Herbivory and drought generate short-term stochasticity and long-term stability in a savanna understory community

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Abstract. Rainfall and herbivory are fundamental drivers of grassland plant dynamics, yet few studies have examined long-term interactions between these factors in an experimental setting. Understanding such interactions is important, as rainfall is becoming increasingly erratic and native wild herbivores are being replaced by livestock. Livestock grazing and episodic low rainfall are thought to interact, leading to greater community change than either factor alone. We examined patterns of change and stability in herbaceous community composition through four dry periods, or droughts, over 15 years of the Kenya Long-term Exclosure Experiment (KLEE), which consists of six different combinations of cattle, native wild herbivores (e.g., zebras, gazelles), and mega-herbivores (giraffes, elephants). We used principal response curves to analyze the trajectory of change in each herbivore treatment relative to a common initial community and asked how droughts contributed to community change in these treatments. We examined three measures of stability (resistance, variability, and turnover) that correspond to different temporal scales and found that each had a different response to grazing. Treatments that included both cattle and wild herbivores had higher resistance (less net change over 15 years) but were more variable on shorter time scales; in contrast, the more lightly grazed treatments (no herbivores or wild herbivores only) showed lower resistance due to the accumulation of consistent, linear, short-term change. Community change was greatest during and immediately after droughts in all herbivore treatments. But, while drought contributed to directional change in the less grazed treatments, it contributed to both higher variability and resistance in the more heavily grazed treatments. Much of the community change in lightly grazed treatments (especially after droughts) was due to substantial increases in cover of the palatable grass *Brachiaria lachnantha*. These results illustrate how herbivory and drought can act together to cause change in grassland communities at the moderate to low end of a grazing intensity continuum. Livestock grazing at a moderate intensity in a system with a long evolutionary history of grazing contributed to long-term stability. This runs counter to often-held assumptions that livestock grazing leads to directional, destabilizing shifts in grassland systems.

Key words: climate; dominance; grazing; livestock; rangeland; resistance; turnover.

Introduction

Herbivory and rainfall, along with fire and soil nutrients, are key drivers of grassland and savanna communities (Bell 1982, Fuhlendorf and Smeins 1997, Sankaran et al. 2005, Anderson et al. 2007, Bond 2008), which together cover ~25% of the world's land surface. Human activities, however, are changing the nature of these fundamental driving variables. Episodic periods of low rainfall, already common in these semiarid ecosystems (Pandey and Ramasastri 2001), are expected to become more frequent and more intense as climate change progresses, regardless of changes in mean annual rainfall (Field 2012).

At the same time, large wild herbivore populations are rapidly declining, often being replaced by domesticated herbivores (Du Toit and Cumming 1999, Ripple et al. 2015). An understanding of how wild herbivores, domestic herbivores, and rainfall interact to structure plant communities is necessary to effectively manage these systems. At the same time, such an understanding can provide new insights into how multiple forms of disturbance interact to shape the dynamics of natural systems.

Intense livestock grazing and other disturbances have been widely observed to lead to land degradation in grassland and savanna systems (Bestelmeyer et al. 2015), and there is a long history of ecologists putting forth different concepts of stability and change for these systems (Westoby et al. 1989, Noy-Meir 1995, Briske et al. 2005, 2006, Bestelmeyer et al. 2015). One challenge is that grazing can be considered both an anthropogenic disturbance

and a natural part of healthy ecosystem functioning (Milchunas et al. 1988). Many rangelands have a long evolutionary history of grazing by wild ungulates; however, contemporary livestock grazing practices may not mimic historical grazing patterns for a variety of reasons. For example, livestock have different foraging habits than those of wild ungulates and are often grazed at higher annual stocking rates with more frequent return intervals than historically wide-ranging wild ungulates (Fuhlendorf and Engle 2001). Thus, depending on the circumstances, livestock grazing may either fill some of the functional role of historic grazing in community and ecosystem dynamics (Veblen et al. 2016) or represent a novel disturbance for which there is no historical analog (Eldridge et al. 2016).

Even for systems with a history of grazing by native herbivores, livestock-dominated systems are often assumed to be less stable and more variable than systems dominated by native ungulates. This may be because (separately or in combination) wildlife communities are more diverse and occupy a broader set of niches than livestock, because livestock are usually stocked at rates that have a higher net grazing intensity than wildlife, or because inappropriate livestock grazing practices have been associated with rangeland degradation around the world (Du Toit and Cumming 1999, Bestelmeyer et al. 2015). In particular, the combination of livestock grazing and "drought" (defined variably in the literature, but generally a period of months to years of moisture deficit; Lloyd-Hughes 2013) has been associated with significant changes in herbaceous community composition, especially increases in unpalatable species (Albertson and Weaver 1944, Fuhlendorf and Smeins 1997, Loeser et al. 2007). In these cases, heavy grazing by livestock can be compounded by low rainfall to cause mortality among palatable plant species, allowing less competitive, more "weedy" species to establish and typically resulting in a less diverse community. Relatively less attention has focused on the lower end of the grazing spectrum, which is often associated with native grazers, and on how drought does or does not lead to plant community change under these grazing conditions. Lightly to moderately grazed systems can become dominated by highly competitive, often palatable, species at the expense of overall species diversity (Olff and Ritchie 1998, Bakker et al. 2006). This dominance could be reduced by drought if it causes mortality among dominant species, or maintained despite drought if the combination of light grazing and drought is insufficient to cause reductions of dominant species. These different possible outcomes of herbivory and drought will impact the degree to which a system is considered stable or not.

Community stability can vary not only depending on ecological context, but also, potentially depending on which aspect of stability is assessed (Pimm 1991, Donohue et al. 2013, 2016). The most typically used measure of stability in ecological experiments is *temporal variability*, or the coefficient of variation in community attributes such

as cover, composition, or biomass, after detrending for any directional changes (Pimm 1984). Other measures include *resistance*, or the inverse of total community change observed in a plot over time compared to a control (Pimm 1984, Donohue et al. 2013); *compositional turnover*, or the extent of change in community composition (change in similarity index) from one time step to another; *robustness*, or the number of extinctions observed in a plot over time; and *number of invasions* or new species arrivals observed in a plot over time. In theory, all of these facets of stability could be independent of each other, some correlated and others independent, or all correlated with each other (Donohue et al. 2013). However, different forms of stability have different implications for management and conservation. For example, short-term stochasticity (high *variability*) may be less important if *resistance* is high and there is no associated long-term destabilization. Thus, it is valuable to clarify the effects of a variety of grazing management scenarios on multiple axes of stability.

