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Western Watersheds Project

Working to protect and restore Western Watersheds and Wildlife

September 25, 2020

Anthony Madrid
Forest Supervisor
Apache-Sitgreaves National Forests
P.O. Box 640
Springerville, Arizona 85938

Submitted via email to: objections-southwestern-apache-sitgreaves@usda.gov

Heber Allotment Analysis EA Objection
Apache-Sitgreaves National Forests

Dear Mr. Madrid,

The following Objection to the Heber Allotment Analysis EA, Draft Decision Notice and Finding of No Significant Impact (DDN/FONSI) is being submitted on behalf of the members of Western Watersheds Project (WWP) who are concerned with the management of our public lands. WWP previously submitted comments for this project on June 15, 2015.

The DDN/FONSI here is insufficiently critical of the need for grazing in the Apache-Sitgreaves National Forests within important habitat for wildlife species, especially the Mexican gray wolf. Wildlife habitat is a precious resource on this allotment and this fact is not adequately considered nor are the impacts of grazing to wildlife habitat adequately analyzed. The alternatives did not adequately reflect the fact that livestock grazing on these allotments is not an activity the permittees are assured of engaging in.

This Objection is filed pursuant to, and in compliance with, 36 C.F.R. Part 218, Subparts A and B. All parties to this objection have filed timely, specific and substantive written comments in accordance with 36 C.F.R. 218(a).

As required by 36 C.F.R. § 218.8(d), Objectors provide the following information:

1. The name and contact information for the Objector is listed below.

2. This Objection was written on behalf of Objector by Cyndi Tuell whose signature and contact information is listed below.
3. Western Watersheds Project is the Objectors. Cyndi Tuell is the Lead Objector for purposes of communication regarding the Objection.

   Western Watersheds Project
   Cyndi Tuell
   738 N. 5th Ave, Suite 206
   Tucson, AZ 85705

4. The project that is subject to this Objection is "Heber Allotment Analysis EA." The Responsible Official is Richard Madril, District Ranger for the Black Mesa Ranger District.
5. Objector submitted, timely, specific, and substantive comments during the Public Comment Period on June 15, 2015.[1] All points and issues raised in this objection refer to issues raised in that comment letter or new information.
6. In the following Statement of Reasons, Objector provides the specific reasons why the decision is being appealed and the specific changes or suggested remedies that he seeks, along with the related evidence and rationale on why the decision violates applicable laws and regulations.

NOTICE OF OBJECTION

Pursuant to 36 C.F.R. § 218, Western Watersheds Project is filing an Objection regarding the Draft DN/FONSI for the Heber Allotment Analysis EA in the Black Mesa Ranger District of the Apache-Sitgreaves National Forests.

INTRODUCTION

The Heber allotment covers approximately 157,000 acres of National Forest Service managed lands on the Black Mesa Ranger District of the Apache-Sitgreaves National Forests. This decision would authorize reauthorize livestock grazing at the current levels (5,430 AUMs/905 head of cattle from May 1 through October 31) initially then authorize AUMs up to 7,600 at some point in the future, authorize new range infrastructure and improvements to existing infrastructure including a new well, 17 miles of new pipeline, 28 new troughs, 2 storage tanks, 7 new water lots, 8 new corrals, 16 new stock tanks, 2 new holding pastures, new trick tanks, and provide for the removal pinon-juniper woodland cover on 81,333 acres of public lands. This is a massive project to provide for industrial scale livestock infrastructure at great expense to the public and the environment.

We describe our concerns more specifically below and hope that clearer heads will prevail in the next steps of this decision-making process.

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[1] Attached as Appendix A.

STATEMENT OF REASONS

The Biological Assessment is from 2015, the Range Report is undated, but presumably from 2015 as well as there is no scientific literature cited after that year. It is unclear why the Forest Service has held this project up for the past five years, but in doing so, the Forest Service has proposed to make a decision based on outdated information. Even the information regarding conditions on the ground are extremely outdated. Furthermore, since 2015 there is new information regarding Mexican gray wolves, the impacts of drought and fire has changed the project area, and there is new scientific information regarding vegetation treatments and livestock grazing the Forest Service has not considered or incorporated in this analysis.

I. Significant new information the Forest Service must consider

a. Mexican gray wolves

The Fish and Wildlife Service made a non-essential determination in 2015 regarding the Mexican gray wolf. That decision was challenged in court and in April of 2018, the court concluded that "because the effect of the 2015 rulemaking was to authorize the release of an experimental population outside its current range, a new essentiality determination was required and the agency's decision to maintain the population's nonessential status without consideration of the best available information was arbitrary and capricious. Therefore, the essential or non-essential status of the Mexican gray wolf is not as described by the Forest Service in the EA, the Forest Service may need to consult with the Fish and Wildlife Service regarding this project and the impacts to the Mexican gray wolf, and all analysis that flows from this outdated 2015 analysis must be reconsidered.

b. New scientific information regarding vegetation treatments and livestock grazing impacts

The Forest Service should closely examine the relationship between livestock grazing and fire.

> "Grassland-to-shrubland state transitions in drylands are the result of changes in disturbance regimes amplified or mitigated by abiotic factors related to climate and soil (Archer and others 2017). For example, livestock grazing coupled with drought reduces fine fuel mass and continuity, thus reducing the probability of fire—a disturbance that historically kept woody plants in check (Higgins and others 2007). In the absence of fire, shrubs can establish and progress to more advanced life-history stages (Higgins and others 2000). At the same time, rates of erosion typically increase with declines in grass cover in arid grasslands, depleting soil resources and concentrating them below developing shrub canopies, as well as increasing disturbance to grasses by burial and abrasion, which constitutes a positive abiotic feedback that impedes future grass recovery while promoting shrub survival (Schlesinger and others 1996; Okin and others 2009)."

Pierce *et al.*, 2019, attached as Appendix B.

New scientific studies more definitively link the presence of livestock grazing with cheatgrass. Time-series data and results in Williamson *et al*. (2019)[2] 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. This concept is applicable to the project area and invasive species of grasses that are spread by livestock use, and the Forest Service must analyze these impacts with a critical eye towards protecting natural resources. The continued spread of invasive species of plants that are likely to alter the fire regime on project area present a clear risk to native plants and wildlife.

II. Alternatives

In our prior comments (at page 1-2) we asked the Forest Service to consider an alternative that excluded livestock from riparian areas. The Forest Service did not respond to our suggestion. This is a violation of the National Environmental Policy Act (NEPA).

This lack of response to our concerns and lack of information renders the analysis in the EA inadequate, precludes a FONSI, and prevented adequate public review.

III. Monitoring is insufficient

WWP raised this issue in our prior comments (at page 2). The Forest Service response stating that utilization and stubble height monitoring are "professionally accepted methods for measuring livestock forage use in the Western United States" does not respond to our concerns that monitoring for stubble height will occur at all, much less prior to pasture moves. Nor does this response address our concerns that the Forest Service relies upon permittees for the monitoring information if it does occur.

We also raised concerns about the frequency of monitoring in riparian areas and expressed grave concern that doing so only every 3-5 years was insufficient. The Forest Service dismissed our concerns as opinion and did not respond substantively, in violation of NEPA.

This lack of response to our concerns and lack of information renders the analysis in the EA inadequate, precludes a FONSI, and prevented adequate public review.

A. Livestock waters

We raised the issue of livestock waters at page 1 of our prior comments. In the EA there is inadequate analysis of the impacts associated with livestock waters. The EA does not identify the area of disturbance associated with the existing and proposed waters, nor does the EA adequately address or analyze the direct and indirect impacts of livestock waters on species in the project area, including species listed as threatened or endangered. The Forest Service has not analyzed how these new waters will impact vegetation, soil erosion, or wildlife. There is no analysis of how distribution of livestock over a larger area due to these new waters will impacts soils, vegetation, or wildlife.

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[2] Attached as Appendix C.

Relief Requested: The Forest Service must withdraw the Draft FONSI/DN and prepare a supplemental analysis, including an EIS for this project.

Thank you for your consideration of this Objection. If you have any questions, or wish to discuss the issues raised in this objection letter in greater detail, please do not hesitate to contact me.

