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SYNTHESIS

Variable effects of long-term livestock grazing across the western United States suggest diverse approaches are needed to meet global change challenges

Stella M. Copeland[1] | David L. Hoover[2] | David J. Augustine[2] | Jonathan D. Bates[1] | Chad S. Boyd[1] | Kirk W. Davies[1] | Justin D. Derner[3] | Michael C. Duniway[4] | Lauren M. Porensky[2] | Lance T. Vermeire[5]

[1]USDA-Agricultural Research Service, Eastern Oregon Agricultural Research Center, Burns, Oregon, USA

[2]USDA-Agricultural Research Service, Rangeland Resources and Systems Research Unit, Fort Collins, Colorado, USA

[3]USDA-Agricultural Research Service, Rangeland Resources and Systems Research Unit, Fort Collins, CO, Cheyenne, Wyoming, USA

[4]US Geological Survey, Southwest Biological Science Center, Moab, Utah, USA

[5]USDA-Agricultural Research Service, Fort Keogh Livestock and Range Research Laboratory, Miles City, Montana, USA

Correspondence
Stella M. Copeland, USDA-Agricultural Research Service, Eastern Oregon Agricultural Research Center, Burns, OR, USA.
Email: stella.copeland@usda.gov

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Abstract

Aims: Livestock production is the most widespread land use globally and occurs across a diverse set of ecosystems. Variability in long-term livestock grazing impacts across ecosystems is poorly characterized, particularly at larger spatial scales, despite strong relationships with various ecosystem services related to soil fertility and stabilization and vegetation productivity. Here we examine the effects of grazing on vegetation and the implications for resistance and resilience to global change.

Methods: We use six long-term research stations in the western United States, spanning two ecoregions, multiple ecosystems, and 311 total site-years of research. Across these sites we evaluate convergence and divergence of vegetation response to grazing vs grazing removal, focusing on interactions with drivers of global change.

Results: We found that at long time scales (multiple decades), grazing has numerous convergent and divergent effects across ecoregions and ecosystems. Similarity among precipitation patterns and plant traits linked to grazing and production timing were key elements explaining convergence or divergence in long-term patterns of livestock grazing response. Ecosystem differences across western US rangelands are also associated with variable effects of grazing on resistance and resilience to invasive species and climate change.

Conclusions: These results suggest that unique ecosystem or ecoregion responses to future global change may result from complex interactions between grazing and environmental factors, such as precipitation timing and plant traits. Adapting livestock and grazing management to specific ecosystem vegetation and climate variability is needed to manage for the myriad global changes affecting rangeland production and diversity.

KEYWORDS
herbivory, long-term ecological research, management, rangeland, resilience, resistance

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Stella M. Copeland and David L. Hoover contributed equally for this study, all other authors listed alphabetically.

1 | INTRODUCTION

Livestock production is the most widespread land use globally, accounting for 77% of all agricultural lands (40 million km^2), with significant impacts on food security, local and global economies, biodiversity, and biogeochemical cycles (FAO, 2017; Maestre et al., 2022). Most livestock production occurs on rangelands, which are defined by both their environmental characteristics (vegetation dominated by grasses and/or shrubs) and land use (grazed or potential to be grazed, managed for natural ecosystem qualities as opposed to pasture systems; Lund, 2007; Reeves & Mitchell, 2011). The effects of grazing by wild and domesticated herbivores on rangeland ecosystem structure and function can vary widely, driven by the complex combinations of climate, soil type, natural disturbance regimes, plant communities, and historic and contemporary grazing practices (Milchunas & Lauenroth, 1993; Bakker et al., 2006; Koerner et al., 2018; Forbes et al., 2019; Maestre et al., 2022). The rate of change in plant community composition and/or bare soil exposure in response to differing grazing intensities can vary substantially across ecosystems and continents (Harrison & Shackleton, 1999; O'Reagain et al., 2014; Veblen et al., 2016; Augustine et al., 2019; Wilmer et al., 2021), and at fine scales across contrasting soil types (e.g. Goheen et al., 2018). Despite such variation, livestock grazing effects are often described in simplistic, binary terms without acknowledging varying levels of impact or nonlinear responses (Davies & Boyd, 2020). In addition, vegetation responses to grazing, and suitable management approaches, from one site or region are often assumed to apply at other sites or regions. This conceptual viewpoint ignores the importance of unique regional characteristics, from biophysical setting to typical management practices, that can affect responses to livestock grazing (Milchunas et al., 1988; Milchunas & Lauenroth, 1993; Cingolani et al., 2005; Oesterheld & Semmartin, 2011; Koerner et al., 2014). Previous studies provide insight into general effects of grazing (e.g. Milchunas & Lauenroth, 1993), yet do not necessarily address specific drivers of change and variation in grazing effects at the temporal and spatial scales relevant to rangeland management. Understanding the relative contribution of regional characteristics to grazing response may also suggest how shifts in grazing management could increase resilience (capacity to recover from change; Pimm 1984; Tilman & Downing 1994) and resistance (capacity to withstand change) to climate change in tandem with atmospheric CO$_2$ increase, invasive species, and altered fire regimes.

Rangelands currently span approximately 30% of the conterminous US land surface (2.07–2.68 million km^2, dependent upon the definition of rangeland), largely concentrated in the Great Plains, southwestern deserts, and Great Basin cold desert, where grazing is the most common land use (Reeves & Mitchell, 2011). In particular, the western United States is an extensive rangeland landscape and encompasses a diverse set of climate conditions, predominant soil types, and dominant plant species, and grazing management systems (Holechek, 1981; Mack & Thompson, 1982; Milchunas & Lauenroth, 1993; Reeves & Mitchell, 2011). Differences in the evolutionary history of native herbivore grazing across the western United States, associated with the prevalence of grazing-tolerant traits among dominant plant species, may also influence plant community responses to contemporary livestock grazing (Milchunas et al., 1988; Anderson, 2006; Spasojevic et al., 2010).

Livestock grazing practices have varied over time across the western United States, complicating efforts to understand the long-term impacts of contemporary grazing practices (Sayre et al., 2012). High livestock densities and unsustainable practices led to widespread environmental degradation in this region from the late 1800s to early 1900s (Stewart et al., 1940; Laycock, 1967). In response, new approaches to livestock management were developed in the mid-1900s, which aimed to avoid degradation through an array of management techniques tailored to key factors like environmental variation and livestock behavior (Holechek, 1981). However, these 20th-century approaches may be insufficient to meet global change drivers, such as warming temperatures, altered precipitation, invasive species, land-use change, and altered fire regimes (Littell et al., 2009; Abatzoglou & Kolden, 2011; Balch et al., 2013; Stocker et al., 2013). Balancing livestock production with conservation, in the western United States and worldwide, in the context of global change may require management adaptations extending beyond current or traditional practices (Reeves et al., 2014), tailored to vegetation and climate characteristics (Bakker et al., 2006; Derner et al., 2018; Koerner et al., 2018).