The Kenya Long-term Exclosure Experiment (KLEE) was designed to facilitate comparison of the long-term effects of domestic vs. wild herbivores (Young et al. 1998). The experiment, established in 1995, includes replicate 4-ha plots grazed by cattle and wild ungulates (divided into meso- and mega-herbivores) separately and in combination. Within this experiment, we have measured change in the herbaceous community through several cycles of average to above-average rainfall punctuated by periods of low rainfall. In our previous work, we showed that herbaceous community composition has diverged substantially across six different herbivore treatments and that this divergence is mediated largely by total herbivore pressure rather than herbivore type (Veblen et al. 2016). Here, using the same 15-yr data set, we (1) focus on the mechanisms, particularly the potential interactions between herbivory and drought, that have driven trajectories of divergence not just among treatments but relative to initial conditions. We then (2) consider the effects of droughts, in the context of the six herbivore treatments, on three aspects of community stability: resistance, variability, and turnover (Table 1; data did not indicate any extinctions or invasions). Finally, we (3) examine how species-level dynamics and changes in richness and dominance in response to drought and herbivory underlie observed differences in community stability and change.

MATERIALS AND METHODS

Study site and experimental design

The Kenya Long-term Exclosure Experiment (KLEE) is located on the Mpala Ranch and Conservancy (36°52′E, 0°17′N) in Laikipia, Kenya. During our study period (1999–2013), rainfall at the site averaged 596 ± 51 mm/yr (mean ± SE; range 364–1003 mm/yr). The "black cotton" ecosystem in which KLEE is located is dominated by the tree *Acacia drepanolobium* Sjost. and the grasses *Pennisetum mezianum* Leeke,

TABLE 1. Summary of measures of stability used to evaluate change in plant community composition over 15 years in response to six herbivore treatments and episodic dry periods, or droughts.

Stability measure	Conceptual definition	Operational (quantitative) definition used in this paper	Responses to herbivore treatment and drought observed in this paper
Resistance (more resistance means more stability)	degree to which community structure remains unchanged in the face of a perturbation	inverse of overall change in community (PRC score) from beginning to end of the study period	plots with less herbivory show less resistance
Temporal variability (more variability means less stability)	variability of a community attribute in time (after accounting for directional change)	standard deviation of the residuals from linear regressions of PRC scores against time for each treatment, divided by the mean PRC score for that treatment	plots with less herbivory had less variability
Compositional turnover (more turnover means less stability)	extent of change in community composition from one time step to another	absolute value of change in PRC score between consecutive sample periods	no differences by herbivore treatment; compositional turnover was greatest during droughts and post-drought periods

P. stramineum Peter, *Themeda triandra* Forssk*.*, and *Brachiaria lachnantha* (Hochst.) Stapf. Mpala is managed for both wildlife conservation and livestock production. Cattle are stocked at low to moderate densities (0.10–0.15 cows/ha).

The KLEE experiment uses semi-permeable barriers to allow access by different combinations of cattle (C), meso-herbivore wildlife 15–1,000 kg (W; e.g., zebras *Equus quagga* Gray, Grant's gazelles *Gazella [Nanger] granti* Brooke, eland *Taurotragus oryx* Pallas, and hartebeest *Alcelaphus buselaphus* Pallas) and mega-herbivore wildlife (M; elephants *Loxodonta africana* Blumenbach and giraffes *Giraffa camelopardalis* L.). The experiment consists of three replicate blocks, each containing six 200 × 200 m (4-ha) treatment plots (18 total plots). Treatments include (1) MWC, accessible to mega-herbivore, meso-herbivore wildlife and cattle; (2) MW, accessible to mega-herbivore and meso-herbivore wildlife; (3) WC, accessible to meso-herbivore wildlife and cattle; (4) W, accessible to meso-herbivore wildlife; (5) C, accessible to cattle; and (6) O, no large herbivore access. Herded groups of cattle are periodically grazed in all cattle-treatment plots to simulate typical cattle management practices in the region. See Appendix S1 for further details on the study site and experimental design.

Data collection

Herbaceous vegetation data have been collected in all 18 KLEE plots annually (in June) or biannually (in February and June) since 1999. Here, we use aerial plant cover data collected by counting the number of pins hit by each species of grass or forb over a 10-point pin frame at gridded sampling stations spread over the innermost hectare of each plot. Details of the sampling are given in our companion paper, Veblen et al. (2016), which made use of the same data set. Because our primary interest was species composition, we use relative cover data only.

Relative cover is the total number of pins hit by each species divided by the total number of pins hit across all species within each plot and sample period. Relative cover provides an index of the contribution of each species to the herbaceous community while controlling for differences in total biomass due to herbivore treatments and rainfall variability. We excluded plant species that occurred in <5% of all samples (all plots over all sample periods), resulting in a data set of 55 taxa (46 species and 9 multi-species groups) accounting for >99.8% of total plant cover (see Veblen et al. [2016] for more details).

Analysis of long-term community change relative to initial conditions and rainfall

To assess the long-term interactive effects of rainfall and herbivore treatments on plant community composition, we used Principal Response Curve (PRC) analysis (Van den Brink and Ter Braak 1999, Pardal et al. 2004, Alday et al. 2012). PRC is a specialized form of redundancy analysis (RDA) designed for multivariate, repeated-measures data. In our previous analyses (Veblen et al. 2016), we used a partial RDA ordination method where time is a covariable to control for temporal trajectories of community change (focusing on the treatment effects, rather than the temporal effects). In the present study, our objective was instead to look specifically at the trajectory of temporal change and to ask questions about plots' divergence from initial conditions, not just from each other. We used a modified Principal Response Curve (PRC) method as described in Van den Brink et al. (2009) where, instead of comparing to a dynamic reference community, we created a static reference that was not allowed to change over time so that the PRC analysis compared all six herbivore treatments to this reference at each time step. The reference community was defined as the cover of each species in 1999 averaged across all herbivore treatments for each block (to create one average value per

block). We chose this reference community because 1999 was an average rainfall year, there were no treatment effects on the relative cover of individual species in the 1999 data, and because non-metric multi-dimensional scaling (NMDS) results showed no significant separation of the herbaceous community by treatment at this time (Veblen et al. 2016).

