Plant community trajectories following livestock exclusion for conservation vary and hinge on initial invasion and soil-biocrust conditions in shrub steppe

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Abstract
Adjustments or complete withdrawal of livestock grazing are among the most common conservation actions in semiarid uplands, but outcomes can vary considerably with ecological context. Invasion by exotic annual grasses and the excessive wildfire they promote are increasing threats to semiarid shrub-steppe, and plant-community response to livestock exclusion in these areas may be complicated by the rapid colonization ability of invaders. We evaluated vegetation-community changes over 14-year interval (2007–2021) in a shrub-steppe landscape where a >100-year history of livestock grazing had been terminated in 1996. Field surveys revealed that bare-soil exposure decreased >20% over the 14 years owing to biomass accumulation, but this was primarily due to large increases in exotic annual “cheatgrass” (Bromus tectorum, +1.8-fold) and the litter it produces (+1.5-fold). Soil biocrusts increased 11.9% and perennial bunchgrasses increased 3% over the 14 years. These community changes varied at the patch scale and entailed inverse relationships of (1) both cheatgrass and biocrusts to plant-community basal cover, (2) cheatgrass to both biocrusts and perennial grasses, and (3) biocrusts to cheatgrass and litter. The spatiotemporal variability in vegetation constituted changes in plant-community states, according to cluster analysis. The modeled probability of a community transitioning to a cheatgrass state was (1) strongly and positively related to the initial (2007) cover of cheatgrass in hotspots where initial cheatgrass cover was >20%, and (2) negatively related to biocrust cover where initial biocrust cover was >4% of ground area. The decision space for this landscape can be framed as a shifting from acceptance towards resisting further degradation by removing livestock and their trampling of soil surfaces and utilization of perennial herbs. However, cheatgrass appears to be the most impactful agent of change and continued invasion appears imminent. Active restoration may help resist further degradation and direct change towards tolerable conditions.

Keywords
bunchgrasses, exotic annual grasses, legacy impacts, lichens, moss, sagebrush steppe
1 | INTRODUCTION

More than half of the terrestrial surface of the earth is dryland that is managed passively for pastoralism, and the utilization can misalign with the adaptive capacity of the grazing regimes applied to cause losses in productivity and ecosystem functioning that resemble desertification (Asner et al., 2004). Relieving plant communities from inappropriate livestock grazing has become one of the most common types of conservation action, globally, and yet evidence on the outcomes is mixed (Filazzola et al., 2020; Jones, 2000). Disturbances such as grazing may alter key native or naturalized plants or biocrust species and thereby influence the space and growth resources for exotic invaders (Davis et al., 2000). This effect appears to operate strongly in semiarid landscapes, where recovery of native plants and biocrusts vital to ecosystem function can be relatively slow (reviewed in Belnap & Eldridge, 2001; Pyke et al., 2016).

Grazing effects on higher plants vary from negative to positive, depending on how the type or level of grazing pressure relates to the adaptive traits of the resident plant species (Milchunas et al., 1988; Milchunas & Lauenroth, 1993). In contrast, biocrusts are vulnerable to trampling by cattle and similar physical disturbances to soil surfaces (Root et al., 2020, O’Connor & Germino, 2021). Grazing can impact invasive plants by directly consuming them, spreading their propagules, altering the abundance of native or naturalized species that compete with invasives for growth resources, or by impacting the physical or biological (i.e., biocrust) condition of the soil surface that affects the ability of seeds to incorporate into soil, germinate, and emerge (Deines et al., 2007; Serpe et al., 2006). Studies have revealed how vulnerability to invasion relates to scarcity of particular native plant types that match the growth requirements of invaders, or, separately, biocrusts—but there are relatively few studies that consider how both plants and biocrusts collectively relate to plant invasions and community transitions (Condon et al., 2020; Condon & Pyke, 2018a; Root et al., 2020). Studies based on repeat sampling over the longer time scales required for whole-community recovery (plants and biocrusts) in response to livestock removal with invasion pressure are even scarcer.