Sincerely,

Cyndi C. Tuell

Cyndi Tuell
Arizona and New Mexico Director
Western Watersheds Project

ATTACHMENTS
Appendix A
Western Watersheds Project, June 15, 2015.

Appendix B
Pierce, N.A., Archer, S.R., Bestelmeyer, B.T., James, D.K. 2019. *Grass-Shrub Competition in Arid Lands: An Overlooked Driver in Grassland–Shrubland State Transition?* Ecosystems (2019) 22: 619–628 https://doi.org/10.1007/s10021-018-0290-9.

Appendix C
Williamson, M.A., Fleishman, E., Mac Nally, R.C., Chambers, J.C., Bradley, B.A., Dobkin, D.S., Fogarty, F.A., Horning, N., Leu, M., and Zillig, M.W., 2020. *Fire, livestock grazing, topography, and precipitation affect occurrence and prevalence of cheatgrass* (Bromus tectorum) *in the central Great Basin, USA*. *Biol Invasions* 22, 663–680 (2020). https://doi.org/10.1007/s10530-019-02120-8

June 15, 2015

Chris James, District Ranger
Black Mesa Ranger District
2748 Highway 260
Post Office Box 968
Overgaard, AZ 85933

Sent by electronic mail

Dear Mr. James:

These are comments on the Heber Allotment analyses, as described in your May 12, 2015 letter. These comments are submitted on behalf of Western Watersheds Project, a non-profit conservation organization dedicated to the conservation and protection of wildlife habitat, range quality, soil productivity, and water quality on public lands in Arizona and throughout the West.

The formula employed by this EA is of course by now familiar to all who follow such things: agree to raise stocking numbers, and justify doing so by having the public fund grandiose range "development" projects, to the tune of a half a million dollars, to artificially water each far-flung area of a broad landscape that has no or very little natural water sources. The theory is that the water developments will further distribute the livestock which will concomitantly reduce grazing impacts overall, and hence support larger numbers of livestock.

In this case, you also propose rather dramatic juniper-removal over 17,000 acres, which will entail opening an undisclosed number of miles of currently closed roads and constructing an undisclosed number of miles of temporary roads.

Your document does not, as far as I have been able to see, explain the cause of the juniper encroachment, but insists that the encroachment is not "natural" and that your decision to conduct this logging will "restore" the area to a more natural state.

But I cannot help but notice that the enthusiasm for restoring the land by logging it is not mirrored in a similar enthusiasm for restoring the riparian areas, none of which are in proper functioning condition, and which your document (always blaming "ungulates," never cows) reveals to be materially impaired by "hoof shear" and lack of riparian vegetation. Riparian areas are among the most important habitat in arid Arizona, and the most endangered, and it seems that some small portion of the attention you devote to logging the junipers might be given to attending to the riparian areas, small and rare as they are, on this allotment.

For example, there are only, you say, 0.8 miles of perennial stream on the entire 157,000 acre allotment, and this area is not functioning properly. Why take some of the $540,000.00 of taxpayer money you are spending to increase the permittees livestock by a very small degree and spend it instead on riparian restoration? Why is there no alternative to exclude livestock from this tiny area, and perhaps also from a few of the areas of intermittent streams that have potential for a healthy riparian area, if only rested from livestock?

I admire the spirit behind the conditions that you have put upon further increases in numbers, but scrutiny shows them to be less burdensome than they first appear. For example, you could increase the numbers by 540 AUMs every year after year three without any monitoring occurring at all: the monitoring does not kick in until you increase AUMs by more than 543 in a given year. You also do not define "monitoring," except in very broad terms and with language like "may include but would not be limited to." I have been quite disappointed in recent years to discover that the term "monitoring" is nearly universally interpreted to mean "what the permittee says he or his range rider estimated utilization to be, by looking at the landscape, in some places, from time to time." You say your monitoring "may" include riparian stubble-height monitoring, and even say that there will be "use guidelines" in riparian areas that entail maintaining stubble height, but I am aware of very, very, very few cases in Arizona where stubble height has been actually measured, and none where it was measured before each pasture move. Are you seriously planning to conduct the riparian stubble-height monitoring that is implied by your statement that "Once riparian utilization guidelines are met, cattle would be moved from the area or to the next scheduled pasture"? EA at 10.

Similarly, your language at page 11 suggests that riparian areas will be monitored "every 3-5 years" but a closer reading suggests that if AUM increases never exceed 10 percent in any given year, that riparian monitoring may never occur at all.

In sum, the EA suffers from its lack of attention or even concern about riparian health. I am pleased that your specialists have at least conducted the reviews necessary to have an intelligent discussion about riparian needs in the area, but the next step is missing -- the step where something is actually done to help those riparian areas. And, given the amount of money you plan to spend on the permittee's economic health, it is dispiriting to see so little time, money, or thought spent on the landscape's ecological health.

We do not believe the riparian monitoring will occur, and we do not believe these riparian areas will improve under this plan. More thorough attention to the tiny, tiny fraction of this allotment that is riparian is needed, along with a balanced plan that provides for livestock reductions should the areas not be found to improve. Right now your plan only provides for increasing livestock numbers, not decreasing those numbers. In times of drought, climate change, decreasing budgets, and because of the radical importance of riparian areas in your Forest, more care is warranted them than your plan provides.

Sincerely,

Erik B. Ryberg
Counsel for Western Watersheds Project

Ecosystems (2019) 22: 619–628
https://doi.org/10.1007/s10021-018-0290-9

ECOSYSTEMS

Grass-Shrub Competition in Arid Lands: An Overlooked Driver in Grassland–Shrubland State Transition?

Nathan A. Pierce,[1]* Steven R. Archer,[1] Brandon T. Bestelmeyer,[2] and Darren K. James[2]

[1]School of Natural Resources and the Environment, University of Arizona, ENR2 - N325, 1064 E Lowell St, Tucson, Arizona 85721, USA; [2]United States Department of Agriculture-Agricultural Research Service Jornada Experimental Range, Jornada Basin Long Term Ecological Research Program, New Mexico State University, Las Cruces, New Mexico 88003, USA

ABSTRACT

Traditional models of state transition in arid lands emphasize changes in disturbance regimes and abiotic feedbacks that promote the degradation of grassland into shrubland, whereas biotic interactions like competition and facilitation are often overlooked. Here, we conducted an experiment to determine whether shrubs have a positive, neutral, or negative effect on grasses and if these interactions may play a role in grassland–shrubland state transition. *Prosopis glandulosa* shrub neighbors within 5 m of *Bouteloua eriopoda* grass patches were left intact (controls) or killed with foliar herbicide, and metrics of grass performance were evaluated over 5 years. We saw no evidence of shrub facilitation of grasses. Instead, grass ANPP responded positively to shrub removal in all years, but more so in years with above-average rainfall. Grass allocation to vegetative reproduction and grass patch size also increased when shrub neighbors were removed. These results demonstrate that biotic interference by shrubs upon grasses reinforce and magnify grazing- and drought-induced abiotic feedbacks during grassland–shrubland transitions. Shrub effects on grass should therefore be considered a key process in desert grassland state transitions.

Key words: *Bouteloua eriopoda*; Chihuahuan desert; Competition; Grassland; *Prosopis glandulosa*; Shrubland; State transition; Woody plant encroachment.

HIGHLIGHTS

- Grasses with shrub neighbors have lower productivity than grasses without shrub neighbors.
- The competitive effect of shrubs on grasses was also evident in allocation to reproductive structures and grass patch size/continuity.

Received 6 April 2018; accepted 29 July 2018;

Author Contributions NAP, SRA and BTB conceived of the study and designed the research; NAP conducted the research; DKJ and NAP analyzed the data; NAP and SRA wrote the manuscript; NAP, SRA and BTB edited the manuscript.

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- Shrub-on-grass competition can reinforce and amplify abiotic feedbacks during grassland–shrubland state transition.