We used the vegan library (version 2.0-8) for R (version 3.0.1) to perform the PRC analysis. Results are given as sample and species scores along a set of constrained PRC axes that relate plant community composition to herbivore treatments and treatment × time interactions. We used permutation tests to evaluate the overall significance of PRC axes and then extracted species and sample scores. Data were not transformed because standard transformations (e.g., Wisconsin square root and log transform) did not qualitatively affect our results but reduced the percentage of variance explained by the PRC axes.

Following the PRC analysis, we analyzed extracted sample scores for the first PRC axis (which explained 67% of the treatment-related variation in plant community structure) using a linear mixed model (LMM). This was done to accomplish two main objectives that could not otherwise be met within the PRC analysis: (1) to separate the effects of treatment from the treatment × time interaction while accounting for the effects of block and temporal auto-correlation, and (2) to enable us to examine the role of additional covariates such as rainfall and their interactions with other predictor variables. In this LMM, block and plot nested within block were treated as random factors, and an autoregressive covariance structure was used to address the non-independence of repeated surveys in the same plots. Fixed effects included herbivore treatment, time, and treatment × time, where "treatment" includes the six herbivore treatments and the initial (reference) community and "time" is a continuous variable (between 0 and 173 months). Previous work has shown that rainfall values in the preceding rainy seasons (both immediately preceding and the two rainy seasons prior to that) are important predictors of plant composition in this system (Porensky et al. 2013). We included three rainfall covariables to account for rainfall-related variability. These were $rain_t$ (total rainfall during the rainy season just before the vegetation survey, summed over four months), $rain_{t-1}$ (total rainfall during the previous rainy season), and $rain_{t-2}$ (total rainfall during the rainy season before that). We also included interaction terms between herbivore treatment and these rainfall variables. All LMMs were performed in R (version 3.0.1) using the nlme package (Pinheiro et al. 2013).

Analysis of community stability and divergence

We calculated three attributes of community-level stability directly from PRC axis 1 scores (Table 1). First, we calculated *community resistance* as the inverse of net change (Pimm 1984, Donohue et al. 2013); in this case, we used

the reciprocal of the difference in PRC axis 1 score between each treatment and the initial community. We calculated resistance for each plot in each of the last three sample periods and averaged these values to get one resistance value for each plot. To test for differences among treatments, we used a one-way ANOVA with treatment and block as main effects. Second, we calculated detrended temporal *variability* in community composition as the standard deviation of the residuals from linear regressions of PRC axis 1 scores (one per block per time step) against time for each treatment, divided by the mean PRC score for that treatment (Tilman et al. 2006, Donohue et al. 2013). Third, we calculated *compositional turnover* (the magnitude of community change from one time step to the next; Donohue et al. 2013) as the absolute value of the difference between PRC 1 score for a given sample period and the preceding sample period ($|PRC_t - PRC_{t-1}|$).

Because we were particularly interested in the roles of herbivore treatment and prolonged dry periods as drivers of change, we conducted two additional analyses to examine (1) the effects of herbivore treatment and rainfall on compositional turnover and (2) the effects of rainfall on change in overall divergence across treatments (a consequence of differences in resistance). To focus on the effects of episodic, prolonged dry periods and their aftermath, we categorized each sample period as one of three rain categories: "drought" (rainfall in the bottom 25th percentile of all sample periods; less than 120 mm in the four-month rainy season preceding sampling), "post-drought" (the two sample periods after drought), and "moderate-wet" (all other rainfall conditions). Post-drought was defined as the two sample periods after drought based on our observations, both in the field and in the data, that it typically takes two rainy seasons for grass biomass to recover. In 2000–2001, there were three consecutive drought periods; for the purposes of defining the post-drought period, this was treated as one continuous drought. We use the term drought for the sake of convenience, although episodic dry period may be more accurate. Drought can mean many different things, but here we use it to mean the situation where one or more consecutive rainy seasons yielded very little rain, rather than to imply an event that was unique on a decadal or multi-decadal scale.

We analyzed compositional turnover as a function of herbivore treatment and rain category using a linear mixed model as described above. We calculated total among-treatment divergence as the difference in PRC 1 score between the two most extreme treatments (O, no herbivores present, and MWC, all herbivores present) for each time step, and from this the absolute value of the change in total divergence from one time step to the next. We analyzed this value as a function of rain category using a one-way ANOVA.

Analyses of dominant species and diversity

Finally, we used a further set of linear mixed models to analyze the patterns of (1) relative cover of the five

species that were most influential in driving community change, (2) the absolute value of change in percent cover of these species across consecutive time steps, in order to understand the effects of rainfall in driving changes in cover, (3) Shannon's diversity index (H'), and (4) Berger-Parker dominance index (cover value for the species with highest cover at time t; Berger and Parker 1970). We analyzed the effects of treatment, rain category, and time on these response variables using the same modeling approach as described above. Cover data for individual species were log- or square-root-transformed when necessary to meet model assumptions.

Results

Rainfall varied substantially over the course of the study period. Sample periods that were preceded by a four-month period with less than 120 mm total rainfall included February 2000, June 2000, February 2001 (we considered these three consecutive sample periods to be part of a single drought), March 2006, February 2008, and June 2009 (Fig. 1a). In contrast, the average four-month cumulative rainfall preceding all other sample periods was 272 mm, with a range of 159–446 mm.

Principal response curves (PRC) analysis showed that time, herbivore treatment, and treatment × time explained a substantial amount of variation (>75%) in plant community composition (Appendix S2: Table S1). Overall permutation test results were significant for all PRC axes combined ($F_{150,350} = 4.00$, $P = 0.005$) and for PRC axis 1 ($F_{1,350} = 402.43$, $P = 0.005$). The patterns of change in scores along PRC Axis 1 (Fig. 1b) accounted for 67% of treatment-related variation.

Trajectories of change over time differed among the treatments, as reflected by a significant treatment × time interaction in the LMM of PRC axis 1 scores ($F_{6,476} = 62.11$, $P < 0.0001$; see Appendix S2: Table S2 for full model). In general, plots with the least grazing showed the most consistent trajectory away from the initial herbaceous community. In particular, the least-grazed treatment (O, no large herbivores) diverged incrementally away from the reference over nearly every time step, exhibiting more or less linear, directional change ($R^2 = 0.61$; Appendix S2: Table S3). In contrast, the most-grazed treatment (MWC, mega-herbivores + meso-herbivores + cattle) showed a period of relatively little change from 2002 to 2006, and thereafter began to converge back toward the reference community. The net consequence was that community resistance was highest in the MWC and WC treatments ($F_{5,17} = 5.84$, $n = 18$, $P = 0.009$; Fig. 2a), while at the same time these two treatments also had the highest temporal variabilities (Fig. 2b).

