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Historical wildfires do not promote cheatgrass invasion in a western Great Plains steppe

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Abstract Plant invasion and wildfire are often tightly linked. Invasive grasses, in particular, can severely alter ecosystems by increasing fire frequency and intensity. In western North America, positive feedbacks between wildfire and *Bromus tectorum* (cheatgrass) invasion have contributed to widespread plant community conversion. Impacts of conversion include reduced biodiversity, wildlife habitat, and livestock weight gains, as well as increased costs associated with fire-fighting and ecosystem restoration. While *B. tectorum* has been studied intensively in the Intermountain West, it is unclear whether fire-invasion feedback cycles observed in the Great Basin operate similarly in the western Great Plains, where annual bromes coexist with fire-adapted native species. In a shrub–grass ecotone in northeastern Wyoming, we asked how wildfires have influenced *B. tectorum* and its congener, *B. arvensis*, and whether the effects of wildfire on annual bromes varied based on landscape context. We sampled annual bromes along 142 transects associated with 28 historical wildfires (2–26 years since fire). Both brome species were equally likely to occur in burned and unburned sites. Cover of *B. tectorum* was lower in burned sites. Soil texture, cover of other plant species, slope, and aspect were strongly associated with annual brome abundance. In the western Great Plains, single wildfires do not appear to promote *B. tectorum* invasion. However, the effects of repeated fires on invasion in this system remain unclear. Our findings stress that relationships between fire and plant invasion are governed not by invader identity alone but by ecosystem-specific interactions among invaders, fire regimes, and resident species.

Keywords *Bromus arvensis* · Fire regime · Great Basin · Shrub–grass interactions · Thunder Basin National Grassland · Winter precipitation

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Introduction

The influence of fire on plant invasion varies widely across invasive species and ecosystems (D'Antonio 2000). Fire can often promote invasion by damaging or killing resident species and releasing resources that can then be used by invasive species, particularly if invasive species are better able to resist or tolerate fire than natives (Alba et al. 2015; D'Antonio and Vitousek 1992). Conversely, where native species are adapted to fire, fire can sometimes inhibit invasion, and even be used as a management tool (Brudvig et al. 2007; DiTomaso et al. 2006).

In North America, the invasive annual grass *Bromus tectorum* L. (downy brome or cheatgrass) is an archetype of problematic fire-invasion interactions (D'Antonio and Vitousek 1992). This highly flammable winter-annual grass increases fire frequency and intensity, often leading to shrub mortality, decreased biotic resistance, and further increases in *B. tectorum* abundance (Balch et al. 2013; Brooks et al. 2004; Knapp 1996; Young and Evans 1978). The positive feedback between *B. tectorum* and fire has facilitated its invasion of tens of millions of hectares in western North America (Bradley and Mustard 2006; DiTomaso 2000; Rice 2005), and invasion continues today. Impacts of this invasion include reductions in plant diversity, wildlife habitat, and livestock weight gain, altered carbon and nitrogen cycling, and increases in costs associated with fighting fires and rehabilitating invaded areas (Bradley et al. 2006; DiTomaso 2000; Haferkamp et al. 2001; Rice 2005).

While *B. tectorum* has been studied intensively in the Intermountain West, much less is known about its invasion east of the Rocky Mountains (Brooks et al. 2016). *B. tectorum* threatens the mixed-grass prairie and grassland–shrubland ecotones of the western Great Plains, which comprise the largest remaining native grasslands in North America (Coupland 1992). In this region, *B. tectorum* can be common enough to reduce productivity of other plant species and livestock weight gains, but it is rarely dominant at broad (>1 ha) scales (Haferkamp et al. 1997; Mealor et al. 2012; Ogle et al. 2003). Both models and experiments, however, suggest that climate change may cause the region to become more susceptible to *B. tectorum* invasion in the future (Blumenthal et al. 2016; Bradley 2009; Prevey and Seastedt 2014).

Currently, *B. tectorum* invasion in the western Great Plains may be constrained by summer-dominated precipitation regimes and the abundance of perennial grasses that are well adapted to grazing by large ungulates (Bradley 2009; Bradley and Mustard 2006; Bradley et al. 2009; Mack and Thompson 1982; Milchunas et al. 1988). It is also possible that fire influences *B. tectorum* differently in this region than it does in the Intermountain West. Given the key role of fire in *B. tectorum* invasion in the Intermountain West, and the possibility that climate change may promote both *B. tectorum* and fire (Abatzoglou and Kolden 2011), learning how fire influences *B. tectorum* in the western Great Plains is critical both for managing existing populations and predicting future invasion.

The few studies relating fire to annual brome invasion in the western Great Plains have shown that prescribed fire can inhibit annual bromes. In Montana, prescribed burning in summer reduced the proportion of mixed-grass prairie vegetation made up of annual grasses, including *B. tectorum*, the related invasive annual *Bromus arvensis* L., and the native *Vulpia octoflora* [Walter] Rydb. (Vermeire et al. 2011, 2014), perhaps in part by damaging seeds on the soil surface (Vermeire and Rinella 2009). A similar result was reported for the effects of prescribed summer burns on *B. arvensis* in northern Texas (Teague et al. 2010). Prescribed burning in the spring or fall, when annual bromes are actively growing, has been found to inhibit *B. arvensis* (Harmoney 2007; Whisenant 1990b; Whisenant et al. 1984; Whisenant and Uresk 1990) or a combination of *B. tectorum* and *B. arvensis* (Munter 2008; White and Currie 1983). Thus, while wildfires in the Intermountain West promote *B. tectorum*, prescribed fires in the western Great Plains appear to have the opposite effect.

The potential drivers of these divergent results include not only climate and disturbance history, but also fire characteristics and brome species identity. Wildfires differ from prescribed burns in that they tend to occur when cheatgrass is inactive, temperatures are especially high, and humidity is especially low. Due in part to these weather conditions, wildfires are also more likely to harm native species (Alba et al. 2015; Ford and Johnson 2006). Indeed, across ecosystems, wildfires are much more likely to promote invasion than are prescribed fires (Alba et al. 2015). Moreover, to our knowledge, all of the existing studies investigating fire impacts on *B. tectorum* in the Great Plains report on *B. tectorum* grouped with *B. arvensis* (Munter 2008; Vermeire et al. 2011, 2014; White and Currie 1983), making it difficult to tell whether these two species respond differently to fire. Both brome species are native to Eurasia and were introduced to North America at least 150 years ago (Mack 1981), but *B. tectorum* is more common in the Intermountain West than in the Great Plains, while the reverse is true for *B. arvensis*. The fact that a fire-invasion feedback cycle has been commonly observed for *B. tectorum,* but not for *B. arvensis*, suggests that fire might differentially affect these two species and/or the ecosystems that they invade. Thus, both fire type and *Bromus* species identity could have important consequences for understanding how fire interacts

with annual brome invasion in the western Great Plains.

Here we describe associations between wildfire and annual bromes for 28 historical wildfires in the Thunder Basin region of northeastern Wyoming. The Thunder Basin is located in the ecotone between grasslands to the east and shrub steppe ecosystems to the west. It is ideal for examining effects of fire due to wide variation in the abundance of both shrubs and grasses. The study area also contains considerable variation in soil type, topography, and human disturbance, allowing us to test how fire interacts with environmental context to influence brome invasion. We ask the following questions: (1) Does wildfire influence *B. tectorum* in the Thunder Basin? (2) Aside from fire, what other environmental factors (including soil type, topography, vegetation cover and disturbance) best predict *B. tectorum* occurrence and abundance in the Thunder Basin? (3) Is the impact of fire on *B. tectorum* contingent on other environmental factors? (4) Do *B. tectorum* and *B. arvensis* respond similarly to fire and other environmental factors? We expected that historical summer wildfires would be associated with higher *B. tectorum* abundance, these effects would be more pronounced in certain environmental contexts, and *B. arvensis* would be less strongly influenced by fire than *B. tectorum.*

Methods

Study site

The study took place in Thunder Basin National Grassland (TBNG), located in northeastern Wyoming, USA (study boundaries: 43°12′–43°57′N; 104°27′–105°23′W). Mean annual precipitation ranges from 250 to 350 mm per year and most of the precipitation falls during the spring and summer. Annual precipitation was above average for 2013 and 2014 (approximately 425 and 375 mm/year, respectively). Mean annual temperature is 6 °C. Winds generally blow from the NW in winter and the SE in summer. The study area is located in an ecotone between northern mixed-grass prairie and sagebrush steppe. In unburned areas, total shrub cover averages 9.1 % (primarily *Artemisia tridentata* Nutt. ssp. *wyomingensis* Beetle & Young), and grass cover averages 52 % (including 26 % C_3 perennial grasses, 13 % C_4 perennial grasses, and 13 % annual grasses; see below for sampling methods). In addition to the two annual *Bromus* species, common understory plant species include *Bouteloua gracilis* [H.B.K.] Lag. ex Griffiths (blue grama), *Carex filifolia* Nutt., *Hesperostipa comata* [Trin. & Rupr.] Barkworth (needle-and-thread), *Pascopyrum smithii* [Rydb.] Á. Löve (western wheatgrass), and *Vulpia octoflora* [Walter] Rydb. (six-weeks fescue).

