

Disentangling drivers of annual grass invasion: Abiotic susceptibility vs. fire-induced conversion to cheatgrass dominance in the sagebrush biome

Alexandra K. Urza^{a,*}, David I. Board^a, John B. Bradford^b, Jessi L. Brown^a, Jeanne C. Chambers^a, Daniel R. Schlaepfer^{b,c}, Karen C. Short^d

^a USDA Forest Service, Rocky Mountain Research Station, Reno, NV, USA

^b U.S. Geological Survey, Northwest Climate Adaptation Science Center & Southwest Biological Science Center, Flagstaff, AZ, USA

^c Center for Adaptable Western Landscapes, Northern Arizona University, Flagstaff, AZ 86011, USA

^d USDA Forest Service, Rocky Mountain Research Station, Missoula, MT 59808, USA

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ABSTRACT

Invasive annual grasses are often facilitated by fire, yet they can become ecologically dominant in susceptible locations even in the absence of fire. We used an extensive vegetation plot database to model susceptibility to the invasive annual grass cheatgrass (*Bromus tectorum* L.) in the sagebrush biome as a function of climate and soil water availability variables. We built random forest models predicting cheatgrass presence or dominance (>15 % relative cover) under unburned (37,219 plots) and burned conditions (6340 plots). We mapped predicted probability of cheatgrass presence and dominance, conditional on burning. We combined predicted susceptibility with burn probability to quantify the 10-year total risk of cheatgrass dominance. Finally, we identified portions of the landscape (1) at risk of fire-induced conversion to cheatgrass dominance, (2) consistently susceptible to cheatgrass dominance, or (3) consistently resistant to cheatgrass dominance. At the scale of the sagebrush biome, we found that abiotic susceptibility to cheatgrass dominance drives total risk, regardless of fire. At local scales (i.e., individual 30 m pixels), burning increased the probability of cheatgrass dominance by a median of 14 %. Threshold-based analyses indicate that 10–31 % of the sagebrush biome was at risk of fire-induced dominance, with 55 % exhibiting abiotic resistance and 5 % exhibiting abiotic susceptibility to dominance regardless of fire. Burn probability was higher in areas predicted to be susceptible to dominance, illustrating how cheatgrass invasion can cause ecosystem conversions that are then sustained by grass-fire cycles. Disentangling the influence of abiotic conditions and fire contributes to our understanding of the mechanisms driving invasion dynamics, and modeling the probability of dominance can help anticipate where ecological transformations are at risk of occurring. Our approach can facilitate the prioritization of management actions in the sagebrush biome and be used as a framework for modeling invasion risk in other disturbance-prone ecosystems.

1. Introduction

Non-native annual grass invasions have caused unprecedented ecological impacts in drylands throughout the world, altering ecosystem processes and contributing to declines in native plant and animal species at landscape scales (Early et al., 2016; Gaertner et al., 2014). Often, annual grass invasions are facilitated by disturbances such as fire (Lodge, 1993), and the subsequent increase in fine fuel continuity can initiate a grass-fire cycle that promotes the progressive dominance of the invader species (Brooks et al., 2004; D'Antonio and Vitousek, 1992). Yet the extent to which conversion to annual grass dominance depends on

fire disturbance is unresolved (e.g., Smith et al., 2023b). Appropriate management responses require a nuanced understanding of the factors contributing to risk, including whether annual grass dominance requires disturbance to overcome biotic resistance or if fire disturbance is one of several potential pathways to invasion in susceptible abiotic environments (Chambers et al., 2019). For example, fire suppression may be critical where the risk of conversion to annual grasses is directly related to fire, yet other management approaches may be more effective in places that are susceptible to invasion even when unburned. Thus, a framework for disentangling the relative roles of underlying environmental conditions and fire disturbance in determining susceptibility to

* Corresponding author at: 920 Valley Rd., Reno, NV 89512, USA.

E-mail address: alexandra.urza@usda.gov (A.K. Urza).

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annual grass dominance will improve prioritization of management efforts.

A notable example of the ecological impact of invasive annual grasses is the proliferation of cheatgrass (*Bromus tectorum* L.) in the western United States (US), which has fundamentally altered the ecology of shrubland (Chambers et al., 2014, 2019), woodland (Floyd et al., 2021), and forest ecosystems (Kerns et al., 2020; Peeler and Smithwick, 2018). Despite its diminutive size, cheatgrass can become a dominant species in a broad range of ecosystem types. Dominant species can be defined as species that are highly abundant relative to other species in the community and have proportional effects on ecosystem function (Avolio et al., 2019). Sagebrush (*Artemisia* spp.) ecosystems have been particularly impacted by cheatgrass invasions, resulting in habitat losses for sagebrush-obligate species (Coates et al., 2016), altered ecosystem processes such as soil water flux and storage (Wilcox et al., 2012), and declines in ecosystem carbon stocks (Nagy et al., 2021). Cheatgrass is estimated to be abundant across nearly 21 million ha (Bradley et al., 2018) and continues to expand rapidly into new areas (Smith et al., 2022), playing a primary role in the ongoing degradation of the sagebrush biome (Chambers et al., 2023b; Doherty et al., 2022). Broad-scale tools to reduce cheatgrass dominance once it has become established are extremely limited (Davies et al., 2021), so anticipating the risk of conversion to cheatgrass dominance is imperative for preventing further sagebrush ecosystem losses (Crist et al., 2019; Doherty et al., 2022; Remington et al., 2021).

Much research has focused on the interaction between cheatgrass and fire, often described as a positive feedback loop that promotes a progressive conversion to cheatgrass dominance (Bradley et al., 2018; Mahood et al., 2023). Burning creates a pulse of resources such as soil water availability and nutrients (Rau et al., 2014; Roundy et al., 2020). Cheatgrass's extreme fecundity and high rates of resource acquisition promote rapid post-fire population growth (James, 2008; Leffler et al., 2013), exerting priority effects that inhibit the recovery of the native plant community (Mazzola et al., 2011; Plouffe et al., 2020). Cheatgrass alters fuel structure by increasing the amount and continuity of fine fuels with lower fuel moisture content during the fire season (Davies and Nafus, 2013), so invaded areas are more likely to burn again (Balch et al., 2013; Fusco et al., 2019). Across the western US, time since wildfire and wildfire frequency are strong predictors of invasive annual grass abundance (Pastick et al., 2021).

Yet, many uncertainties remain about the role of fire in landscape-scale conversions to cheatgrass dominance. Although fire is commonly described as the principal driver of conversion, transformation to invaded states has occurred even in areas that are long unburned (Smith et al., 2023b). Additionally, the influence of fire on conversion risk varies across plant community types (Sofaer et al., 2022), and many burned areas resist invasion because their environmental conditions promote robust native plant recovery and/or are not favorable for cheatgrass establishment (Chambers et al., 2007, 2014; Urza et al., 2019). For proactive management efforts to be most successful at restricting the effects of cheatgrass invasion, it is important to understand the influence of burning on susceptibility to cheatgrass dominance, the potential for converting to cheatgrass dominance in the absence of fire, and how these processes vary across the sagebrush biome (Smith et al., 2023b). Where fire drives conversion to cheatgrass dominance, management focused on fire suppression and post-fire restoration of native plant communities could mitigate impacts at landscape scales (Crist et al., 2019). But where cheatgrass can achieve dominance in the absence of fire, other management strategies are needed, including those focused on disrupting specific invasion processes such as seed dispersal and reproduction.

In this study, we used an extensive vegetation plot database and random forest modeling in a species distribution modeling framework to predict the probability of cheatgrass presence (>0 % cover) and dominance (>15 % relative cover) in burned and unburned conditions, as a function of climate and soil water availability metrics derived from

ecohydrological simulation models. We asked the following questions: 1) What are the biome-scale patterns of susceptibility to cheatgrass presence and dominance, based on predicted probabilities conditional on unburned or burned conditions? 2) What is the total risk of cheatgrass dominance across the sagebrush biome after accounting for burn probability, and to what extent is landscape-scale risk driven by abiotic susceptibility vs. fire? 3) Can our model predictions distinguish between areas that are at risk of fire-induced conversion to cheatgrass dominance and areas that exhibit consistent abiotic susceptibility or abiotic resistance to cheatgrass dominance regardless of fire? Our approach can facilitate the prioritization of management actions in the sagebrush biome and be used as a quantitative framework for modeling invasion risk in other disturbance-prone ecosystems.

