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Savanna woody plants responses to mammalian herbivory and implications for management of livestock–wildlife landscape

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Abstract

1. The need to address wildlife conservation outside of protected areas has become more urgent than ever before to meet environmental and socio-economic goals. However, there is limited knowledge about how woody plants respond to herbivory within landscapes shared by wildlife and domestic herbivores in African savanna, thus management decisions might be based on inaccurate information and ultimately be ineffective.
2. We compared woody vegetation dynamics between two adjacent ranches with different management objectives and subjected to varying levels of herbivory by both wildlife and domesticated mammals using 421 square plots of 400 m² nested on three transects, each 3 km long and purposively selected to minimize bio-physical differences.
3. Both species and structural diversity were significantly higher ($p < 0.05$) in the site with lower levels of herbivory. Conversely, the site with higher levels of herbivory recorded enhanced biomass production for a selection of palatable forage species, perhaps due to compensatory re-growth. This enhanced biomass however dampens as trees grow taller than the browsing zone.
4. A higher intensity of herbivory seems to promote increases in browsing-tolerant *Acacia mellifera* as well as homogenization of the vegetation architecture and lower structural diversity. Conversely, low intensity of browsing modified by environmental factors seems to promote proliferation of encroaching unpalatable species which are increasingly becoming a major rangeland management challenge in the study region.
5. Managing landscapes for the co-existence of both wildlife and livestock demands critical analysis of how vegetation responses to herbivory to ensure suitable ecological niches are maintained. To increase browse biomass for livestock within the landscape would demand that dominant palatable browse-tolerant species are suppressed within the browsing zone of majority of browsing livestock kept by promoting appropriate browsing intensity. On the other hand, if the management objective

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is to promote co-existence of both wildlife and livestock, then the strategy would be to promote structural diversity by varying livestock stocking rate. Given the movement of wildlife between properties, livestock stocking rates should be considered within a wider landscape than just individual private lands.

KEYWORDS

biomass, East Africa, mammalian herbivory, semi-arid, stocking rate, structural diversity, wildlife–human landscapes

1 | INTRODUCTION

Savanna systems cover more than half the area of the African continent and support a large fraction of its human population, majority of its rangeland and livestock biomass and are home to the greatest density of wild herbivores and carnivores of any ecosystem on Earth (Sankaran and Anderson, 2009). In addition to their obvious socioeconomic importance, several savanna grazing systems suffer from woody/bush encroachment in both Southern Africa (Moleele et al., 2002; Roques et al., 2001; Trollope et al., 1998) and Eastern Africa (Angassa, 2012; Dalle et al., 2006). Bush encroachment has been associated with decline in grass resources for livestock (Macharia and Ekaya, 2005; Moleele et al., 2002), decreases in soil carbon (Hudak et al., 2003) and declines in biodiversity (Angassa, 2012; Gordijn et al., 2012). Several causal factors have been brought forward to explain mechanisms behind woody plant encroachment and key among them include changes in: the intensity of grazing, fire, browsing and rainfall (Angassa, 2012; Archer et al., 2017; Dalle et al., 2006; Roques et al., 2001). The role of browsers in driving woody plant dynamics however remains unclear. A study by Mills et al. (2005) in South Africa noted that intensive goat production transformed semi-arid thicket with dense shrubby vegetation into open landscape dominated by ephemeral species. Conversely, Roques et al. (2001) observed that browsing pressure had significant but minor impact on the woody plant dynamics only at the early stages of encroachment. Earlier studies ascribed bush/woody encroachment to selective ungulate herbivory that led to a proliferation of unpalatable and/or chemically defended species that outcompete defoliated palatable species; however, other studies have also shown that grazing/browsing-tolerant palatable species often increase with increase in herbivory (Augustine and McNaughton, 1998; Hulme, 1996; Skarpe, 1990).

In Kenya, a number of landscapes under varied land uses have equally suffered from woody plant encroachment. In northern rangelands (especially Laikipia County), bush encroachment has been observed largely on private commercial ranches (Augustine, 2003a; Okello et al., 2001; Wahungu et al., 2013) and some communal pastoral lands in the southern rangelands (Kidake et al., 2015; Macharia and Ekaya, 2005). Both private and communal ranches have lost critical ecosystem services in northern rangelands such as pasture availability, ability of the ecosystem to resist invasion by both native and

non-native species, loss of wildlife habitat among other ecosystem services. Communal ranches in Laikipia County are particularly vulnerable to pasture scarcity compared with private ranches within similar bioclimatic conditions due to land degradation, invasive alien species and woody plants encroachment (Kimiti et al., 2020; Strum et al., 2015). The most common encroaching species in Kenya rangelands include: *Tarchonanthus camphroretus*, *Dodonaea viscosa*, *Acacia reficiens*, *Ipomoea kituensis*, *Sansevieria volkensii*, *Euclea divinorum* among others (see Augustine, 2003a; Kidake et al., 2015; Kimiti et al., 2020; Wahungu et al., 2013). Increase in camel and goat numbers in the region in the recent past is thought to be a strategy to take advantage of increasing browse and/or cope with climate variability (Huho et al., 2011; Vehrs, 2016). Since late 1990s and early 2000s, active wildlife management outside protected areas in both private and community ranches has gained ground and therefore the need for adequate pastures, and landscape ecological integrity cannot be disputed.

Pro-wildlife private ranches have lost suitable wildlife habitats (Riginos and Grace, 2008) resulting in significant decline in wildlife numbers in over at least a decade. Between 1990 and 2005, over 35% decline in total wild herbivore biomass (excluding elephants) occurred (Georgiadis, et al., 2007). Deeper understanding of browse–browsers interactions is therefore needed so as to inform management strategies. This study aims at determining the influence of different level of mammalian herbivory on woody species composition, structural diversity and browse biomass production to inform management of livestock–wildlife-dominated landscapes.