Study design

The study had a hierarchical, stratified sampling design. From the USFS, we obtained a database of fire perimeters for wildfires that had occurred within TBNG since 1988. We identified regions that had burned once but, to the best of our knowledge, had not re-burned since 1988. Within each of these fires, we stratified our sampling by ecological site to ensure that data were representative of existing edaphic variability. We sampled within the seven most common ecological sites (Soil Survey Staff 2015): Loamy (R058BY122WY, covers ~33 % of TBNG, 24 transect pairs), Shallow Loamy (R058BY162WY, 13 %, 16 pairs), Sandy (R058BY150WY, 9 %, 8 pairs), Clayey (R058BY104WY, 7 %, 6 pairs), Shallow Clayey (R058BY158WY, 7 %, 6 pairs), Shallow Sandy (R058BY166WY, 5 %, 6 pairs), and Saline Upland (R058BY144WY, 4 %, 5 pairs).

For each ecological site within each fire we randomly placed a 30 m-long transect. Each burned transect was paired with an unburned transect located outside the burn but within the same grazing allotment and ecological site, and within 1000 m of the fire perimeter. To create each transect pair, we first identified an ecological site occurring within the fire. For that ecological site, we delineated two large polygons (6.2 ± 0.4 ha in size) matched as well as possible for slope, aspect, and topographic wetness index values (Gesch 2007; Soil Survey Staff 2015). One polygon was located inside and one outside the fire perimeter (the latter within 1000 m of the fire perimeter and inside the same allotment and ecological site). Within each polygon, we used a GIS script to randomly place a 30 m-long transect oriented in a random direction. All transects were >30 m from the fire perimeter. This strategy allowed us to sample 71 transect pairs across 28 fires (Fig. 1). Fires ranged from 5 to 3525 ha in size (576 ± 930 ha, mean ± 1

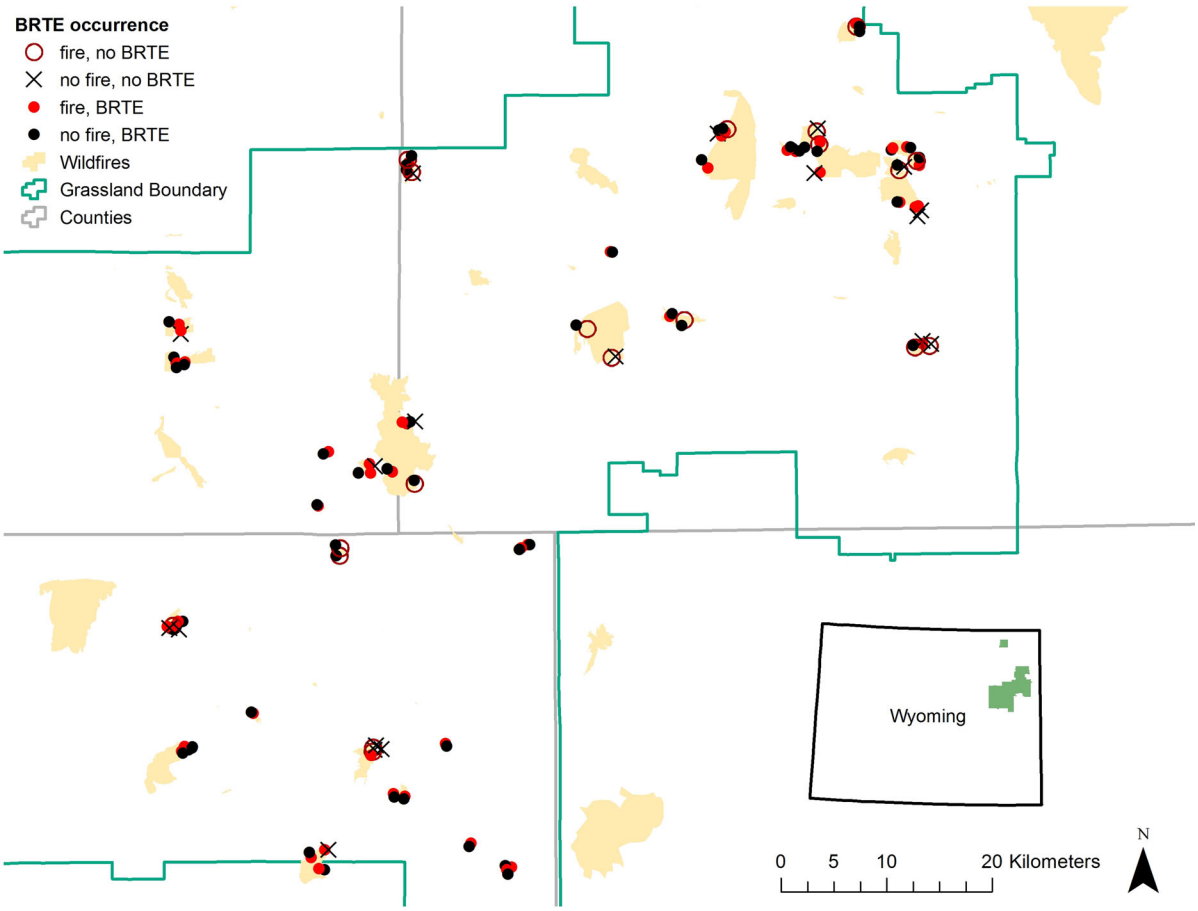

Fig. 1 Sampling locations and *B. tectorum* (BRTE) occurrence in Thunder Basin, including 142 transects (71 pairs) sampled in 28 fires that varied widely in size and shape. Note that all sampling was conducted in association with fires, but perimeters of smaller fires are obscured by sampling points

SD) and occurred 2–26 years prior to sampling (9 ± 7 years, mean ± 1 SD). Most burns (20 out of 28) occurred during July and August, though burn dates ranged from June 12 (5 fires in June) to October 21 (3 fires in October). We sampled all 142 transects from May 29–August 20, 2014. Paired transects were almost always sampled within a 5-day period (68 out of 71 pairs). On average, paired transects were 505 ± 294 m apart (mean ± 1 SD).

Data collection

Vegetation

At every third meter along each transect, we placed nested quadrats (10 sampling locations per 30 m transect). At each sampling location, we first recorded the presence of all species rooted within a 50 × 100 cm quadrat. We then recorded aerial cover of each species within a nested 50 × 20 cm quadrat. For portions of the quadrat with no foliar or basal plant cover, we estimated cover of rock (>0.5 cm), litter and bare ground. We recorded cover using modified (Daubenmire 1959) cover classes (0–1, 1–10, 10–20, 20–30, 30–40, 40–50, 50–60, 60–70, 70–80, 80–90, 90–99, and 99–100 %). When sampling late in the season, we used standing dead plant material to estimate the pre-senescence cover of each species.

Soils

We collected soil cores at 5, 10, 15 and 20 m along each transect. We used a standard soil auger (7 cm dia.) and separated soil into 0–10 and 10–30 cm

layers. Within each layer, samples from the four cores were pooled and a sub-sample of the homogenized material was extracted for analysis. Sub-samples were air dried and passed through a 2 mm sieve. Soil particle size at each depth was determined using a hydrometer method (Bouyoucos 1962). Values from the two depth bands were highly correlated ($r = 0.96$), so we only used data from the shallow depth band for statistical analysis.

Statistical analysis

We generated a set of hypotheses about what factors might influence the occurrence and abundance of *B. tectorum* and *B. arvensis*. We then used AICc-based model selection to determine which hypotheses (or combinations of hypotheses) had the most predictive power. Our model set was based around ten independent hypotheses (Table 1). We constructed one model to match each of these hypotheses. We also included models with additive combinations of hypotheses (e.g., both slope and sandy soils influence bromes, independently), and models with interactions between fire and other factors (e.g., fire promotes bromes, but only in sandier soils). In all cases, we only included combinations for which we could generate a logical and parsimonious hypothesis. This process resulted in 37 candidate models (Table 2), all of which had 9 or fewer predictor variables. Except for the two different formulations of the shrub:perennial grass ratio (see Table 1), predictors were not highly correlated (all correlation coefficients <0.4).

To determine which factors influenced *B. tectorum* or *B. arvensis* occurrence at the transect scale, we ran Generalized Linear Mixed Models (GLMMs) with a binomial distribution. A species was counted as present if observed in one or more of the 50 × 100 cm quadrats. Random factors included fire and ecological site nested within fire (i.e., transect pair).