Native perennials and biocrusts provide community resistance to one of the most problematic invaders of North America, cheatgrass (Bromus tectorum L.), a winter-annual that originates from Eurasia (Chambers et al., 2016; Deines et al., 2007; Serpe et al., 2006). Cheatgrass has spread across 22.7 million hectares that were once dominated by native perennials, and it is expected to continue expansion as climate and disturbance regimes change and more areas are disturbed by fire and human impacts (Boyte et al., 2016; Bradley, 2009; Smith et al., 2022). Cheatgrass is shallow rooted, invades interspaces between perennials, and produces spatially continuous, fine-textured fuel beds that cure relatively early in the growing season and thereby enhance fire risks in space and time (Brooks et al., 2004). The resulting increase in fire frequency further promotes cheatgrass invasion and loss of perennials, biocrusts, ecosystem stability and productivity, wildlife habitat, and biodiversity (Dettweiler-Robinson et al., 2013; Germino et al., 2016; Johansen, 2001; McCann et al., 2021; Ponzetti et al., 2007). Several ecosystem types are impacted by cheatgrass invasion, but the most extensive impacts have occurred in sagebrush-steppe rangelands, which once covered ~1,000,000 km² but have reduced already to half this extent due to the cheatgrass-fire cycle and community state transitions to annual grasslands or to seeded perennial grasslands (Miller et al., 2011).

While some studies have found neutral or sometimes desirable effects of grazing on cheatgrass depending on site context (Davies et al., 2009, 2021; Davies, Bates, & Boyd, 2016; Davies, Bates, Boyd, & Svejcar, 2016), inappropriate livestock grazing is considered to have promoted cheatgrass expansion in sagebrush steppe by causing the selective loss of perennial herbs that are most suited to competing with cheatgrass (Condon & Pyke, 2018a, 2018b; Pyke et al., 2016; Reisner et al., 2013; Williamson et al., 2020). Thus, temporary or permanent cessation of grazing has become by far the most common type of restoration intervention in sagebrush steppe, albeit a passive one (e.g., post-fire rest; Germino et al., 2021). Vegetation changes after livestock exclusion are thus of high interest. In spite of the relatively strong evidence that inappropriate grazing has contributed to less perennial herbs and more exotic annual grasses (Pyke et al., 2016), findings from grazing exclosures have provided mixed evidence for grazing impacts, even though these studies are expected to provide the strongest inference owing to their greater experimental control of confounding factors (Davies et al., 2009, 2021; Davies, Bates, & Boyd, 2016; Davies, Bates, Boyd, & Svejcar, 2016; Porensky et al., 2020; Veblen et al., 2015; Yeo, 2005). The difference in correlative compared to enclosure-experiment findings may relate to a tendency of grazing-exclusion studies in sagebrush steppe to be located in areas in relatively good ecological condition and/or relatively low abundances of cheatgrass (Anderson & Inouye, 2001; Condon et al., 2020; Copeland et al., 2021; Courtois et al., 2004; Davies et al., 2012, 2018; Davies, Bates, & Boyd, 2016; Davies, Bates, Boyd, & Svejcar, 2016; Porensky et al., 2020). Assessments of whole-community responses to grazing exclusion in the presence of invasive threats are thus needed.
To address this need, we capitalized on a long-term, repeat sampling of a grazing exclusion located in relatively low-elevation area of Northwest Colorado that had variable ecological condition, with cattle exclusion beginning when cheatgrass was increasing regionally and attaining local dominance of vulnerable landscapes. We asked (1) if and how plant community composition changed over 14 years (2007–2021) following grazing exclusion in 1997, (2) how changes in cover of cheatgrass or biocrusts related to shifts in other dominant components of the plant-community, (3) if the vegetation changes constituted community state changes, and (4) how the state changes over the 14 years related to initial (2007) cover of cheatgrass, bunchgrasses, or biocrusts. Our primary interest was to determine whether vegetation changes constituted community-state transitions regarding cheatgrass abundance, and to describe the site factors that related most to these changes.

2 METHODS

2.1 Study area

The study was conducted on Browns Park National Wildlife Refuge (BPNWR), established in 1963 by the US Fish and Wildlife Service (USFWS), and adjacent public lands in Moffat County, Colorado, USA (Figure 1). The study area was approximately 8120 ha (60% USFWS, 32% Bureau of Land Management, and 8% Colorado State Land Board) and has an elevation ranging from 1626 m to 2074 m. Average annual temperature was 7.4°C (range: 6.1–8.8°C), with average annual winter, spring, and summer temperatures of 3.7, 7.2 and 18.6°C, respectively (for the 30 years ending in 2015, PRISM model, prism.oregonstate.edu; Figure 2). Annual precipitation was 216 mm (range: 118–331 mm, PRISM). The study area was co-dominated by exotic annual grasses, which were 99% cheatgrass, and mosaics of shrubs, which were primarily sagebrush (Artemisia arbuscula and Artemisia tridentata) and also yellow rabbitbrush (Chrysothamnus viscidiflorus) and greasewood (Sarcobatus vermiculatus); perennial bunchgrasses including bluebunch wheatgrass (Pseudoroegneria spicata), squirreltail (Elymus elymoides), and Indian ricegrass (Achnatherum hymenoides); biological soil crusts such as lichens of the squamulose type (Psora decipiens or Acarospora spp.) or lichens formed by cyanobacteria (Collema sp.), and lesser abundances of short or long mosses and trace amounts of other, rarer biocrust types. The dominant plant communities and soils are described by four Ecological Site Descriptions: Sandy Cold Desert (3923 ha), Cold Desert Breaks (1172 ha), Loamy Cold Desert (546 ha), and Loamy Bottom (204 ha; websoilsurvey.sc.egov.usda.gov).

