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RESEARCH ARTICLE

Disturbances in drylands: Interactions among herbivory, drought, and termite activity in savanna plant communities

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Abstract

1. Climate models predict increases in the frequency and intensity of extreme-weather events. The impacts of these events may be modulated by biotic agents in unpredictable ways, yet few experiments cover sufficient spatiotemporal scales to measure the interactive effects of multiple extreme events.
2. We used 15 years of a 28-year experiment spanning several significant droughts to investigate how rainfall, large herbivores, and soil-engineering termites affect understorey vegetation in a semi-arid savanna.
3. Herbivory was the dominant influence on community structure—decreasing cover, increasing species richness, and favouring occurrence of annuals relative to perennials—but these effects were contingent on rainfall and termitaria in non-additive (hence unpredictable) ways.
4. A separate experiment showed that resource enrichment, mimicking the effects of termitaria, does not straightforwardly compensate for top-down effects of herbivory.
5. *Synthesis*. Our study highlights the potency of top-down forcing in African savannas. It suggests impressive robustness to drought and underscores the value of multi-decadal experiments for studying interactions among multiple drivers of ecosystem dynamics.

KEYWORDS
ecosystem engineers, elephants and ungulates, emergent properties, forecasting global climate change, fourth-corner problem, herbivore exclusion (exclosure) experiment, long-term ecological research, plant functional traits, plant–herbivore interactions, spatial heterogeneity

1 | INTRODUCTION

Disturbance—any biotic or abiotic force that generates deviations from prevailing local background conditions (Graham et al., 2021)—has long been recognised as a fundamental driver of population dynamics, species distributions, and community structure (Pickett & White, 1985; Sousa, 1984). Although the impacts of many types of disturbance have been studied in isolation, the individual and net impacts of multiple interacting disturbances are difficult to disentangle (Turner, 2010). Whether such interactions are additive or non-additive—and in the latter case, whether super-additive or sub-additive (Crain et al., 2008; Piggott et al., 2015)—is rarely established (Porensky & Young, 2013). The potential for non-additive effects and emergent properties in complex systems has important implications because it determines whether or not the consequences of multiple disturbance agents can be predicted from the study of each individually (Buma, 2015; Burton et al., 2020).

The need to understand the impacts and interactions of multiple disturbances is urgent given accelerating change in climate, land use and community structure. Beyond the steadily shifting climatic baseline, models predict increases in the frequency and/or intensity of extreme-weather events (IPCC, 2022), which have severe and long-lasting ecological consequences (Anderegg et al., 2015; Walker et al., 2023). Similarly, the millennia-long decline of large-bodied mammals is currently being punctuated by a spasm of population extirpations, which sharply transform local disturbance regimes (Pringle et al., 2023; Ripple et al., 2015; Smith et al., 2018). The impacts of shifting disturbance regimes may be especially acute in drylands, which cover over 40% of global land area and are often sensitive to even small changes in bottom-up (precipitation) or top-down (herbivory) forces (Maestre et al., 2016, 2022).

We investigated the effects of three dominant drivers of vegetation dynamics in tropical semi-arid grasslands: large-mammal herbivory, rainfall (drought), and soil-nesting termites. Of the possible interactions among these drivers, herbivory × rainfall interactions are the most extensively studied (Carmona et al., 2012; Ebel et al., 2022; Fuhlendorf & Smeins, 1997; Hartvigsen, 2000; Milchunas et al., 1989) and are often non-additive, such that the effects of one are amplified by the other (Augustine & McNaughton, 2006; Gao et al., 2009; Koerner & Collins, 2014; Loeser et al., 2007; Porensky et al., 2013; Riginos et al., 2018). However, the extent to which termite activity modifies the effects of herbivory and/or rainfall remains unclear.

Termites are predominant decomposers in ecosystems worldwide (Zanne et al., 2022) and are ubiquitous in African savannas (~100 kg ha^{-1}, similar to mammalian herbivores; Moe et al., 2009). The centralised nests (termitaria or 'mounds') created by fungus-farming termites (Macrotermitinae) are particularly influential in Paleotropical savannas and affect vegetation at local to landscape scales owing to alterations of soil texture, nutrients and moisture (Pringle et al., 2010; Pringle & Tarnita, 2017; Tarnita et al., 2017). While termitaria typically increase localised productivity, their effects on understorey cover and diversity are variable (Davies et al., 2014; Muvengwi et al., 2017; Muvengwi & Witkowski, 2020; Okullo & Moe, 2012a, 2012b). Termitaria × rainfall and termitaria × herbivory interactions have occasionally been documented. For example, termitaria can enhance grass cover more in drier habitats (Davies et al., 2014), maintain grass cover primarily during the wet season (Okullo & Moe, 2012b), and attract large herbivores (Davies et al., 2016; Odadi et al., 2018).

Theoretical models have predicted that termitaria should enhance the robustness of dryland vegetation to drought by enabling plants to withstand (resistance) and/or recover from (resilience) water limitation (Bonachela et al., 2015; Castillo Vardaro et al., 2021; Tarnita et al., 2017). While some empirical evidence is consistent with this prediction (Ashton et al., 2019; Guirado et al., 2023), it is difficult to test directly. In addition, few studies have explored the role of herbivory in mediating termite (Okullo & Moe, 2012a, 2012b; Trisos et al., 2021). For example, productive conditions on termitaria might help plants tolerate herbivory; however, given that the capacity for compensatory regrowth is constrained by water limitation and that herbivory at termitaria often intensifies during dry periods (Daskin et al., 2023; Davies et al., 2016), any buffering effects of termitaria may be negated or outweighed by interactions with bottom-up (drought) and top-down (herbivory) stressors (Trisos et al., 2021). Three-way interactions among rainfall, herbivory, and termitaria have not, to our knowledge, been experimentally evaluated and might provide insights that are overlooked by studies of individual or pairwise effects (Kercher & Zedler, 2004; Koerner & Collins, 2014).

Plant responses to these three drivers (herbivores, rainfall, and termitaria) are likely to depend on plant functional traits, such as life form and life history. For example, herbivory often benefits annuals relative to perennials and alters the balance of forbs and grasses (Anderson et al., 2007; Loeser et al., 2007; Pakeman, 2004; Pérez-Camacho et al., 2012), and annual grasslands may be more sensitive to interannual variation, including droughts, than perennial grasslands (Ruppert et al., 2015; Werner et al., 2024). However, such studies often analyse aggregate responses of functional groups, which are driven by their dominant species, and thus do not necessarily enable reliable inferences about the responses of species of the same functional type in other similar ecosystems.

