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RESEARCH ARTICLE

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Fine-scale variation in soil and topography influences herbaceous vegetation and the distribution of large mammalian herbivores

Robert O. Ang'ila[1,2] | **Duncan M. Kimuyu**[2,3] | **Geoffrey M. Wambugu**[1,4] | **David Kenfack**[5] | **Paul M. Musili**[6] | **Tyler R. Kartzinel**[2,7,8]

[1]Department of Environmental Studies, Karatina University, Karatina, Kenya

[2]Mpala Research Centre, Nanyuki, Kenya

[3]Department of Natural Resources, Karatina University, Karatina, Kenya

[4]Wildlife Works, Voi, Kenya

[5]ForestGEO, Smithsonian Tropical Research Institute, Washington, D.C., USA

[6]East African Herbarium, Botany Department, National Museums of Kenya, Nairobi, Kenya

[7]Department of Ecology, Evolution, and Organismal Biology, Brown University, Providence, Rhode Island, USA

[8]Institute at Brown for Environment and Society, Brown University, Providence, Rhode Island, USA

Correspondence

Robert O. Ang'ila and Duncan M. Kimuyu, Mpala Research Centre, P.O. Box 555, 10400, Nanyuki, Kenya.
Email: robert.o.angila@gmail.com and dkimuyu@gmail.com

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Abstract

Current understanding of the distribution of vegetation and large mammalian herbivores (LMH) is based on a combination of biogeographic studies and highly controlled field experiments, but a more complete understanding of these patterns requires study of their natural co-occurrence patterns at intermediate spatial scales. The study was conducted in the 120-ha Mpala Forest Global Earth Observatory (ForestGEO) plot, Kenya. We examined differences in herbaceous plant communities and habitat use by LMH among three topographic habitats with distinct soil types, namely steep slopes, valley and plateau. Each pair of habitats differed in plant and animal composition. The steep slopes and plateau respectively had ≥1-fold higher percentage herbaceous cover than the valley, whereas the steep slopes and valley had >1.5-fold greater grass species richness and diversity than the plateau. The activity of LMH was ≥1.7-fold higher in the valley than the steep slopes and plateau, reflecting a positive relationship between LMH activity index and richness and diversity of grass species. Results indicate that fine-scale variation in topography and soil are associated with both the distribution of herbaceous vegetation and LMH, suggesting a need to account for local habitat characteristics when examining the distributions of plants, animals, and plant-herbivore interactions in natural systems.

KEYWORDS

grazer-browser Spectrum, Laikipia, landscape ecology, megaherbivore, primary productivity, rangeland

Abstract

La compréhension actuelle de la distribution de la végétation et des grands mammifères herbivores (GMH) repose sur une combinaison d'études biogéographiques et d'expériences de terrain hautement contrôlées. Cependant, une compréhension plus complète de ces schémas nécessite l'étude de leurs schémas de co-occurrence naturelle à des échelles spatiales intermédiaires. L'étude a été menée dans la parcelle de 120 ha de l'Observatoire mondial de la Terre (ForestGEO) de la forêt de Mpala, au Kenya. Nous avons examiné les différences entre les communautés de plantes herbacées et l'utilisation de l'habitat par les GMH dans trois habitats topographiques avec des types de sol distincts, notamment les pentes abruptes, la vallée et le plateau. Chaque paire d'habitats présentait une composition végétale et animale différente. Les pentes abruptes et le plateau présentaient respectivement un pourcentage de couverture herbacée ≥1 fois supérieur à celui de la vallée, tandis que les pentes abruptes et la vallée présentaient une richesse et une diversité d'espèces d'herbes >1,5 fois supérieures à celles du plateau. L'activité des GMH était ≥1,7 fois plus élevée dans la vallée que sur les pentes abruptes et le plateau, reflétant une relation positive entre l'indice d'activité des GMH et la richesse et la diversité des espèces d'herbes. Les résultats indiquent que les variations à petite échelle de la topographie et du sol sont associées à la fois à la distribution de la végétation herbacée et des GMH, ce qui suggère la nécessité de prendre en compte les caractéristiques de l'habitat local lors de l'analyse de la distribution des plantes, des animaux et des interactions plantes-herbivores dans les systèmes naturels.

1 | INTRODUCTION

Savannah ecosystems cover about an eighth of the global terrestrial environment (Cavelier et al., 1998; Sankaran et al., 2005; Scholes & Archer, 1997) and host one-fifth of the world's human population alongside a diverse assemblage of LMH, defined here as weighing ≥2.5 kg (Beerling & Osborne, 2006; Scholes & Archer, 1997). In these ecosystems, myriad abiotic factors including topography, soil composition, tree cover, precipitation, and the distribution of surface waters contribute to spatial and temporal heterogeneity in the herbaceous communities of savannah ecosystems (Bergström & Skarpe, 1999; Coe et al., 1976; Frost, 1986). The resulting differences in vegetation cover, primary productivity, and plant species composition can in turn influence variation in LMH abundance and distribution through space and time (Du Toit & Cumming, 1999; Reid, 2012). Advancing understanding of the landscape ecology of savannah ecosystems requires spatial analyses of associations between vegetation and LMH at scales that bridge more traditional large-scale biogeographic and small-scale experimental research programs.

