

Fine-scale habitat heterogeneity influences browsing damage by elephant and giraffe

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Abstract

Effects of large mammalian herbivores on woody vegetation tend to be heterogeneous in space and time, but the factors that drive such heterogeneity are poorly understood. We examined the influence of fine-scale habitat heterogeneity on the distribution and browsing effects of two of the largest African terrestrial mammals, the elephant and giraffe. We conducted this study within a 120-ha (500 x 2,400 m) ForestGEO long-term vegetation monitoring plot located at Mpala Research Center, Kenya. The plot traverses three distinct topographic habitats (“plateau,” “steep slopes,” and “valley”) with contrasting elevation, slope, soil properties, and vegetation composition. To quantify browsing damage, we focused on *Acacia mellifera*, a palatable tree species that occurs across the three habitat categories. Overall tree density, species richness, and diversity were highest on the steep slopes and lowest on the plateau. *Acacia mellifera* trees were tallest and had the lowest number of stems per tree on the steep slopes. Both elephant and giraffe avoided the steep slopes, and their activity was higher during the wet season than during the dry season. Browsing damage on *Acacia mellifera* was lowest on the steep slopes. Elephant browsing damage was highest in the valley, whereas giraffe browsing damage was highest on the plateau. Our findings suggest that fine-scale habitat heterogeneity is an important factor in predicting the distribution of large herbivores and their effects on vegetation and may interact with other drivers such as edaphic variations to influence local variation in vegetation structure and composition.

KEYWORDS

Acacia mellifera, ForestGEO, Laikipia, megaherbivores, Mpala Research Center, savanna, slope, topography

1 | INTRODUCTION

Savanna ecosystems are characterized by highly dynamic vegetation cover, which usually oscillates between woody dominated to grass-dominated phases (Scholes & Archer, 1997; Skarpe, 1992; Staver, Bond, Stock, van Rensburg, & Waldram, 2009). In these

systems, stochastic factors such as inter-annual variation in rainfall and multiple interacting press and pulse disturbances such as herbivory and fire play critical roles in influencing vegetation dynamics (Augustine & McNaughton, 2004; van Langevelde et al., 2003; Roques, O'Connor, & Watkinson, 2001; Sankaran et al., 2005; Sankaran, Ratnam, & Hanan, 2008; Staver et al., 2009). Knowledge

of the underlying drivers of spatial-temporal dynamics of vegetation is fundamental to understanding the existence of savanna ecosystems as well as for management and conservation.

Megaherbivores (large mammalian herbivores, especially elephant and giraffe) exert significant top-down regulation of woody vegetation in savanna ecosystems (Ben-Shahar, 1996; Bond & Loffell, 2001; Ihwagi, Vollrath, Chira, Douglas-Hamilton, & Kironchi, 2010; Midgley, Lawes, & Chamaillé-Jammes, 2010; Staver, Bond, Cramer, & Wakeling, 2012), but their effects tend to be spatially heterogeneous (Kerley et al., 2008; Nellemann, Moe, & Rutina, 2002). Understanding factors that influence spatial heterogeneity in megaherbivore distribution and effects on vegetation has been an important goal for ecologists. However, many studies have either focused on large-scale patterns across large altitudinal gradients, different vegetation zones, and different rainfall regimes (Bell, 1982; Bohrer, Beck, Ngene, Skidmore, & Douglas-Hamilton, 2014; Fritz & Duncan, 1994; Holdo, 2003; Howes, Doughty, & Thompson, 2019; Mysterud, Langvatn, Yoccoz, & Nils Chr, 2001; Ngene, Skidmore, Van Gils, Douglas-Hamilton, & Omondi, 2009), or patterns associated with proximity to focal points such as surface water sources (Chamaillé-Jammes, Mtare, Makuwe, & Fritz, 2013a; Ndlovu et al., 2018; Wato et al., 2018), human settlements (Neupane, Kwon, Risch, Williams, & Johnson, 2019), and roads (Gaynor et al., 2018), but see (Bond & Loffell, 2001; Coetsee & Wigley, 2016). Consequently, we know little about how fine-scale habitat patch characteristics such as local variation in topography and edaphic-driven contrasts in vegetation structure and resource densities may influence megaherbivore effects on vegetation. Yet, such fine-scale habitat heterogeneity is a prominent feature of most savanna ecosystems.

Usually browsing pressure within an habitat is positively correlated with the amount of time animals spend in an area (Bond & Loffell, 2001; Milligan & Koricheva, 2013), but the factors that influence foraging decisions vary remarkably across herbivore species and over time (Fortin et al., 2015; Lagendijk et al., 2015; Stephens, 2008). For megaherbivores, movement patterns are driven more by maximizing forage intake and minimizing energy expenditure rather than avoiding predators (Riginos, 2015; Sinclair, Mduma, & Brashares, 2003). The general expectation therefore is that megaherbivores will select the most resource-rich patches within a habitat. However, the relative accessibility of such resource-rich patches may complicate foraging decisions. For example, megaherbivores may avoid resource areas with rugged terrain, such as steep slopes and depressions, because of the high energy expenditure in navigating such terrain and the associated risk of injury through accidental fall (Leblond, Dussault, & Ouellet, 2010; Wall, Douglas-Hamilton, & Vollrath, 2006). Areas thus avoided may become habitat refugia, with greater diversity and density of forage resources than frequently visited areas. Additionally, seasonality may also influence foraging decisions by megaherbivores.