2. Materials and methods

2.1. Study area

This study focused on sagebrush, pinyon-juniper, and salt desert ecosystems within the geographic extent of the sagebrush biome of the US (Jeffries and Finn, 2019), in which cheatgrass has contributed to extensive habitat losses (Doherty et al., 2022). The biome encompasses multiple Level II EPA ecoregions – Cold Deserts, Western Cordillera, small portions of the West-Central and South-Central Semi-Arid Prairies, and very small portions of the Warm Deserts (Mojave Basin and Range) – that exhibit different environmental characteristics and ecosystem attributes (Omernik and Griffith, 2014; Winthers et al., 2005). The Cold Deserts are characterized by warm to hot summers and cold winters. The proportion of summer precipitation increases across a west-to-east gradient, resulting in vegetation that is characterized largely by woody (shrubland and woodland) vegetation in the western Cold Deserts but transitions to warm-season grass dominance in the east. The portion of the Western Cordillera that is included in the sagebrush biome is characterized by high-elevation mountains and foothills, short summers, very cold winters, and relatively high precipitation. Upper elevations are dominated by coniferous forests, the foothills are partly wooded or shrub-dominated, and the intermontane valleys are grass- or shrub-covered. The West-Central Semi-Arid Prairies have a mostly dry climate characterized by warm to hot summers and cold winters; climate patterns favor grassland communities, although sagebrush species are present.

2.2. Database and data

2.2.1. Plot data

We used plot-based vegetation cover data collected between 2004 and 2019 and spatial location information from a dataset compiled from USDOI Bureau of Land Management Assessment Inventory and Monitoring (AIM) TerrADat and Landscape Monitoring Framework (Herrick et al., 2017), USDA Forest Service Forest Inventory and Analysis (FIA; Bechtold and Patterson, 2005), Rehabilitation Success Project (RSP; Pyke et al., 2024), and Sagebrush Steppe Treatment Evaluation Project (SageSTEP; McIver and Brunson, 2014). We identified and excluded plots with forest tree species, focusing on plots that represented salt desert, sagebrush, and pinyon-juniper woodland ecosystems. For more details on the dataset compilation and cleaning process, see Chambers et al. (2023a). The dataset included 43,442 unique sampling plot locations (Fig. 1), which had a total of 50,464 sampling events (1898 plots were sampled more than once, and some were sampled up to seven times). For each sampling event, we extracted cheatgrass percent areal cover and total vegetation cover, which were used to calculate cheatgrass relative cover. Evaluating cheatgrass cover relative to total vegetation is more useful for quantifying vegetation dominance than cheatgrass cover relative to total plot area, because it standardizes across gradients of ecosystem productivity that drive biomass production of both cheatgrass and co-occurring species.

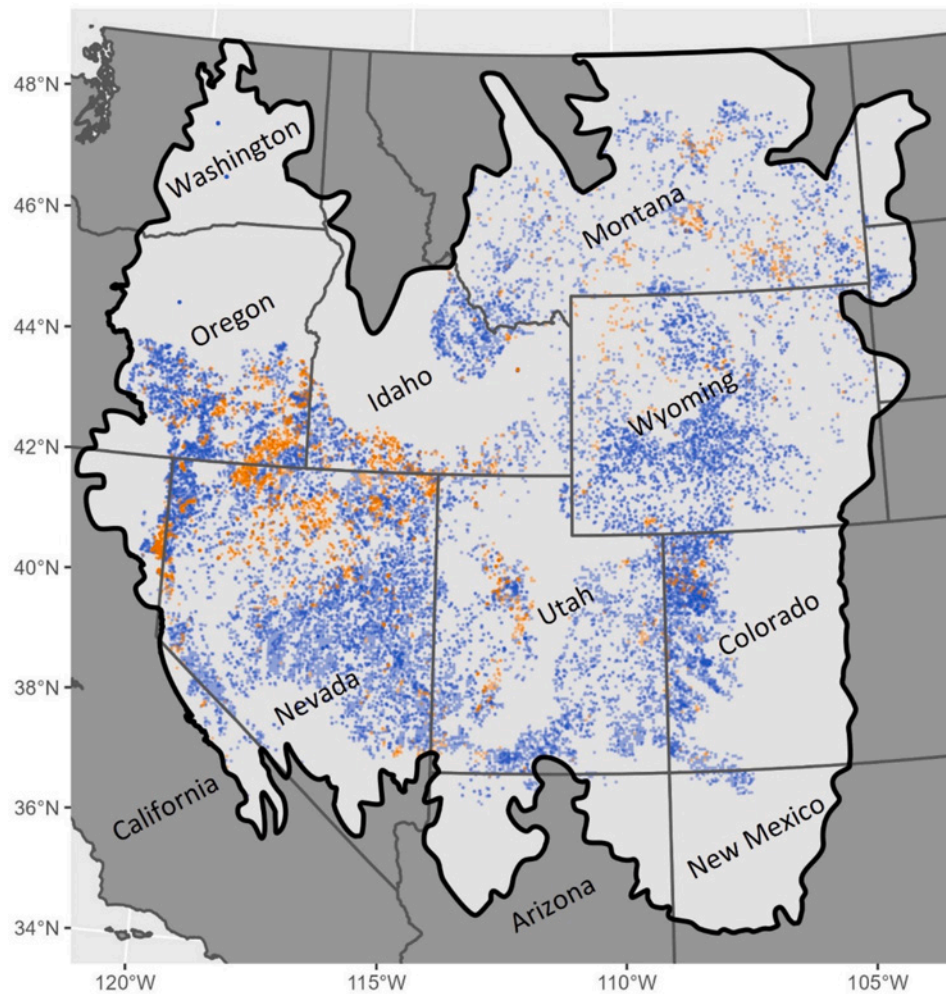


Fig. 1. Locations of plots in our dataset. Blue dots represent plots that were unburned prior to sampling, whereas orange dots represent plots that burned between 1984 and the date of sampling. U.S. State boundaries are in black. Areas outside the sagebrush biome study area are dark grey. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

2.2.2. Fire history data

Recent burn history for each sampling event was obtained by overlaying the plot locations with a spatial data layer representing fire history. The fire history layer was created using two publicly available databases: the Monitoring Trends in Burn Severity (MTBS) – Burned Areas Dataset (MTBS, 2017, accessed 10/27/2021) and the National Interagency Fire Center – Interagency Fire Perimeter History (IFPH) – All Years (National Interagency Fire Center, 2020, accessed 10/19/2021). The two databases overlap, but the IFPH dataset provides information on smaller fires that are not contained in the MTBS database. Our database included fires (wildfires, prescribed fires, and wildland fire use) occurring between 1984 and 2019; we excluded any fires occurring before 1984 because older fires were inconsistently recorded. We combined the IFPH and MTBS data products after removing duplicate polygons of fire perimeters from the dataset based on fire names, fire year, and spatial overlap, preferring the MTBS polygon when duplicates occurred due to its more precise fire perimeter delineations.

Plot locations were overlaid with the fire database to attribute sampling events with burn history (1984–2019) information: whether any fire occurred prior to sampling in that location, and the number of years between the last fire and the sampling event. The plot vegetation data were then divided into two datasets. The first was a dataset of unburned plots that included the first sampling event without a prior recorded fire at each plot location (37,219 sampling events). The second was a dataset of burned plots that included the first sampling event after

burning (6340 sampling events).

2.2.3. Climate and soil water availability data

Climate and soil water availability metrics were simulated using the open-source SOILWAT2 ecohydrological model (SOILWAT2 v6.2.1; R packages rSOILWAT2 v5.0.1 and rFSW2 v4.3.1). SOILWAT2 is a process-based ecosystem water balance simulation model that incorporates daily weather data, multiple soil layers, snowpack dynamics, multiple vegetation types responsive to atmospheric CO₂ concentrations, and hydraulic redistribution (details available in: Schlaepfer and Andrews, 2021; Schlaepfer and Murphy, 2021). We used a set of 33 metrics that quantify overall growing conditions, seasonal variability and timing of moisture, occurrence of extreme drought conditions, and conditions indicating recruitment potential for perennial plants in drylands (Table 1; Chenoweth et al., 2023). Our list included variables that have previously been found to be strong predictors of annual forb and grass invasion (McMahon et al., 2021), resilience to disturbance and resistance to annual grasses (Chambers et al., 2023a), and responses to vegetation management treatments such as prescribed fire (Roundy et al., 2018). We opted to retain a relatively large predictor set to optimize model predictions. Random forest models are generally robust against model over-fitting (Hastie et al., 2009), particularly for large datasets where the sample size far exceeds the number of predictors.