The variable interactions among herbivory, termitaria and drought documented in previous studies may stem in part from their short duration. This is particularly pertinent for episodic disturbances, such as extreme weather, because studies encompassing just one event cannot robustly test interactions. Moreover, communities dominated by slow-growing perennial plants can take years for experimental effects to manifest fully (Porensky et al., 2017; Riginos et al., 2018). The handful of active multi-decade experiments is therefore inordinately valuable for untangling multi-disturbance interactions, especially those that are intermittent and unpredictable (Gaiser et al., 2020).

Since 1995, the Kenya Long-term Exclosure Experiment (KLEE) has manipulated large-mammal herbivory in replicated 40,000-m^2 plots of semi-arid African savanna (two to three orders of magnitude larger than the typical exclosure experiment; Pringle et al., 2023). Using 15 years of data from KLEE and 2 years of data from an adjacent small-scale resource-addition experiment with crossed herbivore exclusion, water-addition, and fertilisation treatments, we applied hierarchical multispecies models to test (a) the individual and interactive effects of herbivory, rainfall, and termites on understorey vegetation cover and species richness, and (b) how these responses were mediated by plant life-form (graminoid/forb) and life history (annual/perennial). We hypothesised a three-way interaction among herbivory, drought, and termitaria, whereby the more-than-additive suppression of understorey plants by herbivory and drought would be dampened on termitaria.

2 | MATERIALS AND METHODS

2.1 | Kenya Long-term Exclosure Experiment

KLEE is located at Mpala Research Centre in Laikipia, central Kenya (0°17′ N, 36°52′ E, 1800 m elevation) and consists of 18 four-hectare ($200 \times 200\,m^2$) plots on heavy-clay vertisol soils. The overstorey is dominated (over 95%) by a single tree species, *Acacia (Vachellia) drepanolobium*. The understorey is dominated by the perennial grasses *Brachiaria lachnantha*, *Themeda triandra*, *Pennisetum stramineum*, *P. mezianum*, and *Lintonia nutans* (collectively exceeding 75% of total cover). Common large herbivores are elephant (*Loxodonta africana*), giraffe (*Giraffa camelopardalis*), plains zebra (*Equus quagga*), Grevy's zebra (*E. grevyi*), eland (*Tragelaphus oryx*), hartebeest (*Alcelaphus buselaphus*), oryx (*Oryx beisa*), buffalo (*Syncerus caffer*), Grant's gazelle (*Nanger granti*), and domestic cattle (*Bos indicus*). For context on herbivory pressure, we present herbivore species abundances and biomass densities at the experimental plots as reported by Veblen et al. (2016) in Table S1. Termitaria in this system are functionally monotypic as far as we know, although genetic analysis shows that they are occupied by two closely related *Odontotermes* spp., *O. montanus* (~90%) and *O. anceps* (~10%) (Castillo Vardaro et al., 2021).

Rainfall at KLEE is weakly trimodal with a short, pronounced dry season (December–March). Between 2001 and 2023, annual rainfall averaged 601 mm $year^{-1}$ (range: 331–1099 mm $year^{-1}$, interannual coefficient of variation: 30%). Owing in part to the low annual rainfall, abbreviated dry seasons, and unpredictable temporal distribution of rainfall fires are uncommon in this region.

We used understorey data collected over 15 years of KLEE (2009–2023). This period contained 5 years that coincided with regionally significant droughts (2009, 2014, 2017, 2021, 2022). During these drought years, the 4-month cumulative rainfall preceding vegetation sampling (February–May, which includes the primary growing season) fell below the 25% quantile of all years from 2001 to 2023. For this study, we focused on two herbivory treatments, each replicated three times, for a total of six 4-ha treatment plots: (1) excludes all large (>15 kg) wild and domestic herbivores, and (2) unfenced control accessible to all herbivores. For more details of this experimental study system, see Riginos et al. (2012) and Young et al. (2018).

2.2 | Resource-addition experiment

In 2017, a separate experiment was established immediately adjacent to KLEE. In this experiment, all factorial combinations of ± fertilisation (0.11 kg m^{-2} NPK applied as 17:17:17 pellets every 6 months), ± watering (12 mm per week, thus doubling baseline rainfall) and ± herbivore exclusion (as described above for KLEE) were replicated three times in 9-m^2 plots ($n = 24$ total plots). We used this experiment to independently probe the interaction of soil-nutrient enrichment (as occurs on termitaria), water limitation, and herbivory. Specifically, we used data from 2021 to 2022 (during the Horn of Africa Drought) to test the effects of experimentally alleviating bottom-up constraints in the presence and absence of large herbivores.

2.3 | Data collection

In KLEE, the occurrence (presence-absence) of understorey plant species was recorded in $1 \times 1\,m^2$ quadrats at 50 stations located every 20 m along 10 parallel 100-m transects in a 1-ha grid in each treatment plot (total $n = 300$ quadrats $year^{-1}$). At a subset of these occurrence sampling stations (20 sampling stations, 20-m spacing), understorey cover was measured by counting the number of pin hits by each species using a 10-point pin frame (5 cm between pins; maximum one hit pin^{-1} $species^{-1}$) within each treatment plot (total $n = 120$ stations $year^{-1}$). The distance to the edge of the nearest termitarium was calculated for each vegetation sampling station (Charles et al., 2021). Because many small termite nests emerge after reproductive swarms but do not last long enough to affect vegetation, we followed Castillo Vardaro et al. (2021) by including only termitaria larger than ~0.8 m^2 (corresponding to ~1-m diameter for a circular mound) to avoid confounding effects of 'incipient' colonies. We recorded negative distances from the edge if sampling stations were located on termitaria (Baker et al., 2020). Although the termitaria were mapped in 2015, mound structures greater than 1 m in diameter are perennially stable (often being recolonised after the death of the founding colony and sometimes persisting for centuries; Pringle & Tarnita, 2017), and are thus very likely to have persisted throughout the study period.

In the resource-addition experiment, species occurrence and cover were measured at nine sampling locations arranged in a 3 × 3 m grid within each of the 24 treatment plots (total $n = 216$ sampling stations year^{-1}). Cover was measured using total hits of 10-point pin frames (5 cm between pins, counting all hits of all species on all pins), and species occurrence was measured within 0.25-m^2 quadrats (0.5 × 0.5 m).

2.4 | Data analysis

Data from KLEE were analysed at the scale of individual sampling stations. To investigate the response of understorey species occurrence and richness to large mammalian herbivores, termitaria, and rainfall, we analysed the quadrat presence-absence data by fitting a joint species distribution model (Warton et al., 2015) using the Hierarchical Modelling of Species Communities (HMSC) framework (Ovaskainen et al., 2017). We investigated the response of total understorey cover (sum of pin hits) in a separate model due to the different sampling methodologies (20 stations per treatment plot for cover versus 50 stations for species occurrence).

