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RESEARCH ARTICLE

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Assessing the rate and reversibility of large-herbivore effects on community composition in a semi-arid grassland ecosystem

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Abstract

Questions: What are the rate, reversibility, and degree of symmetry in plant species compositional change in response to the addition and removal of cattle grazing in the shortgrass steppe? Specifically, how does the imposition and removal of grazing affect the abundance of perennial C_4 shortgrasses and C_3 midgrasses that are of primary importance for livestock production in the region?

Location: Shortgrass steppe, northeastern Colorado, USA, in the North American Great Plains.

Methods: We evaluate rates and magnitude of basal cover change in newly ungrazed and newly grazed sites (established in 1991), relative to change in long-term (grazed and ungrazed) comparison treatments (established in 1939) over 25 years. We also compare shifts in species basal cover in newly implemented treatments relative to baseline community composition measured at the start of the study.

Results: Unlike the limited change observed in long-term treatments between 1939 and 1991, we documented more rapid, reversible and largely symmetric effects of both the imposition and removal of grazing between 1992 and 2017. This was primarily due to differences in the rate of increase in basal cover of C_3 midgrasses, litter, and bare ground. However, the rate and direction of change differed when assessed relative to continuously evaluated and (early-treatment) baseline cover data.

Conclusions: Studies of plant community change in response to large-herbivore grazing under varying ecological conditions and management regimes are needed to effectively guide the development and revision of state-and-transition models (STMs) for grassland managers, and to better detect and plan for dynamic ecological conditions. Effective adaptive management and STM development under a changing climate will recognize that effects of grazing and removal of grazing on shortgrass steppe can be reversible in a relatively symmetrical pattern, occurring within 6–16 years.

KEYWORDS

climate change, grazing, plant–herbivore interactions, semiarid grassland, shifting baselines, shortgrass steppe, state and transition models

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1 | INTRODUCTION

Plant community responses to large-herbivore grazing under varying ecological conditions, evolutionary histories, and herbivore management regimes are only beginning to be quantified by experimental studies. This emergent research has been limited by the long temporal scales over which these dynamics occur, and by changing climatic conditions. Recent empirical studies addressing vegetation responses to long-term grazing treatments have enhanced the development of State-and-Transition Models (STM) in grasslands globally (Westoby et al., 1989; Fynn and O'Connor, 2000; Suding and Hobbs, 2009). State-and-Transition Models (STMs)communicate potential alternative vegetation states and thresholds, within-state shifts in community composition, and management drivers of these dynamics (Knapp et al., 2011b; Stringham et al., 2003; Westoby et al., 1989). However, managers and researchers have expressed concern that in many ecosystems we lack long-term experiments to guide and revise existing models (Knapp et al., 2011a; Twidwell et al., 2013). Empirical evaluation of the temporal scales at which plant community shifts occur in multiple directions and how these scales may be changing are needed to help prioritize management strategies and achieve ecological objectives. Moreover, because livestock grazing management is a primary strategy indicated in STMs to drive community and state shifts (Twidwell et al., 2013) there is a need to evaluate rates of vegetation change in relation to both increases and decreases in grazing intensity.

1.1 | Empirical development of state-and-transition models

State-and-Transition Model development in grassland ecosystems has often evaluated vegetation compositional shifts across a range of grazing intensities (Fynn and O'Connor, 2000; Cingolani et al., 2003), and relied on evidence from space-for-time substitution methods, which identify multiple pathways for state and community transitions from point-in-time sampling. For example, Kachergis et al. (2012) built evidence-based STMs in sagebrush steppe with plant community composition data from plots with different management and disturbance histories. Here, grazing at different intensities accounted for two of six possible transition pathways and "no grazing or low grazing intensity" was indicated to maintain diverse (reference) communities in a claypan site (Kachergis et al., 2012). In other cases, long-term observational datasets have been used to assess potential transitions among plant community states, but did not experimentally assess the effects of grazing on such transitions (Bagchi et al., 2012 for Sonoran Desert grasslands; Jamiyansharav et al., 2018 for Mongolian grasslands; Sims et al., 2019 in Australia). Longer-term experiments are needed to test such hypothesized thresholds and community shifts without space-for-time substitution.

Experimental evaluations of whether the imposition and the removal of grazing have equivalent effects on vegetation dynamics are uncommon (Huang, et al., 2018; Suding and Hobbs, 2009). Globally, many long-term exclosure studies were established following a historical period of intensive grazing pressure from domestic livestock during European colonial expansion, for example in the USA, Uruguay, and Australia (Witt et al., 2011; Sayre, 2017; Ferreira et al., 2020). Early grazing experiments typically involved the establishment of exclosures or other protected areas, but did not examine the effects of adding or increasing grazing pressure (Milchunas, 2011). The long temporal and large spatial scales needed to evaluate these shifts are also logistically challenging (Scheffer and Carpenter, 2003).

Even when long-term data are available, transition dynamics are difficult to observe experimentally (Suding and Hobbs, 2009). For example, Chihuahuan Desert grasslands failed to exhibit state-transition dynamics after a pulse disturbance–recovery experiment because vegetation cover recovered with rest from grazing regardless of historical grazing treatment after 13 years (Bestelmeyer et al., 2009). Sims et al. (2019) evaluated the effects of grazing removal on grassy woodlands in southeastern Australia over 17 years and found that grazing removal initiated limited divergence from grazed sites but did not lead to convergence with reference sites.

1.2 | Plant community dynamics in the western Great Plains

Our study specifically informs STM development in grasslands with an evolutionary history of heavy grazing from large and small herbivores, fire, and periodic drought, as is the context in the western Great Plains of North America (Milchunas et al., 1988). Here, we report on a grazing reversal experiment conducted with exclosures established in 1939 and in which grazing treatments were modified beginning in 1992. This study was designed to examine the rate and reversibility of moderate cattle grazing effects on shortgrass steppe (Figure 1). Half of each exclosure was opened to grazing (with the remainder continuing as a long-term exclosure), and a new exclosure was established in a nearby, previously grazed plot. We report on 25 years of plant species composition measurements within these four treatments consisting of (a) continuously grazed 1939–present, (b) continuously ungrazed 1939–present, (c) grazed 1939–1991, newly ungrazed 1992–present, and (d) ungrazed 1939–1991, newly grazed 1992–present (Figure 1).

