RESEARCH ARTICLE

The elevational ascent and spread of exotic annual grass dominance in the Great Basin, USA

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Abstract

Aim: In the western United States, sagebrush (*Artemisia* spp.) and salt desert shrublands are rapidly transitioning to communities dominated by exotic annual grasses, a novel and self-reinforcing state that threatens the economic sustainability and conservation value of rangelands. Climate change is predicted to favour annual grasses, potentially pushing transitions to annual grass dominance into higher elevations and north-facing aspects. We sought to quantify expansion of annual grass-dominated vegetation communities along topographic gradients over the past several decades.

Location: Our analysis focused on rangelands among three ecoregions in the Great Basin of the western United States, where several species of exotic annual grasses are widespread among shrub and perennial grass-dominated vegetation communities.

Methods: We used recently developed remote sensing-based rangeland vegetation data to produce yearly maps of annual grass-dominated vegetation communities spanning 1990–2020. With these maps, we quantified the rate of spread and characterized changes in the topographic distribution (i.e. elevation and aspect) of areas transitioning to annual grass dominance.

Results: We documented more than an eightfold increase in annual grass-dominated area since 1990, occurring at an average rate of >2,300 km^2 year^{-1} (0.6% of the area of Great Basin rangelands). In 2020, annual grasses dominated approximately one-fifth (>77,000 km^2) of Great Basin rangelands. This rapid expansion was associated with a broadening topographic niche, with widespread movement into higher elevations and north-facing aspects consistent with predicted effects of a warming climate.

Main conclusions: More than a century after first appearing in the region, exotic annual grasses continue to proliferate and establish dominance in new environments across the Great Basin. Accelerated, strategic intervention is critically needed to conserve vulnerable sagebrush and salt desert shrub communities not yet heavily invaded. In this era of warming, future climate provides important context for selecting from among alternative management actions and judging long-term prospects of success.

1 | INTRODUCTION

Grasses are highly successful invaders globally with the capacity to dramatically reshape rangelands (D'Antonio & Vitousek, 1992; Godfree et al., 2017). Among diverse ecosystems across several continents, consequences of grass invasions include increased risk to human life and property from larger and/or more frequent wildfires (Fusco et al., 2019), impacts on human health (Johnston et al., 2009), disruption of hydrologic and nutrient cycles (Evans et al., 2001; Germino et al., 2016; Rossiter-Rachor et al., 2009), loss of habitat for sensitive species (Coates et al., 2016) and reduced biodiversity across trophic levels (Davies, 2011; Pyšek et al., 2012). Commonly, disruptions to invaded communities are sufficient to force transitions into alternative stable states characterized by dominance of exotic grasses (e.g. "grass-fire cycles;" D'Antonio & Vitousek, 1992). Despite advancements in our understanding of the mechanisms and outcomes of exotic grass invasions on recipient ecosystems, sporadic monitoring has limited our ability to quantify the scope and pace of such ecosystem transformations at broad spatiotemporal scales (Bromberg et al., 2011; Levick et al., 2015).

In the arid and semi-arid Great Basin of the western United States, exotic annual grasses including cheatgrass (*Bromus tectorum*), red brome (*B. rubens*), medusahead (*Taeniatherum caput-medusae*) and ventenata (*Ventenata dubia*) have, collectively, become nearly ubiquitous (Mack, 1981; Nicolli et al., 2020; Young & Evans, 1970). These grasses colonize interstices between native perennial bunchgrasses and shrubs, increasing the amount and continuity of fine fuels (Davies & Nafus, 2013). Consequently, annual grass-infested vegetation communities burn 2–4 times more frequently than relatively uninvaded communities (Balch et al., 2013; Bradley et al., 2018). Post-fire reestablishment of native vegetation often proves exceedingly challenging due in part to pre-emptive resource use by early-germinating annual grasses (Davies, 2010; Eliason & Allen, 1997; Melgoza et al., 1990). Ultimately, this cycle of invasion, fire and exclusion of native competitors can push recipient communities across a threshold into an undesirable state of dominance by exotic annual grasses (hereafter, annual grass dominance). Similar to exotic grass invasions globally (Godfree et al., 2017), transition to annual grass dominance erodes both the economic and conservation values of Great Basin ecosystems (Knapp, 1996).

Climate change may facilitate annual grass dominance in the Great Basin. For example, warmer temperatures and earlier snowmelt are predicted to favour establishment, growth and reproduction of *B. tectorum* throughout much of the region (Blumenthal et al., 2016; Bradley, 2009; Compagnoni & Adler, 2014b), while loss of severe autumn cold may enable range expansion of *B. rubens* (Bykova & Sage, 2012). Larger and more frequent wildfires resulting from extended fire seasons may accelerate transitions to annual grass dominance (Abatzoglou & Kolden, 2011). Potentially exacerbating

these dynamics, rising atmospheric CO_2 may increase biomass and flammability of *B. tectorum* (Ziska et al., 2005). The net effects of climate change on the distribution of annual grass dominance are uncertain, however, as effects of warming are species-specific (Bradley et al., 2016; Bykova & Sage, 2012), contingent upon soil moisture (Compagnoni & Adler, 2014a; Thill et al., 1979; Zelikova et al., 2013) and moderated by the response of the recipient native vegetation community (Chambers et al., 2007; Compagnoni & Adler, 2014b). Range contractions of certain species are predicted under some climate scenarios (Bradley, 2009), but vacated regions may subsequently be invaded by other exotic annual grasses (Bradley et al., 2016; Bykova & Sage, 2012).

Elevational range shifts are among hypothesized responses of annual grasses to climate change (Bradley et al., 2016; Compagnoni & Adler, 2014a, 2014b). The Great Basin is mountainous, with elevations ranging from <700 m to >3000 m. Historically, physiological constraints have limited the spread of *B. tectorum* at higher elevations and on cooler, north-facing slopes (Chambers et al., 2007, 2014). As temperatures warm, timing of snowmelt advances, and precipitation increasingly falls as rain, higher elevations may become suitable for establishment and growth of *B. tectorum* (Compagnoni & Adler, 2014a; Concilio et al., 2013). Furthermore, warming and increasing summer aridity has increased fire in higher elevations across mountainous ecosystems of the western United States (Alizadeh et al., 2021), a phenomenon which could indirectly assist the spread of annual grasses into higher elevations.

The spatiotemporal dynamics of state transitions to annual grass dominance in the Great Basin remain poorly understood. Remote sensing has been successfully used to map annual grass-dominated communities at ecoregional extents (Boyte & Wylie, 2016; Bradley & Mustard, 2005; Peterson, 2005), but these occasional snapshots in time provide limited insight into the rate or trajectory of transitions along bioclimatic gradients. An understanding of these dynamics is needed to inform management and policy. Using a recently developed remotely sensed vegetation cover product that provides continuous coverage of western US rangelands across space and time (Allred et al., 2020; Jones et al., 2020), we quantify the expansion of annual grass dominance in the Great Basin and test for shifts in distribution along topographic gradients over the past three decades.

2 | METHODS

2.1 | Study area

We characterized expansion of annual grass dominance within three level III ecoregions (Omernik & Griffith, 2014) that overlap the hydrologic Great Basin and share similar climates and potential

FIGURE 1 The Great Basin covers >500,000 km² and encompasses parts of 5 US states. Our analysis included the Central Basin and Range (CBR), Northern Basin and Range (NBR) and Snake River Plain (SRP) ecoregions. The colour ramp shows mean per cent cover of annual forbs and grasses between 2015 and 2020

Mean annual forb and grass cover (%), 2015–2020
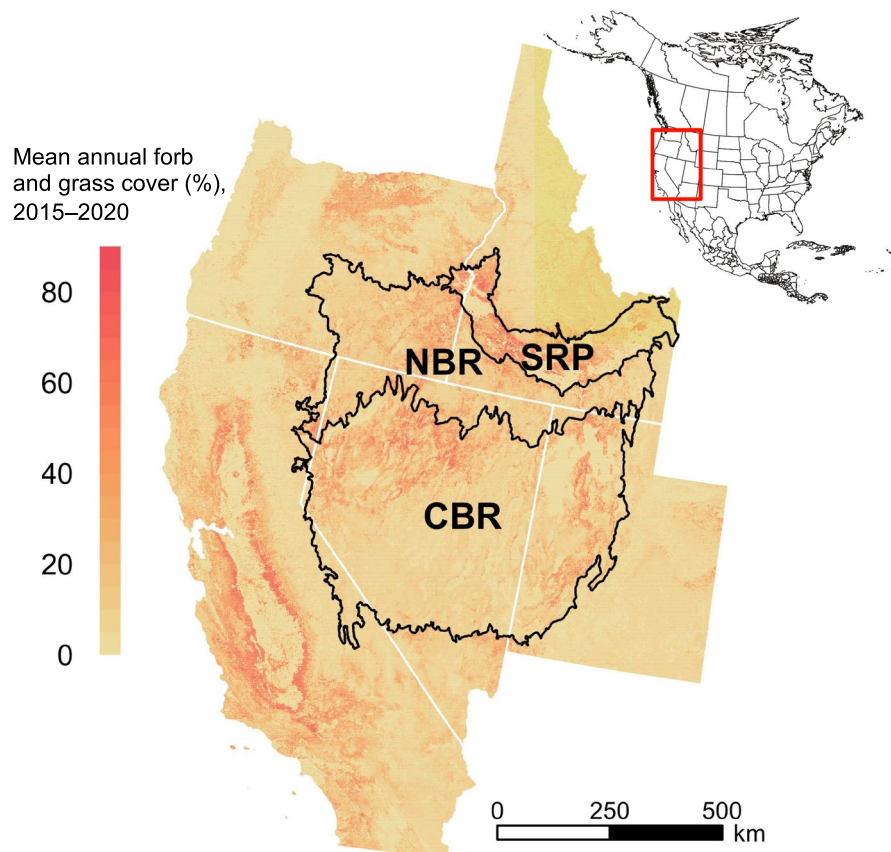
vegetation (Figure 1). These include the Central Basin and Range (CBR), Northern Basin and Range (NBR) and Snake River Plain (SRP). Within these ecoregions, we limited our analyses to rangeland land cover as defined by the USDA Natural Resources Conservation Service's (NRCS) National Resources Inventory (NRI; Nusser & Goebel, 1997) and mapped by Reeves and Mitchell (2011). Briefly, this includes sites >2 ha historically dominated by shrub or herbaceous vegetation suitable for browsing or grazing by domestic or wild herbivores. Sites currently dominated by trees (>20% cover) but otherwise meeting the above definition were considered "afforested rangelands" and were included. For a comprehensive definition and methods used to map rangelands, see Reeves and Mitchell (2011). We also excluded agricultural land cover identified as hay, alfalfa and idle cropland in the USDA National Agricultural Statistics Service Cropland Data Layer (USDA NASS, 2020).