To assess the individual and interactive effects of the three drivers, we coded herbivore exclusion (categorical), distance to termitaria (continuous), precipitation (continuous; cumulative rainfall over the 4 months preceding vegetation sampling), and their pairwise and three-way interactions as fixed effects. To test for lagged effects of precipitation, which have been shown to influence understorey plant occurrence and richness (Porensky et al., 2013), we also included pairwise and three-way interactions among herbivore exclusion, distance to termitaria, and precipitation (of the same 4-month period) in the year preceding the sampling year. To account for potential pseudoreplication and unmeasured environmental variables at the levels of sampling stations, plots, and year, we coded a nested random-effect structure comprising 'station within plot within year'. In the occurrence model (for species occurrence and community composition), we fit a probit regression to quadrat occurrence. To avoid zero-inflation issues, we excluded species occurring in fewer than 1% of sampling occasions, leaving a total of 63 species accounting for over 99% of all occurrences. In the understorey cover model, we fit a log-normally overdispersed Poisson regression to total cover. To explore the influence of functional groups, we examined the main effects of life form (graminoid/forb) and life history (annual/perennial) on species' occurrence responses to the interacting drivers (Abrego et al., 2017). Coding distance to termitaria and precipitation as continuous variables avoids issues relating to selecting arbitrary thresholds to categorise these two variables. However, non-linear main effects of distance to termitaria and/or precipitation may not be well captured. To test the robustness of the results of the continuous models, we also fit alternative formulations of both the understorey cover and multispecies occurrence models, in which we coded distance to termitaria and precipitation as categorical variables: termitaria ('termitaria': ≤10 m vs. 'matrix': >10 m) and precipitation (drought: ≤25% quantile vs. non-drought: >25% quantile). For clarity of graphical illustration of the results of the continuous models and comparability with the results of the categorical models, we binned precipitation into drought/non-drought periods and distance to termitaria into termitaria/matrix using the same thresholds as in the categorical models (Figures 1 and 2). The results of the continuous models (reported in the main text) and of those of the categorical models are qualitatively comparable, as illustrated in Figures S1 and S2.

In the small-scale resource-addition experiment, we tested for individual and interactive effects among soil nutrients, water availability, and herbivory by analysing total understorey plant cover and species richness (both calculated at the level of sampling stations). We coded each explanatory variable (± herbivory, ± watering, ± fertilisation) and their pairwise and three-way interactions as fixed effects, with a 'station within plot' random-effect structure.

All statistical analyses were performed in R version 4.3.2 (R Core Team, 2023). We fitted the models using the *Hmsc* package version 3.0 (Tikhonov et al., 2020), assuming the default prior distributions (Ovaskainen & Abrego, 2020). We sampled the posterior distribution using four Markov chain Monte Carlo (MCMC) chains. For the KLEE species occurrence model, we ran each chain for 300,000 iterations, discarding the first 50,000 as burn-in and thinning by 1000 to yield 250 samples per chain and 1000 posterior samples in total. For all other models, we ran each chain for 30,000 iterations, discarding the first 25,000 as burn-in and thinning by 500 to yield 250 samples per chain and 1000 posterior samples in total. We assessed MCMC chain convergence by visually inspecting trace plots and ensuring that the potential scale reduction factors for all regression parameters were below 1.1 (Gelman & Rubin, 1992). We visually confirmed normality and homoscedasticity of residuals, performed additional posterior predictive checks to assess model performance, and ensured acceptable effective sample sizes of posterior draws (median: 1000, minimum: 548).

We evaluated posterior statistical support (i.e. the proportion of posterior samples for which the focal effect occurs) for the effect of a predictor variable being either positive or negative. For example, if the effect of a predictor variable is positive, the posterior support is the proportion of posterior samples exceeding zero, which can be interpreted as the probability of the effect being positive. Posterior support indicates the probability that a focal effect occurs, while credible intervals provide an indication of the uncertainty surrounding the estimated mean value. Following McElreath (2018), we use 89% credible intervals (within which the mean lies with 89% probability) to infer robust support for an effect. We interpret lesser values (85%–89%) as representing modest but non-negligible support.

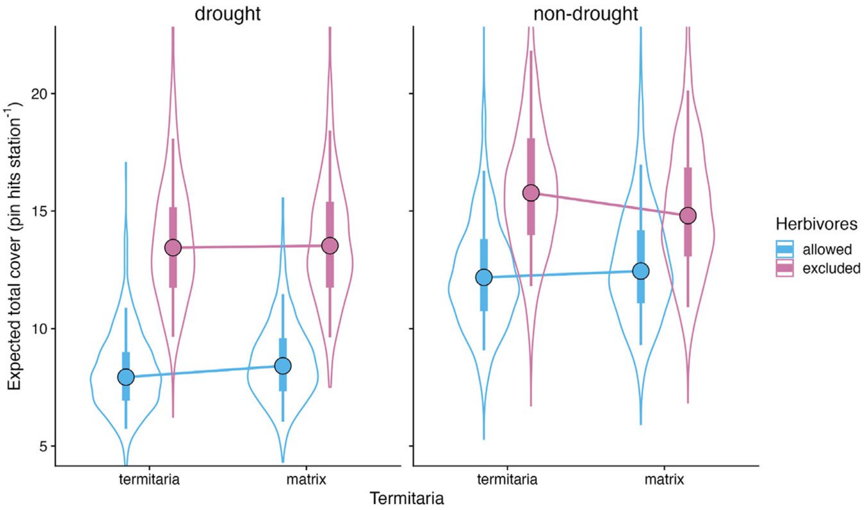

FIGURE 1 Herbivory and drought depleted understorey cover, with effects contingent upon one another, proximity to termitaria, and the three-way interaction. Plots show sampling station-level responses of understorey plant total cover to large herbivores, rainfall, distance to termitaria, and their interactions (medians, 50% and 89% credible intervals). Although precipitation was modelled as a continuous variable, here it is binned into 'drought' (D_1; years with 4-month cumulative antecedent rainfall ≤25% quantile, mean = 115 mm) and 'non-drought' (D_0; cumulative antecedent rainfall >25% quantile, mean = 266 mm) for visualisation and posterior support calculations. Similarly, although distance to termitaria was modelled as a continuous variable, here it is binned into 'termitaria' (T_1; ≤10 m from edge) and 'matrix' (T_0; >10 m) for visualisation and posterior support calculations. H_0: Herbivore exclosure, H_1: Unfenced. Posterior statistical support (proportion of posterior samples in which each effect occurs): Herbivory, $P[H_1 < H_0] > 99\%$; drought, $P[D_1 < D_0] > 99\%$; termitaria, $P[T_1 < T_0] = 52\%$; herbivory × drought, $P[H{:}D < 0] > 99\%$, termitaria × drought, $P[T{:}D < 0] = 93\%$; herbivory × termitaria, $P[H{:}T < 0] = 99\%$; three-way interaction, $P[H{:}D{:}T < 0] = 98\%$. Thus, here we find strong support for all effects except a main effect of termitaria.