2 | MATERIALS AND METHODS

2.1 | Study site

The study was conducted in Mpala private commercial ranch (hereafter refer to PR) and adjacent Il Motiok communal pastoral group ranch (hereafter referred to as GR) in Laikipia County, Kenya centred at 37°53'E and 0°17'N in a semi-arid savanna ecosystem (Figure 1). The area receives mean annual rainfall of 450–600 mm in a weakly trimodal pattern with rain expected in April–May, August and October with January–March being a dry season (Augustine and McNaughton, 2006). Mean annual temperatures for the County is estimated at

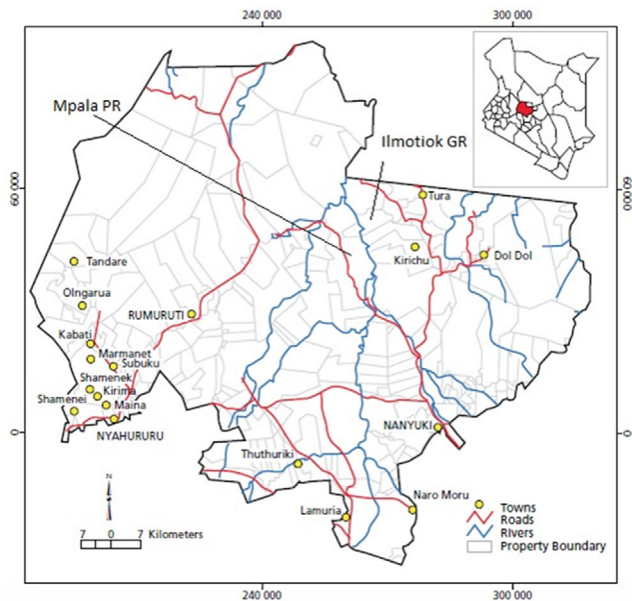


FIGURE 1 Laikipia County map showing properties' boundaries and position of study sites (Mpala PR and Il Motiok GR). Inset, map of Kenya showing the location of the County. Adopted from Ojwang et al., 2010.

16–26°C. The soils in the region are variable from poorly drained black cotton (vertisols) and planosol to well-drained ferric and chromic luvisols (Ngigi, 2006). Topographically, the region has undulating and non-undulating surface with the highest and lowest point having 1800 and 1500 m a.s.l.

Based on historians' understanding, Laikipia region is believed to have been occupied by Laikipiak pastoral Maasai when the European settlers arrived in the late 19th century. At the time, the area had gone through two distressing events; a war pitting Laikipiak Maasai on one side and an alliance of Purko, Kisongo and Keekoyokie clans of the Maasai on the other and a devastating rinderpest outbreak that decimated huge numbers of livestock (estimated at 90%) in some places (Cronk, 2002; Fox, 2018). The colonial administration, through treaties (1904 and 1911) with Maasai *Laibon* Mr. Ole Lenana, moved the Laikipiak Maasai out of the Laikipia (Northern Reserve) to Southern Reserve (Kajiado and Narok) to give way for European settlers (Young et al., 1995). Due to the outbreak of the war in 1914 (World War 1), European settlers seem not to have taken up land vacated by the Maasai until the 1920s (Huxley, 1935). Mpala ranch is a creation of 1911 treaty.

2.1.1 | Mpala ranch

Mpala ranch was one of the lands that were occupied by settlers for use in livestock production since 1920s. Before its demarcation and registration, Mpala was part of the expansive northern rangelands which pastoral communities' practice nomadic pastoralism. From 1933 to 1989, Mpala ranch was managed largely for commercial livestock production. From 1950s to 1969, approximately 2100 cattle,

300 sheep, 100 goats and 150 camels were kept in Mpala when land management objective changed from commercial cattle ranch to joint cattle-wildlife conservancy. In 1989, Mpala Wildlife Foundation and the Mpala Research Trust was established mainly to support wildlife conservation, research as well as a working cattle ranch (Young et al., 1997). The cattle are managed using traditional pastoral (Maasai and Turkana) herding methods. To accommodate wildlife conservation, the management deliberately maintains cattle stocking rate of 10–12 tropical livestock unit (TLU¹)/km² (Augustine, 2003a) and rid the land of goats.

2.1.2 | Il Motiok

Unlike PR that came into private ownership since 1920s, the GR remained under Maasai community control as grazing land for cattle, sheep and goats. Although livestock stocking rate remains doubtful, a number of estimates are greater than 25 TLU/km² (Georgiadis et al., 2007; Kaye-Zwiebel and King, 2014; Ngene et al., 2013) and this value fluctuates in response to prevailing climatic conditions. In mid 1970s, all communal lands in the region were registered as community group ranches to promote pastoral land productivity and control land degradation. Since 1976, Il Motiok community have settled down in four villages, namely Nasirian, Lorupai, Losiagi and Il Motiok within their GR (Kibet et al., 2016). Despite this change in the land tenure system, the management of communal ranches remained unchanged until the early 21st century. Since then, there has been land use changes such as increase in the number of camels, establishment of community wildlife conservancy, mining of sands along dry river beds and most recently subsistence cultivation along Ewaso Ngiro River (Kibet et al., 2016).

The area is dominated by fine-leaved species of *Acacia* genus; *Acacia etbaica* Schweinf., *Acacia brevispica* (Harms), *A. tortilis* (Forssk.) Hayne, *Acacia drepanolobium* Sjostedt and *A. mellifera* (Vahl) Benth (Young et al., 1995).

The region is also a home to several native browsing herbivores such as hares *Lepus saxatilis*, Dik-diks (*Madoqua kirkii*), giraffe (*Giraffa camelopardalis*) and elephants (*Loxodonta africana*) among others. Fire may have been an important component of Laikipia's savannas previously, but has been actively suppressed since European settlement (Augustine and Mcnaughton, 2004).

2.2 | Methods

2.2.1 | Browsing intensity

Livestock stocking rates as well as native herbivore densities per site were used as surrogates for different level of browsing intensity. Herbivore densities were derived from published and grey literature largely wildlife long-term surveys from the study region. The PR has main-

¹ TLU - Tropical Livestock Unit is equivalent to 250 kg live weight; 1 cow = 0.7 TLU, 1 sheep/goat = 0.1 TLU, 1 camel = 1 TLU (FAO, 1986).

tained low livestock stocking rate of 10–12 TLU/km² mainly cattle, camels and sheep over the past 3 decades. The GR stocking rates on the other hand fluctuate depending on prevailing weather conditions with high stocking rates during rainy seasons when pastures and water are plenty and low shortly after major droughts. The GR is estimated to be stocking at higher rate than PR (see Georgiadis et al., 2007; Kaye-zwiebel and King, 2014; Kinnaird and O'Brien, 2012; Kinnaird et al., 2012). In the GR, the grazers kept included cattle, sheep and donkeys and browsers include goats and camels.