Sharp contrasts in environmental conditions can occur on relatively small spatial scales. For example, more soil water may be available to plants on sand-rich soils at great depths whereas more water may be available on clay-rich soils at the surface when topography is otherwise equal (English et al., 2005). In the Mpala ForestGEO plot in Laikipia, Kenya, this type of variation in soil and topography jointly influences the distribution of savannah trees (Mutuku & Kenfack, 2019) and large mammalian herbivores (Freeman et al., 2022; Kimuyu et al., 2021). In this ecosystem, nutrient-rich clay soils and nutrient-poor sandy loams differ in the species of acacia trees that locally dominate the woody plant community due to the differential ability of each species to tolerate the stresses imposed by drying and herbivory (Pringle et al., 2016). Likewise, terrain may contribute to the habitat partitioning of species that prefer rocky terrain as a strategy to avoid competition (Norton, 2011) and those that require flatter terrain (Kimuyu et al., 2021; Wall et al., 2006). Yet whereas the ways that abiotic factors are spatially correlated with the distribution of woody plants and LMH can be readily observed, it is far more difficult to elucidate spatial associations between herbaceous plants and LMH because herbaceous vegetation is more ephemeral, species-rich, and influenced by canopy cover (Bergström & Skarpe, 1999; Coe et al., 1976; Coverdale et al., 2016; Coverdale et al., 2021; Frost, 1986). These relationships are liable to be consequential for the distribution of LMH, however, because understory vegetation contributes substantial annual primary productivity to savannah ecosystems and provides a predominant dietary resource for many local LMH species (Kartzinel et al., 2015; Kartzinel & Pringle, 2020; Potter et al., 2022; Shannon et al., 2013).

While it is reasonable to expect areas with high soil nutrient levels to have higher plant diversity than areas with low soil nutrients, if those soils provide a stressful growth environment they may also limit seedling establishment and hence the diversity of the resultant community (Pringle et al., 2016). Indeed, at the Mpala ForestGEO plot in Kenya, there is greater tree species richness on nutrient-poor sandy loam soils compared to the more nutrient-rich but hydrologically stressful clay vertisols (Mutuku & Kenfack, 2019). Herbivory may also interact with soil fertility to control vegetation. For example the highly defended ant-plant, *Acacia drepanolobium*, thrives on clay vertisols that are nutrient rich but physically stressful, whereas poorly defended *Acacia brevispica* dominates nutrient-poor but otherwise less-stressful sandy loams (Pringle et al., 2016). While evidence for these mechanisms has been documented for tree species (Mutuku & Kenfack, 2019; Pringle et al., 2016), there has been relatively little effort to characterise plant–soil gradients involving herbaceous plants in the African savannahs (Maron et al., 2014), especially at landscape scales (Gandiwa, 2014; Wallgren et al., 2009). This represents a crucial gap between relatively localised field studies where herbaceous vegetation can be well-documented (Goheen et al., 2018; Wells et al., 2021) and relatively large-scale biogeographic studies that often emphasise the distribution of woody vegetation (Daru et al., 2016).

Given that the choice of a habitat by LMH is largely driven by the need to maximise forage intake and to minimise their risk of predation (Lima, 1998), changes in availability and composition of herbaceous plant communities may therefore influence the distribution of LMH as a result of changes in both food availability and cover (Codron et al., 2006; Kartzinel et al., 2015; Shannon et al., 2013; Sponheimer et al., 2003). We examined the relationship between fine-scale ($1200\,\text{km}^2$) variation in soil and topography versus the composition and distribution of herbaceous vegetation and LMH in the ForestGEO plot at Mpala Research Centre in Laikipia, Kenya (Figure 1). The plot has been classified into three distinct topographic habitats ('plateau', 'steep slopes', and 'valley') with dissimilar soil types (Mutuku & Kenfack, 2019). The plateau is relatively flat and has the highest elevation and the steep slope represents the downward sloping transition into the valley (Mutuku & Kenfack, 2019). The plot traverses two distinct soil formations: black-cotton soil and red sandy loams, with an area of transition between them. The black-cotton soils of the plateau undergo shrink-swell cycles that create stressful growth conditions for plants, but they have higher levels of nutrients than do the less stressful sandy loams of the valley (Augustine, 2003; Augustine et al., 2011; Pringle et al., 2016).

Previous study in the Mpala ForestGEO plot demonstrated that the less stressful red sandy loams in the valley habitat maintained a higher diversity of trees as compared to the stressful black-cotton soil in the plateau habitat (Mutuku & Kenfack, 2019). However, how these edaphic variations affect herbaceous community composition remains unknown. Since herbivore movement are controlled by vegetation composition (Venter et al., 2019) it is expected that if the valley will have a high diversity of herbaceous plants it will attract more herbivores as compared to the plateau habitat. Another study in this

