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Fire, livestock grazing, topography, and precipitation affect occurrence and prevalence of cheatgrass (*Bromus tectorum*) in the central Great Basin, USA

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Abstract Cheatgrass (*Bromus tectorum*) has increased the extent and frequency of fire and negatively affected native plant and animal species across the Intermountain West (USA). However, the strengths of association between cheatgrass occurrence or abundance and fire, livestock grazing, and precipitation are not well understood. We used 14 years of data from 417 sites across 10,000 km^2 in the central Great Basin to assess the effects of the foregoing predictors on cheatgrass occurrence and prevalence (i.e., given occurrence, the proportion of measurements in which the species was detected). We implemented hierarchical Bayesian models and considered covariates for which > 0.90 or < 0.10 of the posterior predictive mass for the regression coefficient ≥ 0 as strongly associated with the response variable. Similar to previous research, our models indicated that fire is a strong, positive predictor of cheatgrass occurrence and prevalence. Models fitted to all sample points and to only unburned points indicated that grazing and the proportion of years grazed were strong positive predictors of occurrence and prevalence. In contrast, in models restricted to burned points, prevalence was high, but decreased slightly as the proportion of years grazed increased (relative to other burned points). Prevalence of cheatgrass also decreased as the prevalence of perennial grasses increased. Cheatgrass occurrence decreased as elevation increased, but

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prevalence within the elevational range of cheatgrass increased as median winter precipitation, elevation, and solar exposure increased. Our novel time-series data and results indicate that grazing corresponds with increased cheatgrass occurrence and prevalence regardless of variation in climate, topography, or community composition, and provide no support for the notion that contemporary grazing regimes or grazing in conjunction with fire can suppress cheatgrass.

Keywords *Bromus tectorum* · Hierarchical models · Fire · Great Basin · Livestock grazing · Resilience

Introduction

Increases in the distribution and abundance of non-native grasses have modified fire dynamics world-wide, often leading to loss of human life and property and to substantial financial costs (D'Antonio and Vitousek 1992; Brooks et al. 2004). Cheatgrass (*Bromus tectorum*), an annual grass native to Eurasia, has increased in abundance and geographic distribution across the Intermountain West (USA) in recent decades. For example, the cover of cheatgrass is estimated to be at least 15% across about 210,000 km^2 of the Great Basin, a > 425,000 km^2 desert within the Intermountain West (Bradley et al. 2018). As cheatgrass expands, it drives a cycle of increases in the frequency and extent of fire and further expansion of cheatgrass (Bradley et al. 2018). The area burned has increased by as much as 200% since 1980, accompanied by over US$1 billion in fire-suppression costs (Balch et al. 2013; NCEI 2018). Cheatgrass-induced changes in fire patterns are associated with loss of sagebrush (*Artemisia* spp.), perennial grasses, and forbs that provide habitat for hundreds of plant and animal species. These species include Greater Sage-Grouse (*Centrocercus urophasianus*), which repeatedly has been considered for listing under the U.S. Endangered Species Act (Freeman et al. 2014; USFWS 2015; Germino et al. 2016).

Although the effects of cheatgrass on fire dynamics are well known, the effects of some potential predictors of cheatgrass distribution and abundance at large spatial extents, such as livestock grazing, abundance of native perennial grasses, precipitation, elevation,

and solar exposure, are less clear. For example, it has been suggested that livestock grazing, a major land use in the region, directly and indirectly (e.g., through reductions in the abundance of native perennials) increases the likelihood of invasion (e.g., Reisner et al. 2013). Moreover, the strength of response of both cheatgrass occurrence and prevalence (the proportion of binary occurrence measurements in a given area in which a species is present, and a critical component of the species' effects; Parker et al. 1999) to fire, grazing, and precipitation are unknown. We aimed to clarify these relations.

Several studies assessed environmental correlates of cheatgrass cover, density, or abundance in the Intermountain West (e.g., Gelbard and Belnap 2003; Bradley and Mustard 2006; Compagnoni and Adler 2014; Pilliod et al. 2017). These correlates vary across the range of cheatgrass (e.g., Bradley et al. 2016; Brooks et al. 2016), in relation to fire, and potentially over time. The cover, density, or abundance of cheatgrass can increase rapidly in areas that recently have burned or been disturbed by land uses such as road construction, maintenance, or use; agricultural activities; or grazing by domestic livestock (Mack 1981; Bradley and Mustard 2006; Banks and Baker 2011; Reisner et al. 2013; Pyke et al. 2016; Svejcar et al. 2017).

Previous field research rarely quantified the links between cheatgrass and livestock grazing due to the difficulty of obtaining reliable, quantitative data regarding this land use. Yet management of livestock grazing on the public lands that cover more than half of the Intermountain West, and about 75% of the Great Basin, may have a substantial effect on the expansion and ecological effects of cheatgrass. Livestock trample soil crusts, which can increase potential colonization by cheatgrass; feed on native perennial grasses that can compete with cheatgrass (see below); and disperse cheatgrass seeds (Reisner et al. 2013). In many cases, the US Forest Service (USFS) and US Bureau of Land Management (BLM)—the agencies with jurisdiction over the majority of public lands in the western United States—defer continuation of livestock grazing on active allotments for 2 years following fire (BLM 2007). Although there are advocates for both shorter and longer exclusion periods, there are few empirical data to inform management decisions, especially in areas where cheatgrass has become widespread.

The abundance and cover of native perennial grasses that compete with cheatgrass independent of land use also are directly and negatively associated with the intensity of livestock grazing (Adler et al. 2005; Reisner et al. 2013). These grasses did not coevolve with high abundances of large ungulates (Mack and Thompson 1982). Although fires in Great Basin ecosystems typically remove fire-intolerant shrubs such as sagebrush, most native perennial grasses survive. The cover of cheatgrass and other non-native annual, invasive grasses is negatively related to the cover of perennial native grasses following prescribed fire and other management actions (Davies 2008; Chambers et al. 2014; Roundy et al. 2018). For example, in areas dominated by Wyoming big sagebrush (*Artemisia tridentata wyomingensis*), about 20% cover of perennial, native forbs and grasses is necessary to prevent increases in the cover of annual, invasive grasses after prescribed fire treatments (Chambers et al. 2014; Roundy et al. 2018). Therefore, livestock-grazing history and the abundance of perennial native grasses are likely to be associated with cheatgrass presence and abundance, and to interact with fire.

Establishment of cheatgrass is associated with relatively high levels of precipitation during autumn or spring, which facilitate the species' germination and growth (Bradley et al. 2016). Percent cover and biomass of cheatgrass also are highly responsive to heavy winter and spring precipitation (Knapp 1998). Cheatgrass biomass can increase tenfold following wet winters (Garton et al. 2011), substantially increasing fine-fuel loads and the probability of fire (Balch et al. 2013; Pilliod et al. 2017). Biomass of cheatgrass may remain high during the year following a wet winter, especially when competition from perennial grasses is low (Bradley et al. 2016). There is some evidence that the abundance of cheatgrass is less likely to increase in areas with relatively high summer precipitation and cool annual temperatures (Taylor et al. 2014; Brummer et al. 2016). Therefore, precipitation is likely to be associated with the presence and abundance of cheatgrass.