Average estimates of combined grazing and browsing wildlife and domestic animals in the region (1985–2012) indicate that GR had densities of 43 TLU/km² compared with 28 TLU/km² for PR. Domestic and wildlife browsers, considered the most effective in modifying woody plant structure and perhaps its composition, were estimated at 28 and 17 TLU/km² for GR and PR, respectively (Augustine, 2003b; Kaye-zwiebel and King, 2014; Kinnaird and O'Brien, 2012; Kinnaird et al., 2012; Ngene et al., 2013).

To corroborate on the use of fire as a management tool in the study sites in the last 40 years since the group ranches were established, 10 key informant interviews targeting senior persons who have lived in the region for more than 35 years were conducted. Physical checks for burn stumps as well as burnt scars from older trees were also done.

2.2.2 | Sampling design for structural data

Three transects lines, 3 km long and approximately 200 m apart, were purposively established per site to ensure some similarity in soils types and topography. In each transect, subplots measuring 20 × 20 m were systematically laid in alternating manner at 20 m intervals to make 75 subplots per transect and a total of 225 per site. Sites that indicated signs of human disturbances such as abandoned kraal, charcoal kilns and trees harvesting were avoided and alternative nearby site was selected. Twenty subplots were discarded in PR due to wildlife threats during fieldwork. In each subplot, percent vegetation cover, bare ground, percent slope, elevation and soil texture were recorded. Soil texture was determined in the field based on feel flow chart protocol (see Vagen et al., 2010).

In each subplot, all woody species with stem diameter of 1.0 cm at approximately 50 cm above ground (hereafter referred to as diameter at knee height - DKH) were enumerated. Bedside DKH, height, canopy depth and canopy diameter (CRWN) were measured and recorded. Non-woody invader species were also recorded and their abundance cover estimated. Botanical nomenclature followed Flora of Tropical East Africa (1954). Duplicate copies of specimen for each species were collected for re-distribution between East African Herbarium and Mpala Research Centre.

2.2.3 | Structural diversity

Structural diversity and biomass production estimates were based on four dominant palatable species, *A. brevispica*, *Acacia tortilis*, *Acacia*

mellifera and *A. etbaica* based on Lusigi et al. (1984) rating and from interviewing knowledgeable local herders. *A. mellifera* and *A. etbaica* overlapped in PR and GR and therefore provided basis for comparing browsing effects at species level.

Canopy volumes, canopy area and canopy densities per subplot were then calculated based on structural data collected using the formulas provided below.

$$\text{Canopy Area (CA)} = \pi \left(\frac{D_1 D_2}{4} \right) \quad (1)$$

where D_1 and D_2 are the two perpendicular diameter measurements when projected on the ground. This formula does not assume symmetry of the canopy.

$$\text{Canopy volume (Canvol)} = \pi \frac{2}{3} H_d \left(\frac{D_1 D_2}{4} \right) \quad (2)$$

Based on ellipsoid volume formula, where H_d is the length of canopy depth, while D_1 and D_2 are the two canopy diameter readings (Thorne et al., 2002).

$$\text{Canopy density (CD) per subplot} = \sum \left(\frac{\pi D_1 D_2}{16} \right) \quad (3)$$

This is summation of individual trees canopy area (Equation 1) divided by subplot area of 400 m² then multiply by 100 to make it into a percentage (Manila, 2007).

$$\text{Coefficient of variation (CV)} = \frac{\delta}{\pi} \quad (4)$$

where δ is standard deviation and π is the mean.

Vegetation piospheric effects were tested in GR with apparent grazing/browsing gradient based on two focal points; settlement area (homesteads) and a temporary watering point at the other extreme end. Often livestock spend more time in early mornings, late afternoon and night near homesteads similarly at watering points during the day. The two focal points were 3 km apart. We hypothesized that higher browsing and grazing occur near homesteads and close to watering points. To test this hypothesis, we compared tree densities, tree canopy area and percent bare ground using 20 × 20 m subplots along the transects. It was anticipated that lower tree and canopy densities and higher percent bare ground on subplots near homesteads and at the watering point compared with subplots in the middle of the transects.

2.2.4 | Browse biomass

The browse biomass was estimated using double sampling method as described by Foroughbakhch et al. (2008). Regression equations based on basal branch diameter and browse biomass was derived and used to estimate edible biomass per hectare per site based on number of stems/branches. Foroughbakhch et al. (2008) recommended the use of 15 individuals per species; however, in this study, we took 48, 32, 12 and 37 individuals for *A. mellifera*, *A. brevispica*, *A. tortilis* and *A. etbaica*,

respectively. All individuals per species were then measured using a diameter tape thereafter all leaves and young shoots were harvested. The values obtained per individual were paired with their basal diameters and then regression analyses carried out.

The following equations were derived: *A. etbaica*, $y = 56.24x - 78.981$, $r^2 = 0.685$; *A. mellifera*, $y = 131.76x - 265.6$, $r^2 = 0.714$; *A. brevispica*, $y = 48.74x - 41.17$, $r^2 = 0.24$ and *A. tortilis*, $y = 53.5x - 103.5$; $r^2 = 0.75$, where y is the edible (browsable) biomass and x are branch base diameter. As a result of low coefficient of determination for *A. brevispica* ($r^2 = 0.24$) and absence of *A. tortilis* in sampled plots in PR, the two species were therefore excluded in biomass estimates discussions.

2.2.5 | Soil measurement

To isolate effects of soil properties, 45 soil samples were collected per site picked in a stratified random manner from the subplots described above. Plots were stratified by soil formation (black cotton, transition and sandy) and randomly selecting subplots within each formation. In each subplot, five subsamples were augured 0–30 cm deep from four corners and at the centre and lumped into a composite sample. The composite samples were sun dried and later transported in labelled zip-lock bags to National Agricultural Research Laboratories, Nairobi for further processing and analysis. Standard methods were followed in pH and macro and micronutrients analysis as indicated.

Available nutrient elements (P, K, Na, Ca, Mg and Mn). The Mehlich Double Acid Method was used (Mehlich, 1984). The oven-dried soil samples were extracted in a 1:5 ratio (w/v) with a mixture of 0.1 N HCl and 0.025 N H₂SO₄. The elements Na, Ca and K were determined using a flame photometer and P, Mg and Mn using a spectrophotometer.

Total organic carbon. Calorimetric method was used (Murphy and Riley, 1962): All organic C in the soil sample was oxidized by acidified dichromate at 150°C for 30 min to ensure complete oxidation. Barium chloride was then added to the cool digests. After mixing thoroughly digests were left to stand overnight. The C concentration was then read on the spectrophotometer at 600 nm.

