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Research Article

Analysis of the Spatial Relationship between Cattle and Wild Ungulates across Different Land-Use Systems in a Tropical Savanna Landscape

Geoffrey W. Kinga,[1] **John Mironga**,[2] **and Wilfred O. Odadi**[1]

[1] *Department of Natural Resources, Egerton University, P.O. Box 536–20115, Egerton, Kenya*
[2] *Department of Geography, Egerton University, P.O. Box 536–20115, Egerton, Kenya*

Correspondence should be addressed to Geoffrey W. Kinga; jeffwaki@yahoo.com

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In many African savanna landscapes, domestic and wild herbivores cooccur across different land-use systems, but the role of land-use in shaping their spatial relationship is poorly understood. We evaluated the spatial relationship between cattle and wild herbivores categorized by body sizes and feeding habits across different land-use types, namely, private ranches (PR), transitional lands (TRL), and pastoral grazing areas (PGA), in Laikipia County, Kenya. Cattle and wild herbivores spatial distribution data were obtained from Kenya's Department of Resources Survey and Remote Sensing (DRSRS). Spatial relationships between cattle and different wild herbivore guilds were analyzed using Ripley's bivariate K_{12} function. In PR, wild herbivore guilds showed significant attraction to cattle at short distances. In TRL, wild grazers, mixed feeders, megaherbivores, and medium-sized ungulates exhibited significant attraction to cattle. Additionally, repulsion was observed between cattle and browsers at short distances under this land-use system. In PGA, wild grazers, mixed feeders, and megaherbivores repelled strongly with cattle at short distances while browsers and medium-sized ungulates were significantly attracted to cattle. Cattle and wild herbivores were more randomly and independently distributed in PR than in TRL and PGA. These spatial relationships imply better coexistence between cattle and wild herbivores in PR than in TRL and PGA.

1. Introduction

Savannas are the most widespread ecosystems in the tropics and subtropics. The tropical and subtropical savannas cover nearly a third of the world's land surface and over 50% of Africa [1]. Sub-Saharan Africa supports approximately 162 million poor livestock keepers [2, 3], majority of which are found in savanna rangelands. Cattle population in the Sub-Saharan Africa is estimated at 191 million heads, more than 50% of these cattle are in East Africa [4–6]. In addition to supporting people and livestock production, African savanna rangelands are also important biodiversity reservoirs. These landscapes not only support large population of hoofed herbivores (ungulates) but also very diverse community of indigenous large mammals [7, 8]. Approximately, 46 species of extant ungulates are endemic to the African savanna biome, exceeding that of any other continent [7]. Notably, however, livestock (cattle, goats, and sheep) usually occur in savanna ecosystems in higher numbers than wild herbivores given the advantage of animal husbandry practices such as veterinary care, predator control, and supplementation of feed and water provision, thus putting even higher demands to the ecosystem [9].

Conversion of grassland ecosystems into croplands, afforestation, urbanization, and other detrimental human activities is a global problem [10]. Increasing human population has led to increased need for food production and this has resulted in expansion of croplands; close to 20% of savanna grasslands in Africa has been converted to cropland and urban areas [9]. Furthermore, livestock production has also increased owing to the increasing demand for protein from the increasing human population, a trend projected to continue [11, 12]. These changes continue to increase pressure on rangeland resources, reducing their sustainability and capacity to provide critical ecosystem services and support biodiversity conservation and livestock production. While numerous protected areas have been established across the savanna ecosystems for the purpose of wildlife conservation, large populations of wildlife occur outside protected areas [13] where they share habitats with livestock.

Habitat sharing between domestic and wild ungulates may result in different kinds of ecological interactions between these two herbivore guilds, including competition [14–16], facilitation [15, 17], and transmission of diseases and parasites [18, 19]. However, the intensity of these interactions may vary depending on various factors, for instance, the digestive system and mouth morphology [20, 21], body size and feeding habits of the wild ungulates involved, animal type and intensity [22], season (dry or wet), and land-use type where domestic and wild herbivores cooccur [15, 23, 24]. The kind of ecological interactions and the various factors that affect their strength may determine the nature and magnitude of spatial relationship between domestic and wild ungulates. Previous studies in African savanna ecosystems have shown that livestock has potential or actual adverse effects on native wild ungulates [25–27]. While wild herbivores adapt to presence of competing cattle by using refuge habitat or by modifying their diet, spatial partitioning has also been shown as a strategy employed by wild ungulates [28]. Despite the fact that livestock and wild herbivores cooccur across different land-use systems, the influence of land-use systems on spatial relationship between these ungulate guilds remains poorly understood. Understanding the effect of land-use systems on the spatial relationship between domestic (livestock) and wild herbivore guilds is necessary for their improved management on human-dominated savanna landscapes.

We investigated the influence of land-use system on spatial relationship between cattle and wild mammalian herbivores in Laikipia County, Kenya. The study area is a typical example of a tropical savanna which is of profound socioeconomic and ecological significance. Laikipia was ideal for the study because it hosts a mixture of livestock and a diverse assemblage of wild herbivores. Domestic and wild herbivores commonly share habitats across much of the Laikipia landscape because only approximately 2% of the landscape is formally protected exclusively for wildlife conservation [23, 29].

In this study, we compared the spatial relationship between herds of cattle and mammalian herbivores among three land-use types, namely, private ranches (PR), transitional lands (TRL), and pastoral grazing areas (PGA). Considering the varying densities of cattle and wild herbivores, management regimes, and forage resources availability in the three land-use types, we expected that the spatial relationship between these herbivore guilds would vary among land-use types. Additionally, we expected that the strength of these effects would vary depending on wild herbivore body size (megaherbivores and medium-sized herbivores) and feeding habits (grazers, browsers, and mixed feeder).

2. Materials and Methods

2.1. Study Area. The research was conducted in Laikipia County, Kenya. The county covers approximately 9666 km^2 [23, 30] and lies between latitude 0°17′S–0°52′N and longitude 36°13′E–37°23′E at an elevation of between 1700 and 2000 meters above sea-level (Figure 1).

The study area is located in the central part of Kenya, where it largely falls on the northern side of the equator (0°). To the southwest are the Aberdare highlands and to the southeast is the Mt. Kenya. A climatic gradient occurs longitudinally in Laikipia due to the presence of Mt. Kenya (5199 m) and Aberdare ranges (3999 m). Laikipia experiences a mean annual rainfall range of between 300 mm and 750 mm with a weak trimodal distribution. Long rains fall between March and June, continental rains occur between August and September, and short rains fall between October and December [31], but with marked spatial-temporal variability. The study area has numerous rivers and streams primarily originating from the two major water towers: Aberdares and Mt. Kenya. Various streams join to form two perennial rivers (Ewaso Ng'iro and Ewaso Narok) which flow through Laikipia plains to Samburu [23, 30]. Streams which originate within Laikipia conduct water seasonally only during the rainy season, otherwise remaining dry for the other part of the year. There are two swamps and several springs, dams, and depressions which fill with water during the rainy season [32].