INTRODUCTION

Arid and semiarid grasslands worldwide have undergone state transitions from grassland to shrubland dominated by xerophytic, unpalatable shrubs and bare ground. This transition can represent landscape degradation with regard to primary production (Knapp and others 2008), erosion and nutrient loss (Li and others 2008), biodiversity (Ratajczak and others 2012), and forage production (Fredrickson and others 1998), although specific patterns and interpretations vary globally (Eldridge and others 2011). Grassland-to-shrubland state transitions in drylands are the result of changes in disturbance regimes amplified or mitigated by abiotic factors related to climate and soil (Archer and others 2017). For example, livestock grazing coupled with drought reduces fine fuel mass and continuity, thus reducing the probability of fire—a disturbance that historically kept woody plants in check (Higgins and others 2007). In the absence of fire, shrubs can establish and progress to more advanced life-history stages (Higgins and others 2000). At the same time, rates of erosion typically increase with declines in grass cover in arid grasslands, depleting soil resources and concentrating them below developing shrub canopies, as well as increasing disturbance to grasses by burial and abrasion, which constitutes a positive abiotic feedback that impedes future grass recovery while promoting shrub survival (Schlesinger and others 1996; Okin and others 2009). Inherent in these scenarios is the implicit assumption that grass-shrub interactions in arid grasslands are of little or no significance after shrubs have established. However, this assumption has not been widely tested or rigorously evaluated.

Grass-shrub interactions may be dismissed as a driver of state change in arid lands under the presumption that selection pressures favor adaptations for stress tolerance over competitive ability (Grime 1977; Brooker and Callaghan 1998). Accordingly, a growing body of research supports the notion that facilitation takes precedence over competition with increasing environmental stress (Maestre and others 2009; Dohn and others 2013). This framework helps explain the coexistence of grasses and woody plants in some systems, whereby woody plants facilitate understory grasses via ameliorating harsh environmental conditions (Ludwig and others 2004b) or by providing refugia from grazers (Howard and others 2012). However, in grassland–shrubland transitions, shrub-on-grass facilitation must be eclipsed by other factors detrimental to grass survival, including shrub-on-grass competition. The predominance of facilitation versus competition might also change along a continuum of woody plant abundance, that is, competition increases with increasing shrub size and density (Scholes 2003; Vander-Yacht and others 2017).

The predominance of competition versus facilitation in grass-shrub interactions may also vary at fine spatial scales. Certain xerophytic shrub species have extensive shallow lateral roots (Gibbens and Lenz 2001) and may therefore interact with grasses occurring well beyond their canopies. Such shrubs could facilitate grasses via hydraulic redistribution (Priyadarshini and others 2016). However, shrub lateral roots could also have a negative effect on grasses by utilizing soil resources that grasses would otherwise obtain (Ludwig and others 2004a). In situations where grass and shrub rooting niches are segregated spatially (Walker and others 1981; Ward and others 2013), or where phenology separates their activity patterns temporally, shrubs may have no influence on neighboring grasses (Golluscio and others 1998; Ludwig and others 2001). Net neutral interactions could also occur if competitive and facilitative processes are in balance (Maestre and others 2009). Neutral interactions would support the prevailing assumption that grass loss and shrub proliferation in the course of grassland–shrubland transition are driven primarily by interrelationships among climate, disturbance (grazing, fire), and soil erosion.

Here, we report the outcome of a 6-year field experiment aimed at quantifying grass-shrub interactions to ascertain if shrubs have a positive (facilitation), neutral, or negative (competition) effect on grass production beyond their canopies. We hypothesized that the production of grasses occurring in the vicinity of shrubs with extensive, shallow lateral root systems would be reduced owing to the predominance of competitive interactions. Knowledge of the direction and strength of the influences of shrubs on grasses growing beyond their canopies would help us predict grass patch capacity to recover from disturbance and the extent to which shrub interactions with grasses might either dampen or reinforce abiotic feedbacks during grassland–shrubland state transitions. Support of the hypothesis that shrubs have no discernible effect or a positive effect on grasses would corroborate the prevailing view that competitive grass-shrub interactions are of little consequence compared to facilitation or abiotic drivers. We offer three alternative predictions in testing these hypotheses regarding shrub effects on grasses: (1) no effect, which would suggest abiotic processes triggered by grazing-induced grass losses and subsequent soil erosion are responsible for grassland–shrubland transitions (Okin and others 2006); (2) a positive effect due to hydraulic lift, from which we would infer grasses might be more persistent in the face of grazing and drought stress; and (3) competition, wherein the presence of shrubs would amplify stresses on grasses imposed by grazing and drought.

METHODS

Study Area

The field experiment was conducted on the USDA Agricultural Research Service Jornada Experimental Range (JER), which hosts the Jornada Basin Long-Term Ecological Research (LTER) site, approximately 37 km north of Las Cruces, NM, in the northern Chihuahuan Desert (UTM 13S 336659 3610160; 1325 m a.s.l.; https://jornada.nmsu.edu/lter). The climate is arid (Köppen Climate Classification BWk), with long-term (1926–2015) mean annual precipitation (PPT) of 241 mm (SE ± 9.6, CV = 36%), approximately 65% of which occurs in July–October. June is the warmest month (mean minimum of 17°C and mean maximum 36°C); January is the coldest month (mean minimum and maximum of − 6 and 4°C, respectively).

The study was conducted along a grassland-to-shrubland gradient, reflecting the ongoing spread of shrubs and consequent spatial variations in the rate of state transitions (Bestelmeyer and others 2011). One end of the 3 km × 1 km study area (UTM 13S 334878, 3601198) was grassland dominated by the C_4 perennial grass *Bouteloua eriopoda* (Torr.) Torr. (26% foliar cover), which is a stoloniferous bunchgrass that proliferates via axillary tillers from the genet, as well as stoloniferous ramets. The grassland end was also populated with small, scattered C_3 *Prosopis glandulosa* (Torr.) shrubs (2% canopy cover). The opposing end (UTM 13S 333764, 3604817) was shrubland, with *B. eriopoda* foliar cover of 4% and *P. glandulosa* canopy cover of 18%. Soils are fine-loamy, mixed, thermic Typic Haplargids and Typic Petrocalcids underlain by a petrocalcic horizon 64 to 76 cm beneath the surface (Havstad and Schlesinger 2006).

Experimental Design

Ninety plots were established in 2010 in a stratified random fashion at locations along the grassland–shrubland continuum, ensuring 30 plots within the grassland, the ecotone, and the shrubland portions of the gradient. Plots with a fixed radius of 5 m were centered upon 1 × 1 m subplots containing a *B. eriopoda* patch. Only grass patches with at least one *P. glandulosa* shrub within the 5 m plot radius were chosen. Target grass patches therefore had a broad range of shrub neighborhood configurations, that is, few, small shrub neighbors in the grass-dominated segments of the transect and numerous, larger shrub neighbors in the shrub-dominated segment. Grass patch size and shape was quantified within a grid of 25–20 × 20 cm cells in the 1 × 1 m subplots at the end of the 2010 growing season (October, near peak production) by counting the number of cells occupied by *B. eriopoda*. Clonal reproductive output (number of ramets) was also quantified at this time. Grasses in the entire subplot were then clipped to a height of 10 cm, and current year's biomass was dried and weighed to estimate aboveground annual net primary productivity (ANPP). These measurements were repeated in October of 2011–2013 and 2015 (measurements were not taken in 2014).

The volume of all *P. glandulosa* shrubs within the 5 m radius of each plot was determined in the spring of 2011 by measuring canopy diameter along the longest axis and the diameter perpendicular to the midpoint of the longest axis, as well as plant height. Aboveground ANPP was then determined using a site- and species-specific allometric regression ($R^2 = 0.89$, Gherardi and Sala 2015).

All *P. glandulosa* shrubs located within 45 randomly selected plots were killed in June 2011, prior to the summer rainy season, using a foliar herbicide solution (0.5% triclopyr, 0.5% clopyralid, and 5% diesel fuel) applied in a fine mist. The herbicide mixture was effective at defoliating shrubs within 2 weeks of spraying, and no new growth was observed for the remainder of the growing season. Targeted spot-spraying was conducted as needed to suppress new basal shoots (which typically emerged from only the largest of shrubs) in 2012 and 2013, after which no regrowth occurred.