Total nitrogen. Kjeldahl method was used (Benton, 1991). Soil samples were digested with concentrated sulphuric acid containing potassium sulphate, selenium and copper sulphate hydrated at approximately 350°C. Total N was determined by distillation followed by titration with H₂SO₄.

Soil pH and EC was determined in a 1:1 (w/v) soil–water suspension with pH meter and conductivity meter, respectively.

Available trace elements. Extraction with 0.1 M HCl: The oven-dried soil samples were extracted for trace elements (Fe, Zn and Cu) in a 1:10 ratio (w/v) with 0.1 M HCl. The amounts of elements available were determined with Atomic Absorption Spectrophotometer (Black et al., 1965).

Extractable phosphorus. Olsen method (Olsen et al., 1954) (for soils with pH 7.0 and above was used): The dried soil samples were extracted in a 1:5 ratio (w/v) with 0.5M sodium bicarbonate solution at pH 8.5. Extractable phosphorus was determined spectrophotometrically.

TABLE 1 Floristic composition found at private ranch (PR) and group ranch (GR) in Laikipia County, northern Kenya

Parameter	PR	GR
Number of woody plants	5571	1619
Families	20	7
Genera	30	6
Species	40	15
Shannon diversity index	1.95	1.01
Similarity index	26%	

2.3 | Data analysis

Vegetation data were subjected to canonical correspondence analysis (CCA) to decipher possible linkages between species and environmental variables from those associated with browsing. This analysis was performed using PC-ORD version 5.19 (McCune and Mefford, 2006). Variation within transects (vegetation and soil properties) was tested using Kruskal–Wallis test. Piospheric effects from intense grazing and browsing near homesteads and near watering point at GR were analyzed using polynomial regression (Gardener, 2012). Mann–Whitney U -tests were used to compare structural data, while coefficients of variation (CV) were calculated to estimate structural diversity between sites. Correlation analysis between browse biomass and vegetation structure was done. Q1 Macros Software version 2014.12 was used in all significance tests (KnowWare International Inc., 1996–2014).

3 | RESULTS

The key informants unanimously confirmed that the use of fire as a management tool has not happened in the region in over 30 years; however, accidental fires have occurred in both sites but over very small extents particularly in Mpala ranch. The sampled plots were however not affected based on both the interviews and field observation, with no burned stumps observed in any of the sampled plots. A total of 7190 woody plants were enumerated; 1619 in GR and 5571 in PR. Species diversity varied between sites (Shannon index 1.95 and 1.01 for PR and GR, respectively). Forty-five species belonging to 24 families and 33 genera were identified in the study sites (Table 1). Private ranch with fairly low intensity of browsing had higher structural diversity but low biomass for selected palatable species compared with group ranch.

3.1 | Environmental effects

To isolate possible effects of nutrient, percent slope and elevation, we undertook CCA ordination for measured variables. Observation from the ordination at GR showed that soil fertility declined with increase in distance away from homestead given that all macro-nutrients were negatively correlated with distance. The encroaching species, *S. volkensii* (SANSVO) and *A. reficiens* (ACACRE), dominated less fertile soils

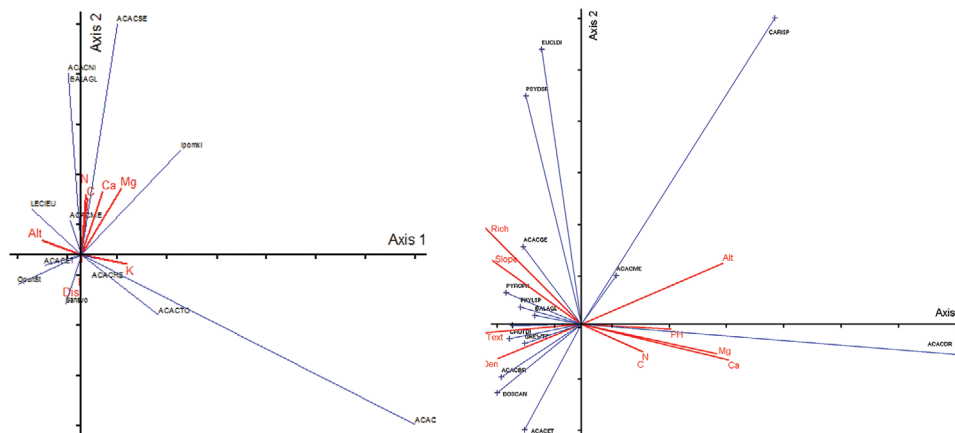


FIGURE 2 Canonical correspondence analysis (CCA) results (a) GR and (b) PR showing correlations between edaphic properties (C, N, Mg, Ca, PH, texture (Text), altitude (Alt) and distance (Dis) as main variates and species attributes species richness (Rich), *Acacia tortilis* (ACACTO), *Acacia mellifera* (ACACME), *Acacia etbaica* (ACACET), *Acacia reficiens* (ACACRE), *Lycium europaeum* (LECIEU), *Acacia drepanolobium* (ACACDR), *Acacia gerrardii* (ACACGE), *Euclea divinorum* (EUCLDI), *Boscia angolensis* (BOSCAN), *Ipomoea kituensis* (IPOM), *Sansevieria volkensii* (Sanvo) as second variates

away from homesteads, while *Ipomoea kituensis* (IPOMKI) dominated the fertile soil and closer to homesteads. *A. tortilis* increased in number away from homesteads with declining soil fertility (Figure 2(a)).

Ordination at PR indicated that the encroaching species such as *Croton dichogamus* (CROTDI) and *E. divinorum* were closely associated with less fertile sandy soils along the sloppy areas. *A. brevispica* (ACACBR), *A. etbaica* (ACACET) and *Acacia gerrardii* were associated with sandy soils at lower elevation, while *Acacia drepanolobium* (ACACDR) in a monodominant stand dominated the higher elevation within black cotton soil high in macro-nutrients (N, C, Mg and Ca) (see Figure 2(b)).

Higher species diversity was observed in areas higher elevation gradient and with lower soil nutrients. Areas dominated by black cotton soil were low in species diversity.