Seasonality creates pulses in forage quality and availability (Duncan, Reid, Thoss, & Elston, 2005; Egea et al., 2019) and affects distribution of surface water as well as the physiological urge to drink (Chamaillé-Jammes, Mtare, Makuwe, & Fritz, 2013b;

Wato et al., 2018). Generally, there are more forage resources and greater availability of water during the wet season than during the dry season. Variation in the timing and spatial distribution of rainfall may increase spatial heterogeneity in forage quality and quantity. Herbivores respond to these dynamics by either adjusting their diet composition (Codron et al., 2006; Kos et al., 2012) or migrating locally or over long distances (Cerling et al., 2006; Purdon, Mole, Chase, & van Aarde, 2018b; Thouless, 1995). For example, elephants have been reported to switch their diet from predominantly grazing during the wet season to predominantly browsing during the dry season (Codron et al., 2006; Kos et al., 2012). Other studies suggest that elephants are partial migrants, with some individuals responding to seasonal scarcity in resources and water by migrating to areas with better resources while others respond by adjusting their foraging patterns locally (Ngene et al., 2009; Purdon et al., 2018a; Tshipa et al., 2017). Both these strategies may have different implications for browsing intensity at habitat scale. On one hand, long-distance migration may temporarily alleviate browsing pressure in a particular habitat, providing a window for trees to escape the browse trap (Staver & Bond, 2014). On the other hand, chronic browsing in areas where seasonal dispersal or migration of herbivores is not possible may limit growth and recruitment of trees. Additionally, lack of opportunities for dispersal may force herbivores to venture into risky or relatively inaccessible sections of the habitat, thus limiting the possibility of topography-mediated vegetation refugia.

This study aimed at examining the extent to which fine-scale habitat heterogeneity may influence the presence of megaherbivores and to assess whether this correlates with browsing intensity. To assess browsing intensity, we focused on *Acacia mellifera*, a tree with highly palatable leaves that occurs across three distinct habitats (plateau, steep slope, and valley), characterized by different soil types and vegetation. We hypothesize that: (i) the presence of elephant and giraffe and their browsing intensity will be high in resource-rich and easily accessible habitats and lowest in resource poor and relatively inaccessible areas; and (ii) elephant and giraffe would avoid areas of difficult terrain during the wet season but increase their use during the dry season when food resources are scarce.

2 | METHODS

2.1 | Study area

We conducted this study within the Forest Global Earth Observatory (ForestGEO) plot located in a semi-arid savanna at Mpala Research Center (Mutuku & Kenfack, 2019). Rainfall at the study site averages 550–600 mm and is weakly trimodal, with a distinct dry season from December to March (Kimuyu, Sensenig, Riginos, Veblen, & Young, 2014). The plot measures 500 × 2,400 m (120-ha) and traverses two distinct soil communities, the heavy clay black cotton soils (Pellic Vertisols), and the red sandy loams (Ferric and Chromic Luvisols), separated by a transition zone. The two soils differ remarkably in terms of drainage, soil texture, and concentration of various

mineral elements. The black cotton soils are poorly drained, with high clay content (60%) and low sand content (26%) (Young, Okello, Kinyua, & Palmer, 1998). The red sandy loams are well drained and contain 15% clay and 74% sand (Augustine, 2003). Generally, the black cotton soils have higher concentrations of *N* and *Ca* than the sandy loams, but both soils have similar total *P* concentration (Augustine, Veblen, Goheen, Riginos, & Young, 2011). Across the entire plot, all trees and shrubs with at least 2 cm diameter at knee height (diameter measured at 50 cm above the ground; here after referred to as “dkh”) have been identified, mapped, and uniquely tagged following the ForestGEO standard protocol (Condit, Lao, Singh, Esufali, & Dolins, 2014). Based on elevation, slope, and convexity, the plot has previously been classified into four topographic habitats (“plateau,” “depressions,” “low flat,” and “cliff”—here referred to as “steep slopes”) (Mutuku & Kenfack, 2019). For the purposes of this study, we combined two of these topographic habitats (“depressions” and “low flat”) into one category (“valley”) (Figure 1a). The “plateau” occurs at the highest elevation and is relatively flat (Figure 1b and c). The “steep slopes” is at an intermediate elevation separating the plateau and the valley and has the highest slope. The “valley” is at the lowest elevation and is gently sloping.