Data Analysis

Overall treatment effects on *B. eriopoda* aboveground ANPP were analyzed using repeated-measures linear-mixed effects models (PROC MIXED; SAS V9.4; SAS Institute, Cary, NC, USA). Shrub removal, year, and their interaction were fixed effects; year was also a repeated effect with plot as the subject. A heterogeneous Topelitz temporal covariance model was used based on Akaike's

Information Criterion (AIC_c). The Kenward–Roger method was used to adjust denominator degrees of freedom to account for bias associated with estimating the fixed effects after the repeated effect. All fixed effects were highly significant; because of the highly significant shrub removal × year interaction, interpretations of the main effects are qualified by year.

We also examined the relationship between *B. eriopoda* ANPP and PPT by regressing annual, growing season (July–October) and dormant season (November–June) PPT (independent variable) against *B. eriopoda* ANPP (dependent variable) and calculating the treatment × PPT interaction coefficients (JMP, Version 13. SAS Institute, Cary, NC, USA). As antecedent precipitation can be a better predictor of current year's ANPP (Sala and others 2012), we also conducted this analysis for previous year's PPT.

ANOVA was used to compare the number of non-stoloniferous and un-rooted stoloniferous ramets on plots with intact and killed shrubs; Tukey's HSD was used to test for significant differences among treatments and years.

Finally, we sought to determine if differences in ramet production translated into changes in grass patch size and continuity over the course of the experiment. We approached this using repeated-measures linear-mixed effects models as described above, but using a heterogeneous compound symmetry covariance structure, which was the best fit based on AIC_c. The response variable was the number of 20 cm × 20 cm cells within the 1 m^2 subplot that was occupied by *B. eriopoda*. An increase in the number of cells occupied over time would reflect net ramet recruitment and genet patch infilling and/or expansion; a decrease in cell occupation would be indicative of patch fragmentation and/or contraction.

RESULTS

Precipitation patterns varied considerably over the course of the experiment (Figure 1). Drought occurred during the first 2 years of the study with annual PPT 54% (2011) and 50% (2012) below the long-term (1926–2015) mean. Similarly, growing season (July–October) PPT was 33% below average in 2011 and 55% below average in 2012. Annual PPT in 2013 and 2014 approximated the long-term average, but growing season PPT was 41 and 37% higher than the long-term mean, respectively. Annual PPT in 2015 was 15% higher than the long-term average, while growing season PPT was near average.

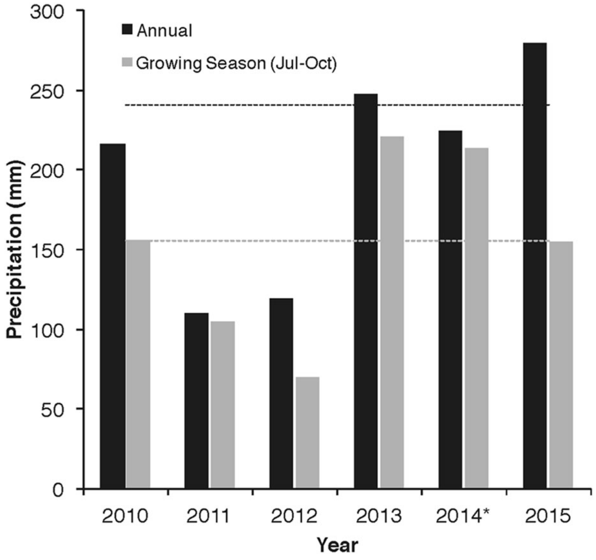
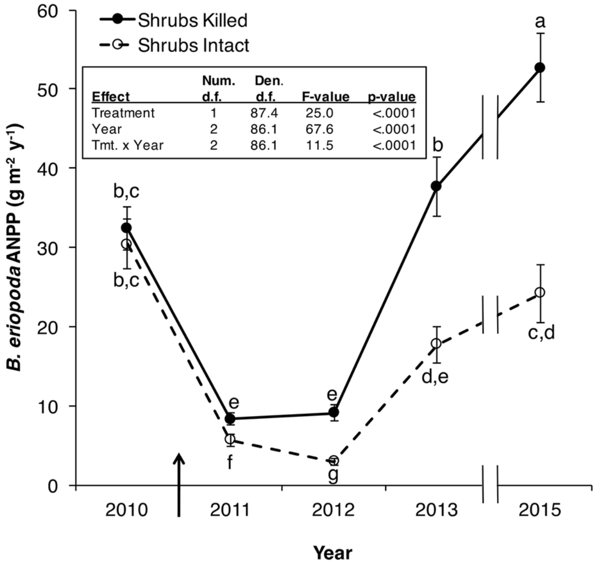


Figure 1. Annual (*black*) and growing season (July–October, *gray*) precipitation (PPT) over the course of the experiment. The *dashed black* and *gray* lines represent long-term (1926–2015) annual and growing season mean PPT, respectively. (*Plot data was not collected in 2014).

B. eriopoda aboveground ANPP in 2010 on control plots and plots slated for shrub removal was nearly identical (Figure 2). Subsequent to shrub



Effect	Num. d.f.	Den. d.f.	F-value	p-value
Treatment	1	87.4	25.0	<.0001
Year	2	86.1	67.6	<.0001
Tmt. x Year	2	86.1	11.5	<.0001

Figure 2. *Bouteloua eriopoda* aboveground ANPP in plots with neighboring shrubs intact (*open circles*) or killed (*closed circles*). Different letters denote significant ($P < 0.05$) differences among treatments and dates. Inset: ANOVA summary table of main effects. The arrow between 2010 and 2011 designates when shrub neighbors were killed in treatment plots. Data were not collected in 2014.

removal, grass ANPP varied by an order of magnitude in both control and treated plots over the course of the 6-year experiment in response to inter-annual variation in PPT (Figure 1). For example, mean (± SE; g m^{-2} y^{-1}) ANPP in control plots was 2.9 (0.7) during the dry year of 2012 and increased to 24.2 (3.9) in the above-average PPT year of 2015.

The presence of shrub neighbors mediated grass ANPP response to precipitation (Figure 2). During the dry period (2011–2012), control plots with shrub neighbors intact had significantly reduced *B. eriopoda* ANPP compared to treatment plots with shrub neighbors killed. Upon return to average and to above-average PPT conditions in 2013 and 2015, differences in grass ANPP between treatment and control plots were amplified: mean *B. eriopoda* (± SE; g m^{-2} y^{-1}) ANPP was 19.9 (4.4) and 28.1 (5.6) higher in plots with shrubs killed than in plots with shrubs intact in 2013 and 2015, respectively.

B. eriopoda ANPP was directly related to PPT in both control and treatment plots. However, *B. eriopoda* ANPP was more responsive to PPT in plots with shrub neighbors killed than in control plots with shrub neighbors intact. This was true for annual PPT, growing season PPT, and dormant season PPT (Figure 3). There was no significant relationship between *B. eriopoda* ANPP and previous year's annual PPT in either the control or treatment plots ($F = 2.07$; $df = 1$; $P = 0.152$; data not shown).

Allocation to clonal reproduction, measured by the number of ramets produced per plot, was near zero in the dry years of 2011–2012 on control and treated plots. During the wet years of 2013 and 2015 ramet production increased, but more so on plots where shrubs had been killed than on plots where shrubs were intact (Figure 4). Vegetative production of axillary tillers also differed in 2013, where the mean number of tillers was significantly higher in plots with shrub neighbors killed than in plots with shrub neighbors intact (Table 1). Despite this difference in tiller number, average ANPP per tiller did not differ between control and treatment plots ($P = 0.37$).