Our primary research objective was to evaluate the rate, reversibility, and symmetry of change in plant composition in response to the addition and removal of cattle grazing in the shortgrass steppe, focusing in particular on the abundance of perennial C_4 shortgrasses and C_3 midgrasses that are of primary importance for livestock production in the region. A second objective was to compare the plant community dynamics detected when comparing treatments to both (a) continuosly grazed and ungrazed sites (exclosures) and (b) to early-treatment assessments of plant community composition, thereby making these results applicable for managers who may use early-treatment assessments or grazing exclosures in adaptive management.

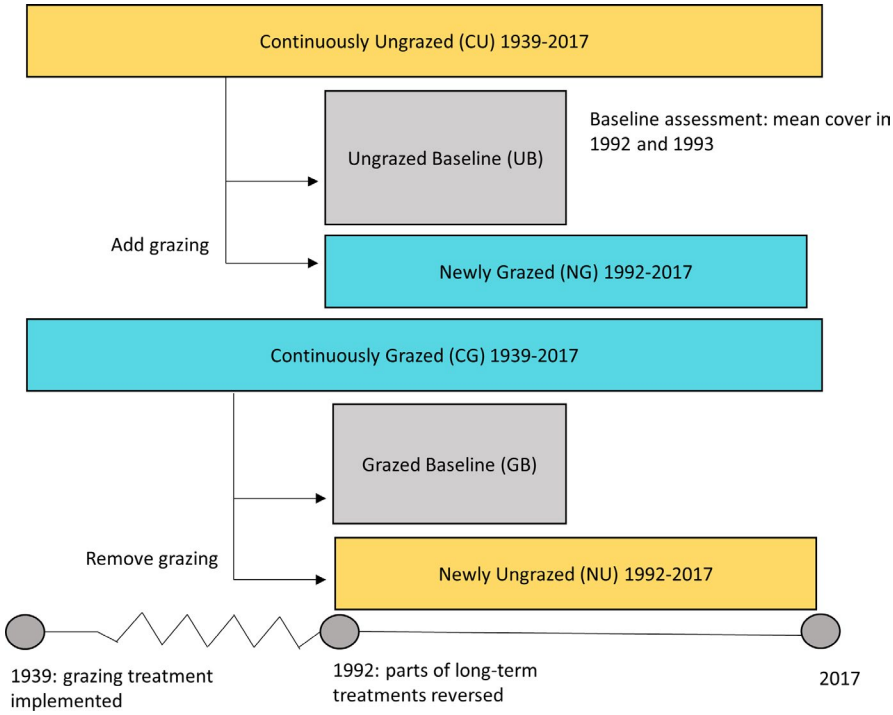

FIGURE 1 Timeline of grazing treatments applied to shortgrass steppe in northeastern Colorado, USA. We compared basal species and functional group composition among (1) grazed baseline (GB) and ungrazed baseline (UB) treatments calculated as the average of 1992–1993 cover on grassland subject to grazed and ungrazed treatments in place from 1939 to 1991 with (2) cover in temporally varying, or continuously grazed and ungrazed treatments (CG and CU), measured annually and maintained for the duration of the study, and with (3) annual measurements on newly implemented grazing (NG) and newly ungrazed (exclosure) treatments (NU) at five replicate sites

We reviewed empirical research from the western Great Plains to develop expectations for our study findings. In grasslands of central North America, which evolved under heavy grazing pressure from mammalian herbivores (Milchunas et al., 1988), several long-term experiments are beginning to document the slow, directional and reversible effects of grazing by livestock and prairie dogs on vegetation dynamics over multiple decades. Working in mixed-grass prairie in Kansas, Harmoney (2017) found that when heavy and light livestock grazing treatments were reversed following a 20-year grazing intensity experiment, community composition also reversed, with a decrease in warm-season perennial shortgrass *Bouteloua dactyloides* and increase in *Pascopyrum smithii* after five years in the heavy-to-light stocked grassland. Similarly, in mixed-grass prairie of Wyoming, Porensky et al., (2016) evaluated plant cover change in a 33-year grazing intensity experiment with reversal to light or no grazing following 25 years of heavy grazing. Where heavy grazing had led to dominance of the C_4 shortgrass *Bouteloua gracilis*, a switch to eight years of light or no grazing allowed C_3 midgrasses to recover (Porensky et al., 2016). The effects of very intensive grazing (by black-tailed prairie dogs), which led to substantial increases in bare soil exposure and reduced perennial grass in shortgrass steppe of Colorado, were reversed over just a five year period following prairie dog removal, even in the presence of continued moderate grazing by livestock (Augustine et al., 2014). These studies all emphasize the capacity for taller structured perennial grasses to increase in abundance following removal of long-term heavy grazing, supporting the contention that central North American grasslands are resilient to grazing (reviewed by Milchunas et al., 2008).

Some of the long-term studies on livestock grazing management in the US western Great Plains have occurred in shortgrass steppe at the Central Plains Experimental Range (CPER) in eastern Colorado. This research station was established in 1937 in response to the extreme drought of the 1930s. In 1939 researchers built a network of livestock grazing exclosures in areas with a range (light, moderate and heavy) of cattle stocking rates (Figure 1, Klipple and Costello, 1960). Over the next two decades, only minimal changes in plant community composition were documented across this grazing intensity gradient, and C_4 shortgrasses (*Bouteloua gracilis* and *Bouteloua dactyloides*) dominated in terms of cover and productivity (Klipple and Costello, 1960). Longer-term (50+ year, from 1939 until the 1990s) exclusion of grazing had a modest effect on species composition, primarily consisting of increases in C_3 midgrasses with light or no grazing (Milchunas et al., 2008). However, during the past two decades (1990s–2010s) vegetation composition responded more rapidly to grazing, with moderate to heavy grazing intensity sustaining dominance of C_4 shortgrass, and long-term lack of grazing shifting the community toward dominance by C_3 midgrasses coexisting with ruderal forbs (Augustine et al., 2017; Porensky et al., 2017). Milchunas published an initial analysis of this experiment in 2011. He found plant species richness in the areas newly opened to grazing converged with long-term grazed areas within 10 years, while plant richness in new exclosures had only partially diverged from those in long-term grazed sites after 16 years.

The current STM for the loamy plains ecological site plant community (USDA NRCS 2014) emphasizes shifts in community phases via changes in relative amounts of grazing-resistant C_4 shortgrasses vs. *Pascopyrum smithii*. The STM suggests reversible community phases among shortgrass and *Pascopyrum smithii*-dominated communities as a result of imposition and relaxation of grazing over multiple decades, but does not specify the time scale over which these changes occur.