To determine which factors influenced aerial cover of *B. tectorum*, we first excluded transects where *B. tectorum* was absent from all ten 50 × 100 cm quadrats ($N = 38$), then ran GLMMs on the remaining transects ($N = 104$). The response variable was average percent cover of *B. tectorum* within each transect, based on ten 20 × 50 cm quadrats. For each transect, midpoints of cover class data from the 10 quadrats were averaged to generate estimates of transect-scale abundance by species (c.f. Hickman and Derner 2007). We tested, for but did not observe, significant relationships between *Bromus* cover and sampling date, suggesting that our cover estimation method effectively minimized potential confounding effects of sampling date on comparisons among locations. We followed the same procedure to model the abundance of *B. arvensis*, which was present in 89 out of 142 transects. As in the occurrence models, random factors

Table 1 Independent hypotheses and associated predictor variables [abbreviations bracketed]

Hypothesis	Hypothesis code	Predictor variables
Fires promote annual bromes	Fire	Fire (yes/no) [F]
Fires promote annual bromes temporarily	Fire age	F, year of burn [Yr], F * Yr
More severe fires promote annual bromes	Fire severity	F, julian day of burn [Day], F * Day
Disturbances occurring along the fire perimeter (e.g., bulldozers) promote annual bromes	Fire disturbance	F, perimeter:area of fire [P:A], F * P:A
Fires promote annual bromes in areas that had higher shrub:perennial grass ratios pre-fire	Pre-fire shrub:grass	F, shrub:perennial grass percent cover from outside fire transect [S:G.out], F * S:G.out
Sandier, rockier soils promote annual bromes	Soils	%Clay: %Sand 0–10 cm [C:S], percent cover rock [R]
Hotter, leeward sites promote annual bromes	Slope/aspect	Slope [Sl], aspect (degrees away from southeast) [A]
Higher shrub:perennial grass ratios promote annual bromes	Shrub:grass	Shrub:perennial grass percent cover [S:G]
Less total vegetation cover promotes annual bromes	Vegetation	Percent cover of other grasses, forbs and shrubs [Veg]
Road-related disturbances promote annual bromes	Disturbance	Distance to road (m) [Road]

Table 2 Full model set

Model name (hypothesis combination)	Model
Null model	Intercept [I]
Fire	I + fire [F]
Fire age	I + F + year [Yr] + F * Yr
Fire severity	I + F + julian day of burn [Day] + F * Day
Fire disturbance	I + F + perimeter:area of fire [P:A] + F * P:A
Soils	I + clay:sand [C:S] + Rock [R]
Slope/aspect	I + slope [Sl] + aspect [A]
Shrub:grass	I + shrub:grass [S:G]
Vegetation	I + cover of other vegetation [Veg]
Disturbance	I + distance to road [Road]
Pre-fire shrub:grass	I + F + shrub:grass outside fire [S:G.out] + F * S:G.out
Soils * fire	I + C:S + R + F + F * C:S + F * R
Slope/aspect * fire	I + Sl + A + F + F * Sl + F * A
Shrub:grass * fire	I + S:G + F + F * S:G
Vegetation * fire	I + Veg + F + F * Veg
Disturbance * fire	I + Road + F + F * Road
Soils + slope/aspect	I + C:S + R + Sl + A
Soils + shrub:grass	I + C:S + R + S:G
Soils + vegetation	I + C:S + R + Veg
Soils + disturbance	I + C:S + R + Road
Slope/aspect + shrub:grass	I + Sl + A + S:G
Slope/aspect + vegetation	I + Sl + A + Veg
Slope/aspect + disturbance	I + Sl + A + Road
Shrub:grass + disturbance	I + S:G + Road
Vegetation + disturbance	I + Veg + Road
(Soils + slope/aspect) * fire	I + C:S + R + Sl + A + F + F * C:S + F * R + F * Sl + F * A
(Soils + Shrub:grass) * Fire	I + C:S + R + S:G + F + F * C:S + F * R + F * S:G
(Soils + vegetation) * fire	I + C:S + R + Veg + F + F * C:S + F * R + F * Veg
Soils * fire + pre-fire shrub:grass	I + C:S + R + S:G.out + F + F * C:S + F * R + F * S:G.out
(Soils + disturbance) * fire	I + C:S + R + Road + F + F * C:S + F * R + F * Road
(Slope/aspect + shrub:grass) * fire	I + Sl + A + S:G + F + F * Sl + F * A + F * S:G
(Slope/aspect + vegetation) * fire	I + Sl + A + Veg + F + F * Sl + F * A + F * Veg
Slope/aspect * fire + pre-fire shrub:grass	I + Sl + A + S:G.out + F + F * Sl + F * A + F * S:G.out
(Slope/aspect + disturbance) * fire	I + Sl + A + Road + F + F * Sl + F * A + F * Road
(Shrub:grass + disturbance) * fire	I + S:G + Road + F + F * S:G + F * Road
(Vegetation + disturbance) * fire	I + Veg + Road + F + F * Veg + F * Road
Disturbance * fire + pre-fire shrub:grass	I + Road + S:G.out + F + F * Road + F * S:G.out

See Table 1 for explanations of hypotheses and predictor variables

included fire and ecological site nested within fire (i.e., transect pair). For abundance models we assumed an inverse Gaussian distribution with log link. This distribution fit our data substantially better than several alternatives (e.g., Gaussian, Gamma, and Gamma with log link; all ΔAICc > 18). For each set of analyses, model structure remained identical except for fixed factors (Tables 1, 2). GLMMs were

conducted in R 3.0.1 using the nlme package (Pinheiro et al. 2013). We compared models using the MuMIn package (Bartoń 2015). Results are reported as means ± 1 SE.

Results

Occurrence of *B. tectorum*

Both inside fires and outside fires, *B. tectorum* was present in 73 % of transects (52 out of 71; Fig. 1). None of the five top-ranked models (ΔAICc < 4) of *B. tectorum* occurrence included fire, either by itself or in combination with other predictors. Rather, our model selection results suggested that the best model included soil parameters and vegetation cover (Table 3). The weight for this model (45 %) was more than double that for the next best model (19 %). Moreover, all five of the top ranked models (cumulative weight >91 %) included soil predictors (Table 3), which emphasizes that soil parameters were particularly important for predicting *B. tectorum* occurrence. *B. tectorum* was more likely to occur on sandier sites (surface soil clay:sand ratio where absent = 0.61 ± 0.10; present = 0.28 ± 0.03) with more rocks (Fig. 2a, b).

After accounting for variation related to soils, *B. tectorum* was more likely to occur in areas with more plant cover (Fig. 2c), and lower shrub:perennial grass ratios (Fig. 2d). *B. tectorum* showed a slight affinity for southeast-facing slopes, which tend to be warmer and more sheltered (Fig. 2e, f). Finally, *B. tectorum* occurred slightly more frequently in locations further from roads (absent: 444 ± 60 m from road; present: 502 ± 49 m from road).

Table 3 Model selection for *B. tectorum* occurrence and abundance

Model name	*df*	logLik	AICc	ΔAICc	Weight
Occurrence					
Soils + vegetation	6	−67.984	148.6	0	0.449
Soils	5	−69.913	150.3	1.68	0.194
Soils + slope/aspect	7	−68.442	151.7	3.13	0.094
Soils + shrub:grass	6	−69.564	151.8	3.16	0.092
Soils + disturbance	6	−69.694	152	3.42	0.081
(Soils + vegetation) * fire	10	−65.885	153.5	4.86	0.039
Soils * fire + pre-fire shrub:grass	10	−66.308	154.3	5.71	0.026
Soils * fire	8	−69.116	155.3	6.72	0.016
(Soils + shrub:grass) * fire	10	−67.817	157.3	8.72	0.006
(Soils + disturbance) * fire	10	−68.84	159.4	10.77	0.002
(Soils + slope/aspect) * fire	12	−67.034	160.5	11.9	0.001
Fire disturbance	6	−76.994	166.6	18.02	0
Shrub:grass	4	−79.682	167.7	19.07	0
Null model (binomial)	3	−80.829	167.8	19.24	0
Abundance					
(Vegetation + disturbance) * fire	9	−292.3	604.5	0	0.406
Slope/aspect	6	−296.225	605.3	0.8	0.272
Slope/aspect + shrub:grass	7	−295.552	606.3	1.76	0.169
Vegetation	5	−299.434	609.5	4.97	0.034
Fire severity	7	−297.594	610.4	5.84	0.022
Vegetation + slope/aspect	7	−297.809	610.8	6.27	0.018
Shrub:grass	5	−300.125	610.9	6.35	0.017
Vegetation + disturbance	6	−299.087	611	6.53	0.016
Null (inverse Gaussian with log link)	4	−301.327	611.1	6.54	0.015

Only models with AICc values lower than or equal to that of the null model are displayed