Here we assess vegetation responses to livestock grazing and environmental variables across six research sites (311 site-years total, six sites, 20–75 years/site; Table 1) representing two key rangeland ecoregions in the western United States (Great Plains and North American Deserts) using long-term data sets and synthesizing extensive site-based literature (Figure 1). The sites are distinguished by a temporal depth and topical breadth of local grazing management research, specific to their respective rangeland ecosystems, and collectively represent millions of km^2 of rangeland integral to the US economy and environmental health. The sites (and their respective ecosystems) overlap to various degrees in attributes known to affect grazing response, such as plant composition, climate, and long-term grazing history (Milchunas et al., 1988; Milchunas & Lauenroth, 1993). We predicted that sites within the same ecoregion would have more convergent responses to grazing, with divergence most notable between ecoregions. We further expected that these patterns would be largely driven by the relationship between vegetation composition and climate.

First, we assess how site attributes, such as native vegetation, climate, and soils, and management practices of these sites and their respective ecoregions may relate to the degree of similarity in plant community responses to livestock grazing. Second, we contrast research from our sites to describe how livestock grazing affects resilience and resistance to global change drivers in the two ecoregions. Third, we address how convergence or divergence in outcomes across sites might shape livestock management strategies to enhance integrity of western US rangeland ecosystems with global change challenges.

TABLE 1 Site locations by ecoregion (Environmental Protection Agency [EPA] Level 1 ecoregions, Commission for Environmental Cooperation [CEC], 1997, revised in 2006; Omernik & Griffith, 2014), environmental characteristics, and peak biomass timing.

Ecoregion	Site name	Code	Location	Ecosystem	Elev. (m)	MAP (mm)	MAT (°C)	CV ppt	AI	Peak biomass
North American Deserts	Canyonlands Research Center	CRC	38°04′ N, 109°34′ W	Colorado Plateau shrublands and grasslands	1600	205	12.7	0.22	0.16	Apr–May
North American Deserts	Northern Great Basin Experimental Range	NGBER	43°29′ N, 119°43′ W	Sagebrush steppe	1430	278	7.3	0.29	0.27	May–Jun
Great Plains	Central Plains Experimental Range	CPER	40°50′ N, 104°43′ W	Shortgrass prairie	1645	352	8.9	0.18	0.30	Jul–Aug
Great Plains	Livestock and Range Research Laboratory	LRRL	46°22′ N, 105°53′ W	Northern mixed-grass prairie	788	327	7.8	0.27	0.31	Jun–Jul
Great Plains	Thunder Basin	TB	43°56′ N, 104°51′W	Sagebrush steppe / Northern mixed-grass prairie ecotone	1400	344	7.3	0.20	0.33	Jul–Aug
Great Plains	High Plains Grasslands Research Station	HPGRS	41°11′ N, 104°54′ W	Mixed-grass prairie	1930	403	7.5	0.18	0.38	Jul–Aug

Note: Climate data including mean annual precipitation (MAP), mean annual temperature (MAT), and the coefficient of variability for annual precipitation (CVppt) were obtained from the NOAA Monthly US Climate Gridded Dataset [NClimGrid] for 1980–2010 (Vose et al., 2014). The aridity index (AI) was calculated using Hargreaves' equation (Hargreaves & Samani, 1985).

2 | DRIVERS OF VARIABLE RESPONSES IN PLANT COMMUNITIES TO LIVESTOCK GRAZING

The six long-term research sites in this study span two major ecoregions, the North American Deserts and the Great Plains (Environmental Protection Agency [EPA] Level I ecoregions, Omernik & Griffith, 2014), and are located within several major western US rangeland ecosystems (Figure 1; Table 1; Appendix S1). The sites in the North American Deserts ecoregion are both in cold desert ecosystems (Colorado Plateau and Great Basin): mixed shrubland and grassland at the Canyonlands Research Center (CRC, southeastern Utah) and sagebrush steppe at the Northern Great Basin Experimental Range (NGBER, eastern Oregon). Great Plains ecoregion sites include the Livestock and Range Research Laboratory (LRRL, eastern Montana) in northern mixed-grass prairie, Thunder Basin (TB, northeastern Wyoming) in an ecotone between sagebrush steppe and northern mixed-grass prairie, High Plains Grasslands Research Station (HPGRS, southern Wyoming) in northern mixed-grass prairie, and the Central Plains Experimental Range (CPER, northeastern Colorado) in shortgrass steppe.

2.1 | Ecoregional differences in precipitation timing drive peak production timing

Across the six sites, mean annual precipitation ranges from 205 (CRC) to 403 mm year^{-1} (HPGRS) with three distinct intra-annual patterns (Table 1, Figure 1). The four sites located in the Great Plains ecoregion (LRRL, TB, HPGRS, and CPER) have a unimodal precipitation regime but vary in seasonal timing (Figure 1). Precipitation peaks in the spring (April, May) in the central sites (TB and HPGRS) while at the northernmost (LRRL) and southernmost sites (CPER) precipitation peaks in early summer (June–July). Meanwhile, the two sites in the North American Desert ecoregion are drier and differ in precipitation regime; NGBER has unimodal precipitation with a cool-season-dominated regime, whereas CRC has a bimodal annual precipitation distribution with peaks in both the early spring and the late summer (Table 1; Figure 1). Interannual precipitation variation (coefficient of variation, CV) was highest at NGBER and lowest at CPER and HPGRS (Table 1). The CRC is also the hottest site, with a mean annual temperature (MAT) of 12.7°C, with MAT at the other sites ranging from 7.3°C to 8.9°C (Table 1). All sites have positive water balance during the cool season, an important period for soil water recharge (Figure 1) and growing-season precipitation is the dominant driver of plant productivity across many of these sites.