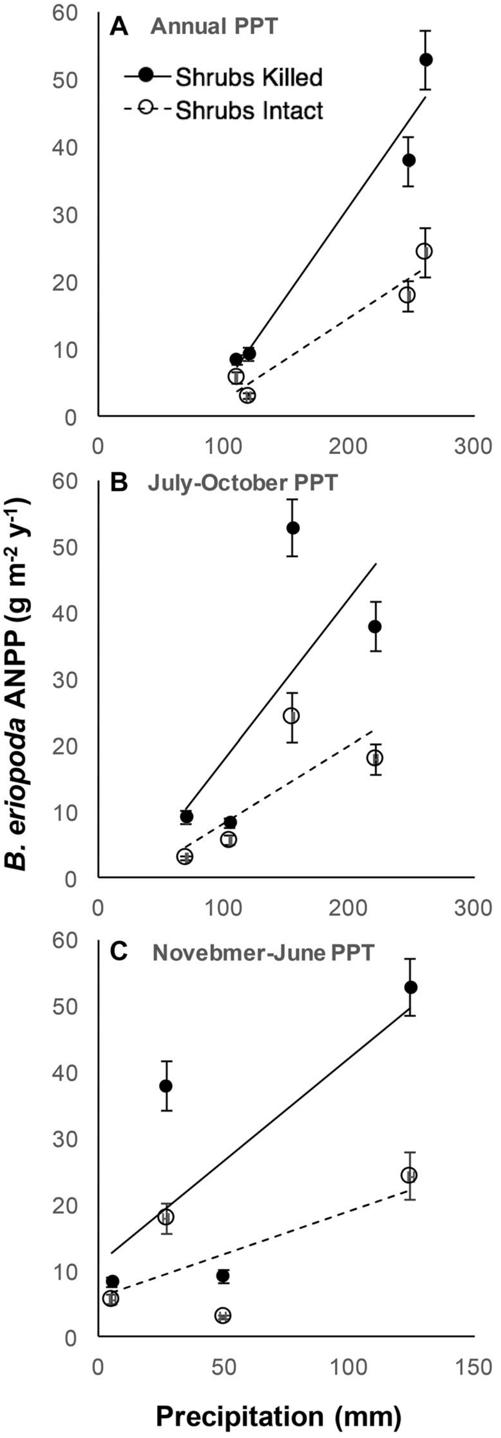
Ramet production, in concert with axillary tiller proliferation, translated into changes in grass patch size over the course of the experiment (Figure 5). Where shrubs were present, the mean number of 20 cm × 20 cm cells within the 1 m^2 subplot occupied by *B. eriopoda* decreased from 2011 to 2012, was stable through 2013 and then returned to 2011 levels by 2015. Conversely, where shrubs had been killed, *B. eriopoda* cell occupancy was maintained through the 2011–2012 dry period and subsequently increased to reach levels 65% higher in 2015.

Discussion

Our results support the hypothesis that competitive effects of shrubs on perennial grasses play an important role in the progression of grassland–shrubland transitions. Shrubs in this Chihuahuan Desert system were relatively short-statured (mean height = 0.6 m, mean canopy diameter = 1.5 m), and focal grass patches occurred well beyond their canopies. Consequently, aboveground interactions related to light competition or temperature amelioration were not likely to have been important. Rather, competitive interactions between grasses and shrubs must have occurred for belowground resources. The presumption of competition for soil water is reflected in the fact that the presence of shrubs significantly reduced grass production during dry periods (2011, 2012) and moderately (2013) to substantially (2015) constrained grass responses to increased rainfall (Figure 2).

Further evidence of belowground competition is demonstrated in the relationship between grass ANPP and PPT. The grass ANPP response to precipitation was positive on plots with and without shrubs; however, this trend was more pronounced for grasses without shrub neighbors than for grasses with shrub neighbors (Figure 3). The contrasting slopes of the ANPP versus PPT lines suggest the competitive influence of *P. glandulosa* shrubs on *B. eriopoda* grasses strengthens with increasing PPT over the rainfall ranges encountered in this study. We hypothesize that intensification of shrub competition with increased PPT may reflect the plastic response of shrub roots to variations in soil moisture availability. *P. glandulosa* plants at the study site have dimorphic root systems, with deep tap roots and lateral roots that extend many times their canopy diameters at depths overlapping grass root systems (Gibbens and Lenz 2001). These shallow coarse lateral roots may opportunistically proliferate fine roots when soil moisture is abundant and curtail this fine root production and lose fine root mass under dry conditions. Competition between grasses and shrubs could thus be more intense when water and other soil resources are more abundant. Such trait-mediated interactions (Callaway and others 2003) have been observed for other dryland plant species (Schwinning and others 2002).

Collectively, the vegetation in our 6-year experiment experienced a dry year with average antecedent conditions (2011); a dry year with dry



Source	d.f.	F-ratio	p-value
PPT	1	205.6	<.0001
Treatment	1	57.9	<.0001
PPT x Treat.	1	28.9	<.0001

Source	d.f.	F-ratio	p-value
PPT	1	91.7	<.0001
Treatment	1	43.8	<.0001
PPT x Treat.	1	11.2	0.0009

Source	d.f.	F-ratio	p-value
PPT	1	85.4	<.0001
Treatment	1	44.5	<.0001
PPT x Treat.	1	13.8	0.0002

Figure 3. Relationship between precipitation (PPT) and *Bouteloua eriopoda* aboveground ANPP on plots where neighboring shrubs were intact (*open circles*) or killed (*filled circles*). **A** Annual PPT; **B** growing season (July–October) PPT; **C** dormant season (November–June) PPT. Analysis of variance summaries are shown beside each panel.

antecedent conditions (2012); a wet year with dry antecedent conditions (2013); and wet years with wet antecedent conditions (2014–2015). Strong seasonality signals also occurred: growing season PPT predominated 2013–2014, whereas rainfall in 2015 was mostly during the cool season when grasses were largely dormant. Our results support those of other research that shows how the intensity of grass-shrub interactions fluctuates as a function of variability in PPT quantity and seasonality. Grasses tend to respond to precipitation more quickly than shrubs (Jobaggy and Sala 2000), which may portend a competitive advantage for grasses under the highly variable precipitation regimes characteristic of drylands (Soriano and Sala 1984). However, recent studies demonstrate the importance of previous years' precipitation in determining current year's grass productivity, wherein wet antecedent conditions lead to higher production than expected based on current year's precipitation alone, and antecedent dry conditions have the opposite effect (Sala and others 2012). Although consecutive wet years are thus a boon for grass productivity, this timescale would also allow for a positive shrub response to the wet conditions. Our data suggest that shrub competition intensifies in multiple, consecutive wet years to constrain increases in grass ANPP that might otherwise occur. Accordingly, we saw no effect of previous year's PPT on current year's grass ANPP. Winter/spring PPT could amplify this effect if a significant proportion of rain falls while grasses are dormant, allowing moisture to percolate to deeper soil layers where it is ostensibly less accessible to grasses when their growth resumes and more accessible to shrubs (Walker and Noy-Meir 1982; Ward and others 2013). Moreover, leaf-level carbon and water relations indicate that *P. glandulosa*, a deciduous shrub, physiologically outperforms *B. eriopoda* under conditions of both low and high soil moisture availability, and for a longer portion of the year (Throop and others 2012), providing a possible mechanism by which shrubs outcompete grasses in this study. This is in direct contrast to interactions between *B. eriopoda* and *Larrea tridentata*, an evergreen shrub species featured in studies of grass-shrub interactions in the Chihuahuan Desert. In these studies, *B. eriopoda* had higher leaf-level photosynthetic rates than the shrub following small rainfall events that characterize dryland systems (Pockman and Small 2010), yet *B. eriopoda* cover declines under long-term drought while *L. tridentata* cover remains consistent (Baez and others 2013). Furthermore, precipitation variability along with changes in aridity can favor one grass species over another (Rudgers and others 2018). This suggests that the relative importance of stress tolerance versus competitive ability as a driver of grassland-to-shrubland transitions may vary with grass and shrub species or functional types.

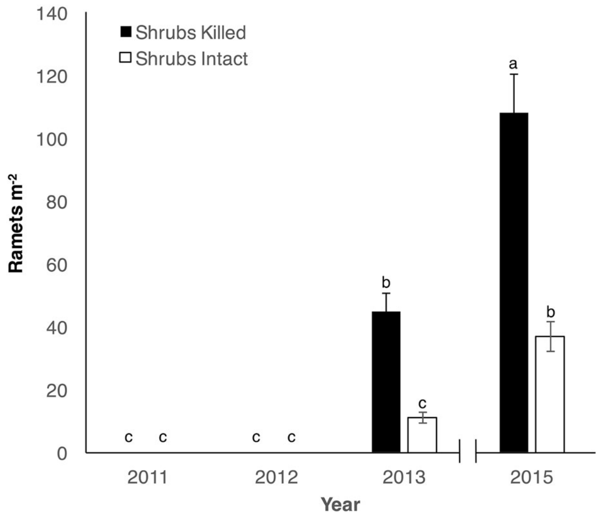


Figure 4. Number of ramets per m^2 in plots with neighboring shrubs intact (*open bars*) or killed (*filled bars*); different letters indicate significant ($P < 0.05$) differences among treatments and years (Tukey's HSD). Years with below-average PPT (2011, 2012) had zero ramet production, but were included in the analysis.

