that are not likely to be replaced. This should not be confused with AUMs that are temporarily suspended due to drought. Suspended AUMs can be viewed as an indicator that past livestock stocking levels were not meeting management objectives (vegetation or soil) and a long-term (quasi-permanent) AUM suspension was deemed appropriate to halt further decline in rangeland condition (Ruyle and Ogen 1993).

For each allotment, we created indices of past (suspended AUMs) and currently active (billed AUMs) grazing and divided them by the number permitted to standardize for differences in the allotment sizes. BLM grazing records immediately

before and after each fire were not accessible for all sites. We used records that were available as of September 15, 2015, from the RAS. According to BLM staff (Lynnda Jackson, personal communication, September 9, 2015), AUMs do not change much making these records an acceptable substitute for pre- and post-fire livestock use. Out of a total of 15 grazing allotments that included all plots in this study, all but one site was reported as having active AUMs and 7 sites had suspended AUMs. Common federal practice at the time of these fires was that livestock grazing be halted for a minimum of two growing seasons following fires and then reinstated (Clark and others 2014), although some offices currently require that recovery objectives be met based on vegetation and soil factors before grazing resumes (Bureau of Land Management 2007).

Data Analysis

Structural equation modeling (SEM) was implemented with AMOS version 23.0.0 (Arbuckle 2014) and was used to evaluate hypothesized effects of fire, grazing, and the interconnections between biocrusts and vegetation with subsequent effects on cover of *B. tectorum* based on an a priori conceptual model (Appendix 1 Figure S1). Specific pathways among environmental factors, grazing impacts, fire impacts, and biotic interactions are described and justified in Table 1. The use of SEM allowed us to assess effects of fire versus grazing on the cover of biocrusts and native bunchgrasses as they relate to site resistance to *B. tectorum*. As opposed to other multivariate analyses, SEM provides confirmatory tests and is more suitable for evaluation of multivariate hypotheses (Grace 2006). Response variables are those that are at the terminal end of a pathway (Appendix 1 Figure S1). Model specification, evaluation, and interpretation followed the guidelines in Grace and others (2012). Global estimation and evaluation methods were chosen for this application. Pathways are summarized by linear relationships based on the relatively short amount of time since fire of 12–23 years.

Non-metric multidimensional scaling (NMS) ordination axes of bunchgrass species cover were used as an indicator of native bunchgrass community composition (McCune and Grace 2002). All variables were z-transformed (the mean was subtracted from each value, and the resulting difference was divided by the standard deviation of the variable), with the exception of the “burned” variable, which was binary (burned or not burned) and so not standardized.