Climatological differences across the sites are linked to variation in peak plant production and composition, with key differences in the timing of precipitation in the growing season and the limitations imposed by low temperatures (Figure 1, Table 1). Among climate variables, precipitation is most closely tied to variation in rangeland productivity for these sites across years (Connell

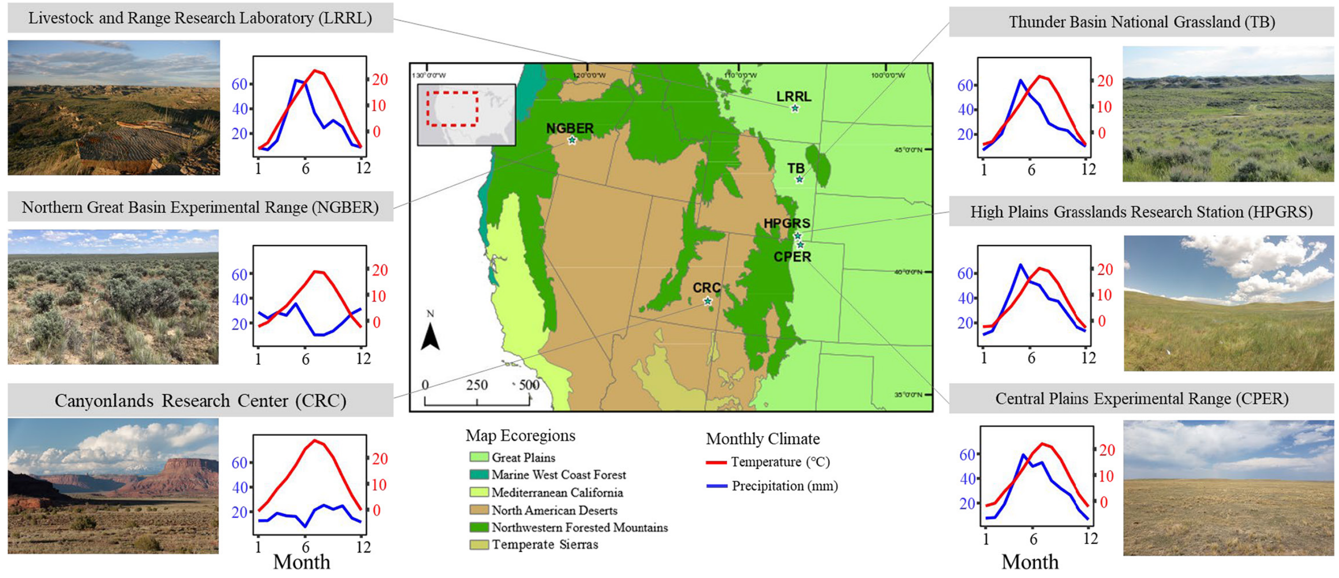


FIGURE 1 Locations and monthly climate for the six sites which are located in two EPA Level 1 ecoregions (CEC, 1997, revised in 2006; Omernik & Griffith, 2014); the Great Plains (CPER, HPGRS, LRRL and TB) and the North American Deserts (CRC and NGBER). Climate variograms (1980–2010) from each site were obtained from NClimGrid (Vose et al., 2014).

et al., 2019), seasons (Derner & Hart, 2007), and multiyear periods (Petrie et al., 2018). The most influential precipitation period affecting vegetation productivity varies by site, and somewhat aligns with ecoregion. Most sites are sensitive to spring precipitation (CPER, HPGRS: Irisarri et al., 2016, Hoover, Lauenroth, et al., 2021; LRRL: Heitschmidt & Vermeire, 2006, Vermeire et al., 2009; NGBER: Bates et al., 2006, Copeland et al., 2022; TB: Connell et al., 2019). The exception is CRC, where a mix of perennial-grass photosynthetic pathways leads to a strong response to both soil water accumulated over the cool season (winter and spring) as well as growing-season precipitation (Gremer et al., 2015; Hoover, Pfennigwerth, & Duniway, 2021). Production at NGBER, the other North American Deserts ecoregion site, is also moderately responsive to cool-season precipitation (Bates et al., 2006; Copeland et al., 2022). The southernmost Great Plains sites (CPER, HPGRS) receive significant growing-season precipitation, which leads to peak production in the summer (Irisarri et al., 2016; Hoover, Lauenroth, et al., 2021), whereas the northernmost Great Plains site, LRRL, is less responsive to precipitation in the summer and fall (Heitschmidt & Vermeire, 2006; Vermeire et al., 2009, Table 1; Vermeire & Rinella, 2020).

In addition to climate and grazing management, plant productivity and composition are influenced by major soil characteristics (e.g., texture) across all ecosystems. For instance, soil type, and associated characteristics such as texture and depth to restriction layer, influence the proportion of cool-season to warm-season grasses in shortgrass steppe (Augustine et al., 2017), the abundance of *Artemisia tridentata* (big sagebrush) in sagebrush grassland (Porensky et al., 2018), the relative dominance of woody shrub vs perennial grass species in the Colorado Plateau (Duniway et al., 2022), and perennial-grass cover and dominant grass species in the sagebrush steppe (Davies et al., 2007).

2.2 | Differences in photosynthetic pathway and growth form drive grazing and weather responses

All six sites are dominated by perennial grasses, with many overlapping plant functional groups and species across sites (Appendix S1). The relative abundance of plant species and associated functional trait values and categories vary due to selection and shifts in species distribution in response to historic climate, herbivore abundance, and fire regime (Janis et al., 2002; Anderson, 2006; Strömberg, 2011). This influences the magnitude and direction of the plant community response to grazing intensity or climate patterns (Milchunas et al., 1988; Milchunas & Lauenroth, 1993; Adler et al., 2004, 2005; Milchunas, 2006). Plant traits related to grazing response are complex combinations of photosynthetic pathway, life history, growth form, morphology, and paleoecology linked to herbivore community composition and abundance (Briske, 1996; Diaz et al., 2007). Livestock grazing can have large impacts on plant community composition by increasing or decreasing the competitive advantage of dominant species (Lezama et al., 2014; Koerner et al., 2018; Li, Dong, et al., 2022; Li, He, et al., 2022).

Climate regime is a major factor determining the relative abundance of plant species with distinct growing seasons across the six sites, and grazing-tolerance traits may be correlated with climate responses, as observed in other systems (Quiroga et al., 2010). Warm-season precipitation is a major factor influencing the herbaceous vegetation across the sites, except for NGBER (Figure 1). This leads to a pattern of much higher abundance of dominant grass species responding to warm-season precipitation in the other sites compared to NGBER. Specifically, warm-season grasses with C_4 photosynthesis are dominant or codominant in these sites compared to cool-season grasses with C_3 photosynthesis because the higher water use efficiency of C_4 photosynthesis outweighs its carbon cost (Vermeire et al., 2009). In contrast, low summer precipitation and cooler temperatures at NGBER are associated with a total absence of warm-season grasses.