2.2 | Classification of invasive annual grass-dominated communities

We used a remote sensing product, the Rangeland Analysis Platform (RAP; Allred et al., 2021; Jones et al., 2018) to produce high resolution (30 m) maps of annual grass dominance throughout the Great Basin for each year from 1990 to 2020. RAP uses Landsat satellite imagery to estimate areal canopy cover (hereafter cover) of major plant functional groups, specifically, perennial forbs and grasses (PFGC), annual forbs and grasses (AFGC), shrubs (SHR), bare ground

(BG), litter (LTR) and trees (TREE). Although exotic annual grasses are our primary focus and represent a large portion of the annual herbaceous vegetation in the Great Basin, RAP does not distinguish between native or exotic species, or between forbs and grasses. We therefore used field validation plots to explore the composition of areas we identify as annual grass dominated based on RAP AFGC estimates (see Validation, below).

Cover of herbaceous vegetation in arid environments changes rapidly both within and between years, potentially confounding efforts to quantify trends and identify state transitions (Bradley & Mustard, 2005). To focus our analysis on long-term changes in vegetation state, we first applied a smoothing algorithm to the time series of cover estimates for each pixel. Exponential smoothing methods involve the application of a weighted moving average over a time series, with weights decaying exponentially into the past. We used Holt's linear exponential smoothing method (Holt, 2004), which employs smoothing equations for the level and trend components of the time series. The parameters α and β, which can range from 0 to 1, determine the decay rate of weights for the level and trend, respectively, with values closer to 1 giving greater weight to more recent observations (i.e. less smoothing). We selected smoothing parameters by applying them to 1000 randomly selected pixels from within the study area and selecting the parameters that minimized mean absolute error between one-step ahead annual forb and grass cover estimates produced by the smoothing function and raw cover values. This dampened sharp year-to-year fluctuations while still revealing longer-term trends

and abrupt shifts following disturbances such as wildfires (Figure S1.1).

Although vegetation may fall anywhere along a continuum from uninvaded to complete annual grass dominance, we sought to identify highly invaded communities where herbaceous vegetation is predominantly composed of exotic annual grasses and cover of woody vegetation is absent or diminished. This severely invaded condition is thought to represent a stable state from which a return back to a perennial-dominated understory with a well-developed shrub overstory is unlikely without intensive management (Bagchi et al., 2013; Davies et al., 2012). We took a data-driven approach to identifying which pixels fell into this annual grass-dominated state, using unsupervised clustering following the analytical framework outlined by Bagchi et al. (2013), Bagchi et al. (2012). Specifically, we used k-means++ clustering (Arthur & Vassilvitskii, 2007) to group pixels into a finite number of clusters representing discrete vegetation "states," and selected the number of clusters (k) using the silhouette method (Rousseeuw, 1987).

A strength of unsupervised clustering, as opposed to imposing analyst-defined thresholds on the data (e.g. AFGC > PFGC, or AFGC > 50% of total vegetation cover), is that it reduces the influence of arbitrary rules which can lead to unexpected or nonsensical class assignments. The k-means algorithm divides observations (pixels) into k clusters in a way that minimizes the residual sum of squares (MacQueen, 1967). Each new pixel is assigned to the cluster centroid to which it is most similar (i.e. nearest in Euclidean distance). The analyst must only choose the relevant variables and specify the number of clusters, k. The silhouette method is an automated method of selecting a value of k that seeks to maximize consistency within, and isolation among, clusters. Briefly, a "silhouette" is calculated for each observation, which expresses its similarity to other observations within its assigned cluster, relative to its similarity to observations in its nearest neighbouring cluster (see Rousseeuw, 1987 for details). The value of k that maximizes the mean silhouette width across all observations is selected as the optimal solution.

We then examined the characteristics of the resulting clusters to identify the cluster most closely associated with annual grass dominance. Selection of k and characterization of clusters were performed in R (v4.0.5; R Core Team, 2021) on 10,000 pixels sampled randomly in time and space from the raw RAP cover time series. Once we selected k, training and clustering of the smoothed RAP cover time series and all other raster processing steps were completed in Google Earth Engine (GEE; Gorelick et al., 2017) via the GEE code editor. We clustered the RAP cover time series beginning in 1990, such that cover estimates from 1984 to 1989 served to initialize smoothing.

2.3 | Validation

We validated our annual grass dominance mapping procedure by comparing the remote sensing-derived vegetation cluster dataset to an independent (i.e. not used in the training of RAP models) set of 1,486 field-measured monitoring plots from the US Bureau of Land Management's Assessment, Inventory and Monitoring programme (AIM; Taylor et al., 2014) and the NRI (USDA NRCS, 2015). These plots were measured between 2004 and 2019, with the majority of plots (92%) sampled after 2010. The AIM and NRI line-point intercept data were first converted to cover by species using the first hit pin drop data and then aggregated to functional groups (annual forbs and grasses, perennial forbs and grasses, and shrubs) based on definitions in the USDA NRCS PLANTS database (USDA NRCS, 2018). Bare ground and litter calculations were retained from the first hit pin drop calculations. We applied the same trained clusterer used on the smoothed RAP cover time series to the field data to determine the cluster identity of each of the field plots. From these cluster labels, we assigned each plot a binary class label distinguishing annual grass dominance from other clusters. The resulting field plot-based classes (hereafter field class) were then compared with the smoothed RAP imagery-based classes (hereafter RAP class) from the year corresponding to the sampling date. Agreement between field classes and RAP classes was assessed with statistics based on the resulting confusion matrix, including kappa, sensitivity/specificity and positive/negative predictive value. To assess the extent to which the focal cluster represented exotic annual grasses as opposed to annual forbs or native annual grasses, we calculated cover of exotic and native forbs and grasses from the field data and report the proportion of plots assigned to the annual grass dominance cluster where exotic annual grasses were present (cover >0%) and abundant (cover >10%).

Temporal shifts in the errors of RAP-estimated cover values, especially in the annual forb and grass functional group, could confound our ability to quantify spread of annual grass-dominated rangelands. Additionally, differential shifts between high and low elevations could introduce bias into our estimates of the rates of elevational movement of transitions. We therefore tested for the presence of such shifts using the same set of validation plots and used the results to conduct a sensitivity analysis of our main findings. Details of this sensitivity analysis are provided in Appendix S2. Because the estimated bias was small (Figure S2.1), effects on parameter estimates were too minor to qualitatively alter our inference (Figure S2.2,S2.3), and the detrending procedure itself relied on highly uncertain extrapolation of trends in errors, we used the original RAP AFGC data for inference.

2.4 | Characterizing trends

We summed the area of pixels in the annual grass-dominated cluster in each year to derive yearly estimates of the areal extent of annual grass dominance within each ecoregion. To quantify trends in extent of annual grass dominance, we used the non-parametric Theil–Sen estimator (Sen, 1968; Theil, 1950). Estimates and 95% confidence intervals of the Theil–Sen estimator were calculated using the `sens.slope` function in the "trend" package (Pohlert, 2020) in R.

We examined trends in elevation to test whether the topographic distribution of pixels transitioning to annual grasslands changed over the duration of the time series. For pixels classified as annual grassland in ≥1 year, we determined the earliest year in the time series that the pixel was assigned to the annual grassland cluster (transition year). Omitting pixels already classified as annual grasslands at the beginning of the time series (1990), we randomly sampled $n = 1000$ pixels from each transition year in each ecoregion (for a total of 30,000 transitioned pixels per ecoregion) and determined their elevation and aspect from the USGS National Elevation Dataset (NED) ⅓ arc-second digital elevation model. We used the cosine of aspect (in radians, θ) as an index, ranging from −1 to 1, differentiating north-facing slopes (cos(θ) >0) from south-facing slopes (cos(θ) <0). Hereafter, we refer to cos(θ) as "northness." To characterize trends in elevation, we used quantile regression to estimate temporal trends in the 10th ($\tau = 0.1$), 50th ($\tau = 0.5$) and 90th percentiles ($\tau = 0.9$) of elevations. Quantile regression gave us the flexibility to characterize dynamics of the leading and trailing edges of the distribution in addition to the central tendency. This could, for example, allow us to detect a broadening or narrowing elevational distribution through time. We used AIC to select from among several *a priori* models of the relationship between elevation, northness, year and ecoregion, including two- and three-way interactions, which were biologically plausible given the wide range of abiotic conditions represented by the three ecoregions under study. Candidate models and AIC are provided in Table S1.1. We estimated regression coefficients with the "quantreg" package (v 5.67; Koenker et al., 2020) in R, and computed standard errors and confidence intervals from 1,000 bootstrap samples.