3.2 | Community woody structure

Density of woody species between sites varied significantly ($p < 0.05$) with mean of 739 and 180 trees per ha for PR and GR, respectively. In the PR, *A. brevispica*, *A. drepanolobium* and *C. dichogamus* were the three most abundance species in terms of densities. Twenty-six species had less than 1% relative abundance, six of which were represented by only one individual. The three most dominant palatable species (*A. brevispica*, *A. mellifera* and *A. etbaica*) contributed relative density of 43.1%. Similarly, species densities in GR were highly skewed with the three most dominant species *A. tortilis*, *A. etbaica* and *A. mellifera* cumulatively contributing more than 70% of density.

Beside the four acacia species analyzed in detail, other browse species that occurred in more than 3% relative density included *A. drepanolobium* (19%), *C. dichogamus* (17%), *E. divinorum* (6%) and *Grewia similis* (4%). Other occurred at relatively low percentages that included *Balanites glabra*, *Grewia tenax*, *Searcia natalensis*, *Acacia nilotica* and *A. gerrardii* preferred by majority of browsing animals.

TABLE 2 Mann–Whitney U -test results comparing mean values of structural parameters for four dominant-palatable species (*Acacia mellifera*, *A. brevispica*, *A. etbaica*, and *A. tortilis*) within lightly browsed private ranch (PR) and intensely browsed group ranch (GR) within Semi-arid Savanna, northern Kenya

Parameters	PR	GR	Z value	p value
DKH (cm)	3.8 (± 4)	7.7 (± 3.9)	39.5	*
Basal area (cm ²)	24 (± 94)	58 (± 70)	39.5	*
Height (m)	2.1 (± 1)	3 (± 1.1)	26	*
Canopy volume (m ³)	4.9 (± 11)	18.4 (± 24)	39.3	*
Canopy diameter (m)	1.7 (± 1.2)	3.4 (± 1.4)	39.8	*
Canopy depth (m)	1.3 (± 0.8)	2.1 (± 0.9)	30.4	*
Canopy area (m ²)	3.5 (± 5.6)	11 (± 9)	40	*
Density (ha ⁻¹)	1175	175		
Bare ground	20 (± 20)	29 (± 23)		*

Statistical significance level indicated * $p < 0.05$; standard deviation in parentheses.

Mean values for structural data varied significantly between PR and GR for all parameters measured. Trees on GR on average had larger stems, canopy diameters and heights. This translated into significantly larger mean values for basal area, canopy area and canopy volume ($Z = 39.5$, $p < 0.05$; $Z = 40$, $p < 0.05$ and $Z = 39.3$, $p < 0.05$) respectively (Table 2).

A. mellifera and *A. etbaica* were compared between sites. *A. mellifera* had a significantly ($p < 0.05$) taller and wider canopy at GR compared with PR. However, *A. etbaica* individuals were significantly taller and wider at PR than GR. The stem size class distribution for the two species differed significantly between sites. At GR, *A. mellifera* showed a coarse-grained dome-shaped distribution curve with fewer individuals below 4.9 cm and above 8.9 cm and more in the middle. Similar

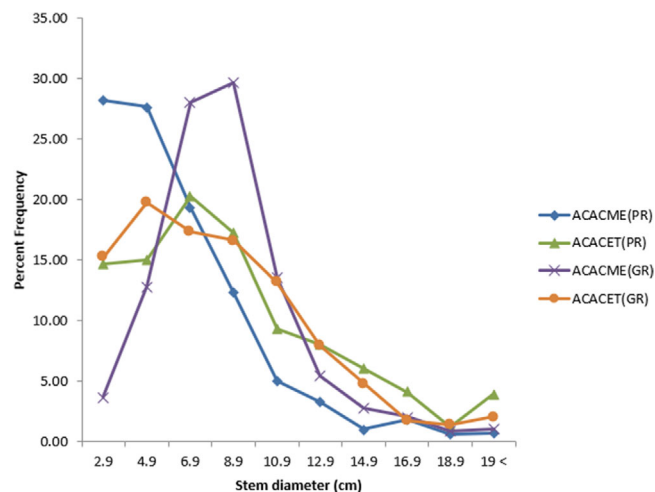


FIGURE 3 Size class distribution of *A. mellifera* (ACACME) and *A. etbaica* (ACACET) for PR and GR, respectively

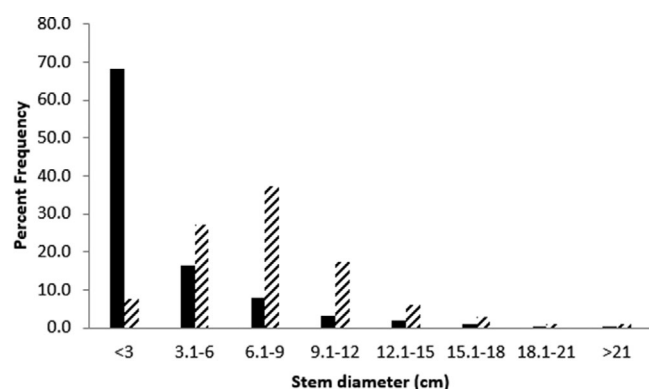


FIGURE 4 Combined size class distribution of all target species at PR (solid bands) with perfect reversed J-shaped curve and GR (Hatched bands) displaying a dome-shape curve.

pattern was observed with *A. etbaica*. A relatively fine-grained reverse J-shaped curve with a greater number of smaller size class individuals that decline gradually with increasing diameters was observed for *A. mellifera* within the PR (Figure 3). A similar trend was observed when all target species were compared between sites, PR exhibited a reversed J-shaped characteristic of actively regenerating plant community, while GR exhibited a dome-shaped distribution with more individuals in the middle size class and fewer at smaller and larger size class (Figure 4).

3.3 | Piospheric effects

Using distance as a proxy indicator of grazing and browsing intensity (see Wesuls et al., 2013), we analyze tree densities, percent bare ground and canopy area along the transects. Descriptive statistics indicates low tree densities near homesteads followed by progressive rise numbers with increasing distance until about 2.7 km where a downward trend was observed (Figure 5(a)). High percent bare ground near homesteads and near watering point and less in subplots at the mid-

TABLE 3 Structural diversity attributes based on coefficient of variations (CV) for private ranch and group ranch in semi-arid savanna, northern Kenya

Study site	Private ranch			Group ranch		
	Standard deviation (δ)	Mean (π)	CV	Standard deviation (δ)	Mean (π)	CV
DKH (cm)	4	3.8	1.05	3.9	7.7	0.51
Basal area (cm ²)	94	24	3.92	70	58	1.21
Height (m)	1	2.1	0.47	1.1	3	0.37
Canopy volume (m ³)	11	4.9	2.24	24	18.4	1.30
Canopy diameter (m)	1.2	1.7	0.71	1.4	3.4	0.41
Canopy depth (m)	0.8	1.3	0.62	0.9	2.1	0.42
Canopy area (m ²)	5.6	3.5	1.60	9	11	0.81
Bare ground	20	20	1.00	23	29	0.79

point of the two was noted (Figure 5(b)). Tree canopy area on average was low for subplots closer to homesteads with the highest canopy area occurring around 0.6 km distance from homesteads thereafter a steady decline towards the watering point was observed (Figure 5(c)).