Rainfall was a strong driver of compositional turnover and treatment divergence. The effects of rainfall on composition varied in direction, but not magnitude, across herbivore treatments (Fig. 1b). In the LMM where rainfall was treated as a continuous variable, treatment interacted with rainfall in terms of both the preceding rainy

season (four-month period immediately before vegetation sampling; treatment × rain$_t$, $F_{6,476} = 3.9$, $P = 0.001$) and two rainy seasons before that (treatment × rain$_{t-2}$, $F_{6,476} = 2.44$, $P = 0.025$), although not the intervening rainy season (treatment × rain$_{t-1}$, $F_{6,476} = 1.38$, $P = 0.22$; see Appendix S2: Table S2 for full model). These results suggest a lagged effect, in addition to a short-term effect, of rainfall variation. The LMM on compositional turnover, or the magnitude of change in PRC Axis 1 score between consecutive time steps, showed that turnover differed significantly by rainfall category ($F_{2,396} = 24.29$, $P < 0.0001$; see Appendix S2: Table S4 for full model). In all treatments, change was greatest during drought and post-drought periods and least during moderate-wet periods (Fig. 2c). Although the magnitude of change did not differ across treatments, the direction of change often did differ by treatment, particularly after 2006. Thus, differential responses to rainfall patterns, and particularly droughts, contributed to a general increase in the level of divergence among the six herbivore treatments over time. Change in the total divergence between the two most extreme treatments (O and MWC) was significantly higher during post-drought times than during drought and moderate-wet times (Fig. 2d; $F_{2,21} = 3.32$, $P = 0.049$).

The species with the highest weights associated with PRC Axes 1, 2, and 3 scores (a relative index indicating the greatest contribution to community change from initial conditions) were the perennial bunchgrasses *Brachiaria lachnantha*, *Themeda triandra*, *Lintonia nutans*, *Pennisetum stramineum*, and *Pennisetum mezianum* (see Appendix S2: Table S5 for a complete list of species weights for PRC axes 1–3). These are also the five most numerically dominant species in KLEE (Porensky et al. 2013). For all five species, rainfall category was the predominant predictor of both relative cover and change in relative cover (Appendix S2: Table S6). Change was greatest for all species during drought and/or post-drought periods (Fig. 3). However, the direction of these changes varied across species, leading to different outcomes over time. Cover of *B. lachnantha* increased during post-drought periods (Fig. 3a) leading to an increase in cover over time, especially in the least-grazed treatments (O, W, MW; Appendix S2: Fig. S7). Although there was not a significant interaction between treatment and rainfall over the entire time series, there was a noticeable change in dynamics beginning in 2006, after which *B. lachnantha* cover in the different herbivore treatments appears to have diverged progressively during each drought/post-drought cycle (Appendix S2: Fig. S7). Cover of *T. triandra* decreased during drought and post-drought periods (Fig. 3b), especially in the least-grazed treatments (significant treatment × herbivore interaction). As a result of this interaction, cover of *T. triandra* was maintained in more heavily grazed treatments but declined substantially in the less grazed treatments (Appendix S2: Fig. S7). For the remaining three dominant species, rainfall responses were consistent across herbivore treatments. Cover of
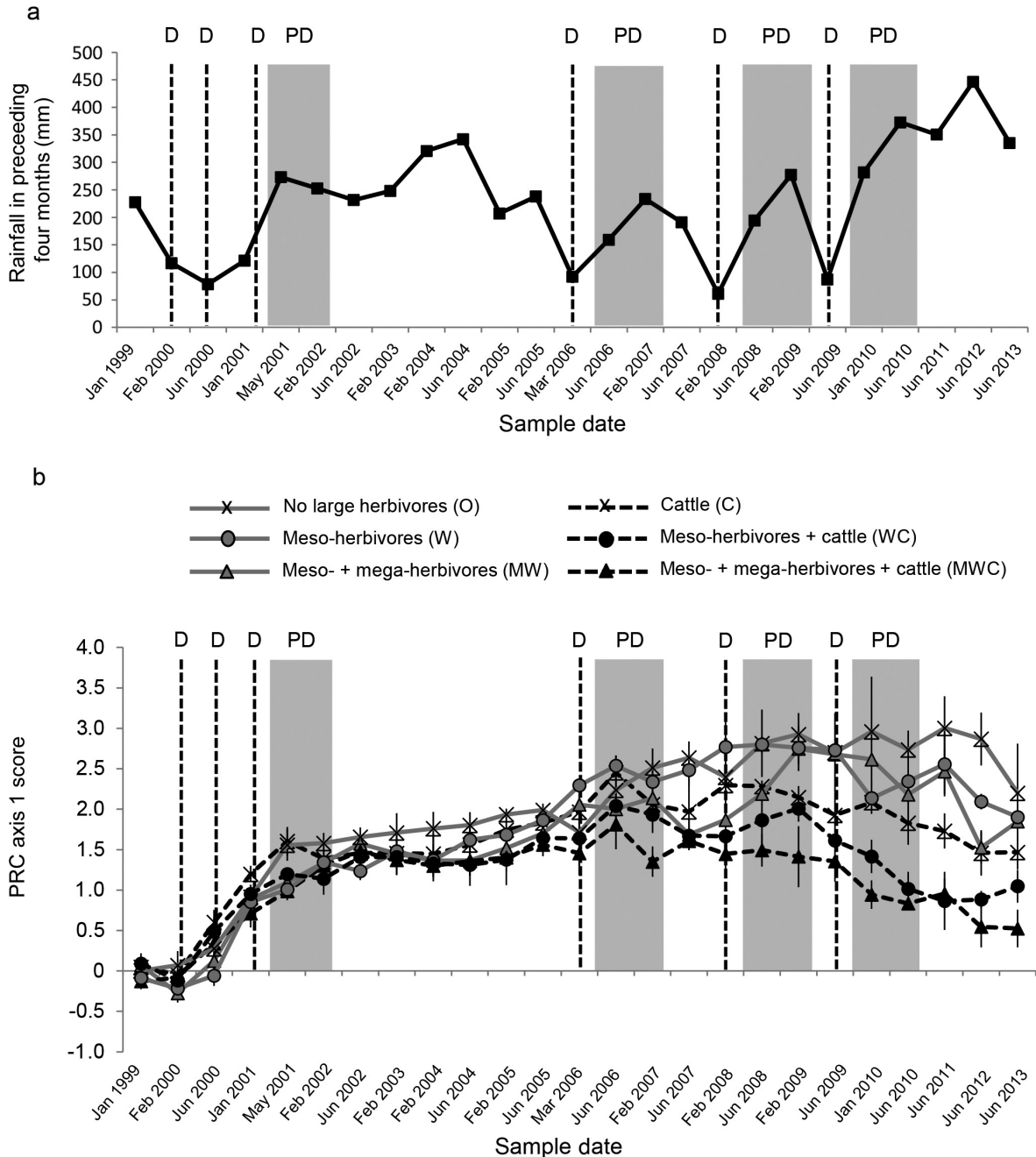
Fig. 1. (a) Total rainfall during the four-month period preceding each vegetation sampling period from January 1999 to June 2013. Six drought periods (D; each <100 mm of rain and below the 25th percentile of rainfall for all sample periods) are indicated with vertical dashed bars, and post-drought periods (PD; the two sample periods after each drought) are indicated in gray. (b) Principal response curves showing the change in PRC Axis 1 score (mean ± SE) over time for six herbivore treatments; treatments in order of increasing grazing intensity are O, W, MW, C, WC, MWC. Treatments are described in *Materials and methods: Study site and experimental design*. Treatment values are shown in reference to 1999 PRC Axis 1 scores averaged across all treatments and plots, which is represented by the line at PRC Axis 1 = 0.