1.3 | Improving manager assessment of plant community change

Experimental evaluations of plant community dynamics hypothesized in STMs can inform managers conducting their own monitoring and adaptive management. Our secondary research objective was to compare the dynamics detected relative to two different "baseline" measurements, data similar to those gathered from grazing exclosures and from pre or early-treatment monitoring. Shifts in atmospheric CO_2 levels and observations of increased C_3 graminoid abundance in both long-term grazed and long-term ungrazed areas at our study site (Augustine et al., 2017) led us to hypothesize that different ways of calculating changes in plant communities would lead to a different understanding of these dynamics. Under dynamic climatic and atmospheric conditions, managing grazing to return grassland species composition to previous "reference" conditions described in STMs may be impractical (Milchunas, 2006), though long-term studies of climate change and grazing interactions are rare (Dangal et al., 2016; Augustine et al., 2017; Jamiyansharav et al., 2018). A comparison of how grazing imposition and removal affects community composition when viewed in relation to a fixed (i.e., "desired" or "reference") plant community, as well as in relation to a temporally dynamic community (e.g., what one could observe annually within ungrazed reference plots/exclosures) are both needed to fully interpret rates of change and reversibility in the STM context.

Therefore, we present contrasting analyses of community change based on (a) comparison to an early-study reference community, derived from data collected at the time the reversal experiment started in the early 1990s, and (b) comparisons between continuously grazed vs. continuously ungrazed plant communities measured annually, as they might be when managers maintain grazing exclosures, to account for dynamic and potentially directional shifts in composition over time.

Our research questions were: (a) what are the rate, reversibility, and degree of symmetry in plant species compositional change in response to the addition and removal of cattle grazing in the shortgrass steppe; (b) how does the imposition and removal of grazing affect plant communities and specifically the abundance of perennial C_4 shortgrasses and C_3 midgrasses that are of primary importance for livestock production in the region; and (c) how does an assessment of this change differ when grazing treatments are compared to continually implemented comparative treatments (e.g., continually maintained exclosures) and to the early-study reference community (e.g., a baseline assessment).

2 | METHODS

2.1 | Study site

We conducted this study at the Central Plains Experimental Range, a ~6,400 ha Long-Term Agroecosystem Research (LTAR) Network site in northeast Colorado, USA (40°50′ N, 104°43′ W). Mean annual water-year (October–September) precipitation (1940–2017) is 343 mm and varies widely (coefficient of variation [CV] = 26%). During the study period (1992–2017), annual water-year precipitation ranged from 231 mm (2012) to 612 mm (1999), and three years (2002, 2004, and 2012) received less than 75% of the long-term mean precipitation (see Appendix S1). The shortgrass steppe is dominated by drought- and grazing-tolerant palatable C_4 shortgrasses (*Bouteloua gracilis and Bouteloua dactyloides). Pascopyrum smithii* is a palatable mid-height C_3 grass, which declines under heavy grazing (Porensky et al., 2017). Other species include cactus *Opuntia polyacantha*, forb *Sphaeralcea coccinea*, subshrub *Gutierrezia sarothrea*, and the palatable shrub *Atriplex canescens*.

2.2 | Experimental design

As reported in Klipple and Costello (1960) and Milchunas (2011), long-term grazing treatments and exclosures (~100 m × 100 m) were established at CPER in 1939. Moderately grazed areas enclosed by fencing (130 ha) were stocked with an average of 2.6 ha/yearling cattle for the six-month growing season (early May through October or early November). Grazing exclosures prevented access by cattle but not small herbivores (lagomorphs and rodents). Pronghorn antelope (*Antilocapra americana)* may pass under the lowest wire of the fences, but are rarely observed inside exclosures.

In 1992, grazing treatments were reversed to assess how this semiarid grassland transitions among states and to examine short-term responses to both the release from and imposition of grazing. Half of each of six long-term exclosures were opened to grazing and new large-herbivore exclosures were constructed adjacent to the historical exclosures on formerly long-term grazed land. This resulted in four treatments consisting of continuously grazed 1939–present (CG), continuously ungrazed 1939–present (CU), grazed 1939–1991, newly ungrazed 1992–present (NU), and ungrazed 1939–1991, newly grazed 1992–present (NG) (see Figure 1). One historical exclosure site was colonized by black-tailed prairie dogs mid-way through the study, which fundamentally altered the grazing regime. This site was discontinued and removed from the study, giving a total of five replicate sites.

We measured basal cover in 30 Daubenmire quadrats (0.1 m^2) in each of the four treatments at each site, each year from 1992 to 2017, with the exception that no measurements occurred in 1994 or 2013. We visually estimated basal cover of each plant species and bare ground, fungi, dung, and litter using six classes of 1 = <5%; 2 = 5–14%; 3 = 15–24%; 4 = 25–39%; 5 = 40–59%; 6 = 60–100%. We converted values to class mid-points, removed rare species (fewer than 5% of observations; see McCune and Grace, 2002), and calculated relative cover, such that each plot was scaled to 100% cover (including individual plant species, plus relative cover of litter and bare ground).

Plots where continuously-grazed (CG) and ungrazed (CU) treatments were maintained for the duration of the study period (1992–2017) are analogous to small grazing exclosures managers establish

in their grasslands to monitor trends in vegetation and evaluate how grazing affects community composition relative to a continuously ungrazed (and measured or observed annually) community. Managers without access to annually measured reference sites may use a specific, desired reference community, such as those defined in STMs or measured at one point in time from a desired community state, to evaluate management outcomes. We calculated an analogous baseline community composition as the average of the community composition measurements during the first two years of our study (1992 and 1993) in the original continuously grazed and ungrazed treatments (see Figure 1). We refer to the community composition measured in these first two years of the study as the grazed baseline (GB) and ungrazed baseline (UB) communities (Figure 1).

2.3 | Analytical approach

To evaluate the rate, reversibility and symmetry of reversal of the effect of grazing on plant communities within the experiment we used a combination of three analyses. First, we calculated Bray–Curtis dissimilarity in relative basal cover for each combination of treatments and used general additive mixed models (GAMMs) to compare community dissimilartiy over time, accounting for experimental block and preciptiation. This enabled an evaluation of the rate of non-linear plant community change, but did not enable us to see which species accounted for that change. Then, we used unconstrained ordinations on the multi-variate community abundance data set and ploted species scores to determine how communities in continuous and newly implemented treatments diverged from and converged with one another and from data collected during the baseline years (1992–1993) in ordination space over time. Finally, we focused on the dominant grasses using univariate analyses of change in relative cover of the C_3 mid-grass, *Pascopyrum smithii* and the C_4 shortgrass functional group (the sum of *Bouteloua gracilis and Bouteloua dactyloides* cover). We describe the specific details of these three steps below.