The competitive influence of shrubs on grasses was also apparent via changes in grass patch structural attributes. When shrub neighbors were present, grass patches contracted and became fragmented, and did not rebound to their initial configuration until after three consecutive years of above-average PPT (Figure 5). Plots without shrub neighbors, on the other hand, did not contract/fragment during the dry period, and dramatically expanded/infilled during the wet period. Grass patch size and bare soil connectivity can be used as leading indicators of state transitions in arid systems (Kefi and others 2007; Dakos and others

Table 1. Mean (± SE) Values for *B. eriopoda* Patch-Scale Aboveground ANPP (g m^{-2} y^{-1}), Number of Tillers per m^{-2}, and One-Way ANOVA Results for Differences Between Control and Treatment Plots in 2013

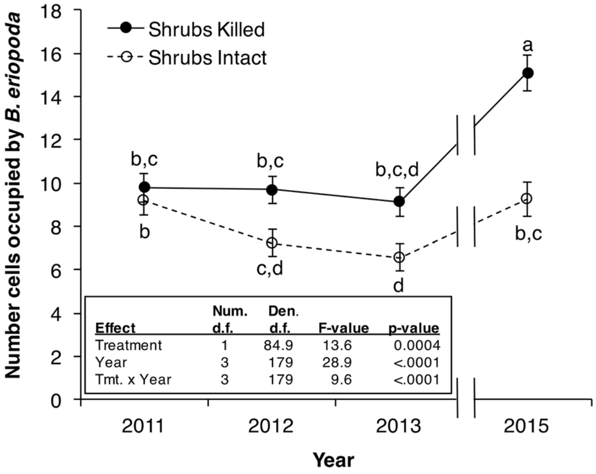
Variable	Treatment		*F* ratio	*P* value
	Shrubs intact	Shrubs killed		
ANPP	17.3 (3.1)	37.7 (3.1)	21.4	< 0.0001
Number tillers	145.0 (19.2)	268.1 (19.0)	20.7	< 0.0001

Tiller production was near zero in the dry years of 2011–2012.

2011), and abiotic soil erosion processes are considered the primary drivers of grass patch contraction (Okin and others 2009). Our results demonstrate that biotic interference can also influence grass patch size and level of fragmentation and hence bare soil connectivity and susceptibility to erosion forces.

Grass ANPP is a combined function of the total number of tillers and the mass per tiller, that is, similar productivity could be achieved with fewer large tillers or with a greater number of small tillers. Our results suggest that grass ANPP at the Jornada site was more dependent on the number of tillers. Although the number of 20 cm × 20 cm cells occupied by *B. eriopoda* was similar between control and treatment plots in 2013 (Figure 5), axillary tiller number was higher in plots with shrubs removed than in plots with shrub neighbors intact (Table 1). This could help explain the increasing ANPP difference between control and treatment plots following consecutive years of wet conditions, as current year ANPP is related to previous year tiller density (Reichmann and others 2013).

Some evidence suggests shrub effects on grasses shift from net negative to net positive along gradients of increasing environmental stress (Maestre and others 2009). Annual precipitation at our site during this experiment (216–279 mm) was well below the threshold (479 mm) that has been proposed for this shift (Dohn and others 2013), so our findings of competitive suppression in this arid grass-shrub system do not support this idea. Instead, our results are more in line with predictions that have been reported for grass-woody plant interactions in mesic savanna systems. Shrubs do, however, appear to facilitate some grass species at this Chihuahuan Desert site. Whereas our study focused on *B. eriopoda* patches in areas beyond shrub canopies, *Muhlenbergia porteri* has been observed growing within and seemingly confined to *P. glandulosa* and *Larrea tridentata* canopies (Welsh and Beck 1976). It is unclear if this is because shrubs ameliorate microclimate conditions, enhance nutrient availability, or provide refugia from grazers. This study supported the stress gradient hypothesis in that shrub-on-grass competition intensified with increasing precipitation. However, we detected no facilitative influence of shrubs on grasses. Due to the small stature of *P. glandulosa* shrubs and the occurrence of *B. eriopoda* grass patches beyond their canopies, aboveground shrub facilitation of grasses via environmental amelioration is irrelevant between these species. If *P. glandulosa* at our site carried out beyond-canopy hydraulic redistribution (Bleby and others 2010) as has been shown in other systems (Zou and others 2005), the redistributed water was not utilized by grasses to a degree that overcame soil water competition with shrubs (Barron-Gafford and others 2017).



Effect	Num. d.f.	Den. d.f.	F-value	p-value
Treatment	1	84.9	13.6	0.0004
Year	3	179	28.9	<.0001
Tmt. x Year	3	179	9.6	<.0001

Figure 5. Number of 20 × 20 cm cells per 1 m^2 plot containing rooted *Bouteloua eriopoda* genets or ramets in control (*open circles*) and treatment (*closed circles*) plots; an increase in number of cells occupied represents grass patch expansion/infilling, whereas a decrease represents grass patch size constriction/fragmentation. Different letters denote significant ($P < 0.05$) differences among treatments and dates. Inset: ANOVA summary table of main effects.

Land-management practices have long sought to restore herbaceous cover and production in shrub-invaded grasslands using herbicides, mechanical treatments, or prescribed fire. Such treatments often do not produce the expected results, however, and reasons for this are not clear (Archer and Predick 2014). Under the assumption that abiotic factors are largely driving system dynamics, shrub removal at broad scales could be expected to exacerbate grass loss because of increased erosion potential. Similarly, if hydraulic lift was important, removing shrubs could render grasses more susceptible to stresses imposed by grazing and drought. Our results, however, confirm that shrub removal in this Chihuahuan Desert system has the potential to be an effective restoration tool in that grass patches expanded in size, connectivity, and productivity when shrub neighbors were removed. Although not addressed in this study, reducing shrub cover could also reduce the density and/or activity of mammalian herbivores to the benefit of grasses, particularly in dry years when C_3 forbs with large seeds are less available (Daniel and others 1993; Whitford 1993; Kerley and Whitford 2009).

Traditional models of grassland–shrubland transition in drylands emphasize changes in disturbance regimes and abiotic feedbacks that promote the degradation of grassland into shrubland (Schlesinger and others 1990, 1996). In this study, we demonstrate that shrub-on-grass biotic interference has the potential to reinforce grazing- and drought-induced stresses on mesophytic grasses that would amplify positive abiotic feedbacks driving grassland–shrubland transition. Accordingly, competitive ability may be as, or more, important than stress tolerance in shaping community structure and function in this arid grassland. Shrub-driven declines in grass cover and production also help explain observations of shrub encroachment into arid grasslands where disturbances related to livestock grazing (Browning and Archer 2011) and fire (O'Connor and others 2014) have been eliminated. Further development of dryland state-and-transition models (for example, Bestelmeyer and others 2011) should incorporate biotic interactions as a mechanistic driver of state change.