Based on the dominant type of sagebrush and annual precipitation, the study area is characterized as having low resilience to disturbance and resistance to exotic annual grass invasion (Chambers et al., 2014).

The area has a long and extensive history of use for cattle grazing dating to the 1850s, with large pastures and long, repeated grazing seasons starting in early winter that continued following establishment of the refuge in 1965. Cattle stocking densities reached nearly 1.63 ha per...
animal unit month (AUM) in the mid-1980s. In 1988, refuge managers assumed that livestock grazing was having a negative effect on vegetation and thus wildlife habitat, and corroborating assessments by the US General Accounting Office and the US Congress deemed cattle use incompatible with the mission of the refuge (GAO, 1989). Thereafter, grazing was reduced by 50% to 3.51 ha per AUM in 1994, then further reduced to 289.29 ha per AUM in 1995, and then reduced again to 0 AUMs in 1996. Current land uses are wildlife habitat and recreation, the latter largely associated with the Green River (e.g., rafting, angling).

2.2 Site characteristic monitoring

Sampling occurred in 2021 on 68 plots that were initially established and measured in 2007 by Williams (2010). All cover data reported here for 2007 were obtained from the US Fish and Wildlife Service. Plots were dispersed over four plant community conditions (Figure 1). Cover of plant species, litter, biocrusts (by type, moss, lichen, or cyanobacterial), bare ground, and rock was measured at 0.5 m intervals along three 25-m transects arranged in a spoke design around the plot center, using the line-point intercept method. We measured biocrust cover in April 2021 under relatively cool and wet early season conditions, when biocrusts were at their most active time of year, and measured total vegetation cover including higher plants and biocrusts again in June 2021, during warmer and dry conditions at the time of peak biomass. The same sampling methods were used in 2007 and 2021.

2.3 Data analysis

All analyses were performed in R Version 4.1.0 (R Core Team, 2020). Differences in plant-community cover types for all plots combined between 2007 and 2021 were evaluated using 95% confidence intervals (CI) around the means for each year, with mean differences considered significant if the CI did not overlap zero. Next, relationships between the difference in cheatgrass or biocrust cover from 2007 to 2021 and 19 plant-community variables were evaluated using linear regression (Table 1; R packages included glmmTMB, generalized linear mixed model builder; GGally, correlation of independent variables; and MuMIN, model selection, Magnusson et al., 2017). The most parsimonious models (i.e., cheatgrass or biocrust) were identified by first eliminating variables that had a correlation coefficient ≥ 0.6 (eliminating the single variables from each pair that appeared least likely to contribute to a parsimonious model) and eliminating variables that had extremely low values (forbs), and then using a backward stepwise elimination of variables having the highest p values until Akaike’s Information Criterion did not decrease appreciably with further elimination of variables.

To determine if vegetation changes from 2007 to 2021 constituted community-state transitions, K-means clustering (kmeans in R) was used to identify distinct plant community groups based on the cover components which differed most among plots according to sum of squares values in a general linear model with plotID as the response variable and all macro vegetation cover as independent variables (GLM). The optimal number of clusters was determined using the “elbow method,” that is, the smallest number of clusters that attained the greatest minimization of within-cluster sum of squares. We verified significant differences among clusters using analysis of similarities (ANOSIM), a nonparametric ANOVA of Bray–Curtis dissimilarity matrix values instead of raw data (vegan package in R, Oksanen et al., 2020). We estimated the probability of a site transitioning from biocrust or perennial bunchgrass dominated to cheatgrass dominated between 2007 and 2021 using multinomial logistic
TABLE 1  Predicted direction of change for cheatgrass or total biocrust in relation to other community components, from 2007 to 2021