Cheatgrass occurs over extensive topographic gradients (Brooks et al. 2016), but the likelihood of presence or the abundance of cheatgrass generally decreases as elevation increases (Compagnoni and Adler 2014; Chambers et al. 2016). For example, in both 1973 and 2001, probability of cheatgrass presence in the central Great Basin was highest at elevations from 1200 to 1400 m (Bradley and Mustard 2006). Between those years, cheatgrass expanded into lower elevations, but did not expand at elevations above 1700 m, and the probability of cheatgrass presence above 2500 m was almost zero (Bradley and Mustard 2006). The mechanisms underlying the relation between cheatgrass presence or abundance and elevation are fairly well understood. Germination, growth, and reproduction of cheatgrass generally are highest at intermediate elevations with moderate temperatures and water availability, limited at low elevations by relatively high temperatures and low precipitation, and limited at high elevations by low soil temperatures (Meyer et al. 2001; Chambers et al. 2007, 2017; Compagnoni and Adler 2014). Strong competitive interactions between perennial grasses and cheatgrass affect density and cover of cheatgrass across elevational gradients (Chambers et al. 2007; Reisner et al. 2013; Larson et al. 2017). Soil moisture and nutrient levels generally increase as elevation increases, leading to an increase in primary productivity and higher levels of competition between cheatgrass and other species (Chambers et al. 2007; Compagnoni and Adler 2014).

Some work has suggested that cheatgrass is more likely to be present and abundant on certain topographic aspects, although relations with aspect may vary across the Great Basin and among assessment methods. On the basis of Landsat data for the central Great Basin, Bradley and Mustard (2006) found that likelihood of cheatgrass presence was greatest on west- and northwest-facing slopes. However, fine-resolution empirical analyses in the northern Great Basin and in the Rocky Mountains suggested that cheatgrass abundance was greatest on south-facing slopes (Banks and Baker 2011; Svejcar et al. 2017), especially at relatively high elevations (Brooks et al. 2016).

Here, we use a 14-year time-series of data collected within a bounding area of $\sim 10{,}000$ km^2 of the central Great Basin (Fig. 1) to assess empirically the relative strengths of association of cheatgrass occurrence and prevalence with fire, livestock grazing, precipitation, and other abiotic environmental conditions. Our selection of predictor variables was motivated by the ecological theories and previous research summarized above, and facilitated by the unusually extensive topographic gradients and duration covered

Fig. 1 Locations of the 417 sample points that were distributed among 29 canyons in four mountain ranges in the central Great Basin (Lander, Eureka, and Nye Counties, Nevada, USA). We sampled cheatgrass at each point for a minimum of three years and a maximum of eight years
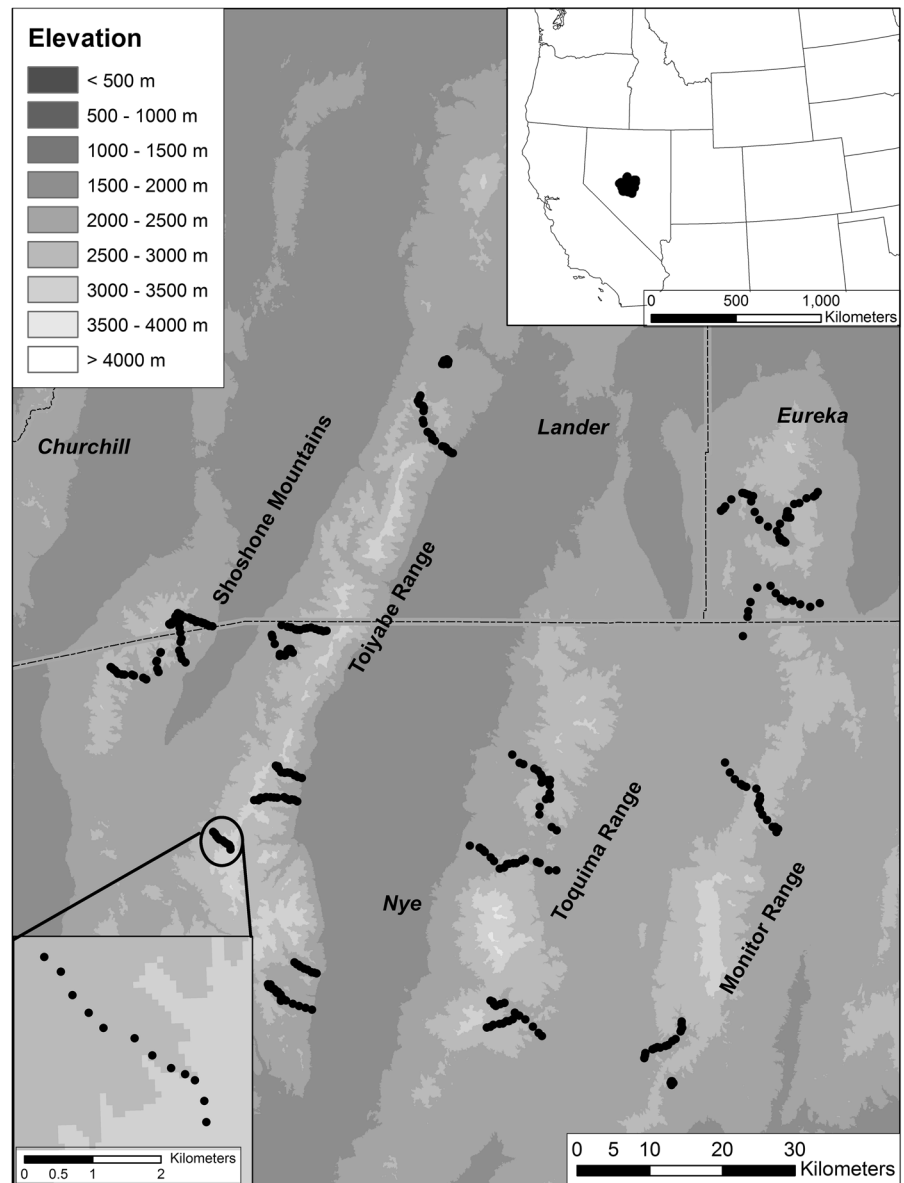
by our data. Our ultimate aim is to inform policy and management actions that may minimize the further expansion and undesirable direct and indirect effects of cheatgrass on species and ecosystem function across the Intermountain West. Our results also may inform research priorities or sampling designs to more thoroughly examine interactive effects of drivers of cheatgrass colonization and dominance.

Methods

Data collection and development

We used two sets of data collected from 2001 through 2015 in 29 canyons in four mountain ranges (Shoshone, Toiyabe, Toquima, and Monitor) in Lander, Nye, and Eureka Counties, Nevada (Fleishman 2015) (Fig. 1). Within those canyons, we sampled cheatgrass at elevations from 1886 through 3219 m over a range of disturbance histories. Complete

vegetation data and metadata are in Chambers et al. (2010) and Fleishman (2015). Detailed information about data collection methods also is in Urza et al. (2017).

First, we collected data on cheatgrass and other elements of vegetation structure and composition from 30 to 50 m point-intercept transects (10–31 locations per transect per year) along elevational gradients of the 29 canyons. We refer to each transect as a *sample point*. We collected data from each sample point for 3–8 years from 2001 to 2015.

Second, we collected vegetation data in three pairs of adjacent alluvial fans on burned and unburned sites at elevations of 2073, 2225, and 2347 m on a north-facing slope within one watershed in the Shoshone Mountains. We established three sampling plots of ca 0.1 ha within burned and unburned plots at each elevation. We measured areal cover of herbaceous species and shrubs within 50, 2-m^2 quadrats per plot in 2001, prior to a prescribed fire. We remeasured the same plots in 2002, 2004, and 2006, after the fire. We measured areal cover of herbaceous species within 25–30, 0.25-m^2 quadrats. We converted these quadrats to presence–absence estimates for a sample point assigned to the geographic center of the plots to allow combination with the transect data (i.e., the number of the 50 quadrats in which cheatgrass was detected).