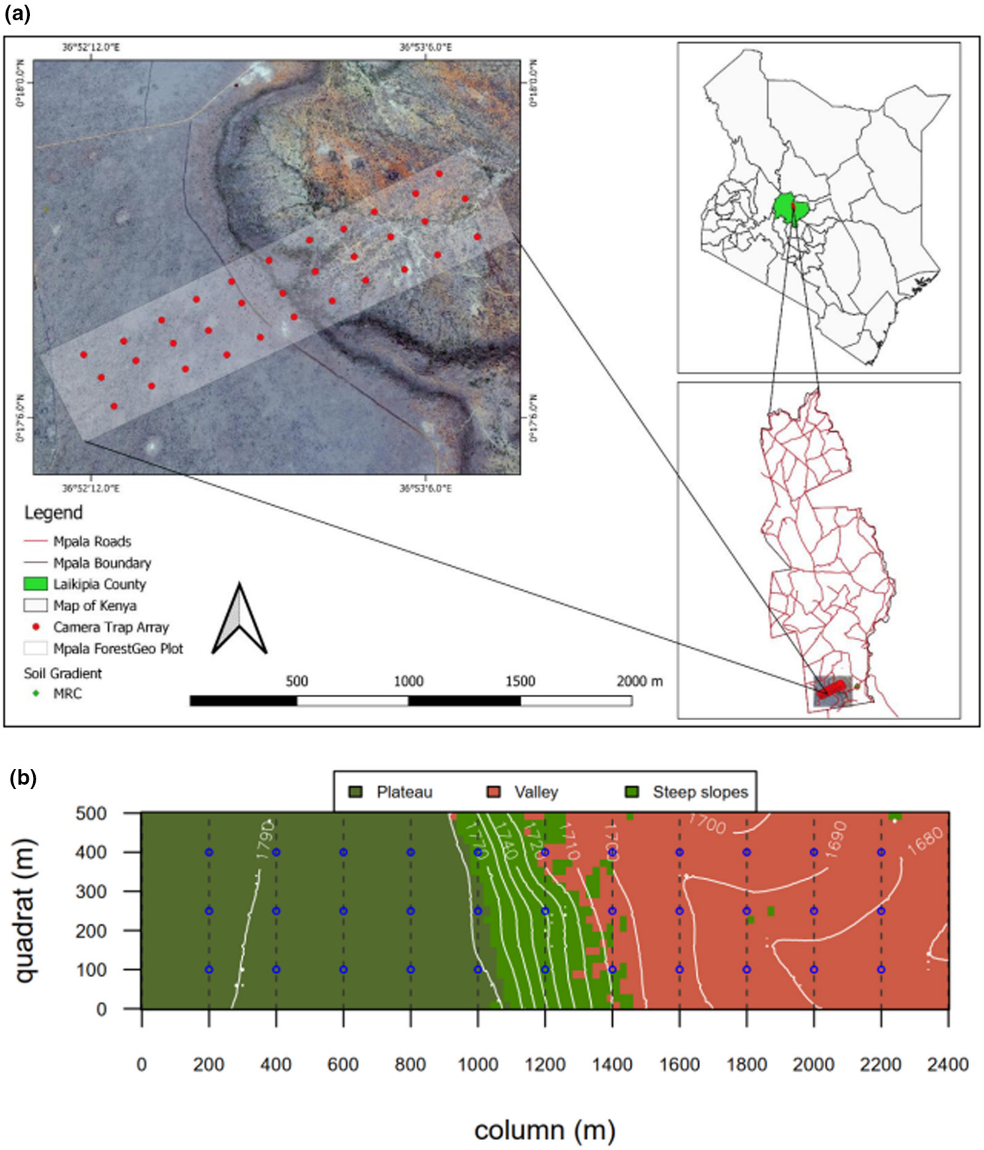

FIGURE 1 Map of the study area showing the location of Mpala ForestGEO plot. (a) The maps show imagery of the plot area inset within Mpala Research Centre in Laikipia county, Kenya (scale bar pertains to the inset map of the plot). (b) In greater detail, the three topographic habitats are shown within the 120-ha (2400 × 500 m) plot, with the blue circles showing the 33 camera trap locations.

plot has shown that topography influences the browsing damage by elephant and giraffe with the steep slopes habitat being avoided by both of these megaherbivores (Kimuyu et al., 2021). While the role of topography in influencing megaherbivore movement in the Mpala ForestGEO plot has been documented, how topography influences other herbivores' use of the plot still remain elusive. Based on these previous observations, we therefore predicted that: (1) the valley has higher herbaceous percentage cover, species richness, and diversity than the plateau and steep slopes; (2) overall LMH activity is higher in the valley than the plateau and steep slopes, but the distribution patterns differ among LMH species; and (3) overall LMH activity is strongly and positively related with percentage herbaceous cover, richness, and diversity.

2 | MATERIALS AND METHODS

2.1 | Study area

The Mpala ForestGEO plot covers 120 ha (500 × 2400 m) and an altitude range of 1660–1800 m above sea level (Figure 1). The area receives annual rainfall that is weakly trimodal, averaging 550–600 mm per year, with a distinct dry season in December to March (Kimuyu et al., 2014). The plot traverses two distinct soil formations: black-cotton soil (Pellic Vertisols) and red sandy loams (Ferric and Chromic Luvisols) with an area of transition between them. The black-cotton soils of the plateau habitat are poorly drained due to their clay content of 60% and sand content of 24% on average (Young et al., 1997). The red sandy soil in the valley habitat contain clay content of 15% and sand content of 74% on average, resulting in better drainage (Augustine, 2003). The black-cotton soils of the plateau have higher N and Ca content than do the sandy loams of the valley, making them more nutrient-rich despite having similar amounts of total P (Augustine et al., 2011). Woody vegetation is more diverse in the valley than the plateau, where *Acacia drepanolobium* is the most dominant tree species and constitutes ~94% of tree cover (Mutuku & Kenfack, 2019). The area hosts a diverse community of LMH, including elephant (*Loxodonta africana*), reticulated giraffe (*Giraffa reticulata*), African buffalo (*Syncerus caffer*), eland (*Taurotragus oryx*), impala (*Aepyceros melampus*), Grevy's zebra (*Equus grevyi*), plains zebra (*Equus quagga*), East African oryx (*Oryx beisa*), hartebeest (*Alcelaphus buselaphus*), and Grant's gazelle (*Gazella granti*). Livestock, mostly cattle, share the same habitats as wildlife in this system (Goheen et al., 2018).