3 | RESULTS

3.1 | Understorey cover

In KLEE, herbivores reduced understorey cover by 27% on average (10.7 vs. 14.6 hits station^{-1}; posterior support >99%) under average rainfall and distance to termitaria. Droughts (≤25% quantile of 4-month antecedent precipitation) reduced understorey cover by 21% on average (11.0 vs. 14.1 hits station^{-1}; posterior support >99%). Termitaria had no net effect averaged across herbivory treatments and rainfall conditions (12.5 vs. 12.5 hits station^{-1}; posterior support = 52%). Thus, understorey cover was reduced most strongly by herbivory and to a slightly lesser extent by droughts, while the net effect of termites on understorey cover was negligible (Figure 1).

However, the effect of termitaria (≤10 m vs. >10 m from visible edge) on understorey cover changed from positive to negative depending on herbivory (+0.9 vs. −0.6 hits station^{-1}; posterior support >99%) and drought (+0.4 vs. −0.4 hits station^{-1}; posterior support = 96%; Figure 1). Therefore, the effect of termitaria on plant cover depended on rainfall and herbivory, switching from enhancement (in exclosures or non-drought years) to suppression (in unfenced plots or drought years).

Herbivory and precipitation suppressed understorey cover non-additively (posterior support >99%), such that understorey cover in unfenced plots during droughts was lower than expected based on summing the individual effects of drought and herbivory, averaged over distance to termitaria (−4.3 vs. −1.2 hits station^{-1}). Thus, droughts suppressed understorey cover more strongly in unfenced plots, and herbivory suppressed cover more during droughts, regardless of termitaria.

In unfenced plots during droughts, understorey cover near termitaria was lower than expected based on the additive effects of all three drivers (−6.6 vs. −1.3 hits station^{-1}; posterior support for three-way herbivory × drought × termitaria interaction 98%; Figure 1). Thus, understorey cover was lowest in the presence of all three drivers (termitaria, herbivory, and drought), and highest near termitaria in the absence of drought and herbivores.

Taken together, these results suggest that termites locally enhance understorey cover in the absence of stressors, as expected, but that their effect is outweighed by the added combination of top-down (herbivory, which may be more intense on termitaria) and bottom-up (water stress) limiting factors. We obtained similar results from a model in which distance to termitaria and precipitation were coded as categorical variables (Figures S1 and S2).

3.2 | Understorey species richness and composition

In KLEE, large herbivores enhanced understorey quadrat-level species richness by 55% on average (15.0 vs. 9.6 species quadrat^{-1}; posterior support >99%). Droughts reduced richness by 8% on average (11.8 vs. 12.9 species quadrat^{-1}; posterior support = 99%) while termitaria increased richness by 2% on average (12.5 vs. 12.2 species quadrat^{-1}; posterior support = 95%; Figure 2). This strong effect of