Because northness is bounded between −1 and 1, and regression methods are poorly suited to bounded response variables, we took a visual approach to characterizing changes in aspects of transitioning pixels. Masking out slopes <5°, we produced empirical cumulative distribution functions (ECDF) of the aspects of all pixels transitioning to annual grass dominance during each decade spanned by the time series (i.e. 1991–2000, 2001–2010 and 2011–2020) in each ecoregion. We then superimpose these decadal ECDFs to display shifts in aspects of transitioning pixels.

2.5 | Climate trends

To place into context the observed patterns of expansion of annual grass-dominated vegetation, we examined climatic trends among ecoregions of the Great Basin. Responses to abiotic gradients vary among invasive annual grasses in the Great Basin (Brooks et al., 2016; Bykova & Sage, 2012; McMahon et al., 2021), but changes in a few key climate variables are likely to facilitate range expansions and/or shifts into higher elevations among several species. In particular, minimum temperature, climatic water deficit (the difference between potential and actual evapotranspiration) and summer precipitation strongly influence the distributions of *B. tectorum*, *B. rubens* and (with the exception of summer precipitation) *T. caput-medusae* (Bradley,

2009; Jarnevich et al., 2021; McMahon et al., 2021). Warming effects on *B. tectorum* at high elevation are contingent on adequate soil moisture during the growing season (Compagnoni & Adler, 2014a). We therefore derived annual minimum temperature (median temperature of the coldest month), cumulative annual climatic water deficit (sum of monthly differences between potential and actual evapotranspiration), summer (June–September) precipitation and growing season (October–June) precipitation from the monthly TerraClimate dataset (Abatzoglou et al., 2018), calculating the annual value at each pixel (~4 km resolution) and then aggregating (mean) to the ecoregional level. We calculated annual anomalies by subtracting the mean for the base period 1958–2000. We present plots of these time series of anomalies by ecoregion, highlighting trends with generalized additive models employing thin plate regression splines (using the "mgcv" package in R; Wood, 2003, 2011).

3 | RESULTS

3.1 | Classification

Using smoothing parameters $\alpha = 0.25$ and $\beta = 0.01$ for Holt's smoothing method minimized MAE across the 1,000 tested AFGC time series (see Figure S1.1 for examples of smoothing). Average MAE (i.e. the average absolute difference between the smoothed value and raw RAP estimate for a pixel-year) was 4.7%.

Using *k*-means++ clustering and the silhouette method, we identified $k = 4$ as the optimal number of clusters in the data (Figure S1.2). Cluster 0 was characterized by high annual forb and grass cover (median AFGC = 29%), annual dominance (median ratio AFGC:PFGC = 1.57:1) and low shrub cover (median SHR = 9%); therefore, this cluster was selected to represent annual grass dominance (Figure 2, Table 1). The other 3 clusters identified areas mostly devoid of vegetation (cluster 3), areas composed predominantly of bare ground and shrubs (cluster 2) and areas characterized by varying degrees of co-dominance of shrubs and perennial grasses and forbs (cluster 1; Table 1). Although clusters occupied distinct regions of the multivariate space, boundaries between clusters were more-or-less continuous (Figure 2). Pixels assigned to cluster 1 often displayed substantial cover of annual forbs and grasses (median = 7%), but they consistently comprised the minor component of herbaceous vegetation cover (median ratio AFGC:PFGC = 0.2:1, 95th percentile = 0.76:1). Annual GeoTIFFs of the clustered RAP data from 1990 to 2020 are available online at: http://rangeland.ntsg.umt.edu/data/rap/rap-derivatives/great-basin-classes/.

3.2 | Validation

Functional group composition of validation field plots is shown in Figure S1.3. Using RAP class as the prediction and field class as the reference, accuracy (per cent correctly classified) was 0.88, and kappa was 0.66. Sensitivity, or the fraction of positive (i.e. annual
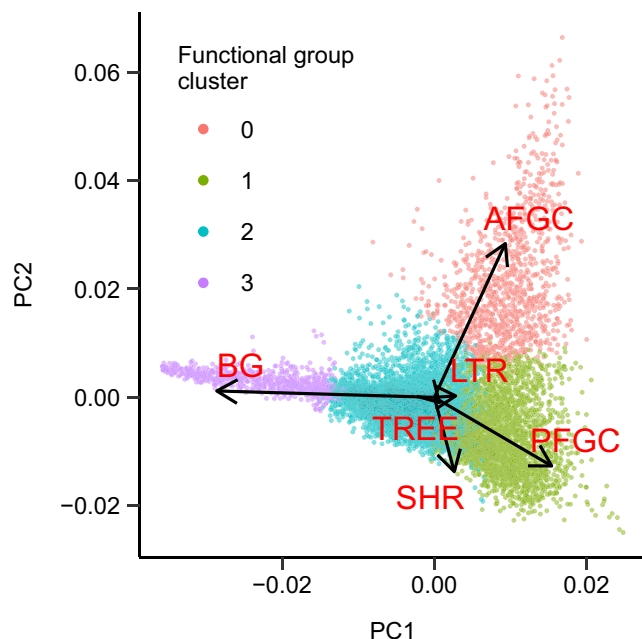
FIGURE 2 Composition of $k = 4$ functional group cover clusters along the first two principal components (PC), which explained 77% of the total variance. Vectors indicate loadings of all function group cover components (AFGC = annual forb and grass cover; BG = bare ground; LTR = litter; PFGC = perennial forb and grass cover; SHR = shrub cover; TREE = tree cover)

grass dominance) reference cases correctly predicted to belong to the annual grass dominance cluster, was 0.64. Specificity, or the fraction of negative (not annual grass dominance) reference cases correctly assigned to non-annual grass dominance clusters, was 0.97. Positive predictive value, or the fraction of predicted positive cases that were actually annual grass-dominated, was 0.88, and negative predictive value was 0.88. The substantially lower sensitivity relative to specificity suggests the true extent of annual grass dominance at any point in time is underestimated by our methods.

The relatively low sensitivity was partly a consequence of smoothing prior to clustering. The smoothed value in a given year is a weighted function of that year's estimate and past years' estimates, with the weight decaying into the past. When cover of a functional group trends quickly in either direction, the smoothed value will lag behind in reflecting that change (Figure S1.1). Because the extent of annual grass dominance is generally increasing and sometimes increases rapidly following disturbance, smoothed annual forb and grass cover values will tend to underestimate current cover and the transition of pixels into the annual grass dominance cluster will lag behind the true transition on the ground by a short period.

To confirm this, we compared the field classes to RAP classes 1 year after field measurements were made. As expected, agreement between RAP and field class assignments improved: kappa increased to 0.69 and sensitivity increased to 0.68, with little change in specificity (0.96). Still, a false-negative rate of >0.3 indicates a systematic underestimation of the extent of annual forb and grass-dominated vegetation communities.

TABLE 1 Composition (per cent cover) of Great Basin rangeland vegetation functional group clusters identified via k-means partitioning. Percentiles were calculated independently for each functional group among $n = 10,000$ randomly selected pixels

| Cluster ID	Functional group	Percentile				
		5	25	50	75	95
0[a]	AFGC	12	21	29	38	57
	BG	3	7	11	16	27
	LTR	8	12	15	18	26
	PFGC	4	11	18	27	40
	SHR	3	6	9	15	23
	TREE	0	0	0	1	3
1	AFGC	0	3	7	12	22
	BG	2	5	9	14	24
	LTR	4	9	12	15	19
	PFGC	17	25	32	44	73
	SHR	2	11	18	26	40
	TREE	0	0	1	2	16
2	AFGC	0	3	5	10	21
	BG	7	15	23	31	41
	LTR	7	11	13	15	18
	PFGC	1	4	8	12	19
	SHR	6	13	18	24	32
	TREE	0	0	0	4	38
3	AFGC	0	0	1	2	5
	BG	46	57	74	87	100
	LTR	0	0	4	6	11
	PFGC	0	2	4	6	16
	SHR	0	0	5	9	14
	TREE	0	0	0	0	1

Abbreviations: AFGC, annual forb and grass cover; BG, bare ground; LTR, litter; PFGC, perennial forb and grass cover; SHR, shrub cover; TREE, tree cover.

[a]Cluster selected to represent annual grasslands.

Among validation plots, RAP annual forb and grass cover estimates were strongly correlated ($\rho = 0.79$) with first hit (upper canopy) cover of exotic annual grasses measured in the field. Annual forb and grass cover of validation plots assigned to Cluster 0 based on RAP data was predominantly composed of exotic annual grasses (Figure S1.4). Exotic annual grasses were present (>0% first hit cover) in 90% of plots and exceeded 10% first hit cover in 80% of plots assigned to Cluster 0.