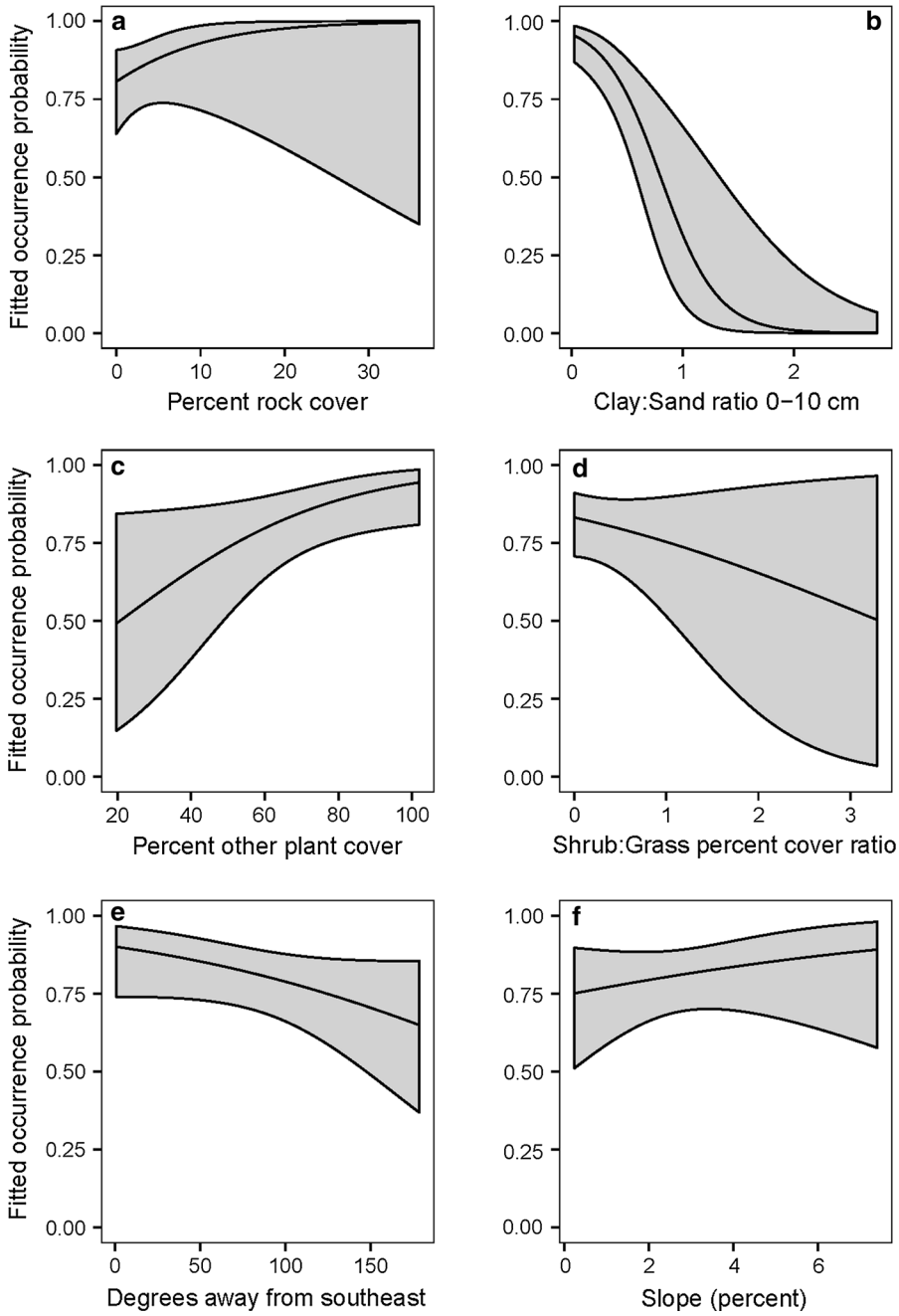

Fig. 2 Effects of **a** rock cover, **b** clay:sand ratio, **c** vegetation, **d** shrub:perennial grass ratio, **e** aspect, and **f** slope on *B. tectorum* occurrence. Fitted occurrence probabilities (mean ± 95 % CI) were determined from binomial models of *B. tectorum* occurrence. **a**–**c** 'Soils + vegetation' model predictions. **d** 'Soils + shrub:grass' model predictions. **e**, **f** 'Soils + slope/aspect' model predictions. For visualizations using raw data, see Online Resource 1

Abundance of *B. tectorum*

Bromus tectorum cover values ranged from 0 to >40 % (Online Resource 1). The top-ranked model (weight = 41 %) for *B. tectorum* abundance included fire in combination with vegetation cover and distance to road (Table 3). Burned transects had approximately 30 % lower *B. tectorum* cover than unburned transects (Fig. 3a), and this effect was more pronounced in sites with less other vegetation cover and sites closer to roads (Fig. 3b, c). In unburned areas, vegetation cover had a strong, negative relationship with *B. tectorum* cover (Fig. 3c). The second- and third-ranked models (ΔAICc = 0.8 and 1.76; weights = 27 and 17 %, respectively) indicated that *B. tectorum* was somewhat more abundant on slopes, irrespective of aspect (Table 3; Fig. 3d, e), and in areas with less shrub cover (Fig. 3f). The small differences among these three top models suggest that all these factors may be important in predicting *B. tectorum* abundance.

We were unable to run the Fire Age model using an inverse Gaussian distribution (it failed to converge), and this model was therefore excluded from the full model selection process. However, we did compare

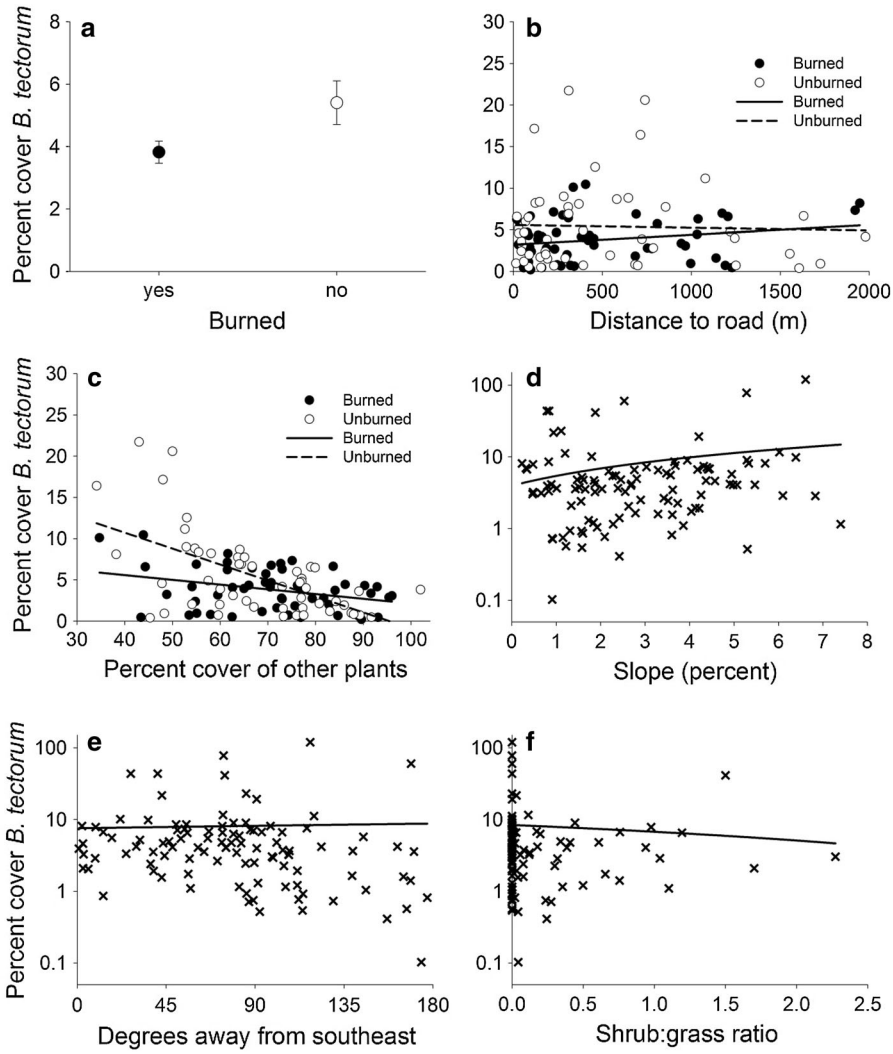

Fig. 3 Effects of **a** fire, **b** disturbance, **c** vegetation, **d** slope, **e** aspect, and **f** shrub:perennial grass ratio on *B. tectorum* abundance. **a–c** '(Vegetation + disturbance) * fire' model predictions. **d–f** 'Slope/aspect + shrub:grass' model predictions. For visualizations using raw data, see Online Resource 1

Fire Age to a Null model using a different distributional assumption (normal distribution and log-transformed *B. tectorum* cover data). This process indicated that the Fire Age model had much less explanatory power than the Null model (ΔAICc = 18.8).