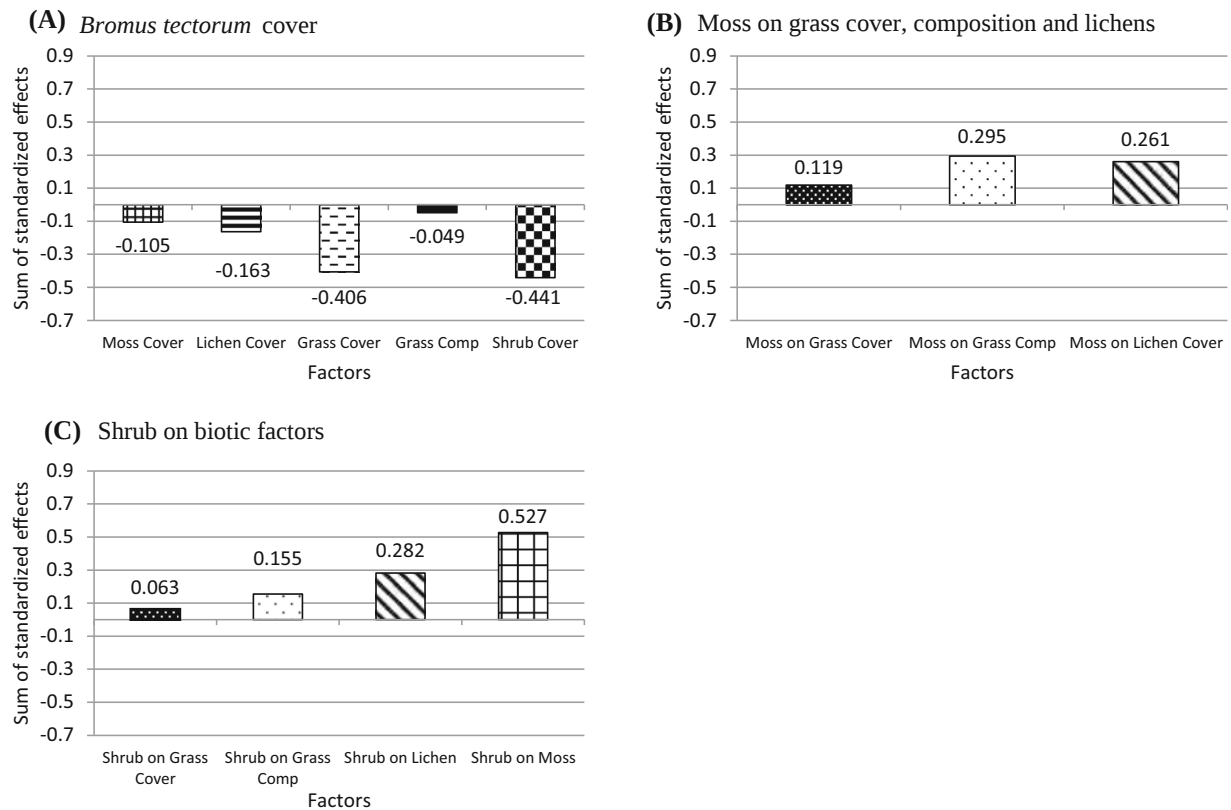


Figure 3. Sum of the standardized effects of **A** biotic factors on *Bromus tectorum*, **B** moss cover on native bunchgrass cover, composition, and lichens, **C** shrub cover on native bunchgrass cover, composition, lichens, and mosses. Abbreviations for significant factors are as follows: grass cover–native bunchgrass cover, grass comp–native bunchgrass composition. Y-axis is unitless. Pathways used to calculate these effects are presented in Figure S3.

We included all resulting pathways from Reisner and others (2013) in our a priori conceptual model. The relationship between perennial herbaceous cover and cheatgrass in the presence of fire was established in Condon and others (2011), but here we replace perennial herbaceous cover with native bunchgrass cover so as to be consistent with Reisner and others (2013). Hypothesized pathways that were added to characterize disturbances were first visually examined in scatterplots for relationships among variables of interest before being added to our conceptual model. Season of fire, as represented by the Julian date of ignition (Table 1), did not show a relationship with biocrust or bunchgrass recovery and so it was not included in our a priori model. Although fire severity as calculated by MTBS was included in our selection of surveyed sites, the ecologically meaningful metrics do not always relate well to MTBS (Table 1, Kolden and others 2015). Instead, we used the amount of shrub cover lost to fire to represent fire severity, which showed stronger relationships in the model compared with fire severity from MTBS. Other

hypothesized pathways were as described above (Table 1, Figure S1). In an effort to achieve parsimony, pathways were only kept in the model if the associated p value was less than 0.1. Model fit was evaluated with both a Chi-squared test and a root-mean-squared error of approximation (RMSEA). A RMSEA takes into account the sample size and the number of pathways evaluated. A RMSEA that includes zero and an insignificant Chi-squared test indicates that the model fits the data well. Sum of standardized effects were calculated for factors of interest following methods described in Grace (2006).

RESULTS

A model only including significant pathways showed a reasonable fit to the data (RMSEA 0.000, $X^2 = 77.5$, $p = 0.309$, $df = 72$). Neither fire nor grazing produced direct effects on *B. tectorum* cover, but their impacts were expressed indirectly through impacts on other biotic factors (Figure S2). The model provides evidence that increases in cover of