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ORIGINAL PAPER

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 worldwide, 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 $\sim 10{,}000\ \mathrm{km}^2$ 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

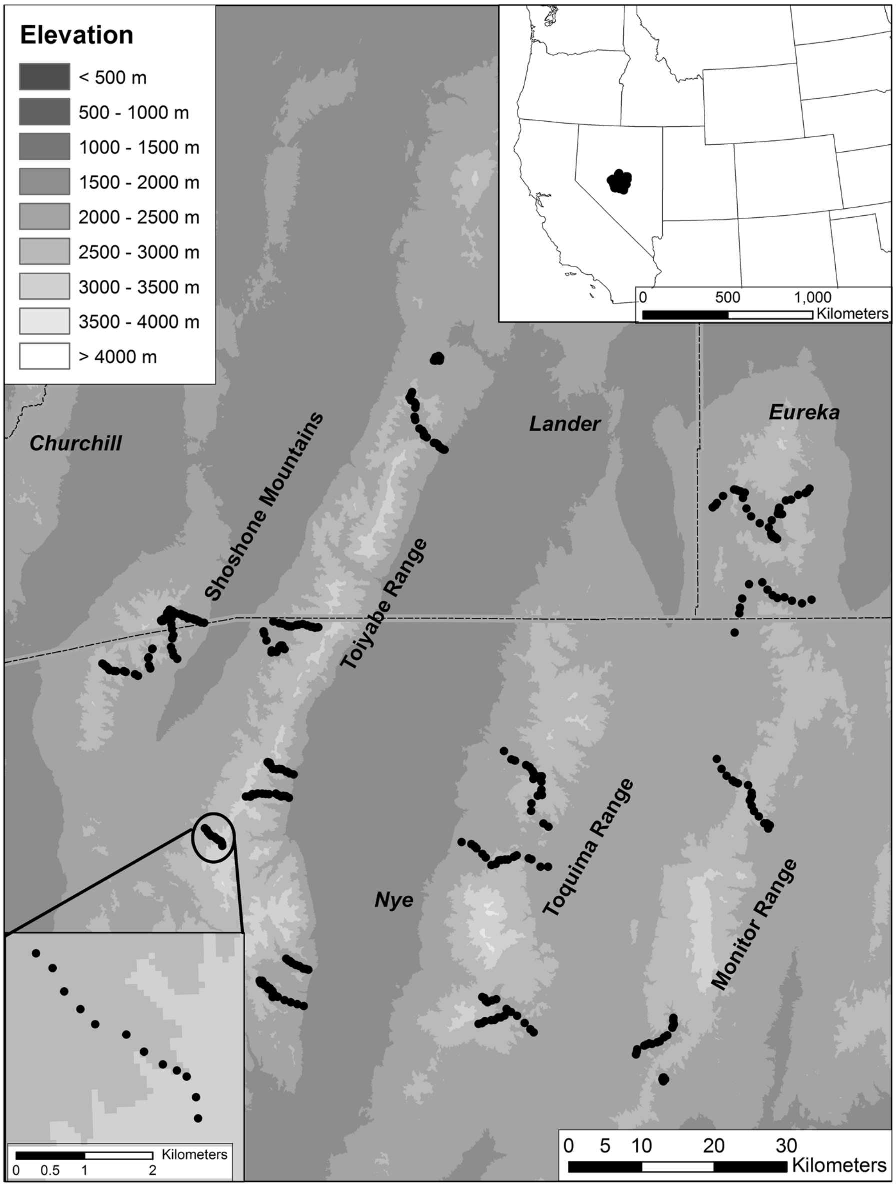

Fig. 1 Locations of the 417 sample points that were distributed among 29 canyons in four mountain ranges in the central Great Basin (Lander, Eureka, and Nye Counties, Nevada, USA). We sampled cheatgrass at each point for a minimum of three years and a maximum of eight years

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; $\boldsymbol{X}_{obs}$, Table 1).

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

$$logit\left(p_{i,j,k,s}\right) = \alpha_{j,k,s} + \beta_{obs}\boldsymbol{X}_{obs}. \tag{2}$$

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, $\boldsymbol{X}_{point}$, Table 1).

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

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

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

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

$$\alpha_{k,s} \sim Normal\left(\mu_{k,s}, \sigma_{s}\right), \tag{6}$$

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

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

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 ($\boldsymbol{X}_{obs}$, Table 1).

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

$$logit\left(p_{i,j,k,s}\right) = \alpha_{j,k,s} + \beta_{obs}\boldsymbol{X}_{obs}. \tag{13}$$

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 ($\boldsymbol{X}_{point}$, Table 1).

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

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

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

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

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

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

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

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 ~ 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 ($\mu_{j,k,s}$):

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

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

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

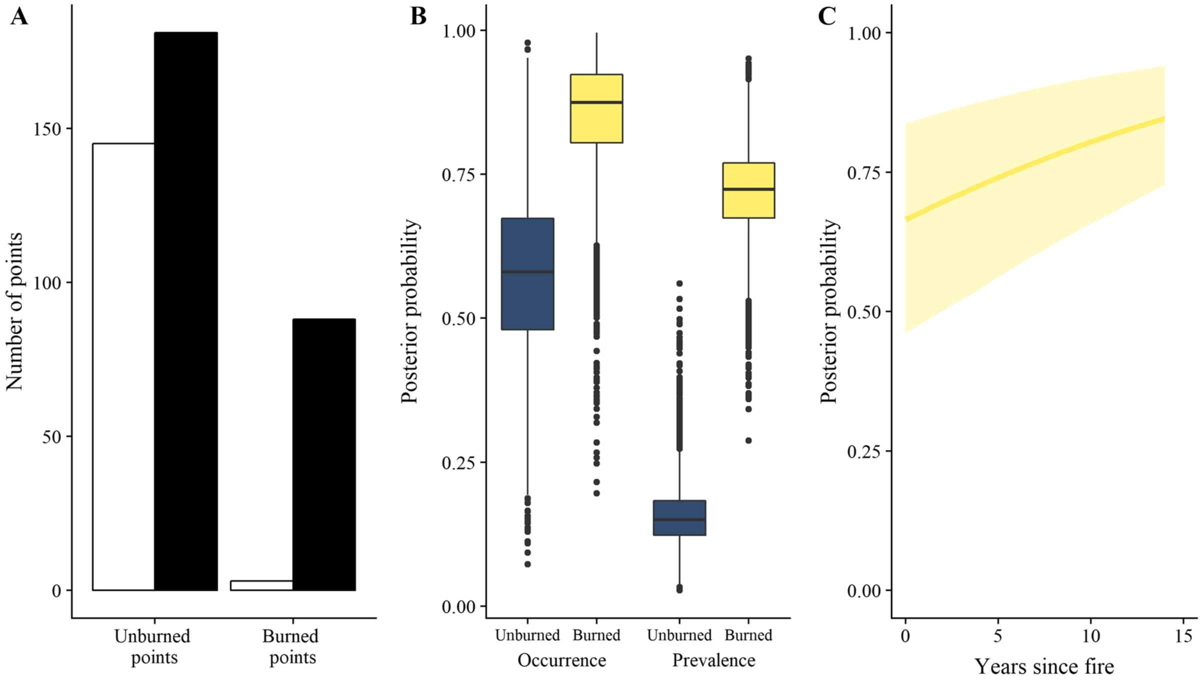

Fig. 2 Relations between fire and the occurrence of cheatgrass and prevalence of cheatgrass (i.e., given occurrence, the likelihood that cheatgrass was recorded present in any sample in a given point in a given year). Posterior probabilities for the occurrence and prevalence models are based on the likelihoods 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),