Occurrence of *B. arvensis*

Bromus arvensis was present at 62 % of unburned transects (44 out of 71) and 63 % of burned transects (45 out of 71). None of the six top-ranked models (ΔAICc < 4; cumulative weight = 82 %) included fire, either by itself or in combination with other predictors (Table 4). All six top-ranked models included either vegetation cover or slope and aspect, and the best model included both of these predictors (Table 4). *B. arvensis* was most likely to occur on southeast-facing slopes with high cover of other plants (Fig. 4a–c).

Secondary predictors of *B. arvensis* occurrence included shrub:perennial grass ratio, soils, and distance to road (Table 4). *B. arvensis* was somewhat more likely to occur on sites with lower shrub:perennial grass ratios (Fig. 4d), less rock cover (Fig. 4e), higher clay:sand ratios (Fig. 4f), and sites closer to roads (absent: 578 ± 67 m to road; present: 432 ± 47 m to road).

Abundance of *B. arvensis*

In areas where *B. arvensis* was present, few models of abundance performed substantially better than the null model (ΔAICc for null model = 4.09). The top-ranked model (weight = 27 %) included fire in combination with distance to road (Table 4). Fire was associated with lower *B. arvensis* cover at sites close to roads, but not at sites farther from roads (Fig. 5a, b). Where it occurred, *B. arvensis* was slightly more abundant in areas with more vegetation cover, higher clay:sand ratios and fewer rocks (Fig. 5c–e). Models with less support (ΔAICc from 3 to 4) included fire in combination with distance to road and either slope and aspect (preferring steeper slopes) or pre-fire shrub:perennial grass ratios (preferring grassier sites; Table 4; Fig. S4).

Table 4 Model selection for *Bromus arvensis* occurrence and abundance

Model name	df	logLik	AICc	ΔAICc	Weight
Occurrence					
Vegetation + slope/aspect	6	−62.263	137.1	0	0.307
Slope/aspect + shrub:grass	6	−62.854	138.3	1.18	0.17
Vegetation	4	−65.191	138.7	1.53	0.143
Vegetation + soils	6	−63.642	139.9	2.76	0.077
Slope/aspect	5	−64.757	140	2.81	0.075
Vegetation + disturbance	5	−65.154	140.7	3.6	0.051
Slope/aspect + disturbance	6	−64.751	142.1	4.98	0.025
Vegetation * fire	6	−64.873	142.4	5.22	0.023
Soils + shrub:grass	6	−65.157	142.9	5.79	0.017
Slope/aspect + soils	7	−64.064	143	5.82	0.017
Shrub:grass	4	−67.523	143.3	6.19	0.014
Null model (binomial)	3	−68.732	143.6	6.49	0.012
Abundance					
Disturbance * fire	7	−187.356	390.1	0	0.273
Vegetation + soils	7	−187.731	390.8	0.75	0.187
(Vegetation + disturbance) * fire	9	−185.517	391.3	1.22	0.148
Vegetation	5	−190.817	392.4	2.26	0.088
(Disturbance + slope/aspect) * fire	11	−184.083	393.6	3.5	0.047
Disturbance * fire + pre-fire shrub:grass	9	−186.776	393.8	3.74	0.042
Pre-fire shrub:grass	7	−189.387	394.2	4.06	0.036
Null (inverse Gaussian with log link)	4	−192.856	394.2	4.09	0.035

Only models with AICc values lower than or equal to that of the null model are displayed

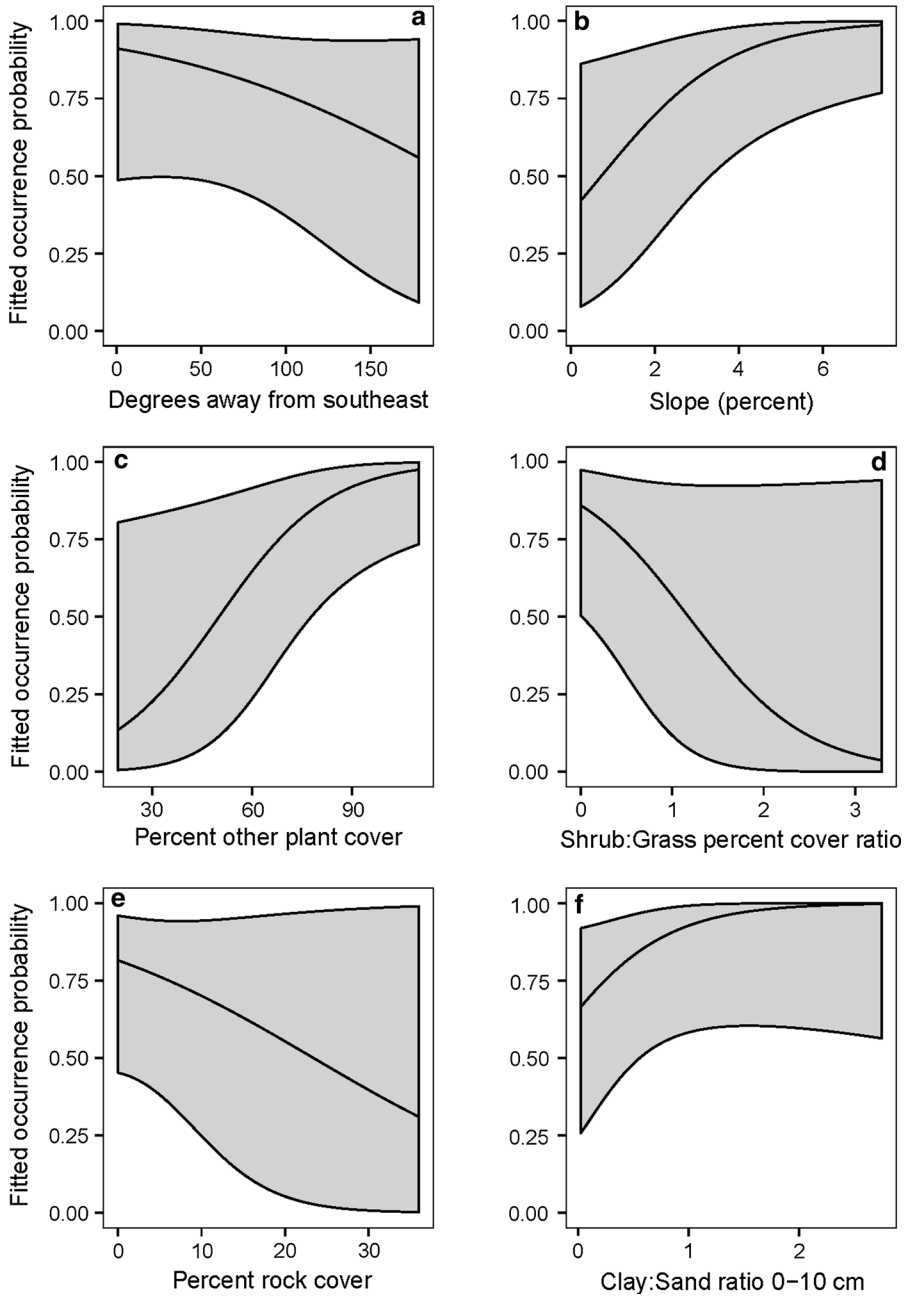

Fig. 4 Effects of **a** aspect, **b** slope, **c** vegetation, **d** shrub:perennial grass ratio, **e** rock cover, and **f** clay:sand ratio on *B. arvensis* occurrence. Fitted occurrence probabilities (mean ± 95 % CI) were determined from binomial models of *B. arvensis* occurrence. **a**–**c** 'Vegetation + slope/aspect' model predictions. **d** 'Slope/aspect + shrub:grass' model predictions. **e**, **f** 'Vegetation + soils' model predictions. For visualizations using raw data, see Online Resource 1

As with *B. tectorum*, we were unable to run the Fire Age model using an inverse Gaussian distribution. Using a different distributional assumption (normal distribution and log-transformed *B. arvensis* cover data), we found that the Fire Age model had much less explanatory power than the Null model (ΔAICc = 19.4).

Across all 142 transects, *B. tectorum* and *B. arvensis* displayed a non-significant negative correlation with each other ($r = -0.12$; $P = 0.16$). There were no transects in which both species had >10 % cover.