We assessed cheatgrass occurrence by considering sample points at which cheatgrass was not recorded during the study period as absences, and sample points at which cheatgrass was recorded present in ≥ 1 year during the study period as presences. For each sample point at which cheatgrass was recorded present, we estimated local prevalence of cheatgrass by summing the number of point intercepts (or quadrats) where cheatgrass was recorded present and comparing that to the total number of point intercepts (or quadrats) taken at each point in a given year.

We characterized the grazing and fire history of each sample point for each year during the period in which we collected vegetation data. Each year from 2001 through 2015, EF or JC made multiple visits (generally 3–6) to each point at which data were collected and recorded whether it was grazed by domestic cattle and whether a fire occurred during the growing season or between the previous and current growing season. We augmented these observations with information on whether grazing by domestic cattle was permitted on each allotment (i.e., whether

the allotment was active) from 2006 through 2015 (M. West, USFS, personal communication). We assigned a binary value to indicate whether the allotment in which a given sample point was embedded was grazed during each year. Because data on realized (as opposed to permitted) grazing intensity are not maintained by the USFS, which manages virtually all of the land on which our sample points were located, we assumed that all active allotments were grazed. Although permitees may use a portion of an allotment rather than an entire allotment, or engage in short-term non-use of an allotment, it is reasonable to assume that active allotments were grazed recently or during the years in which data were collected. We calculated the proportion of years during which each sample point was grazed (years grazed/years during the study period prior to collection of data in a given year) to estimate levels of livestock use. We classified sampled points as burned if a fire occurred at the sample point from 2000 through 2015.

For burned points, we calculated the number of growing seasons between the fire and a given field sample. We included both linear and quadratic terms for number of growing seasons between the fire and the sampling event because Miller et al. (2013) suggested that cheatgrass could decrease in abundance after about 12 years if the abundance of other grasses, forbs, and shrubs increases. To examine the potential effect on cheatgrass of competition from perennial native grasses, we also estimated the prevalence of perennial native grasses at each sample point by summing the number of points along transects or within quadrats at which perennial native grass was recorded present and dividing by the total number of points.

We derived the elevation of each sample point from the 10-m National Elevation Dataset (lta.cr.usgs.gov/NED). We calculated a hillshade index (an indication of the extent to which a given location receives direct sunlight or is shaded) in ArcGIS 10.4 (Esri, www.esri.com/en-us/home) for each sample point (at the geographic center of transects or quadrats) on the basis of the sun angle and azimuth at the center of study area on 21 June at 15:00. The date and time represent maximum solar exposure on summer solstice (Blackard and Dean 1999). Values of the hillshade index ranged from 0 to 254, with higher values indicating greater solar exposure on southwest-facing slopes. We estimated solar radiation on the basis of a hillshade index

Table 1 Predictors included in models of the probability of presence (occurrence) of cheatgrass and prevalence of cheatgrass (i.e., given occurrence, the likelihood that cheatgrass was recorded present in any sample in a given point in a given year)

Model	Level	Predictor
Occurrence		
All sample points	Point	Elevation
		Hillshade index (an indication of the extent to which a given location receives direct sunlight or is shaded)
		Median annual winter precipitation over the study period
		Median annual proportion of precipitation falling in winter over the study period
	Observation	Burned (yes/no) (whether a fire occurred during the growing season or between the previous and current growing season)
		Grazed (yes/no) (whether grazing by domestic cattle was permitted on the allotment within which the point was located)
Unburned points	Point	Elevation
		Hillshade index
		Median annual winter precipitation over the study period
		Median annual proportion of precipitation falling in winter over the study period
	Observation	Grazed (yes/no)
Prevalence		
All points	Point	Elevation
		Hillshade index
		Median annual winter precipitation over the study period
		Median annual proportion of precipitation falling in winter over the study period
	Observation	Burned (yes/no)
		Proportion of years grazed
		Prevalence of perennial grasses
		Spring precipitation in the year of sampling
		Winter precipitation in the year of sampling
		Proportion of precipitation falling in winter in the year of sampling
Unburned points	Point	Elevation
		Hillshade index
		Median annual winter precipitation over the study period
		Median annual proportion of precipitation falling in winter over the study period
	Observation	Proportion of years grazed
		Prevalence of perennial grasses
		Spring precipitation in the year of sampling
		Proportion of precipitation falling in winter in the year of sampling
Burned points	Point	Elevation
		Hillshade index
		Median annual winter precipitation over the study period
		Median annual spring precipitation over the study period
		Median annual proportion of precipitation falling in winter over the study period
	Observation	Time since fire
		Time since fire^2
		Proportion of years grazed
		Prevalence of perennial grasses
		Spring precipitation in the year of sampling
		Winter precipitation in the year of sampling
		Proportion of precipitation falling in winter in the year of sampling

rather than aspect because it is difficult to differentiate between opposite aspects (e.g., north vs. south or east vs. west) within a statistical model. We estimated precipitation at each sample point with data from the Parameter-elevation Regressions on Independent Slopes Model (PRISM). We calculated both cumulative precipitation in the winter (1 October–31 March) and spring (1 April–30 June) preceding sampling and the proportion of precipitation in those two seasons that fell in winter. We included the latter variable to distinguish associations with precipitation seasonality from those with cumulative precipitation.

We restricted the data to years for which data on cheatgrass and predictors were available for each sample point. In some cases, the bivariate correlation between winter and spring precipitation was > 0.7. We retained the precipitation estimate that had the lowest correlation with all other predictors in the model. We scaled all predictors to a mean of zero and unit variance to facilitate model convergence and to represent the predictors on a common scale.

Statistical modeling

We modeled associations between predictors and occurrence across the 14-year study period, and between predictors and annual variation in prevalence throughout the 14-year study period. To evaluate associations with predictors in the presence and in the absence of fire, we applied these models to (1) all of the data ($N_{occurrence} = 417, N_{prevalence} = 624$), (2) only those points that had not been burned ($N_{occurrence} = 326, N_{prevalence} = 314$), and (3) only those points that had been burned ($N_{occurrence} = 91, N_{prevalence} = 310$). We did not fit occurrence models to burned points because cheatgrass was recorded present in 88 of those 91 points, preventing the model from discriminating between the determinants of presence and absence.

We classified sample points as *recorded present* if cheatgrass was detected at any time during the study period (occurrence = 1) and *recorded absent* if cheatgrass was not observed during the study period (occurrence = 0). We used a Bernoulli response model to link occurrence with candidate predictors (Table 1). We then used a binomial response model to identify predictors that were associated strongly with the prevalence of cheatgrass in the sample points at

which cheatgrass was recorded. We used separate response models rather than zero-inflated models (e.g., hurdle models sensu Mullahy 1986) because the spatial–temporal processes almost certainly are not statistically stationary. Hurdle models assume that occurrence is stationary, but cheatgrass is still spreading throughout our study area.

Cheatgrass occurrence

For each sample point, we calculated winter and spring precipitation as the median annual value across the study period. We assigned binary values for fire and grazing that reflected whether the point had been burned or grazed in any year of the study period prior to the year in which cheatgrass first was recorded present or, if cheatgrass consistently was recorded absent, the final year of sampling.