3.3 | Annual grass trends

The area of annual grass dominance in the Great Basin increased >8-fold during the study period, from 8964 km^2 in 1990 to 77,617 km^2 in 2020 (Figure 3). Aggregated across the Great Basin, this represents an estimated annual rate of increase of
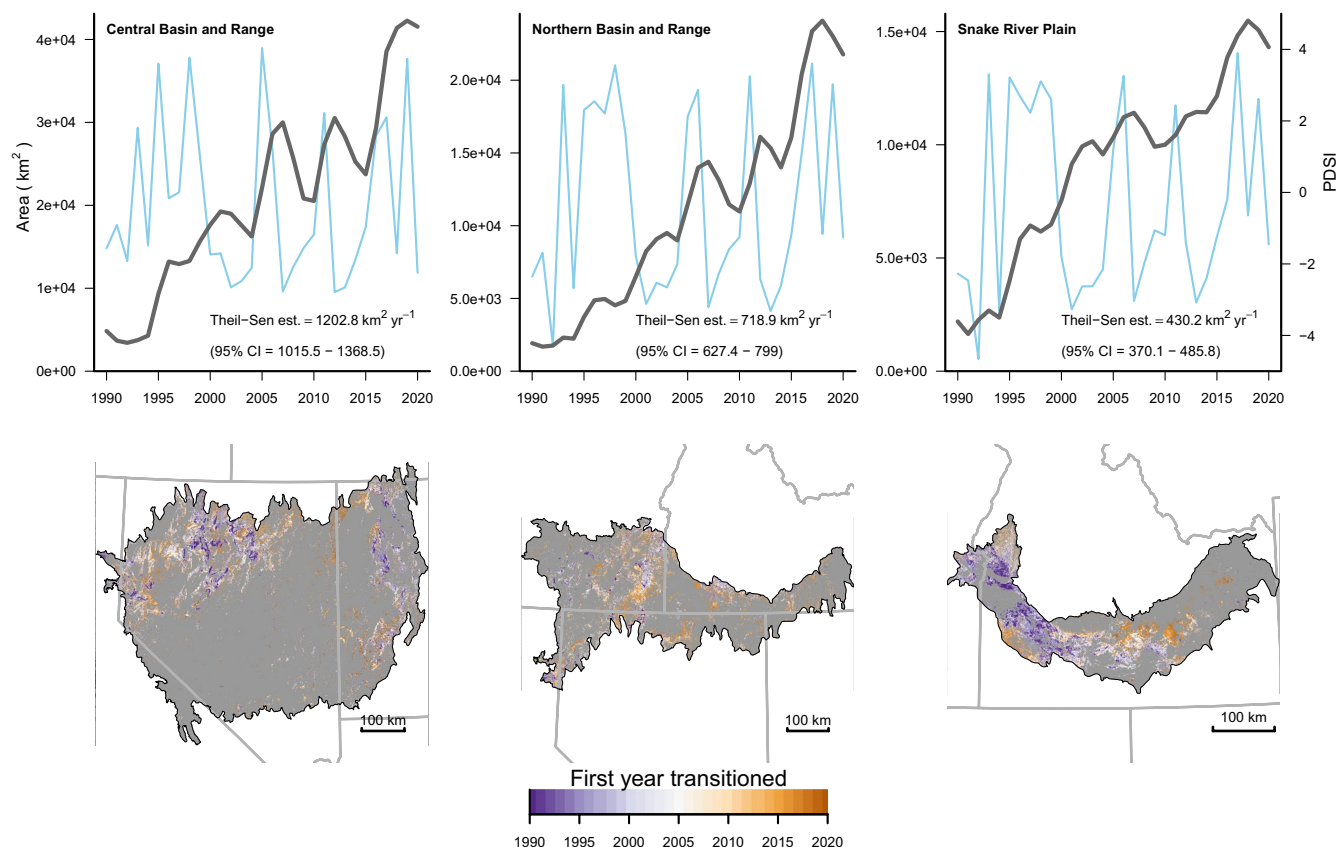
FIGURE 3 Estimated area of exotic annual grass-dominated vegetation communities in the Central Basin and Range, Northern Basin and Range and Snake River plain from 1990 to 2020 (dark grey line; top row). The June Palmer Drought Severity Index (PDSI; blue line) over the same period is shown for reference (source: Abatzoglou, 2013). Drought (PDSI ≪ 0) consistently preceded temporary ebbs in area of annual grass dominance. The Theil-Sen estimate characterizes growth in area from 1990 to 2020. Maps (bottom row) show the spatial distribution of pixels characterized by annual grass dominance at least once in the time series, with colours indicating the first year transitioned. The darkest purple indicates transition in or prior to 1990, the first year in the time series

2373 km^2 year^{-1} (95% CI = 2055–2638 km^2 year^{-1}) or a geometric mean proportional increase of 7.5%. At the ecoregional scale, estimated annual rates of increase ranged from 430.2 km^2 year^{-1} (95% CI = 370.1–485.8 km^2 year^{-1}) in SRP to 1202.8 km^2 year^{-1} (95% CI = 1015.5–1368.5 km^2 year^{-1}) in CBR (Figure 3). Geometric mean proportional rates of increase were 7.4% in CBR, 8.4% in NBR and 6.4% in SRP. In 2020, the annual grass dominance cluster occupied 17% (41,537 km^2) of rangelands in CBR, 18% (21,771 km^2) of rangelands in NBR and 43% (14,309 km^2) of rangelands in SRP, or 19.8% of rangelands across ecoregions.

Elevations of transitions to annual grass dominance increased through time (Table 2; Figure 4), though the rate of increase differed by ecoregion and aspect. For all quantiles, the three-way year × northness × ecoregion interaction model received unequivocal support based on AIC (Table S1.1). Elevations of transitions were highest in the most southerly ecoregion (CBR) and decreased through the most northerly ecoregion (SRP). On east- and west-facing aspects (i.e. northness = 0), the median elevation of transitions (τ = 0.5) increased 4.6 m year^{-1} (95% CI = 4.2–4.9 m year^{-1}) in CBR,

6.9 m year^{-1} (95% CI = 6.5–7.2 m year^{-1}) in NBR and 15.3 m year^{-1} (95% CI = 15.0–15.7 m year^{-1}) in SRP.

Empirical CDFs revealed shifts towards more north-facing aspects through time across all three ecoregions, with the greatest shifts in CBR and NBR occurring during the last decade (Figure 5). While most transitions still occur on north-facing aspects in CBR and NBR, transitions were roughly uniformly distributed across aspects in the most recent decade in SRP.

3.4 | Climate trends

Ecoregional-scale changes in climate variables relevant to the distributions of several key species of exotic annual grasses in the Great Basin from 1958 to 2020 are shown in Figure S1.5. Across ecoregions, generalized additive models indicate climatic water deficit and annual minimum temperature have increased, especially in the past 3 decades, while summer precipitation has steadily declined and growing season precipitation has changed little over the past 60 years.

TABLE 2 Coefficient estimates of quantile regression models describing relationships between elevation, aspect and year of transition to invasive annual grass dominance among three Great Basin ecoregions, 1990–2020. Continuous variables were standardized by subtracting the mean and dividing by two standard deviations

| τ	Coefficient	Estimate	SE	t	p(>|t|)
0.1	Intercept	−0.11	0.00	−58.25	<0.001
	Ecoregion: NBR[a]	−0.24	0.00	−60.94	<0.001
	Ecoregion: SRP	−0.78	0.00	−281.46	<0.001
	Aspect	−0.13	0.00	−39.25	<0.001
	Year	0.02	0.00	5.68	<0.001
	Ecoregion: NBR × aspect	0.07	0.01	8.62	<0.001
	Ecoregion: SRP × aspect	0.13	0.01	25.11	<0.001
	Ecoregion: NBR × year	0.18	0.01	19.86	<0.001
	Ecoregion: SRP × year	0.14	0.01	27.13	<0.001
	Aspect × year	−0.03	0.01	−4.19	<0.001
	Ecoregion: NBR × aspect × year	−0.07	0.02	−4.14	<0.001
	Ecoregion: SRP × aspect × year	−0.02	0.01	−1.70	0.09
0.5	Intercept	0.28	0.00	112.85	<0.001
	Ecoregion: NBR	−0.20	0.00	−62.21	<0.001
	Ecoregion: SRP	−0.72	0.00	−172.02	<0.001
	Aspect	−0.25	0.01	−49.27	<0.001
	Year	0.12	0.00	28.05	<0.001
	Ecoregion: NBR × aspect	0.03	0.01	4.96	<0.001
	Ecoregion: SRP × aspect	0.21	0.01	26.12	<0.001
	Ecoregion: NBR × year	0.06	0.01	9.46	<0.001
	Ecoregion: SRP × year	0.3	0.01	44.76	<0.001
	Aspect × year	−0.08	0.01	−8.23	<0.001
	Ecoregion: NBR × aspect × year	−0.04	0.01	−2.80	0.005
	Ecoregion: SRP × aspect × year	0.03	0.01	2.31	0.021
0.9	Intercept	0.77	0.00	204.81	<0.001
	Ecoregion: NBR	−0.19	0.01	−36.96	<0.001
	Ecoregion: SRP	−0.72	0.00	−167.52	<0.001
	Aspect	−0.39	0.01	−49.82	<0.001
	Year	0.19	0.01	25.12	<0.001
	Ecoregion: NBR × aspect	0.06	0.01	5.24	<0.001
	Ecoregion: SRP × aspect	0.37	0.01	41.74	<0.001
	Ecoregion: NBR × year	0.05	0.01	4.33	<0.001
	Ecoregion: SRP × year	0.05	0.01	6.07	<0.001
	Aspect × year	−0.02	0.02	−1.36	0.174
	Ecoregion: NBR × aspect × year	−0.04	0.02	−1.67	0.095
	Ecoregion: SRP × aspect × year	−0.02	0.02	−1.19	0.235

[a]Ecoregions are abbreviated: Northern Basin and Range = NBR, Snake River Plain = SRP; Central Basin and Range (CBR) was used as the reference level.