In addition to their responses to climate, cool- and warm-season grasses differ in grazing-tolerance characteristics. Prostrate growth forms are relatively common for warm-season, but not cool-season, grasses in the Great Plains sites, which is attributed to the favorable climate and coevolution with abundant native herbivores, particularly *Bos bison* (American bison), over the past several thousand years (Towne et al., 2005; Augustine et al., 2021). At LRRL, even though warm-season grasses are present, the generally cooler spring temperatures favor a higher abundance of cool-season grasses. While all grasses at NGBER are cool-season species, their grazing-related trait values also vary, with at least one common species, *Poa secunda* (Sandberg bluegrass) having shorter stature and a mat-forming habit in contrast to the taller, co-occurring bunchgrasses. A higher proportion of cool-season precipitation is also associated with shrub abundance, with the desert ecoregion sites, CRC, NGBER, and the ecotonal TB site having a higher proportion of shrubs, particularly *Artemisia tridentata* at NGBER and TB (Cook & Irwin, 1992).

2.3 | Grazing management varies in livestock densities and movement

Timing and intensity of livestock grazing (defined by utilization and/or other measurement of effects; Jasmer & Holechek, 1984; Holechek et al., 1998) varies among the six sites and two ecoregions and is largely driven by spatiotemporal variability in production for key forage species (Appendix S2). Grazing regimes in the North American Deserts ecoregion sites are distinct from the Great Plains sites. Lower elevations (e.g., desert valleys) at the CRC are grazed from winter through spring (November–May) and higher elevations (e.g., mountains) are grazed in the summer and fall due to differences in water availability in the cool vs warm seasons (Figure 1). The typical grazing regime in the NGBER area is moderate intensity with seasonal deferment alternating between the growing season (April–July) and post-growing season, with occasional rest years. For the Great Plains sites, grazing regimes in the shortgrass steppe (CPER) and mixed-grass prairie sites (TB, HPGRS, LRRL) vary in intensity and range from season-long to rotational grazing (Kachergis et al., 2013; Wilmer et al., 2018).

2.4 | The magnitude and direction of grazing effects varies broadly with ecoregion

We assessed the relative effects of livestock grazing vs removal at multidecadal grazing-exclusion experiments at each of the study sites. The sites used various methods, but all measured herbaceous cover by species (Appendix S1 and S2). The relative effects of livestock grazing on perennial herbaceous cover and richness, and invasive annual-grass cover are not consistent across ecoregions (Figure 2). The North American Desert sites exhibited different responses to the removal of moderate grazing. Livestock grazing reduces native perennial herbaceous cover and diversity (species number) at the driest site (CRC), compared to removal, but only slightly reduced native perennial cover at NGBER (Figure 2; Figure S1). Functional group composition was not affected by removal of livestock grazing at the CRC, although the relative abundance of palatable vs unpalatable shrubs may decrease with livestock grazing (Miller et al., 2011). Moderate livestock grazing removal only weakly affects composition and functional group relative abundance at NGBER (Sneva et al., 1984; Davies et al., 2009, 2018; Copeland et al., 2021). However, intense, repeated early-season livestock grazing can have long-lasting impacts in this ecosystem (Laycock, 1967) resulting in multidecadal recovery trajectories after a shift to more moderate grazing practices (including: rest years, later-season grazing, and lower stocking rates; Sneva et al., 1984; Copeland et al., 2021). Greater differences between grazed and ungrazed (grazing removal) plant communities occurred at the Great Plains sites for most variables, with livestock grazing removal leading to generally decreasing native perennial herbaceous cover and richness and increasing non-native annual cover (Figure 2; Figure S1).

The response of plant composition to grazing removal in the Great Plains is related to the codominance of short-statured, grazing-resistant warm-season grasses with taller cool-season grasses that are less resistant to grazing (Briske, 1996). Livestock densities can shift the dominance of these two plant functional types with higher stocking densities favoring warm-season grasses and lower stocking densities favoring the cool-season grasses (CPER: Augustine et al., 2017, Porensky et al., 2017; TB: Porensky et al., 2020; HPGRS: Porensky et al., 2016). Warm-season grass abundance in the Great Plains seems to preclude the expansion of cool-season non-native annual grasses (primarily *Bromus* spp., cheatgrass, *B. tectorum* and field brome, *B. arvensis*), which tend to increase with grazing removal at some Great Plains sites (HPGRS: Porensky et al., 2016; TB: Porensky et al., 2020). At the LRRL site, climate conditions (cooler springs) favor the dominance of cool-season grasses and less capacity for shifts in functional group composition in response to changes in grazing intensity (Vermeire et al., 2008).

The relative abundance of species with different trait values also affects how plant communities shift with the combination of livestock grazing and climate change. If changing climate shifts precipitation seasonality to favor dominant species with high palatability, livestock grazing may dampen the potential effects of climate change on composition. This scenario may be responsible for dampened increases in cool-season grasses at CPER in recent decades with climate change and CO_2 increase (Augustine et al., 2017), which tend to favor cool-season (C_3) grasses.

3 | RESISTANCE AND RESILIENCE TO GRAZING AND INTERACTIONS WITH GLOBAL CHANGE

Rangelands can vary in resistance (capacity to withstand change) and resilience (capacity to recover from change) to grazing, with