2.2 | Measurements of herbaceous vegetation

To estimate herbaceous vegetation composition, we used the canopy-intercept method; also known as point-quadrat method (Frank & McNaughton, 1990), point-intercept (Jonasson, 1988), or point-contact method (Catchpole & Wheeler, 1992). This method is based on the number of contacts ("hits") that a pin makes with vegetation at a point location (Radloff & Mucina, 2007). To enable comparisons of herbaceous plant distributions and LMH species distributions, we conducted vegetation surveys at the same sampling stations where LMH activity was also monitored using camera traps (see below). We had a total of 33 sampling stations distributed along a regular 150 × 200-m grid across the plot (Figure 1a,b). At each sampling station, we established four 20-m transects in cardinal directions from the camera. Along each transect, we placed a ten-point pin frame at 10-, 15- and-20 m intervals to record the total number of hits per plant species, avoiding termite mounds and the undergrowth of tree canopies. Species richness and diversity were estimated based on the total number of pin hits in each of the 33 sapling stations. In addition, we estimated percentage herbaceous cover using a 50 × 50-cm quadrat in the same stations where we quantified species richness and diversity. We conducted vegetation surveys during the peak growing season when most plants are flowering to aid identification and maximise completeness of species coverage.

In order to assess how well the pin-hits could be used to estimate local herbaceous biomass, we conducted an experimental plant harvest. We used shears to clip vegetation at the base of each shoot within thirty-three 50 × 50-cm quadrats located 30 m from the camera trap along the southern transect. Quadrats were kept at this distance in order to avoid manipulating the area near the camera, where non-destructive sampling was conducted. The clipped biomass was placed in paper bags and dried to constant weight using sun drying and a wooden oven until a constant weight was achieved using a high-resolution spring balance. A total 437 pin-hits across the 33 quadrats were used to evaluate the correlation between the number of pin hits per sampling station and the final dry weight of the clipped biomass. There was a significant, positive correlation between the number of pin hits and the clipped biomass across the 33 quadrats ($F_{2,32} = 140.8$, $R^2 = 0.82$, $p < 0.001$), indicating that the canopy-intercept method produced accurate estimates of forage availability and plant community composition (Figure S1).

2.3 | Abundance and distribution of large mammalian herbivores

The use of the plot by LMH was monitored for twenty-three months (from April 2018 to March 2020), using 33 infrared motion detector camera traps (Bushnell Trophy Cam 2013 and 2017 HD). We characterised the location of each camera trap as either within the valley (13 camera traps), steep slopes (8 camera traps) or plateau (12 camera traps) based on an existing map of the topographic habitats (Kimuyu et al., 2021; Figure 1b). All cameras were mounted on trees at a height of 50 cm, avoiding obstacles within 25 m to the front of each camera. Additionally, we regularly slashed grass within 10 m to the front of each camera trap in order to minimise chances of tall grass blades triggering the camera traps. The cameras were set to capture one photograph per trigger with a 1 s delay between successive triggers. All photographs were processed using WildID to assign metatags containing information on animal species identities and number of individuals present in each photograph (Bolger et al., 2011). Image metadata including date and time, species identity, and number of individuals in a photograph were exported for statistical analysis.

2.4 | Data analyses

To examine differences in herbaceous community cover, species richness, and diversity across the three habitats, we analysed data from 396 quadrats and 4678 pin hits. Species diversity was estimated using effective number of species based on Hill numbers representing the exponential of the Shannon Weiner index (Blackwood et al., 2007). We tested for significant differences in herbaceous species richness, diversity, and & cover between habitats using generalised linear models (GLMs). We used Poisson error structure in the GLMs for species richness and we used quasi-Poisson error structure for diversity and percentage cover (Crawley, 2012).

We calculated an LMH activity index as a measure of presence of wildlife at each camera trap location. The activity index is based on the number of independent detections of each species of LMH per camera per day. Successive photographs of the same species were considered independent detections only when the time interval between photographs was at least 30 min. We tested for significant differences in LMH activity across the three topographic habitats using GLMs with quasi-Poisson error structure. We then tested for significant relationships between overall LMH activity as functions of herbaceous percentage cover, richness, and diversity using GLMs with quasi-Poisson error structure. All GLMs were fitted using the package glm2 (Marschner et al., 2018) in R version 4.0.5 (R Development Core Team, 2021). Prior to performing the GLM analyses, we checked the data (herbaceous cover, grass species richness and diversity, forb species richness and diversity as well as LMH activity index) for normality and homeodasticity to verify whether assumptions were met. We constructed analysis of deviance tables with Type II Wald χ^2 tests using the function *Anova* in the package car (Fox & Weisberg, 2011). We separated means for statistically significant factor levels using the *emmeans* function in the R package *emmeans* (Russell, 2021).

3 | RESULTS

3.1 | Herbaceous vegetation cover and composition across habitats

Our study revealed 57 grass species and 69 forb species in the ForestGEO plot. The forb group consisted of 30 families. The Acanthaceae with 9 individuals were the most abundant family, tailed by Malvaceae, Asteraceae, Leguminosae, Amaranthaceae, Lamiaceae and Convolvulaceae (Table S1). We recorded a total of 4678 pin hits, out of which 4286 (92%) were grasses (Table S1). Relatively few species were widespread across habitats, with only 8 grass (14%) and 7 (10%) forb species occurring in all the three habitats. Of the more specialised species from both groups of plants, the largest proportion of grasses ($N=23$, 40%) and forbs ($N=26$, 38%) occurred exclusively in the valley. We found significant differences in the herbaceous community across habitats. Both the plateau and the steep slopes had higher percentage cover than the valley ($\chi^2=0.45$; $p=0.003$; Figure 2a). Despite the lower percentage cover in the valley, both the valley and steep slopes had significantly higher grass richness ($\chi^2=31.83$; $p<0.001$) and diversity ($\chi^2=3.50$; $p<0.001$) than the plateau (Figure 2b,c). While there was no significant difference in forb species richness ($\chi^2=4.34$; $p=0.114$) or diversity ($\chi^2=0.11$; $p=0.808$) between habitats (Figure 2d,e), the abundances and distributions of some forb species did differ significantly between habitats (Table S1).