2.3.1 | Evaluating when the effect of grazing treatments on plant communties reversed

We used dissimilarity analysis to reduce multi-dimensional measures of many species in two communities to a single number indexing the degree of dissimilarity between the two communities. This approach has frequently been used to compare effects of grazing on community composition across multiple studies and ecosystems (Milchunas et al., 2008; Milchunas and Lauenroth, 1993). All of the community dissimilarity values we present were calculated using the Bray–Curtis method using the R (R Core Team version 3.5.0, 2018) package vegan (Dixon, 2003; R package version 2.5-6, 2019).

We calculated Bray–Curtis dissimilarity in relative basal cover for each combination of treatments. Visual inspection of the results indicated potential non-linear changes in community dissimilarity for some treatment combinations over time, which precluded fitting of linear models. We implemented GAMMs via the gamm4 package in R (R package version 0.2-6, 2020) to evaluate change in dissimilarity over time for each relevant treatment pair. GAMMs use a non-parametric smoothing term to fit the data, and hence are suitable for detecting potential non-linear trends in data. The mixed-model framework allowed us to incorporate experimental block (four treatments each replicated in five blocks) in the models as a random effect (Wood, 2017). We considered models in which the smoothing term could vary by treatment pair based on a cubic regression spline with a maximum of four knots to minimize the complexity of the non-linear form of the models (Wood, 2017).

We also sought to account for the potential influence of precipitation variability among years on community dissimilarity. Wet years often lead to increases in forb species richness and increase abundance of C_3 grasses, whereas dry years may have lower overall species richness and greater community dominance by C_4 shortgrasses. This could in turn affect the magnitude of dissimilarity among grazing treatments, with reduced dissimilarities hypothesized to occur in dry years. We therefore examined models with and without current years' growing season precipitation (March–June) and previous years' spring (March–May) and summer (June–August) precipitation as separate fixed effects. We used Akaike Information Criteria (AICs) to select final models.

For each set of community dissimilarity values, we calculated a 95% confidence interval (CI) as two standard errors from the predicted mean, and we interpret rates of convergence and divergence among pairs of treatments on the basis of the degree of overlap in CIs. To address our secondary objective, which was to evaluate plant community responses relative to two different "baselines" in order to make the results applicable for managers, we separately report results (a) comparing newly implemented treatments (NG, NU) and continuous treatments (CG, CU) and (b) comparing newly implemented treatments to early-treatment baseline assessments from 1992 to 1993 (GB and UB).

2.3.2 | Evaluating how plant communities changed as grazing treatments were reversed

We used Non-metric Multi-dimensional Scaling (NMDS) ordinations of relative cover with the R library vegan (Dixon, 2003; R package vegan version 2.5-6, 2019) to examine variation in plant community composition among plots (in five sites) in the four grazing treatments at the start of our study. We ran separate ordinations comparing the first two years of measurements (1992–1993), then two years in which divergence was detected in the GAMMs (2006–2007) and finally the last two years of measurements (2016–2017). We calculated treatment centroids and associated 95% CIs, as well as individual species scores. To further interpret patterns in the species composition change, we evaluated correlation among the ordinations and treatment centroids using the envfit function in vegan. We used the ordinations to compare the degree of divergence between grazed and ungrazed grassland that occurred during the first half-century of grazing exclusion

(1939–1993), with the degree of divergence between grazed and ungrazed treatments during the subsequent 25 years, in terms of both newly grazed vs. continuously ungrazed (NG vs. CU) and continuously grazed vs. ungrazed communities.

We then conducted univariate analyses of change in relative cover of the dominant C_3 mid-grass, *Pascopyrum smithii*, and the shortgrass functional group (the sum of *Bouteloua gracilis and Bouteloua dactyloides* cover), again using GAMMs with block as a random effect to account for potential non-linear changes over time and examining models with and without the above precipitation variables as separate fixed effects, selecting models using AIC.

3 | RESULTS

3.1 | Community change following grazing reversal

Our analyses show that the effects of the imposition and exlusion of grazing were reversible, relatatively symmetrical, and occurred within 16 years when assessed relative to continuously grazed and continuously ungrazed treatements (black line, Figure 2a,b). For our comparison of newly implemented treatments to continuous treatments, the most parsimonious models of dissimilarity all included grazing treatment and current growing season precipitation. The significant coefficient for current growing season precipitation ($p < 0.001$) in the model comparing NG and CG treatments indicates that increasing precipitation in current and past growing seasons enhanced community dissimilarity (Appendix S2). Our models of community dissimilarity therefore account for interannual variation in precipitation in terms of estimating the rate of grazing imposition and removal on community composition.

At the beginning of the study, the newly ungrazed treatment was relatively similar to the continuously grazed treatment (CG; e.g., fitted value of 0.15 in 1992; blue curve; Figure 2a) compared to higher dissimilarity between continuously grazed and continuously ungrazed treatments (CG vs. CU; dissimilarity of 0.24 in 1992). However, note that 95% CIs for these two sets of dissimilarity values still overlapped in 1992–1993. The newly ungrazed treatment