Vegetation communities differ dramatically across the three habitat types. The plateau has low tree diversity, dominated by one tree species, *Acacia drepanolobium*, that constitutes 94% of all woody trees (Mutuku & Kenfack, 2019). The valley and the steep

slopes have more diverse vegetation (Mutuku & Kenfack, 2019). Unlike most tree species whose range is largely restricted to specific habitat type, *Acacia mellifera* occurs in all the three habitats, thus an ideal species for comparing browsing intensity across the three habitats. *Acacia mellifera* is a multi-stemmed shrub that grows up to a height of 9 m. It produces leaves that are highly palatable but has recurved spines that make it difficult for smaller browsers (e.g., antelope, goats) to strip leaves from its branches. These recurved spines also affect browsing by giraffe more than they affect browsing by elephants. In the absence of browsing and fire, *A. mellifera* tends to form dense impenetrable thickets, posing concerns about bush encroachment (Britz & Ward, 2007). However, in habitats like the Laikipia ecosystem where elephant, giraffe, and other large mammalian browsers still occur in large numbers, *A. mellifera* is heavily browsed and maintained at low densities (Augustine et al., 2011; Sankaran, Augustine, & Ratnam, 2013).

2.2 | Data collection

We continuously monitored elephant and giraffe activity in the plot over a period of twelve months, using 33 infrared motion detector camera traps. The camera traps were distributed across the plot on a regular 150 × 200 m grid (Figure 1a) following (Jansen, Forrester, & Shea, 2014). All cameras were mounted on trees at a height of

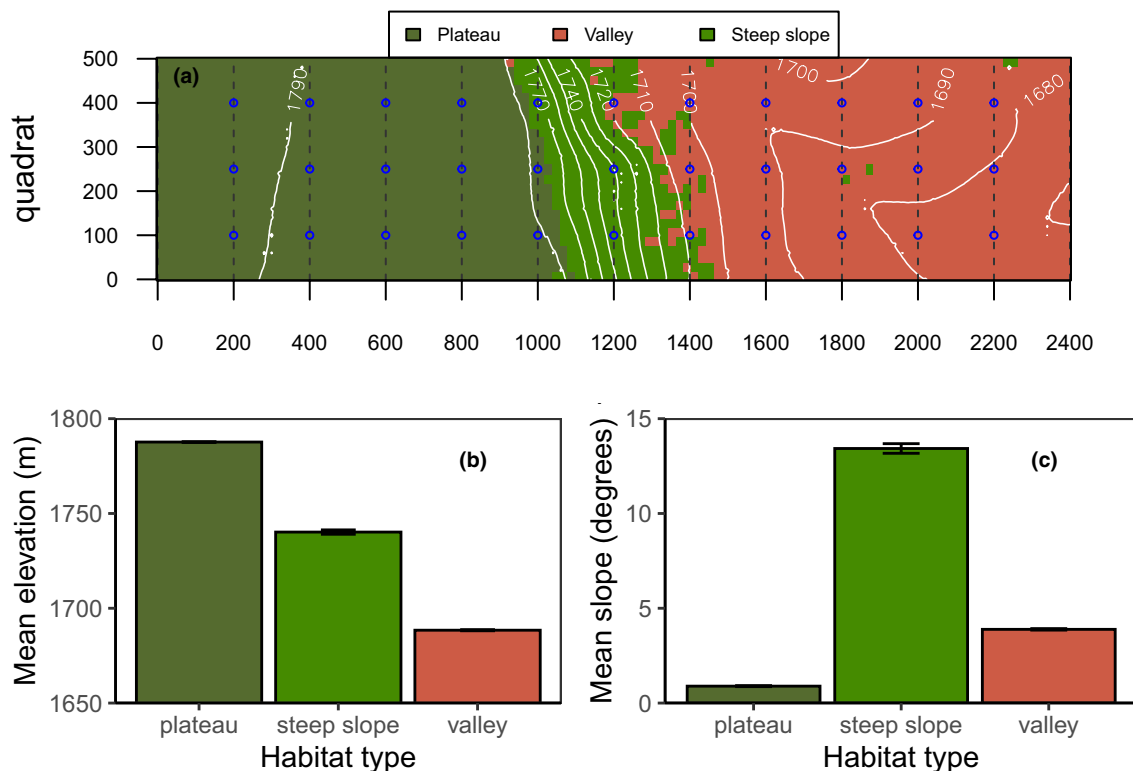


FIGURE 1 Habitat categories within the 120-ha (2,400 × 500 m) Mpala ForestGEO plot: (a) map of the three habitat categories, (b) differences in elevation, and (c) differences in slope. The dotted gray lines on plate (a) indicate the locations of the transects used to survey browsing damage on *Acacia mellifera*, and the blue circles indicate to locations of the camera traps used to assess the activity of elephant and giraffe. Means in panel (b) and (c) are based on 20 × 20 m quadrats and the error bars depict standard error

50 cm, avoiding any obstacles within 25 m in front of each camera. We replaced camera trap batteries and downloaded photographs once after every 30 days. All the downloaded photographs were processed using WildID (Bolger, Vance, Morrison, & Farid, 2011) to assign metatags containing information on animal species and number of individuals occurring in each photograph.