We produced two sets of simulation runs with SOILWAT2: the first to provide metrics at the individual plot locations used for initial model

Table 1

List of predictor variables, grouped into categories. Metric identifies the function used to calculate the long-term predictor variables (1980–2019) from annual time series. CV = coefficient of variation; SD = standard deviation; WDD = wet degree days; DDD = dry degree days; SWA = soil water availability; CWD = climatic water deficit; MAT = mean annual temperature; PET = potential evapotranspiration; AET = actual evapotranspiration; DSI = dry soil interval.

Category	Predictor variable	Metric (across years)
Overall growing conditions	Wet degree days (WDD)	Mean
	Dry degree days (DDD)	Mean; CV
	Soil water availability (SWA)	Mean; CV
	Climatic water deficit (CWD)	Mean
	Annual precipitation	Mean; CV
	Annual precipitation as rainfall	Mean
	Precipitation in July, August, and Sept	Mean
	Precipitation in driest month	Mean; CV
	Mean annual temperature (MAT)	Mean
	Mean temperature of coldest month	Mean; SD
	Mean temperature of hottest month	SD
	Maximum monthly mean temperature	SD
	Minimum monthly mean temperature	SD
	Diurnal temperature range	Mean; CV
	Potential evapotranspiration (PET)	CV
	Actual evapotranspiration (AET)	Mean; CV
	Deep water drainage	Mean
	CWD seasonal variability	Mean
	SWA seasonal variability	Mean
Seasonal variability	Fall recruitment index	Mean
Recruitment potential	Spring recruitment duration	Mean
	Dry soil interval (DSI) length	Mean
Seasonal moisture timing	Number of DSI	Mean
	SWA seasonality	Mean
	CWD seasonality	Mean
	Precipitation seasonality	Mean
Fire history ^a	Time since fire	Years since last fire

^a Burned models only; includes fires since 1984.

training, and the second to produce raster surfaces (30-m spatial resolution) for projecting the model predictions across the sagebrush biome. Annual values were calculated for 1980–2019 and summarized into long-term normals (mean across years) and interannual variability (coefficient of variation [CV] for variables with only positive values; standard deviation [SD] for variables with negative values [e.g., temperature]). A more detailed description of the climate and water availability data development can be found in [Chenoweth et al. \(2023\)](#) and [Chambers et al. \(2023a\)](#).

2.3. Data analysis

2.3.1. Statistical model building and evaluation

We used a random forest species distribution modeling approach to predict the probability of cheatgrass based on environmental conditions. To directly evaluate the conditional effect of fire on cheatgrass probability across our study area, we created separate models for the burned and unburned plot datasets. For each dataset, we calculated two binary response variables. First, we modeled cheatgrass presence (>0 % cheatgrass cover), as is commonly used in species distribution modeling (e.g., [McMahon et al., 2021](#)). Second, we created a binary cheatgrass dominance metric to characterize plots in which cheatgrass is highly abundant relative to other species in the plant community ([Avolio et al., 2019](#)). We defined ‘cheatgrass dominance’ as >15 % relative cover, calculated as follows:

$$\text{cheatgrassrelativecover} = \frac{\text{cheatgrass\%arealcover}}{\text{totalvegetation\%arealcover}} * 100$$

In plots with >15 % cheatgrass relative cover, cheatgrass was the most abundant species 65 % of the time, and was among the three most abundant species >99 % of the time (Fig. S1-1). We thus developed four models: probability of cheatgrass presence (cover >0 %) and probability of cheatgrass dominance (relative cover >15 %), each conditional on unburned vs. burned conditions. All models included the full set of environmental predictor variables (Table 1). In the burned models, we also included time since fire (years) as a predictor.

All modeling was done in R version 4.3.0 ([R Core Team, 2023](#)). We built the random forest models as probability forests ([Malley et al., 2012](#)) with the ranger package ([Wright and Ziegler, 2017](#)). Data were partitioned into training (70 %) and testing (30 %) datasets and were centered and scaled prior to analysis. Models used the Gini splitting rule and were iteratively tuned with the caret package ([Kuhn, 2008, 2023](#)), with spatial cross-validation using the blockCV package version 2.1.4 ([Valavi et al., 2018, 2023](#)). We used ten folds generated from 100-km² blocks randomly allocated across the study area. Models used cost-sensitive learning to compensate for class imbalances, with class weights inversely proportional to their prevalence ([Chen et al., 2004](#)). Models were then evaluated using the withheld testing dataset. For each model, we produced lists of ranked variable importance using the Shapley Additive exPlanations (SHAP) method ([Lundberg and Lee, 2017](#)). SHAP values describe overall variable effect strength while accounting for dependence between features, and we present the mean of absolute Shapley values for each predictor and Accumulated Local Effects (ALE) plots to visualize the marginal average effect of each predictor variable.

2.3.2. Model projections

We projected the predictions from our four models across the sagebrush biome using the raster surfaces for the climate and soil water predictors. The burned and unburned models were projected separately to predict susceptibility to cheatgrass conditional on burn status: the unburned prediction assumed that the entire region had never burned, while the burned prediction assumed that the entire region had burned once since 1984, 10 years prior to sampling. We mapped the difference in burned and unburned model predictions as a continuous surface to show fire-related changes in susceptibility to cheatgrass. Interpreting the map requires cross-referencing the raw prediction surfaces, as two areas with similar fire-related changes would appear equivalent despite differences in susceptibility.

The Type 2 Novelty metric (NT2) developed by [Mesgaran et al. \(2014\)](#) was used to identify the amount of model extrapolation in the prediction maps. NT2, a metric of multivariate novelty in predictor space, measures the Mahalanobis distance between environmental conditions of the training and predicted data. Values between 0 and 1 indicate similarity in environmental conditions, while values greater than one indicate increasing novelty (extrapolations into novel conditions).

2.3.3. Total 10-year cheatgrass dominance risk maps

From here onward, we focused only on predictions of cheatgrass dominance (not cheatgrass presence). To calculate the total 10-year probability (total risk) of cheatgrass dominance, we combined our model predictions of the conditional probability of cheatgrass dominance given burn status with published burn probability estimates. Annual burn probability was derived using a geospatial fire modeling application ([Finney et al., 2011](#)) and ca. 2020-vintage landscape data calibrated specifically for use in quantitative wildfire risk assessment for the sagebrush biome ([Short et al., 2023, 2024](#)). We derived 10-year burn probability by calculating the complement to the probability of not burning in all ten years.

The model-predicted conditional probability of cheatgrass dominance given unburned conditions was multiplied by the 10-year probability of not burning to produce the risk of unburned dominance (joint probability of not burning within 10 years and susceptibility to dominance in unburned conditions). The same process was followed to produce the risk of burned dominance. Finally, the risk of unburned and risk of burned dominance were summed to produce the total 10-year probability (total risk) of cheatgrass dominance across the landscape.

2.3.4. Categorical cheatgrass dominance susceptibility maps

We created a categorical map of susceptibility to cheatgrass dominance based on the spatial relationships between the unburned and burned cheatgrass dominance predictions. These maps are intended to illustrate potential applied uses of our model outputs, and specific thresholds for visualizing categorical predictions would likely differ based on management objectives. “Susceptible to dominance” represents areas predicted to be susceptible to cheatgrass dominance (probability >0.50) in both unburned and burned conditions. “Resistant to dominance” represents areas predicted to be not susceptible to cheatgrass dominance (probability <0.50) in both unburned and burned conditions. “Fire-induced dominance” represents areas predicted to be susceptible to cheatgrass dominance only if burned. “Fire-reduced dominance” represents areas predicted to be susceptible to dominance if unburned, but not susceptible if burned. Predicted transitions between susceptibility and resistance were considered marginal if either the unburned or burned predicted probabilities were within 10 % of the 0.50 probability threshold.

We then incorporated modeled burn probability to represent the expected risk of cheatgrass dominance given estimates of current burn probability (Short et al., 2023). We created a binary map of 10-year burn probability, using 10 % as a threshold distinguishing high and low probability of burning within a 10-year period. 10 % was selected as a burn probability threshold because it represented an approximate inflection point in the distribution of the data (Fig. S1-2), with most of the study area falling below this threshold. We overlaid this binary burn probability map with the categorical map of susceptibility to cheatgrass dominance described above to calculate the percent of each category with low vs. high burn probability.