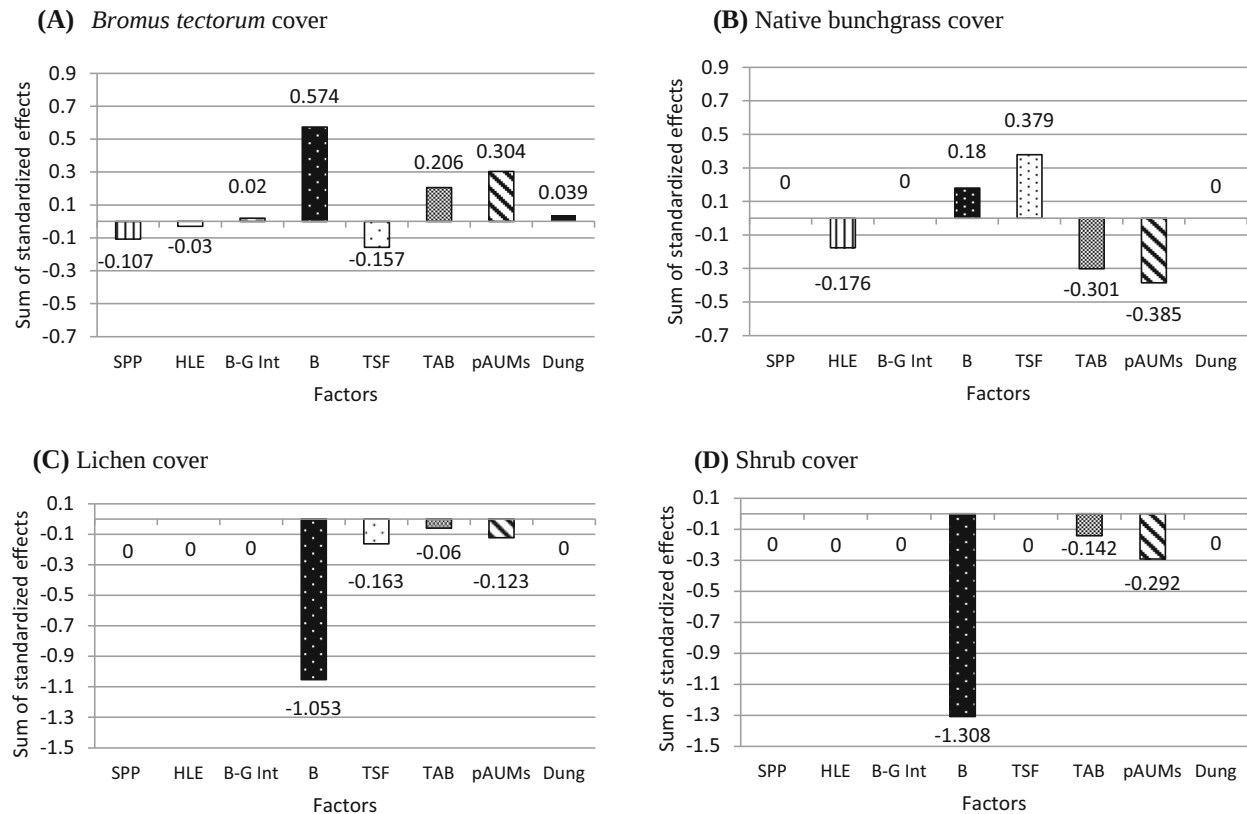


Figure 4. Sum of the standardized effects of fire, grazing, and environmental factors on **A** *Bromus tectorum* cover, **B** native bunchgrass cover, **C** lichen cover and **D** shrub cover. Abbreviations for significant factors are as follows: SPP—soil physical properties, HLE—heat load exposure, B—burned, B-G Int—burned area–grazing interaction, TSF—time since fire, TAB—total area burned, pAUMs—proportion of suspended AUMs. Y-axis is unit less. Pathways used to calculate these effects are presented in Figure S4. *Bromus* is also affected by gaps among perennials with a standardized effect of 0.204.

bare ground, shrubs, native bunchgrasses, and lichens along with decreases in the variation in sizes of gaps among perennial plants are directly associated with reduced cover of *B. tectorum*. Given that cover of *B. tectorum* was largely driven by the response of the biotic community to disturbance, we present our results in the following order: relationships among biotic factors including *B. tectorum*, relationships between biotic factors and disturbance, and relationships between biotic and abiotic factors. Additionally, pathways included in each sum of standardized effects are outlined in Figure S3 for Figure 3 and Figure S4 for Figure 4 for repeatability.