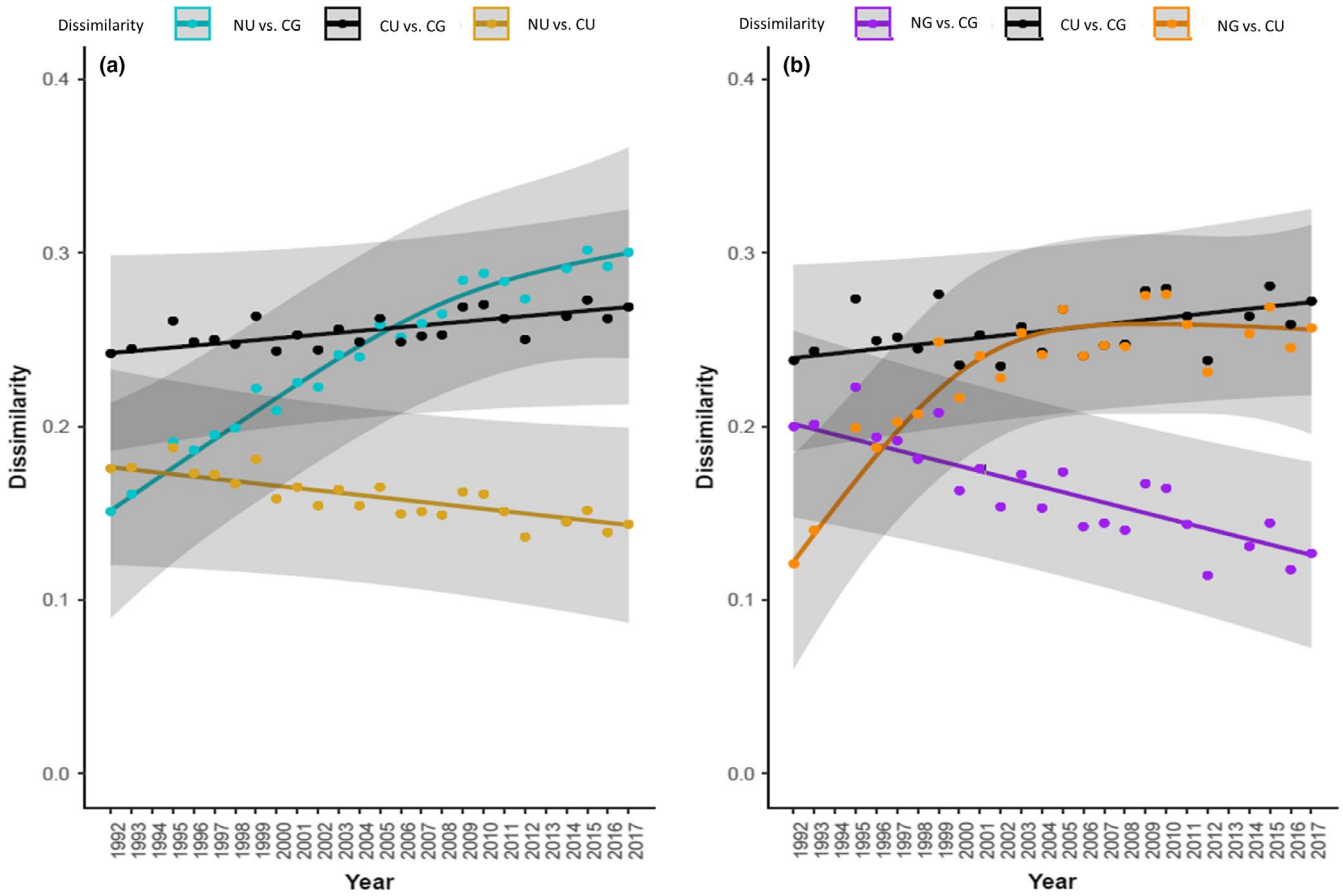

FIGURE 2 Divergence in community composition between grazing treatments in shortgrass steppe of northeastern Colorado as measured by Bray–Curtis dissimilarity (ranging from 0 = no dissimilarity to 1 = completely dissimilar). Curves show predicted changes over time based on a generalized additive mixed model fit to allow for potential non-linear trends, points are fitted values, and grey shading shows 95% CIs around predicted values for each treatment pair assuming a normal distribution. Panel (a) illustrates removal of cattle from formerly grazed shortgrass steppe, as shown by declining dissimilarity over time between the newly ungrazed vs. continuously ungrazed treatment (NU vs. CU; yellow curve), and increasing dissimilarity between the newly ungrazed vs. the continuously grazed treatment (NU vs. CG; blue curve). Panel (b) illustrates the addition of cattle to formerly ungrazed shortgrass steppe, as shown by increasing dissimilarity over time. For comparison, we also show the dissimilarity between continuously grazed continuously ungrazed treatments (CG vs. CU; black lines)

then diverged rapidly and relatively linearly from the continuously grazed treatment, reaching a maximum of ~0.3 by 2015 (blue curve; Figure 2a). For comparison, the continuously ungrazed vs. continuously grazed treatments diverged at a lower, linear rate (CU vs. CG, black line), such that GAMM-estimated dissimilarities for CU vs. CG and NU vs. NG both reached the same level in 2006 at 0.25 (blue and black curve intersection; Figure 2a).

In contrast, dissimilarity between the newly ungrazed and continuously ungrazed (NU vs. CU; yellow line) declined approximately linearly over the entire 25-year period, from 0.18 in 1992 to 0.14 in 2017 (Figure 2a). Based on the 95% CIs, NU vs. CU dissimilarity diverged from NU vs. CG dissimilarity by 2007, indicating grazing effect reversal, and remained lower until 2017 (Figure 2a).

Changes in the newly grazed communities showed a relatively similar pattern. The newly grazed treatment was similar to the continuously grazed treatment in 1992 (dissimilarity ~0.13 in 1992, orange curve in Figure 2b), reflecting the modest divergence in community composition at the start of our measurement period. Over the next 14 years, newly grazed treatments diverged rapidly from the continuously ungrazed treatment. GAMM-estimated dissimilarities between NG vs. CU and CG vs. CU became nearly identical (at ~0.26), indicating full reversal of the exclosure effect by 2003 (orange and black curves; Figure 2b). Thereafter (2003–2017), NG vs. CU dissimilarity remained stable. In contrast, dissimilarity between the newly grazed treatment and the continuously grazed treatment (NG vs. CG) declined approximately linearly over the entire 25-year period, from a predicted mean of 0.20 in 1992 to 0.13 in 2017. Based on the 95% CIs, NG vs. CG dissimilarity diverged from NU vs. CG dissimilarity beginning in 2007, indicating a reversal of the exclosure effect, and remained lower until 2017 (Figure 2b). These comparisons indicate a greater rate of effect of grazing imposition (converging with the continuously grazed treatment by 2003) vs. grazing removal (diverging from grazed treatments by 2007). Overall, the patterns revealed by the shapes of the dissimilarity curves for both the removal of grazing