Laikipia is a species-rich savanna rangeland in both animal and plant life-forms. It harbors over 95 mammal species of which 25 are ungulate species, 540 bird species, and close to 1000 species of invertebrates [29]. Common ungulates include plains zebra *(Equus burchelli)*, impala *(Aepyceros melampus)*, dik-dik *(Madoqua kirkii)*, Grant's gazelle *(Gazella granti)*, African elephant *(Loxodonta africana)*, hartebeest *(Alcelaphus buselaphus)*, oryx *(Oryx beisa)*, eland *(Taurotragus oryx)*, giraffe *(Giraffa camelopardalis)*, buffalo *(Syncerus caffer)*, gerenuk *(Litocranius walleri)*, black rhino *(Diceros bicornis)*, white rhino *(Ceratotherium simum)*, Grevy's zebra *(Equus grevyi)*, and waterbuck *(Kobus ellipsiprymnus)* [33]. Common large carnivores include lion *(Panthera leo)*, cheetah *(Acinonyx jubatus)*, leopard *(Panthera pardus)*, African wild dog *(Lycaon pictus)*, and spotted hyena *(Crocuta crocuta)*.

Habitat types in Laikipia are largely characterized by the dominant plant community or plant species. In the grassland and open woodlands, several species of *Acacia* and *Commiphora* dominate the woody vegetation layer. Various graminoids and forb species dominate the understory vegetation. *Acacia* and *Commiphora* woodland is predominant in the dry central and the northern part of Laikipia; *Acacia mellifera* is the dominant species in this habitat type. In the dry upland forest habitat type, African olive *(Olea africana)* and cedar *(Juniperus procera)* dominate. In the evergreen bushland forest, the dominant vegetation type is *Euclea divinorum* with *Acokanthera schimperi* and *Carissa spinosa* also being present. In the west Laikipia and along the escarpments *Leleshwa* bushes *(Tarchonanthus camphoratus)* and the sand olive *(Dodonaea angustifolia)* exist especially in the overgrazed areas. The yellow fever

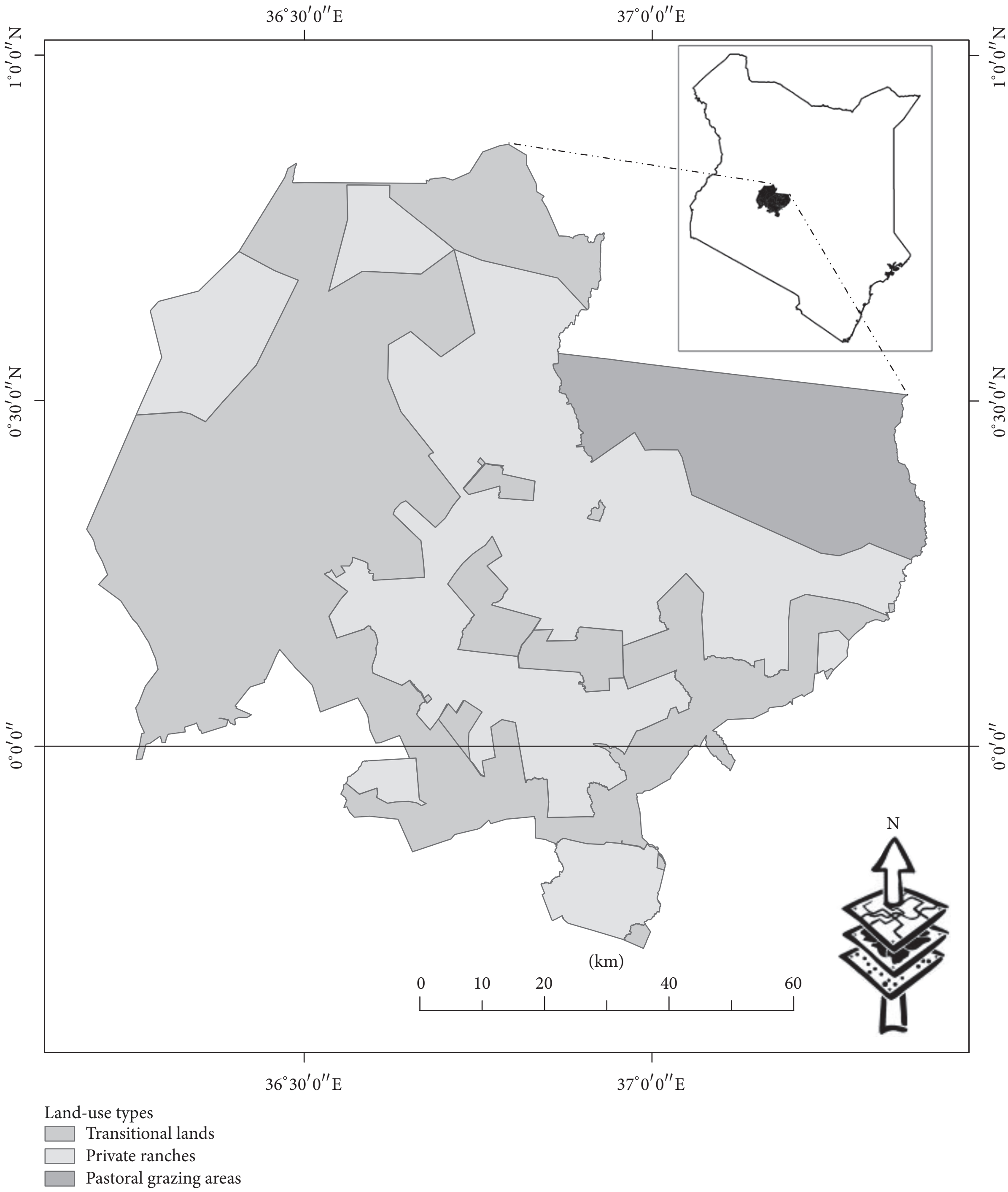

Figure 1: Laikipia county broad land-use types (equator: 0°0′0″). Source: LWF, 2012.

tree *(Acacia xanthophloea)* dominates along the riverine and papyrus dominates in the wetlands [29]. Dominant grasses include *Pennisetum stramineum, Lintonia nutans, Themeda triandra, P. mezianum, Cynodon dactylon, Cynodon plectostachyus, Tragus berteronianus, Cymbopogon pospischilii, Digitaria milanjiana, Bothriochloa insculpta,* and *Brachiaria lachnantha* [34, 35]. Forbs and herbs also constitute the plant community in Laikipia.