P. stramineum and *P. mezianum*, both less desirable forage species, increased significantly during drought and post-drought periods relative to moderate-wet periods (Fig. 3c,e). Cover of *L. nutans* decreased substantially during droughts and appears to have been unable to

recover during post-drought periods (Fig. 3d), which perhaps contributed to the significant decline in this species across all treatments (Appendix S2: Fig. S7).

Species diversity was characterized by a significant interaction between treatment and rainfall category
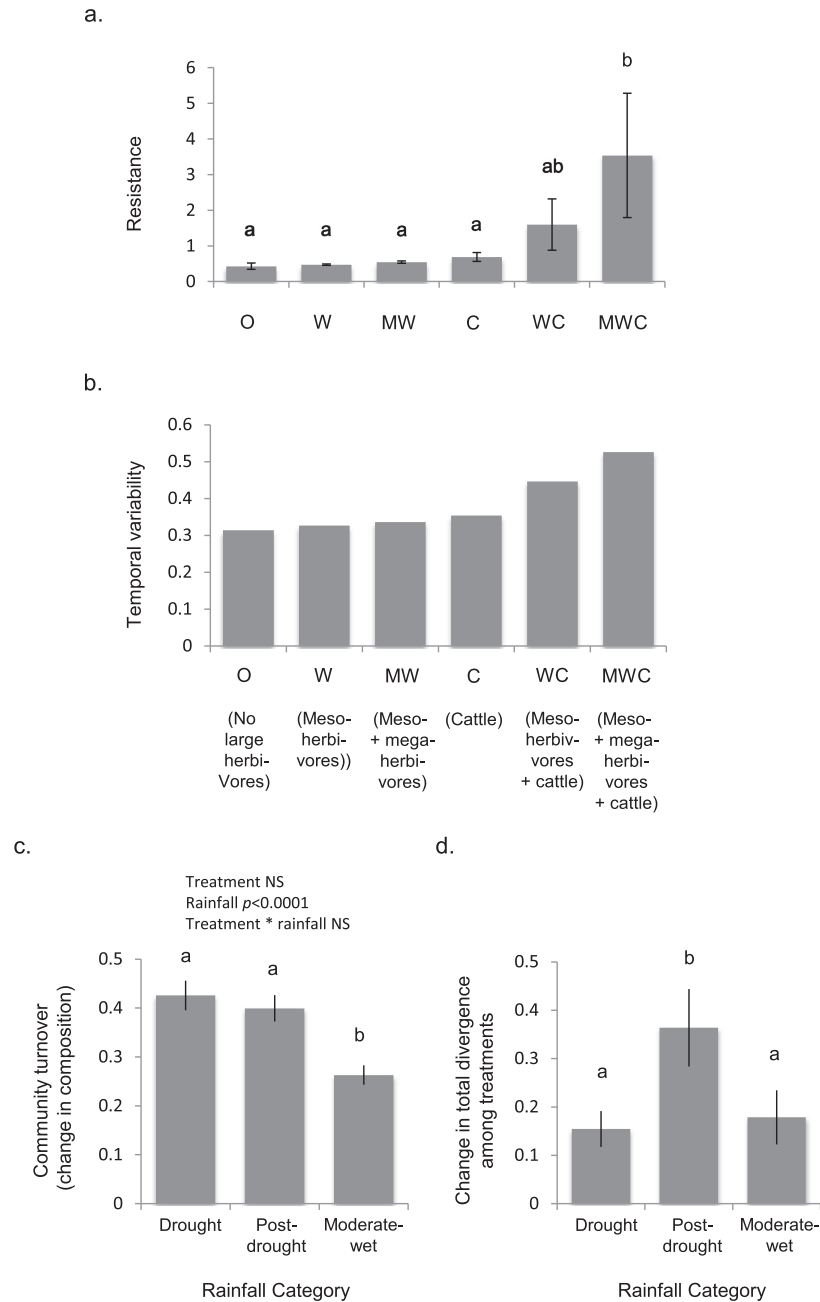
a.

b.

c.

Treatment NS
Rainfall *p*<0.0001
Treatment * rainfall NS

d.

FIG. 2. (a) Resistance (mean $\pm$ SE) for each of six herbivore treatments. Resistance (PRC Axis 1 score^{-1}) was first averaged within each plot for the last three sample periods, then averaged across replicate plots within each treatment to compare treatment means. Significant differences ($P \leq 0.05$) among treatments are indicated with different lowercase letters. (b) Temporal variability in PRC Axis 1 score (standard deviation of residuals of linear fit of [score by time]/[mean score]) for each of six herbivore treatments. Because there is one value per treatment, error bars are not applicable. (c) Absolute value of change in PRC Axis 1 score (from one sample period to the next; mean $\pm$ SE) for three categories of rainfall conditions, with significant differences indicated by different letters, and (d) absolute value of change in the difference (from one sample period to the next; mean $\pm$ SE) in PRC Axis 1 score between the two most divergent treatments (O and MWC), given for three categories of rainfall conditions with significant differences indicated by different letters.

