

Herbivory and drought interact to enhance spatial patterning and diversity in a savanna understory

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Abstract The combination of abiotic stress and consumer stress can have complex impacts on plant community structure. Effective conservation and management of semi-arid ecosystems requires an understanding of how different stresses interact to structure plant communities. We explored the separate and combined impacts of episodic drought, livestock grazing, and wild ungulate herbivory on species co-occurrence and diversity patterns in a relatively productive, semi-arid *Acacia* savanna. Specifically, we analyzed 9 years of biannual plant community data from the Kenya long-term exclosure experiment, a broad-scale manipulative experiment that has excluded different combinations of large mammalian herbivores from 18 4-ha plots since 1995. During droughts, we observed low species diversity and random species co-occurrence patterns. However, when rain followed a major drought, areas

exposed to moderate cattle grazing displayed high species diversity and evidence of significant species aggregation. These patterns were not apparent in the absence of cattle, even if other large herbivores were present. To explore possible mechanisms, we examined patterns separately for common and rare species. We found that aggregation patterns were likely driven by rare species responding similarly to the availability of open micro-sites. Our results indicate that in a productive, fire-suppressed savanna, the combination of periodic drought and moderate cattle grazing can enhance plant biodiversity and fine-scale spatial heterogeneity by opening up space for species that are otherwise rare or cryptic. Our findings also emphasize that domestic herbivores can have significantly stronger impacts on plant community dynamics than wild herbivores, even in an ecosystem with a long history of grazing.

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Introduction

In an era of global climate change and pervasive land-use alterations, ecologists and managers are increasingly challenged to understand the separate and combined effects of different stresses on ecological communities (Sala et al. 2000; Ni et al. 2006). Grassland and savanna plant communities, which cover more than 25 % of the world's land surface (Asner et al. 2004; Bond 2008), are likely to be particularly sensitive to multiple drivers of global change (Sala et al. 2000). Severe, episodic droughts are common in semi-arid grasslands and savannas (Weaver and Albertson 1936; Pandey and Ramasastri 2001), and climate change is

likely to increase drought frequency and intensity (IPCC 2012). At the same time, wild herbivores in these landscapes have often been replaced by domestic herbivores—which may place additional or novel stresses on the system (Weisberg et al. 2002; Asner et al. 2004). An understanding of how wild herbivores, domestic herbivores, and drought interact to structure plant communities is necessary to effectively conserve and manage semi-arid systems. In particular, it is important to understand how different stresses affect the spatial configuration of plant communities. Changes in fine-scale spatial patterning can influence ecosystem processes such as erosion, invasion, and fire in semi-arid systems (Okin et al. 2009; Davies et al. 2010; Prevey et al. 2010). However, few studies have quantified the interactive effects of drought and herbivory on spatial patterning.

Abiotic stress can affect spatial patterning by altering interspecific interactions within plant communities. The stress-gradient hypothesis predicts that positive interspecific interactions will be more common when the physical environment is more stressful (Bertness and Callaway 1994). Numerous studies in arid and semi-arid systems have found evidence for greater plant–plant facilitation at more stressful sites (e.g., Arredondo-Nunez et al. 2009; Forey et al. 2009) or at more stressful times (Veblen 2008). Such facilitation often occurs via nurse-plant effects or associational resistance, wherein plants of one species shade, shelter, or hide plants of another (typically less common) species (e.g., Riginos and Young 2007; Veblen 2008). In contrast to the evidence for facilitation, several studies suggest that abiotic stress can lead to increased competition for scarce resources (e.g., Bowker et al. 2010; Holmgren and Scheffer 2010), which may cause spatial segregation among competing species.

In some cases, the net effect of stress on plant–plant interactions depends on the presence or absence of large herbivores (i.e. herbivores larger than rodents), but there is little consensus on whether herbivory increases or decreases the likelihood of facilitation (Milchunas et al. 1989; Riginos and Young 2007; Veblen 2008; Gao et al. 2009). These variable findings may reflect the fact that interactions can shift depending on the severity of stresses (Holmgren and Scheffer 2010), the types of plant species and stresses involved (Maestre et al. 2009), the type of herbivory, or a combination of these (Veblen 2008). For example, herbivory by domestic livestock can have different effects on plant community structure than herbivory by wild ungulates (Veblen and Young 2010). This is likely to be particularly true where a single domestic species (e.g., cattle) has replaced a diverse community of large herbivores, as is the case in large parts of sub-Saharan Africa (Du Toit and Cumming 1999).

In addition to their impacts on plant–plant interactions, drought and large herbivores have broader consequences

for plant community structure and dynamics. In grasslands, it is well known that both droughts (e.g., Weaver and Albertson 1936; Coupland 1958; Dunnett et al. 1998; Morecroft et al. 2004; Stampfli and Zeiter 2004) and large herbivores (e.g., Heady 1966; Silvertown and Smith 1989; Bullock et al. 1995; Veblen and Young 2010; Dreber et al. 2011) can initiate major shifts in plant community composition and structure. Fewer studies have examined the combination of drought and large herbivores in this context. Existing findings suggest that, in the short-term, the combination of herbivory and drought can be associated with lower diversity and higher dominance (often by less desirable or palatable plant species) than either stressor alone (e.g., Milchunas et al. 1989; Gao et al. 2009). Over the longer term, grasslands impacted by both herbivory and drought tend to experience faster or larger community changes than grasslands impacted by only one of the two stresses (Albertson and Weaver 1944; Fuhlendorf and Smeins 1997; Loeser et al. 2007; Stubbendieck and Tunnell 2008; Dreber and Esler 2011). It is important to note that most existing studies on the combination of drought and large herbivores have focused exclusively on domestic herbivores; here, we extend this approach to compare the effects of wild and domestic herbivores at the same site.