Finally, we compared the current level of cheatgrass abundance to our dominance susceptibility categories. We used a raster layer of remotely sensed mean cheatgrass cover from 2016 to 2020 (30-m resolution; Dahal et al., 2022). We calculated the amount of cheatgrass areal cover corresponding to 15 % relative cover (index of dominance) in our plot database, using this value to classify each pixel as either previously converted or not converted to cheatgrass dominance and calculating how much of each dominance susceptibility category had already converted. We then overlaid estimated cheatgrass cover in burned and unburned areas with our predicted susceptibility categories, removing pixels that had burned since 2014 and likely would not yet have had a post-fire increase in cheatgrass abundance by 2016. Remotely sensed estimates of cheatgrass cover are not directly comparable to our cheatgrass dominance predictions for two reasons: 1) our distribution modeling approach produces estimates of abiotic suitability rather than abundance; and 2) the relationship between areal cover and relative cover varies based on total vegetation cover or ecosystem productivity. For these reasons, we did not use the remotely sensed cover estimates to evaluate the performance of our models, using them instead to provide an estimate of the level of current cheatgrass abundance across our predicted susceptibility categories.

3. Results

3.1. Susceptibility to cheatgrass in unburned and burned conditions

3.1.1. Models of cheatgrass presence (>0 % cover)

Our models predicted cheatgrass presence across broad areas within

the sagebrush biome (Table 2; Fig. 2a–b). SHAP variable importance rankings and ALE plots show that the probability of cheatgrass presence in unburned conditions was greatest in locations with high variability in the temperature of the coldest month, low summer precipitation (July, August, September), high mean annual temperature, and a negative correlation between monthly precipitation and temperature (Appendix S2-1). This corresponds to a high probability of cheatgrass presence across the Snake River Plain in southern Idaho, the northern Great Basin in northwest Nevada, the Wasatch Front in western Utah, the Columbia Plateau in eastern Washington, and portions of Wyoming, northwest Colorado, and northeast Utah (Fig. 2a). The probability of cheatgrass presence after fire was predicted to be greatest in locations with low summer precipitation, higher annual climatic water deficit, longer dry soil intervals, higher temperature of the coldest month, and a positive correlation between monthly climatic water deficit and temperature (Appendix S2-2). Overall, the burned model predicted cheatgrass presence in a larger portion of the study area than the unburned model, extending the area of predicted susceptibility into the southern portion of the sagebrush biome (Figs. 2b, 3a). Burning increased the probability of cheatgrass presence in 92 % of pixels (Fig. 3b; median change = 15 % increase; Fig. S3-1a).

3.1.2. Models of cheatgrass dominance (>15 % relative cover)

Our models predicted cheatgrass dominance (Fig. 2c–d) in a much smaller area of the sagebrush biome than the predictions of cheatgrass presence. The probability of cheatgrass dominance in unburned conditions was greatest in locations with high variability in temperature of the coldest month, low summer precipitation, a positive correlation between monthly climatic water deficit and temperature, higher mean annual temperature, and higher annual climatic water deficit (Appendix S2-3). The probability of cheatgrass dominance after fire was predicted to be greatest in locations with high annual climatic water deficit, low variability in monthly climatic water deficit, low summer precipitation, a positive correlation between monthly climatic water deficit and temperature, and moderately high mean temperature of the coldest month (Appendix S2-4). Burning increased the predicted probability of cheatgrass dominance in 94 % of pixels (Fig. 3d; median change = 14 % increase; Fig. S3-1b).

3.1.3. Area of applicability mapping

The maps of multivariate novelty in predictor space (NT2 metric; Fig. S4-1) indicate that the plot data used to train the models were most representative of abiotic conditions in the Northern Basin and Range in northwest Nevada, the Semi-Arid Prairies in eastern Montana, and the Snake River Plain in southern Idaho (mapped as white-to-yellow in Fig. S4-1). Other regions had greater novelty in predictor space, with especially high levels of novelty (mapped as pink-to-black) in the Colorado Plateau and Four-Corners Region (Utah, Colorado, New Mexico, and Arizona). Novelty indicates differences between the model training conditions and the conditions that were projected into, and areas with higher levels of novelty should be assumed to have greater uncertainty in model predictions.

3.2. Total risk of cheatgrass dominance across the sagebrush biome

Burn probability over a 10-year period was predicted to be low except in specific portions of the landscape, such as southern Idaho, northern Nevada, and small portions of other regions (Short et al., 2023). Because most of the study area was much more likely to remain unburned than to burn, the predictions of dominance in unburned conditions were generally more influential than predictions of dominance in burned conditions when calculating total risk of cheatgrass dominance (Fig. 4). Thus, the total 10-year risk of dominance (Fig. 4g) closely resembled the model predictions of susceptibility to cheatgrass dominance in unburned conditions (Figs. 2c and 4a). Widening the interval of the risk prediction (e.g., using 50-year burn probability)

Table 2
Model evaluation metrics for the four models that were developed. Models were evaluated using the withheld testing dataset (30 % of data points).

Model name	N	% of samples above cover threshold	Cross-validated AUC	Sensitivity	Specificity	Brier score
Cheatgrass presence (>0 % cover), unburned	37,219	34.7 %	0.864	0.763	0.809	0.150
Cheatgrass presence (>0 % cover), burned	6340	82.7 %	0.890	0.954	0.549	0.086
Cheatgrass dominance (>15 % rel. cover), unburned	37,219	18.7 %	0.822	0.384	0.945	0.107
Cheatgrass dominance (>15 % rel. cover), burned	6340	55.6 %	0.788	0.796	0.625	0.169

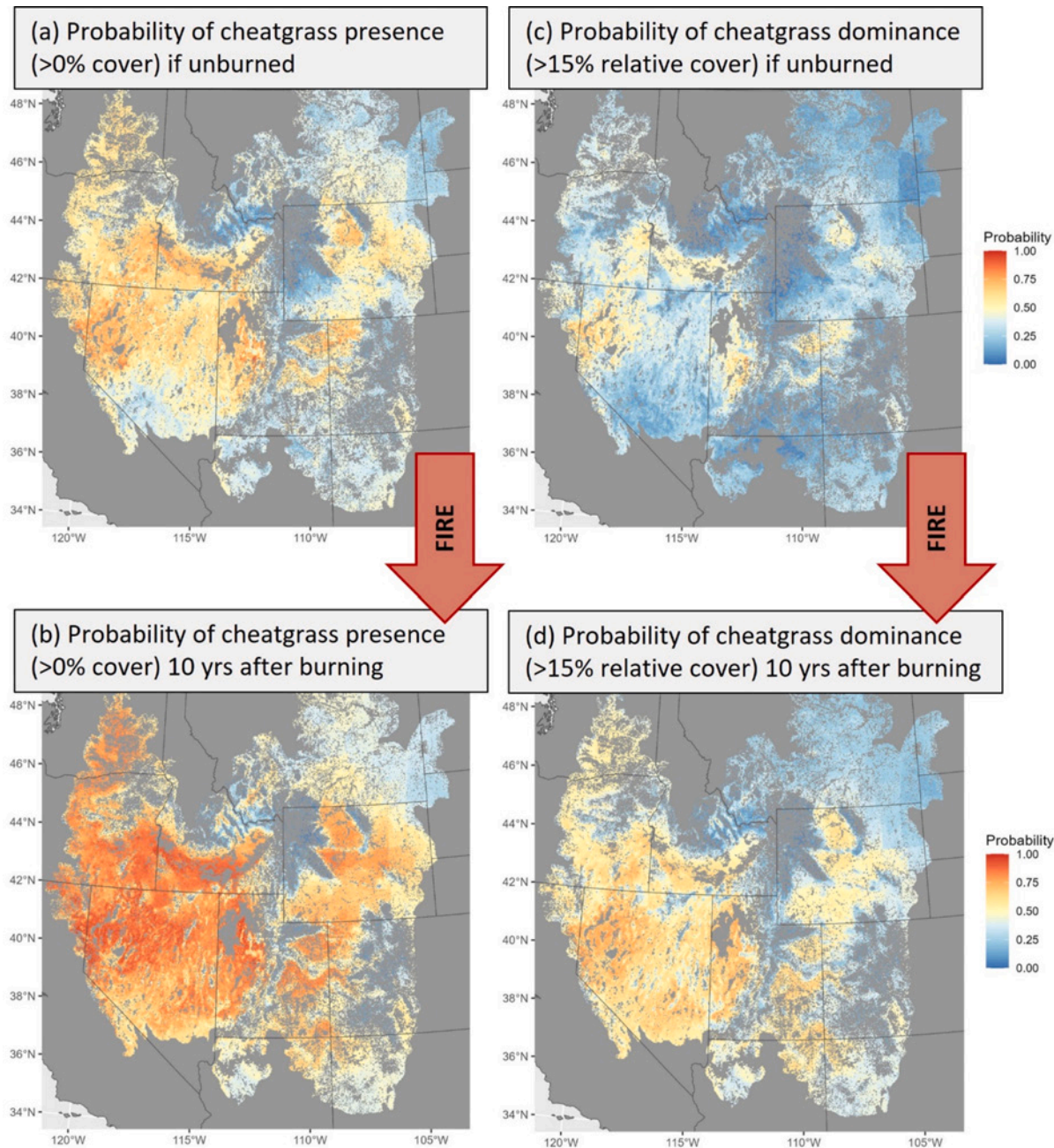


Fig. 2. Model predictions of (a) probability of cheatgrass presence if unburned, (b) probability of cheatgrass presence 10 years after burning, (c) probability of cheatgrass dominance (>15 % relative cover) if unburned, and (d) probability of cheatgrass dominance 10 years after burning. U.S. State boundaries are in black. Areas outside the study area are dark grey.