3.2 | Herbivore activity across habitats

We recorded 714 independent photographic events for all LMH species from a total of 215,744 photographs across 22,250 camera-trap days. We compared the activity of 15 LMH species, but excluded three from further analysis due to sparse data (duiker were detected exclusively in the plateau; greater kudu and hippopotamus occurred mainly in the valley). We found a significant difference in the LMH activity index across the three habitats ($\chi^2=100.92$; $p<0.001$), where LMH activity index was 2.4- and 1.7-times greater in the valley than the plateau and steep slopes, respectively (Figure 3). The 15 species of LMH for which we had sufficient data differed markedly in their activity across habitats. Some species were strongly associated with the plateau, including steenbok, Grant's gazelle, oryx, hartebeest, and plains zebra (Figure 4a–e): steenbok were recorded only in the plateau and hartebeest activity was at least 95.2- and 18.4-fold higher in the plateau than the valley and steep slopes, respectively. Several species were also strongly associated with the valley, including dik-dik, waterbuck, impala, buffalo, Grevy's zebra, and elephant (Figure 4i–o). Many herbivore species avoided the steep slopes, including giraffes, which had roughly equal activity levels in the plateau and valley but strongly avoided the slopes. Eland and warthog distributions trended towards the valley and/or plateau, but there was not a significant difference in eland activity across habitats (Figure 4).

There was a positive relationship between overall LMH activity and herbaceous plant composition and cover. We found a negative relationship between herbaceous percentage cover and LMH activity ($\chi^2=4.86$; $p=0.027$; Figure 5a). Nevertheless, there was a significant positive relationship between LMH activity and grass species richness ($\chi^2=9.12$; $p=0.003$) and grass species diversity ($\chi^2=7.59$; $p=0.006$; Figure 5b,c). The LMH activity index was not, however, significantly related with either forb species richness ($\chi^2=2.47$; $p=0.116$) or forb species diversity ($\chi^2=0.73$; $p=0.392$; Figure 5d,e).

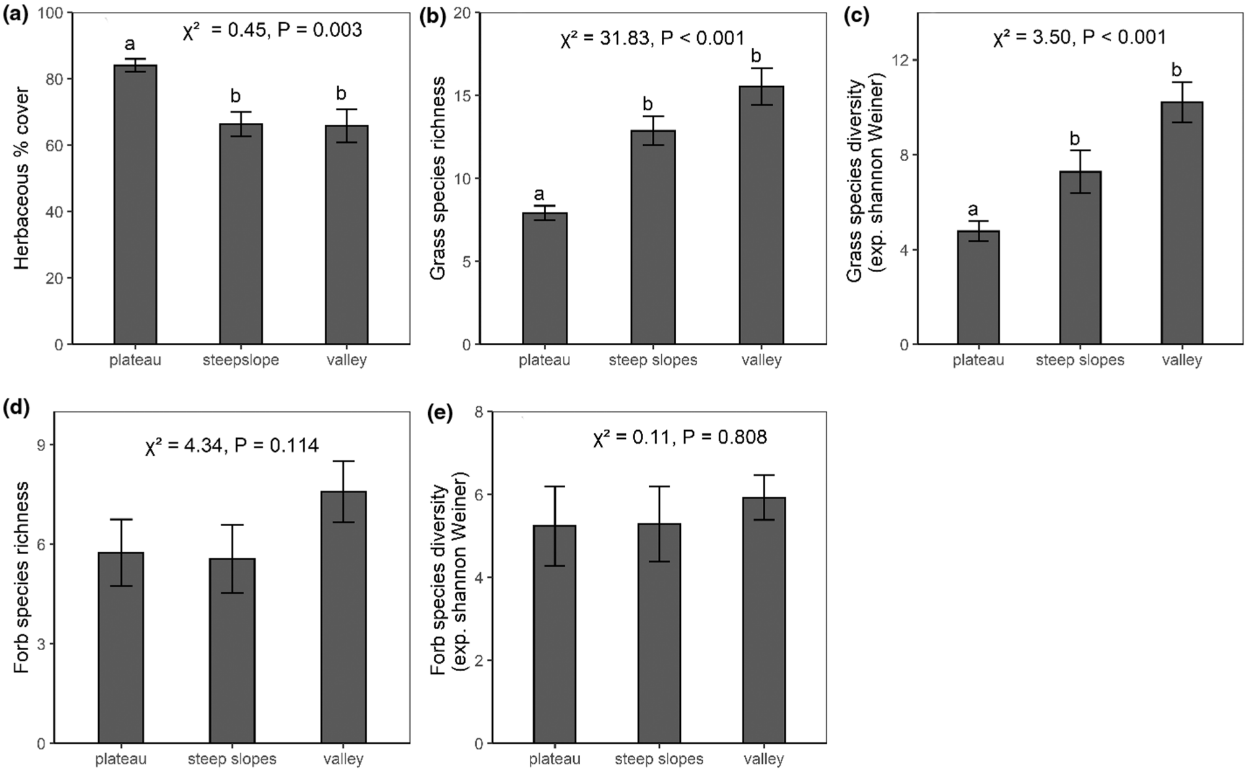

FIGURE 2 Variation in herbaceous vegetation cover and composition across the three habitats of the Mpala ForestGEO plot. Plots show GLMs of (a) herbaceous % cover, (b) grass species richness, (c) grass species diversity, (d) forb species richness and, (e) forb species diversity. Error bars represent one standard error.