This paper also moves beyond previous work by evaluating the separate and combined impacts of domestic herbivory, wild ungulate herbivory, and episodic drought on fine-scale spatial patterning. Fine-scale spatial patterning within the plant community can affect soil and water movement (Okin et al. 2009), fire behavior (Davies et al. 2010), species invasion (Melbourne et al. 2007; Yurkonis et al. 2012), and species diversity (Chesson 2000; Porensky et al. 2012). Thus, it is important for ecologists and managers to understand how various stresses alter spatial pattern. We used null model analysis of species co-occurrence patterns to determine how fine-scale spatial patterning changed in response to different stresses. Random co-occurrence patterns indicate a lack of fine-scale structuring within a community, while segregation (i.e. negative patterns of co-occurrence among species across sites) and aggregation (i.e. positive patterns of co-occurrence among species across sites) indicate that the community is spatially structured.

Co-occurrence patterns can provide clues about the relative strength of different ecological processes driving a community (Gotelli 2000, 2001; Horner-Devine et al. 2007). For example, communities structured by competition may show significant segregation across sites (Osnas and Ankeny 2003; Pfeiffer et al. 2008). Even within a given community, segregation may be stronger among more common than less common species (Osnas and Ankeny 2003). A co-occurrence pattern indicating significant aggregation across sites can be driven by multiple

mechanisms. Facilitative relationships (e.g., nurse plants or associational defenses) may cause persistent fidelities between species (Tirado and Pugnaire 2005; Forey et al. 2009). Alternatively, species with similar habitat requirements (e.g., abiotic conditions) may cluster together in specific micro-sites (Jackson et al. 1992).

In this study, we analyzed 9 years of herbaceous plant community data from a long-term manipulative experiment in which different combinations of herbivores have been excluded since 1995. We quantified impacts of livestock herbivory, wild ungulate herbivory, and drought on species co-occurrence, aerial cover, and species diversity (compositional patterns will be examined in a subsequent publication). Furthermore, we explored potential mechanisms underlying observed co-occurrence patterns by asking whether patterns were more consistent with interspecific facilitation or environmental filtering.

Materials and methods

Study site

The Kenya long-term enclosure experiment (KLEE) is located in central Kenya's Laikipia County (0°N, 37°E; 1,800 m elevation). KLEE is situated on a flat plateau underlain with clay-rich vertisol ('black cotton') soils. These soils support an understory plant community with high cover and relatively few bare patches. The vegetation is wooded savanna in which *Acacia drepanolobium* trees account for more than 95 % of woody cover (Young et al. 1998). Seven grass species and six forb species account for more than 95 % of the herbaceous cover (see Online Resource 1). From January 2001 through December 2010, rainfall at the site averaged 581 mm/year (range 428–783 mm/year). Rainfall was weakly trimodal with major peaks in April–May and November, a minor peak in July, and usually a distinct dry season from December to February.

The KLEE experiment was established in 1995 and consists of three replicate blocks, each with six 200 × 200 m treatment plots (Young et al. 1998). Treatments include different combinations of cattle (C), meso-herbivore wildlife (W; 15–1,000 kg, e.g., gazelles and zebras), and megaherbivores (M; elephants and giraffes). In addition to total enclosure plots (O), treatment combinations include C, W, WC, MW, and MWC, where letters indicate the types of animals allowed into the plots (e.g., WC plots allow meso-herbivores and cattle). Smaller herbivores (steinbucks, hares, rodents, and invertebrates) have access to all plots. These non-excluded herbivores help to keep total enclosure plots (O) from becoming moribund. Meso-herbivore and megaherbivore use does not fluctuate

greatly across seasons (Kimuyu and Young, unpublished data). Dung data collected in treatment and control plots indicate that (1) treatments are >90 % effective, and (2) experimental fences do not deter wild herbivores from using the plots they are intended to access (for more details, see Young et al. 1998).

Four to eight times per year (across all seasons), individually herded groups of cattle are allowed to graze in C, WC, and MWC plots. Timing of cattle runs varies, but C, WC, and MWC plots are usually grazed <8 weeks before each vegetation survey, and these plots rarely experience >16 weeks without cattle grazing. During each grazing period, one herd of about 100 animals grazes in each C, WC and MWC plot for 2 h. These grazing and herding practices reflect typical cattle management on both private and communal properties in the region, and produce impacts similar to the overall ranch stocking density (Odadi et al. 2007). Fire has not been an active part of this ecosystem since the 1960s (R.L. Sensenig, personal communication). In Kenyan rangelands, long-term fire suppression is common and becoming even more widespread as managers seek to remove rank grass using intensive grazing rather than fire.

Data collection

The herbaceous vegetation in all 18 KLEE plots is sampled biannually (in February and June). During each survey, the innermost hectare of each plot is divided into a square grid of 100 sampling stations separated by 10 m. Every other grid point (50 per plot) is sampled for the presence or absence of each herbaceous species in 0.5 × 0.5 m quadrats. Except where noted, species richness (per plot) refers to the total number of species found in these 50 quadrats. Every fifth grid point (20 per plot) is sampled for aerial plant cover, counting the number of pins hit by each species over a ten-point pin frame. Pins are vertical and separated by 5 cm. We analyzed data from 18 surveys between June 2001 and June 2010 (the June 2003 survey was excluded because data from some plots were missing). Vegetation data collected prior to June 2001 were not comparable to later data due to improvements in species identification. For each plot at each sampling date, we calculated species co-occurrence (see below), aerial plant cover (summed pin hits), species richness (total number of species observed per plot), and species evenness (the probability of an interspecific encounter; Hurlbert 1971). Rainfall was measured on-site after each rain event, using standard gauges.