Laikipia County communities engage in various socioeconomic activities; agriculture in various forms dominates. In the northern part of the county where rainfall is scarce, pastoralism is the dominant economic activity being practiced on communally owned land. Agropastoralism and small scale mixed farming dominate the rest of the county especially in areas where land ownership is small-holding and rainfall permits arable farming. Agropastoralism refers to land-use

Table 1: Categorization of Laikipia wild herbivores based on body size and feeding habits.

Wild herbivore species	Body size		Feeding habits		
	Megaherbivore	Medium-sized	Grazers	Browsers	Mixed-feeders
African elephant	Yes				Yes
Rhino	Yes			Yes	
Giraffe	Yes			Yes	
Burchell's zebra		Yes	Yes		
Grevy's zebra		Yes	Yes		
Thomson's gazelle		Yes	Yes		
Grant's gazelle		Yes	Yes		
Hartebeest		Yes	Yes		
Impala		Yes			Yes
Cape buffalo		Yes	Yes		
Eland		Yes			Yes
Warthog		Yes	Yes		
Beisa oryx		Yes			Yes
Greater kudu		Yes		Yes	
Lesser kudu		Yes		Yes	
Waterbuck		Yes	Yes		
Reedbuck		Yes	Yes		
Gerenuk		Yes		Yes	

Source: author, 2017.

where a parcel of land is either on crop farming (during wet season) or on livestock (during dry periods). Where land owners or government entities have large tracts of land, cattle ranching, game ranching, and tourism are practiced [36]; moreover, large scale intensive horticultural farming is done in the uplands. Livestock in Laikipia include cattle, donkeys, sheep and goats, and camels. An aerial survey conducted in 2012 estimated that Laikipia hosts approximately 149,910 heads of cattle and 1,454 donkeys. Sheep and goats were estimated at 380,312 while camels were estimated at 4,150 [37].

2.2. Study Design. In this study, we assessed the spatial relationship between cattle and wild herbivores of different feeding habits and body sizes (Table 1) across three broad land-use categories discernible in the study area. Based on feeding habits, wild herbivores were grouped as grazers, browser, and mixed feeders. Grazers comprise herbivores that consume herbaceous plants including grass, grass-like plants, and forbs; browsers predominantly consume leaves, twigs or reproductive parts of shrubs, woody vines, and tree while mixed feeders graze or browse depending on habitat and/or season [38, 39]. Based on the body size, the wild herbivores were classified as megaherbivores or medium-sized ones. Megaherbivores refer to herbivores whose individuals may weigh over 1000 kg while medium-sized herbivores refer to herbivores that weigh above 20 kg [15, 40].

Land-use was classified based on (1) the dominant economic activity, (2) presence of cattle and wildlife, and (3) land ownership regime. This categorization is similar to the previous categorizations in the study area [23, 33]. The land-use categories used were private ranches (PR; also known as prowildlife properties or ranches), pastoral grazing areas (PGA; also known as group ranches), and transitional lands (TRL). These categories are briefly described below.

2.2.1. Private Ranches. This land-use type comprises large scale land holdings which are acquired or leased to individuals or private entities by the government. The private proprietors manage these properties which can either be fenced or unfenced. The "owners" of these properties utilize the land primarily for wildlife conservation while at the same time keeping livestock as a secondary utility for varied reasons; therefore wildlife density is usually higher compared to livestock density [23, 33]. Cattle are usually accompanied by a herdsman. Private ranches tend to provide sufficient pasture to both wild and domestic ungulates due to various land-use management interventions; however, range utilization by cattle is seasonal depending on forage availability.

2.2.2. Pastoral Grazing Areas. These are properties which are registered under a limited number of families from the local pastoral community who communally own and manage their land. Unlike the private ranches where property management is centralized, some group ranches have a much decentralized land management system where each group ranch elects a committee which manages grazing, tourism, and other land utilization activities [33]. The group ranch members may practice mixed farming but they are largely pastoralists; livestock density is usually higher than wildlife and to some extent exceeding the recommended stocking density thus displacing wildlife [23, 33]. Livestock herds are normally accompanied by herdsmen. Due to the "open-access" nature of grazing and unregulated stocking rate in this land-use type, forage resources get exhausted quickly especially during the dry seasons forcing herders to move their livestock to other areas in search of adequate pasture.

2.2.3. Transitional Lands. These are lands which have been subdivided into small plots (1–10 ha) and are owned by the small scale holders by way of having free-hold title deed. Land owners manage their individual properties. Occupants practice mixed farming or agropastoralism when rain permits; in the unoccupied plots, the pastoral communities dominate with their livestock thus displacing wildlife in those areas. There are also some large scale farms and ranches which may or may not tolerate wildlife but do not actively favor wildlife conservation; as a result, wildlife densities are varied in these transitional properties [23]. Cattle herds are usually accompanied by herders. In this land-use type, livestock utilize the range seasonally depending on forage availability. During the dry seasons, herders move with their livestock to other areas with abundant pasture.

2.3. Data Acquisition and Processing. Livestock and wild ungulates spatial data collected during November 2012 aerial census was obtained from the Department of Resources Survey and Remote Sensing (DRSRS), a Kenyan government department mandated with collecting, storing, analyzing, updating, and disseminating geospatial information on natural resources. DRSRS has over the years conducted aerial surveys for both wildlife and livestock in Laikipia where each detected group of either livestock or wild ungulates is mapped using the Global Positioning System (GPS) and the individuals counted. The spatial data was processed based on species and the land-use type in which the species occurred; individual species vector data (points) were then grouped according to the respective wild ungulate category based on feeding habit or body size. Spatial analysis was done using *splancs* package [41] in the R environment [42].

2.4. Data Analysis. Ripley's bivariate K_{12} function [43] was used to evaluate the spatial relationship between cattle herds and wild herbivore herds at different scales of distance at an interval of 250 meters up to a maximum distance (s) of 5000 meters. This function assesses whether the events (cattle herds and wild herbivore herds) being studied are aggregated, independently distributed, or segregated. It measures the average amount of event 2 (wild herbivore herds) located within a distance (s) of randomly chosen event 1 (cattle herd), divided by the overall density of event 2 [44]. Equation (1) defines Ripley's bivariate K_{12} function:

$$\widehat{K}_{12}(s) = \frac{1}{\lambda_2} E(N_{2s}), \quad (1)$$

$$\lambda_2 = \frac{N_2}{A}, \quad (2)$$

where

N_{2s} is number of type 2 events within a distance s of an arbitrary type 1 event,

λ_2 is the intensity of the type 2 events,

N_2 is number of groups of type 2 event,

A is unit area occupied by type 1 and type 2 events,

s is distance of type 2 events from type 1 events (radius).