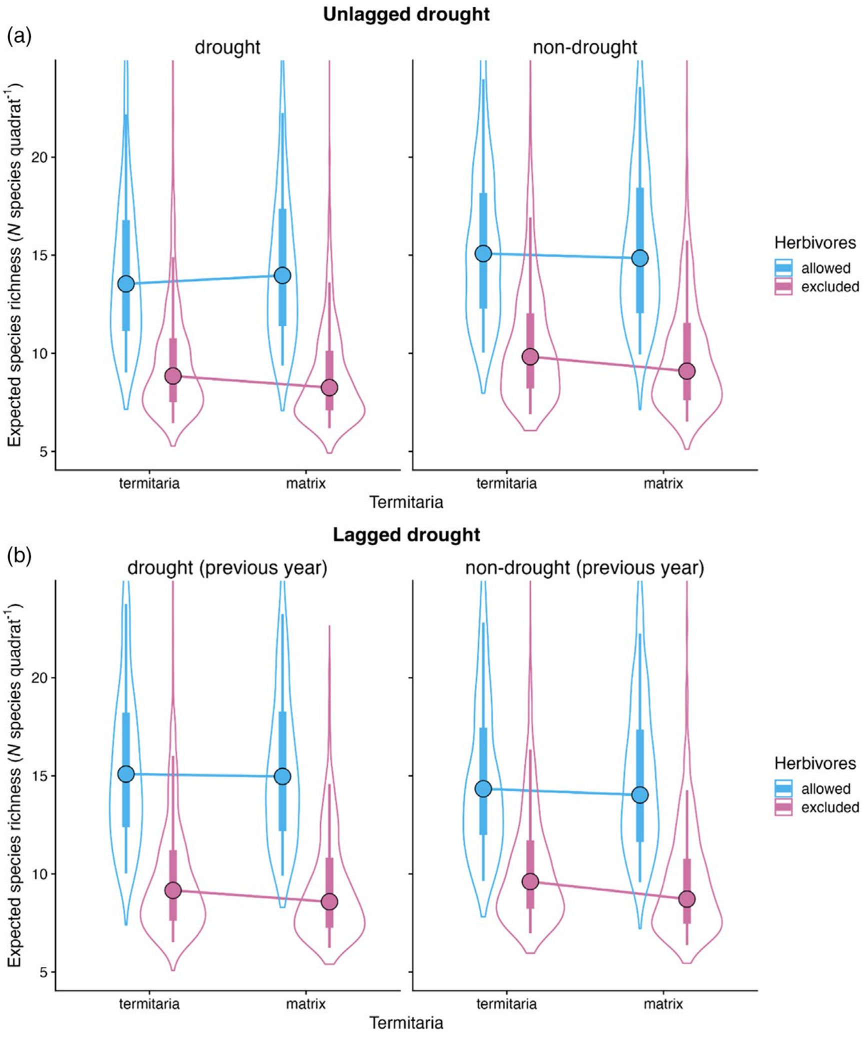

FIGURE 2 Herbivore exclusion and drought reduced local species richness, with effects contingent upon one another and proximity to termitaria, but with no three-way interaction [Correction added on 23 May 2025, after first online publication: The wording 'Herbivory and drought reduced' has been updated to 'Herbivore exclusion and drought reduced'.]. Plots show sampling station-level responses of species richness to herbivory, drought, distance to termitaria, and their interactions, for unlagged (a) and lagged (b) drought (medians, 50% and 89% credible intervals). Although precipitation and distance to termitaria were modelled as continuous variables, here they are binned into 'drought' (D_1)/'non-drought' (D_0) and 'termitaria' (T_1; ≤10 m from edge)/'matrix' (T_0; >10 m) for visualisation and posterior support calculation, as in Figure 1. H_0: herbivore exclosure, H_1: unfenced. Posterior statistical support: herbivory, $P[H_1 > H_0] > 99\%$; drought, $P[D_1 < D_0] = 99\%$; lagged drought, $P[Dlag_1 > Dlag_0] = 60\%$; termitaria, $P[T_1 > T_0] = 95\%$; herbivory × drought $P[H{:}D < 0] = 55\%$; herbivory × lagged drought, $P[H{:}Dlag > 0] = 89\%$; termitaria × drought $P[T{:}D < 0] = 85\%$; termitaria × lagged drought, $P[T{:}Dlag < 0] = 63\%$; herbivory × termitaria, $P[H{:}T < 0] = 88\%$; unlagged three-way interaction, $P[H{:}T{:}D < 0] = 59\%$; lagged three-way interaction, $P[H{:}T{:}Dlag < 0] = 50\%$. Thus, here we find strong support for main effects of herbivory, drought, and termitaria (posterior support ≥95%), moderate support for several two-way interactions between herbivory, termitaria, and drought (posterior support ≥0.85 but ≤0.89), and no support for three-way interactions with either lagged or unlagged drought terms.

herbivory on richness, relative to precipitation and distance to termitaria, is also evident in plant species-specific responses (Figure 3) and the results of variance partitioning (Figure 4) and community ordination (Figure S3).

Termitaria switched from enhancing understorey richness in exclosures to suppressing it in unfenced plots (+0.7 vs. −0.1 species quadrat^{-1}; posterior support = 99%) and enhanced richness less during droughts (+0.1 vs. +0.4 species quadrat^{-1}; posterior support = 85%), indicating non-additive termitaria × herbivory and termitaria × drought interactions. We also observed a non-additive interaction between herbivory and lagged drought (posterior support >99%): in post-drought years, species richness was reduced in exclosures but increased in unfenced plots (−0.4 vs. +0.6 species quadrat^{-1}; Figure 2).

We found no strong statistical support for a three-way interaction on plant species richness (posterior support ≤59% for lagged and unlagged drought terms). We again obtained similar results from a model in which distance to termitaria and precipitation were coded as categorical variables (Figures S1 and S2). Thus, understorey species richness was disproportionately affected (positively) by large herbivores, with weaker and contingent effects of drought and termitaria (herbivory × lagged drought,