We modeled whether cheatgrass was recorded present ($\Phi_{i,j,k,s}$) during a given year (i) at sample point j within canyon k within mountain range s as the outcome of a Bernoulli trial with probability $p_{i,j,k,s}$. We modeled probability $p_{i,j,k,s}$ as a function of the point-level intercept ($\alpha_{j,k,s}$) and the product of observation-level regression parameters (β_{obs}) and observation-level standardized predictors (some predictors vary among years; X_{obs}, Table 1).

$$\Phi_{i,j,k,s} \sim Bernoulli(p_{i,j,k,s}), \tag{1}$$

$$logit(p_{i,j,k,s}) = \alpha_{j,k,s} + \beta_{obs}X_{obs}. \tag{2}$$

We modeled the point-level intercepts as the outcome of a canyon- and range-specific, point-level intercept ($\alpha_{k,s}$) and the sample point-level regression parameters (β_{point}) and sample point-level predictors (i.e., predictors with values that were constant throughout the study period, X_{point}, Table 1).

$$\alpha_{j,k,s} \sim Normal(\mu_{j,k,s}, \sigma_{k,s}), \tag{3}$$

$$\mu_{j,k,s} = \alpha_{k,s} + \beta_{point}X_{point}, \tag{4}$$

$$\sigma_{k,s} \sim HalfNormal(0, 1). \tag{5}$$

We modeled mountain range-specific, canyon-level intercepts ($\alpha_{k,s}$) as

$$\alpha_{k,s} \sim Normal(\mu_{k,s}, \sigma_s), \tag{6}$$

$$\mu_{k,s} = \alpha_s, \tag{7}$$

$$\sigma_s \sim HalfNormal(0, 1). \tag{8}$$

We modeled mountain range-level intercepts as specific outcomes of a global mean (μ_0):

$$\alpha_s \sim Normal(\mu_0, \sigma_0), \tag{9}$$

$$\mu_0 \sim Normal(0, 2), \tag{10}$$

$$\sigma_0 \sim HalfNormal(0, 1). \tag{11}$$

This hierarchical structure accounted for potential systematic variation among points within the same canyon and among canyons within the same mountain range, and for potential spatial organization in the data.

Cheatgrass prevalence

For sample points at which cheatgrass was recorded present, we modeled cheatgrass prevalence as functions of topographic, climatic, and land-use variables (Table 1). We attributed observation-level predictor values to each point for the corresponding year of sampling. We included the annual estimate of each precipitation variable as an observation-level predictor and the median of the annual values of each precipitation variable throughout the study period as a point-level predictor. We used the proportion of years grazed as the grazing predictor in these analyses.

We modeled the prevalence of cheatgrass ($y_{i,j,k,s}$) in a given year (i) at sample point j within canyon k within mountain range s as the binomial outcome of the number of detections, which in turn was a function of the number of samples taken at that point in that year ($n_{i,j,k,s}$), where cheatgrass is present with probability $p_{i,j,k,s}$. We modeled the probability $p_{i,j,k,s}$ as a function of the point-level intercept ($\alpha_{i,j,k,s}$) and the product of an array of observation-level slope parameters (β_{obs}) and observation-level predictors (X_{obs}, Table 1).

$$y_{i,j,k,s} \sim Binomial(n_{i,j,k,s}, p_{i,j,k,s}), \tag{12}$$

$$logit(p_{i,j,k,s}) = \alpha_{j,k,s} + \beta_{obs}X_{obs}. \tag{13}$$

We modeled the point-level intercepts as the outcome of a point-specific, canyon-level intercept ($\alpha_{k,s}$) and

the product of an array of point-level slope parameters (β_{point}) and point-level predictors (X_{point}, Table 1).

$$\alpha_{j,k,s} \sim Normal(\mu_{j,k,s}, \sigma_{k,s}), \tag{14}$$

$$\mu_{j,k,s} = \alpha_{k,s} + \beta_{point}X_{point}, \tag{15}$$

$$\sigma_{k,s} \sim HalfNormal(0, 1). \tag{16}$$

We modeled mountain range-specific, canyon-level intercepts ($\alpha_{k,s}$) as

$$\alpha_{k,s} \sim Normal(\mu_{k,s}, \sigma_s), \tag{17}$$

$$\mu_{k,s} = \alpha_s, \tag{18}$$

$$\sigma_s \sim HalfNormal(0, 1). \tag{19}$$

We modeled mountain range-level intercepts as specific outcomes of a global mean (μ_0):

$$\alpha_s \sim Normal(\mu_0, \sigma_0), \tag{20}$$

$$\mu_0 \sim Normal(0, 2), \tag{21}$$

$$\sigma_0 \sim HalfNormal(0, 1). \tag{22}$$

Model fitting

We fitted models in R (v3.4.1, R Core Team 2017; Williamson 2019) with the rstan package (Stan Development Team 2018), a wrapper to the Hamiltonian Monte Carlo program Stan (Stan Development Team 2017). We used four sampling chains, each with 2000 iterations (1000 iterations for warmup), and set the adaptation parameter (adapt delta) to 0.95. The latter reduces the step-size of the sampler to allow sampling of complex posterior geometries of model parameters and reduces the potential that bias will result from chains that do not sample the posterior distribution effectively (Stan Development Team 2017).

Assessing model fit

We assessed goodness-of-fit of the occurrence model by evaluating the area under the receiver-operating curve [AUC; implemented in package pROC (Robin et al. 2011)]. AUC > 0.75 is regarded as a good model fit and AUC $\sim$ 1 as an excellent fit to the data. We evaluated the AUC for the lower quartile, median, and

upper quartile values for posterior predictions of p (the posterior estimate of the probability of occurrence) to evaluate the sensitivity of our AUC calculations across the posterior distribution of p.

For the binomial models, we sampled values from the posterior of the parameterized model ($y_{i,jk,s}^{sampled}$) and calculated the Freeman-Tukey measure of discrepancy for the observed ($y_{i,j,k,s}^{obs}$) or sampled data, given their fitted values ($\mu_{j,k,s}$):

$$D_{obs} = \sum_i \sqrt{\left(y_{i,j,k,s}^{obs} - \mu_{j,k,s}\right)^2}; \qquad (23)$$

$$D_{sampled} = \sum_i \sqrt{\left(y_{i,j,k,s}^{sampled} - \mu_{j,k,s}\right)^2} \qquad (24)$$

Any number of samples from the posterior can be drawn and corresponding discrepancies calculated. The posterior predictive fit is the proportion of sampled discrepancies that exceed the observed discrepancy. Values of posterior predictive fit near 0.5 indicate excellent model fits, but values from 0.05 through 0.95 are regarded as plausible fits of the parameterized model to the data (Gelman et al. 2013).

Strength of association of individual predictors

We assessed the strength of evidence that a predictor was strongly associated with the probability of occurrence (Bernoulli model) or with the prevalence (binomial model) of cheatgrass by calculating the proportion of the posterior probability distribution that exceeded zero for each predictor's regression coefficient. Predictors for which > 0.90 or < 0.10 of the posterior predictive mass for the regression coefficient ≥ 0 were regarded, respectively, as strongly and positively or strongly and negatively associated with the response variable. Given our use of uninformative priors (i.e., half of the posterior predictive mass ≥ 0), posterior proportions > 0.90 correspond to odds ratios of > 10, which are strong positive associations (Jeffreys 1961). Similarly, posterior proportions < 0.10 equate to odds ratios of < 0.1, which are evidence of strong negative associations.