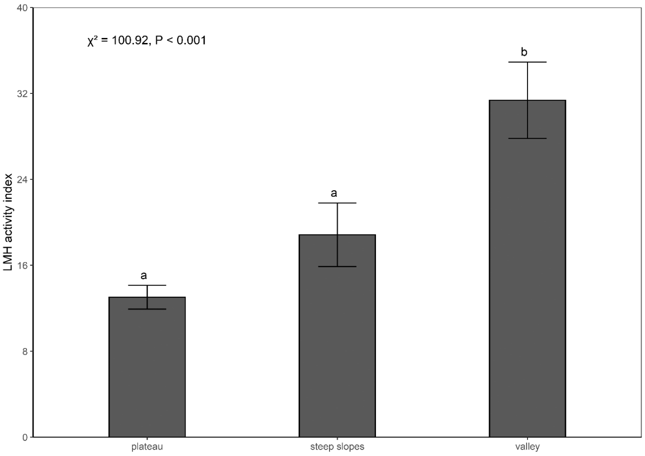

FIGURE 3 Variation in the LMH activity index across the three habitats of the Mpala ForestGEO plot (GLMs). The bar chart shows the mean ± one standard error for all LMH activity indices, with letters above the bar indicating significant pairwise differences.

4 | DISCUSSION

Across the Mpala ForestGEO plot, soil and topography influenced herbaceous plant and animal community compositions. Consistent with a growing body of evidence that physically stressful black-cotton soils may serve as a filter against the establishment of many species that are less tolerant of this type of stressor, we showed that the less stressful yet more nutrient limited sandy loams of the valley habitat sustained higher herbaceous vegetation species richness despite their relatively low abundance of herbaceous plants (Mutuku & Kenfack, 2019; Pringle et al., 2016). Together with the distribution of herbaceous vegetation, topography was related with the space use patterns of LMH species, which tended to be strongly associated with either the plateau or valley habitat.

One of the clearest results from our study was that more herbaceous plant species occur in the valley than the plateau. There are several possible reasons for this pattern. The high percentage cover and low diversity of herbaceous plants in the plateau can be attributed to the suppressive edaphic conditions of black-cotton soils (Pringle et al., 2016). Black-cotton soils go through shrink-swell and cracking cycles, with poor water infiltration and low water potentials during dry periods (Pringle et al., 2016). These edaphic conditions could reduce herbaceous plant seedling establishment, resulting to low species richness and diversity. The corresponding high percentage cover in the plateau could be attributed to the stressful nature of black-cotton soils that leads to proliferation of a few dominant species that are adapted to the stressful edaphic conditions of this habitat (Mutuku & Kenfack, 2019). Additionally, combination of the stressful edaphic conditions of black-cotton soils and herbivory may also impede plant growth (Pringle et al., 2016).

The steep slopes habitat had intermediate herbaceous percentage cover and grass diversity, and there are several possible explanations. One possible explanation for this intermediacy is that the slopes are

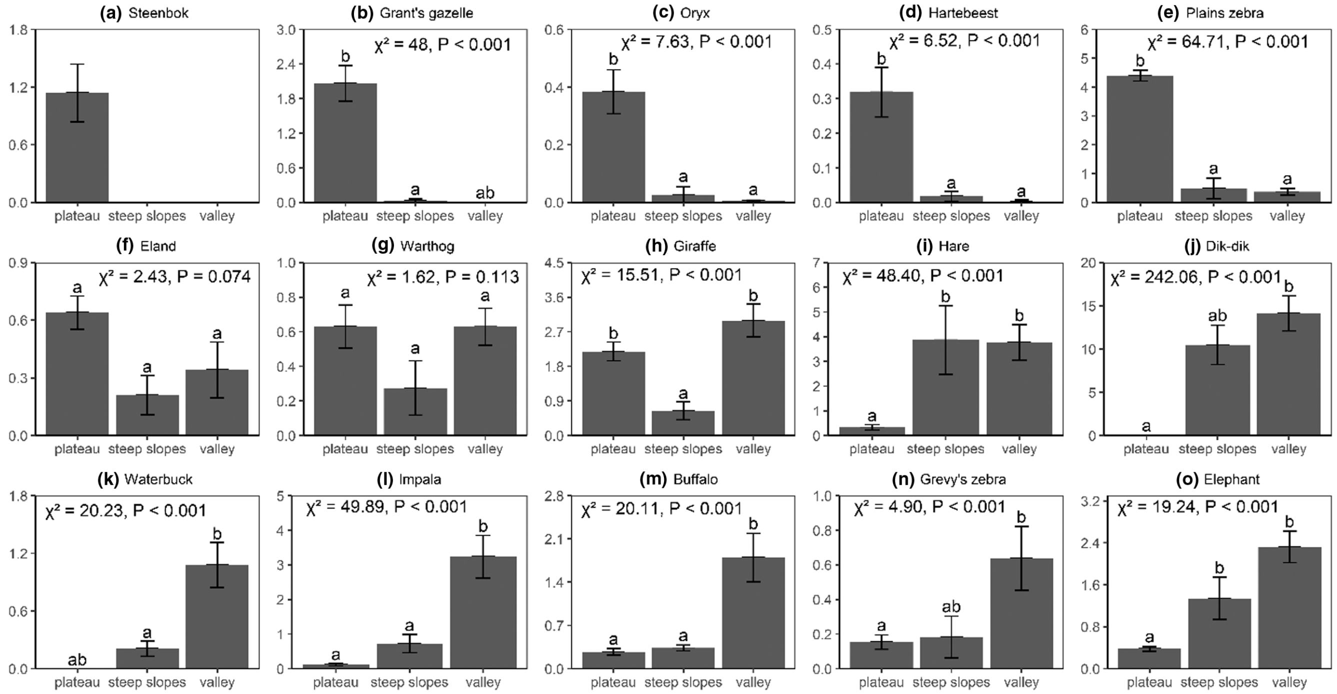

FIGURE 4 GLMs comparison of the incidence of LMH species across three habitats in the Mpala ForestGEO plot. Means are calculated for 33 camera traps, 13 of which were in the valley, 8 in the steep slope and 12 in the plateau. The mean LMH activity indexes of two habitats differed significantly if the bars did not share the same letter and the error bars depict standard error. Note that the scale bars on the y axes differ across panels, depending on the frequency of each species in the camera trap data. Panels are organised according to the strength of association with one habitat versus the other.