($F_{10,413} = 2.60$, $P = 0.004$). Species diversity was generally lowest during drought periods and highest during post-drought periods (Fig. 4a). However, during drought and moderate-wet periods, diversity patterns did not differ significantly across treatments, whereas during post-drought periods diversity was higher in the more heavily grazed treatments than the less-grazed treatments (Fig. 4a). Patterns of dominance were the

inverse of diversity patterns; on average, dominance was highest in the less-grazed treatments and lowest in the most-grazed treatments (Fig. 4b), largely due to higher cover of *B. lachnantha* in less-grazed treatments. There was a marginally significant effect of treatment on dominance ($F_{2,413} = 2.65$, $P = 0.08$) but no significant interaction between rainfall and treatment ($F_{10,413} = 1.54$, $P = 0.12$). Dominance was significantly higher during drought than post-drought and moderate-wet periods (main effect of rain category, $F_{2,413} = 16.75$, $P < 0.0001$;

drought = 0.36 ± 0.013, post-drought = 0.33 ± 0.013, moderate-wet = 0.31 ± 0.012), likely because cover of most species was low during these times, inflating relative cover of the less palatable *P. stramineum* (Fig. 3c).

DISCUSSION

Rainfall and herbivory are two fundamental drivers of grassland and savanna plant dynamics. As in most savannas, our system is characterized by variable rainfall
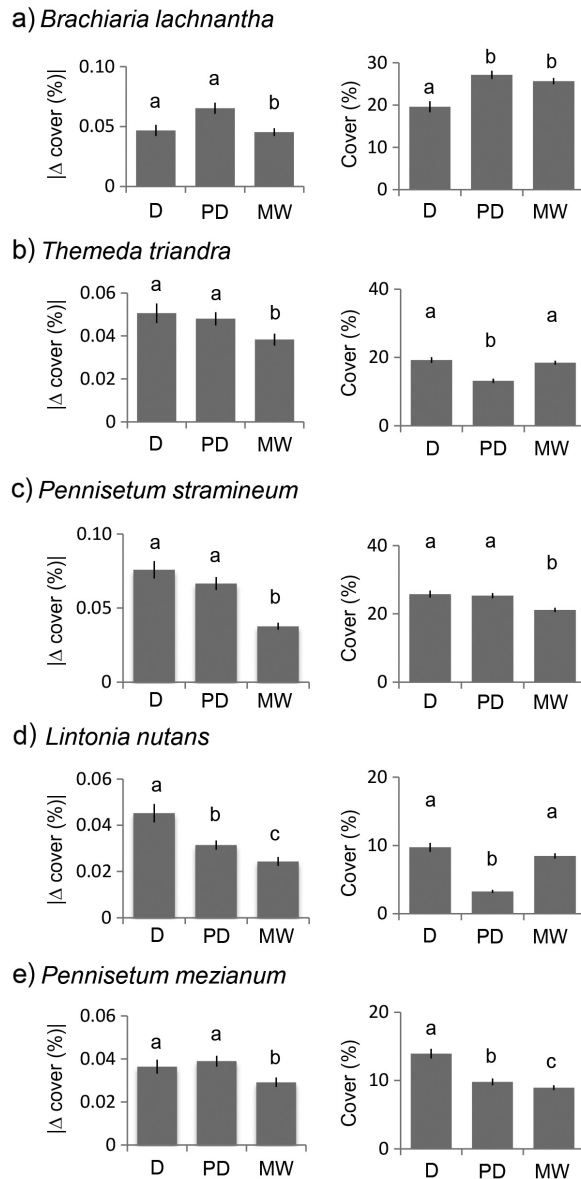

FIG. 3. Patterns of absolute value of change in relative cover (Δ; from one sample period to the next) and relative cover for the five species of grasses that had the greatest influence in driving community change over time. Bar graphs show means (± SE) during drought (D), post-drought (PD), and moderate-wet (MW) rainfall conditions, with significant differences ($P \leq 0.05$) indicated by different lowercase letters.
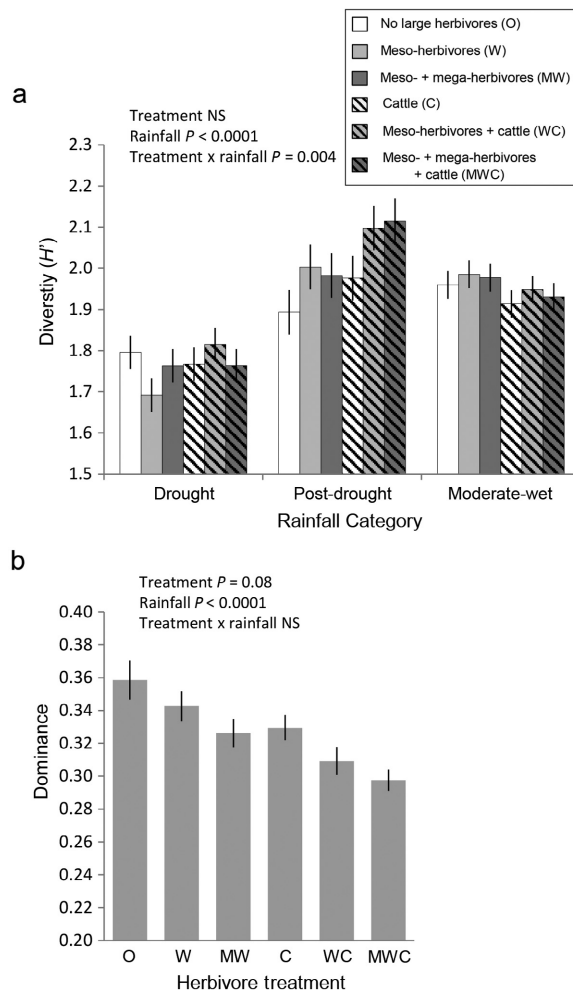
FIG. 4. (a) Shannon diversity (mean ± SE) in six herbivore treatments under three different rainfall conditions, averaged across all sample periods and (b) Berger-Parker dominance (mean ± SE) in six herbivore treatments, averaged across all sample periods.

including episodic dry periods or droughts. In our companion paper, we showed that six KLEE treatments have diverged from each other in terms of herbaceous community composition primarily along a gradient of total herbivore pressure with cattle having a greater impact than wild herbivores because they have a higher biomass density and exert greater total grazing pressure (Veblen et al. 2016). Here we expand on our prior work to examine (1) trajectories of community change in relation to the initial herbaceous community, (2) the role of rainfall variability, particularly droughts, in shaping those trajectories, and (3) implications for community stability.