To estimate elephant and giraffe browsing damage on *A. mellifera*, we sampled all trees along eleven 20 × 500 m belt transects. The eleven belts transect were placed at intervals of 200 m and overlapped with the locations of the camera traps (Figure 1a). We estimated elephant and giraffe damage separately. Browsing damage by each of the two megaherbivores is quite distinct. Giraffe feed on leaves and young branch tips leaving behind thin stripped ends on the canopy. In addition to toppling trees and snapping branches or stems, elephant also feed on branch tips leaving behind jugged outlines or stripped bark. We scored elephant browsing based on the presence of browse marks typical of elephant browsing and based on the proportion of canopy removed through broken or snapped branches and stems. A score of "0" was assigned to trees without any apparent elephant browse damage, "1" for trees with between 1% and 24% of the canopy removed, "2" for trees with 25%–49% of canopy removed, "3" for trees with 50%–74% of canopy removed, "4" for trees with 75%–99% of canopy removed, and "5" for trees that were completely pushed over or with 100% canopy removed. We scored giraffe damage based on the proportion of truncated terminal branch tips above the height that is not accessible to other larger herbivores (besides elephant) and based on

the presence of a browse line above 2.5 m (Bond & Loffell, 2001). A score of "0" was assigned to trees that did not have truncated terminal branches typical of giraffe browsing, "1" for trees with between 1% and 24% of the canopy consisting of truncated terminal branches but no visible browse line, "2" for trees with between 25% and 49% of the canopy consisting truncated terminal branches but no visible browse line, "3" for trees with between 50% and 74% of the canopy consisting truncated terminal branches or trees with a visible (but not distinct) browse line, "4" for trees with over 75% of the canopy consisting truncated terminal branches or trees with a distinct browse line, and "5" for (unlikely) cases where the whole canopy was removed or a tree was dead as a result of browsing damage by giraffe. For each tree, we also measured the height of the tallest live branch.

2.3 | Data analyses

To estimate variation in overall tree density, species diversity, dkh, and the density of *A. mellifera* trees, we analyzed existing plot-wide data from the first census conducted between 2011 and 2015 (Mutuku & Kenfack, 2019). We estimated tree density, species richness, and diversity at the level of 20 m × 20 m quadrats. We used linear mixed models in lme4 package (Bates, Mächler, Bolker, & Walker, 2015) in R version 3.5.2 (R Development Core Team 2009) to test for differences in tree density, dkh, and species richness and diversity (effective number of species) across

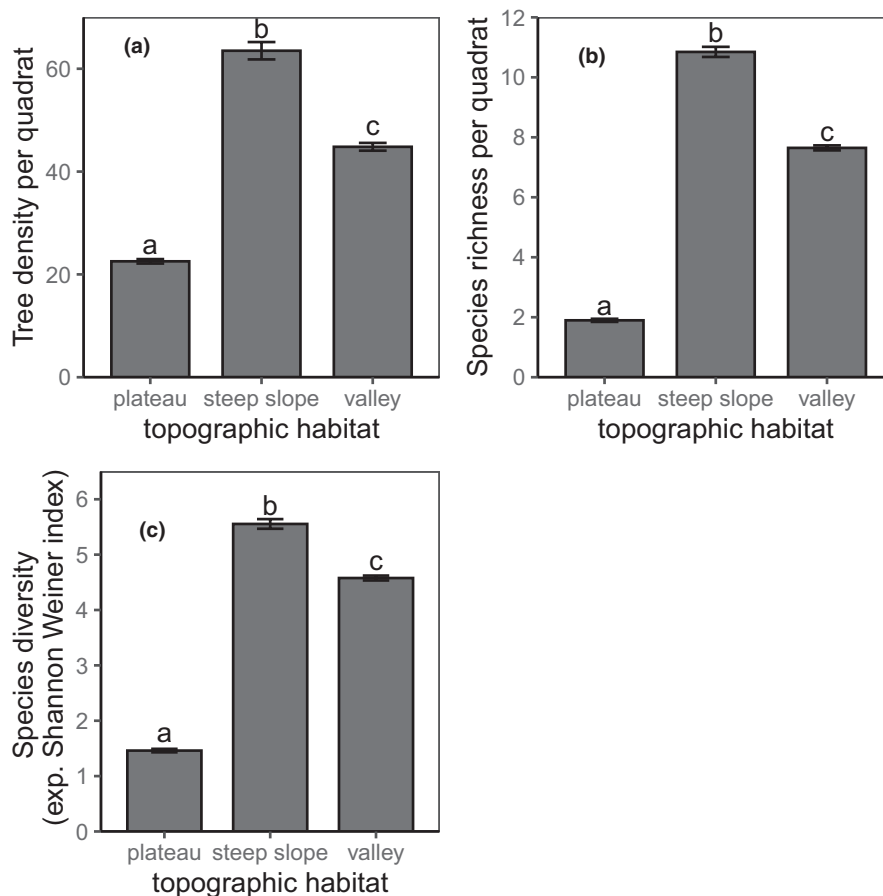


FIGURE 2 Variation in (a) overall tree density (b) species richness, and (c) species diversity across three habitat categories within Mpala ForestGEO plot. Bars not sharing the same letter indicate that the means were significantly different and the error bars depict standard error

the three habitats. We also analyzed for differences in *A. mellifera* canopy traits (height, dkh, and number of stems) using a similar approach. To account for pseudoreplication as a result of quadrats being spatially clustered in each habitat, we specified quadrat as a random effect in the linear mixed models. We used Tukey's test to separate significant means.