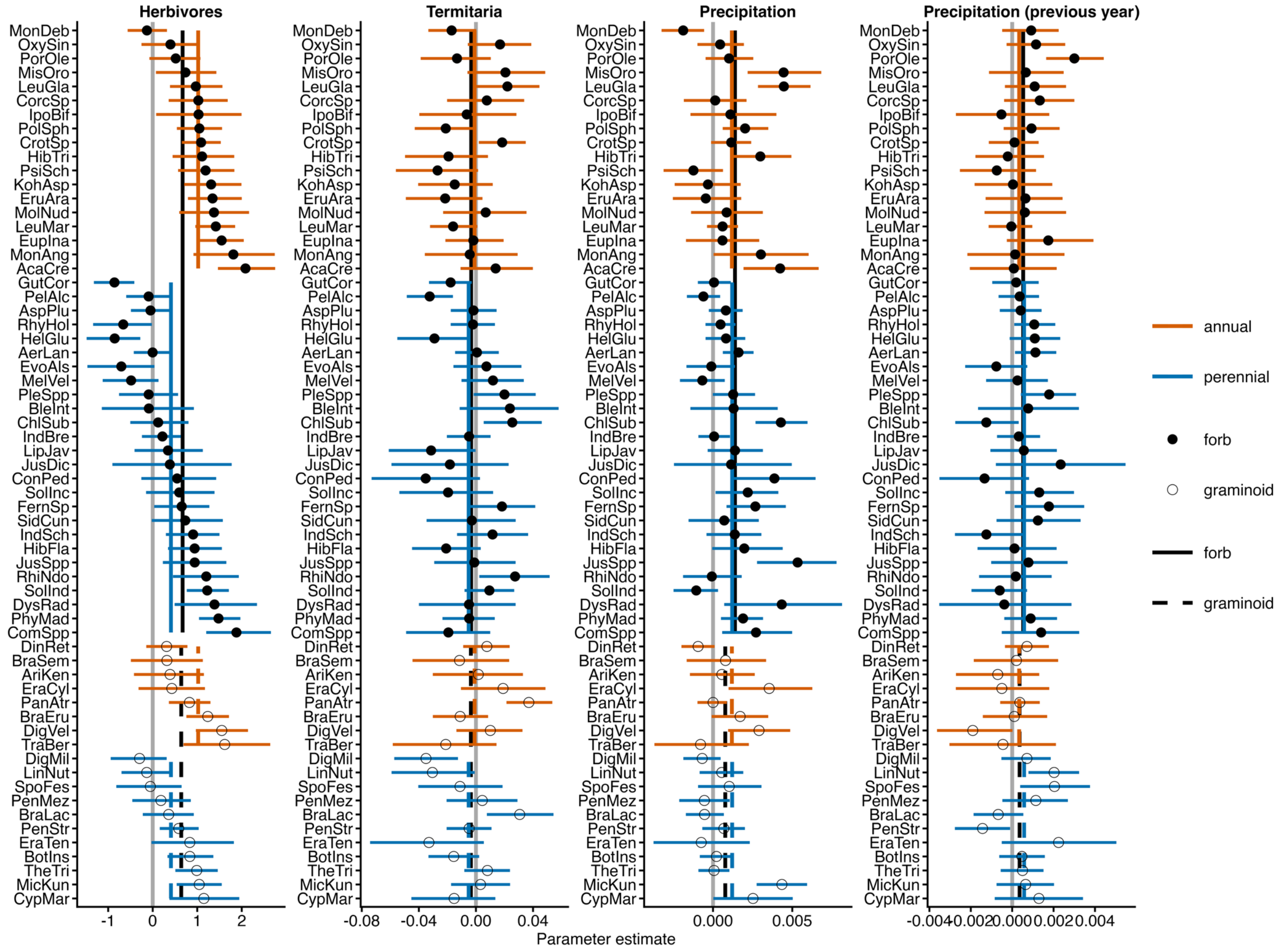

FIGURE 3 Herbivory promoted annual plants more than perennials, while rainfall and termitaria altered species' occurrences independently of plant functional group. Responses of quadrat-level species occurrence to herbivory (*H*), distance to termitaria (*T*), and 4-month antecedent precipitation (*R*), ordered by plant functional group (medians and 89% credible intervals). Grey reference line indicates zero; coloured vertical lines show overall mean effect sizes for functional groups (red = annuals; blue = perennials; dashed/open = graminoids; solid/filled = forbs; dashed/black = graminoids; solid/black = forbs). For species codes, see supplementary Table S2. Posterior statistical support: $P[H_{\text{annual}} < H_{\text{perennial}}] = 99\%$, $P[H{:}R_{\text{graminoid}} > H{:}R_{\text{forb}}] = 91\%$, all other functional type effects <81%. Thus, the effect of herbivores on the occurrence of annuals (H_{annual}) was more positive than that of perennials ($H_{\text{perennial}}$; blue vs. red), while the effect of the herbivory × precipitation interaction on the occurrence of graminoids ($H{:}R_{\text{graminoid}}$) was more positive than that of forbs ($H{:}R_{\text{forb}}$; Figure S4). For clarity, only main effects are visualised here; for all effects, see Figure S4.

termitaria × drought, termitaria × herbivory) and no indication of a three-way interaction [Correction added on 23 May 2025, after first online publication: The wording 'was disproportionately affected (negatively)' has been updated to 'was disproportionately affected (positively)'.].

3.3 | Influence of plant functional type on species occurrence responses

Herbivory increased the occurrence (presence) of annuals, perennials, graminoids, and forbs, but on average promoted the occurrence of annuals more than that of perennials (posterior support = 99%). However, there was considerable interspecific variation around these general tendencies (Figure 3). The non-additive herbivory × drought interaction effect on plant species occurrence varied by life form, such that the occurrence of forbs tended to be lower than expected based on the additive effects of herbivory and drought, whereas this was not true for graminoids (Figure S4). There was less evidence of a generalisable influence of life history (annual/perennial) or life form (graminoid/forb) on the responses of plant species occurrence to termitaria or drought (posterior support all <78%).

3.4 | Comparing effects of fertilisation and termitaria on the understorey

In the resource-addition experiment adjacent to KLEE, large herbivores reduced total understorey cover by 29% on average

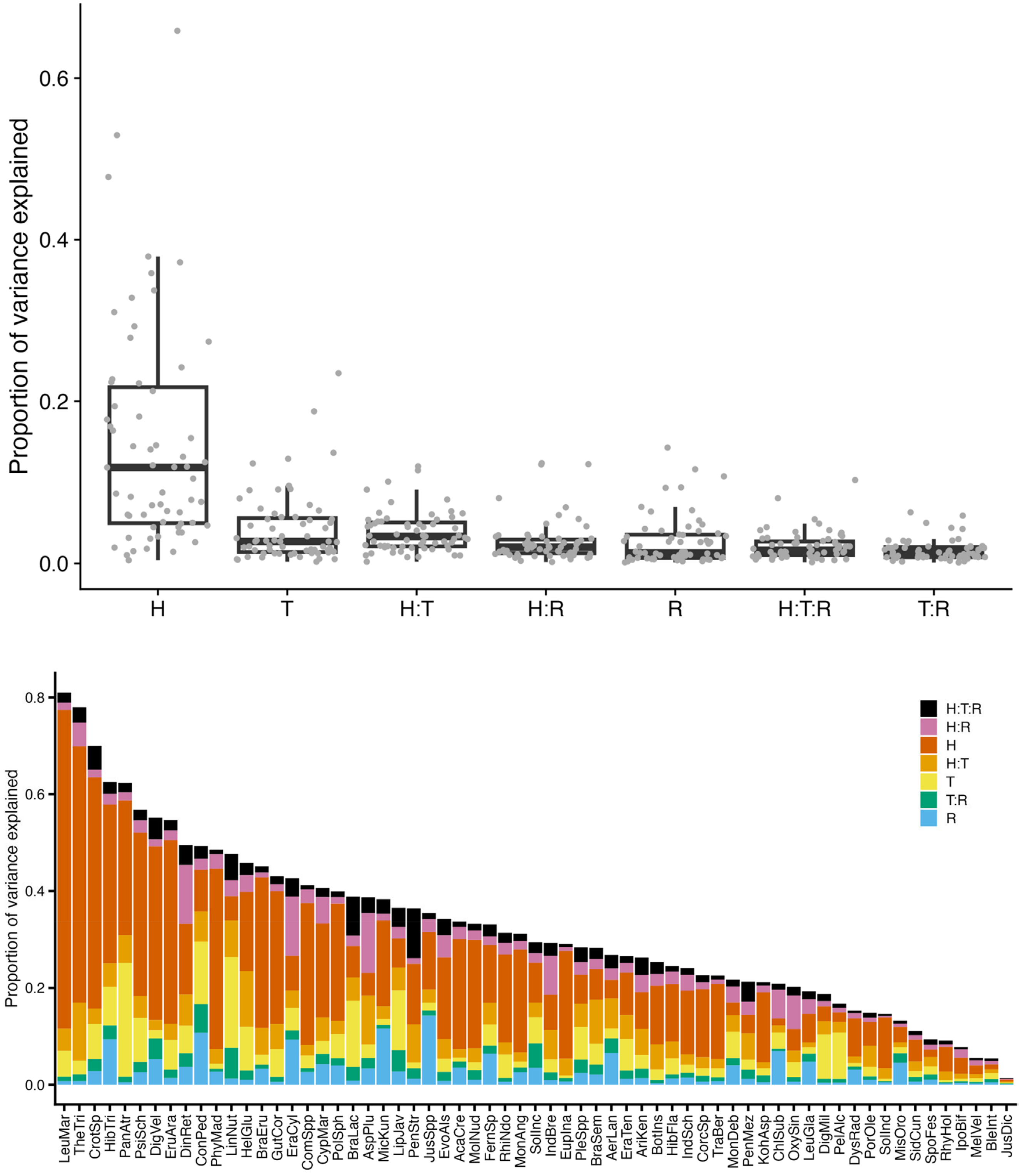

FIGURE 4 Variance partitioning shows the dominant effect of large mammalian herbivores on understorey plant species occurrence patterns. *H* = herbivory, *R* = precipitation, *T* = distance to termitaria; colons between letters signify interactive effects. Each point in the boxplot corresponds to one species. Stacked bars (bottom) show the variance explained by each factor on each species. For species codes, see Table S2.