| Difference in cover (%) from 2007 to 2021 | Description                                                                 | Predicted direction of effect (cheatgrass, biocrust) |
|----------------------------------------|-----------------------------------------------------------------------------|-----------------------------------------------------|
| Sagebrush                              | Basin big sagebrush & low sagebrush                                         | (−, +)                                              |
| Non-sagebrush shrubs                   | Greasewood, spiny hopsage, winterfat, shadscale saltbrush, shortspine horsebrush & yellow rabbitbrush | (−, −)                                              |
| Bare soil                              | Bare mineral soil                                                           | (+, −)                                              |
| Exotic forbs                           | Clasping pepperweed, desert madwort, western tansymustard & saltlover       | (+, −)                                              |
| Cheatgrass                             | Current year’s cheatgrass (senesced or not)                                 | (na, −)                                             |
| Lichen crust                           | Lichen component of biocrusts                                               | (−, na)                                              |
| Total biocrust                         | Cyanobacteria, lichen, and moss components of biocrusts                     | (−, na)                                              |
| Total litter                           | Total herbaceous and woody litter                                           | (+, −)                                              |
| Moss                                   | Early and late successional short and tall mosses                           | (−, na)                                              |
| Native forb                            | Hooker’s buckwheat, scarlet globemallow, douglas dustymaiden, basin cryptantha, povertyweed & woolly plantain | (−, +)                                              |
| Perennial bunchgrass                   | Squirreltail, sandberg’s bluegrass, thurber’s needlegrass, alkali cordgrass, sand dropseed, & Indian ricegrass | (−, −)                                              |
| Total foliar cover                     | Vertical projection of the aerial portion of plants                         | (−, −)                                              |
| Basal cover                            | Soil surface covered by plant bases                                         | (−, −)                                              |
| Total ground cover                     | Bare soil and biocrust soil surfaces                                       | (+, na)                                              |
| Ground cover between plant cover       | Bare soil and biocrust soil surfaces between plant foliar cover             | (−, na)                                              |
| Ground under plant cover               | Bare soil and biocrust soil surfaces under plant foliar cover               | (−, na)                                              |
| Litter cover between plant cover       | Herbaceous and woody plant litter between foliar plant cover                | (+, −)                                              |
| Litter under plant cover               | Herbaceous and woody plant litter under foliar plant cover                  | (+, −)                                              |

Note: In (), the direction of change can be positive (+) or negative (−) and the effect is listed first for cheatgrass and secondly for biocrust.

TABLE 2  Mean and 95% confidence intervals of cover of the major plant functional groups across all plots in 2007 and 2021 in Brown’s park National Wildlife Refuge; n = 68

| Variable                | 2007     | 2021     |
|-------------------------|----------|----------|
|                         | $\bar{x}$ | 95% CI LL | 95% CI UL | $\bar{x}$ | 95% CI LL | 95% CI UL |
| Sagebrush               | 5.8      | 4.7      | 6.9       | 4.2      | 3.2      | 5.1       |
| Bare soil               | 41.6     | 39.9     | 43.4      | 18.1     | 16.4     | 19.8      |
| Exotic forbs            | 0.5      | 0.3      | 0.6       | 0.1      | 0.02     | 0.3       |
| Cheatgrass              | 8.8      | 7.3      | 10.3      | 27.2     | 24.4     | 30.1      |
| Lichen crust            | 1.2      | 0.9      | 1.6       | 12.3     | 10.6     | 14.0      |
| Litter                  | 39.8     | 38.0     | 41.5      | 54.8     | 52.3     | 57.3      |
| Moss                    | 3.9      | 3.2      | 4.6       | 4.7      | 4.0      | 5.5       |
| Native forbs            | 3.2      | 2.7      | 3.8       | 0.1      | 0.01     | 0.2       |
| Non-sagebrush shrubs    | 17.5     | 15.9     | 19.0      | 17.1     | 15.3     | 19.0      |
| Perennial bunchgrasses  | 2.0      | 1.5      | 2.6       | 5.0      | 4.1      | 5.9       |
| Total biocrust          | 5.1      | 4.4      | 5.9       | 17.0     | 15.2     | 18.9      |
regression (nnet package in R, multinomial log-linear model builder, Ripley et al., 2016). The significance of differences in cheatgrass cover from 2007 to 2021 in each of the original plant-community states was determined with a two-way general linear model with year and plant community states as fixed factors, and Tukey’s mean separation.