We quantified elephant and giraffe activity (presence) in the plots based on the number of independent detections of each species per camera trap. Successive photographs of the same individual or multiple individuals in a group were considered as independent detections only when the time interval between the exposures was at least 20 min. To account for isolated cases when some camera traps would malfunction, we divided the total number of independent photographic events with the total number of known working time (calculated from the total number of days each camera was active). We used package glm2 version 1.2.1 (Marschner, 2018) to fit generalized linear models with quasi-poisson error structure to test for the differences in wildlife activity and browsing intensity across the three habitat categories and to test for correlations between browsing intensity by both elephant and giraffe activity.

3 | RESULTS

3.1 | Differences in community composition across the three habitats

There were 113,337 individual trees and 63 tree morphospecies across the entire 120-ha plot, and the overall tree density was 38.8

per 20 m² quadrat (944.5 trees per ha). There were significant differences in overall tree density ($\chi^2 = 906.07$, $p < .001$), species richness ($\chi^2 = 2,864.5$, $p < .001$), and diversity ($\chi^2 = 2,562.8$, $p < .001$) across the three habitat categories. The steep slopes had the highest density of trees per quadrat (63.5 ± 1.23), the highest species richness (10.8 ± 1.13), and the highest species diversity (Effective number of species: 5.55 ± 0.07) (Figure 2). Most species (65%) occurred across all the three habitat categories, with both the valley and steep slopes having only three unique species and the plateau having only one unique species (Table S1). These unique species were among the least dominant, represented by less than five individual trees per species. More than 69% (44 out of 63) of the tree species occurred at higher densities on the steep slopes than in any of the two other habitat categories (Table S1).

3.2 | Differences in *A. mellifera* density and canopy traits across the three habitat categories

We found significant differences in *A. mellifera* density per quadrat ($\chi^2 = 145.05$, $p < .001$), number of stems per individual tree ($\chi^2 = 708.8$, $p < .001$), dkh ($\chi^2 = 67.46$, $p < .001$), and average tree height ($\chi^2 = 17.1$, $p < .001$) across the three habitat types. Generally, *A. mellifera* occurred at a higher density in the valley (6.1 ± 0.23) than on the steep slopes (3.6 ± 0.20) and the plateau (1.7 ± 0.09) (Figure 3a). Both dkh and the total number of stems per tree were highest in trees occurring within the plateau (dkh = 274.9 ± 10.40 cm², total number of stems = 7.4 ± 0.19) than in either the valley (dkh = 200.9 ± 2.50 cm², total number of stems = 3.6 ± 0.04)

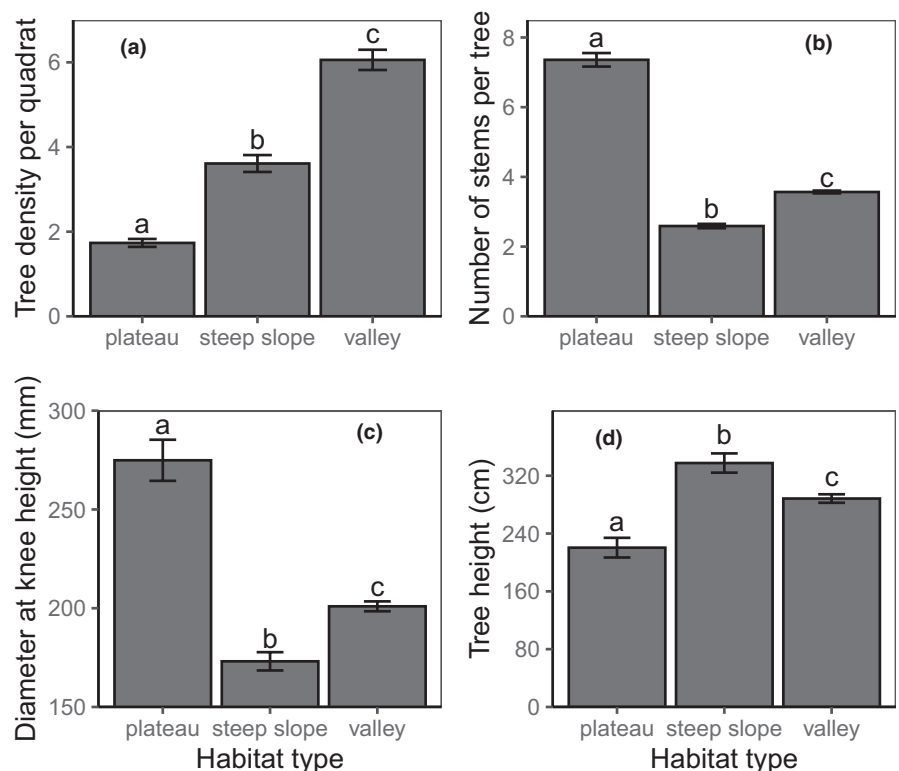


FIGURE 3 Variation in *A. mellifera* (a) tree density (trees 20 m × 20 m quadrat), (b) stem density (number of stems), (c) diameter at knee height (cm), and tree height (cm) across the three habitat categories within Mpala ForestGEO plot. Bars not sharing the same letter indicate that the means were significantly different and the error bars depict standard error

or the steep slopes ($\text{dkh} = 173.1 \pm 4.63 \text{ cm}^2$, total number of stems = 2.6 ± 0.06) (Figure 3b,c). Trees were on average taller on the steep slopes ($348.9 \pm 19.64 \text{ cm}$) than on the plateau ($233.08 \pm 20.84 \text{ cm}$) and in the valley ($326.8 \pm 10.20 \text{ cm}$) (Figure 3d).