4 | DISCUSSION

Annual grass dominance has expanded with alarming speed in recent decades, increasing approximately eightfold in area since 1990 in rangelands of the Great Basin. We estimate annual grass dominance now characterizes one-fifth (19.8%, >77,000 km^2) of Great Basin rangelands and has expanded by >2,300 km^2 annually,

a rate proportionally greater than recent deforestation of the Amazon[1]. The most rapid expansion occurred in the last decade (2011–2020), averaging >3700 km^2 annually across the Great

[1]Brazil's Instituto Nacional de Pesquisas Espaciais (INPE) PRODES program annual deforestation estimates for the Brazillian Legal Amazon averaged 10,129 km^2 from 2004 to 2019, or 0.2% of the 5 million km^2 region. 2,373 km^2 represents 0.6% of the total area of rangelands in our study area.
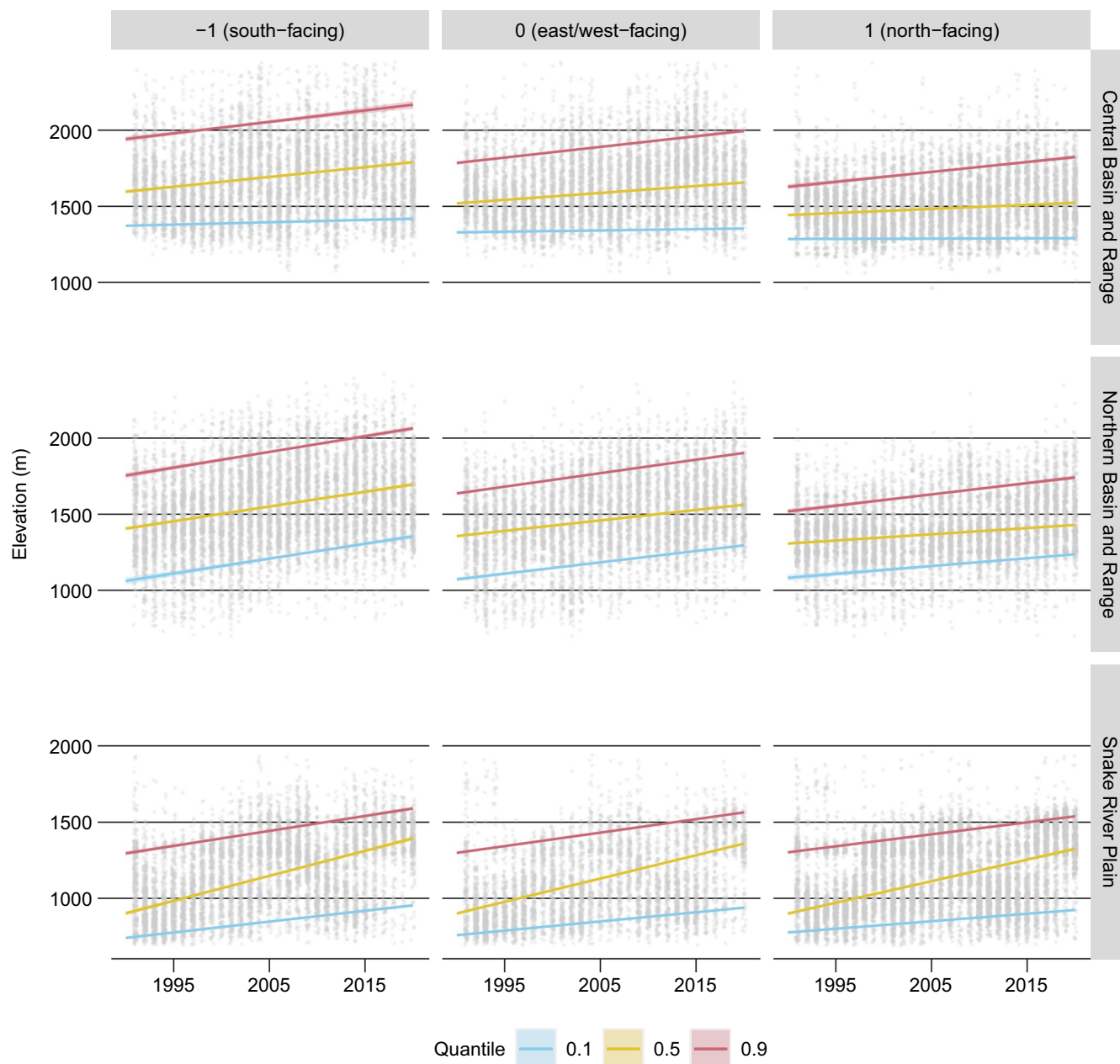
FIGURE 4 Trends in elevation of transitions to exotic annual grass dominance in the Central Basin and Range (top row), Northern Basin and Range (middle row) and Snake River Plain (bottom row) from 1990 to 2020. Trends in the 0.1, 0.5 and 0.9 quantiles (colours) are shown for south-facing (northness = −1; left column), east or west-facing aspects (northness = 0; middle column) and north-facing aspects (northness = 1; right column). Points indicate elevations of n = 1000 transitions sampled from each year and ecoregion, with a small amount of noise added to the x-axis to aid visibility. Elevational trends in all quantiles were best explained by a three-way interaction between year, aspect and ecoregion

Basin. Consistent with predictions based on warming trends, movement into higher elevations has allowed expansion to continue more-or-less unabated (Figure 3). This steady ascent of annual grasses now threatens higher elevation rangelands formerly thought to be minimally vulnerable to transition (Chambers et al., 2007; Johnson et al., 2019).

Our estimates of the extent of annual grass dominance were broadly consistent with previous studies, though differences among study areas make direct comparisons imprecise. For example, Pellant

and Hall (1994) estimated 10,027 km^2 (2,477,837 ac) of Bureau of Land Management rangelands across Idaho, Oregon, Utah, and Nevada was dominated by either *B. tectorum*, *T. caput-medusae* or a combination of the two species, in the early 1990s (Table 2). Our estimate identifies 8964 km^2 of annual grass dominance across Great Basin rangelands in all land ownerships in 1990. Bradley and Mustard (2005) estimated 20,000 km^2 was dominated by *B. tectorum* across the hydrologic Great Basin, a region roughly corresponding to the Central and Northern Basin and Range ecoregions, using
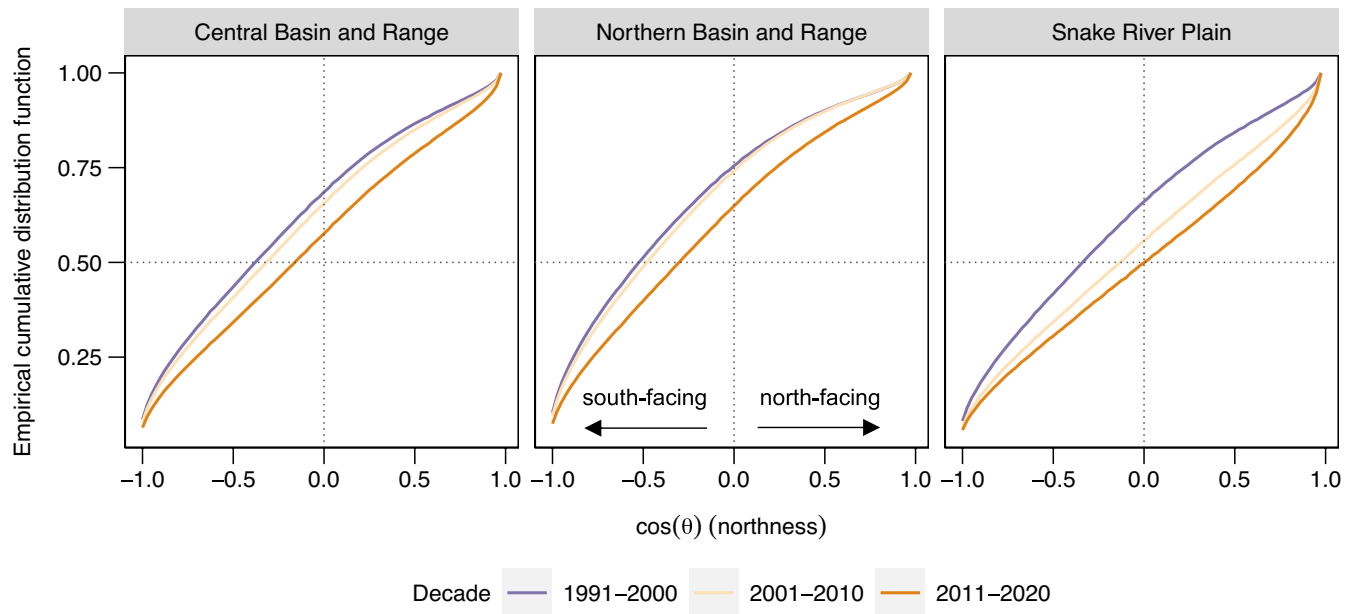
FIGURE 5 Distributional change in aspect of transitions to exotic annual grass dominance among three level III ecoregions of the Great Basin. Values of cos(θ) near −1 represent south-facing aspects, values near zero represent east- or west-facing aspects, and values near 1 represent north-facing aspects. Shifts towards more north-facing aspects in recent decades are evident across ecoregions
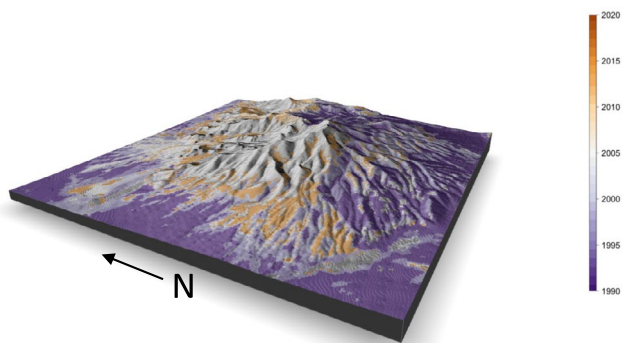
FIGURE 6 Example of elevational movement of transitions to annual grass dominance south of Interstate 80 in Humboldt and Pershing Counties, Nevada, USA. The depicted area is approximately 5 km from east to west, and elevations range from 1424 to 2029 m. Annual grass-dominated vegetation is shown by the purple-to-orange colour ramp depicting the year of transition, and other land cover is shown in grey. Recent transitions on north-, east- and west-facing aspects have occurred at elevations up to approximately 1800 m. Earlier upslope movement is evident on south-facing aspects. Large (>400 ha) wildfires burned the south-eastern portion of the map in 1985, 1996 and 2006. Most transitions to annual dominance within the last decade, however, have occurred in areas unaffected by fire since at least 1984. (Topographic relief is slightly exaggerated to aid visualization.)

a time series of Landsat imagery through 2001. Our method places the extent of annual grass dominance among rangeland land cover in those two ecoregions at 27,500 km² in 2001.