The corresponding linearized $\widehat{L}_{12}$ function was calculated from the resultant $\widehat{K}_{12}$ function to enable the graphical interpretation of the relationship between cattle and wild ungulate guilds. The linearized $\widehat{L}_{12}$ was given by

$$\widehat{L}_{12} = \sqrt{\frac{\widehat{K}_{12}(s)}{\pi}} - s. \quad (3)$$

Assuming two events are independently distributed, the location of type 2 events (wild ungulate groups) should be randomly distributed with respect to the location of type 1 events (cattle herds) [44, 45]. From equation 2, the expected number of type 2 events within a distance s of a randomly chosen type 1 event when distribution is uniform is $\lambda_2 \pi s^2$. Therefore, if two types of events are independent, the estimate of bivariate $\widehat{K}_{12}$ should equal the area occupied by type 2 events; $\widehat{K}_{12}(s) = \pi s^2$ and $\widehat{L}_{12}(s) = 0$ [44, 46]. If there are more events of type 2 within a distance s of an arbitrary type 1 event than expected under the assumption of independence, then $\widehat{K}_{12}(s) > \pi s^2$ and $\widehat{L}_{12}(s) > 0$, an indication of positive dependence between the two types of events, and this is interpreted as an attraction or aggregation between the two events. If $\widehat{K}_{12}(s) < \pi s^2$ and $\widehat{L}_{12}(s) < 0$, it indicates negative dependence which is interpreted as a repulsion or segregation between the two events [46, 47]. Cattle herds' location remained unchanged, while wild ungulates locations were randomly shifted 100 times within the respective land-use type. The land-use types (study area subunits) were assumed to be torus to enable the shifting of event 2 locations [44, 48]. The 95% upper and the lower confidence bands (envelopes) for the $\widehat{L}_{12}$ function were derived to show where the observed data had greater variation from the random simulations. Table 2 shows the number of cattle and wild herbivore events in each land-use type used in the analysis.

Table 2: Cattle and wild herbivore events in different land-use systems.

Ungulate guild	Land-use type		
	PR	TRL	PGA
Cattle	212	399	22
Wild grazers	1025	379	23
Browsers	271	28	6
Mixed feeders	564	57	24
Megaherbivores	460	45	22
Medium sized ungulates	1431	421	31

Source: author, 2017.

3. Results

3.1. Cattle versus Wild Herbivores of Different Feeding Habits. Cattle and wild grazers showed a significant attraction

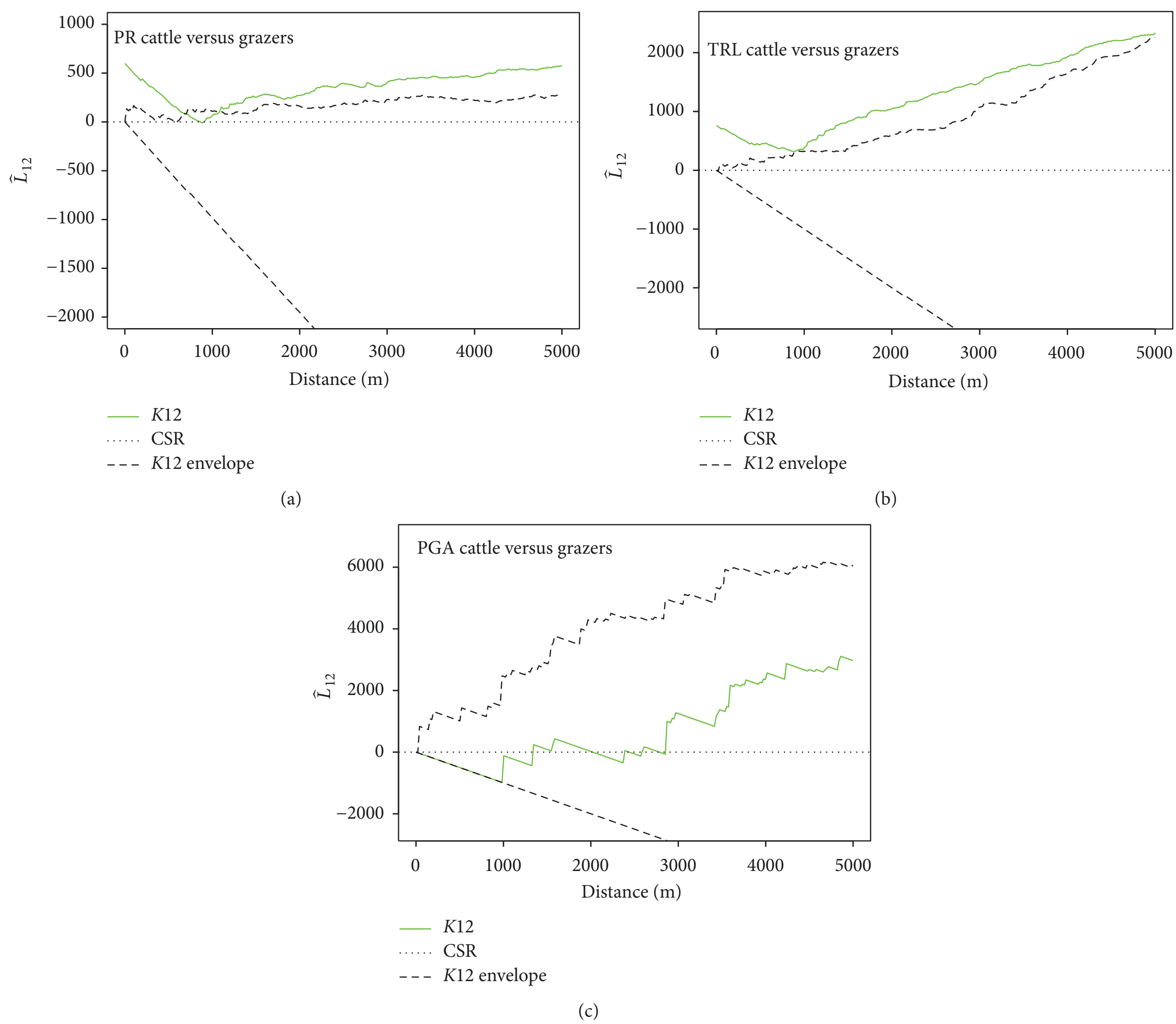

Figure 2: Spatial relationship between cattle and wild grazers across land-use types: (a) private ranches (PR), (b) transitional lands (TRL), and (c) pastoral grazing areas (PGA). Green solid line K_{12} is Ripley's bivariate function estimate; dashed lines (K_{12} envelope) are the 95% upper and lower confidence envelopes while the dotted line is the reference for complete spatial randomness (CSR). Source: author, 2017.

towards each other up to approximately 700 m and from approximately 1400 m to 5000 m in PR (Figure 2(a)). In TRL, the two guilds exhibited significant attraction at all distances up to 5000 m (Figure 2(b)). In PGA, cattle and wild grazers exhibited two different departures from independence. At distances up to approximately 1400 m, between 2000 m and 2600 m, and at around 2900 m, linearized K_{12} function (L_{12}) was less than 0, indicating repulsion. However, below 1000 m, it was not clear whether repulsion was significant or not because L_{12} overlapped with the lower confidence envelope. Attraction was observed between approximately 1400 m and 2000 m, between 2600 m and 2800 m, and from approximately 2900 m to 5000 m. The observed L_{12} curve did not go beyond the upper envelope and thus the attraction between cattle and wild grazers was not significant in PGA unlike in PR and TRL (Figure 2(c)).