3.4 | Structural diversity

GR had significantly higher structural mean values in all variables measured (Table 3); however, in terms of structural diversity, the site was less diverse. High structural diversity as indicated by high values of CV was observed in basal area, canopy volume, canopy area and DKH, while height, canopy diameter and canopy depth showed low structural diversity in PR and GR.

3.5 | Browse biomass production

Cumulative biomass for *A. mellifera* and *A. etbaica* varied significantly ($p < 0.05$) between GR and PR. In GR, the two species produced cumulative browse biomass of 2631 kg dry matter (DM) with a mean of 292 kg DM ha⁻¹, while PR produced 1284 kg DM with a mean of 157 kg DM ha⁻¹ ($z = 89, p < 0.05$). *A. mellifera* biomass production was 272 against 110 kg DM ha⁻¹ for PR and GR, respectively. *A. etbaica* on the other had 54 and 19 kg DM ha⁻¹ of biomass for PR and GR, respectively. This suggest that *A. mellifera* produced more biomass per unit area in the GR than PR, whereas *A. etbaica* performed better in PR. Equally, *A. mellifera* individuals in GR produced significantly more biomass ($z = 125, p < 0.05$) mean of 481 g DM stem⁻¹ compared with mean of 407 g DM stem⁻¹ for PR. *A. mellifera* biomass production at all size classes within GR was higher ($p < 0.05$) than PR. Although *A. etbaica* biomass was generally higher in PR, it was not consistent for all size classes. There was no difference in biomass between sites on height below 1 m and 1.1–2.0 m ($z = 0.31, p < 0.76$ and $z = 1.3, p < 0.19$, respectively) (see Table 4).

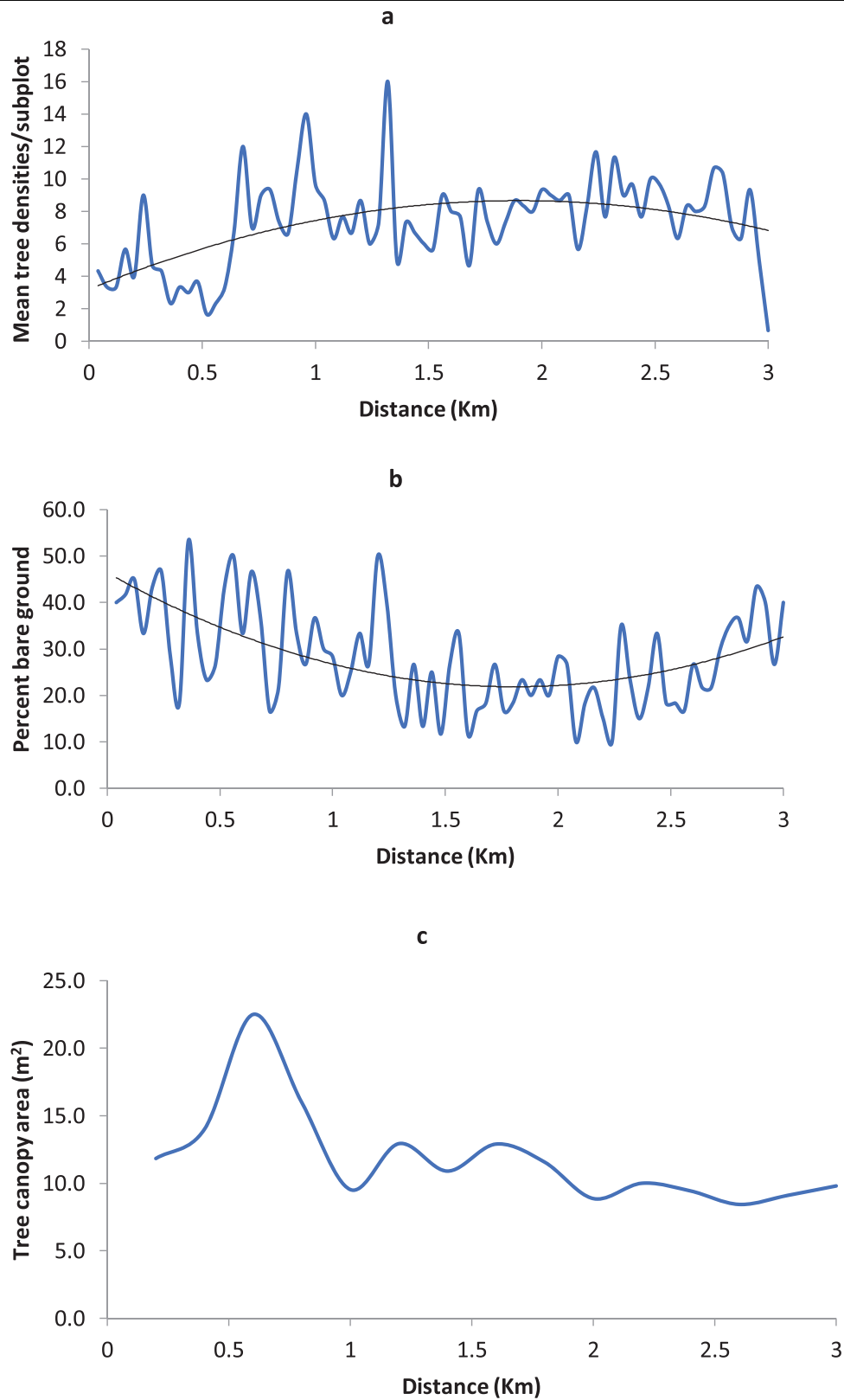


FIGURE 5 Piospheric effect of increase intensity of grazing and browsing along transects starting near homesteads at and ending close to watering point at 3 km creating two focal points at extreme ends. Changes along the transect using means values for (a) tree densities, (b) percent bare ground and (c) tree canopy areas

TABLE 4 Browse biomass mean values (gDM) per species per height class in group ranch (GR) and private ranch (PR) in semi-arid savanna, northern Kenya