We did not interpret the strength of associations of predictors on the basis of the magnitudes of the regression coefficients for two reasons. First, only the continuous predictors were scaled given that the mean of a binary predictor is not relevant, making comparisons with the binary predictors inappropriate. Second, although expressing the continuous predictors on a common scale facilitates model fitting, it results in regression coefficients that indicate the predicted change in outcome associated with a unit standard deviation change in the predictor value. As such, the regression coefficients provide an estimate of the relative effect of the predictor subject to its measured variation and conditional on all other predictors in the model. Given that our continuous predictors had different standard deviations, use of the magnitude of the regression coefficients to compare the relative strength of the predictors in our models would be inappropriate. Instead, we provide marginal effects plots to illustrate the effect of multiple standard deviation changes in the predictor on the response while all other predictors are held at their mean.

Results

Occurrence models for all sample points and unburned points fitted the data well (AUC > 0.98 for the median, lower, and upper quartile posterior estimates of p). Posterior predictive checks indicated that the prevalence models also fitted the data well, with posterior predictive fits of 0.25, 0.32, and 0.26 for models that included all sample points, unburned points only, and burned points only, respectively.

The probabilities of cheatgrass occurrence and prevalence were associated strongly with fire. Results of the model that included all sample points (Fig. 2A) indicated that fire occurrence was associated with an increase in the probability of cheatgrass occurrence (Table 2, Fig. 2B) and an increase in prevalence (conditional on cheatgrass presence; Table 3, Fig. 2C). In models restricted to burned points, cheatgrass prevalence increased as time since fire increased. However, the strength and sign of the quadratic term suggested that this relation may peak at intermediate values of time since fire.

Grazing and prevalence of native perennial grasses were associated with the probability of cheatgrass occurrence and prevalence. Models that included either all sample points or only unburned points (Fig. 3A) indicated that grazing occurrence and an increase in the proportion of years grazed were associated positively with an increase in the
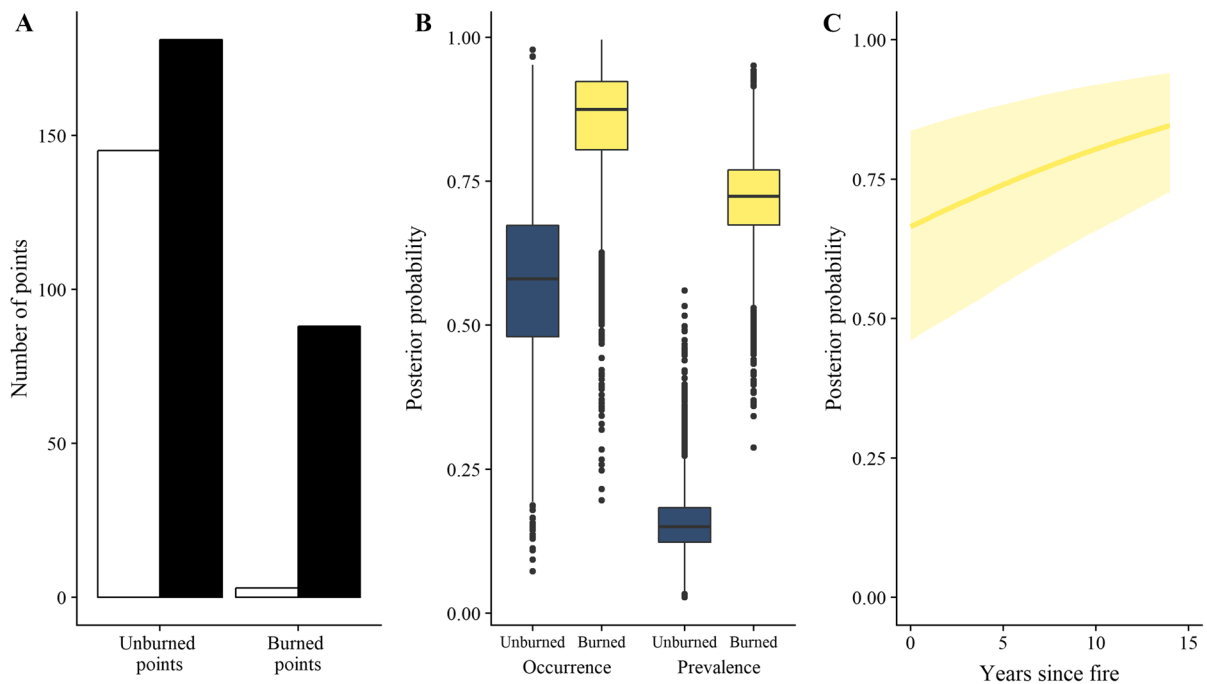
Fig. 2 Relations between fire and the occurrence of cheatgrass and prevalence of cheatgrass (i.e., given occurrence, the likelihood that cheatgrass was recorded present in any sample in a given point in a given year). Posterior probabilities for the occurrence and prevalence models are based on the likelihoods described in Eqs. 1 and 12 (and their associated models and priors), respectively. **A** The number of sample points in which cheatgrass was recorded present (black) was much greater than the number of sample points in which it was recorded absent

(white); cheatgrass was recorded present in 97% of burned points. **B** Probability of occurence of cheatgrass and of prevalence of cheatgrass were higher in models that included only burned points (yellow) than in models that included only unburned points (blue). **C** In the model restricted to burned points, the marginal effect of time since fire on cheatgrass prevalence (conditional on cheatgrass presence) was strongly positive. SD, standard deviation from the mean value of time since fire

Table 2 Regression coefficients and standard deviations (SD) of the parameter estimates for predictors (standardized if continuous) included in models of cheatgrass occurrence

Variable	All sample points Mean (SD)	Unburned points Mean (SD)
Elevation	− 0.46 (0.23)*	− 0.43 (0.24)*
Hillshade index	0.17 (0.15)	0.14 (0.17)
Median winter precipitation	− 0.07 (0.23)	− 0.02 (0.25)
Median proportion of precipitation falling in winter	− 0.47 (0.23)*	− 0.42 (0.25)*
Burned (yes/no)	1.64 (0.56)*	NA
Grazed (yes/no)	0.64 (0.44)*	0.25 (0.45)

Mean, mean posterior estimate for each slope coefficient. NA, not included in model. Asterisks indicate strong positive or negative associations with occurrence (defined as > 0.90 or < 0.10 of the posterior predictive mass for the regression coefficient ≥ 0)

probability of cheatgrass occurrence (Table 2, Fig. 3B) and in the prevalence of cheatgrass (Table 3, Fig. 3C). However, in models restricted to burned points, prevalence of cheatgrass remained quite high,

but decreased slightly as the proportion of years grazed increased (Table 3, Fig. 3D). Few burned points (8 of 91) were not grazed. In models that included all sample points or only unburned points,

Table 3 Regression coefficients and standard deviations (SD) of the parameter estimates for predictors (standardized if continuous) included in models of prevalence of cheatgrass (i.e., given occurrence, the likelihood that cheatgrass was recorded present in any sample in a given point in a given year)