Elevational ascent of annual grass dominance has long been presumed (e.g. Concilio & Loik, 2013; Davies et al., 2011), but our analysis is the first to empirically confirm this widespread phenomenon by capitalizing on advanced remote sensing products. Across the Great

Basin, the median elevation of transitions to annual grass dominance has increased by 138–459 m (453–1,506 ft) over the last 30 years (Figures 4 and 6). Ascent was faster on hot and dry south-facing aspects historically most susceptible to invasion (Figure 4), but transitions have increasingly affected cooler north-facing aspects across elevations (Figure 5).

Our analysis does not explicitly attribute these topographic shifts to a particular driver, but the patterns we observed are consistent with expected effects of warming based on considerable experimental research (Blumenthal et al., 2016; Compagnoni & Adler, 2014a, 2014b; Concilio et al., 2013; Zelikova et al., 2013). Upslope movement could also result from invasion proceeding outward from early-invaded areas, assuming initial invasion occurred at lower elevations. However, given that the earliest and most successful among the annual grass invaders, *B. tectorum*, achieved widespread distribution throughout the Great Basin by 1928 (Mack, 1981), and the rapid potential population growth rates of it and other annual grasses, it is doubtful that the upslope increase in dominance we observed is due only to a delayed legacy of initial introductions. Moreover, the interaction between aspect and elevation strongly suggests that environmental factors are at play: for instance, transitions to annual dominance on north-facing slopes lags behind those on south-facing slopes by more than a decade across ecoregions (Figure 4). Regardless of the mechanism(s), our findings suggest frequently invoked generalities about how susceptibility of rangelands to annual invasion changes across elevation gradients may not hold in the future (e.g. Chambers et al., 2007; Johnson et al., 2019).

The explosive expansion of annual grass dominance was unambiguous despite short-term fluctuations corresponding with periodic spring droughts (Figure 3). Consistent with the high interannual

variability in cover of annuals previously described (Bradley & Mustard, 2005), short-term minima in extent observed in 1992, 2004, 2010 and 2015 predictably followed prolonged droughts. Each retreat, however, was followed by an even higher maximum with the return of wet winters. These short-term ebbs are probably most accurately understood as temporary expressions of low biomass and cover of adult plants, rather than transitions back to less-invaded states. Although droughts may temporarily inhibit their growth and reproduction, exotic annual grasses in the Great Basin have clearly benefited from the climate trajectory of the last 3 decades. Across the region, winters have warmed steadily with little change in precipitation, while summers have become drier and climatic water deficit has increased (Figure S1.5). In combination with periodic wet winters, warming is expected to benefit species such as *B. tectorum* (Compagnoni & Adler, 2014a), especially at higher elevations where temperature is limiting (Chambers et al., 2007), and these predictions are borne out at broad scales.

Among the most threatened biomes of North America (Knick et al., 2003), sagebrush and salt desert shrublands are impacted by a daunting mix of complex ecosystem problems (Boyd et al., 2014). Exotic annual grasses have long played a central role in degradation of these ecosystems. Ongoing transformation of shrublands to exotic annual grasslands, promoted by a warming climate and reinforced by positive feedbacks with wildfire (Bradley et al., 2018; Fusco et al., 2019), comes with dire socio-ecological consequences. For example, vegetation type conversion from native sagebrush shrubland to *B. tectorum*-dominated grassland entails significant loss of biomass carbon (Nagy et al., 2020). Sagebrush and other shrubs lost in transitions are keystones supporting much of the region's wildlife (Coates et al., 2016). Larger and more frequent wildfires directly threaten not only ecosystems but also human health (Reisen et al., 2015; Wettstein et al., 2018) and rural economies (Brunson & Tanaka, 2011).

The pace and scale of transitions supports the need for increased investment and strategic approaches to managing invasive annual grasses in the region (USDA NRCS, 2020; Western Governors' Association, 2020). Our findings suggest vulnerability to transition to annual grass dominance may be strongly controlled by broad-scale climatic drivers (also see Bradford & Lauenroth, 2006; Brummer et al., 2016), highlighting the importance of this context—current and future—when considering alternative management actions. We recommend land managers prioritize efforts to proactively prevent less-invaded rangelands from transitioning over reactive restoration of large-scale annual grasslands to their historical native plant communities, which is costly and ineffective (Davies et al., 2011; Pilliod et al., 2017). Such proactive management requires reducing exposure to annual grass seed sources (Sebastian et al., 2017), increasing resistance to invasion by promoting perennial plants (Chambers et al., 2014), strategic implementation of appropriate fuel treatments in fire-prone areas (Pilliod et al., 2021) and building adaptive capacity of local communities to respond early to the problem (Maestas et al., In Review). We acknowledge, however, that managers have few tools at their disposal and commonly lack sufficient resources to implement those tools at scales commensurate with the problem. Without increased investment and a paradigm shift in management mindset, the archetypal shrubland ecosystems of the Great Basin could be largely transformed into highly flammable, depauperate annual-dominated grasslands and woodlands within a lifetime.

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REFERENCES

Abatzoglou, J. T. (2013). Development of gridded surface meteorological data for ecological applications and modelling. *International Journal of Climatology*, *33*(1), 121–131. https://doi.org/10.1002/joc.3413

Abatzoglou, J. T., Dobrowski, S. Z., Parks, S. A., & Hegewisch, K. C. (2018). TerraClimate, a high-resolution global dataset of monthly climate and climatic water balance from 1958–2015. *Scientific Data*, *5*, 170191. https://doi.org/10.1038/sdata.2017.191

Abatzoglou, J. T., & Kolden, C. A. (2011). Climate change in western US deserts: Potential for increased wildfire and invasive annual grasses. *Rangeland Ecology & Management*, *64*(5), 471–478. https://doi.org/10.2111/REM-D-09-00151.1

Alizadeh, M. R., Abatzoglou, J. T., Luce, C. H., Adamowski, J. F., Farid, A., & Sadegh, M. (2021). Warming enabled upslope advance in western US forest fires. *Proceedings of the National Academy of Sciences*, *118*(22), e2009717118.

Allred, B. W., Bestelmeyer, B. T., Boyd, C. S., Brown, C., Davies, K. W., Duniway, M. C., Ellsworth, L. M., Erickson, T. A., Fuhlendorf, S. D., Griffiths, T. V., Jansen, V., Jones, M. O., Karl, J., Knight, A., Maestas, J. D., Maynard, J. J., McCord, S. E., Naugle, D. E., Starns, H. D. … Uden, D. R. (2021). Improving Landsat predictions of rangeland fractional cover with multitask learning and uncertainty. *Methods in Ecology and Evolution*, *12*(5), 841–849.

Arthur, D., & Vassilvitskii, S. (2007). k-means++: The advantages of careful seeding. SODA '07: Proceedings of the Eighteenth Annual ACM-SIAM Symposium on Discrete Algorithms, 1027–1035.

Bagchi, S., Briske, D. D., Bestelmeyer, B. T., & Wu, X. B. (2013). Assessing resilience and state-transition models with historical records of cheatgrass *Bromus tectorum* invasion in North American sagebrush-steppe. *Journal of Applied Ecology*, *50*, 1131–1141.

Bagchi, S., Briske, D. D., Wu, X. B., McClaran, M. P., Bestelmeyer, B. T., & Fernández-Giménez, M. E. (2012). Empirical assessment of state-and-transition models with a long-term vegetation record from the Sonoran Desert. *Ecological Applications*, 22(2), 400–411. https://doi.org/10.1890/11-0704.1

Balch, J. K., Bradley, B. A., D'Antonio, C. M., & Gómez-Dans, J. (2013). Introduced annual grass increases regional fire activity across the arid western USA (1980–2009). *Global Change Biology*, 19(1), 173–183. https://doi.org/10.1111/gcb.12046

Blumenthal, D. M., Kray, J. A., Ortmans, W., Ziska, L. H., & Pendall, E. (2016). Cheatgrass is favored by warming but not CO_2 enrichment in a semi-arid grassland. *Global Change Biology*, 22(9), 3026–3038.

Boyd, C. S., Johnson, D. D., Kerby, J. D., Svejcar, T. J., & Davies, K. W. (2014). Of grouse and golden eggs: Can ecosystems be managed within a species-based regulatory framework? *Rangeland Ecology & Management*, 67(4), 358–368. https://doi.org/10.2111/REM-D-13-00096.1

Boyte, S. P., & Wylie, B. K. (2016). Near-real-time cheatgrass percent cover in the northern Great Basin, USA, 2015. *Rangelands*, 38(5), 278–284. https://doi.org/10.1016/j.rala.2016.08.002

Bradford, J. B., & Lauenroth, W. K. (2006). Controls over invasion of *Bromus tectorum*: The importance of climate, soil, disturbance and seed availability. *Journal of Vegetation Science*, 17(6), 693–704.

Bradley, B. A. (2009). Regional analysis of the impacts of climate change on cheatgrass invasion shows potential risk and opportunity. *Global Change Biology*, 15(1), 196–208. https://doi.org/10.1111/j.1365-2486.2008.01709.x

Bradley, B. A., Curtis, C. A., & Chambers, J. C. (2016). *Bromus* response to climate and projected changes with climate change. In M. J. Germino, J. C. Chambers, & C. S. Brown (Eds.), *Exotic Brome-Grasses in Arid and Semiarid Ecosystems of the Western US: Causes, Consequences, and Management Implications* (pp. 257–274). Springer International Publishing.