increases the weight given to the predictions of dominance in burned conditions, yet predictions of total risk remained quite stable, with the highest total risk of dominance concentrated within the regions predicted to be susceptible in both burned and unburned conditions (Fig. S5-1).

3.3. Distinguishing fire-induced conversion to cheatgrass dominance from consistent abiotic susceptibility or abiotic resistance

The categorical map of susceptibility to cheatgrass dominance (Fig. 5) illustrates the spatial relationships between the unburned and

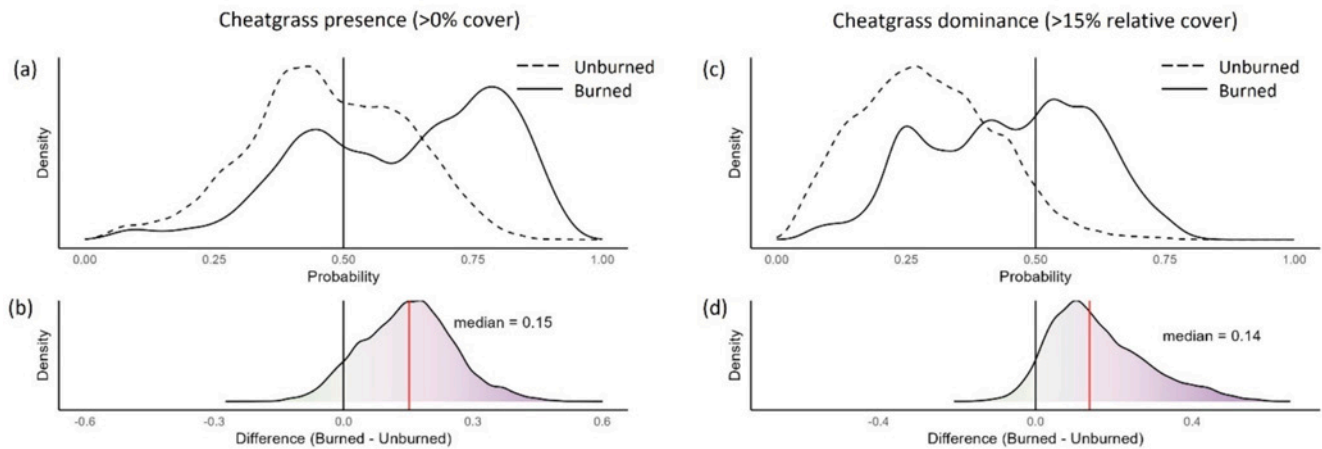


Fig. 3. Probability density functions of predicted probabilities for models of (a) cheatgrass presence and (c) cheatgrass dominance. Difference figures show the distribution of pixel-level differences between the unburned and burned model predictions (conditional probability given burned conditions – conditional probability given unburned conditions) for cheatgrass presence (b) and cheatgrass dominance (d). Positive values represent a fire-related increase in probability of cheatgrass, and negative values represent a fire-related decrease in probability. Red vertical line indicates the median difference. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

burned cheatgrass dominance predictions. 55 % of the study area was predicted to be resistant to cheatgrass dominance in both burned and unburned conditions, including much of the eastern half of the study area. In contrast, <5 % of the study area was predicted to be susceptible to cheatgrass dominance in either burned or unburned conditions, concentrated primarily in the northern Great Basin in northern Nevada, the Snake River Plain in southern Idaho, and the Wasatch Front in western Utah. A total of approx. 31 % of the study area was predicted to be at risk of fire-induced cheatgrass dominance, although more than half of that land area was near the threshold (marginally resistant or marginally susceptible). The regions at risk of robust fire-induced dominance (yellow areas in Fig. 5) were concentrated in central Nevada and at the intersection of Utah, Arizona, Colorado, and New Mexico. Fire-reduced dominance was predicted in only 0.02 % of the study area.

The regions categorized as susceptible to dominance generally coincided with the areas of high burn probability (Fig. 6a), with 42 % of susceptible areas mapped as likely to burn. In contrast, only 12 % of the resistant areas and 10 % of the robust fire-induced dominance areas had high burn probability. Comparison with remotely sensed estimates of cheatgrass cover (Fig. 6b) showed that 74 % of areas classified as susceptible to dominance have already converted to cheatgrass dominance (cheatgrass areal cover >11.3 %, a level that corresponded to 15 % relative cover in the plot data; Fig. S7-1), compared to 17 % of the robust fire-induced dominance areas and 9 % of the resistant to dominance areas. The distribution of cheatgrass cover was consistent with expected patterns (Fig. S7-2): cheatgrass cover was relatively high in susceptible to dominance areas, relatively low in resistant to dominance areas, and strongly influenced by burn history in fire-induced dominance areas.

4. Discussion

The proliferation of cheatgrass (*Bromus tectorum* L.) in western North America poses major challenges to the management of sagebrush ecosystems, prompting the need to identify drivers of cheatgrass dominance to help anticipate and mitigate ecological impacts. Cheatgrass has been a central focus of invasive species management due to its widespread distribution, known impacts to fire regimes, and well-documented detrimental ecological effects (Balch et al., 2013). Our study used an extensive plot database to disentangle underlying abiotic susceptibility from fire-induced susceptibility to cheatgrass dominance. However, many other invasive annual grass species also have the capacity to

impact ecological processes and alter fire behavior, including *Bromus rubens*, *B. arvensis*, *Schismus barbatus*, *Taeniatherum caput-medusae*, and *Ventenata dubia* (Fusco et al., 2019; McMahon et al., 2021). Additionally, many invasive annual forb species have been shown to displace native vegetation (Prevéy et al., 2010). The results of our study can be used to anticipate the drivers of cheatgrass-fire cycles in the western US, and our approach can be used as a framework for modeling susceptibility to other invasive species in disturbance-prone ecosystems.

4.1. Fire increases susceptibility to cheatgrass dominance, but its effects are geographically variable

We found that fire generally increased local susceptibility to cheatgrass dominance, consistent with much previous research on fire-facilitated annual grass invasion. Invasive species' establishment is often facilitated by disturbances, which produce a pulse of resources and provide new niche opportunities for invaders (Davis et al., 2000; Shea and Chesson, 2002). Fire-facilitated expansion and growth of annual grass populations increase the abundance and continuity of fine fuels that promote rapid fire spread, initiating a grass-fire cycle that supports more extensive and more frequent fires (Balch et al., 2013; Bradley et al., 2018; Fusco et al., 2019). However, the simple presence of invasive species does not necessarily lead to ecosystem transformations (Jarnevich et al., 2021), and cheatgrass is present at low abundance in many landscapes without dominating the vegetation community (Duniway et al., 2023; Sofaer et al., 2022). Disturbances such as fire create opportunities for rapid growth of annual grass populations, and extant cheatgrass populations often increase following fire due to residual seeds in the soil seedbank and acquisitive life-history traits (James, 2008; Leffler et al., 2013; Mahood et al., 2023; Prévéy et al., 2024), exerting priority effects that impede the recovery of native species (Ploughe et al., 2020). We found that predicted cheatgrass dominance was constrained to a geographic subset of predicted presence, indicating a narrower range of abiotic conditions suitable for ecological dominance despite the species' widespread presence across the region (Jarnevich et al., 2022; McMahon et al., 2021). Cheatgrass dominance risk may be underestimated by our species distribution modeling approach, because ongoing expansion of cheatgrass and changing environmental conditions (Smith et al., 2022) indicate that suitability is not static.