(posterior support >99%), and fertilisation reduced species richness by 15% on average (posterior support >99%). There was modest statistical support that fertilisation reduced cover (posterior support = 86%) and that watering increased it (posterior support = 85%), but no appreciable support for 2- or 3-way interactions among fertilisation, watering, and herbivory (posterior support all <74%; Figure 5).

Thus, as in KLEE, herbivory and water limitation decreased understorey cover. Watering buffered the reduction of cover by herbivory, but fertilisation did not, analogous to the effects of natural

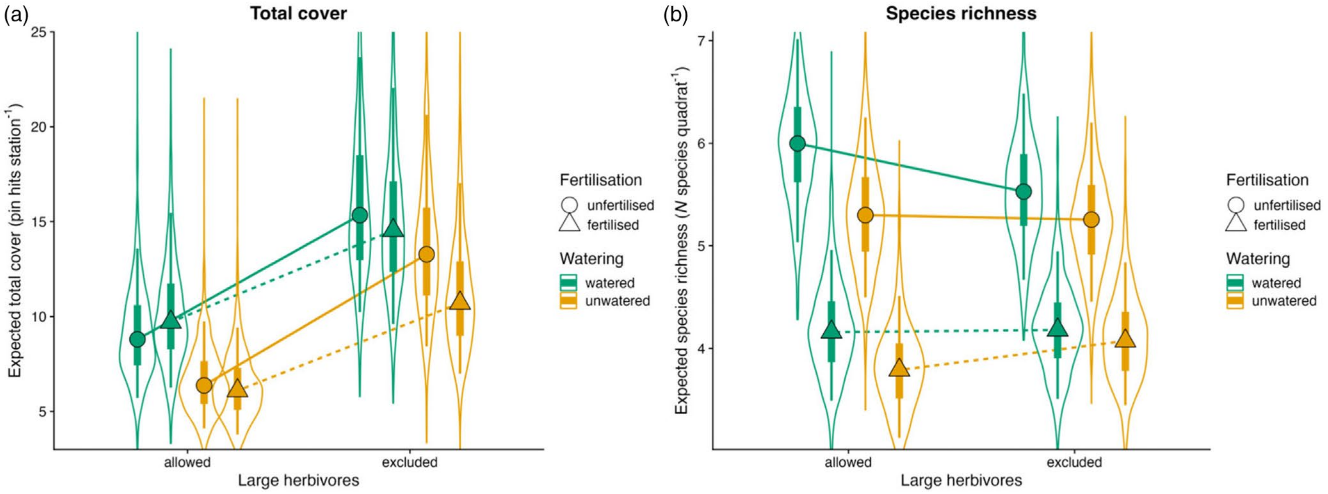

FIGURE 5 A factorial resource-addition experiment independently corroborated several patterns observed at larger scales in KLEE. Effects of large herbivores, fertilisation (mimicking soil enrichment by termites), and supplemental water (the equivalent of an average year's rainfall over 52 weekly waterings) on understorey cover (a) and species richness (b) in 9-m^2 plots during a drought. (a) As in KLEE, herbivory and water limitation decreased understorey cover. Supplemental watering recovered some of the cover lost to herbivory, such that mean cover in watered unfenced plots approached that in unwatered exclosure plots, but fertilisation had no comparable buffering effect, which is similar to what we found for real termitaria (Figure 1). Posterior support: herbivory, $P[H_1 < H_0] > 99\%$; fertilisation, $P[F_1 < F_0] = 86\%$; watering, $P[W_1 < W_0] = 85\%$; herbivory × fertilisation, $P[H{:}F > 0] = 72\%$; herbivory × watering, $P[H{:}W > 0] = 74\%$; fertilisation × watering, $P[F{:}W > 0] = 69\%$; three-way interaction, $P[H{:}F{:}W > 0] = 52\%$. (b) Unlike in KLEE, herbivory had negligible net effect on local species richness, which was strongly reduced by fertilisation (circles vs. triangles) and weakly reduced by water limitation (green vs. brown). While statistical support for interactions was low (posterior support ≤74%), highest richness occurred when herbivores were present and resources were low, which is qualitatively consistent with results from KLEE (cf. Figure 2). Posterior support: Herbivory, $P[H_1 > H_0] = 54\%$; fertilisation, $P[F_1 < F_0] > 99\%$; watering, $P[W_1 < W_0] = 71\%$; herbivory × fertilisation, $P[H{:}F < 0] = 74\%$; herbivory × watering, $P[H{:}W > 0] = 74\%$; fertilisation × watering, $P[F{:}W < 0] = 59\%$; three-way interaction, $P[H{:}F{:}W < 0] = 51\%$.

termitaria (Figure 2). Unlike in KLEE, herbivory had little effect on species richness, which was strongly reduced by fertilisation and slightly reduced by water limitation (Figure 5). The highest richness occurred in unfenced, unfertilised, watered plots, qualitatively consistent with results from KLEE (Figure 2).

4 | DISCUSSION

We experimentally tested the individual and interactive effects of large-mammal herbivory, drought, and termite activity on understorey vegetation cover, species richness, and community composition in an African savanna. The main effect of herbivory was the strongest driver of cover, richness, and community structure. Droughts substantially reduced understorey cover, particularly in conjunction with herbivory (see also Augustine & McNaughton, 2006; Gao et al., 2009; Koerner & Collins, 2014; Loeser et al., 2007), but the resilience of understorey cover was also evident from the high cover observed in intervening non-drought years (Figure 1). The negative effect of droughts on species richness was both quantitatively small and short-lived, with a non-additive increase in richness in the presence of herbivores in post-drought years relative to years not preceded by drought (see also Porensky et al., 2013; Riginos et al., 2018).

Previous research on savanna stressors has emphasised herbivory and drought and their interactions but have not incorporated termite effects. We had reasons to expect that these effects might be as great or even greater than those of herbivory and drought, and might interact strongly with them. Termitaria have been shown to exert strong effects on the occurrence of multiple plant species and hence on understorey community composition (Odadi et al., 2018; Okullo & Moe, 2012a, 2012b), and we also observed this effect (Figure 3; Figures S3 and S4). Nonetheless, their overall effects on cover and richness were considerably weaker in this system than those of herbivory and drought (Figures 1 and 2). Effects of termitaria are often strongest in nutrient-poor soils (Muvengwi et al., 2017), and the high fertility of the clay soils in KLEE might be one reason for the comparatively weak effects of termitaria in this study.