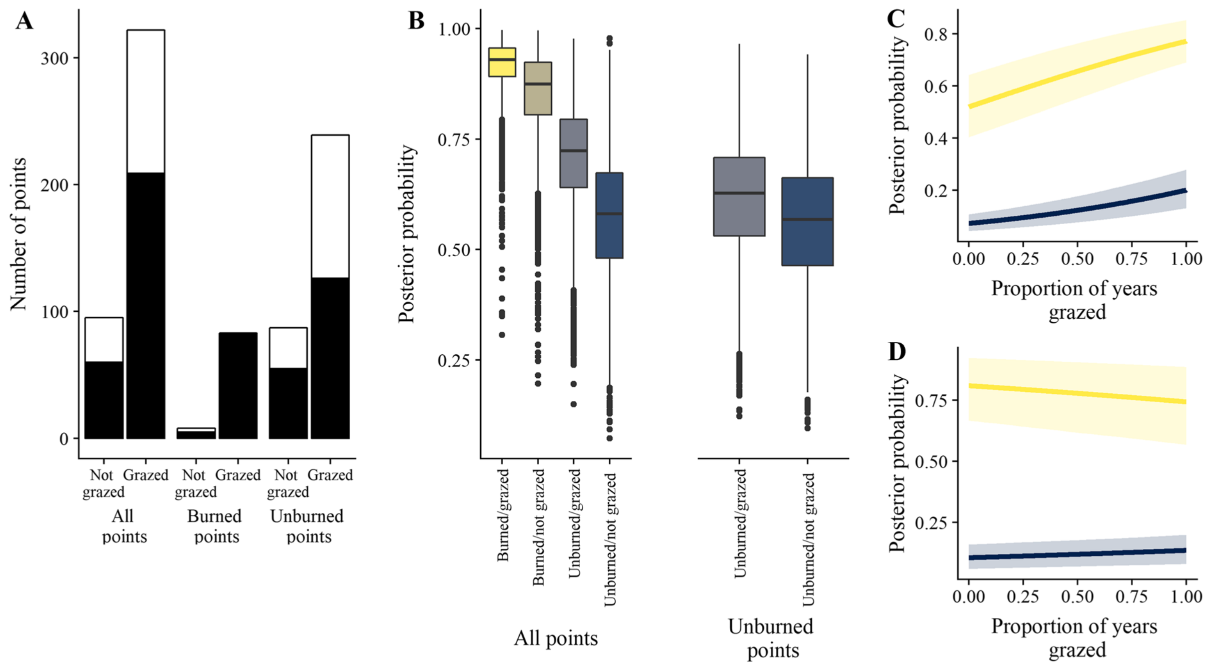

Fig. 3 Response of the occurrence of cheatgrass and prevalence of cheatgrass (i.e., given occurrence, the likelihood that cheatgrass was recorded present in any sample in a given point in a given year) to the interaction between livestock grazing and fire. Posterior probabilities for the occurrence and 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

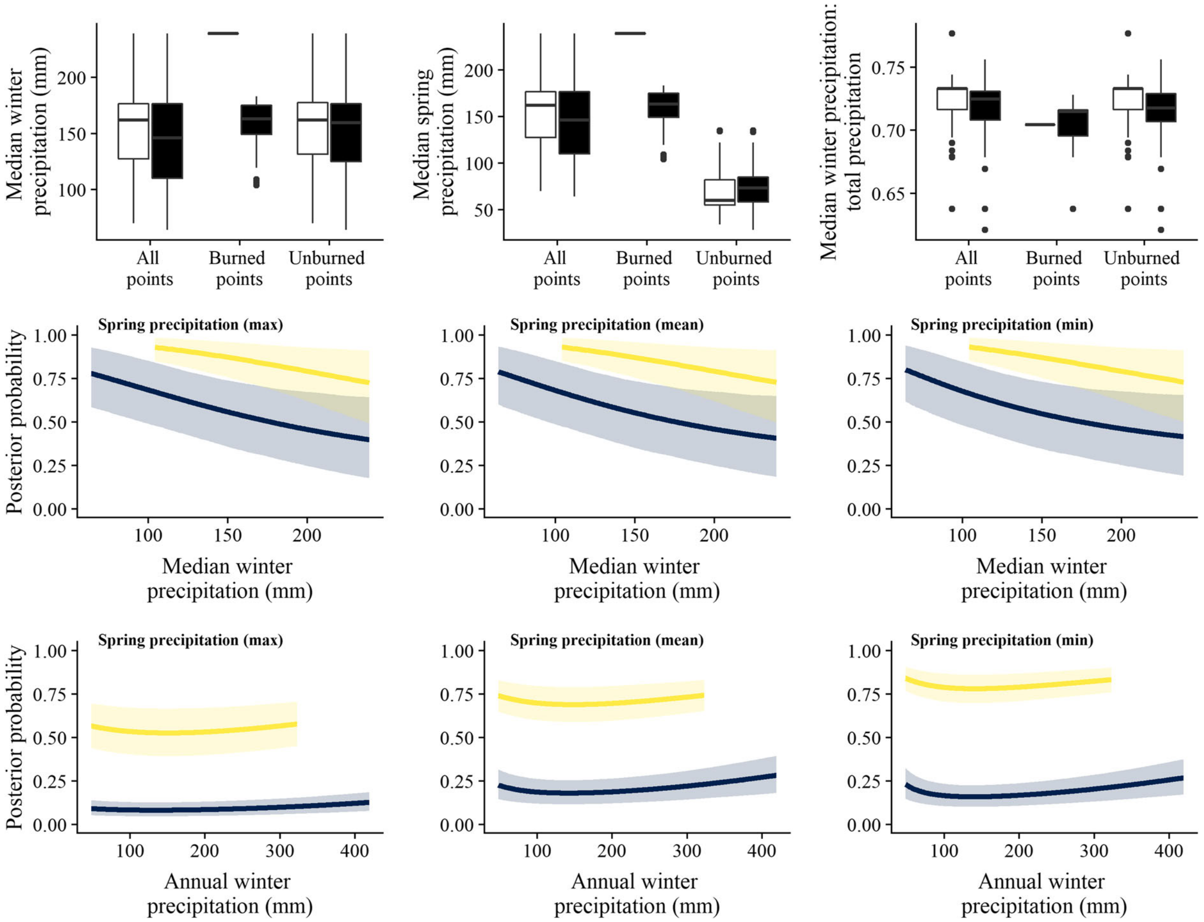

Fig. 4 Response of the occurrence of cheatgrass and prevalence of cheatgrass (i.e., given occurrence, the likelihood that cheatgrass was recorded present in any sample in a given point in a given year) to precipitation. Posterior probabilities for the occurrence and prevalence models are based on the 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).

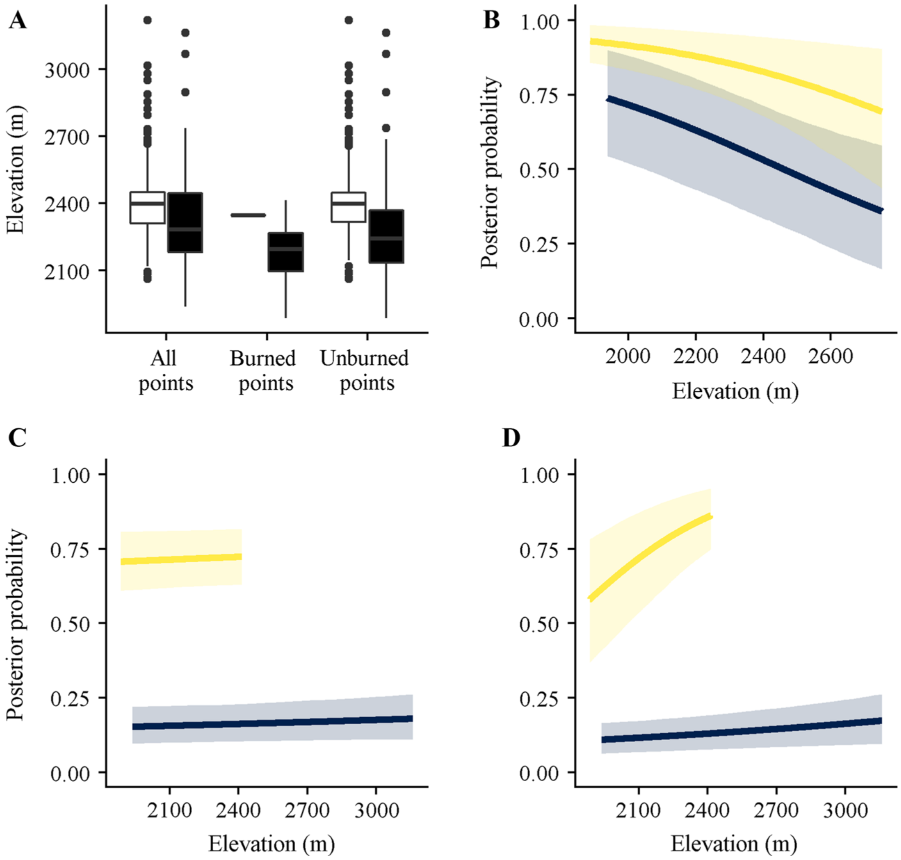

Fig. 5 Response of the occurrence of cheatgrass and prevalence of cheatgrass (i.e., given occurrence, the likelihood that cheatgrass was recorded present in any sample in a given point in a given year) to elevation. Posterior probabilities for the occurrence and prevalence models are based on the likelihoods 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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