3 | RESULTS

The cover of all functional groups, except moss and nonsagebrush shrubs, changed between 2007 and 2021 based on mean differences and 95% CI. The largest increases from 2007 to 2021 were observed in cheatgrass, which increased 1.8-fold to 27% cover (95% CI: 1.5–2.1 fold), in litter primarily from cheatgrass (1.5-fold increase, 95% CI: 1.3–1.8) and in total biocrusts (1.2-fold increase, 95% CI: 1.0–1.4). Bare soil decreased most of all variables, decreasing by 23.5 percentage points between 2007 and 2021 (95% CI: −21.4 to −25.7). Mean cover increased 3% for perennial bunchgrasses (95% CI: 2.2–3.8) and 11.1% for lichen crust (95% CI: 9.5–12.7, Table 2, Figure 3). According to multiple regression, cheatgrass increased ~18% for every 15% decrease in bare soil cover over the 14 years. Similar but smaller increases in cheatgrass occurred with decreases in perennial bunchgrasses (increasing ~10% per 15% decrease in perennial bunchgrasses cover), biocrusts (increasing ~10% per 12% decrease in biocrust cover), and plant basal cover (increasing ~10% per 5% decrease in plant basal cover) (Figure 4, Table 3, whole model $R^2 = 0.61$, AIC = −76.3).

Multiple regression also revealed that increases in biocrust cover were inversely related to concurrent changes in cover of cheatgrass (increasing ~6% per 45% decrease in cheatgrass), bare ground (increasing ~10% per 12% decrease in bare ground), basal area of all plants (increasing ~10% per 8% decrease in plant basal area), and litter (increasing ~11% per 20% decrease in litter) (Figure 5, Table 3, whole model $R^2 = 0.73$, AIC = −197.6).

The k-means clustering based on plant cover revealed five distinct community conditions (Figures 6 and 7, see species list in Table 1). In 2007, sites were classified as either bare-soil dominated ($n = 41$), intact sagebrush ($n = 10$), non-sagebrush shrub ($n = 9$) or becoming cheatgrass invaded ($n = 8$). In 2021, there were 12, 8, 9, and 26 plots in each of these respective community states, and the remaining 13 sites were classified as fully cheatgrass-invaded. The most common site transitions were from bare-soil dominated to becoming-cheatgrass or fully-cheatgrass invaded, and, to a lesser extent, communities retaining their bare-soil dominated or intact sagebrush conditions. The probability of plots having a plant-community transition from bare-soil dominated to cheatgrass-invaded (but not fully invaded, blue lines in Figure 8) over the 14 years was negatively related to...
initial (i.e., in 2007) biocrust cover values >12\% ($\beta \pm SE = -14.3 \pm 4.4$, 95\% CI: -22.9 to -5.7) and to initial perennial bunchgrass cover >7\% ($\beta \pm SE = 30.4 \pm 15.9$, 95\% CI: -0.8 to 61.5). The probability of a site transition from partially to fully cheatgrass-invaded conditions (purple lines in Figure 8) increased appreciably and in a threshold-like fashion for plots that initially (in 2007) had >~15\% cover and especially 20\% cheatgrass cover ($\beta \pm SE = 31.5 \pm 7.2$, 95\% CI: 17.4–45.6). In contrast, sites were less likely to transition to fully invaded by cheatgrass as cover of all biocrust types increased beyond 4\% ($\beta \pm SE = -19.7 \pm 5.6$, 95\% CI: -30.7 to -8.6).

Increases in cheatgrass from 2007 to 2014 were not uniform among the plant-community states identified in 2007, and instead were (1) greatest in plots initially classified as non-sagebrush shrublands, increasing 32\% from 2007 ($\bar{x} = 5.1$, CI: 0.5–10.0) to 37.8\% (CI: 25.6–49.9) in 2021, and (2) second greatest in plots initially classified as bare-soil dominated, increasing from 5.4\% (CI: 3.9–6.9) in 2007 to 26.8\% (CI: 20.8–32.7) in 2021 (Figure 9).

![Figure 5](https://example.com/figure5.png)

**Table 3** Estimate of effect (coefficient estimates $\beta$) and 95\% CI for each variable in the best-fit model of cover change from 2007 to 2021 according to Akaike’s information criterion for cheatgrass (AIC = 166.2; 8 parameters), and biocrusts (AIC = 196.3; 5 parameters)

| Variable (difference in % cover from 2007 to 2021) | $\beta$ estimate | 95% CI |
|--------------------------------------------------|------------------|--------|
| Response of cheatgrass                           |                  |        |
| Bare soil                                        | -0.01            | [-0.01, -0.01] |
| Total biocrust                                   | -0.80            | [-1.14, -0.47] |
| Plant basal                                      | -0.02            | [-0.03, -0.01] |
| Perennial bunchgrass                             | -0.62            | [-1.37, 0.12] |
| Response of biocrusts                            |                  |        |
| Cheatgrass                                       | -0.14            | [-0.23, -0.05] |
| Bare ground                                      | -0.01            | [-0.01, -0.01] |
| Plant basal                                      | -0.01            | [-0.01, -0.01] |
| Total litter                                     | -0.01            | [-0.01, -0.01] |