In our study, burning increased the modeled local probability of cheatgrass dominance in 94 % of pixels in our study area (median change = 14 % increase in probability). However, using a 50 %

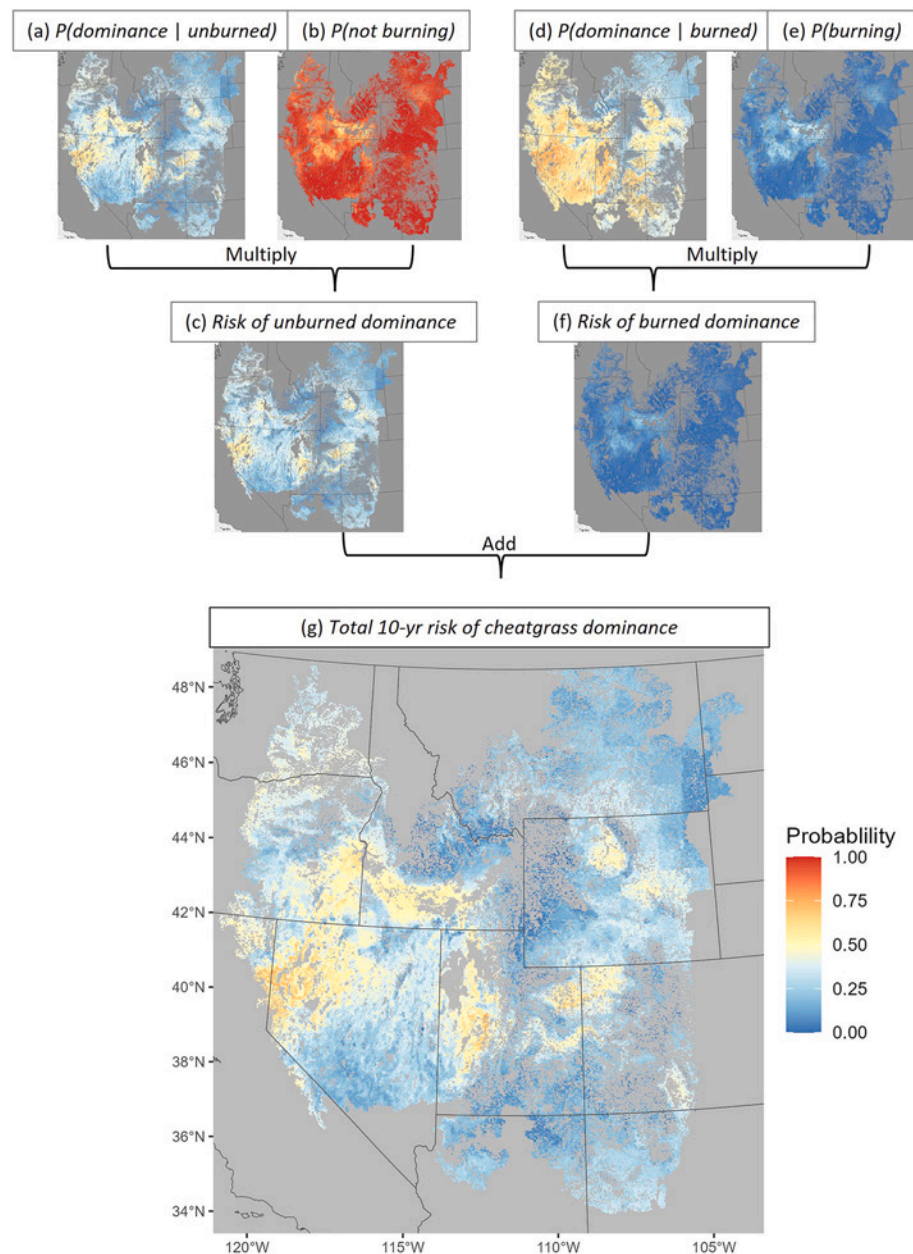


Fig. 4. Workflow for calculating total 10-year risk of cheatgrass dominance (> 15 % relative cover). (a) The conditional probability of cheatgrass dominance given unburned conditions was multiplied by (b) the 10-year probability of not burning to produce (c) the 10-year risk (joint probability) of unburned dominance. (d) The conditional probability of cheatgrass dominance given burned conditions was multiplied by (e) the 10-year probability of burning to produce (f) the 10-year risk (joint probability) of burned dominance. The joint probabilities in (c) unburned and (f) burned conditions were summed to produce (g) the total 10-year risk of cheatgrass dominance. U.S. State boundaries are in black. Areas outside the study area are dark grey.

threshold of susceptibility, we found that only 10–31 % of the study area (depending on the strength of fire-induced change) was predicted to shift from resistant to susceptible to cheatgrass dominance if a fire were to occur, which we classified as at risk of fire-induced conversion to dominance. Fire-induced dominance was predicted in large areas in southern Nevada and the Four-Corners area at the intersection of Utah, Arizona, Colorado, and New Mexico, suggesting that in these areas, fire occurrence can catalyze ecosystem transformation and potentially initiate a grass-fire cycle. Within those suitable environments, fire-induced dominance is more likely where pre-fire annual grass cover is already relatively high (Barker et al., 2019) or where pre-fire herbaceous understory cover is low (Chambers et al., 2014; Urza et al., 2019).

In contrast to the 10–31 % of the sagebrush biome predicted to be at risk of fire-induced cheatgrass dominance, we found the majority of the

study area (55 %) to be resistant to dominance regardless of fire. Post-fire recovery of natives and thus resistance to cheatgrass dominance varies based on the environment, and resistance is generally higher in relatively cool and moist locations (Chambers et al., 2007, 2014; Taylor et al., 2014; Urza et al., 2019). The environmental conditions that we identified as supporting resistance to cheatgrass dominance were consistent with previous research that found higher resistance to invasion in places with greater summer precipitation, lower mean annual and winter temperatures, and lower climatic water deficit (Chambers et al., 2023a; Prev  y et al., 2024). These conditions tend to occur at higher elevations and in the eastern portion of the sagebrush biome, where favorable climate conditions promote greater abundance of native perennial grasses, which are capable of rapid post-fire recovery and can out-compete cheatgrass (Chambers et al., 2007; Prev  y and