simply representative of a transition zone between the clay vertisols that are nutrient rich but physically stressful and nutrient-poor but otherwise less-stressful sandy loams, generating an intermediate quantity and composition of herbaceous plants. Another possibility is that this pattern arises from the distinctive environmental properties of the steep slopes, such as shallow soils and drier conditions imposed by runoff, which might impede herbaceous plants directly (Coughenour & Ellis, 1993). Relatedly, the shallow soils on steep slopes contribute to a relatively high density of trees (Ludwig et al., 2004; Riginos & Grace, 2008) with distinctive canopy architectures and shading patterns (Linstädter et al., 2016), which modulate moisture availability (Van Der Waal et al., 2009) and nitrogen availability (Ludwig et al., 2004). A third possibility involves the suppressive effects of terrain on LMH activity as the study plot has contrasting convexity, elevation, and slope (Mutuku & Kenfack, 2019). Because activity was lower on the slopes than either other habitat for many species, and especially large grazers such as zebras, the slopes could provide a refuge from top-down herbaceous growth limitation on plant species that might be suppressed or competitively excluded from the plateau habitat and thereby enhance diversity. Yet diversity may still not be as great—or biomass so supressed—on the slopes as compared to the valley because the relatively high activities of herbivores in the valley could maintain or even boost herbaceous species diversity by suppressing otherwise dominant herbaceous species and trees (Olff & Ritchie, 1998; Riginos et al., 2018). The possibility of such a terrain-based refuge stands in contrast to a recent study of woody plant abundance and diversity in the Mpala ForestGEO plot, which were more clearly maximised (as opposed to intermediate) on the steep slopes, where there is a conspicuous absence of browsing effects by the largest browsers, such as elephants and giraffes, on tree growth in this habitat (Freeman et al., 2022; Kimuyu et al., 2021).

Whether the high diversity of grass species in the valley can be mechanistically linked to the correspondingly high levels of LMH activity in this habitat is a topic of considerable interest. While there is higher herbaceous percentage cover on the plateau than the other two habitats, these dominant grass species are not necessarily palatable to all large grazers; rather, at least some of these grasses may rise to dominance in this habitat because of their ability to resist grazing in the otherwise challenging substrate of black-cotton soils. Of the 7 common grass species on the plateau, only *Themeda triandra* and *Brachiaria lachnantha* are considered palatable (Odadi et al., 2013). In contrast, the high diversity of grasses in the valley ensures that LMH have enough forage to choose from in a system that supports even less palatable species such as *Bothriochloa insculpta*, *Pennisetum mezianum*, and *Pennisetum stramineum* (Odadi et al., 2013; Veblen et al., 2016). Likewise, the high LMH activity in the valley could generate positive feedbacks that subsequently contribute to the high diversity of grass species capable of colonising a community based on mechanisms that involve herbivores' differential utilisation of competitively dominant food species (du Toit, 2003; Ganjurjav et al., 2015; Van Coller & Siebert, 2020).The complexity of savannah plant-herbivore trophic networks has traditionally been simplified