Interactive and individual effects of grazing and rainfall

Initially, from 2000 to 2001, all treatments showed a similar trajectory away from the reference community, likely because of a prolonged drought and possibly due to release from more intense livestock grazing prior to 1992. Starting in the post-drought period during the second half of 2001, however, treatments began to diverge from each other in terms of herbaceous community composition, an effect that was amplified in each of the subsequent three drought/post-drought cycles.

The effects of herbivore treatment on the herbaceous community interacted significantly with rainfall from both the preceding rainy season and two rainy seasons prior, indicating both immediate (e.g., drought) and lagged (e.g., post-drought) effects of rainfall. Such lagged effects of precipitation are not surprising in a system dominated by perennial plants and are consistent with findings from other grassland communities (Dunnett et al. 1998, Farrer et al. 2010, Reichman et al. 2013). However, whereas drought and post-drought periods contributed to fairly consistent directional change in the least-grazed treatments, they had more variable effects in the more heavily grazed treatments, sometimes contributing to divergence away from the initial community (e.g., 2001–2002) and sometimes contributing to convergence toward it (e.g., 2006 and 2010) (Fig. 1b). Community turnover was greatest for all treatments during drought and post-drought periods (Fig. 2c), but divergence among the treatments also largely occurred during post-drought periods (Fig. 2d). Although the magnitude of change caused by droughts was similar across herbivory treatments (no significant interactive effect of herbivory and drought), it is clear that droughts and subsequent recovery periods precipitated periods of change and reorganization in the herbaceous community with outcomes that were contingent upon herbivore treatment.

Other studies have shown that both heavy grazing by large herbivores (e.g., Heady 1966, Loeser et al. 2007) and drought (e.g., Coupland 1958, Morecroft et al. 2004, Stampfli and Zeiter 2004) can initiate major shifts in plant composition. Further, the combination of these factors has been associated with lower diversity and higher dominance (often by less desirable or less palatable plant species) than either stressor alone (e.g., Milchunas et al. 1989, Gao et al. 2009). Previous studies have largely concluded that drought accelerates community change under heavy grazing but not under light or no grazing. In a Texas grassland, for example, Fuhlendorf and Smeins (1997) found that a significant drought led to rapid, divergent change in a heavily grazed treatment, but not in moderately grazed or ungrazed treatments. Similarly, Loeser et al. (2007) found herbaceous community change in a high-impact cattle grazing treatment after a severe drought in Arizona. In South Africa, the combination of heavy grazing and drought led to the near-elimination of several species of palatable grasses, whereas a much less dramatic compositional shift occurred under the combination of light grazing and drought (O'Connor 1995). In all of these cases, more intense livestock grazing and drought together caused significant perennial plant mortality, allowing colonization by more short-lived, weedy species. In

contrast, our results show the least resistance (greatest net community change) at the less intense end of the grazing continuum (O, W, MW, and perhaps C; Fig. 2a), with droughts promoting long-term change in these treatments and dampening it in the more heavily grazed treatments.

One important difference between our study and some others is that KLEE does not include a heavily grazed treatment. Cattle stocking rates are moderate, and even the most intensely grazed treatment (MWC) cannot be considered a heavy grazing (i.e., degradative) scenario. In the context of this experiment, community change appears to be driven not by drought acting disproportionately in more heavily grazed treatments, but rather by drought either acting equally (but at times in different directions) across treatments, or by drought combining with light grazing to favor one grass species at the expense of others. It is also important to note that only one of the four drought periods we observed (2000–2001) might be considered prolonged and we lack historic records to gauge its broader severity. It is possible that we might observe different community responses to a more exceptional drought, i.e., outside the range of normal rainfall variability, than the dry periods that we observed here.

Implications for community stability

These patterns of change over time can be placed more formally within the conceptual framework of "stability." We measured three different components of community stability that capture different temporal scales: resistance, temporal variability, and compositional turnover (Table 1). More heavily grazed treatments, especially MWC and WC, exhibited greater resistance (less overall community change from initial conditions) but also greater temporal variability than other treatments. This combination of more variability in the short term and more resistance in the long term suggests the presence of resilience, the ability to recover from (shorter-term) disturbance shifts. It is also interesting to note that resistance was more variable across replicate plots in the MWC and WC treatments than in other treatments (Fig. 3a), indicating spatial variability in addition to temporal variability. Unlike resistance and temporal variability, however, compositional turnover was similar across herbivore treatments and was instead strongly influenced by rainfall patterns. Thus by one measure (resistance to change), the most heavily grazed MWC and WC communities were most stable, whereas by a second measure (turnover), all treatments had similar stability, and by a third measure (temporal variability), the MWC and WC communities were least stable (Table 1).

These conclusions illustrate how various components of stability can exhibit different responses to perturbations, suggesting that different processes and mechanisms may be driving them (Donohue et al. 2013). Here resistance and temporal variability were negatively correlated, similar to the findings of Donohue et al. (2013),

which may reflect the constraints of how these are calculated. Stability may also depend on the type of disturbance and the time scale being considered. For example, one interpretation of the greater overall community change in the less grazed treatments is that these treatments had lower resilience to a pulse disturbance (drought). Another interpretation is that all treatments except the most heavily grazed MWC were changing steadily, with low temporal variation, in response to a press disturbance (experimentally imposed change in herbivory regime) and perhaps moving toward new equilibria. Despite the long-term nature of this study, it is still too early to determine whether these treatments will continue to diverge from initial conditions or not.

It is also difficult to say whether total grazing pressure or herbivore type played a greater role in affecting stability. The general pattern of community composition (e.g., Fig. 1b) arrays along a gradient of divergence from reference community, with MWC < WC < C < MW < W < O, following the gradient in total herbivore pressure (Veblen et al. 2016). However, resistance and variability (Fig. 2a,b) as well as diversity (Fig. 4a) were all markedly higher in WC and MWC than in C, MW, and W; this suggests an alternative hypothesis that cattle and the diverse suite of wild herbivores each play a unique role in shaping understory dynamics. It is possible that cattle fill the role of bulk-feeding grazers such as zebras and buffalo, which were once more abundant in Laikipia.