Variable	All sample points Mean (SD)	Unburned points Mean (SD)	Burned points Mean (SD)
Elevation	0.03 (0.04)	0.09 (0.06)*	0.41 (0.10)*
Hillshade index	− 0.08 (0.02)*	− 0.13 (0.03)*	− 0.31 (0.03)*
Median spring precipitation over the study period	NA	NA	− 0.53 (0.09)*
Median winter precipitation over the study period	0.15 (0.03)*	0.04 (0.06)	0.25 (0.06)*
Median proportion of precipitation falling in winter over the study period	− 0.18 (0.04)*	0.01 (0.06)	0.04 (0.04)
Burned (yes/no)	2.69 (0.06)*	NA	NA
Time since fire	NA	NA	1.03 (0.05)*
Time since fire^2	NA	NA	− 0.73 (0.03)*
Proportion of years grazed	0.47 (0.03)*	0.13 (0.06)*	− 0.13 (0.04)*
Prevalence of perennial grasses	− 0.08 (0.03)*	− 0.18 (0.04)*	− 0.01 (0.03)
Spring precipitation in the year of observation	− 0.31 (0.08)*	0.00 (0.04)	− 0.22 (0.11)*
Winter precipitation in the year of observation	0.27 (0.07)*	NA	0.26 (0.09)*
Proportion of precipitation falling in winter in the year of observation	− 0.27 (0.07)*	− 0.16 (0.04)*	− 0.27 (0.11)*

Mean, mean posterior estimate for each slope coefficient. NA, not included in model. Asterisks indicate strong positive or negative associations with prevalence (defined as > 0.90 or < 0.10 of the posterior predictive mass for the regression coefficient ≥ 0)
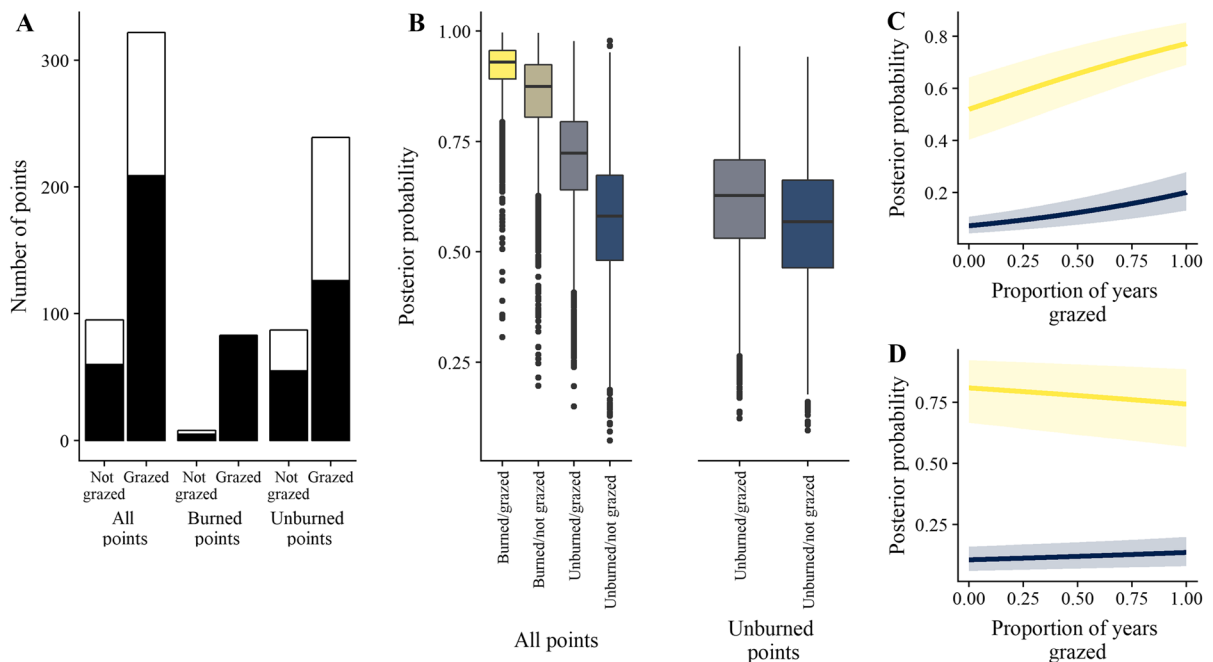
prevalence of cheatgrass decreased as prevalence of perennial grasses increased (Table 3). We did not estimate relations between prevalence of perennial grasses and probability of cheatgrass occurrence because we did not have a complete record of perennial grass prevalence and, therefore, could not estimate the median prevalence of perennial grasses across the study period.

The response of cheatgrass to longer-term precipitation (median winter and spring precipitation and the median proportion of precipitation falling in winter) was inconsistent. Median winter precipitation was not strongly associated with probability of cheatgrass occurrence (Table 2) but was associated positively with cheatgrass prevalence in models that included all sample points or only burned points (Fig. 4A). The median proportion of precipitation falling in winter was negatively associated with the probability of cheatgrass occurrence in models that included all sample points or only unburned points (Table 2, Fig. 4B). Similarly, the proportion of precipitation falling in winter in the year of observation was negatively associated with cheatgrass prevalence in all three models (Table 3, Fig. 4C). We did not include median spring precipitation as a predictor because it was highly correlated with median winter

precipitation. However, regardless of the amount or proportion of winter precipitation, prevalence of cheatgrass in models restricted to burned points increased as median spring precipitation decreased.

Precipitation in the year of observation was associated strongly with the prevalence of cheatgrass. In models that included all sample points or only burned points, cheatgrass prevalence increased as winter precipitation increased (Table 3, Fig. 4C). The effect could not be estimated in the model restricted to unburned points, in which winter precipitation was excluded given its high correlation with other variables.

Elevation was associated strongly with cheatgrass occurrence in all models and with prevalence of cheatgrass in models restricted to unburned or burned points (Tables 2, 3; Fig. 5A). Probability of cheatgrass occurrence increased as elevation decreased, and prevalence increased as elevation increased when controlling for fire (i.e., restricting the data to either burned or unburned points, Tables 2, 3; Fig. 5B, C). This may be due to the occurrence of most fires at the lower end of the range of elevations occupied by cheatgrass. Solar exposure was not strongly associated with probability of cheatgrass occurrence (Table 2),

Fig. 3 Response of the occurrence of cheatgrass and prevalence of cheatgrass (i.e., given occurrence, the likelihood that cheatgrass was recorded present in any sample in a given point in a given year) to the interaction between livestock grazing and fire. Posterior probabilities for the occurrence and prevalence models are based on the likelihoods described in Eqs. 1 and 12 (and their associated models and priors), respectively. **A** The number of points at which cheatgrass was recorded present (black) or recorded absent (white) in models that included all sample points, burned points only, or unburned points only. **B** Livestock grazing and fire both increased the probability of cheatgrass occurrence. Yellow, grazed and burned; tan, burned only; gray, grazed only; blue, neither grazed nor burned. Values derived from models that included either all sample points or unburned points. **C** Marginal effect of the proportion of years grazed on cheatgrass prevalence in models that included all sample points. Yellow, burned points; blue, unburned points. SD, standard deviation from the mean value of proportion of years grazed. **D** Marginal effect of the proportion of years grazed on cheatgrass prevalence in models that were restricted to either burned points (yellow) or unburned points (blue)

but prevalence increased as exposure decreased (Table 3).

Discussion

We capitalized on spatially and temporally extensive data on cheatgrass in both burned and unburned areas to evaluate explicitly the associations of fire, livestock grazing, precipitation, elevation, and solar exposure with probability of occurrence and with prevalence of cheatgrass across a large area and extensive topographic gradients. Our results generally were consistent with expectations that fire and a history of livestock grazing are associated positively with probability of cheatgrass presence and prevalence, and that ongoing disturbance is likely to induce expansion and increases in cover, density, abundance, or similar

measures. Moreover, our work highlights that the potential response of cheatgrass to any one predictor, regardless of whether that predictor can be managed, is affected by other biotic and abiotic environmental attributes and feedbacks.