Bradley, B. A., Curtis, C. A., Fusco, E. J., Abatzoglou, J. T., Balch, J. K., Dadashi, S., & Tuanmu, M.-N. (2018). Cheatgrass (*Bromus tectorum*) distribution in the intermountain western United States and its relationship to fire frequency, seasonality, and ignitions. *Biological Invasions*, 20(6), 1493–1506. https://doi.org/10.1007/s10530-017-1641-8

Bradley, B. A., & Mustard, J. F. (2005). Identifying land cover variability distinct from land cover change: Cheatgrass in the Great Basin. *Remote Sensing of Environment*, 94(2), 204–213. https://doi.org/10.1016/j.rse.2004.08.016

Brooks, M. L., Brown, C. S., Chambers, J. C., D'Antonio, C. M., Keeley, J. E., & Belnap, J. (2016). Exotic annual *Bromus* invasions: Comparisons among species and ecoregions in the Western United States. In M. J. Germino, J. C. Chambers, & C. S. Brown (Eds.), *Exotic Brome-Grasses in Arid and Semiarid Ecosystems of the Western US: Causes, Consequences, and Management Implications* (pp. 11–60). Springer International Publishing.

Bromberg, J. E., Kumar, S., Brown, C. S., & Stohlgren, T. J. (2011). Distributional changes and range predictions of downy brome (*Bromus tectorum*) in Rocky Mountain National Park. *Invasive Plant Science and Management*, 4(2), 173–182.

Brummer, T. J., Taylor, K. T., Rotella, J., Maxwell, B. D., Rew, L. J., & Lavin, M. (2016). Drivers of *Bromus tectorum* abundance in the western North American sagebrush steppe. *Ecosystems*, 19(6), 986–1000. https://doi.org/10.1007/s10021-016-9980-3

Brunson, M. W., & Tanaka, J. (2011). Economic and social impacts of wildfires and invasive plants in American deserts: lessons from the Great Basin. *Rangeland Ecology & Management*, 64(5), 463–470. https://doi.org/10.2111/REM-D-10-00032.1

Bykova, O., & Sage, R. F. (2012). Winter cold tolerance and the geographic range separation of *Bromus tectorum* and *Bromus rubens*, two severe invasive species in North America. *Global Change Biology*, 18(12), 3654–3663.

Chambers, J. C., Bradley, B. A., Brown, C. S., D'Antonio, C., Germino, M. J., Grace, J. B., Hardegree, S. P., Miller, R. F., & Pyke, D. A. (2014). Resilience to stress and disturbance, and resistance to *Bromus tectorum* L. invasion in cold desert shrublands of western North America. *Ecosystems*, 17(2), 360–375.

Chambers, J. C., Roundy, B. A., Blank, R. R., Meyer, S. E., & Whittaker, A. (2007). What makes Great Basin sagebrush ecosystems invasible by *Bromus tectorum*? *Ecological Monographs*, 77(1), 117–145.

Coates, P. S., Ricca, M. A., Prochazka, B. G., Brooks, M. L., Doherty, K. E., Kroger, T., Blomberg, E. J., Hagen, C. A., & Casazza, M. L. (2016). Wildfire, climate, and invasive grass interactions negatively impact an indicator species by reshaping sagebrush ecosystems. *Proceedings of the National Academy of Sciences*, 113(45), 12745–12750. https://doi.org/10.1073/pnas.1606898113

Compagnoni, A., & Adler, P. B. (2014a). Warming, soil moisture, and loss of snow increase *Bromus tectorum*'s population growth rate. *Elementa*, 2, 000020.

Compagnoni, A., & Adler, P. B. (2014b). Warming, competition, and *Bromus tectorum* population growth across an elevation gradient. *Ecosphere*, 5(9), art121.

Concilio, A. L., & Loik, M. E. (2013). Elevated nitrogen effects on *Bromus tectorum* dominance and native plant diversity in an arid montane ecosystem. *Applied Vegetation Science*, 16(4), 598–609.

Concilio, A. L., Loik, M. E., & Belnap, J. (2013). Global change effects on *Bromus tectorum* L. (Poaceae) at its high-elevation range margin. *Global Change Biology*, 19(1), 161–172.

D'Antonio, C. M., & Vitousek, P. M. (1992). Biological invasions by exotic grasses, the grass/fire cycle, and global change. *Annual Review of Ecology and Systematics*, 23(1), 63–87. https://doi.org/10.1146/annurev.es.23.110192.000431

Davies, G. M., Bakker, J. D., Dettweiler-Robinson, E., Dunwiddie, P. W., Hall, S. A., Downs, J., & Evans, J. (2012). Trajectories of change in sagebrush steppe vegetation communities in relation to multiple wildfires. *Ecological Applications*, 22(5), 1562–1577. https://doi.org/10.1890/10-2089.1

Davies, K. W. (2010). Revegetation of Medusahead-invaded sagebrush steppe. *Rangeland Ecology & Management*, 63(5), 564–571. https://doi.org/10.2111/REM-D-09-00127.1

Davies, K. W. (2011). Plant community diversity and native plant abundance decline with increasing abundance of an exotic annual grass. *Oecologia*, 167(2), 481–491. https://doi.org/10.1007/s00442-011-1992-2

Davies, K. W., Boyd, C. S., Beck, J. L., Bates, J. D., Svejcar, T. J., & Gregg, M. A. (2011). Saving the sagebrush sea: An ecosystem conservation plan for big sagebrush plant communities. *Biological Conservation*, 144(11), 2573–2584. https://doi.org/10.1016/j.biocon.2011.07.016

Davies, K. W., & Nafus, A. M. (2013). Exotic annual grass invasion alters fuel amounts, continuity and moisture content. *International Journal of Wildland Fire*, 22(3), 353–358. https://doi.org/10.1071/WF11161

Eliason, S. A., & Allen, E. B. (1997). Exotic grass competition in suppressing native shrubland re-establishment. *Restoration Ecology*, 5(3), 245–255. https://doi.org/10.1046/j.1526-100X.1997.09729.x

Evans, R. D., Rimer, R., Sperry, L., & Belnap, J. (2001). Exotic plant invasion alters nitrogen dynamics in an arid grassland. *Ecological Applications*, 11(5), 1301–1310.

Fusco, E. J., Finn, J. T., Balch, J. K., Nagy, R. C., & Bradley, B. A. (2019). Invasive grasses increase fire occurrence and frequency across US ecoregions. *Proceedings of the National Academy of Sciences*, 116(47), 23594–23599. https://doi.org/10.1073/pnas.1908253116

Germino, M. J., Belnap, J., Stark, J. M., Allen, E. B., & Rau, B. M. (2016). Ecosystem Impacts of Exotic Annual Invaders in the Genus *Bromus*. In M. J. Germino, J. C. Chambers, & C. S. Brown (Eds.), *Exotic Brome-Grasses in Arid and Semiarid Ecosystems of the Western US: Causes, Consequences, and Management Implications* (pp. 61–95). Springer International Publishing.

Godfree, R., Firn, J., Johnson, S., Knerr, N., Stol, J., & Doerr, V. (2017). Why non-native grasses pose a critical emerging threat to biodiversity conservation, habitat connectivity and agricultural production in multifunctional rural landscapes. *Landscape Ecology*, *32*(6), 1219–1242. https://doi.org/10.1007/s10980-017-0516-9

Gorelick, N., Hancher, M., Dixon, M., Ilyushchenko, S., Thau, D., & Moore, R. (2017). Google Earth Engine: Planetary-scale geospatial analysis for everyone. *Remote Sensing of Environment*, *202*, 18–27. https://doi.org/10.1016/j.rse.2017.06.031

Holt, C. C. (2004). Forecasting seasonals and trends by exponentially weighted moving averages. *International Journal of Forecasting*, *20*(1), 5–10. https://doi.org/10.1016/j.ijforecast.2003.09.015

Jarnevich, C. S., Sofaer, H. R., & Engelstad, P. (2021). Modelling presence versus abundance for invasive species risk assessment. *Diversity & Distributions*, *00*, 1–11. https://doi.org/10.1111/ddi.13414

Johnson, D., Cahill, M., Boyd, C., Schroeder, V., Foster, L., Sitz, A., Kerby, J., Svejcar, T. J., & Cupples, J. (2019). *Threat-Based Land Management in the Northern Great Basin: A Manager's Guide.* Catalog.extension.oregonstate.edu. https://catalog.extension.oregonstate.edu/pnw722/html

Johnston, F. H., Hanigan, I. C., & Bowman, D. M. J. S. (2009). Pollen loads and allergic rhinitis in Darwin, Australia: a potential health outcome of the grass-fire cycle. *EcoHealth*, *6*(1), 99–108. https://doi.org/10.1007/s10393-009-0225-1

Jones, M. O., Allred, B. W., Naugle, D. E., Maestas, J. D., Donnelly, P., Metz, L. J., Karl, J., Smith, R., Bestelmeyer, B., Boyd, C., Kerby, J. D., & McIver, J. D. (2018). Innovation in rangeland monitoring: annual, 30 m, plant functional type percent cover maps for U.S. rangelands, 1984-2017. *Ecosphere*, *9*(9), e02430.

Jones, M. O., Naugle, D. E., Twidwell, D., Uden, D. R., Maestas, J. D., & Allred, B. W. (2020). Beyond inventories: emergence of a new era in rangeland monitoring. *Rangeland Ecology & Management*, *73*(5), 577–583. https://doi.org/10.1016/j.rama.2020.06.009

Knapp, P. A. (1996). Cheatgrass (*Bromus tectorum* L) dominance in the Great Basin Desert: History, persistence, and influences to human activities. *Global Environmental Change: Human and Policy Dimensions*, *6*(1), 37–52. https://doi.org/10.1016/0959-3780(95)00112-3

Knick, S. T., Dobkin, D. S., Rotenberry, J. T., Schroeder, M. A., Haegen, W. M. V., van Riper, C. III. (2003). Teetering on the edge or too late? Conservation and research issues for avifauna of sagebrush habitats. *The Condor*, *105*(4), 611–634. https://doi.org/10.1093/condor/105.4.611

Koenker, R., Portnoy, S., Ng, P. T., Zeileis, A., Grosjean, P., & Ripley, B. D. (2020). *quantreg: Quantile Regression (Version 5.67) [Computer software].* https://CRAN.R-project.org/package=quantreg

Levick, S., Setterfield, S., Rossiter-Rachor, N., Hutley, L., McMaster, D., & Hacker, J. (2015). Monitoring the distribution and dynamics of an invasive grass in tropical savanna using airborne LiDAR. *Remote Sensing*, *7*(5), 5117–5132. https://www.mdpi.com/2072-4292/7/5/5117. https://doi.org/10.3390/rs70505117

Mack, R. N. (1981). Invasion of *Bromus tectorum* L. into Western North America: An ecological chronicle. *Agro-Ecosystems*, *7*(2), 145–165.