Biotic factors reduced cover of *B. tectorum*. Standardized effects of shrub, native bunchgrass, lichen, and moss cover, and to a lesser degree, native bunchgrass composition were all associated with reduced cover of *B. tectorum* (Figure 3). Increased moss cover was associated with increased lichen cover, native bunchgrass cover, and composition (Figure 3). Increased shrub cover was directly

associated with reduced cover of *B. tectorum* and increased lichen and moss cover. Increased shrub cover was indirectly associated with increased native bunchgrass cover and composition. Increased variation in the size of gaps among perennials is a measure of disturbance effects on the biotic community, which had a subsequent direct effect on facilitating cover of *B. tectorum* (Figure 4, Figure S2).

Fire and grazing affected biotic factors (Figure 4). Cover of *B. tectorum* increased following fire and with greater total area burned (Figure 4a). Cover of *B. tectorum* decreased with increasing time since fire. Active AUMs did not have a role in the model explaining biotic response, but increased historical grazing pressure represented by suspended AUMs, and to a lesser degree, increases in dung density increased *B. tectorum* cover. Further increases in grazing pressure were observed on burned sites, leading to further increases in cover of *B. tectorum* (burned area–grazing interaction, Figure 4a).

Native bunchgrass cover increased with fire and time since fire although reductions in cover were observed on sites with greater amounts of heat load, of total area burned, and of historical grazing pressure as represented by suspended AUMs (Figure 4b). Lichens were observed to be sensitive to fire, time since fire, total area burned, and historical grazing pressure as represented by suspended AUMs (Figure 4c). Shrub cover was reduced in both the presence of fire and on sites with greater amounts of total area burned (Figure 4d). Additional reductions in shrub cover were seen on sites with increased grazing pressure as represented by suspended AUMs.

Environmental factors of soil physical properties and heat load content also contributed to the explanation for *B. tectorum* cover. Increases in both soil physical properties (sand content) and heat load index were associated with reduced cover of *B. tectorum* (Figure 4a). In addition, increases in heat load index demonstrated reduced cover of native bunchgrasses on warmer and drier sites (Figure 4b).

DISCUSSION

We are the first to quantify that site resistance to *B. tectorum* across the sagebrush steppe of the Great Basin is mediated through changes in the biotic community and those changes are driven by fire and livestock grazing. None of our studied disturbance factors had direct impacts on ecosystem resistance to *B. tectorum*, but rather they negatively impacted other biotic factors that in turn reduced site resistance. Factors relating to reduced *B. tectorum* cover were high cover of shrubs, perennial bunchgrasses, mosses, lichens, and bare ground and low variation in gap distances among perennial plants supporting previous models (Condon and others 2011; Reisner and others 2013) and studies (Chambers and others 2007). We had hypothesized that the proportion of active AUMs, representing grazing disturbance, and that the three factors representing fire disturbance: burning, time since fire, and acres burned, would be directly related to *B. tectorum* cover. However, none of these relationships were supported by the model. In addition, the sign of the relationship between cover of bare ground and *B. tectorum* cover in our model was reversed from that seen by Reisner and others (2013), but we believe differences in study designs may explain these opposing results.

Our study did not attempt to find locations within 100 m of livestock water points to describe conditions of areas with extreme livestock use

(Reisner and others 2013). We accepted whatever distance occurred, and since more lands within the Great Basin are beyond 100 m from water, we were less likely to sample highly trampled lands with sustained overuse by livestock. The highly trampled areas near water in Reisner and others (2013) had both high *B. tectorum* cover and high cover of disturbed bare ground. Livestock hoof action likely broke up biocrusts, and killed perennial plants, while also working *B. tectorum* seed into the soil providing safe sites for establishment. Tolerance to grazing likely allowed *B. tectorum* to maintain high cover each year (Pyke 1987; Hempy-Mayer and Pyke 2009). In contrast, higher cover of bare ground in our study was associated with areas having larger distances from water and more native bunchgrass cover. These are likely locations where perennial plants and their roots dominate interspaces (Aguiar and Sala 1999; Reisner and others 2015) making it more difficult for *B. tectorum* to establish and produce high cover or large populations (Reichenberger and Pyke 1990).