3.3 | Megaherbivore activity

From a total of 10,075 camera trap days (5,300 of which were during the dry season and 4,775 during the wet season), we recorded 758 and 1,327 independent photographic events for elephant and giraffe, respectively. Both elephant and giraffe activity in the plot varied across the three habitat categories and seasonally (Figure 4). Elephant activity in the valley was 4.3 times higher ($Z = 2.93, p = .009$) and 4.8 times higher ($Z = 5.22, p < .001$) than on the steep slopes and the plateau, respectively, but there was no significant difference in elephant activity between the plateau and the steep slopes ($Z = -0.16, p = .985$). Giraffe activity was 40.1 times higher ($Z = 2.76, p = .012$) in the valley and 20.4 times higher ($Z = 2.29, p = .047$) on the plateau than on the steep slopes. Additionally, elephant and giraffe activity across the entire plot was, respectively, 4.9 times higher ($Z = 5.43, p < .001$) and 1.9 times higher ($Z = 3.47, p = .001$) during the wet season than in dry season. Interaction between season and habitat was not significant, implying that the dry season reduction in elephant and giraffe activity was consistent across all the three habitat categories.

3.4 | Megaherbivore browsing damage

Both elephant and giraffe browsing damage on individual *A. mellifera* trees varied significantly across the three habitat types (Figure 5). Elephant browse damage was 1.9 times higher in the valley ($Z = 8.91, p < .001$) and 1.5 times higher on the plateau ($Z = 3.87, p < .001$) than on the steep slopes. Giraffe browse damage was 5.0 times higher in the valley ($Z = 7.2, p < .001$) and 13.8 times higher on the plateau ($Z = 17.0, p < .001$) than on the steep slopes. There was 1.2 times more elephant browse damage during the dry season than during the wet season ($Z = 3.41, p = .001$), but giraffe damage did not differ significantly between wet and dry season ($Z = 0.76, p = .44$).

3.5 | Relationship between megaherbivore activity and browsing damage

After controlling for seasonal effects, elephant activity was positively correlated with their browsing intensity in the valley ($t = 2.15, p = .042$) but not on the steep slopes ($t = 0.04, p = .971$) and on the plateau ($t = -0.42, p = .679$) (Figure 6a). Similarly, we found a significant positive correlation between giraffe activity and their browsing intensity in the valley ($t = 2.37, p = .026$) but not on the steep slopes ($t = 0.59, p = .571$) and on the plateau ($t = -0.37, p = .701$) (Figure 6b).

4 | DISCUSSION

This study underscores the importance of fine-scale habitat heterogeneity in predicting local activity of megaherbivores and explaining their effects on vegetation. Our results concur with earlier studies indicating that megaherbivores play a dominant role in selectively suppressing growth and survival of some tree species on the plateau and in the valley, thus amplifying the effects of edaphic factors (Augustine et al., 2011; Pringle, Prior, Palmer, Young, & Goheen, 2016). Further, we provide evidence that both elephant and giraffe tend to avoid areas with steep slopes. We also demonstrate that browsing pressure in areas with steep slopes is lower than in the other more accessible habitats. Due to limited accessibility and low browsing pressure, we argue that steep slopes may become habitat refugia, with higher diversity and density of trees than at intensely browsed habitats.

The observed reduction in presence of elephant and giraffe on the steep slopes is consistent with growing evidence that topography is an important predictor of distribution of herbivores and their effects on vegetation (Bałazy, Ciesielski, Stereńczak, & Borowski, 2016; Stirnemann, Mortelliti, Gibbons, & Lindenmayer, 2015; Takeuchi, Kobayashi, & Nashimoto, 2011; Wall et al., 2006). Previous work on factors driving herbivory patterns across the landscape has focused on animal-driven responses such as landscape of fear and species or guild specific habitat selection patterns (Anderson et al., 2016; Atkins et al., 2019; Goheen, Palmer, Keesing, Riginos, & Young, 2010; Riginos, 2015). This study is an excellent example of how abiotic factors such as topography also contribute to mosaic habitats that characterize savannas.