Regardless of fire history, cheatgrass was more likely to be recorded present at lower elevations. However, given presence, cheatgrass prevalence was greater at higher elevations and in areas with lower solar exposure. These areas likely have relatively high soil water availability while meeting the thermal requirements of cheatgrass for establishment, growth, and seed production (Chambers et al. 2007, 2016). Many of these areas are in canyons and occur in association with pinyon (*Pinus monophylla*) and juniper (*Juniperus osteosperma, J. occidentalis*) trees, which may reduce the exposure of cheatgrass to sunlight and heat stress. Higher prevalence of
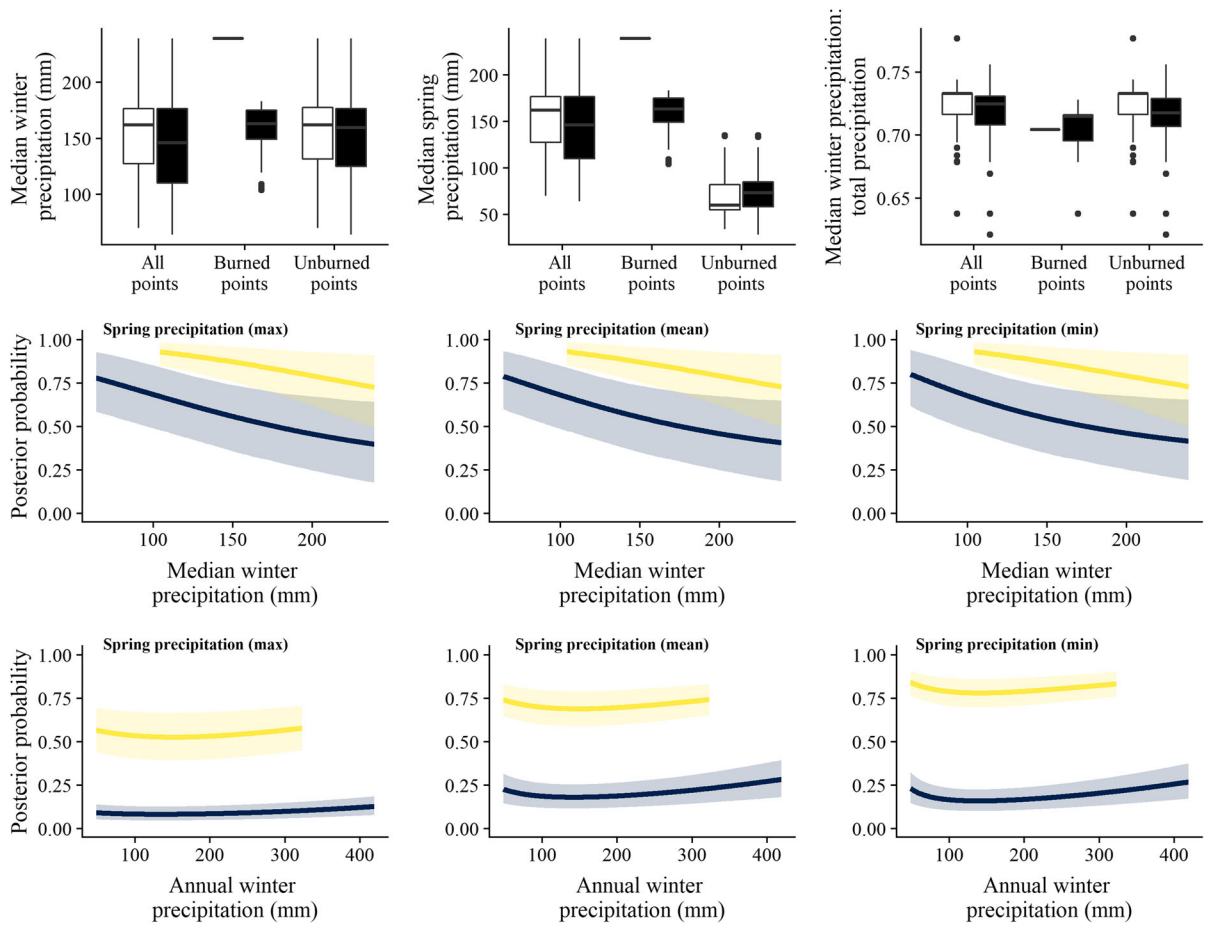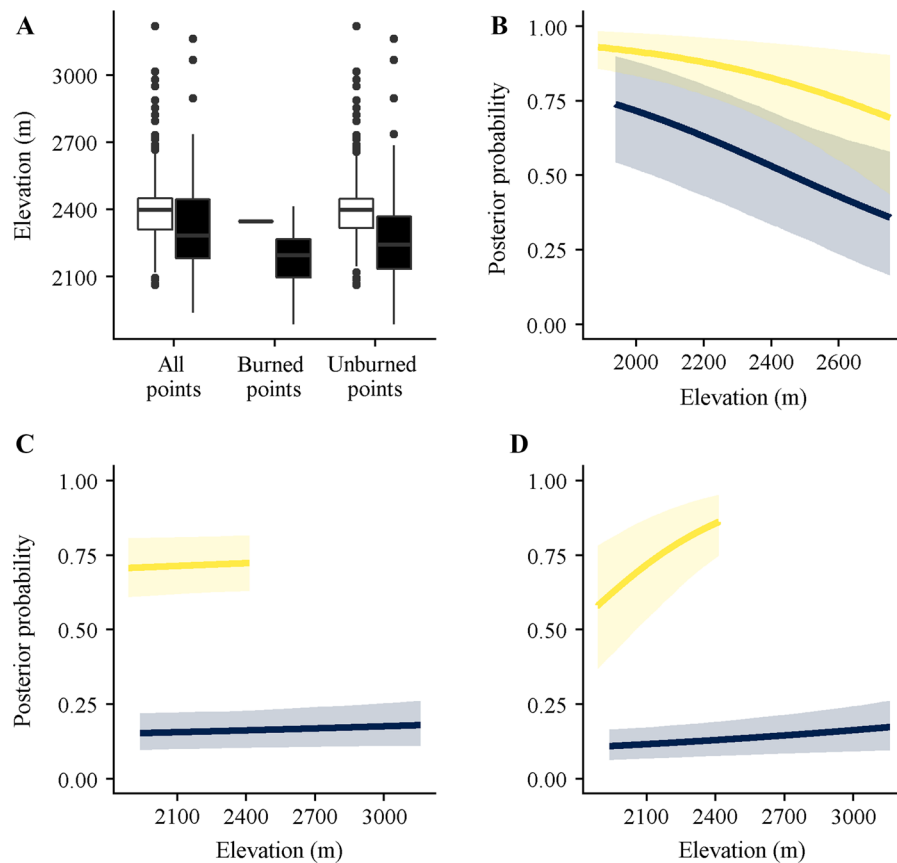
Fig. 4 Response of the occurrence of cheatgrass and prevalence of cheatgrass (i.e., given occurrence, the likelihood that cheatgrass was recorded present in any sample in a given point in a given year) to precipitation. Posterior probabilities for the occurrence and prevalence models are based on the likelihoods described in Eqs. 1 and 12 (and their associated models and priors), respectively. Top row: Median winter precipitation, spring precipitation, or proportion of precipitation falling in winter at sample points at which cheatgrass was recorded present (black) or recorded absent (white) in models that included all sample points, burned points only, or unburned points only. Middle row: The probability of cheatgrass occurrence decreased as median winter precipitation (or the median proportion of precipitation falling in winter) increased when the maximum, mean, or minimum spring precipitation was held constant. Values derived from models that included all sample points. Yellow, burned points; blue; unburned points. SD, standard deviation from the mean value of median winter precipitation. Bottom row: The probability of cheatgrass prevalence increased as median winter precipitation (or the median proportion of precipitation falling in winter) over the study period increased when the maximum, mean, or minimum spring precipitation was held constant. Values derived from models that included all sample points. SD, standard deviation from the mean value of winter precipitation in the year of sampling

cheatgrass at relatively high elevations at the edges of unoccupied areas suggests that cheatgrass is likely to expand to higher elevations if thermal conditions are consistent with its requirements and if ground disturbances continue.