Of the 100 plant taxa observed between June 2001 and June 2009, 67 (comprising 96 % of all pin hits and 84 % of all occurrences) were identified to species (Online Resource 1). Most other taxa were identified to genus.

Plants not identified to species or genus accounted for only 0.01 % of pin hits and 0.25 % of occurrences (Online Resource 1). For many of the less common taxa, life-history and functional trait details are unknown or uncertain, and efforts to collect such data are ongoing. Due to the paucity of species-specific data, our analyses focused on numerical dominance rather than functional traits or life history traits.

Statistical analysis

Co-occurrence

To explore how rainfall and herbivores affected species co-occurrence, we used null model analysis (Gotelli and Graves 1996), comparing observed co-occurrence patterns to patterns from randomized assemblages. Randomized assemblages were created using the fixed-equiprobable model (SIM2), an algorithm robust to both type I and II errors (Gotelli 2000) in EcoSim v.7 (Gotelli and Entsminger 2006). In these null models, the row totals, which represent the total number of sampling stations at which a species was present, were fixed to be equivalent to the observed row totals. However, the columns, which represent sampling stations ($n = 50$), were treated as equally suitable for each species. Thus, species occurred at the same frequency in the randomized as in the observed assemblages, but species occurrence per sampling station was not constrained in the randomized assemblage.

To evaluate species co-occurrence patterns, we used the *C*-score (Stone and Roberts 1990), which measures the average number of ‘checkerboard units’ of all species pairs of an assemblage. Each checkerboard unit is calculated by $(r_a - S) \times (r_b - S)$, where S is the total number of ‘sites’ (e.g., sampling stations) shared by the species pair, and r_a and r_b are the row totals for species a and b, respectively. Species pairs that always occur together (complete aggregation) will have a *C*-score of zero. Species pairs that never occur together (complete segregation) will have a large positive *C* score. Observed *C* scores were compared to the average *C* scores generated from 5,000 randomized matrices. Results are reported in terms of the standard effect size (SES), which scales results in terms of standard deviations (Gurevitch et al. 1992). Large positive SES values (>1.96) indicate statistically significant species segregation. Large negative SES values (<-1.96) indicate statistically significant species aggregation. SES values between -1.96 and 1.96 are also informative, in that they can suggest the relative strength of segregation or aggregation across different treatments, species subsets or guilds.

To explore which species were driving the observed co-occurrence patterns, we also evaluated co-occurrence patterns separately for numerically dominant and non-

dominant species (defined below). Thus, three different matrices (all species, dominant species, and non-dominant species) were analyzed for each plot at each sampling date ($n = 972$ matrices).

Impacts of rainfall and herbivores

To investigate the impacts of rainfall patterns and herbivore treatments on aerial cover, co-occurrence, species evenness, and species richness, we used linear mixed models with maximum likelihood estimation and Satterthwaite’s approximation for degrees of freedom. For each of the four response variables, we included block and survey date as random effects, and we addressed the non-independence of repeated surveys by treating consecutive surveys within the same plot as repeated measures. We considered date², date \times treatment, date \times block, plot (i.e. block \times treatment), and date \times plot as additional random factors, including these only if they improved model AIC by more than 10 points.

After selecting random factors, we identified appropriate fixed factors pertaining to rainfall. Rainfall factors were chosen based on the fact that plant communities often display a lag when responding to rainfall events (Dunnett et al. 1998; Farrer et al. 2010). In our study system, rainfall exhibits major peaks in November and April–May. Vegetation surveys occur after each of these rainy seasons (in February and June). We therefore defined ‘rain_{*t*}’ as the total rainfall during the rainy season just before the vegetation survey (summed over 4 months), ‘rain_{*t-1*}’ as the total rainfall during the previous rainy season, and ‘rain_{*t-2*}’ as the total rainfall during the rainy season before that. For example, for a survey in February 2010, rain_{*t*} = rainfall from October 2009 to January 2010, rain_{*t-1*} = rainfall from March to June 2009, and rain_{*t-2*} = rainfall from October 2008 to January 2009. During model selection, we began with a full model that included the following fixed effects: treatment, rain_{*t*}, rain_{*t-1*}, rain_{*t-2*}, trt \times rain_{*t*}, trt \times rain_{*t-1*}, trt \times rain_{*t-2*}, (rain_{*t*})², (rain_{*t-1*})², (rain_{*t-2*})², trt \times (rain_{*t*})², trt \times (rain_{*t-1*})², trt \times (rain_{*t-2*})². Treatment, a pre-assigned factor, was always retained in the final model. Rainfall factors were selected using a backwards stepwise procedure with the goal of minimizing model AIC.

In each of the four final models, significance of different fixed factors was assessed at the $\alpha = 0.0125$ level (Bonferroni correction). In models with significant treatment effects and no significant interactions between treatment and rainfall, we used three planned contrasts to compare (1) treatments including and excluding cattle, (2) treatments including and excluding meso-herbivores, and (3) treatments including and excluding megaherbivores. Significance of these tests was assessed at the $\alpha = 0.016$ level (Bonferroni correction).

To examine correlations among response variables, we also performed a repeated measures MANOVA with block, treatment and rain_{t-1} (the most consistently significant rainfall predictor across all response variables) as predictors. Sampling events were treated as the repeated factor, and response variables included SES values (results of co-occurrence analyses), species richness, evenness, and cover. We examined the partial correlation matrix from this model to see whether response variables were correlated after taking block, treatment, and rainfall (rain_{t-1}) into account.