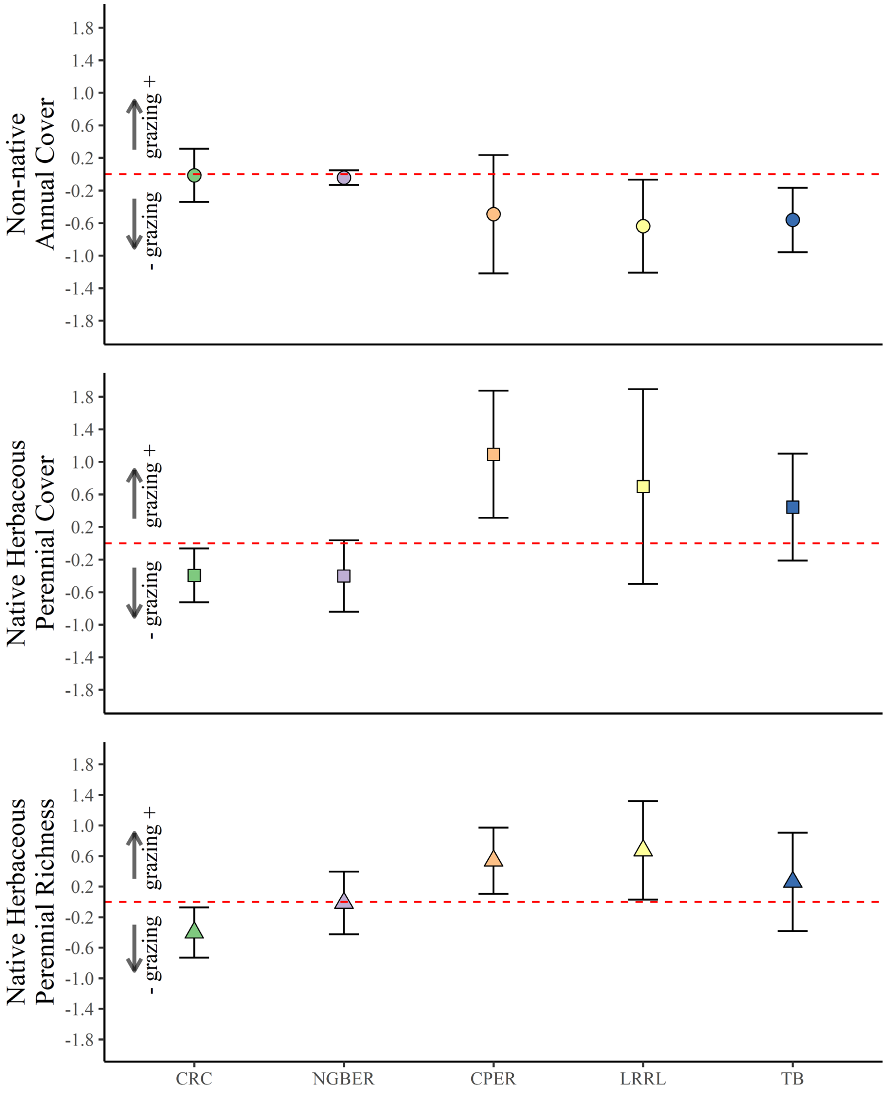


FIGURE 2 Effect size and 95% confidence intervals for difference in vegetation characteristics (non-native annual and perennial herbaceous percent cover and perennial herbaceous species richness, number of species) with long-term moderate livestock grazing compared to ungrazed areas (exclosures) across all sites (North American Desert sites: CRC, Canyonlands Research Center; NGBER, Northern Great Basin Experimental Range; Great Plains sites: CPER, Central Plains Experimental Range; LRRL, Livestock and Range Research Laboratory; TB, Thunder Basin [National Grassland]) for a recent year (see Appendix S2 for site dataset details). Points above or below the dashed red line indicate higher or lower values with moderate grazing, respectively. The effect size statistic calculated here is Hedge's *g*, which uses a pooled standard deviation weighted by sample size (Hedges & Olkin, 1985) with a correction applied for paired plots (Gibbons et al., 1993) for all sites but CRC (R *effsize* package; Torchiano, 2020). Effect size could not be calculated for the HPGRS site due to low replication at the pasture level.

implications for balancing production and conservation, in the context of global change. Responses of rangeland productivity and composition to grazing can vary in rate (e.g., rapid or gradual), type (e.g., reversible or alternative stable states), and magnitude as a function of climate, paleoecology, and associated plant community composition (Mack & Thompson, 1982; Milchunas et al., 1988; Milchunas & Lauenroth, 1993). These dynamics are difficult to detect without long-term observations due to intra- and interannual weather variability, and tend to fall within a continuum of speed, trajectory, and reversibility (Briske et al., 2003).

3.1 | Resilience and resistance to grazing-induced change is associated with ecoregion

Long-term plant community responses to grazing (compared to removal) at these sites vary from abrupt shifts with alternate stable states to slow and reversible compositional changes (Box 1). The most resilient sites are in the Great Plains, with no shifts to distinct alternate stable states observed at any sites (Milchunas et al., 1998) and reversible effects on the plant community. For example, compositional responses to high grazing intensity in areas previously excluded from livestock grazing appear within a decade for dominant perennial grasses and are reversible if intensity is reduced over a similar timeframe in mixed-grass prairie (HPGRS, Box 1, Porensky et al., 2016). In the northern mixed-grass prairie (LRRL) there were no lasting effects of six years of overutilization compared to moderate grazing after a year of rest (Vermeire et al., 2008). Similarly, grass composition in shortgrass steppe (CPER) recovered from seven to 10 years of continual, intense grazing by prairie dogs after they had been removed for five years (Augustine et al., 2014). Additionally, the introduction or removal of moderate cattle grazing in shortgrass steppe induced slow but predictable and similar changes in species composition (Wilmer et al., 2021).

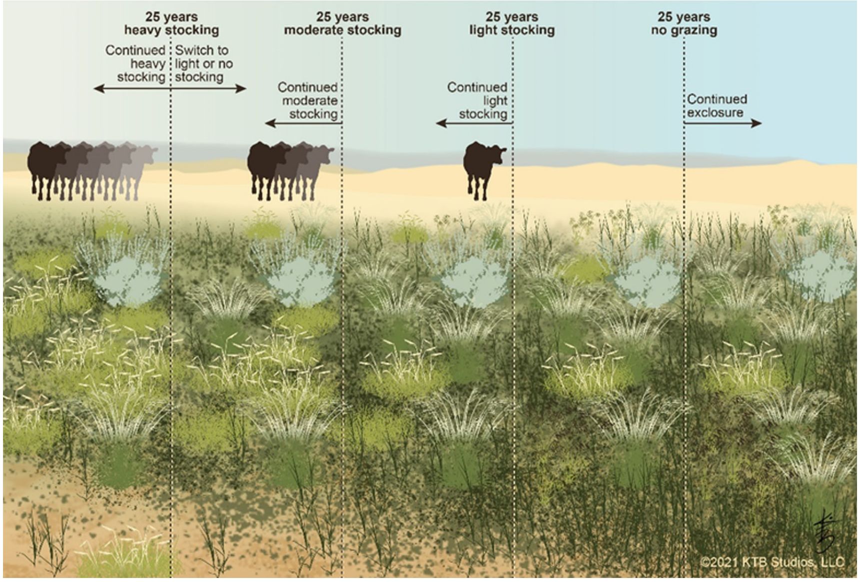
Plant composition may be more resistant, but less resilient, to livestock grazing in the North American Desert ecoregion sites (CRC and NGBER) compared to the Great Plains sites (Figure 2). Additional evidence suggests that the resilience of desert ecoregion sites to grazing differs by grazing intensity, with lower resilience to higher intensity livestock grazing (Box 1). The magnitude and type of change with high-intensity livestock grazing across desert sites may depend on aridity, with a shift to an alternative stable state observed at the driest site (CRC, Box 1) and slow recovery over several decades in the less arid, more temperature-limited, Northern Great Basin (NGBER, Sneva et al., 1984; Copeland et al., 2021). In general, shifts to alternate stable states are more likely where livestock grazing is associated with increased soil exposure and erosion, or conversion to exotic grass- or woodland-dominated states, which is documented in the desert sites included here (Davies et al., 2014; Davies, Bates, & Boyd, 2016; Duniway et al., 2018). In the dry rangelands of the Colorado Plateau (CRC ecosystem), sparse vegetation occurs with interspace soils stabilized by biological soil crusts, which are rapidly lost with livestock trampling at higher densities (Box 1; Schwinning et al., 2008; Belnap et al., 2009; Miller et al., 2011; Munson, Belnap, & Okin, 2011) with the highest biocrust values observed in sites naturally excluded from native herbivores (Belnap et al., 2006). Soil erosion following loss of biological soil crusts in this ecosystem can lead to alternate stable states, due to both the slow nature of soil development and accelerated wind and water erosion which further damage plants and soils and hamper recovery (Box 1; Miller et al., 2011; Nauman et al., 2018).