Height class	GR	PR	Z	p values
<i>A. mellifera</i>				
≤1	78 ± 232	-80 ± 52	6.5	0.001
1.1-2.0	224 ± 285	216 ± 369	3.11	0.001
2.1-3.0	393 ± 285	348 ± 389	4.43	0.001
3.1-4.0	501 ± 306	633 ± 880	0.64	0.52
≥4.1	729 ± 461	702 ± 579	1.49	0.13
Mean	481	407	125	0.001
<i>Acacia etbaica</i>				
≤1	112 ± 179	112 ± 239	0.31	0.76
1.1-2.0	62 ± 46	128 ± 246	1.3	0.19
2.1-3.0	203 ± 190	250 ± 204	2.64	0.01
3.1-4.0	327 ± 202	381 ± 245	2.4	0.02
≥4.1	487 ± 251	414 ± 338	2.39	0.02
Mean	215	301	7.3	0.001

The U-test significant values are indicated in bold. Note *A. tortilis* and *A. brevispica* did not occur across the ranches.

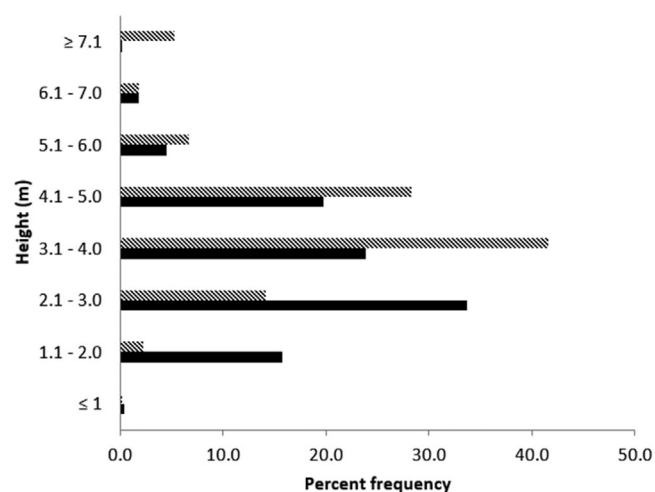


FIGURE 6 Combined vertical canopy volume for selected forage species between PR (Solid bands) and GR (hatched bands) in Laikipia County, Kenya

We compared canopy volume for PR and GR and noted similar trends as those in Figure 3. PR had more canopy volume in lower height classes, while GR had higher values for tree taller than 3 m (Figure 6).

4 | DISCUSSION

This study shows that mammalian herbivory, in association with abiotic factors, influence plant species diversity, structural diversity and biomass production as an ecosystem process. Heterogeneity in vegetation structure influences functioning of African savannas, such as for-

age production as well as providing habitat for a wide variety of plants and animals.

4.1 | Species composition

The intensely browsed site (GR) had fewer woody species compared with PR although they shared 26% of the same species. Often herbivore species selection is low under higher browsing intensity and therefore both palatable and less palatable species are browsed (see Augustine and McNaughton, 1998) and under such circumstances, browsing-tolerant species will thrive at the expense of less tolerant species. Low species diversity in GR therefore may suggest a case of filtering out of species intolerant to heavy browsing or declining competitiveness resulting in low reproduction ability as noted in studies by Díaz et al. (2001) and Fornara and du Toit (2007). Although the study sites had fairly similar biophysical properties, *A. drepanolobium* with more than 1600 individuals in PR was represented by only two individuals within GR. This could have been linked to limited successful recruitment of younger individuals into the system. A study by Goheen et al. (2007) observed that resource re-allocation to defence instead of reproduction occurs under heavy browsing and this decreases recruitment of seedlings. Low numbers of the species could be due to recruitment bottlenecks that could be both biotic and abiotic or both.

Notably, species with high abundance in the GR, except one, were of medium to high palatability based on Lusigi et al. (1984), implying that these species are either browsing tolerant and/or browsing resistant. This implies that intense herbivory not only facilitates an upsurge of unpalatable species as noted by Riginos and Hoffman (2003), but also promotes proliferation of browsing-tolerant palatable species. Encroachment by palatable species into rangeland is therefore less obvious and less problematic for pastoralists given their forage value and therefore its negative ecological effects such as declining wildlife habitat will go undetected until serious impacts are realized. Interviews with local community at GR did not classify *A. mellifera* as an invasive/encroaching species because the word 'invasive' has a negative connotation, and the species was not perceived as negative.

High occurrence of encroaching species such as *Sansevieria sp.*, *I. kituensis* and emergence of *A. reficiens* in GR suggest potential increase in resource availability associated with low intensity of competition and/or existence of unoccupied ecological niches (see Alpert et al., 2000; Schellberg and Pontes, 2013). Similarly, we suggest that the decline in *I. kituensis* abundance with increasing distance from homesteads is a function of soil fertility and/or disturbance (trampling). The species has been shown to thrive in overgrazed sites (Kidake et al., 2015; Macharia and Ekaya, 2005).

4.2 | Woody community structure

In the absence of fire within the study sites in recent decades, we suggest that soil, climate and herbivory are possible vegetation determinants within this savannah ecosystem. Differences in herbivory levels

seemed a plausible regulator of vegetation dynamics within the study sites given similarities in climatic and edaphic factors. Low woody plant density of 180 trees/ha in GR compared with 706 trees/ha at PR suggest possible poor recruitment of seedlings over the years. Size class distribution analysis for *A. mellifera* and *A. etbaica* (see Figure 3) indicated fewer seedlings and mature individuals and more individuals in middle size classes. Possible explanation to such observation could include: low seed development associated with declining fitness of heavily defoliated plants (see Fornara and du Toit, 2008); increase reallocation of resources to defence instead of reproduction (see Goheen et al., 2007); or death of younger individuals attributed to heavy browsing and trampling by browsers (see Augustine and McNaughton, 2004; van Langevelde et al., 2003). The last argument is most plausible within the study site. Trees below 3 m are accessible to majority of animals (sheep from ground level up to 0.87 m, goats at up to 2 m and camels up to 3 m high); this means shorter individual trees would suffer more defoliation than taller ones (Rutagwenda et al., 1989). *A. mellifera* individuals differed significantly at size classes below 3 m but less above 3 m. Augustine and McNaughton (2004) observed that browsing at Dik-diks' (*M. kirkii*) height (i.e., <0.5 m) had more profound effect on the recruitment of *A. mellifera* and *A. etbaica* species to next height class (0.5–1.5 m). This observation however does not explain why the three target species (*A. mellifera*, *A. etbaica* and *A. tortilis*) continue to remain dominant with over 70% of woody plant relative density in GR and more than 40% in PR. We suggest that dominant palatable species in GR may be employing tolerance and/or avoidance strategies to remain dominant amid exposure to higher level of herbivory. Studies elsewhere in Africa have observed faster replacement of lost biomass through compensatory photosynthetic process (Sebata, 2013) as some of the strategies common with browsing-tolerant species to minimize negative effect of defoliation. Unlike GR where palatable species dominates, high trees densities in PR were attributed to high abundance of unpalatable species (*C. dichogamus* and *E. divinorum*) with fairly high vegetative regeneration mode (see Lusigi et al., 1984, Personal Communication from local herder G.M, 2013).