Cattle and browsers exhibited both attraction and repulsion in the PR; at short distances of up to approximately 700 m, there was significant attraction between the two guilds. From 700 m up to 5000 m, the L_{12} curve was less than 0 indicating repulsion, notably; the repulsion was weak and near complete spatial randomness ($L_{12} = 0$) (Figure 3(a)). In TRL, cattle and browsers exhibited repulsion. At short distances up to approximately 600 m, the repulsion appeared strong though it could not be established whether it was significant or not because the L_{12} curve overlapped with the lower confidence envelope; beyond this distance up to 5000 m, the repulsion was moderate (Figure 3(b)). In PGA, significant attraction was exhibited at short distances up to approximately 500 m; beyond 500 m up to 5000 m, cattle and browsers tended to show strong attraction which was not significant (Figure 3(c)).

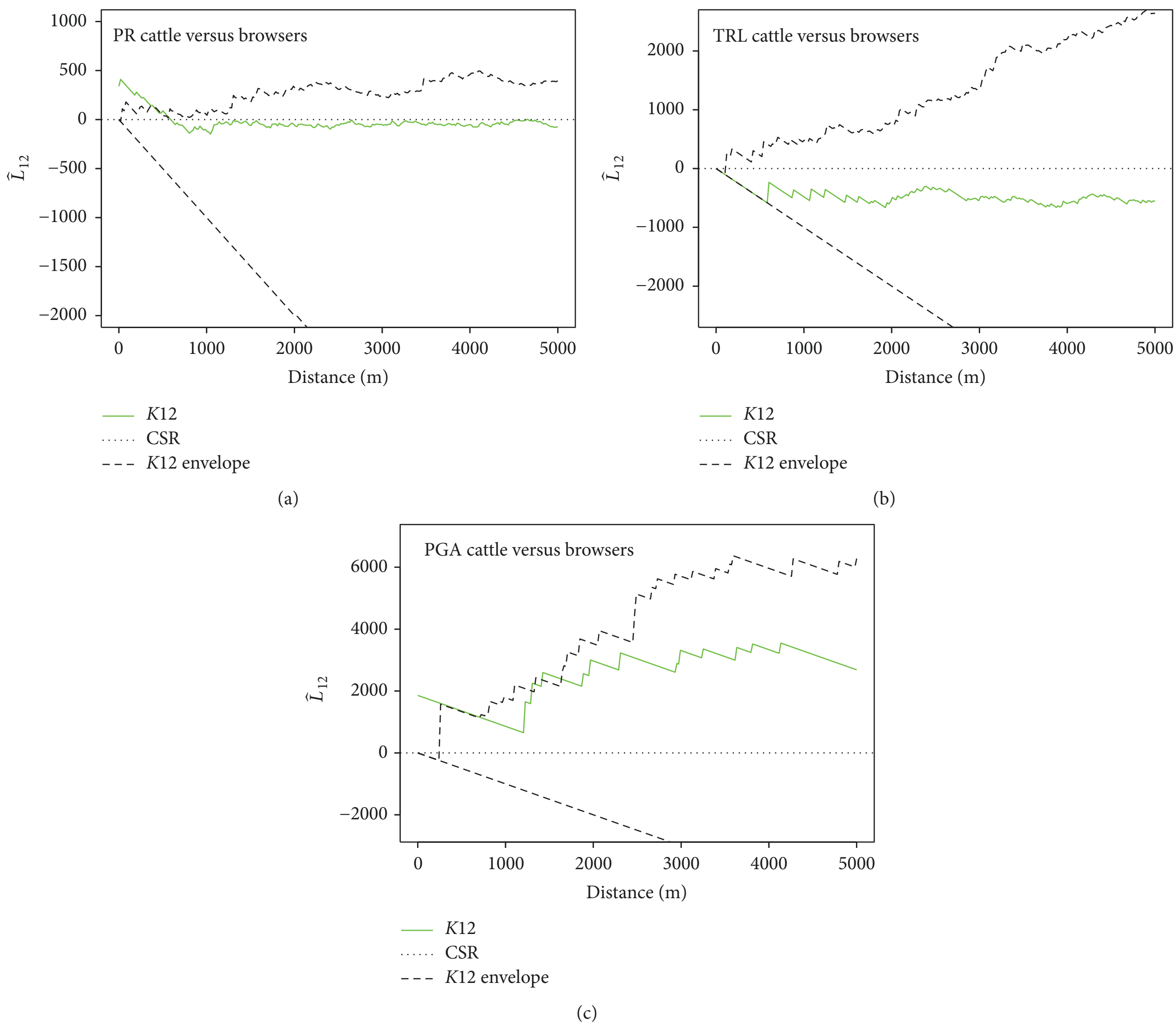

FIGURE 3: Spatial relationship between cattle and wild browsers across land-use types: (a) private ranches (PR), (b) transitional lands (TRL), and (c) pastoral grazing areas (PGA). Green solid line K_{12} is Ripley's bivariate function estimate; dashed lines (K_{12} envelope) are the 95% upper and lower confidence envelopes while the dotted line is the reference for complete spatial randomness (CSR). Source: author, 2017.

Cattle and mixed feeders exhibited two different departures from independence across all the three land-use systems unlike in the cases of cattle and grazers and cattle and browsers. In the PR, significant attraction was observed up to approximately 700 m followed by a weak repulsion up to around 1200 m. A weak attraction was observed from 1200 m to 5000 m, the observed spatial relationships between cattle and mixed feeders in PR conspicuously oscillated very close to complete spatial randomness (Figure 4(a)). In TRL, there was a weak but statistically significant attraction between cattle and mixed feeders up to approximately 400 m followed by repulsion between 500 m and approximately 3300 m. A short stint of weak attraction was observed followed by weak repulsion up to around 4400 m and then an attraction up to 5000 m (Figure 4(b)). In the PGA, there was strong repulsion at short distances (<300 m) but it could not be established whether it was significant or not because L_{12} overlapped with the lower confidence envelope. This was followed by moderate attraction at all distances up to 5000 m (Figure 4(c)).