Drivers of community structure

We undertook further analysis of the KLEE dataset to explore potential mechanisms driving community structure. Although confirmation of specific mechanisms will require further experimental testing, we were able to determine whether different potential mechanisms were consistent with existing data. To begin, we asked whether observed aggregation patterns were driven by dominant species, non-dominant species, or associations between these two groups. As explained above, aggregation within each group could indicate either positive interactions within the group or similar responses to spatially variable environmental conditions (e.g., micro-sites). Positive associations between these two groups could indicate nurse plant effects where dominant species facilitate non-dominant species. Finally, to obtain more information about the possibility of environmental filtering, we asked whether dominant or non-dominant species responded to the availability of open micro-sites.

In the first step of this analysis, we compared overall co-occurrence values among only dominant species, only non-dominant species, and across the entire community while controlling for block, herbivore treatments, and rainfall. If non-dominant species associate with each another, then we expect non-dominant species to show stronger positive co-occurrence patterns (aggregation) than the total community. Dominant species could potentially show a similar pattern. However, if dominant species facilitate non-dominant species, then separating dominant from non-dominant species will remove many instances of co-occurrence, and we expect the entire community to be more aggregated than either dominant or non-dominant species alone.

We identified numerically dominant species by calculating the sum of all pin hits from June 2001 to June 2009 for each species (Online Resource 1). Thirteen species with more than 1,000 pin hits were labeled ‘dominants’. These seven perennial bunchgrasses and six forbs (a mixture of semi-woody perennials and annuals) accounted for >95 % of all pin hits (Online Resource 1). The remaining taxa (mostly annuals, ephemeral geophytes or weak perennials,

Online Resource 1) were labeled ‘non-dominants’. To compare co-occurrence values across groups, we used a repeated measures MANOVA with dominant species co-occurrence scores, non-dominant species co-occurrence scores, and total community co-occurrence scores as response variables. Predictors included block, treatment and rainfall (using rain_{t-1}). Sampling events were treated as the repeated factor. Profile contrasts were used to compare among species groups.

Finally, to determine whether species aggregation might be driven by colonization of open sites at the 0.5×0.5 m patch scale, we analyzed patterns associated with individual quadrats nested within plots (50 quadrats per plot). For each quadrat, we used data from the 18 sampling events to regress dominant species richness and log-transformed non-dominant species richness at sampling time t against bare ground at sampling time $t - 1$. We saved the slope of each regression; positive slopes indicate that species richness is tracking bare ground at the quadrat scale. For each species group, we then used slope values (one value per quadrat) as the response variable in a linear mixed model with maximum likelihood estimation and Satterthwaite’s approximation for degrees of freedom. Treatment was included as a fixed effect, random factors included block and plot (i.e. block \times treatment), and data were inverse variance-weighted to meet model assumptions. In these models, response values significantly greater than zero indicate a significant, positive relationship between bare ground at time $t - 1$ and species richness at time t , suggesting that species tend to opportunistically colonize open sites. All statistical analyses were conducted in SAS 9.2 (SAS Institute, Cary, NC, USA) using Proc MIXED (for mixed models) and Proc GLM (for MANOVAs).

Results

Impacts of rainfall and herbivores

Aerial cover

Aerial cover displayed a quadratic (humped) relationship with rainfall during the previous rainy season (rain_{t-1}) and a linear relationship with rainfall during the current rainy season (rain_t , Table 1). In both cases, cover increased with increased rainfall (Fig. 1a, b). Cover differed significantly across herbivore treatments, but there was no significant interaction between herbivore treatment and rainfall (Table 1). Cattle exclusion increased cover by 35 % (contrast $F_{1,84} = 125.0$, $p < 0.0001$). After Bonferroni corrections, meso-herbivore and megaherbivore presence did not have significant impacts on aerial cover (meso-herbivore

contrast $F_{1,84} = 4.3$, $p = 0.04$; megaherbivore contrast $F_{1,84} = 0.8$, $p = 0.4$).

Co-occurrence

Species co-occurrence displayed a quadratic relationship with rainfall during the previous rainy season (rain_{t-1}) and there was a significant interaction between prior rainfall (rain_{t-1}) and herbivore treatment (Table 1; Fig. 1c). After droughts (i.e. when rain_{t-1} was very low), plots with cattle displayed significant aggregation (SES scores < -1.96), but there was no significant aggregation in plots without cattle (Fig. 1c). At higher rainfall, most co-occurrence scores revealed random species arrangements. Co-occurrence also displayed a quadratic relationship with rainfall during the

current rainy season (rain_t). Higher rainfall was associated with more aggregation, though the effect size of this result was small (Table 1; Fig. 1d).

Species richness

Species richness displayed quadratic relationships with all three rainfall predictors (rain_t , rain_{t-1} , and rain_{t-2} ; Table 1). Species richness in the present was much higher when rainfall in the past (rain_{t-1} and rain_{t-2}) was low (Fig. 2a, b). However, the relationship between recent rainfall and species richness was markedly different; as recent rainfall increased, richness also increased (Fig. 2c). The relationship between rain_{t-1} and species richness differed significantly across herbivore treatments (Table 1;