![Figure 6](https://example.com/figure6.png)

**Figure 6** Mean ±95\% CI composition of plant communities identified by K-means clustering in 2007 and 2021. Only cover types that were significantly different among plant-community types are presented.

![Figure 5](https://example.com/figure5.png)

**Figure 5** Relationship between modeled change (difference) in cover of biocrusts (%) from 2007 to 2021 and measured difference in cover from 2007 to 2021 of bare ground, cheatgrass, plant basal area, and total litter on Browns Park National Wildlife Refuge, USA. Dotted lines are 95\% confidence intervals. See Table 3 for statistics.
Ecosystem responses to livestock exclusion can provide strong inference on livestock grazing effects. Although our study could not formally control for cattle removal effects owing to the lack of replicated ungrazed and grazed areas, important insights were possible from the space × time heterogeneity in plant-community recovery as cheatgrass invaded the large and varied exclosure we sampled. The observed patterns reveal that cheatgrass invasion likely has been a stronger driver of plant community condition than grazing exclusion in recent decades, although these factors are interactive and not trivial to separate. The salient plant-community responses to grazing exclusion were dominated by increases in relatively slow-growing biocrusts and perennial herbs and rapid increases in cheatgrass and the copious litter it produces—all of which were interactive and inversely related to the amount of bare soil. It is perhaps not surprising that perennial herbs and especially deeper-rooted bunchgrasses were among the most significant changes in relation to cheatgrass, because bunchgrasses are well known to provide resistance to cheatgrass invasion via their resprouting ability and moderate overlap with the growth form and requirements of cheatgrass (reviewed in Chambers et al., 2014; Chambers et al., 2016), and biological soil crusts can also contribute to resistance to cheatgrass invasion by affecting seed incorporation into soil and germination (Serpe et al., 2006; Peterson 2013; Slate et al. 2019). Bunchgrasses and biocrusts are also most directly impacted by livestock, compared to all components of shrub steppe.

4.1 | Thresholds portending cheatgrass invasion, or resistance to invasion

Increases in cheatgrass over the 14 years at Brown’s Park NWR were substantial: cheatgrass cover more than doubled to cross a threshold of 20%, above which exponential increases in cheatgrass cover by 2021 were observed for each incremental increase in 2007 cover. Communities with an initial mean cheatgrass cover of >20% in 2007 (i.e., “becoming invaded” state) had cheatgrass cover increase to 40% by 2021. The 20% cheatgrass threshold identified here as portending conversion of mixed perennial communities to annual grasslands is notable, because (1) the threshold has been presumed by land managers to identify where or when cheatgrass is likely to transform plant-community and ecosystem integrity, and (2) the threshold has thus guided significant land-management decisions and action—and both of these points are despite few datasets and analyses available to corroborate the threshold (Creutzburg et al., 2022; Germino et al., 2021). The increased cheatgrass abundance is a serious threat because of the accompanying greater likelihood of wildfire, and cheatgrass would be expected to increase further in the post-fire environment.
imposing a competitive disadvantage to perennials and thereby engaging the cheatgrass-fire cycle (Brooks et al., 2004).

We also asked if thresholds in the relationships of biocrusts and perennial herb cover in 2007 to cheatgrass change from 2007 to 2021 were evident and if they could indicate minimum target cover for these native vegetation types. The probability of community-state conversion to (or towards) annual grasslands also decreased with (1) greater biocrust cover above thresholds of 4%–12% and (2) greater bunchgrass cover above thresholds of 7% bunchgrass cover in 2007, although the relationships between these cover classes and cheatgrass were hump-shaped. Nonetheless, the implication is that any loss of biocrusts or bunchgrasses, especially to <7%–10% cover, would be expected to confer little or no preemption of cheatgrass.

The pattern for bunchgrasses does not agree with a commonly assumed threshold of 20%, perennial grass abundance, above which perennial grass stands are considered less likely to diminish or be heavily invaded by cheatgrass (reviewed in Germino et al., 2021 and citations therein). The lack of detection of a clear uni-modal relationship depicting a 20% perennial-grass threshold may be due to too few plots in our dataset having >20% perennial bunchgrasses in either sampling year.