4.3 | Structural diversity

Structural diversity measurement indicates specific height classes that are under intense pressure from herbivory, which otherwise would not have been observed if vegetation structure mean values were used. Structural diversity, besides indicating how heights mean values differed between sites, also indicated how different height classes varied within and between sites. The different management systems in PR and GR together with some abiotic factors may have contributed to the observed difference in vegetation heterogeneity between sites. Higher intensity of herbivory in GR and/or low species diversity could be responsible for relative homogeneity in vegetation architecture at GR. On the other hand, higher heterogeneity observed in PR may be a factor of selective herbivory and/or presence of higher species diversity with diverse lifeforms – trees and shrubs. High livestock stocking rate reduces species selection during feeding and this may promote

establishment of 'browsing lawn' (see Cromsigt and Kuijper, 2011; Fornara and du Toit, 2007). Depending on the dominant resident herbivores, species are browsed to a certain constant height and maintained through constant re-browsing. Although this phenomenon is thought to promote available edible biomass to herbivores, it does reduce the structural heterogeneity required for enhanced habitat suitability for a wide range of organisms (see Asner et al., 2009).

4.4 | Edible biomass production

Biomass production per unit plant as well as unit area was significantly higher in intensely browse site (GR) and could be linked to both biotic and abiotic factors. This observation was particularly pronounced among *A. mellifera* individuals below 3 m high. This was demonstrated by a greater number of stems per ramet and wider canopies associated with breaking up of apical dominance and increase in growth of lateral buds. Importantly, biomass of individuals taller than 3 m did not differ significantly between sites. Except for camels, most domestic herbivores browse below 3 m (Rutagwenda et al., 1989) and therefore taller individuals within GR, even though subjected to higher stocking rate, escape intense browsing. Compensatory re-growth among browsing-tolerant species has been noted in other studies; *A. tortilis* by Oba and Post (1999); *A. nilotica* and *A. karroo* (Sebata, 2013); *A. nigressens* (Fornara and du Toit, 2007) and *Indigofera spinosa* by (Oba et al., 2000). Browsing enhances biomass production of browsing-tolerant species through increased photosynthesis, cell division and reduction in rate of leaves senescence (Sebata, 2013). This implies that palatable species are able to survive intense browsing by strategically investing resources for faster growth to escape the 'browse trap' – browsing may impose height-structured recruitment limitations on trees (see Staver and Bond, 2014). We suggest that the formation of an hourglass-shaped architecture is one such strategy where browsed saplings initially form a 'browsing lawn' at the height of about 1 m that spreads laterally thus creating a buffer/safe zone for shoots at the middle of a ramet to grow and achieve a height beyond 3 m (Figure 7). Once the trees are fully established the lower branches senescence out and the individuals escape browsing trap altogether in the absence of larger herbivores such as elephants and giraffes. Interestingly, there was no significant variation in biomass above 3 m for *A. mellifera* for the two sites. This suggests that compensatory photosynthesis necessary to replace loss biomass is no longer tenable at that height (Table 4).

Unlike *A. mellifera*, intense browsing generally had negative effect on *A. etbaica* biomass production typified by fewer lateral stems and smaller canopy diameters. Similarity in biomass for individuals with height below 2 m between PR and GR remains unclear. Effective resistance to herbivory at seedling and/or sapling stage through chemical defence or due to presence of effective thorns may be a plausible explanation for the observation. Studies have shown that mammalian herbivores prefer mature compared with juvenile tissues in woody plants due to enhanced chemical defence at juvenile stages (see Augustine and McNaughton, 2004b; Barton and Koricheva, 2010). Positive correlation



FIGURE 7 Hour-glass structural architecture created by browsing mammals among browsing-tolerant *Acacia mellifera* (Vahl) Benth. Individual 'c' is beyond browsing height for most herbivores except the giraffes in semi-arid savannah, Kenya.

between biomass values and numbers of individuals and canopy volume per hectare was observed in both sites.

5 | CONCLUSIONS

1. Herbivory modifies vegetation directly through alteration of composition and structure and also indirectly through modification of growing environment such as enhanced nutrients levels, trampling and compaction of soil near kraals and watering points.
2. Intense browsing is thought to alter species composition whereby browsing-sensitive species decline and browsing-tolerant species increase.
3. Browsing of browsing-tolerant species causes the establishment of a temporary browsing lawn where browsed individuals quickly replace loss biomass, increase biomass production and promotes re-browsing. Oddly, the species also enhances the plants defensive strategies thus causing pain to herbivores at the same time benefit from inflicted pain from defoliation. We believe that growth vigour associated with browsed individuals is part of a strategy to escape herbivory given that compensatory growth ceases once the individuals escape the 'browse trap' zone.
4. To increase forage for livestock within the landscape would demand that browse-tolerant species canopies be 'maintained' within browsing height of the main herbivore species kept. However, if the management objective is to promote co-existence of both wildlife and livestock then, the strategy would be to promote structural diversity by varying livestock herbivory intensity.

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AUTHORS' CONTRIBUTIONS

S. K., M. M. N., L. M. and D. K. conceived and designed the research; S. K. carried out data collection and data analysis and wrote the manuscript,

whereas M. N. N., L. M. and D. K. provided technical guidance on methodology, data synthesis and editing of the manuscript. All authors contributed critically to the drafts and gave final approval for publication.

CONFLICT OF INTEREST

The authors declare no conflict of interest.

DATA AVAILABILITY STATEMENT

Data available for the Dryad Digital Repository <https://doi.org/10.5061/dryad.0p2ngf21h> (Kibet et al., 2021)

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