Table 1 Results of linear mixed model analysis

Response	Random factors	Fixed factors	Fixed factor F (num df , den df)	p^*
Aerial cover	Block Date Date ²	Treatment	26.8 (5, 84)	<0.0001***
		Rain _{<i>t</i>}	233.2 (1, 253)	<0.0001***
		Rain _{<i>t-1</i>}	52.0 (1, 249)	<0.0001***
		(Rain _{<i>t-1</i>}) ²	31.8 (1, 257)	<0.0001***
Co-occurrence (SES)	Block Date	Treatment	4.5 (5, 175)	0.0007***
		Rain _{<i>t</i>}	12.1 (1, 259)	0.0006***
		Rain _{<i>t-1</i>}	63.6 (1, 263)	<0.0001***
		Rain _{<i>t-2</i>}	0.2 (1, 321)	0.7 ns
		(Rain _{<i>t</i>}) ²	18.4 (1, 262)	<0.0001***
		(Rain _{<i>t-1</i>}) ²	24.7 (1, 247)	<0.0001***
		Rain _{<i>t-1</i>} × treatment	3.9 (5, 317)	0.002**
		Rain _{<i>t-2</i>} × treatment	2.8 (5, 318)	0.02 ns
Species evenness ^a	Block Date	Treatment	6.3 (5, 273)	<0.0001***
		Rain _{<i>t</i>}	60.1 (1, 317)	<0.0001***
		Rain _{<i>t-1</i>}	15.0 (1, 308)	0.0001***
		Rain _{<i>t-2</i>}	15.0 (1, 321)	0.0001***
		(Rain _{<i>t-1</i>}) ²	14.3 (1, 306)	0.0002***
		(Rain _{<i>t-2</i>}) ²	14.1 (1, 320)	0.0002***
		Rain _{<i>t-1</i>} × treatment	3.6 (5, 314)	0.004**
		Treatment	7.7 (5, 196)	<0.0001***
Species richness	Block Date Date ²	Rain _{<i>t</i>}	59.3 (1, 237)	<0.0001***
		Rain _{<i>t-1</i>}	134.7 (1, 315)	<0.0001***
		Rain _{<i>t-2</i>}	8.3 (1, 316)	0.004**
		(Rain _{<i>t</i>}) ²	16.3 (1, 257)	<0.0001***
		(Rain _{<i>t-1</i>}) ²	65.9 (1, 312)	<0.0001***
		(Rain _{<i>t-2</i>}) ²	10.9 (1, 318)	0.001**
		Rain _{<i>t-1</i>} × treatment	5.1 (5, 315)	0.0002***
		Rain _{<i>t-2</i>} × treatment	2.5 (5, 317)	0.03 ns

For all responses, measurements from different surveys within the same plot were treated as repeated measures. Final models were chosen via backwards stepwise model selection with the goal of minimizing model AIC. Treatment, a pre-assigned factor, was never removed from models

* Significance after Bonferroni correction (* $p < 0.0125$, ** $p < 0.01$, *** $p < 0.001$)

^a Data squared and inverse variance-weighted to meet model assumptions

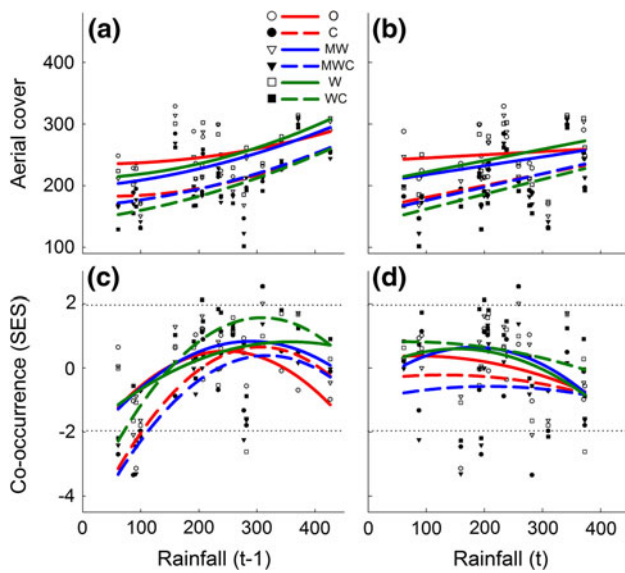
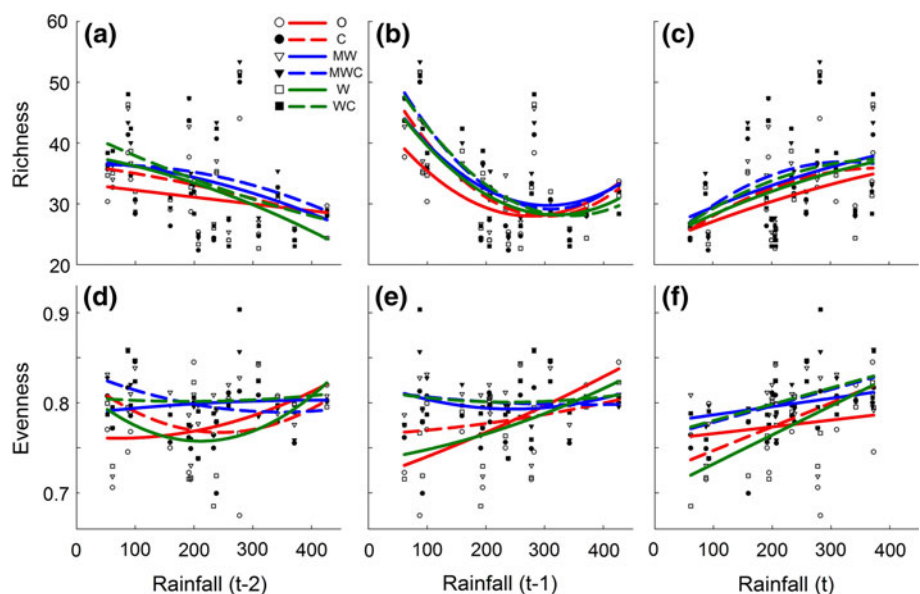