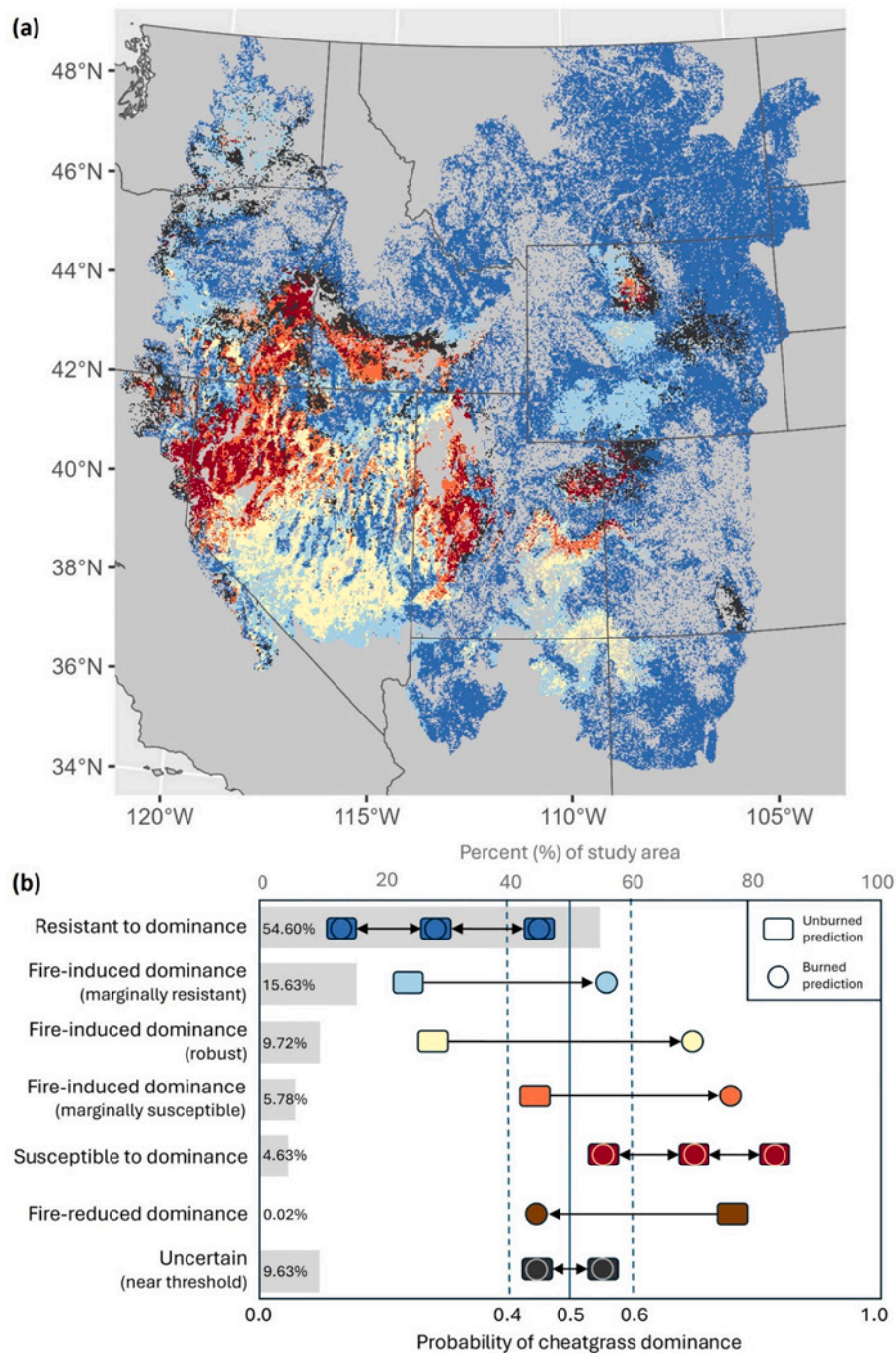


Fig. 5. Categorical predictions of the probability of cheatgrass dominance. (a) Distribution of dominance categories. (b) Graphical description of the categories (colored boxes and arrows; bottom axis) and the percent of the modeled landscape represented by each category (grey bars; top axis). The categories were defined by combining predictions from the unburned and burned models of cheatgrass dominance. The arrows indicate the direction of change from the unburned (rectangles) to the burned prediction (circles). Arrows are bi-directional (i.e., probability of dominance could be increasing or decreasing) where predicted probability of dominance was above or below the 0.50 threshold in both burned and unburned conditions (Resistant and Susceptible categories), or where burned and unburned predictions were both near the threshold (Uncertain category). Arrows are one-directional for categories predicting fire-related transitions across the threshold, and transitions were considered marginal if either the unburned or burned predicted probabilities were within 10 % of the 0.50 probability threshold. See Appendix S6 for more detail. (For interpretation of the references to color in this figure, the reader is referred to the web version of this article.)

Seastedt, 2014). In the eastern portion of the sagebrush biome where cheatgrass co-occurs with fire-adapted native plant species, the occurrence of fire can increase native species abundance and, consequently, decrease cheatgrass abundance (Porensky and Blumenthal, 2016; Symstad et al., 2021). However, annual grass species differ in the climatic conditions suitable for their establishment and reproduction, and some areas resistant to cheatgrass dominance may be susceptible to

dominance by another annual grass species, which may have detrimental ecological effects similar to cheatgrass (McMahon et al., 2021).

4.2. Abiotic susceptibility to cheatgrass dominance, not fire, drives landscape-scale risk

Our study challenges the common assertion that ecological

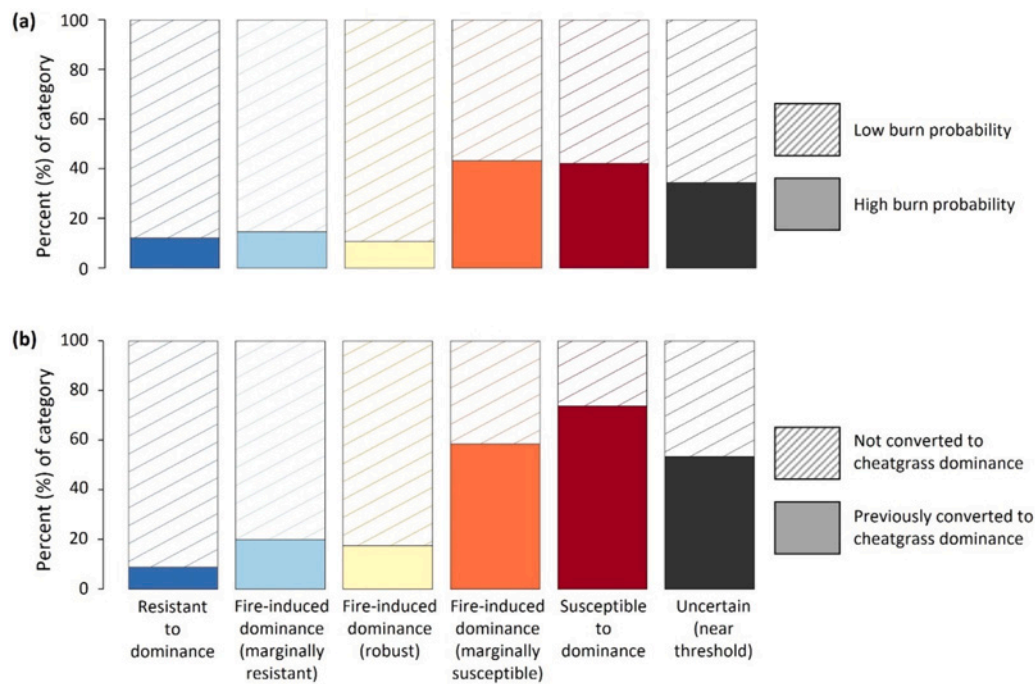


Fig. 6. (a) Percent of each cheatgrass dominance category in which burn probability was high (solid bars) or low (hashed bars). Burn probability (from Short et al., 2023) was considered high if the 10-year probability of burning exceeded 10 %. (b) Percent of each cheatgrass dominance category that had previously converted to cheatgrass dominance (solid bars) or was not converted to cheatgrass dominance (hashed bars). Conversion to cheatgrass dominance was based on remotely-sensed cheatgrass cover estimates (mean cover from 2016 to 2020; Dahal et al., 2022). Pixels were considered to have converted to cheatgrass dominance if cheatgrass cover was >11.3 %, a level that corresponded to 15 % relative cover in our plot data (Fig. S7-1). Fire-reduced dominance (brown in Fig. 5) was rare and was excluded from these overlays.

conversions to cheatgrass dominance are driven primarily by fire, finding that 5 % of the sagebrush biome is highly susceptible to cheatgrass dominance even in the absence of recent fire, and an additional 15 % is predicted to be near the threshold of susceptibility when unburned. This finding is consistent with a recent study by Smith et al. (2023b), which found that almost 80 % of transitions to annual grass dominance occurring over the last three decades in the Great Basin Region were not preceded by fire in the previous 10 years and concluded that fire is overemphasized as a driver of change. We found that abiotic susceptibility to cheatgrass dominance was predicted in unburned conditions across large areas, particularly within portions of the northern Great Basin and Snake River Plain. An overlay with current estimates of cheatgrass cover indicate that >70 % of areas predicted to be susceptible to dominance have already converted, consistent with previous analyses in the Great Basin (Bradley et al., 2018; Smith et al., 2023b). Areas dominated by cheatgrass in the absence of fire have underlying abiotic characteristics that are particularly suitable for cheatgrass population growth, including winter-dominated precipitation regimes and higher winter temperatures (Chambers et al., 2023a; McMahon et al., 2021). Warm fall and winter temperatures accompanied by sufficient precipitation facilitate cheatgrass germination and growth (Bykova and Sage, 2012). In addition, areas with low summer precipitation and relatively warm temperatures tend to support shrub-dominated plant communities with low abundances of perennial grasses, which are the primary competitors with cheatgrass (Chambers et al., 2007; Lauenroth et al., 2014).

Land use legacies and non-fire disturbances may also play an important role in facilitating annual grass invasions where fire is not the primary driver. Heavy grazing by domestic and feral ungulates increases susceptibility to invasion by weakening native plant competitors (Davies and Boyd, 2019; Williamson et al., 2020), breaking up biological soil crusts (Condon and Pyke, 2018; Root et al., 2020), and increasing propagule pressure (Reisner et al., 2013). Our predictions of cheatgrass dominance in the absence of fire may be underestimating the long-term legacies of historic grazing as well as fires occurring before 1984, which

may still be exerting an influence on invasion processes even in plots that have not burned in the intervening 20–35 years. Additionally, invasion is influenced by biotic factors such as animal consumers, seed pathogens, and adaptations of native plant species (Goergen et al., 2011; Mordecai, 2013; St. Clair et al., 2016).