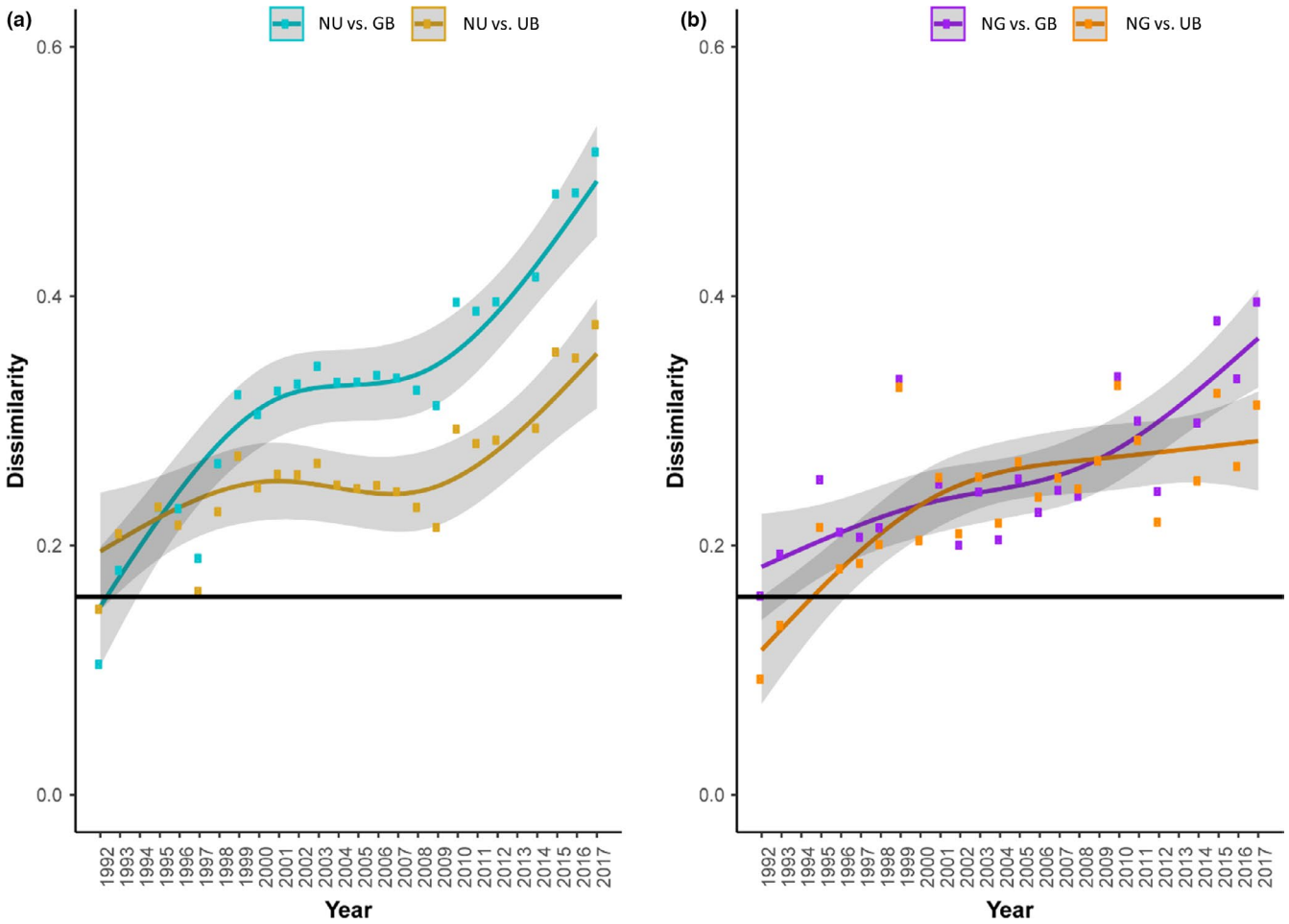

FIGURE 3 Divergence in community composition among newly implemented treatments compared to baseline (1992–1993) data, quantified using the Bray–Curtis dissimilarity index (ranging from 0 = no dissimilarity to 1 = completely dissimilar). Curves show predicted changes based on a generalized additive mixed model fit to allow for potential non-linear trends, points are fitted values, and grey shading shows 95% CIs around predicted values for each treatment pair assuming a normal distribution. Panel (a) shows how the newly ungrazed treatment diverged from the original grazed community over the 25 year period (NU vs. GB; blue line). Panel (b) shows the newly grazed treatment diverged from the original ungrazed baseline over time as expected (NG vs. GB; purple curve). The newly grazed treatment also diverged from the original ungrazed baseline at a similar rate (NG vs. UB; orange curve). For comparison, we show the dissimilarity between ungrazed vs. grazed baseline (UB vs. NU, flat black line)

(Figure 2a) and the addition of grazing (Figure 2b) are similar, indicating that the rate and magnitude of the effects of both treatments are largely symmetric.

3.1.1 | Newly implemented treatments compared to baseline (1992–1993) communities

The picture of these dynamics changes when we assess newly implemented treatments relative to early-treatment assessment data from 1992-1993. The final model for the analysis comparing newly ungrazed to a grazed baseline (NU vs. GB) included a significant treatment effect, but did not include precipitation variables from the current or previous years (Appendix B). Fixed effects for the final model comparing newly grazed and ungrazed baseline (NG vs. UB) included treatment, current year growing season precipitation ($p < 0.001$), and previous year's spring precipitation ($p < 0.05$). The significant coefficients for current year and previous years' spring precipitation indicate that increasing precipitation in either or both seasons resulted in greater community dissimilarity for the newly grazed treatment relative to the baseline community (Appendix B).

Figure 3a shows the rate of change in grassland communities when we excluded cattle from formerly grazed sites and assessed this change relative to early-study baseline data (blue curve). The newly ungrazed communities diverged from grazed communities faster than when we assessed change relative to continuously grazed treatments (which took <16 years) (blue curve in Figure 3a vs. blue curve in Figure 2a). Changes in dissimilarity over the study period were also non-linear, with the most rapid increases occurred during 1992–2001 and 2009–2017, as compared to a period of minimal change during the relatively dry sequence of years from 2000 to 2008 (Figure 3a). Dissimilarity between the newly ungrazed and the early-treatment UB community increased in a similar pattern throughout the 25-year period (at a lower rate than NU vs. GU; Figure 3a), indicating directional changes in community composition unassociated with the effect of grazing.

Relative to the GB data, adding grazing to formerly ungrazed grassland increased dissimilarity rapidly early in the study (1992–2000) before slowing to ~0.3 by 2017 (orange curve in Figure 3b). As with grazing removal, grazing addition to formerly ungrazed grassland changed composition more rapidly when assessed relative to the baseline data (within four years) than relative to the continuously ungrazed treatment (orange curves in Figures 2b vs. 3b).

Surprisingly, dissimilarity between the newly grazed sites and both the ungrazed and the grazed baseline (orange and purple in Figure 3b respectively) increased in a similar manner over the course of the study, the latter indicating a substantial directional shift in composition unassociated with grazing.

3.2 | How plant communities changed

Ordination results and univariate analysis for dominant grasses allow us to evaluate how the relative abundance of plant species changed during the experiment. For the CU treatment established in 1939, community composition in 1992 and 1993 (following 54 years of grazing exclusion) diverged only modestly from composition in the CG treatment (Appendix S3, $k = 3$, stress = 0.15). Ellipses for the two grazed vs. two ungrazed sets of plots overlapped along axis 1, but separated along axes 2 and 3. This separation reflected the expected trend of increased cover of C_3 perennial grasses (especially *Pascopyrum smithii*) and litter, and reduced cover of warm-season perennial grasses (especially *Bouteloua gracilis* and *Bouteloua dactyloides*) and bare soil, in the CU treatment (Appendix S3).