As hypothesised, we found that termitaria interacted with herbivory and rainfall to regulate understorey cover (≥ 93% posterior support for all interactions) and richness (marginally, 85%–89% posterior support for two-way interactions only). However, the directions of these effects did not match our expectations. Bonachela et al. (2015) predicted theoretically that, all else equal, the high primary productivity of termitaria should delay the onset of desertification in drylands under severe, sustained drought. In that model (which did not include effects of herbivory), as rainfall decreases, vegetation disappears first from 'matrix' habitat between mounds and only later from resource-rich termitaria. While the droughts in our 28-year study did not approach the desertification threshold, and plant canopy cover is not necessarily a reliable indicator of population persistence, we still expected that termitaria would act as refugia for understorey vegetation cover under water limitation (Davies et al., 2014). To the contrary, the highest percent cover occurred around mounds in exclosures during non-drought years, and we found no strong effect of proximity to termitaria on cover during drought years in either exclosures or unfenced plots. In unfenced plots, cover if anything increased with distance from termitaria, perhaps owing to elevated consumption of nutrient-rich plants near mounds together with limited compensatory regrowth because of rainfall shortage (Daskin et al., 2023; Davies et al., 2016; Odadi et al., 2018; Trisos et al., 2021). This three-way herbivory × termitaria × drought interaction has not previously been documented and may be an example of an interaction exposure effect, in which the impacts of a focal disturbance (herbivory) are mediated by an underlying condition (termitaria and drought) that increases individuals' exposure to the focal disturbance (Shinoda & Akasaka, 2020). Similarly, local richness declined slightly with distance from mounds in exclosures, but if anything exhibited the opposite trend in unfenced plots, in contrast to one of the only prior experimental studies, which found that termites substantially enhanced understorey diversity both in the absence and (especially) presence of grazers (Okullo & Moe, 2012a). Again, we highlight the baseline productivity of matrix soils as one known source of context-dependency in the relative impact of termitaria across locations.

The results of our smaller-scale (9-m^2) factorial resource-addition experiment did not precisely mirror those observed in the larger (40,000-m^2) KLEE plots, but are nonetheless consistent with the conclusion that herbivory is the primary influence on percent cover and that soil enrichment does not strongly buffer understorey cover or richness against grazing and drought. Here, unfenced plots exhibited a positive effect of fertilisation on understorey cover in the watered treatment that was negated in the unwatered treatment, suggestive of co-limitation, which parallels the negative effect of termitaria on understorey cover during droughts in unfenced KLEE plots. However, termitaria also suppressed understorey cover in unfenced plots during non-drought conditions, suggesting that there may be other co-limiting factors associated with termitaria beyond water and nutrient availability. A buffering effect of soil enrichment would entail equalising interactive effects of resource addition that offset the negative effects of herbivory and/or water limitation to some degree. Yet, even the strongest two- and three-way interactions were only moderately supported (posterior support ≤74%).

The negative main effect of fertilisation on understorey richness is a typical outcome in the absence of herbivory, arising from light limitation and competitive exclusion, but this effect is often attenuated by herbivory (Eskelinen et al., 2022; reviewed in Pringle et al., 2023). We did not find evidence for this fertilisation × herbivory interaction in our resource-addition experiment. We note that there are marked differences between topical NPK addition and the modifications created by real termitaria, which include not just nutrient enrichment but strong effects on soil texture (elevated sand: clay ratio) and structure (bioturbation and fungus gardens). A previous study in our system that also used fertilisation as a proxy for termitaria found that the two factors had divergent effects on soil microbiota, attributable in part to differences in soil pH (Baker et al., 2020). Moreover, in contrast to fertilisation, natural termitaria are typically marked by localised disturbance atop the mounds arising from termite activities (e.g. creation of vents). These discrepancies probably explain some of the differences between our two experiments.

As reported in other grasslands, herbivory favoured the occurrence of annuals over perennials (Loeser et al., 2007; Pakeman, 2004; Pérez-Camacho et al., 2012). However, we found considerable variation among plant species (Figure 3) that is overlooked by typical approaches that analyse aggregate responses of functional groups, which are driven by dominant species. The overall promotion of annuals over perennials by herbivores may be due to the improved access to light reduced dominance, and/or greater availability of microsites for colonisation by annuals due to large herbivore grazing and trampling (Koerner et al., 2018; Porensky et al., 2013; Wells et al., 2022). Our results suggest that plant species' responses to large mammalian herbivores can, in general, be predicted based on the species' life-history strategies. By contrast, evidence of non-additive effects suggests that the consequences of interactions will be hard to predict.

Other factors may also prove to be important to plant communities, such as the relative timing of different interacting drivers (Kollars et al., 2021; Lear et al., 2023). For example, if droughts become more frequent, which is a predicted effect of climate change, then the impacts of individual droughts of comparable magnitude may be more severe because the ecosystem will have had less time to recover from the preceding drought. Similarly, shifts in the timing, duration, and/or intensity of grazing by domestic herbivores could help to mitigate detrimental effects on vegetation, particularly during droughts. The continued maintenance of long-term experiments will be invaluable for future attempts to understand the combined impacts of interacting environmental forces on ecosystem dynamics.

AUTHOR CONTRIBUTIONS

Harry B. M. Wells conceived the study, led the writing of the manuscript and analysed the data. Harry B. M. Wells, Mathew Namoni, Jackson Ekadeli, Samson Kurukura, Abdikadir A. Hassan, John Ekeno, Buas Kimiti, Duncan M. Kimuyu, Corinna Riginos, Kari E. Veblen and Lauren M. Porensky conducted the fieldwork and prepared the datasets. Truman P. Young designed and established the exclosures. Robert M. Pringle designed and supervised the resource-addition experiment. All authors made significant contributions to the drafts and approved them for publication.

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CONFLICT OF INTEREST STATEMENT

The authors declare no conflicts of interest.

PEER REVIEW

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DATA AVAILABILITY STATEMENT

Data are available from the Dryad Digital Repository https://doi.org/10.5061/dryad.18931zd7q (Wells et al., 2025).

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SUPPORTING INFORMATION

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

Table S1: Abundance and biomass densities of major herbivore species at the Kenya Long-term Exclosure Experiment reported by Veblen et al. (2016).

Table S2: Plant species code key.

Figure S1: Alternative model structure with categorical termite and drought effects, as opposed to continuous, provide qualitatively comparable results for total cover.

Figure S2: Alternative model structure with categorical termite and drought effects, as opposed to continuous, provide qualitatively comparable results.

Figure S3: Community ordination also demonstrates the dominant effect of large mammalian herbivores on understory plant species occurrence patterns.

Figure S4: Large mammalian herbivores promote the occurrence of annual plants more than that of perennials and the herbivory × drought interaction is more negative for the occurrence of forbs than graminoids.

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