3.2. Cattle versus Wild Herbivores of Different Body Sizes. A weak significant attraction existed between cattle and megaherbivores in PR at distances less than approximately 700 m. Weak repulsion was exhibited between 700 m and 3300 m, followed by weak oscillations of attraction and repulsion up to around 3900 m. Further, a weak attraction was observed up to 5000 m (Figure 5(a)). In TRL, a weak significant attraction was observed at short distances (<300 m). From approximately 600 m up to 5000 m, repulsion between cattle and megaherbivores was observed (Figure 5(b)). In PGA, a very strong repulsion was exhibited at short distances (<400 m) followed by moderate attraction up to 5000 m (Figure 5(c)).

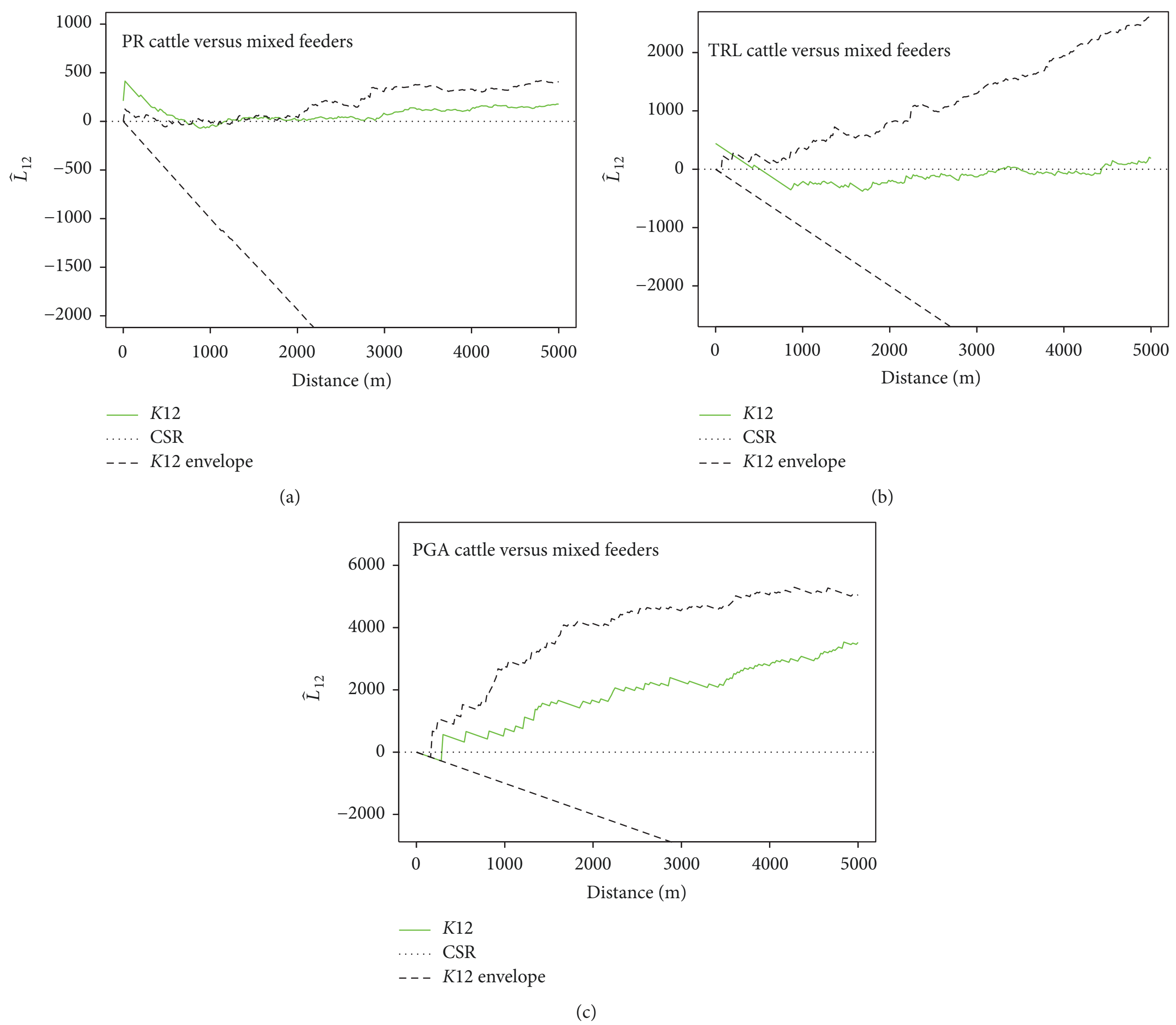

FIGURE 4: Spatial relationship between cattle and mixed feeders across land-use types: (a) private ranches (PR), (b) transitional lands (TRL), and (c) pastoral grazing areas (PGA). Green solid line K_{12} is Ripley's bivariate function estimate; dashed lines (K_{12} envelope) are the 95% upper and lower confidence envelopes while the dotted line is the reference for complete spatial randomness (CSR). Source: author, 2017.

A significant positive dependence between cattle and medium-sized ungulates was observed throughout all the scales of distances in the PR; however, the strength of the relationship weakened towards the 5000 m mark (Figure 6(a)). In the TRL, the relationship between the two ungulate guilds indicated a significant attraction up to 5000 m (Figure 6(b)). In PGA, cattle and medium-sized ungulates showed significant attraction at short distances (<400 m); a short stint of repulsion was exhibited between approximately 700 m and 1000 m followed by attraction behavior up to 5000 m (Figure 6(c)).

4. Discussion

The wild grazers largely exhibited significant attraction to cattle in PR and TRL unlike in PGA where they showed both repulsion and attraction. In a parallel study, mean NDVI in PR and TRL (excluding forested areas) was higher than in PGA (excluding forested areas) indicating higher forage availability (G.W. Kinga, unpublished data). The observed attraction between cattle and wild grazers in PR and TRL is consistent with previous studies where niche overlap between cattle and some wild grazers has been reported especially when forage resources are abundant [26, 49]. The observed spatial attraction in PR and TRL could be as a result of both habitat and dietary niche overlap between cattle and wild grazers. In PGA, the spatial repulsion at short distances (≤1400 m) could be as a result of differential use of space and/or forage resources which is associated with resource scarcity [26]. At moderate to larger scale distances (≥2900 m) cattle and wild grazers exhibited a positive relationship (attraction). The deviation of the observed spatial