By 2016–2017, the NU treatment (centroid 0.05, 0.09, 0.09) ordinated along axes 2 and 3 near cool-season perennial C3 grasses (*Pascopyrum smithii* −0.27, 0.42, 0.11) and *Hesperostipa comata* (0.63, 0.22, −0.07) while the CG treatment ordinated along axes 2 and 3 near *Bouteloua gracilis* (−0.14, −0.06, −0.20), and *Bouteloua dactyloides* (−0.38, −0.36, −0.06) ($k = 3$, stress 0.16, Appendix S3).

3.2.1 | Cover of dominant grass species

The most parsimonious models of cover of dominant C_4 shortgrass species (*Bouteloua gracilis* and *Bouteloua dactyloides*; hereafter *Bouteloua* cover) included grazing treatment, current growing season precipitation, and the previous year's spring and summer precipitation (Appendix S2 for coefficients). During 1992–2002, basal cover of C_4 shortgrasses increased rapidly in both continuously CG (black line) and NG (orange line) treatments, reaching peak abundance during 2007–2009 (Figure 4). In the NU (blue line), *Bouteloua* cover also increased at the beginning of our study period, but reached a maximum in 2000, five years earlier than the grazed treatments, and declined in cover thereafter (Figure 4). All three treatments attained mean *Bouteloua* basal cover of >20% during the three consecutive years of 1999–2001. Only in the CU treatment did *Bouteloua* remain at a relatively stable and low GAMM-estimated mean basal cover of 9–17% during the entire decade from 1992 to 2001. From 2001 onward, *Bouteloua* cover in the NU treatment showed a downward trend, and converged with *Bouteloua* cover in the continuously ungrazed treatment during 2009–2017. In contrast, *Bouteloua* cover in both grazed treatments reached maximal values during 2002–2009, and declined during 2009–2017. Despite the latter decline, the GAMM-estimated 95% CIs show that *Bouteloua* cover remained significantly greater in both CG and NG compared to both CU and NU treatments from 2008 to 2017 (Figure 4).

The final model for *Pascopyrum smithii* cover included grazing treatment but not a main precipitation effect from current or previous years (Appendix S2). *Pascopyrum smithii* cover increased linearly in the CU and NG treatments over the 25-year study period, whereas cover remained stable in CG and NG treatments (Figure 5). In 1992, none of the treatments differed significantly in *Pascopyrum smithii* cover. *Pascopyrum smithii* cover increased more rapidly in the NU treatment than any other treatment, converged with the CU treatment in 2010, and continued to increase to a maximum cover of about five percent by 2017 (Figure 5). We note that because of

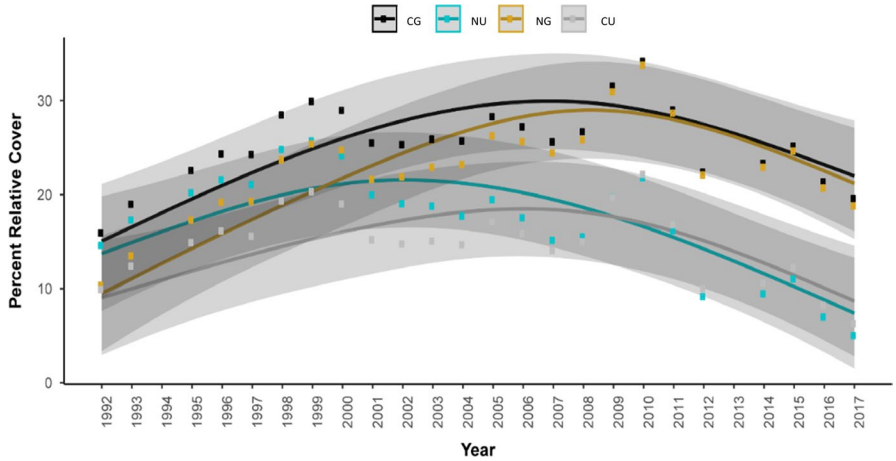

FIGURE 4 Changes over 25 years in relative basal cover of the dominant C4 shortgrasses, *Bouteloua gracilis* and *Bouteloua dactyloides*, in four grazing treatments in the shortgrass steppe of northeastern Colorado, USA. Curves show predicted changes over time based on a generalized additive mixed model fit to allow for potential non-linear trends, points are fitted values, and grey shading shows 95% CIs around predicted values for each treatment pair assuming a normal distribution. CG = continuously grazed; NU = previously grazed/newly ungrazed; NG = previously ungrazed/newly grazed; CU = continuously ungrazed

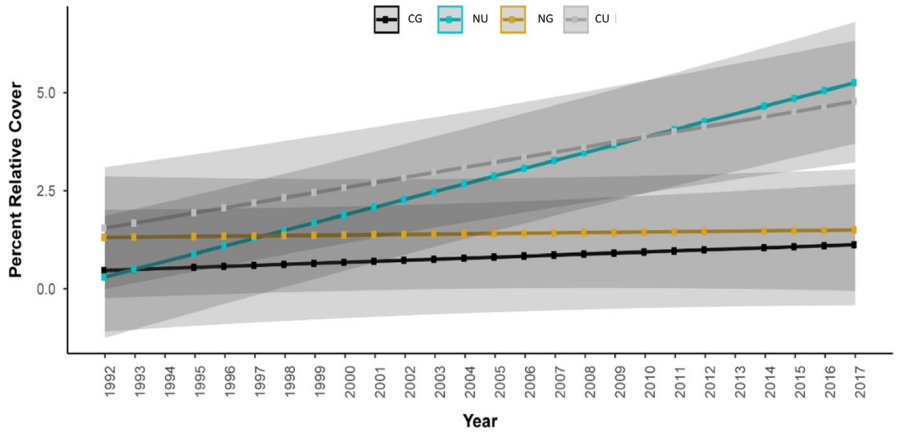

FIGURE 5 Changes over 25 years in basal cover of the dominant C_3 midgrass, *Pascopyrum smithii*, in four grazing treatments (solid lines) in the shortgrass steppe of northeastern Colorado, USA. Curves show predicted changes over time based on a generalized additive mixed model fit to allow for potential non-linear trends, points are fitted values, and grey shading shows 95% CIs around predicted values for each treatment pair assuming a normal distribution. CG = continuously grazed; NU = newly ungrazed; NG = newly grazed; CU = continuously ungrazed

the vertical growth form of *Pascopyrum smithii* tillers, this species' relative contribution to total above-ground biomass is much greater than its relative basal cover. In the NG treatment, *Pascopyrum smithii* cover remained nearly constant over the entire 25-year study period, albeit with large CIs. *Pascopyrum smithii* cover in the NU treatment diverged significantly from cover in the CG treatment beginning in 2010, and from the NG treatment beginning in 2013 (Figure 5).