Consistent with previous studies on the cheatgrass-fire cycle (Balch et al. 2013; Germino et al. 2016; Bradley et al. 2018), the presence of fire was the predictor most strongly associated with probability of

cheatgrass presence and was positively related to prevalence. In models restricted to burned points, prevalence of cheatgrass increased as time since burn increased. A lag in increases in cheatgrass density and cover of one to three years after fire is common (Chambers et al. 2016). Subsequent increases in cover and density can occur over time as the abundance of cheatgrass in the seed bank increases (Chambers et al. 2016).

Fig. 5 Response of the occurrence of cheatgrass and preva-lence of cheatgrass (i.e., given occurrence, the likelihood that cheatgrass was recorded present in any sample in a given point in a given year) to elevation. Posterior probabilities for the occurrence and prevalence models are based on the likelihoods described in Eqs. 1 and 12 (and their associated models and priors), respectively. **A** Elevational distribution of sample points at which cheatgrass was recorded present (black) or recorded absent (white) in models that included all sample points, burned points only, or unburned points only. **B** Probability of cheatgrass occurrrence decreased as elevation increased in a model that included all sample points (yellow, burned; blue, unburned). SD, standard deviation from the mean value of elevation. **C** Prevalence of cheatgrass, conditional on cheatgrass presence, increased as elevation increased in a model that included all sample points. **D** Prevalence of cheatgrass, conditional on cheatgrass presence, increased as elevation increased in models that were restricted to either burned points (yellow) or unburned points (blue). Differences in line lengths reflect different elevational ranges covered by the points included in the three models

Abundance of perennial native herbaceous species often is associated negatively with the abundance of cheatgrass or other non-native invasive annual grasses following prescribed fire and other management treatments (Davies 2008; Chambers et al. 2014). We found negative associations between prevalence of native perennial grasses and prevalence of cheatgrass in models that included all sample points or only unburned points, but not in models restricted to burned points. Following fire, loss of sagebrush and other fire-intolerant woody species increases the area of habitat for cheatgrass, soil water content, and nutrient content,

and typically leads to increases in cheatgrass presence and abundance (Roundy et al. 2014, 2018). Cheatgrass likely will persist on these burned sites. However, maintaining or increasing the abundance of native perennial grasses can increase resistance to cheatgrass (Chambers et al. 2016; Pyke et al. 2016). The longer-term trajectories of these systems are unknown, but the strength and sign of the quadratic form of time-since-fire suggests that prevalence may stabilize or even decrease slightly at some point beyond the 14-year period we examined.

Consistent with Reisner et al. (2013), our analyses of all sample points and of only unburned points support the inference that, over an extensive area, both the presence of livestock grazing and the proportion of years in which a location is grazed are associated with an increase in the probability of presence and prevalence of cheatgrass. However, the negative association between the proportion of years grazed and prevalence of cheatgrass in models restricted to burned points may reflect a modest reduction in cheatgrass growth and seed production. This decrease in cheatgrass prevalence was accompanied by a decrease in the incidence of perennial grasses, suggesting that grazing on burned sites may lead to an overall decrease in herbaceous cover or biomass rather than selectively suppressing cheatgrass per se. Regardless, that the probability of encountering cheatgrass at any observation around a sample point (i.e., probability of prevalence) was > 0.5 on burned sites suggests that cheatgrass is likely to remain fairly dense on sites that are both burned and grazed, even if prevalence decreases modestly from its absolute peak.

It has been suggested that livestock grazing can reduce fuel loads and the likelihood of severe fires in sagebrush ecosystems (Davies et al. 2010). In the Owyhee Front in southern Idaho, the BLM has begun implementing intensive grazing in an effort to create fuel breaks, although evidence that fuel breaks reduce the spread and undesirable effects of fire is lacking (Shinneman et al. 2019). Grazing often reduces the abundance of perennial native grasses, which can facilitate increases in the presence and relative abundance of cheatgrass (Reisner et al. 2013, 2015); as our work suggests, these increases can occur over large areas, especially after fire. Widespread increases in cheatgrass presence and abundance, in turn, can increase fine-fuel loads and the likelihood of more frequent and extensive wildfires (Balch et al. 2013). We acknowledge that our characterization of grazing history includes some uncertainty. Grazing by cattle and sheep has occurred throughout our study region for well over a century, and likely for at least 75 years on allotments that were active during the study period, but reliable records are limited. Although we do not have precise information on number of livestock per unit area, duration of grazing, or intensity of grazing, livestock grazing long has been the single most widespread land use across the Intermountain West. Our results suggest a strong positive relation between the probability of presence and prevalence of cheatgrass and livestock grazing, particularly in unburned locations, where resistance to cheatgrass is greater than in burned locations.

Cheatgrass prevalence tended to be lower in years in which precipitation at a given point was high relative to that point's long-term median, but higher when regional winter precipitation was high and regional spring precipitation was at or below the median for the study period. This result is consistent with observations that growth and reproduction of cheatgrass occur earlier than that of many native shrubs and grasses (Peterson 2005). As a result, cheatgrass abundance may respond more strongly than abundance of native species to precipitation early in the water year. For example, at relatively low elevations, autumn precipitation may lead to germination and establishment of cheatgrass, provided the thermal requirements of cheatgrass are met (Roundy et al. 2018). By contrast, native species that compete with cheatgrass may respond more strongly than cheatgrass to precipitation later in the water year. Many of our observations of high prevalence of cheatgrass that coincided with relatively high proportions of precipitation in winter were associated with water-years in which precipitation was low. Thus, the amount of precipitation falling during periods favorable for cheatgrass establishment and growth may be more important than the total precipitation for the year (Bradley and Mustard 2006; Chambers et al. 2014; Jones et al. 2015).

The frequency of wet days in the Intermountain West is projected to decrease during the 21st century, whereas the amount of precipitation on wet days (Polade et al. 2014) and variability in precipitation are projected to increase (Dettinger et al. 2011; Gershunov et al. 2013; Kunkel et al. 2013). It is unclear how these projected changes will affect water availability, and how water availability may affect land uses, such as livestock grazing. Our results suggest that both the timing and amount of precipitation may affect the abundance of cheatgrass. Moreover, increases in temperature may lead to expansion of cheatgrass at higher elevations. We believe that interactions between land use and climate change will continue to affect the composition, structure, and function of ecosystems throughout the arid western United States and globally. Our work may inform prioritization of management actions to minimize anthropogenic

drivers of climate change that independently and cumulatively drive expansion of cheatgrass, changes in fire cycles, and the status of species and ecosystems across the Intermountain West. Our results, which derive from a novel time-series of data on cheatgrass and covariates from within an extensive area, do not support the use of livestock grazing to suppress cheatgrass and its undesirable effects on the habitats of native species or regional fire dynamics. Livestock grazing with the aim of suppressing cheatgrass may be especially counterproductive in unburned areas in which native perennial grasses may remain viable.

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