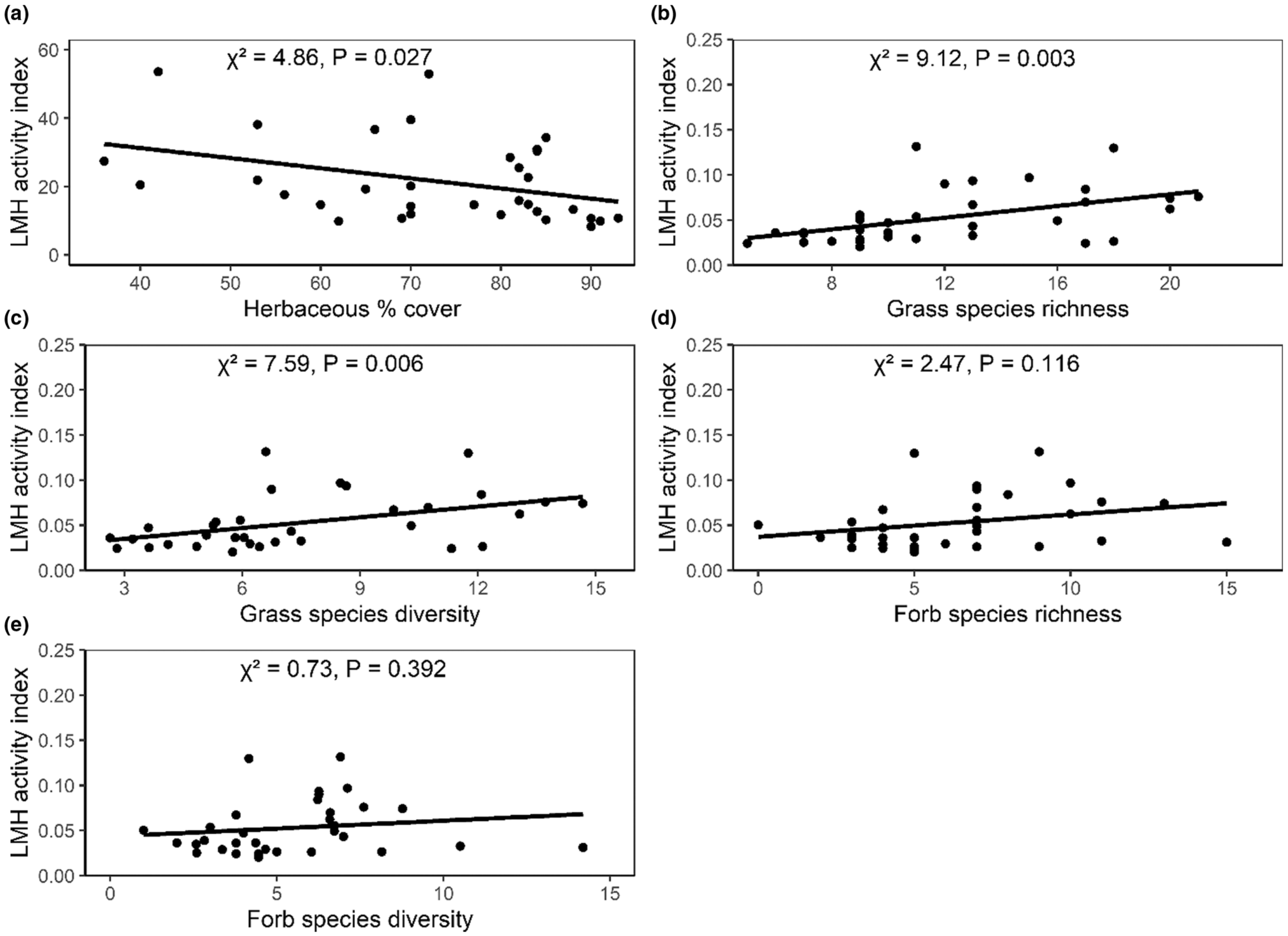

FIGURE 5 Relationship between the LMH activity index and herbaceous vegetation composition in the Mpala ForestGEO plot. GLM comparison revealed significant differences in (a) herbaceous percentage cover, (b) grass species richness, (c) grass diversity, but not for (d) forb species richness, or forb species diversity (e).

into discrete feeding guilds (grazers, browsers, and mixed feeders), but recent evidence based on dietary DNA metabarcoding at Mpala Research Centre has suggested that the local diversity of plants and large mammalian herbivores may be more tightly linked than previously recognised (Kartzinel et al., 2015; Kartzinel & Pringle, 2020).

Habitat heterogeneity drives the distribution patterns of grazers (Cromsigt et al., 2009) and browsers (Kimuyu et al., 2021) through resource partitioning (Djagoun et al., 2016; Kleynhans et al., 2011; Potter et al., 2022). Overall, our study suggests that grass species richness and diversity are associated with differences in LMH activity, while LMH distributions were less dependent on forb species richness and diversity. Notably, however, grasses were more abundant than forbs and thus the effects of the pairwise interactions between grasses and large herbivores may be stronger and/or easier to discern than are those involving forbs. Because of their high protein content, forbs play a vital role in nutritionally enhancing the diets of ungulate species that utilise the herbaceous layer (Odadi et al., 2011; Zimmermann, 1980). Despite forbs being considered a highly nutritious forage category and constituting a vital part of ungulate diets at given times of the year (Odadi et al., 2013), forbs are generally unnoticed or grouped together into a "non-grass" class in most of the savannah studies (Scott-Shaw & Morris, 2015; Van Coller & Siebert, 2020) making their functional ecology to remain elusive (Van Coller & Siebert, 2020).

5 | CONCLUSIONS

We investigated how soil and topography influence the abundance and distribution of herbaceous vegetation and LMH in an East African savannah. Vegetation cover and composition changed across an environmental gradient of soil and topography. The red soil (valley) supported more species of herbaceous vegetation and LMH than the black-cotton (plateau) and transition habitats (steep slopes), generating strong positive relationships between LMH activity and grass species richness and diversity. Overall, our results indicate that fine scale variations in topography and soil can generate spatial patterns of correspondence involving the abundance and/or diversity of plants and large mammalian herbivores. Although the mechanisms by which these associations develop require further investigation, the emergent pattern establishes evidence that microhabitat heterogeneity in savannah ecosystems can be critical to the generation and maintenance of local biodiversity hotspots.

AUTHOR CONTRIBUTIONS

R.O.A., D.M.K. and T.R.K. conceived the study and designed methodology. D.M.K. and T.R.K. obtained the funding for the study. R.O.A. and D.M.K. conducted field work. R.O.A., D.M.K., T.R.K. and G.M.W. executed the statistical analysis. D.M.K., T.R.K. and G.M.W. coordinated the study. D.M.K., T.R.K., P.M.M., D.K. and G.M.W. contributed critically to the drafts. All authors gave final approval for publication.

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CONFLICT OF INTEREST STATEMENT

We have no conflict of interest concerning our manuscript.

DATA AVAILABILITY STATEMENT

The data of vegetation composition, plant biomass calibration, LMH distribution and environmental variables on the studied plot is deposited in the Dryad Digital Repository: https://doi.org/10.5061/dryad.stqjq2c7j (Ang'ila et al., 2023).

ORCID

Robert O. Ang'ila https://orcid.org/0000-0003-2133-4600
Duncan M. Kimuyu https://orcid.org/0000-0001-6077-4970
Geoffrey M. Wambugu https://orcid.org/0000-0001-6050-3011
Tyler R. Kartzinel https://orcid.org/0000-0002-8488-0580

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SUPPORTING INFORMATION

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

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