3.2 | Climate and soil controls on reversibility of grazing responses

Precipitation amount, seasonal timing, and evaporative demand are major factors linked to the ratio of perennial-grass cover to bare ground and the potential for soil erosion across these sites. Lower growing-season precipitation and higher bare ground tends to occur in North American Deserts compared to the Great Plains ecoregion. More bare ground increases erosion potential with livestock grazing and is further influenced by characteristics such as soil texture and biological soil crusts. Rangelands within the North American Deserts and other arid

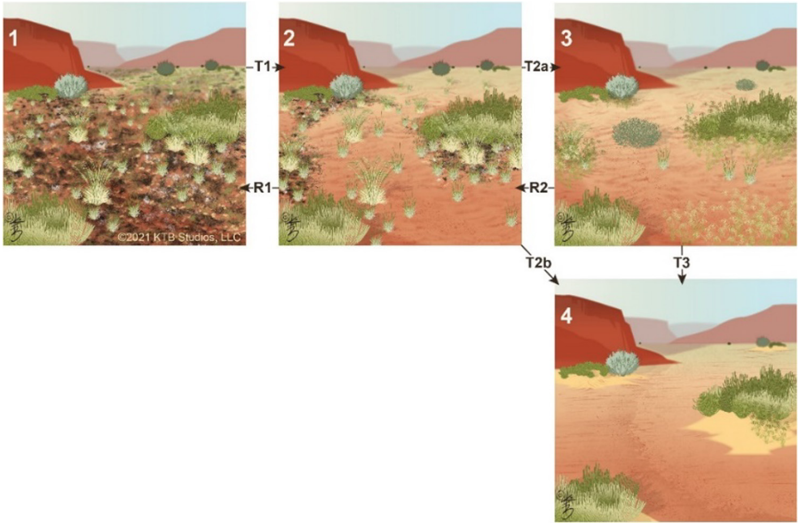
BOX 1 Contrasting grazing resilience: Great Plains vs North American Deserts. ©2021 Kate Galloway KTB Studios LLC, all rights reserved

Northern Mixed-Grass Prairie (Great Plains) — high grazing resilience, reversible change.



At the High Plains Grasslands Research Station (HPGRS), different long-term grazing intensity treatments caused slow, continuous and directional changes with important management implications, but these changes were reversible and did not provide evidence for alternative stable states. Heavier stocking rates led to reduced cover of dominant cool-season (C_3) grasses and litter, and increased cover of bare soil and the dominant warm-season (C_4) grass *Bouteloua gracilis*. For this and similar ecosystems, quantifying the timescales and compositional gradients associated with key phase shifts may be more important than identifying thresholds between alternative stable states (adapted from Porensky et al., 2016).

Colorado Plateau (North American Deserts) – low grazing resilience, alternative stable states.



Response to grazing on the deep, sandy loam soils at the Canyonlands Research Center (CRC) are best described by a threshold and alternative-stable-state model. A biological soil crust (BSC) and perennial-grass state with stable soils due to abundant and diverse BSC cover is observed with no or very light current or historic livestock use (state 1). Light to moderate livestock use leads to a state with similar plant communities as state 1 but with lower BSC cover and diversity, leading to increases in bare ground and erosion risk (state 2). States 3 and 4 represent states with loss of BSC and native perennial vegetation, dominance by bare soil and non-native annuals, and accelerated soil erosion risk with no known restoration or recovery pathway. Threshold changes with grazing pressure (arrows T1 through T3) are difficult to reverse with grazing removal (arrows R1 and R2). Transitions to degraded states (arrows T2a and T2b) are often driven by improper grazing management, especially during drought (adapted from Duniway et al., 2016).

rangelands are not universally susceptible to grazing-induced shifts to irreversible, alternative states (Pei et al., 2008; Yayneshet et al., 2009; Perryman et al., 2021), and can be influenced by other environmental factors, such as soil texture. For example, in Colorado Plateau rangelands, plant communities growing in soils derived from shale parent material are less resilient to grazing due to salt-induced limitations (Munson et al., 2016; Duniway et al., 2018) and extremely sandy soils also appear more sensitive to intense grazing due to risk of accelerated erosion (Bowker et al., 2012; Nauman et al., 2018). Similarly, soil and climate determine the abundance and composition of biological soil crusts, and the impact of their potential loss via livestock trampling, across the North American Deserts ecoregion (Condon & Pyke, 2020).

3.3 | Diverse and complex grazing effects on resistance and resilience to global change drivers

Livestock grazing can influence the future resistance and resilience of rangelands to global change via complex interactions. In western US rangelands, major change drivers include invasion by non-native annual grasses, increased wildfire frequency and extent, climate change, and CO_2 increases, among other factors. Climate change is predicted to alter precipitation amounts, seasonality and intensity, and have consequences for vegetation productivity and livestock production for the Great Plains and North American Desert ecoregions (Derner et al., 2018; Snyder et al., 2019; Briske et al., 2021). Climate change may impact Great Plains vegetative dynamics by shifting the ratio of warm- to cool-season grasses, which differ in their response to precipitation (Irisarri et al., 2016) and CO_2 (Augustine et al., 2018). In the Colorado Plateau ecosystem, cool-season grasses are more vulnerable to increases in temperature and drought than warm-season grasses (Munson, Belnap, Schelz, et al., 2011; Hoover et al., 2015). This could lead to shifts in the ratio of cool- to warm-season grasses in low-elevation winter pastures, with potentially large impacts on livestock operations as cool-season grasses are an important source of high-quality forage during spring green-up.