Fig. 1 Relationships between precipitation (mm rainfall over 4 months) in the previous rainy season [rainfall ($t - 1$)] and current rainy season [rainfall (t)] and **a, b** aerial cover (pin hits) and **c, d** species co-occurrence (SES). Points represent mean values for each survey, averaged across the three blocks. Best fit curves are shown for significant linear or quadratic relationships (see Table 1). C cattle allowed, W meso-herbivore wildlife allowed, M mega-herbivores allowed, and O all large herbivores excluded. Horizontal dotted lines in (c, d) indicate significant segregation (SES values >1.96) and aggregation (SES values <-1.96)

Fig. 2b). In seasons of recovery after droughts (i.e. when $rain_{t-1}$ was very low), plots with cattle tended to have higher species richness than plots without cattle (Fig. 2b). Across most rainfall levels, plots exposed to both cattle and meso-herbivores (WC and MWC) had the highest species richness (Fig. 2a–c).

Fig. 2 Relationships between rainy season precipitation and **a–c** species richness and **d–f** species evenness. Refer to Fig. 1 and “Materials and methods” for explanations of rainfall time periods, points, curves, and treatment codes



Species evenness

Species evenness displayed a linear relationship with rainfall during the current rainy season ($rain_t$) and quadratic relationships with rainfall during previous rainy seasons ($rain_{t-1}$ and $rain_{t-2}$) (Table 1; Fig. 2d–f). In general, higher rainfall was associated with more evenness (Table 1; Fig. 2d–f). For rainfall during the previous rainy season ($rain_{t-1}$), the strength of this response varied significantly across herbivore treatments (Table 1; Fig. 2e). After droughts (i.e. when $rain_{t-1}$ was low), treatments with mega-herbivores or cattle had higher evenness than treatments without mega-herbivores or cattle (Fig. 2e).

Relationships among response variables

After accounting for the impacts of block, treatment, and rainfall during the previous rainy season ($rain_{t-1}$), none of the four response variables were significantly correlated with each other. Apparent correlations between response variables (e.g., patterns visible in Figs. 1, 2) appear to be driven by correlated responses to treatments and rainfall patterns.

Drivers of community dynamics

Dominance groups and co-occurrence

After accounting for block, treatment, and rainfall ($rain_{t-1}$), we found that dominant species were significantly less aggregated than the total community (repeated measures MANOVA profile contrast $F_{1,10} = 77.4, p < 0.0001$), while non-dominant species were significantly more aggregated than the total community ($F_{1,10} = 143.4,$

$p < 0.0001$; Fig. 3). This suggests that overall community aggregation is driven primarily by positive associations among non-dominant species rather than by associations among dominant species or by associations between dominants and non-dominants.

Bare ground

At the scale of individual 0.5×0.5 m quadrats, we found that higher bare ground at time $t - 1$ was associated with slightly lower species richness of dominant plants at time t (after accounting for treatment, estimate of slope = -0.03 ± 0.01 , $t = -2.6$, $p = 0.02$). The relationship between bare ground and dominant species richness did not differ significantly across herbivore treatments ($F_{5,897} = 1.2$, $p = 0.3$; Fig. 4a).

In contrast to the results for dominant species, bare ground at time $t - 1$ was significantly and positively associated with the log-transformed species richness of non-dominant plants at time t (after accounting for treatment, estimate of slope = 0.11 ± 0.007 , $t = 15.3$, $p < 0.0001$). The relationship between bare ground and non-dominant species richness varied significantly across herbivore treatments ($F_{5,900} = 12.7$, $p < 0.0001$; Fig. 4b). Plots with cattle or meso-herbivores showed a stronger response to the amount of bare ground than plots without cattle or meso-herbivores (cattle contrast $F_{1,900} = 22.5$, $p < 0.0001$; wildlife contrast $F_{1,900} = 25.0$, $p < 0.0001$), probably due to a relatively weak relationship in total exclusion plots (Fig. 4b). The presence or absence of megaherbivores had no significant effect on the relationship between bare ground and non-dominant species richness (contrast $F_{1,900} = 0.4$, $p = 0.5$). Note that plots

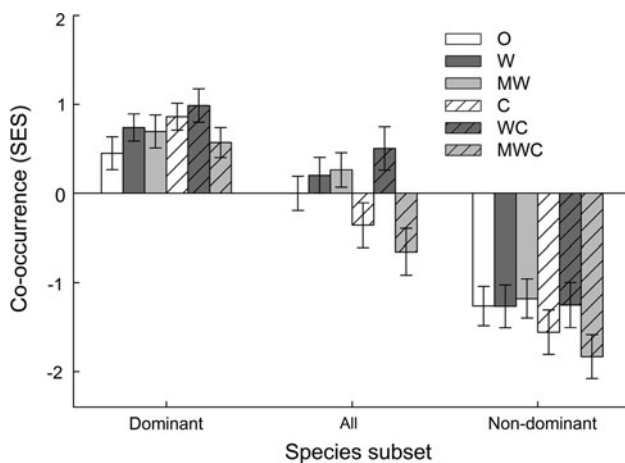


Fig. 3 Mean species co-occurrence (SES) for dominant species, all species and non-dominant species within each treatment. Bars display values (± 1 SE) averaged across surveys and blocks. Refer to Fig. 1 for explanation of treatment codes