Discussion

Wildfire and plant invasion are often tightly linked (Alba et al. 2015; D'Antonio 2000; D'Antonio and Vitousek 1992). In the Intermountain West, cheatgrass

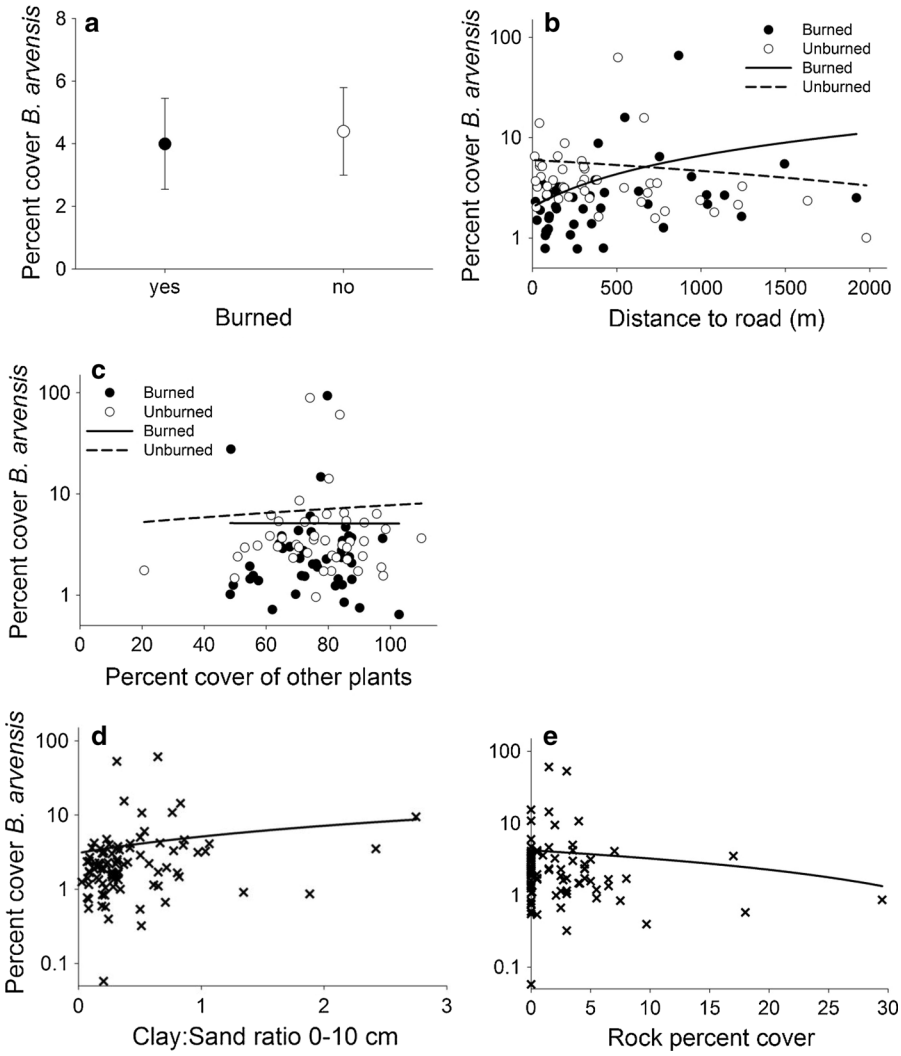

Fig. 5 Effects of **a** fire, **b** disturbance, **c** vegetation, **d** clay:sand ratio, and **e** rock cover on *B. arvensis* abundance. **a**–**b** 'Disturbance * fire' model predictions. **c** '(Vegetation + disturbance) * fire' model predictions, **d**–**e** 'Vegetation + soils' model predictions. For visualizations using raw data, see Online Resource 1

invasion can initiate a positive feedback cycle in which invasion promotes wildfire, which promotes further invasion (Balch et al. 2013; Brooks et al. 2004; Chambers et al. 2007; Knapp 1996; Young and Evans 1978). However, our data support a largely untested hypothesis suggesting that the same relationships do not hold in the western Great Plains (Brooks et al. 2016). Wildfires in northeast Wyoming were not associated with the occurrence of two invasive brome species. Moreover, burned areas were associated with slightly lower cover of *B. tectorum*. Our study cannot rule out the possibility that fire was less likely to occur in areas with more *B. tectorum*. However, paired transects were close together and matched to minimize differences in landscape position, topography, grazing management, and soil type. Furthermore, we have no reason to expect that areas with more *B. tectorum* would be less likely to burn, given that the opposite is often observed. Therefore, it seems likely that wildfire does not promote, and may even inhibit, *B. tectorum* in this ecosystem.

Our results suggest that (1) wildfires occurring mainly during the annual brome dormant season have qualitatively similar effects to prescribed burns

conducted in Nebraska, Kansas, South Dakota and Montana mixed-grass prairie (Harmoney 2007; Munter 2008; Vermeire et al. 2011, 2014; Whisenant 1990b; White and Currie 1983); and (2) wildfires do not facilitate either *B. arvensis* or *B. tectorum*, even in a shrub–grass ecotone located relatively close to the Great Basin. Our analysis focused on areas that, to the best of our knowledge, had not experienced multiple burns within the study time frame (1988–2012). It remains unclear whether, when compared to a single wildfire, multiple fires would display the same relationships with brome occurrence and abundance in this ecosystem. Similarly, bromes may respond differently to fires occurring during extreme weather conditions. Our Fire Severity model (Table 1) used date as a proxy for climatic conditions due to data limitations for the older fires, but future research could explore fire weather in more detail.

Both evolutionary history and climate may be causing the lack of wildfire-annual brome invasion feedbacks in Thunder Basin, as well as prescribed fire-annual brome invasion feedbacks in other parts of the western Great Plains (Harmoney 2007; Munter 2008; Vermeire et al. 2011, 2014; Whisenant 1990b; White and Currie 1983). Compared to the Intermountain West, the Great Plains historically experienced more frequent wildfires (Brown and Sieg 1999; Ratajczak et al. 2014; Whisenant 1990a), and most plants native to the region are tolerant of above-ground disturbances, including fire and grazing (Brudvig et al. 2007; Fuhlendorf and Engle 2004). Thus, wildfires in the western Great Plains may not reduce biotic resistance of native plant communities as much as wildfires in the Great Basin (Chambers et al. 2016). Compared to the Great Basin, the western Great Plains also receives a higher proportion of annual precipitation during the summer when annual bromes are dormant, many native plants are still active, and wildfire season is at its peak. When rains occur after summer wildfires, native plants (especially C_4 species) may be able to quickly resprout and utilize available nutrients at the expense of annual bromes (Pyke et al. 2010). In support of this hypothesis, modeling work suggests that summer precipitation is negatively associated with *B. tectorum* invasion potential (Bradford and Lauenroth 2006; Bradley 2009).

The lower *B. tectorum* abundance we observed in burned sites suggests that wildfire may even increase the resistance of some Great Plains ecosystems to annual brome invasion. Two mechanisms could contribute to such resistance. First, previous studies suggest that wildfires can hinder bromes in the northern Great Plains by removing litter, which, when present, increases water availability to and ameliorates microclimatic conditions experienced by overwintering brome seedlings (Whisenant 1990b; Whisenant and Uresk 1990). Second, our data from Thunder Basin indicate that perennial grass cover increases over time in burned areas, presumably as a result of reduced competition with shrubs. We expect that perennial grasses at burned sites are efficient competitors with annual bromes, and this competitive interaction helps to keep bromes out of burned areas over the long term. This hypothesis is supported by the negative correlation we observed between plant cover and *B. tectorum* cover in sites where *B. tectorum* occurred (Fig. 3c). However, we note that a study on chemical shrub thinning in north-central Wyoming suggests that this logic may not apply in all Great Plains steppe ecosystems; in that study, a reduction in shrub cover was associated with higher cover of both *B. tectorum* and perennial grasses (Blumenthal et al. 2006).

Based on previous studies (e.g., Chambers et al. 2007), we expected that fire might promote annual brome invasion, but only (or more strongly) in certain environmental contexts, such as in areas experiencing additional disturbance. Our data revealed few interactive effects of fire and other environmental factors on annual brome invasion. For occurrence of *B. tectorum* and *B. arvensis*, none of the top ranked models included fire, even in combination with other factors, and we did not observe positive associations between fire and bromes in any environment (Tables 3, 4; Figs. 2, 4). At sites with less other vegetation cover, *B. tectorum* cover was lower on burned than unburned transects, but this pattern was absent at sites with more other vegetation cover. (Fig. 3). If vegetation cover is correlated with site productivity, these results could indicate that burning and the associated loss of nutrients, particularly nitrogen, had a stronger negative impact on *B. tectorum* in less productive sites (Perry et al. 2010). Alternatively, there might be a facilitative effect of other vegetation on *B. tectorum* after fire. In a multi-site Great Basin experiment, lack of perennial vegetation accentuated the positive effects of fire on *B. tectorum* (Chambers et al. 2007), but in the present

study, lower cover of other vegetation accentuated the negative effects of fire on *B. tectorum*.