3.4 | Grazing effects on resistance to annual-grass invasion diverge across ecosystems

Non-native annual grasses (e.g., *Bromus* spp.) are a major management concern in rangelands in both the North American Deserts and Great Plains ecoregions, with expected increases in distribution and abundance likely with climate change and increased fire frequency in many ecosystems (Bradley, 2009; Smith et al., 2022). Livestock grazing has complex interactions with invasive annual grasses, with outcomes depending upon ecological context and grazing management. In the Great Basin ecosystem, grazing timing (growing season vs dormant season), intensity (utilization), and multiyear duration of a particular grazing system combine to determine whether grazing effects on resistance to invasive annual grasses are slightly positive, neutral, or negative. For instance, repeated, high-intensity grazing in the growing season can increase the abundance of the invasive annual grass *Bromus tectorum* (Reisner et al., 2013) while moderate to intense grazing in the fall (dormant season) can reduce its abundance (Davies, Bates, Perryman, & Arispe, 2021) and seedbank (Perryman et al., 2020), potentially favoring perennial grasses (Schmelzer et al., 2014; Davies, Bates, Perryman, & Arispe, 2021). At NGBER, *Bromus tectorum* abundance was not affected by long-term (decadal) moderate grazing (Davies et al., 2009, 2018) nor a range of grazing intensities, including high utilization, over a seven-year period (Bates & Davies, 2014), likely due to a grazing system with alternating grazing timing (growing season and non-growing season) and occasional rest years. At the drier Colorado Plateau site (CRC), high livestock numbers historically increased the abundance of non-native annual grasses and forbs (Miller et al., 2011; Duniway et al., 2018), in contrast to neutral effects observed with moderate grazing (Figure 2). Mechanisms for increasing annual grasses with livestock grazing include the loss of perennial grasses and biocrust cover (lichens and mosses on the soil surface) that can compete with annual species for space and resources (Condon & Pyke, 2018; Root et al., 2020).

Grazing suppresses cheatgrass in the Great Plains sites, likely by enhancing cover of dominant short-stature warm-season grasses like *Bouteloua gracilis* (blue grama, Vermeire et al., 2008; Porensky et al., 2016), a species which is either absent (NGBER) or less common (CRC) in the North American Deserts. Similarly, *Bromus tectorum* increases were associated with livestock removal at TB (Porensky et al., 2020) and non-native or weedy species are more common in ungrazed areas in CPER as well (Milchunas et al., 1990; Augustine et al., 2017). Furthermore, the non-native *Bromus arvensis* tends to be more abundant in ungrazed sites leading to greater pre-fire litter at the LRRL site (Reinhart et al., 2020).

3.5 | The capacity for grazing to alter the effects of fire are driven by vegetation

Wildfire is a widespread natural disturbance in most rangelands, including these six sites in the western United States. Fire regime varies widely across our study sites in association with vegetation productivity and climate regime, with a more frequent fire return interval, less than five years, in the northern Great Plains (Allen & Palmer, 2011) and over a century in the lower-elevation Great Basin rangelands (Mensing et al., 2006). The potential for livestock grazing to increase resilience (recovery capacity) to wildfire has major implications for rangeland ecosystems where increasing wildfire is associated with flammable invasive annual grasses, such as in the Great Basin (Balch et al., 2013). The potential for grazing to alter the effects of fire appears to be dependent upon vegetation response to both fire and grazing. In the Great Plains, grazing has little effect on ecosystem resilience to wildfire, perhaps due to the greater resilience of perennial grasses to fire and grazing and relatively high sensitivity of annuals to both grazing and fire (Vermeire et al., 2014; Porensky & Blumenthal, 2016; Dufek et al., 2018). At the Great Basin site (NGBER) and nearby plant communities, moderate livestock grazing increased resistance to (capacity to withstand) invasion by annual grasses post-fire (Figure 3, NGBER; Davies et al., 2009; Davies, Bates, Boyd, & Svejcar, 2016; Davies, Bates, Boyd, et al., 2021). The strong impact of grazing in the Great Basin is likely due to reduction of pre-fire fuels, associated with lower bunchgrass mortality, with livestock grazing compared to exclosure sites (Davies et al., 2010, 2018), and the ability of bunchgrasses to effectively compete with annual grasses post-fire (Davies et al., 2009; Davies, Bates, Boyd, & Svejcar, 2016). In contrast, a similar experiment with pre-fire grazing demonstrated little impact of grazing on vegetation response to fire in the northern Great Plains site (Figure 3, LRRL; Vermeire et al., 2018).

Grazing intensity and timing may also be crucial factors in managing for resilience post-fire. For instance, higher intensity and/or repeated early-season pre-fire grazing in the Great Basin (NGBER ecosystem) can decrease resilience to fire and favor exotic annual-grass conversion by increasing woody vegetation and decreasing bunchgrass abundance (Laycock, 1967; Strand et al., 2014). Shifting

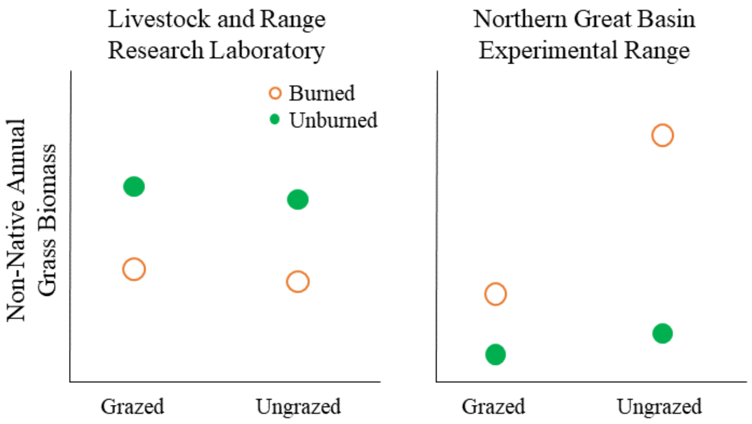


FIGURE 3 Contrasting effects of moderate livestock grazing on change in non-native annual grasses (*Bromus* spp.) after burning with main effects only at a Great Plains site, the Livestock and Range Research Laboratory (adapted from Vermeire et al., 2018), and an interactive effect at a North American Desert site, the Northern Great Basin Experimental Range (adapted from Davies et al., 2009).

climate could also increase or decrease general site resistance to post-fire invasion by cheatgrass in the Great Basin where and when altered climate conditions favor cheatgrass over perennial species (Bradley, 2009; Chambers et al., 2014; Roundy et al., 2018). This suggests that the appropriate grazing management regime for wildfire resilience and resistance may vary within the Great Basin ecosystem, depending upon temporal and spatial environmental conditions.