4 | DISCUSSION

We found that both the imposition and removal of grazing induced long-term shifts in shortgrass community composition, primarily due to changes in the relative cover of C_4 shortgrasses, C_3 midgrasses (especially *Pascopyrum smithii*), litter, and bare ground. These shifts were largely similar in terms of the rate of response to both addition and removal of grazing, as indicated by similar patterns in the dissimilarity analyses for both grazing addition and removal (Figure 2a vs. b), and by shifts in both overall basal cover composition and cover of the dominant C_4 shortgrasses (*Bouteloua gracilis* and *Bouteloua dactyloides*) and dominant C_3 midgrass (*Pascopyrum smithii*). The only notable non-symmetric response we detected was in the rate of response of *Bouteloua* cover, which increased rapidly with imposition of grazing (NG diverging from the CU treatment beginning in 2001, or after ten years), but showed a more delayed decline in response to the removal of grazing (NG diverging from the CG treatment beginning in 2007, or after 16 years).

Divergence of NG and NU treatments from long-term, continuous treatments was constrained during dry periods throughout the mid-2000s, when total cover of *Pascopyrum smithii* was low regardless of grazing treatment. Historical presence of grazing tended

to hinder *Pascopyrum smithii* response to precipitation in the early 2000s in the newly ungrazed treatments, and enhance *Bouteloua* response to precipitation early in the study in the newly grazed treatments. However, these effects dissipated later (2009–2017) as plant communities in newly imposed treatments diverged from their long-term treatments of origin.

Furthermore, we found that the rate of divergence of grazed vs. ungrazed grassland is increasing over time. Species composition (based on foliar cover measurements) during the 1940s and 1950s was similar between grazed and ungrazed treatments (Klipple and Costello, 1960). Ordinations show only modest separation of grazed vs. ungrazed communities by 1992–1992, followed by complete community-level divergence beginning in 2002 (Figure 2), significant differences in cover of the dominant perennial grasses by 2007–2008 (Figures 4, 5), and substantial separation of grazed vs. ungrazed communities by 2016–2017. These results are consistent with, and provide a more detailed temporal picture of, the finding that in the absence of grazing, C_3 grasses have increased more in recent decades than during the mid-twentieth century (Porensky et al., 2016, 2017; Augustine et al., 2017).

Our analysis of treatment effects relative to the early-study baseline composition of communities measured early in our study (1992–1993 Figure 3) also shows that we would interpret a change in composition over the past 25 years differently without access to both long-term treatments (exclosures) and the 1992–1993 baseline data. In particular, we documented rapid divergence between the newly ungrazed and the fixed baseline grazed communities during 2009–2017 (Figure 3a), even though dissimilarity between annually measured grazed vs. ungrazed communities remained relatively constant throughout this time period (Figure 2).

These results are consistent with the idea that shortgrass plant communities are undergoing directional shifts in composition that are not driven by grazing, and may be related to changes in the climate system. In particular, multiple field experiments in the western Great Plains show that C_3 perennial grasses can benefit from elevated atmospheric [CO_2] (Morgan et al., 2004; Polley et al., 2011; Zelikova et al., 2014, Augustine et al., 2018), which is consistent with our finding of increased divergence in grazed vs. ungrazed communities over the past 25 years as a result of increasing dominance of *Pascopyrum smithii* in the absence of grazing. A directional change in precipitation did not occur during the 25-year period, so this does not appear to be a likely explanation, but other ongoing changes such as shifts in the timing of the growing season, increasing temperature, and increasing N deposition can not be ruled out. Finally, we note that the low rate of community divergence during 1939–1992 could be related to the impact of severe drought during 1930–1939, from which plant communities may have been slowly recovering in the mid-twentieth century.

Such directional shifts create challenges for managers trying to interpret the effects of their grazing management relative to weather and climate-related effects on grassland communities. "Shifting baselines" is described as a problem where successive generations of resource managers perceive their current conditions as a natural baseline, without recognition of trends and patterns occurring over longer time scales (Olson, 2002; Jorgenson, et al., 2019). Applying that line of thinking to our study, the grazing removal treatment, implemented in 1939, spans the same historical period during which the United States Forest Service grazing permits have been managed in cooperation with some of the oldest grazing associations in the US near the Central Plains Experimental Range (Furman and Ball, 1943; Shoop et al., 1989), and the later period during which agency STMs were first developed (Knapp et al., 2011a). As in grasslands throughout the world, multi-generational ranchers here may have decades of collective experience and local ecological knowledge which can bolster the capacity of ranching communities to anticipate and cope with complex, dynamic, and uncertain drivers and outcomes of plant–herbivore interaction (Knapp et al., 2011a; Fernández-Giménez and Estaque, 2012; Reid et al., 2014). However, local knowledge based on the ecological dynamics in the mid–late 20th century, such as the limited change we observed in basal cover among long-term grazed and long-term ungrazed sites after 59 years (1939–1992), does not account for a grassland system changing as rapidly as we observed in the early 21st century, with shifts in C_4 and C_3 species composition and overall cover occurring within 6–16 years. Management decision-making (and STM-based decision support) informed by running, long-term comparison treatments and comparison to pre- or early-treatment data over multiple decades may help managers disentangle the effects of rising atmospheric CO_2 and other climatic changes from grazing management decisions. On the other hand, ranching operational strategies, public lands grazing management, and STMs that assume fixed relationships between large-herbivore grazing and grassland community dynamics may miss opportunities to adapt to these dynamic grazing outcomes.

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AUTHOR CONTRIBUTIONS

DGM established the study, led data collection, and assisted with data analysis and conceptual framing; DJA led data collection for the last five years; HW and DJA led data analysis and writing; JDD contributed with analysis and writing; all authors discussed the results and contributed to editing.

DATA AVAILABILITY STATEMENT

Data (https://doi.org/10.15482/USDA.ADC/1519153) are publically availaåble at: https://data.nal.usda.gov/dataset/assessing-rate-and-reversibility-large-herbivore-effects-community-composition-semi-arid-grassland-ecosystem-gztx-data-central-plains-experimental-range-nunn-colorado-usa-1992-2017

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

Appendix S1. Precipitation summary during study period

Appendix S2. Summary of GAMM models

Appendix S3. Ordination results and species code look-up table

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