MacQueen, J. (1967). Some methods for classification and analysis of multivariate observations. *Proceedings of the Fifth Berkeley Symposium on Mathematical Statistics and Probability*, *1*, 281–297.

Maestas, J. D., Porter, M., Cahill, M., & Twidwell, D. (In Review). Defend the core: Maintaining intact rangelands by reducing vulnerability to invasive annual grasses. Rangelands.

McMahon, D. E., Urza, A. K., Brown, J. L., Phelan, C., & Chambers, J. C. (2021). Modelling species distributions and environmental suitability highlights risk of plant invasions in western United States. *Diversity & Distributions*, *27*(4), 710–728. https://doi.org/10.1111/ddi.13232

Melgoza, G., Nowak, R. S., & Tausch, R. J. (1990). Soil water exploitation after fire: competition between *Bromus tectorum* (cheatgrass) and two native species. *Oecologia*, *83*(1), 7–13. https://doi.org/10.1007/BF00324626

Nagy, R. C., Fusco, E. J., Balch, J. K., Finn, J. T., Mahood, A., Allen, J. M., & Bradley, B. A. (2020). A synthesis of the effects of cheatgrass invasion on U.S. Great Basin carbon storage. *Journal of Applied Ecology*, *58*(2), 327–337. https://doi.org/10.1111/1365-2664.13770

Nicolli, M., Rodhouse, T. J., Stucki, D. S., & Shinderman, M. (2020). Rapid invasion by the annual grass *Ventenata dubia* into protected-area, low-elevation sagebrush steppe. *Western North American Naturalist*, *80*(2), 243–252. https://doi.org/10.3398/064.080.0212

Nusser, S. M., & Goebel, J. J. (1997). The National Resources Inventory: a long-term multi-resource monitoring programme. *Environmental and Ecological Statistics*, *4*(3), 181–204.

Omernik, J. M., & Griffith, G. E. (2014). Ecoregions of the conterminous United States: evolution of a hierarchical spatial framework. *Environmental Management*, *54*(6), 1249–1266. https://doi.org/10.1007/s00267-014-0364-1

Pellant, M., & Hall, C. (1994). Distribution of two exotic grasses on intermountain rangelands: status in 1992. *Proceedings--Ecology and Management of Annual Rangelands*. (Eds SB Monsen, SG Kitchen) USDA Forest Service, Intermountain Forest and Range Experiment Station, General Technical Report INT-GTR-313, 109–199.

Peterson, E. B. (2005). Estimating cover of an invasive grass (*Bromus tectorum*) using tobit regression and phenology derived from two dates of Landsat ETM+ data. *International Journal of Remote Sensing*, *26*(12), 2491–2507.

Pilliod, D. S., Jeffries, M. A., Welty, J. L., & Arkle, R. S. (2021). Protecting restoration investments from the cheatgrass-fire cycle in sagebrush steppe. *Conservation Science and Practice*, *3*(10), 1–12. https://doi.org/10.1111/csp2.508

Pilliod, D. S., Welty, J. L., & Toevs, G. R. (2017). Seventy-five years of vegetation treatments on public rangelands in the Great Basin of North America. *Rangelands*, *39*(1), 1–9. https://doi.org/10.1016/j.rala.2016.12.001

Pohlert, T. (2020). trend: Non-Parametric Trend Tests and Change-Point Detection. https://CRAN.R-project.org/package=trend

Pyšek, P., Jarošík, V., Hulme, P. E., Pergl, J., Hejda, M., Schaffner, U., & Vilà, M. (2012). A global assessment of invasive plant impacts on resident species, communities and ecosystems: the interaction of impact measures, invading species' traits and environment. *Global Change Biology*, *18*(5), 1725–1737. https://doi.org/10.1111/j.1365-2486.2011.02636.x

R Core Team (2021). *R: A language and environment for statistical computing.* R Foundation for Statistical Computing. https://www.R-project.org/

Reeves, M. C., & Mitchell, J. E. (2011). Extent of coterminous US rangelands: Quantifying implications of differing agency perspectives. *Rangeland Ecology & Management*, *64*(6), 585–597. https://doi.org/10.2111/REM-D-11-00035.1

Reisen, F., Duran, S. M., Flannigan, M., Elliott, C., & Rideout, K. (2015). Wildfire smoke and public health risk. *International Journal of Wildland Fire*, *24*(8), 1029–1044. https://doi.org/10.1071/WF15034

Rossiter-Rachor, N. A., Setterfield, S. A., Douglas, M. M., Hutley, L. B., Cook, G. D., & Schmidt, S. (2009). Invasive *Andropogon gayanus* (gamba grass) is an ecosystem transformer of nitrogen relations in Australian savanna. *Ecological Applications*, *19*(6), 1546–1560.

Rousseeuw, P. J. (1987). Silhouettes: A graphical aid to the interpretation and validation of cluster analysis. *Journal of Computational and Applied Mathematics*, *20*, 53–65. https://doi.org/10.1016/0377-0427(87)90125-7

Sebastian, D. J., Nissen, S. J., Sebastian, J. R., & Beck, K. G. (2017). Seed bank depletion: the key to long-term downy brome (*Bromus tectorum* L.) management. *Rangeland Ecology & Management*, *70*(4), 477–483. https://doi.org/10.1016/j.rama.2016.12.003

Sen, P. K. (1968). Estimates of the regression coefficient based on Kendall's tau. *Journal of the American Statistical Association*, *63*(324), 1379–1389. https://doi.org/10.1080/01621459.1968.10480934

Taylor, J. M., Kachergis, E., Toevs, G. R., Karl, J. W., Bobo, M. R., Karl, M. G., Miller, S. W., & Spurrier, C. (2014). AIM-monitoring: a component of the BLM assessment, inventory, and monitoring strategy. https://www.ars.usda.gov/research/publications/publication/?seqNo115=296736

Theil, H. (1950). A rank-invariant method of linear and polynomial regression analysis, 3; confidence regions for the parameters of polynomial regression equations. *Indagationes Mathematicae. New Series*, *1*(2), 467–482.

Thill, D. C., Schirman, R. D., & Appleby, A. P. (1979). Influence of soil moisture, temperature, and compaction on the germination and emergence of downy brome (*Bromus tectorum*). *Weed Science*, *27*(6), 625–630.

USDA, NASS (2020). *Cropland Data Layer*. CropScape; USDA-NASS. https://nassgeodata.gmu.edu/CropScape/

USDA, NRCS (2015). The National Resources Inventory grazing lands on-site database, 2004 – 2014 (Unreleased). Compiled by the Resource Inventory Division; processed by the Resource Assessment Division, Conservation Effects Assessment Project-Grazing Land Component.

USDA, NRCS (2018). *The PLANTS Database* (http://plants.usda.gov). National Plant Data Team.

USDA, NRCS. (2020). Tackling Idaho's Cheatgrass Challenge. https://www.nrcs.usda.gov/wps/PA_NRCSConsumption/download?cid=nrcseprd1560032&ext=pdf

Western Governors' Association. (2020, July). A Toolkit for Invasive Annual Grass Management in the West.

Wettstein, Z. S., Hoshiko, S., Fahimi, J., Harrison, R. J., Cascio, W. E., & Rappold, A. G. (2018). Cardiovascular and cerebrovascular emergency department visits associated with wildfire smoke exposure in California in 2015. *Journal of the American Heart Association*, *7*(8), 1–15. https://doi.org/10.1161/JAHA.117.007492

Wood, S. N. (2003). Thin plate regression splines. *Journal of the Royal Statistical Society. Series B. Statistical Methodology*, *65*(1), 95–114. https://doi.org/10.1111/1467-9868.00374

Wood, S. N. (2011). Fast stable restricted maximum likelihood and marginal likelihood estimation of semiparametric generalized linear models. *Journal of the Royal Statistical Society Series B-Statistical Methodology*, *73*, 3–36. https://doi.org/10.1111/j.1467-9868.2010.00749.x

Young, J. A., & Evans, R. A. (1970). Invasion of Medusahead into the Great Basin. *Weed Science*, *18*(1), 89–97. https://doi.org/10.1017/S0043174500077419

Zelikova, T. J., Hufbauer, R. A., Reed, S. C., Wertin, T., Fettig, C., & Belnap, J. (2013). Eco-evolutionary responses of *Bromus tectorum* to climate change: implications for biological invasions. *Ecology and Evolution*, *3*(5), 1374–1387.

Ziska, L. H., Reeves, J. B., & Blank, B. (2005). The impact of recent increases in atmospheric CO_2 on biomass production and vegetative retention of Cheatgrass (*Bromus tectorum*): implications for fire disturbance. *Global Change Biology*, *11*(8), 1325–1332. https://doi.org/10.1111/j.1365-2486.2005.00992.x

BIOSKETCH

The research team that co-authored this paper has diverse backgrounds in wildlife biology, rangeland management, remote sensing, plant ecology and conservation implementation. Their work is currently focused on the dynamics and drivers of vegetation change in sagebrush ecosystems to inform rangeland management and wildlife conservation on public and private lands in the western United States.

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