4.2 Colonization of bare soil patches after grazing exclusion

The initial plant-community states most vulnerable to transition towards annual grasslands, aside from the one labeled “becoming invaded,” were states depleted in either overstory or understory perennials, that is, the “bare-soil dominated” or “other shrubs,” that is, greasewood stands with scarce understory herbs and presumably large bare-soil patches. A stronger negative correlation of changes from 2007 to 2021 in cheatgrass and bare soil compared to changes in biocrusts to bare soil indicated that cheatgrass more readily occupied the bare soil than biocrusts, assuming that the correlations reflect direct relationships. Negative relationships observed between cheatgrass and bunchgrass or total community cover on Brown’s Park NWR could have resulted from a priority effect (Vaughn & Young, 2015; Weidlich et al., 2021) in which initial colonization of bare soil by cheatgrass preempted some of the recovery potential of bunchgrasses and biocrusts, compounding their relatively slower growth to limit their abundances. Cheatgrass can displace perennial seedlings through competition (reviewed in Chambers et al., 2016), and the shade-inducing litter mats cheatgrass produces combined with its occupation of otherwise bare-soil patches to reduce biocrust growth (Dettweiler-Robinson et al., 2013; Ponzetti et al., 2007; Serpe et al., 2013). Where perennial grasses are recovering, it is possible that future increases in their basal cover may reduce the available soil area for biocrusts such that a negative perennial-biocrust relationship emerges, which would be indicative of the site attaining higher invasion resistance.

It is possible or perhaps likely that the biocrust and bunchgrass covers on Brown’s Park NWR had not reached their maximum potential cover by 2021, and additional years of observation may reveal increases in perennials relative to cheatgrass—provided that wildfire does not impact the site as could be expected if cheatgrass continues to increase in abundance. Biocrust communities can be slow-growing and this likely contributes to biocrust declines after fire (Johansen, 2001; McCann et al., 2021). Compared to our observations, Anderson et al. (1982) and Yeo (2005) reported larger, 15%–30% increases in crusts up to 30–38 years after grazing exclusion, and Anderson and Inouye (2001) reported many-fold increases in perennial bunchgrasses with additional decades of rest, minimal cheatgrass, and absence of fire—all in sagebrush steppe. Recovery of perennial bunchgrasses was still occurring 90 years after passive recovery from more severe disturbances in other areas of sagebrush steppe where cheatgrass was prominent in the...
initial post-disturbance colonization phase but eventually subsided as perennials recovered (Morris et al., 2011). Multiple decades were required for full recovery of perennial grasses in relatively wetter sagebrush steppe of British Columbia following rest from grazing without wildfire, even in the absence of cheatgrass (McLean & Tisdale, 1972).

4.3 | Plant-community states relating to cheatgrass change

In addition to the evidence for cheatgrass as a driver of community change, several patterns of patch-scale community change indicated ways that the whole-community condition likely imparted partial resistance to cheatgrass invasion over the 14 years. Our observations corroborated previous studies that observed high resistance of intact sagebrush steppe to cheatgrass (Prevéy et al., 2010). Sagebrush itself may confer some resistance to cheatgrass, perhaps through its dimorphic, shallow and deep rooting and soil-water use (Germino & Reinhardt, 2014), although there are many communities with sagebrush overstories and cheatgrass understories. In contrast, greasewood commonly functions as a phreatophyte using deeper groundwater and has much fewer shallow roots and thus less potential for competitive interactions with cheatgrass (Harr & Price, 1972), and we observed greasewood stands, which generally had very few perennial herbs, to be more readily invaded by cheatgrass.

4.4 | Relating to other exclosure studies

Not all exclosure or observational studies in sagebrush steppe have reported negative impacts of grazing on cheatgrass (Davies et al., 2009, 2021; Davies, Bates, & Boyd, 2016; Davies, Bates, Boyd, & Svejcar, 2016), especially where grazing practices were more amenable to maintaining community resistance to invasion (Davies et al., 2018; Davies, Bates, Boyd, & Svejcar, 2016). Cheatgrass increased in less severe ways than observed on Brown’s Park NWR after longer periods of exclusion in sagebrush steppe of US National Parks (Bangert & Huntly, 2010; Banks & Baker, 2011; Bishop et al., 2019; Rodhouse et al., 2021). Several observational studies that reported increased cheatgrass with grazing identified integrity of both perennial grasses and biocrusts as factors promoting increases in cheatgrass (Condon et al., 2020; Reisner et al., 2013; Root et al., 2020). Where grazing effects on cheatgrass have been inferred from exclosures, increases in biocrusts and/or perennial grasses and smaller increases in cheatgrass than observed in Brown’s Park NWR have been repeatedly observed (Anderson et al., 1982; Anderson & Inouye, 2001; Condon et al., 2020; Courtois et al., 2004; Davies et al., 2012; Porensky et al., 2020; Veblen et al., 2015; Yeo, 2005). In the notable case of the 1000 km² grazing exclosure established in the upper Snake River Plain at the Idaho National Lab in 1950, many-fold increases in bunchgrass cover occurred prior