For both brome species, burned sites had lower cover in areas <500 m away from roads (Figs. 3, 5). This is a surprising result which runs counter to the idea that disturbance tends to promote invasion (Bradley and Mustard 2006; Lowry et al. 2013). The fact that this pattern was present for both brome species suggests that it was not driven by a few spurious data points. However, we do have more data from locations closer to roads, and so it could be that we simply have more power to detect a difference in locations closer to roads. More research is needed to understand this pattern and potential mechanisms driving it.

A second objective of this study was to learn what factors beyond fire can be used to predict the occurrence and abundance of *B. tectorum* and *B. arvensis*. In the Great Basin, multiple studies have explored which environments are most susceptible to *B. tectorum* invasion (e.g., Bradley 2009; Bradley and Mustard 2006; Chambers et al. 2014, 2007), but similar studies are lacking for the Great Plains (Brooks et al. 2016). Our data suggested that for both brome species, occurrence was related to soils, slope and aspect, and the cover of other plants. In northeastern Wyoming, niche partitioning between the two brome species may be at least partially driven by soil texture. *B. tectorum* was more likely to occur on sandier, rockier sites, but *B. arvensis* was more likely to occur on sites with more clay and fewer rocks (Figs. 2, 4). Although the literature suggests a lack of consensus concerning optimal soil textures for *B. tectorum* (Belnap and Phillips 2001; Chambers et al. 2007; Miller et al. 2006; Reisner et al. 2013), a study in the northern Great Plains found relatively more *B. tectorum* on a silty site and more *B. arvensis* on a clay site (Heitschmidt et al. 1995). It is unclear what mechanisms are driving soil texture results, but previous work suggests that complex relationships among soil texture, soil moisture and nutrient availability can regulate annual brome abundance (Belnap et al. 2016).

Although the two brome species had contrasting responses to soil texture, they responded similarly to other environmental parameters. Both species were more likely to occur on southeastern slopes, which tend to be warmer, more sheltered from winter wind, and possibly more likely to accumulate winter moisture in the form of snow than other slope/aspect combinations (Blumenthal et al. 2012). Associations between brome species and microclimatic conditions could be contingent on weather, and we note that our sampling took place during a particularly wet period. Nevertheless, our results match findings from the Intermountain West in which *B. tectorum* presence or abundance have been positively correlated with winter precipitation, winter or spring temperature, incident solar radiation, heat load, or southerly slopes (Bradley 2009; Bradley and Mustard 2006; Condon et al. 2011; Kulpa et al. 2012; Lovtang and Riegel 2012; Reisner et al. 2013). Climate change predictions for the northern Great Plains include increased temperatures and increased winter precipitation (Program 2014). According to both our study and previous work (Blumenthal et al. 2016; Bradley 2009; Prevey and Seastedt 2014), these changes should promote annual brome invasion in this ecosystem.

Both brome species were more likely to occur on sites with higher cover of other plants and lower shrub:perennial grass ratios. This result may suggest that other herbaceous species facilitate bromes, or that bromes prefer more productive, nutrient-rich sites. The latter result matches findings from work in the Great Basin (Bradley 2009; Bradley and Mustard 2006; Chambers et al. 2007).

In most cases, environmental influences on occurrence were paralleled by environmental influences on abundance. However, total cover of other plants affected *B. tectorum* occurrence and abundance differently. Where *B. tectorum* occurred, its abundance was negatively correlated with cover of other plants, especially in unburned areas. A negative relationship between *B. tectorum* and native plant cover has been observed repeatedly in the Great Basin (Chambers et al. 2014; Condon et al. 2011; Reisner et al. 2013) and by at least one study in the northern Great Plains (Ogle et al. 2003). Thus, our findings support a growing body of literature suggesting that although *B. tectorum* is more likely to occur at sites with higher cover of other plants, its abundance within those sites is negatively correlated with cover of other plants. These patterns likely reflect a combination of abiotic (site productivity) and biotic (competition) filtering mechanisms (Tonn 1990). Alternatively, however, our results could suggest that co-occurring plants lead to facilitation at the seedling stage but competition at the adult

stage (Leger and Espeland 2010). More research is needed to differentiate between these alternative hypotheses.

Conclusions and management implications

Positive feedbacks between wildfire and *B. tectorum* invasion have contributed to plant community conversion across millions of hectares of land in western North America. This species has been used as a key example of problematic wildfire-invasion interactions. Using the very same species, our work offers a prime example of an important caveat to invasion-fire linkages: relationships between fire and plant invasion hinge not just on invader identity, but on interactions between invaders and their environments (D'Antonio 2000; Mack and D'Antonio 1998). In situations where resident species are relatively well-adapted to fire, invasive species may not be able to reap the benefits of increased nutrient availability and reduced competition in post-fire environments. This appears to be the case in the grassy Great Plains, where single wildfires do not appear to promote *B. tectorum* invasion.

Our work suggests that from the perspective of annual brome invasion, infrequent fires may be a safe method for influencing plant communities and wildlife habitat in the western Great Plains. However, we emphasize that this analysis did not consider other potentially negative impacts of fire (e.g., removal of shrubs) or the effects of repeated fires on invasion trajectories. For managers attempting to control *B. tectorum* in this region, our study suggests that the largest populations are likely to occur on sandier soils and southeast-facing slopes. Using soil survey and topographic information, managers may be able to target invasion hotspots. While *B. tectorum* was not strongly associated with fire under current climatic conditions, our results do suggest that future climate conditions could favor increased invasion in this ecosystem, which in turn could lead to shifts in fire-invasion feedback cycles.

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References

Abatzoglou JT, Kolden CA (2011) Climate change in western US deserts: potential for increased wildfire and invasive annual grasses. Rangel Ecol Manag 64:471–478

Alba C, Skalova H, McGregor KF et al (2015) Native and exotic plant species respond differently to wildfire and prescribed fire as revealed by meta-analysis. J Veg Sci 26:102–113

Balch JK, Bradley BA, D'Antonio CM et al (2013) Introduced annual grass increases regional fire activity across the arid western USA (1980–2009). Glob Change Biol 19:173–183

Bartoń K (2015) MuMIn. R package version 1.13.4

Belnap J, Phillips SL (2001) Soil biota in an ungrazed grassland: response to annual grass (*Bromus tectorum*) invasion. Ecol Appl 11:1261–1275

Belnap J, Stark JM, Rau BM et al (2016) Soil moisture and biogeochemical factors influence the distribution of annual *Bromus* species. In: Germino MJ, Chambers JC, Brown CS (eds) Exotic brome-grasses in arid and semi-arid ecosystems of the western US: causes, consequences, and management implications. Springer, New York

Blumenthal DM, Norton U, Derner JD et al (2006) Long-term effects of tebuthiuron on *Bromus tectorum*. West N Am Nat 66:420–425

Blumenthal DM, Norton AP, Cox SE et al (2012) *Linaria dalmatica* invades south-facing slopes and less grazed areas in grazing-tolerant mixed-grass prairie. Biol Invasions 14:395–404

Blumenthal DM, Kray JA, Ortmans W et al (2016) Cheatgrass is favored by warming but not CO_2 enrichment in a semi-arid grassland. Glob Change Biol. doi:10.1111/gcb.13278

Bouyoucos GJ (1962) Hydrometer method improved for making particle size analyses of soils. Agron J 54:464–465

Bradford JB, Lauenroth WK (2006) Controls over invasion of *Bromus tectorum*: the importance of climate, soil, disturbance and seed availability. J Veg Sci 17:693–704

Bradley BA (2009) Regional analysis of the impacts of climate change on cheatgrass invasion shows potential risk and opportunity. Glob Change Biol 15:196–208

Bradley BA, Mustard JF (2006) Characterizing the landscape dynamics of an invasive plant and risk of invasion using remote sensing. Ecol Appl 16:1132–1147

Bradley BA, Houghtonw R, Mustard JF et al (2006) Invasive grass reduces aboveground carbon stocks in shrublands of the Western US. Glob Change Biol 12:1815–1822

Bradley BA, Oppenheimer M, Wilcove DS (2009) Climate change and plant invasions: restoration opportunities ahead? Glob Change Biol 15:1511–1521

Brooks ML, D'Antonio CM, Richardson DM et al (2004) Effects of invasive alien plants on fire regimes. Bioscience 54:677–688

Brooks ML, Brown CS, Chambers JC et al (2016) Exotic annual *Bromus* invasions: comparisons among species and ecoregions in the western United States. In: Germino MJ,

Chambers JC, Brown CS (eds) Exotic brome-grasses in arid and semi-arid ecosystems of the western US: causes, consequences, and management implications. Springer, New York

Brown PM, Sieg CH (1999) Historical variability in fire at the ponderosa pine—Northern Great Plains prairie ecotone, southeastern Black Hills, South Dakota. Ecoscience 6:539–547