Shrub and bunchgrass cover were the two most important biotic factors relating to site resistance, with direct and nearly equal negative relationships on *B. tectorum* cover. Increases in shrub cover facilitated increases in cover and composition of native bunchgrasses, and to a greater degree, increases in cover of lichens and mosses. Mosses facilitated both native bunchgrasses and lichens. These relationships were observed over the complete range of precipitation and temperature gradients present across the Great Basin.

Site resistance was also directly related to low variation in gap distances among perennials and lichen cover on *B. tectorum* cover. Gap variation was reduced when cover and composition of native bunchgrasses increased, likely due to having fewer long gaps and more short gaps among perennials, which is consistent with Reisner and others (2013). Although low variation could result from a large number of long gaps among perennial plants, only one plot fit this scenario of low perennial gap variation with high cheatgrass cover.

Abiotic factors resulted in some unexpected relationships, likely due to the regional scope of our study compared to both Condon and others (2011) and Reisner and others (2013). The positive relationship between high sand and bare ground cover was anticipated, but the positive relationship between heat load and bare ground was not hypothesized largely because it was not a significant factor in the model by Reisner and others (2013). However, both Condon and others (2011) and Reisner and others (2015) did find that warmer

and drier sites are more prone to *B. tectorum* invasion which our model supports. Simultaneously, the idea that more arid sites experienced greater increases in gaps among perennial plants fits within the concepts of resistance and resilience, under which, arid sites are more susceptible to invasion by *B. tectorum* following disturbance (Chambers and others 2014).

When perennial plants and biocrusts are intact, sites are resistant to *B. tectorum* and the subsequent creation of continuous fuels (Condon and others 2011; Reisner and others 2013). When *B. tectorum* is present in the ecosystem, fuels and subsequent fires are likely to be continuous and of larger extent. When grazing is light, perennial grasses remain in the interspaces (Reisner and others 2015) where they are more likely to survive fire. The acute disturbance of fire was strongly associated with reduced cover of shrubs, largely the fire-intolerant *A. tridentata*, and of biocrusts, leaving a void for increases in cover of *B. tectorum*. Large fires reduced bunchgrass cover and may relate to changes in fire behavior (for example, higher fire intensity producing lethal temperatures for bunchgrasses), but the mere fact that a fire burned the area tended to favor bunchgrass cover. In addition, some recovery of site resistance was observed with increasing time since fire of 12–23 years. Fire also had the biggest impact on increasing gap distances among perennials and adding to a net increase in *B. tectorum* cover following fire, likely due to the removal of shrubs (Pyke and others 2014). Native perennial grasslands with scattered sagebrush are thought to be maintained by fire (Wright and others 1979), which corroborates our finding of a positive effect of fire on bunchgrass cover. Recovery of shrubs following fire in the Great Basin is slow and patchy (Nelson and others 2014; Condon and Weisberg 2016) corroborating our observed lack of shrub recovery.

We expected that the effect of fire on native herbaceous flora would be temporary. Bunchgrasses and mosses increased in cover with increasing time since fire and were associated with decreased cover of *B. tectorum*. However, lichens did not increase with increasing time since fire. Bowker and others (2004) observed no significant differences in species composition of mosses or lichens following fire on sites that were ungrazed by livestock for 20 years in the Columbia Basin. Their burned locations tended to have lower mean cover on burned versus unburned areas. Our locations were grazed both before and shortly after the fires.