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**FIGURE 9** Percent cheatgrass cover measured in 2007 and 2021 in each of the four plant-community types prevailing in 2007 on Brown’s Park National Wildlife Refuge, USA. Letters denote significant differences *p* < .05 within community clusters according to Tukey’s test. See Figure 7 for representative photos of community types.
to the onset of cheatgrass invasion into the surrounding region, and by 1995, cheatgrass had reached low abundances (<6% cover) on only a modest number of plots (Anderson & Inouye, 2001). However, Bagchi et al. (2013) later reported greater invasion levels, which notably followed a decade of extensive wildfire.

Increases in exotic invasive species after cessation of livestock grazing can be generally expected where native perennials are depleted and invasive species are present prior to the livestock withdrawal, owing to the rapid population growth potential of invaders (Davies et al., 2009, 2021; Davies, Bates, Boyd, & Svejcar, 2016; Davies, Bates, & Boyd, 2016 for sagebrush steppe, and Milchunas et al., 1992 more generally). This effect is expected to be exacerbated in areas similar to Brown’s Park NWR, that is, semiarid rangelands where native perennials are relatively slow growing, especially compared to the rapid colonization and biomass development of exotic invaders such as cheatgrass.

4.5 | Spatial uncertainty in grazing pressure, temporal uncertainty in cheatgrass and biocrust cover

A key challenge in assessing cheatgrass and other annual herb abundances is that (1) their abundance in a given year are strongly coupled to weather patterns prevailing prior to data collection, more so than for perennials, and (2) weather, especially spring precipitation, is highly variable among years (Applestein et al., 2021; Pilliod et al., 2017). Wet winters and springs favor cheatgrass, and experimentally blocking rain during these times can greatly reduce cheatgrass population sizes, especially in undisturbed sites (Prevéy et al., 2010). Variable weather was a major driver of temporal changes in cheatgrass (alternating increases and decreases) over the decades of plant community change following grazing exclusion on the Idaho National Lab (Anderson & Inouye, 2001). Thus, weather variations between 2007 (wetter) and 2021 (drier, Figure 2) may cause our assessment to underestimate both the increase in cheatgrass and its response to landscape factors.

5 | CONCLUSIONS

Land managers increasingly recognize that their resources, such as wildlife habitat, are nonstationary and that future change is likely and the decision “space” for addressing the changes can be framed as accepting, that is, no action, or resisting or direct the changes towards a tolerable condition via intervention (Schuurman et al., 2022). Withdrawal of livestock grazing by Brown’s Park NWR over two decades ago is an example of an effort to resist the change. However, cheatgrass has expanded faster than perennial bunchgrasses or biocrusts in a 14-year segment of recovery from grazing on Brown’s Park NWR, and cheatgrass cover has reached levels that portend greater likelihood of further transitions to annual grasslands. Patches of resistance to cheatgrass were evident where biocrusts or perennials grasses—ecosystem attributes that can be directly impacted by livestock—remained intact or increased over the 14 years. Even greater resistance could be attained through application of active restoration by using herbicides to reduce cheatgrass and the competitive pressure it places on perennials and by using seeding or planting of perennials in the landscape patches impacted by cheatgrass.

AUTHOR CONTRIBUTIONS

Matthew J. Germino conceived of and supervised the study, Chad R. Kluender collected the field data and led the data processing and analyses, Christopher R. Anthony assisted in analyses, Matthew J. Germino led the writing with assistance from the other authors, and all authors edited and approved the manuscript.

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CONFLICT OF INTEREST

The authors have no conflicts of interest to declare. Any use of trade, firm, or product names is for descriptive purposes only and does not imply endorsement by the U.S. Government.

DATA AVAILABILITY STATEMENT

Data for this study are available at https://doi.org/10.5066/P9SO99W8 (Kluender & Germino, 2022).

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