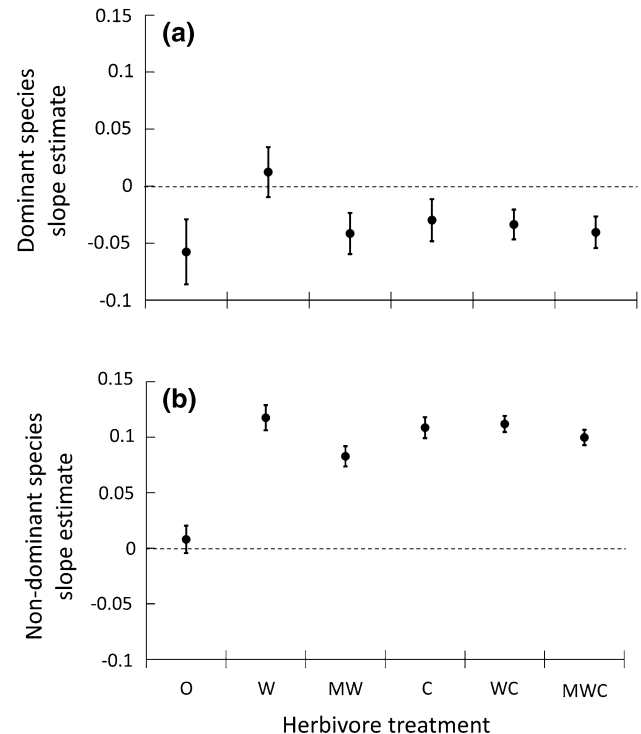


Fig. 4 Slope estimates for species richness versus bare ground across herbivore treatments for **a** dominant and **b** non-dominant species. Positive values indicate that bare ground at time $t - 1$ is positively associated with species richness at time t . A separate slope was determined for each sampling quadrat within each plot (50×18 regressions; for each regression, $n = 18$ surveys). Non-dominant species richness data were log-transformed. Points represent LS mean (± 1 SE) slope estimates. Refer to Fig. 1 for explanation of treatment codes

allowing megaherbivores (MW and MWC) also allow meso-herbivores.

Discussion

Over the course of this 9-year study, cattle grazing and drought (two layers of contingency) interacted to increase biodiversity and fine-scale spatial patterning in the herbaceous layer of a semi-arid savanna. In contrast to some other arid and semi-arid systems, patterns of positive spatial association and diversity did not appear to be driven by facilitation but instead by competition and disturbance. We suggest that cattle grazing—particularly in the absence of fire—may play an important role in maintaining species diversity and fine-scale spatial heterogeneity in this relatively productive savanna.

Separate impacts of rainfall and herbivores

The herbaceous community responded strongly to rainfall variability over the 9 years of this study. Community-level

metrics responded most strongly to rainfall that occurred in the previous rainy season (the season which ended 5–7 months prior to the survey; Figs. 1, 2). Time-lagged responses are consistent with other studies which found time-lagged effects of precipitation on grassland community dynamics (e.g., Dunnett et al. 1998; Farrer et al. 2010).

Not surprisingly, herbaceous cover was higher when recent rainfall (during both the current and prior rainy season) was higher. Interestingly, however, there did not appear to be any longer-term impacts of rainfall variability on plant cover; current plant cover was not significantly affected by rainfall that occurred over 12 months ago. This suggests that biomass production in this system is highly resilient to rainfall variation.

Herbivory, like periods of low rainfall, had a negative effect on total plant cover. Consistent with previous results from the KLEE experiment (Young et al. 2005), cattle had a greater impact on plant cover (reducing total cover by approximately 18 % relative to total herbivore exclusion plots) than either meso-herbivores alone (which reduced cover by 2.4 %) or meso-herbivores in combination with megaherbivores (which reduced cover by approximately 6.1 %). Cover was highest and least affected by rainfall in the total herbivore exclusion treatment (Fig. 1a, b).

Across most rainfall levels, species richness was highest in plots to which cattle and meso-herbivores had access (WC and MWC). High species richness in these plots is likely driven by high spatial variability, which increases the number and type of available micro-sites (including patches of bare ground, see below).

Synergistic impacts of rainfall and herbivores

In the KLEE experiment, herbivory and drought appear to act synergistically: these two factors together had a far greater impact than either factor alone. In plots experiencing herbivory, and particularly cattle grazing, periods of especially low rainfall (<100 mm over 4 months) were associated with aggregation among non-dominant plant species, high species richness, and reduced species evenness after the next rainy season (Figs. 1, 2). Said differently, conditions of low plant cover—specifically, in plots grazed by cattle during a time of low rainfall—resulted in higher species richness and community aggregation after the next rainy season. These results appear to be driven primarily by non-dominant species colonizing bare patches after drought. We suggest that cattle grazing and drought act together to create favorable micro-sites (open gaps in this otherwise high-cover landscape) that are subsequently colonized by rare species (Online Resource 2). Although we were not able to explicitly examine responses by different plant functional groups, we note that the break between common and rare species tended to fall along a

functional fault-line: robust perennials versus annuals, geophytes, and short-lived perennials.

Separate elements of this scenario are consistent with earlier work in other, similar systems. Previous studies have shown that ephemeral gaps in grasslands can be generated by both large mammalian herbivory (Heady 1966; Silvertown and Smith 1989; Bullock et al. 1995; Renne and Tracy 2007) and drought (Weaver and Albertson 1936; Morecroft et al. 2004; Stampfli and Zeiter 2004). Ephemeral gaps can provide opportunities for other plant species, sometimes in the form of release from the seed bank (Bullock et al. 1995; Renne and Tracy 2007). In some cases, species colonizing ephemeral gaps were present in the pre-disturbance community, but gap colonizers can also be transient species that appear at the end of the disturbance and may or may not be replaced by dominants as the gaps gradually disappear (Albertson and Weaver 1944; Coupland 1958; Stampfli and Zeiter 2004). In perennial grasslands, species ‘released’ after droughts are often forbs or short-lived grasses (Weaver and Albertson 1936; Dunnett et al. 1998; Sternberg et al. 1999; Morecroft et al. 2004; Stampfli and Zeiter 2004). Similarly, herbivory by large mammals can cause an increase in forbs, shorter-lived plants, or weeds at the expense of perennial grasses (Heady 1966; Renne and Tracy 2007; Dreber et al. 2011). Finally, herbivory has been shown to cause permanent increases in the fine-scale spatial aggregation of the understory (Rayburn and Monaco 2011).