Brudvig LA, Mabry CM, Miller JR et al (2007) Evaluation of central north American prairie management based on species diversity, life form, and individual species metrics. Conserv Biol 21:864–874

Chambers JC, Roundy BA, Blank RR et al (2007) What makes Great Basin sagebrush ecosystems invasible by *Bromus tectorum*? Ecol Monogr 77:117–145

Chambers JC, Bradley BA, Brown CS et al (2014) Resilience to stress and disturbance, and resistance to *Bromus tectorum* L. invasion in cold desert shrublands of western North America. Ecosystems 17:360–375

Chambers JC, Germino MJ, Belnap J et al (2016) Plant community resistance to invasion by *Bromus* species: the roles of community attributes, *Bromus* interactions with plant communities, and *Bromus* traits. In: Germino MJ, Chambers JC, Brown CS (eds) Exotic brome-grasses in arid and semi-arid ecosystems of the Western US: causes, consequences, and management implications. Springer, New York

Condon L, Weisberg PJ, Chambers JC (2011) Abiotic and biotic influences on *Bromus tectorum* invasion and *Artemisia tridentata* recovery after fire. Int J Wildland Fire 20:597–604

Coupland RT (1992) Mixed Prairie. Ecosystems of the world 8A: natural grasslands, introduction and western hemisphere. Elsevier, New York, pp 151–182

D'Antonio CM (2000) Fire, plant invasions, and global changes. In: Mooney HA, Hobbs RJ (eds) Invasive species in a changing world. Island Press, Washington, pp 65–93

D'Antonio CM, Vitousek PM (1992) Biological invasions by exotic grasses, the grass fire cycle, and global change. Annu Rev Ecol Syst 23:63–87

Daubenmire RF (1959) Canopy coverage method of vegetation analysis. Northwest Sci 33:43–64

DiTomaso JM (2000) Invasive weeds in rangelands: species, impacts, and management. Weed Sci 48:255–265

DiTomaso JM, Brooks ML, Allen EB et al (2006) Control of invasive weeds with prescribed burning. Weed Technol 20:535–548

Ford PL, Johnson GV (2006) Effects of dormant- vs. growing-season fire in shortgrass steppe: biological soil crust and perennial grass responses. J Arid Environ 67:1–14

Fuhlendorf SD, Engle DM (2004) Application of the fire-grazing interaction to restore a shifting mosaic on tallgrass prairie. J Appl Ecol 41:604–614

Gesch DB (2007) The national elevation dataset. In: Maune D (ed) Digital elevation model technologies and applications: The DEM users manual, 2nd edn. American Society for Photogrammetry and Remote Sensing, Bethesda, pp 99–118

Haferkamp MR, Heitschmidt RK, Karl MG (1997) Influence of Japanese brome on western wheatgrass yield. J Range Manag 50:44–50

Haferkamp MR, Grings EE, Heitschmidt RK et al (2001) Suppression of annual bromes impacts rangeland: animal responses. J Range Manag 54:663–668

Harmoney KR (2007) Grazing and burning Japanese brome (*Bromus japonicus*) on mixed grass rangelands. Rangel Ecol Manag 60:479–486

Heitschmidt RK, Grings EE, Haferkamp MR et al (1995) Herbage dynamics on 2 Northern Great Plains range sites. J Range Manag 48:211–217

Hickman KR, Derner JD (2007) Blackland tallgrass prairie vegetation dynamics following cessation of herbicide application. Rangel Ecol Manag 60:186–190

Knapp PA (1996) Cheatgrass (*Bromus tectorum* L.) dominance in the Great Basin Desert—history, persistence, and influences to human activities. Glob Environ Change Hum Policy Dimens 6:37–52

Kulpa SM, Leger EA, Espeland EK et al (2012) Postfire seeding and plant community recovery in the Great Basin. Rangel Ecol Manag 65:171–181

Leger EA, Espeland EK (2010) The shifting balance of facilitation and competition affects the outcome of intra- and inter-specific interactions over the life history of California grassland annuals. Plant Ecol 208:333–345

Lovtang SCP, Riegel GM (2012) Predicting the occurrence of downy brome (*Bromus tectorum*) in central Oregon. Invasive Plant Sci Manag 5:83–91

Lowry E, Rollinson EJ, Laybourn AJ et al (2013) Biological invasions: a field synopsis, systematic review, and database of the literature. Ecol Evol 3:182–196

Mack RN (1981) Invasion of *Bromus tectorum* L. into Western North America: an ecological chronicle. Agro Ecosyst 7:145–165

Mack MC, D'Antonio CM (1998) Impacts of biological invasions on disturbance regimes. Trends Ecol Evol 13:195–198

Mack RN, Thompson JN (1982) Evolution in steppe with few large, hoofed mammals. Am Nat 119:757–773

Mealor BA, Cox S, Booth DT (2012) Postfire downy brome (*Bromus tectorum*) invasion at high elevations in Wyoming. Invasive Plant Sci Manag 5:427–435

Milchunas D, Sala O, Lauenroth W (1988) A generalized model of the effects of grazing by large herbivores on grassland community structure. Am Nat 132:87–106

Miller ME, Belnap J, Beatty SW et al (2006) Performance of *Bromus tectorum* L. in relation to soil properties, water additions, and chemical amendments in calcareous soils of southeastern Utah, USA. Plant Soil 288:1–18

Munter EJ (2008) Seasonal and prescribed fire effects on cheatgrass and native mixed grass prairie vegetation. Education. Chadron State College, Chadron, p 82

Ogle SM, Reiners WA, Gerow KG (2003) Impacts of exotic annual brome grasses (*Bromus* spp.) on ecosystem properties of northern mixed grass prairies. Am Midl Nat 149:46–58

Perry LG, Blumenthal DM, Monaco TA et al (2010) Immobilizing nitrogen to control plant invasion. Oecologia 163:13–24

Pinheiro J, Bates D, DebRoy S et al (2013) nlme: Linear and nonlinear mixed effects models. R package version 3

Prevey JS, Seastedt TR (2014) Seasonality of precipitation interacts with exotic species to alter composition and phenology of a semi-arid grassland. J Ecol 102:1549–1561

Program U (2014) National climate assessment full report. http://www.energyandclimatechange.org/view/article/537bc46d0cf226e0bdbfef38

Pyke DA, Brooks ML, D'Antonio C (2010) Fire as a restoration tool: a decision framework for predicting the control or enhancement of plants using fire. Restor Ecol 18:274–284

Ratajczak Z, Nippert JB, Briggs JM et al (2014) Fire dynamics distinguish grasslands, shrublands and woodlands as alternative attractors in the central Great Plains of North America. J Ecol 102:1374–1385

Reisner MD, Grace JB, Pyke DA et al (2013) Conditions favouring *Bromus tectorum* dominance of endangered sagebrush steppe ecosystems. J Appl Ecol 50:1039–1049

Rice PM (2005) Downy brome, *Bromus tectorum* L. In: Duncan CA, Clark C (eds) Invasive plants of range and wildlands and their environmental, economic, and societal impacts. Weed Sci Soc Am, Lawrence, pp 147–170

Soil Survey Staff NRCS, USDA (2015) Soil survey geographic (SSURGO) database. http://sdmdataaccess.nrcs.usda.gov/

Teague WR, Dowhower SL, Baker SA et al (2010) Soil and herbaceous plant responses to summer patch burns under continuous and rotational grazing. Agric Ecosyst Environ 137:113–123

Tonn WM (1990) Climate change and fish communities: a conceptual framework. Trans Am Fish Soc 119:337–352

Vermeire LT, Rinella MJ (2009) Fire alters emergence of invasive plant species from soil surface-deposited seeds. Weed Sci 57:304–310

Vermeire LT, Crowder JL, Wester DB (2011) Plant community and soil environment response to summer fire in the Northern Great Plains. Rangel Ecol Manag 64:37–46

Vermeire LT, Crowder JL, Wester DB (2014) Semiarid rangeland is resilient to summer fire and postfire grazing utilization. Rangel Ecol Manag 67:52–60

Whisenant SG (1990a) Changing fire frequencies on Idaho's Snake River Plains: ecological and management implications. General technical report—US Department of Agriculture, Forest Service, pp 4–10

Whisenant SG (1990b) Postfire population dynamics of *Bromus japonicus*. Am Midl Nat 123:301–308

Whisenant SG, Uresk DW (1990) Spring burning Japanese brome in a western wheatgrass community. J Range Manag 43:205–208

Whisenant SG, Ueckert DN, Scifres CJ (1984) Effects of fire on Texas wintergrass communities. J Range Manag 37:387–391

White RS, Currie PO (1983) Prescribed burning in the Northern Great Plains: yield and cover responses of 3 forage species in the mixed grass prairie. J Range Manag 36:179–183

Young JA, Evans RA (1978) Population dynamics after wildfires in sagebrush grasslands. J Range Manag 31:283–289