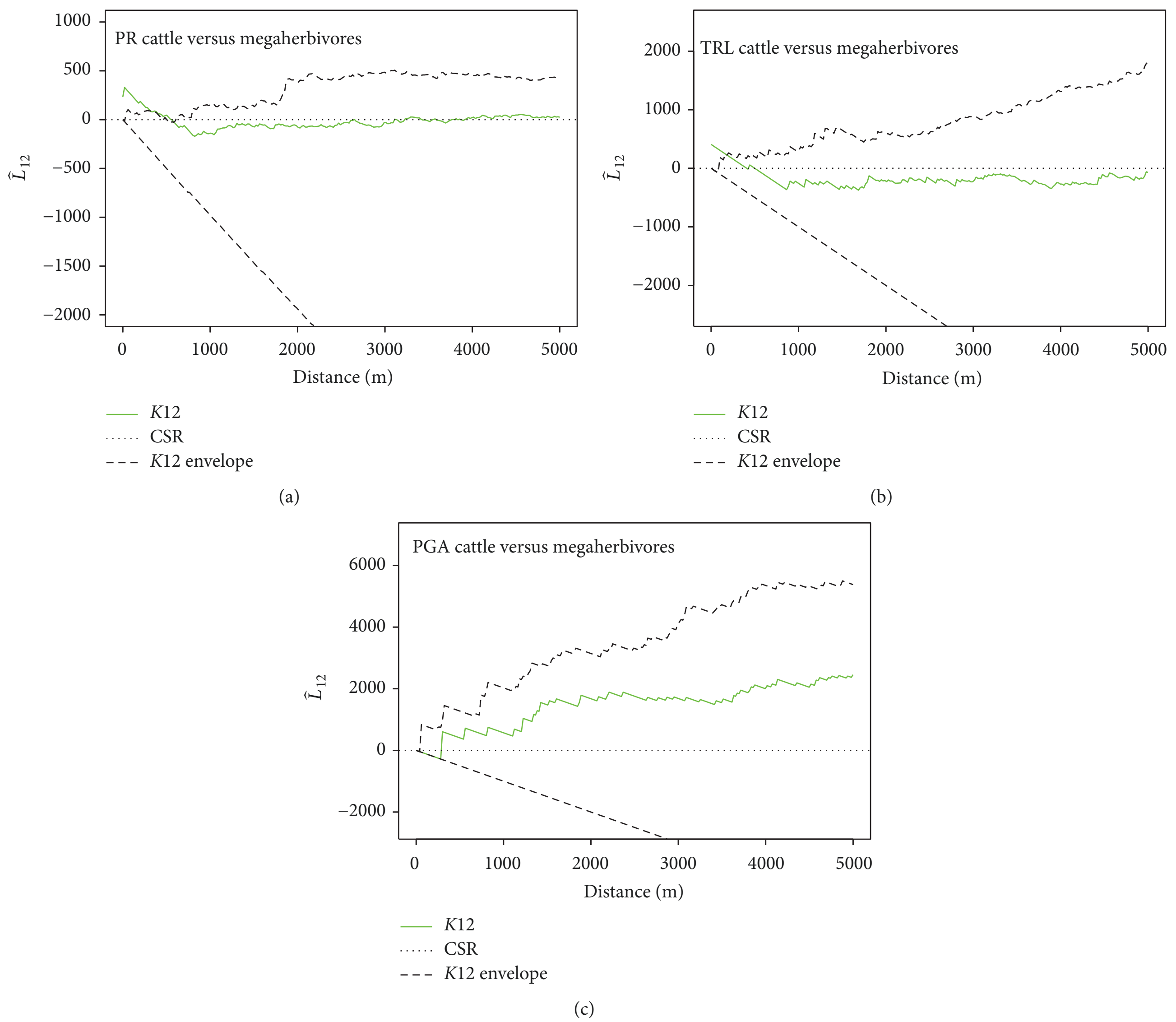

Figure 5: Spatial relationship between cattle and megaherbivores across land-use types: (a) private ranches (PR), (b) transitional lands (TRL), and (c) pastoral grazing areas (PGA). Green solid line K_{12} is Ripley's bivariate function estimate; dashed lines (K_{12} envelope) are the 95% upper and lower confidence envelopes while the dotted line is the reference for complete spatial randomness (CSR). Source: author, 2017.

relationship (L_{12} curve) from complete spatial randomness (CSR) was greatest in PGA followed by TRL and least in PR, suggesting that "randomness" was relatively higher in PR followed by TRL and finally the PGA, a phenomenon which is thought to correlate well with relative forage resources abundance across the different land-use types.

Browsers had a significant attraction to cattle at distances (≤700 m) in PR; however, they largely exhibited negative dependence in PR and TRL. Conversely, they generally exhibited attraction in PGA which was significant at distances (approximately ≤500 m). The observed repulsion between cattle and browsers in both PR and TRL could be due to lack of dietary niche overlap as the two guilds have exclusively different feeding styles as was observed in some browser species [50]. The attraction between cattle and browsers in PGA could possibly be due to sharing of same resource patches even though exploiting different forage materials. Although there was general repulsion in PR, its strength was very weak (slightly below CSR) unlike in TRL.

Mixed feeders exhibited both departures from CSR in all the three land-use types considered in this study. This is presumed to be due to their dynamic feeding style allowing them to conveniently adjust their spatial interaction with cattle. Attraction, independence, and repulsion at different scales of distance were evident (Figures 4(a)–4(c)), an observation closely consistent with [44] on three different mixed feeder species. Just like in the case of grazers and browsers, the departures from CSR were lowest in PR, moderate in TRL, and highest in PGA.

Megaherbivores exhibited attraction towards cattle at short distances (≤700 m and ≤500 m) in PR and TRL, respectively, possibly due to habitat niche overlap as compared