Significant factors in our study that characterized relationships between grazing intensity and vege-

tation relating to resistance to *B. tectorum* were indicators of long-term impacts: suspensions of AUMs, increases in the standard deviation of gap size among perennials, and dung from cattle since dung tends to persist in the cold desert of the Great Basin due to the absence of dung beetles and termites (Mack and Thompson 1982). Given our results, the first two factors should be thought of as indicators that the plant community has not yet recovered from past grazing disturbances (ecosystem resilience) and has not regained resistance to *B. tectorum*. Suspensions of AUMs may have been due in part to historical high levels of grazing by sheep (USDA, Forest Service 2012). The Animal Unit Equivalent of a mature sheep is 0.2, meaning that five sheep will consume the equivalent forage of one cow (Pratt and Rasmussen 2001). Sheep will browse shrubs and tend to be more selective in the grasses that they graze compared with cattle (Wilson and Harrington 1984; USDA, Forest Service 2012). Assuming that animal unit equivalents are maintained, a site being grazed by sheep is subjected to five times the number of hoofs compared with a site being grazed by cattle. Sheep also apply more total hoof pressure than cattle at the same animal units because sheep apply half the static pressure per animal 83 kPa relative to 192 kPa for cattle, but five times as many animals (Willatt and Pullar 1983). If suspended AUMs were due to sheep, the increased consumption of shrubs and increased level of trampling may explain why we observed reduced cover of shrubs with increased proportions of suspended AUMs, as sagebrush seedlings can be eliminated by trampling (Owens and Norton 1992). Although we do not have dates for when long-term grazing suspensions were implemented, we observed reduced cover of shrubs and bunchgrasses where these suspensions occurred. Even though one might expect the opposite with a reduction in grazing pressure, these indicators of grazing intensity are associated with increased cover of *B. tectorum*, but this is typical of a site that has crossed a threshold to a new stable state where nonequilibrium system processes are operating at the community level (Briske and others 2017).

Separating the current and historic effects of grazing on our study sites is nearly impossible with the use of dung counts. Dung that was present before fires likely burned on plots within fire perimeters and yet we still saw increases in dung density on burned, relative to unburned, plots, with effects associated with increased cover of *B. tectorum*. It is notable that active AUMs did not demonstrate a relationship with *B. tectorum* in our

study. Effects of the current grazing on cover of *B. tectorum* are complex as grazing can lead to reductions in cover of *B. tectorum* (Hempy-Mayer and Pyke 2009), but the timing of grazing is critical, which we were not able to account for here. However, we demonstrate a small but significant interaction between fire and grazing, as burned sites experience increased grazing pressure, leading to net negative effects on site resistance to *B. tectorum*.

This relationship between grazing history, climate, and plant responses is common across shrub grassland environments. In Australian rangelands with similar livestock grazing histories to the Great Basin (James and others 1999), plant species that responded inconsistently to grazing pressure were more likely to increase in response to grazing at higher rainfall locations and decrease at lower rainfall locations (Vesk and Westoby 2001). Grazing history of an ecosystem dictates the likelihood that the plants species present are increasers or decreasers in response to grazing. Following overgrazing of grazing-sensitive species, only increasers remain until they too are overgrazed and removed from the system (Hacker 1987; Fensham and others 1999) often leading to alternative stable states based on nonequilibrium systems. This relationship can be contrasted with rangelands in the eastern Mediterranean that have experienced domesticated grazing for approximately 5000 years and as a result, relatively fewer species are found to dramatically decrease with grazing and a greater proportion of species are found to increase likely due to selection for grazing-tolerant species (Noy-Meir and others 1989). In our system, where native perennial bunchgrasses still exist, the droughty sites may be more prone to alternative stable states and these sites may benefit from monitoring those biotic indicators more directly related to site resistance, cover of shrubs, perennial grasses, lichens, mosses, and bare soil along with distances among perennial plants. These may provide early warning indicators of resilience from fire and grazing and resistance to invasive species triggering adaptive management before alternative stable states result in undesirable invasive species. Unfortunately, we did not have data on how long a rest from grazing our sites were given following fire. Future research could examine management practices that favor the documented recovery of the biotic community following fire if maintaining site resistance to *B. tectorum* is a management goal.

We present a holistic view of fire, in the context of a history of livestock grazing for semiarid shrub grasslands, using the sagebrush steppe of the

northern Great Basin as an example ecosystem. Resistance to invasive species that may result in alternative stable states appears to be linked to cover and structural composition of native perennial life-forms, including the biocrusts. Future work should examine mechanisms behind which bunchgrass and biocrust communities dictate post-disturbance site resistance and ultimately predict resilience to disturbances before these disturbances occur, thus allowing managers to prioritize their management options.

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