4 | THE IMPORTANCE OF CONTEXT FOR SUSTAINABLE RANGELAND MANAGEMENT WITH GLOBAL CHANGE

Research from six long-term rangeland research sites within the western United States illustrates a high degree of variability in the effects of livestock grazing on vegetation, particularly when long timescales (e.g., decades) are considered. Despite such variability, there were several general patterns observed. First, all sites converged in their sensitivity of plant growth and composition to local climatological conditions — particularly the timing and amount of precipitation. While the exact sensitivity varied by site, the tight coupling between production and precipitation was a key driver of vegetation dynamics and in turn the response of vegetation to grazing. Second, there tended to be more divergence between ecoregions, and more convergence within ecoregions, with especially high convergence among sites with similar plant community traits and climate. At sites in the Great Plains ecoregion, plant dynamics were primarily driven by growing-season precipitation and there was high resistance to grazing, with slow, reversible, and directional change. Grazing also reduced invasive species and had little effect on wildfires in this region. On the other hand, responses to grazing within the North American Deserts were less similar, likely due to the higher proportion of warm-season precipitation and associated C_4 grasses in the Colorado Plateau and interactions between cool-season precipitation, C_3 annual-grass abundance and fire-driven shifts in plant composition in the Great Basin. Third, convergence or divergence in grazing effects on the plant community across ecoregions and ecosystems directly relates to the potential for grazing management to impact the resistance and/or resilience of these rangelands to global change.

These findings from synthesizing over three centuries of combined research at six research stations are consistent with key conceptual models on grazing (Milchunas et al., 1988; Cingolani et al., 2005) as well as recent global meta-analyses and syntheses based on short-term data sets (1–10 years; Bakker et al., 2006; Koerner et al., 2018; Maestre et al., 2022; Price et al., 2022). Price et al. (2022) describe three key factors influencing the effects of grazing on plant diversity: (1) evolutionary history of grazing; (2) resources available for plant growth; and (3) contemporary grazing intensity; all of which also relate to grazing effects on plant dynamics across these study sites. Milchunas et al. (1988) also proposed that moisture availability linked to productivity and evolutionary history of grazing are key forces that have shaped rangeland plant communities by influencing the physical structure and resistance to the effects of grazing. Such differences may underlie, for example, the lower resilience to livestock grazing with higher and uniform stocking rates (O'Reagain et al., 2014) in Australia (Eldridge et al., 2016), which has a low evolutionary history of grazing, as compared to central Asia (Pei et al., 2008; Liu et al., 2015) and Africa (Porensky et al., 2013; Charles et al., 2017), which have longer histories of grazing. Differences in evolutionary history across global rangelands, such as across continents, are much more profound than in the ecosystems in this synthesis. However, the divergent vegetation responses to grazing between Great Plains and North American Desert ecoregions do align with evolutionary history of grazing as well as climate. The Great Plains sites have a long evolutionary history of grazing (Mack & Thompson, 1982; Axelrod, 1985), with high abundance of large grazing herbivores, particularly *Bos bison* (American bison) providing a keystone role shaping the structure and function of these rangeland ecosystems (Knapp et al., 1999). Large herbivores were likely less abundant in the North American Desert ecoregion due to climate limitations on productivity (Mack & Thompson, 1982; Price et al., 2022). In addition to a gradient in evolutionary history of grazing, there is also a related gradient in the most limiting resource, water, between the two ecoregions (Table 1; Figure 1). Supporting the effects of water availability, the site in this synthesis with the lowest water availability (CRC) was also the least resilient site to grazing, leading to rapid transitions to alternate stable states with heavy grazing (Box 1).

While this study focuses on just six sites, each one represents decades of research on a particular ecosystem, as well as representing distinct rangeland vegetation types of broad extent in the western United States. All sites demonstrate that livestock grazing can play a large role in resilience and/or resistance to global change, as found in other systems (e.g. Chaneton et al., 2002; Al-Rowaily et al., 2015). However, contrary to predictions, the relationships between livestock grazing and global change agents were generally ecoregion-specific and complex. Some of the specific causes of variation in grazing response to global change are shifting rapidly, such as climate, whereas others, such as soil properties and common native plant species, are changing to a lesser degree or at a slower rate. Large changes in soil water availability are likely across western US rangeland ecosystems with climate change (Bradford et al., 2020), but the identity and associated traits of dominant native perennial species in each region are unlikely to change rapidly via dispersal, competitive dynamics, and/or adaptation even with dramatic changes in climate. This suggests that the current regional vegetation composition will determine the potential for grazing management to impact ecosystem responses to climate change in the near future (decadal time scales). For instance, in the Great Basin, a more limited range of species traits with respect to growing-season precipitation and grazing may limit the capacity for livestock grazing to affect climate-driven community change. The exception, however, is the relationship of livestock grazing to invasive species in the Great Basin, because fuel reductions driven by livestock grazing have the potential to limit the conversion of large swathes of native vegetation to invasive species with fire. In the Great Plains and Colorado Plateau, livestock grazing could either accelerate or dampen changes in vegetation composition with climate change depending upon the timing and intensity of use, because combinations of species with varying grazing response traits and primary seasons of growth (cool vs warm) coexist in these ecosystems.

Climate, soil texture, and vegetation composition are associated with highly variable, even reversed grazing effects on ecosystems services across global rangelands (Maestre et al., 2022). These broadscale differences are further linked to vegetation composition as a function of evolutionary history (Price et al., 2022) and/or the relative dominance of grazing-tolerant species (Koerner et al., 2018). Our results suggest that sustainable rangeland management in an era of global change may be informed by understanding how more static factors, such as soil texture and common native plant species, as well as changing properties, such as climate change and invasive species, control ecosystem grazing response. As a whole, the unique combination of these factors within rangeland ecosystems will likely determine where and when adaptively managing livestock distribution and grazing (Derner et al., 2021) can increase plant community resilience to global change in western North American rangelands, and beyond. Best practices in the near future are more likely to be unique than shared across sites, and should be tailored based on robust, context-specific understanding, informed by data on long-term outcomes. Successfully balancing livestock production and conservation with global change will require adaptive grazing management reflective of the high complexity and variation across rangeland ecosystems.

AUTHOR CONTRIBUTIONS

All authors discussed the ideas and contributed to writing the paper, with David L. Hoover and Stella M. Copeland taking the lead in writing.

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DATA AVAILABILITY STATEMENT

Unpublished data (in Figure 2 and Figure S1) are in Appendix S3.

ORCID

Stella M. Copeland https://orcid.org/0000-0001-6707-4803

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

Appendix S1. Site vegetation details.

Appendix S2. Site grazing experiment and measurement details.

Appendix S3. Data in Figure 2 and Figure S1 described in Appendix S2.

Figure S1. Absolute values for cover and richness by site and grazing treatment.

Supporting information S1. Supplementary material.

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