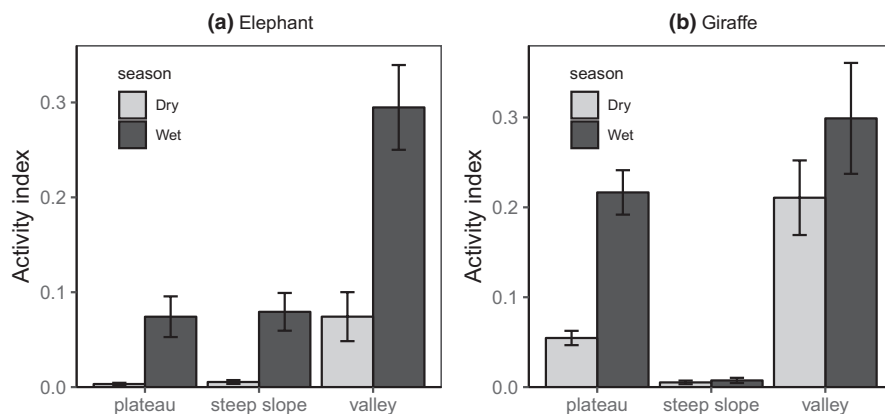


FIGURE 4 Seasonal differences in elephant and giraffe activity in each of the three habitats within Mpala ForestGEO plot. Error bars depict standard error

FIGURE 5 Differences in browsing intensity by elephant and giraffe on *Acacia mellifera* across three habitat categories within Mpala ForestGEO plot. The error bars depict standard error

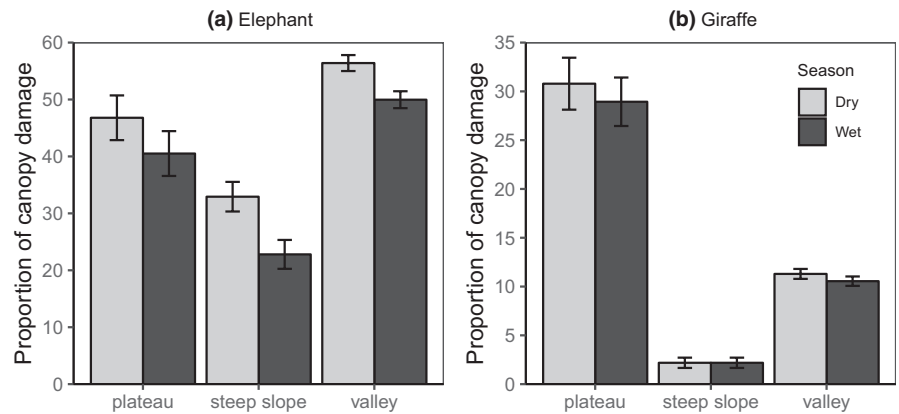
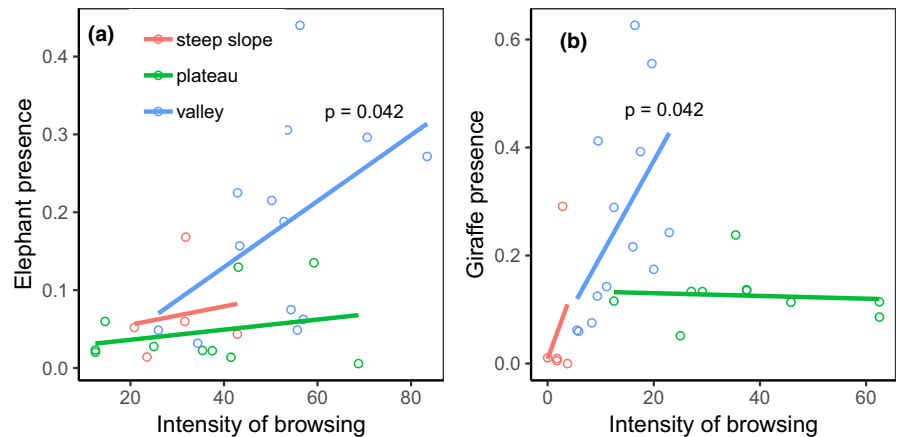


FIGURE 6 Correlation between megaherbivore presence and browsing intensity (proportion of canopy removed) on *A. mellifera* in Mpala ForestGEO plot



Our prediction that elephant and giraffe would avoid areas with steep slopes during the wet season when forage resources are abundant but intensify their visitation during the drier period when resources become scarce was not supported by this study. Instead, we found a general reduction in the presence of elephant and giraffe across all three habitat categories, suggesting that the two megaherbivore species responded to shortages in forage resources by dispersing to other, potentially favorable areas in the landscape rather than adjusting their activity locally. Similar changes in elephant densities in response to rainfall have also been reported in our study system (Augustine, 2010) and elsewhere (Chamaillé-Jammes, Valeix, & Fritz, 2007; Purdon et al., 2018a). While such seasonal movements may be important in alleviating adverse effects on vegetation, the movement of animals is increasingly constrained in human-dominated landscapes (Schlossberg, Chase, & Griffin, 2018; Tucker et al., 2018).

Browsing pressure on *A. mellifera* was unevenly distributed across the three habitat categories and seasonally. Consistent with other studies indicating that elephant browsing pressure increases during the dry season when there is limitation in grass availability (Ihwagi et al., 2010), we found disproportionately more *A. mellifera* trees with fresh elephant damage during the dry season than during the wet season, despite the fact that elephant presence was low in the dry season (Figures 4 and 5). *Acacia mellifera* trees occurring on the steep slopes suffered less browsing damage, probably due to limited presence of both elephant and giraffe. Consequently, trees

on the steep slopes were on average taller and with fewer stems than in any of the two other habitats. Elephant browse damage was highest in the valley, while giraffe browse damage was highest on the plateau. Meanwhile, elephant and giraffe browse damage increased predictably with their presence in the valley but not on the plateau. We suggest two possible explanations for these habitat-specific differences in elephant and giraffe browsing intensity, which are not mutually exclusive.