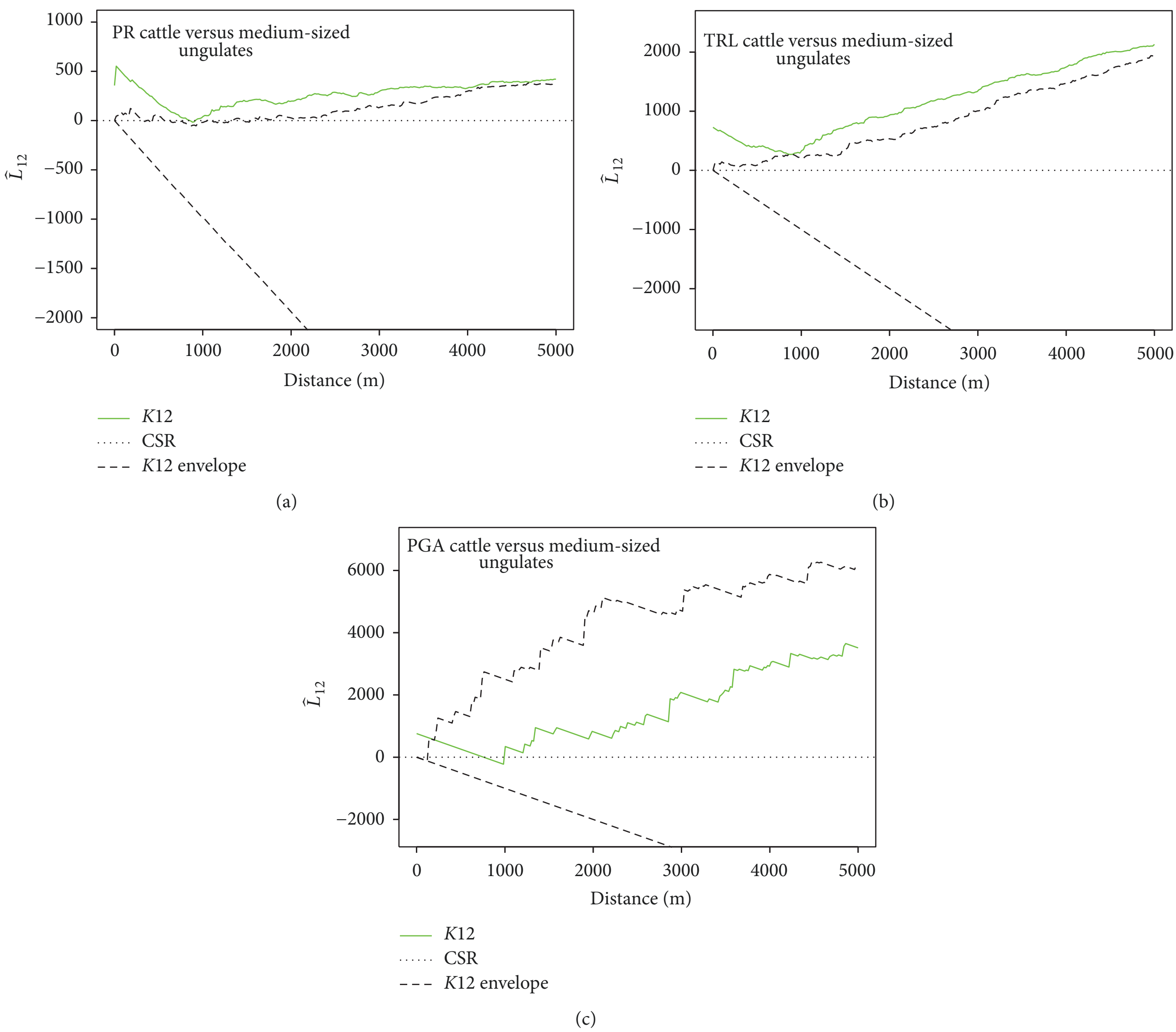

Figure 6: Spatial relationship between cattle and medium-sized ungulates across land-use types: (a) private ranches (PR), (b) transitional lands (TRL), and (c) pastoral grazing areas (PGA). Green solid line K_{12} is Ripley's bivariate function estimate; dashed lines (K_{12} envelope) are the 95% upper and lower confidence envelopes while the dotted line is the reference for complete spatial randomness (CSR). Source: author, 2017.

to dietary niche overlap. This is more so because no pure grazer was in this ungulate guild (megaherbivore). The spatial repulsion observed at fairly short to moderate distances in PR (≈700 m to ≈3300 m) and short to larger distances in TRL (≈600 m to 5000 m) broadly conforms with previous studies indicating that particular species of megaherbivores (elephants) segregate with cattle even at larger scales of distance [44]. This could be as a result of the two ungulate groups exploiting different habitat types within the respective land-use type. The variation of L_{12} curve from CSR was minimal in PR than in TRL, possibly indicating some degree of independence in PR than in TRL. The higher attraction in PGA especially at larger scales of distance could be as a result of the two guilds using same habitat patches within the land-use type.

The medium-sized ungulates broadly indicated attraction to cattle at nearly all scales of distance in all the three land-use types (Figures 6(a)–6(c)); this was attributed to the fact that some wild ungulates in this guild are pure grazers and mixed feeders that not only shared the same habitat but also used same dietary niche with cattle. This ungulate group showed greater deviation from CSR in the PGA than in TRL and PR, implying that more independence was exhibited in PR.

The observed spatial relationships (attraction, independence, and repulsion) between cattle and different wild herbivore guilds in the three different land-use types can largely be attributed to pasture resources availability and the density of cattle and wild herbivores in the specific land-use types. Pasture resource availability is a requisite conditional requirement for interspecific competition to occur between sympatric populations [14]; wild ungulates have previously employed spatial partitioning to counter the competitive effects from cattle [28]. And cattle therefore are a possible cause of the observed spatial relationships. On the other hand, the density of either cattle or wild herbivore guilds in the respective land-use type may potentially affect the spatial relationship between them. Cattle density has previously been highest in TRL followed by PR and PGA while wild ungulates density has been highest in PR followed by TRL and PGA having the lowest density [23]. The observed spatial relationships in this study cannot therefore be singly attributed to competition arising from pasture resource use or varying densities of cattle and specific wild ungulate guilds across the land-use types. However, it is also important to consider the departure of the observed spatial relationship (L_{12} curve) from CSR and how it changes across land-use systems and correlate it with other community attributes in future studies.

5. Conclusions

The five wild ungulate guilds considered in this study exhibited varying spatial relationships with cattle at different scales of distance, a phenomenon which is possibly attributed to habitat and/or dietary niche overlap amidst other possible biotic and abiotic factors. Stronger attractions were exhibited in PGA than in TRL and PR. Moreover, most important is the consistent observation that the variation of the observed spatial relationship (L_{12}) from CSR increased from PR through TRL to PGA for all the wild ungulate guilds analyzed. This is perceived as an indicator of randomness and therefore implying that both domestic and wild ungulate guilds were more independently distributed in PR followed by TRL and finally the PGA. This order is to some extent associated with forage resources available and accessible to wild and domestic ungulates in these three land-use types. The near independent spatial distribution between cattle and different wild herbivores in PR could possibly be an indicator of better coexistence between these two guilds especially in ranches which are better managed ecologically compared to the other land-use systems. The spatial attraction in PGA could be an indicator of complete niche overlap between cattle and wild herbivores in exploiting forage resources in this land-use type which are fairly scarce due to the uncontrolled stocking rate by the community and the "open-access" nature of resources in PGA, potentially leading to competition. The extent of departures from CSR in the three land-use systems shows clearly that cattle have less effect on wild herbivores in PR than in TRL and PGA; this is a possible indicator of better coexistence between the two herbivore guilds in PR than in the other two land-use systems. However, more studies on this subject area need to be done and specifically focus on individual species, effects of seasonality, predator presence, forage availability, habitat type, and patchiness and other anthropogenic factors that may influence the spatial relationship between cattle and wild ungulates.

Conflicts of Interest

The authors declare no conflicts of interest regarding publishing this paper.

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