At the scale of the sagebrush biome, abiotic susceptibility to cheatgrass dominance, not fire, was the primary driver of the 10-year probability (total risk) of cheatgrass dominance, consistent with results from process-based modeling (Bradford and Lauenroth, 2006). We estimated the total risk of cheatgrass dominance by combining predictions of cheatgrass dominance in burned and unburned conditions with estimates of burn probability from Short et al. (2023). The resulting map of total 10-year risk of cheatgrass dominance closely reflects areas susceptible to dominance in the absence of fire. Because fire occurs with a low probability in most places, the risk of transitioning to cheatgrass dominance because of a fire is generally lower than transitioning in the absence of fire (see Fig. 4 for underlying math). The burn probability estimates used a 2020 fuelscape that was calibrated specifically for use in quantitative wildfire risk assessment for the sagebrush biome, with fuel models that were adjusted to reflect annual grass fuels in invaded portions of the landscape (Short et al., 2024). These results illustrate how cheatgrass invasion, rather than fire, can be the primary driver of grass-fire cycles (Bradley et al., 2018; Smith et al., 2023b). In portions of the landscape that are highly invaded by cheatgrass, the abundance of fine fuels increases rates of fire spread and elevates burn probability if ignition sources are present (Fusco et al., 2019). Burn probability was thus highest in the portion of the study area that was predicted to be susceptible to dominance in either burned or unburned conditions, much of which has already converted to cheatgrass dominance in the absence of fire (Smith et al., 2023b).

In the portions of the study area at risk of fire-induced dominance, the occurrence of a fire has the potential to abruptly initiate a grass-fire cycle that would otherwise have been less likely to establish. Our burn probability models were based on static fuelscapes, but it is critical to

recognize that annual grass invasions rapidly change fuels and introduce more interannual variability in fine fuel loading (Smith et al., 2023a). In the current predictions, areas at risk of fire-induced conversion contributed little to overall cheatgrass dominance risk because they generally have lower burn probability (Short et al., 2023). This reflects a feedback loop that maintains an uninvaded state: unburned areas are unlikely to be invaded, and the absence of fine fuels makes them less likely to burn (Bradley et al., 2018). However, a fire that occurs in favorable climatic conditions (Pilliod et al., 2017) or following anthropogenic ignitions (Fusco et al., 2021) has the potential to catalyze conversion to cheatgrass dominance and propel the ecosystem into a new feedback loop characterized by an annual grass-fire cycle (Underwood et al., 2019).

4.3. Identifying drivers of cheatgrass dominance can help prioritize management actions

Understanding the drivers of conversion to cheatgrass dominance, and the conditions in which fire plays a primary role, is a critical step towards implementing targeted management actions that more effectively mitigate the impacts of invasion. Current management strategies for the sagebrush biome rely on identifying relevant risks and how they vary spatially (Chambers et al., 2017; Crist et al., 2019; Remington et al., 2021). As our results show, the likelihood of fire-induced cheatgrass dominance and subsequent initiation of a grass-fire cycle is not uniform across the sagebrush biome. Model predictions of susceptibility to dominance can help land managers anticipate potential spread into new areas and mitigate the impacts of increasing cheatgrass abundance in otherwise intact native plant communities (McMahon et al., 2021). Using spatially explicit predictions of susceptibility to dominance and burn probability, fire management can be prioritized to decrease the likelihood of invasion initiating grass-fire cycles, protect prior restoration investments, and maintain areas with high ecological integrity (Chambers et al., 2023b; Doherty et al., 2022; Pilliod et al., 2021).

Our results suggest that much of the sagebrush biome likely has inherent abiotic resistance to cheatgrass dominance regardless of fire, consistent with recent indices of invasion resistance (Chambers et al., 2023a). Within these areas, broad-scale management focused on mitigating the impacts of cheatgrass dominance is likely unnecessary, and efforts should instead be focused on other threats to sagebrush ecological integrity, such as other invasive plant species and human development (Doherty et al., 2022). Prescribed fire may be a valuable management tool in these areas, as long as other fire-adapted invasive species are not a concern.

Other areas are likely susceptible to cheatgrass dominance regardless of their fire history, and past conversion in these areas has resulted in well-established grass-fire cycles (Bradley et al., 2018; Smith et al., 2023b). Management within these areas can focus on activities that can reduce the strength of the grass-fire feedback loop, such as reducing fine fuel loads with herbicides or targeted grazing (Gornish et al., 2023) or taking advantage of cyclical cheatgrass die-off events to restore native grass species that can compete with cheatgrass (Baughman et al., 2016). Within areas that are susceptible to dominance but currently supporting a native-dominated plant community, management can focus on preventing transmission of fire from nearby areas that have converted to dominance (Shinneman et al., 2023), minimizing disturbances, and reducing opportunities for cheatgrass seed dispersal, such as reducing grazing intensity in especially susceptible areas (Reisner et al., 2013).

Some portions of the landscape are at risk of conversion to cheatgrass dominance as a direct result of fire, and in these areas, fire suppression is critical to prevent the initiation of the grass-fire cycle and eventual ecological transformation via cheatgrass dominance. Areas mapped as at risk of fire-induced cheatgrass dominance are most vulnerable where herbaceous understory species capable of post-fire recovery and competition with cheatgrass are absent (Chambers et al., 2014, 2019). In these places, the ecological consequences of burning are very high, even

if the current burn probability is low, and management efforts aimed at preventing fire are likely to have a meaningful impact on invasion risk. Activities may include reducing anthropogenic ignition sources, wild-land fire suppression, early invasion detection programs, targeted removal of invasive annuals from fire-vulnerable locations, and improved livestock management (Crist et al., 2019; Fusco et al., 2021). Following fires, these susceptible locations may benefit from intensive seeding of native plant species (Havrilla et al., 2020; Ott et al., 2019; Urza et al., 2019). However, plant establishment is often challenging in the warmer and drier portions of the landscape (Shackelford et al., 2021), emphasizing the importance of protecting these landscapes from fire and other disturbances (Chambers et al., 2023b).

Land management strategies must also consider the impacts of climate change, and assessing susceptibility to cheatgrass under anticipated future climate conditions is an important next step. Recent observations of increases in cheatgrass cover as well as expansion into new areas suggest that environmental shifts are already favoring invasive annual grasses, consistent with predictions of climate warming ameliorating the cold-related geographic constraints on population processes (Blumenthal et al., 2016; Boyte et al., 2016; Prev  y et al., 2024; Smith et al., 2022). At the biome scale, projected climate change-related increases in ecological drought (Bradford et al., 2020) are expected to reduce resistance to cheatgrass invasion (Schlaepfer and Bradford, 2024), although some regions may be less impacted (Larson et al., 2017). Changing climate conditions will likely also alter both burn probability (Holdrege et al., 2024; Pilliod et al., 2017) and habitat suitability for native plant species (Renwick et al., 2018), necessitating meaningful adaptive management approaches with sufficient flexibility to respond to changing risks.

CRediT authorship contribution statement

Alexandra K. Urza: Writing – original draft, Methodology, Formal analysis, Conceptualization. **David I. Board:** Writing – review & editing, Visualization, Methodology, Formal analysis, Data curation. **John B. Bradford:** Writing – review & editing, Investigation, Conceptualization. **Jessi L. Brown:** Writing – review & editing, Validation, Methodology, Data curation. **Jeanne C. Chambers:** Writing – review & editing, Project administration, Investigation, Funding acquisition, Conceptualization. **Daniel R. Schlaepfer:** Writing – review & editing, Software, Methodology, Formal analysis, Data curation. **Karen C. Short:** Writing – review & editing, Investigation, Formal analysis, Data curation.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data availability statement

Data and map products associated with this manuscript are available for download: Board, D.I.; Urza, A.K.; Bradford, J.B.; Brown, J.L.; Chambers, J.C.; Schlaepfer, D.R.; Short, K.C. 2024. Maps of abiotic susceptibility vs. fire-induced conversion to cheatgrass dominance in the sagebrush biome and associated data. Fort Collins, CO: Forest Service Research Data Archive. doi:<https://doi.org/10.2737/RDS-2024-0041>.

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use of trade, firm, or product names is for descriptive purposes only and does not imply endorsement by the U.S. Government.

Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.biocon.2024.110737>.

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