Our results add to this wealth of prior knowledge in three ways. First, our study bolsters a relatively small literature showing that the interaction of herbivory and drought can drive gap creation and subsequent community change more strongly than either stressor alone (see also Albertson and Weaver 1944; Fuhlendorf and Smeins 1997; Loeser et al. 2007; Stubbendieck and Tunnell 2008; Gao et al. 2009; Dreber and Esler 2011). Second, results show that at our site, domestic herbivores are stronger drivers of gap creation than wild herbivores. Third, we demonstrate that the combination of drought and herbivory can cause the spatial structure of the understory community to undergo predictable, temporary shifts from random to significantly aggregated (Fig. 1c).

Although cattle grazing had the most dramatic impacts on plant community structure, areas grazed by native wild herbivores also exhibited relatively high species richness and community aggregation after periods of low rainfall. Moreover, bare ground during the previous season was positively associated with subsequent non-dominant species richness in all but the total herbivore exclusion treatment. Taken together, these results suggest that wild and domestic herbivores have qualitatively similar effects on herbaceous community structure, but the magnitude of domestic herbivore impacts is much greater.

Cattle probably have larger impacts than wild ungulates because of their higher biomass density (cattle have 5–10 times higher biomass per km² than wild ungulates). However, wild ungulate herbivory also differs from domestic herbivory in other ways. Each C, WC, and MWC plot experiences a relatively short-duration cattle grazing event every 8–16 weeks. By contrast, wild ungulate herbivory is more continuous. Cattle and wild ungulates also have different diets, although dietary overlap is fairly large (the dominant wild ungulate species are grazing zebras and mixed-feeding antelopes). The dominant understory plant species in this system are grasses (Online Resource 1), so browsing herbivores (e.g., giraffe, eland) are unlikely to create understory gaps. Finally, because wild ungulates have a longer evolutionary history in this system, plants may have adaptations that make them more resilient to wild ungulate herbivory than cattle herbivory.

Regardless of mechanism, our results suggest that in the absence of fire, herbivory (and particularly livestock grazing) can help to maintain understory plant diversity and spatial heterogeneity in savanna ecosystems. It is important to note that our system is a relatively productive savanna with a long evolutionary history of grazing, and current levels of grazing are relatively moderate. Our results may not apply to other systems or to sites with heavier grazing intensities (Milchunas and Lauenroth 1993). Outcomes of grazing can also be affected by the timing of herbivory relative to precipitation (Vermeire et al. 2008). Finally, creating space for ephemeral and annual species may not be a central goal for managers who want to maximize perennial grass biomass. Nevertheless, carefully managed livestock grazing may be a useful tool for maintaining high plant biodiversity in many rangelands.

Insights about drivers of community structure

Relationships among response variables were quite strong in general but broke down once herbivore treatment and rainfall were accounted for. This suggests that herbivores and rainfall are major drivers of several linked aspects of this herbaceous vegetation community. Fire has been excluded from our study site for several decades, but in many other grasslands it is also a key driver of community dynamics (Archibald et al. 2005; Collins and Smith 2006).

In contrast to previous studies in arid and semi-arid systems (e.g., Tirado and Pugnaire 2005; Forey et al. 2009), our data did not support the idea of increased plant-plant facilitation during times of drought. In fact, droughts (i.e. low rain,) were associated with significantly higher SES scores, though the effect size of this result was relatively small (Table 1; Fig. 1d). Recent studies suggest that

facilitation may be more common when the abiotic stress is non-resource-based (e.g., temperature rather than water stress; Maestre et al. 2009), and that facilitation might be most common in mild environments (Holmgren and Scheffer 2010). In our system, plants may be so water-stressed during droughts that microclimate amelioration does little to facilitate growth. It is also possible that facilitation occurs at a scale different from that of our measurements. For example, palatable grasses can be facilitated by less palatable grasses at a scale finer than 0.25 m² (Veblen 2008).

Rather than supporting the stress-gradient hypothesis (Bertness and Callaway 1994), our results support the concept of a disturbance-limited community. Without both drought and grazing, non-dominant species appear to be out-competed by more common plant species, primarily perennial grasses and forbs. The more common species in our system did not exhibit aggregation and, in fact, were somewhat segregated, suggesting that competition drives their dynamics (see also Osnas and Ankeny 2003). In addition to similarities to other grassland systems (see above), these dynamics are reminiscent of post-fire herbaceous communities in chaparral (e.g., Guo 2001) or post-tree fall herbaceous communities in forests (e.g., Dirzo et al. 1992). It is possible that disturbance would be a less important influence on the community in a system with lower biomass and more large-scale spatial patterning; although rainfall is relatively low at our study site, herbaceous cover is nearly continuous and the understory relatively homogenous. In other savannas, tree understories and termite mounds can harbor plant species not found in the background vegetation. In our system, however, trees and termite mounds are characterized by higher cover of a few common grass and forb species (Riginos et al. 2009) and do not appear to be favorable micro-sites for the less common plant species.

Our results emphasize that drivers of community structure are highly contextual in the face of established patterns of aggregation, facilitation, and disturbance. As we seek to develop general theories of community ecology, we must remain open to the power of contingency to reveal a far more complicated world of species interactions.

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