First, *A. mellifera* trees growing in the valley (characterized by high conspecific neighborhood as well as higher diversity of heterospecific palatable tree species such as *A. etbaica*, *A. brevispica*, and *A. gerrardii*) experience on average less giraffe browse damage than trees on the plateau (where conspecific density is low and 94% of the other trees in the neighborhood are highly defended against browsers by symbiotic ants; Mutuku & Kenfack, 2019). This inference is consistent with predictions of the Marginal Value Theorem (Charnov, 1976) and optimal foraging (Stephens & Krebs, 1986) that the amount of time an herbivore spends in one habitat patch and the proportion of resources still remaining by the time it decides to leave is influenced by the quality of the other patches and the distance between them. Further supporting this idea is the fact that with low browsing intensity trees are able to grow past the height at which they are most vulnerable to giraffe (Figure S1). Studies demonstrate that although giraffe can forage on trees up to 5 m tall, their foraging rates diminish dramatically for trees taller than 3 m (Young & Isbell, 1991). Twenty-one percent

(21%) of trees in the valley were at least 3 m, while only 5% of trees on the plateau were above 3 m tall. We suggest that trees on the plateau are maintained within the giraffe “browse trap” due to their vulnerability associated with growing in isolation in a neighborhood of symbiotically defended *A. drepanolobium* trees. Elsewhere, intense browsing by giraffe has been attributed to the decline and even local extirpation of their preferred species (Bond & Loffell, 2001; Parker & Bernard, 2005). These findings may provide insights to the maintenance of monodominance of *A. drepanolobium* in the plateau. Indeed, in nearby herbivore exclosures (located within the plateau), the density of *A. mellifera* and other tree species has increased by more than three times, and trees are on average taller in plots where large herbivores have been kept away for the last 25 years (Kimuyu, unpublished data).

Second, because *A. mellifera* trees in all height classes are accessible to elephant, the intensity of elephant browsing should vary with the density of trees rather than tree height mediated limitation on accessibility. Consistent with this prediction, elephant browse damage was positively correlated with their activity in the valley and not on any other habitats where their activity was generally low (Figure 4).

Our study focused on responses of the two largest herbivores in African savannas. It is important to note that other smaller herbivores may respond differently to habitat heterogeneity or to presence of the two megaherbivores. For example, smaller herbivores such as klipspringer (*Oreotragus oreotragus*) and mountain reedbuck (*Redunca fulvorufula*) prefer steep or rocky habitats due to low perceived predation risk and availability of specific forage items, and their proliferation in such habitats may offset the effect from reduced presence of megaherbivores. However, the “browse trap” for these smaller herbivores is shorter than that of megaherbivores and trees may easily escape it, thus remaining only vulnerable to megaherbivore browsing (Augustine & McNaughton, 2004). Browsing effects by megaherbivores may either benefit these smaller herbivores by maintaining tree canopies at lower accessible heights (Kohi et al., 2011) or may intensify competition for forage resources (Legendijk et al., 2015).

Previous studies using herbivore exclosures have demonstrated that megaherbivores have profound effects on growth, recruitment, and mortality of the dominant trees in the valley and on the plateau (Augustine & McNaughton, 2004; Maclean, Goheen, Doak, Palmer, & Young, 2011; Sankaran et al., 2013; Wigley et al., 2019). In both habitats, protecting trees from browsing resulted in a dramatic increase in recruitment and reduced mortality of trees. To the extent that megaherbivores have limited access to the steep slope, this may positively influence survival, recruitment, and growth patterns of trees. Our argument that the steep slopes may serve as a habitat refugia is supported by the fact that there was higher density (more than 69% of tree species occurred at the highest density on the steep slopes) and diversity of trees on the steep slopes than in any of the two other habitats. Further, we found reduced presence of elephant and giraffe and lower browsing intensity by these two megaherbivores on the steep slopes. While we cannot rule out the potential

contribution of other factors (such as variation in soil characteristics) to the observed patterns, we argue that topography has a major influence, particularly by limiting megaherbivore access to the steep slopes. However, the ecological role of topography-mediated habitat refugia requires further scrutiny to understand how it may influence persistence of plant species that are heavily browsed and perhaps depleted in other areas and to elucidate how the observed patterns may interact with other potentially confounding abiotic drivers such as variation in soil texture and chemistry, and soil drainage patterns.

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DISCLOSURE STATEMENT

The corresponding author confirms on behalf of all authors that there have been no involvements that might raise the question of bias in the work reported or in the conclusions, implications, or opinions stated.

DATA AVAILABILITY STATEMENT

Data available from the Dryad Digital Repository: <https://doi.org/10.5061/dryad.bzkh1896c> (Kimuyu et al. 2020).

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SUPPORTING INFORMATION

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

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