In terms of long-term community composition, however, it is clear that the presence of large herbivores dampens net change whereas the loss of large herbivores initiates community changes that are reinforced by the effects of episodic droughts. Although it is important to consider multiple dimensions of stability, we suggest that resistance (lack of net compositional change) and the maintenance of species diversity through multiple cycles of drought are likely the most holistic and meaningful measures of stability in systems such as this one for at least two reasons. First, semiarid systems with variable precipitation are expected to exhibit short-term instabilities such as temporal variability and compositional turnover, but these changes do not necessarily translate into long-term directional change. Second, in grazing systems herbaceous composition and diversity are closely related to forage quality, which in turn affects the system's ability to support the diverse dietary needs of different herbivores (Kartzinel et al. 2015). Thus, we conclude that large mammal herbivory contributed to one of the most important components of stability, resistance in long-term community composition.

Species-specific responses

In addition to the community-wide patterns, many of the changes in cover of common species in KLEE appear to have occurred in association with drought/post-drought cycles. The grass *L. nutans*, as well as at least two common forbs (*Monechma debile* and *Aspilia pluriseta*; results not

shown) declined significantly during post-drought periods, and between 2006 and 2013 it appears that droughts occurred too frequently for these species to fully recover (Appendix S2: Fig. S7). The decline of these species over time may explain why all six treatments diverged to some extent from the initial community. However, the particular sensitivity of these species to post-drought periods may also be linked to the second pattern of change over time: the substantial increase in cover of *B. lachnantha*. The large decrease in cover of *T. triandra* in the less-grazed, especially cattle-absent, treatments was likely also associated with the increase in *B. lachnantha*.

Both *B. lachnantha* and *T. triandra* share characteristics of what O'Connor (1991) calls an "extinction-prone perennial bunchgrass," as they are both palatable, long-lived plants that do not reproduce vegetatively. At our study site, both are preferred forage species (Odadi et al. 2007). *Themeda triandra,* a widespread and important forage species in sub-Saharan Africa, has been shown in multiple studies to decrease substantially under the combination of heavy grazing and drought (O'Connor 1995, Fynn and O'Connor 2000). Here, we found a somewhat different pattern. *Themeda triandra* decreased in cover during droughts, consistent with other studies, but its recovery was reduced in the less grazed, rather than more grazed, treatments. This was likely due to the coincident dynamics of *B. lachnantha*, which increased in cover during post-drought periods, especially when it was lightly grazed. *Themeda* cover, on the other hand, only recovered after droughts in the more heavily grazed treatments, possibly because there was less *B. lachnantha* in those treatments (and possibly because no treatments experience more than a moderate level of grazing intensity).

The ability of *B. lachnantha* to increase in the less-grazed treatments after droughts may also have contributed to suppression of species diversity in the less-grazed treatments relative to the more-grazed treatments. Dominance was 17–21% higher in the W and O treatments than in the MWC and WC treatments (Fig. 4b), largely because of the very high relative cover of *B. lachnantha* in those treatments. At the same time, species diversity was highest in the more heavily grazed treatments (e.g., MWC, WC) particularly after droughts (Fig. 4a). From previous work in this system, we know that the combination of higher herbivory levels and drought creates small patches of bare ground that allow less common species to establish (Porensky et al. 2013). Our current results indicate that the relative sensitivity of *B. lachnantha* to grazing may contribute to the creation of these bare patches in the more heavily grazed treatments.

Similar patterns of dominance by a palatable, competitive species that apparently suppresses overall species diversity have been well documented, particularly in nutrient-rich grasslands (Olff and Ritchie 1998, Bakker et al. 2006). Under these conditions, intermediate levels of herbivory are thought to maintain species diversity by removing some, but not all, biomass of dominant species (Bakker et al. 2006, Loeser et al. 2007). Our results extend further to illustrate how, under very low herbivory, drought cycles can function as a facilitator of persistent, step-wise increases in single-species dominance. Rather than drought counter-balancing the effects of light grazing on *B. lachnantha* (e.g., by causing high mortality in this species), it instead appears to favor this species to the detriment of other species in the community. Interestingly, Koerner et al. (2014) found a similar effect, in which both fire and herbivore removal favored a dominant grass with negative consequences for herbaceous species richness in the Konza prairie grasslands in North America, although they found no such effect in a South African savanna (see also Smith et al. 2016: Fig. 8). They attribute this to the difference in herbivore community; since the diverse African herbivores consume both grasses and forbs, they might be expected to have less net effect on species richness than bison in North America, which consume only grass. In partial contrast, we found that the combination of cattle (bulk grazers, like bison) and wild herbivores (with diverse diets) was most effective at keeping dominance in check and promoting diversity, suggesting that both guilds can play important and potentially distinct roles in these regards.

Management implications

These findings add to our understanding of how herbivory and rainfall can act together to cause large changes in grassland communities not only at the high, but also at the low end of the grazing continuum. As droughts are likely to become an increasingly common occurrence in grazing systems, managing herbivory to promote long-term ecosystem resilience is gaining a new level of importance. At the same time, as large wild herbivores decline worldwide due to habitat losses and land-use changes (Ripple et al. 2015), it is increasingly important to understand the role that livestock play in their stead (Cingolani et al. 2014, Veblen et al. 2016). Our results suggest that a moderate level of herbivory, especially by a combination of herbivore types, may be necessary to prevent run-away dominance by one or a few species that outcompete other species when not heavily grazed. Intermediate herbivory may be more likely to promote compositional stability in systems such as ours that are reasonably productive and have a long evolutionary history of grazing and other disturbances, such as fire (Eldridge et al. 2016). However, we caution that even at moderate stocking rates, domestic livestock may contribute to destabilizing ecosystems under different historical and environmental contexts. Even in our system, the greatest long-term stability and diversity were achieved under the combination of cattle and wild herbivores. Further research is needed to better understand the long-term impacts of wild ungulates vs. domestic livestock on the stability of ecosystem functions such as nutrient cycling and hydrological processes, in addition to their impacts on species composition.

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SUPPORTING INFORMATION

Additional supporting information may be found online at: http://onlinelibrary.wiley.com/doi/10.1002/eap.1649/full

DATA AVAILABILITY

Data available from figshare: https://doi.org/10.6084/m9.figshare.3175561.v1.