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Source: Tropical Conservation Science, 12(1)

Published By: SAGE Publishing

URL: https://doi.org/10.1177/1940082919870371

Research Article

Tropical Conservation Science
Volume 12: 1–12
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Unfenced Borders Cause Differences in Vegetation and Fauna Between Protected and Unprotected Areas in a Tropical Savanna

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Abstract

Protected areas generally occur within a matrix of intensively human-modified landscapes. As a way to maintain the biodiversity in these areas, enclosure by fencing is often preferred. This strategy, however, is costly and little is known about the effectiveness of the alternative of unfenced borders on the vegetation and fauna. The objectives of this study are to assess whether there is a distinct difference in biodiversity and composition of plants and mammals between the protected Lake Mburo National Park and the adjacent ranchlands across an unfenced border and to determine the associations between vegetation and faunal species over the same border. We recorded herbaceous vegetation, woody vegetation, and mammal species composition in plots 300 to 500 m away from the border both inside the protected area and in the adjacent ranchlands. The species composition of herbs and mammals in the protected area differ from the adjacent ranchlands, but there is no difference for trees and shrubs. After accounting for land-use type, distance from the border did not significantly account for any additional variation. We also find a correlation between the species composition of vegetation and fauna. Our results suggest that unfenced borders around protected areas create a clear effect.

Keywords

border, disturbance, fauna, herbaceous vegetation, plant-herbivore interaction, protected area, ranchlands, savanna

Introduction

Protected areas are vital for the maintenance of biodiversity and other ecosystem services (Dudley, 2008). The International Union for Conservation of Nature (IUCN) classifies protected areas along a gradient from highly restrictive categories to those that allow sustainable use of resources inside the protected area (Dudley, 2008; Dudley, Parrish, Redford & Stolton, 2010). Protected areas in African savannas are mostly restrictive and most of them have been established for the conservation of wildlife. At the same time, protected areas may harbor resources desirable for human livelihoods, which can create a conflict with the conservation interests (Lindsey, Masterson, Beck, & Romañach, 2012; Mistry & Beradi, 2000). To preserve the conservation value of such protected areas, they are usually separated from adjacent landscapes by fences, trenches, or other restrictions to prevent access by domesticated animals (Hayward & Kerley, 2009).

Fenced borders are commonly used to mitigate biodiversity threats such as wildlife–cattle disease transmission, human–wildlife conflict (disturbance and harvesting), and to protect threatened species (Hayward & Kerley, 2009; Newmark, 2008). Because of these perceived benefits, Lake Mburo National Park

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Received 20 March 2019; Revised 25 June 2019; Accepted 23 July 2019

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(LMNP) plans to fence its border that was demarcated in 1992 to reduce human–wildlife conflict such as competition for pasture for livestock, predation of livestock, and raiding of crops as well as to address the issue of landless pastoralists who resented the gazettement of the park (Kagoro-Rugunda, 2004; Tweheyo, Tumusiime, Turyahabwe, Asiimwe, & Orikiriza, 2012; Uganda Wildlife Authority [UWA], 2015). However, physical fencing is not benign and there are negative effects on biodiversity. A study by Massey, King, and Foufopoulos (2014) found that the effects of fencing on species composition of mammals varied with time. In the early stages of fence establishment, there was an increase in mammal populations and diversity, but later they declined because of insufficient enforcement against illegal activities that could not be thwarted by fencing. At relatively short distances from the border, studies have indicated that a border can have a significant effect on vegetation (Broadbent et al., 2008). Edge effects are often caused by fencing and isolating the protected area can cause population extinction due to dispersal barriers (Lasky, Jetz, & Keitt, 2011; Massey et al., 2014; Newmark, 2008). Fencing may also negatively affect vegetation by enhancing herbivore trampling and overgrazing in the fenced area and hence unbalance the carrying capacity of the vegetation community. Hayward and Kerley (2009) recommend that fencing of protected areas should not be used permanently because in the long run they may cause the biodiversity threats that they were meant to solve.

Because of the negative effects of fencing and the cost of establishing and maintaining fences, unfenced borders, as opposed to enclosed protected areas, could be a viable alternative. Of special interest in such cases is what happens at the border of the protected area: If the borders show no difference to the adjacent ranchlands, the effective area of the park will decrease. A number of studies have looked at the effects of protected areas in general (Di Minin et al., 2013; Fabricius, Burger, & Hockey, 2003; Leverington, Costa, Pavese, Lisle, & Hockings, 2010) and found contrary results for species diversity and composition. For example, species diversity and composition of vegetation (Mureithi et al., 2016; Schindler, Poirazidis, & Wrbka, 2008; Schmidt et al., 2016; Wasiolka & Blaum, 2011), reptiles (Schindler et al., 2008), and arthropods (Fabricius et al., 2003) differ significantly between an unfenced-border conservation area and adjacent land used for livestock grazing and agriculture. Conversely, Fabricius et al. (2003) and Bhagwat, Kushalappa, Williams, and Brown, (2005) found no significant difference in composition of reptiles and birds between the protected area and the ranchlands and farms when the borders were unfenced. Previous studies suggest the effect of an unfenced border on vegetation influences herbaceous plants differently to woody plants (Schmidt et al., 2016; Wasiolka & Blaum, 2011) and also varies with the land-use type (Bhagwat et al., 2005; Fabricius et al., 2003). Therefore, we cannot yet infer how an unfenced border will affect the effective size of the protected area.

The Lake Mburo area in Uganda is a tropical savanna ecosystem in which the major land-use types are a protected area for wildlife conservation (LMNP) and private land used for livestock rearing (Kagoro-Rugunda, 2004). LMNP has an unfenced border and harbors the country's largest population of eland (*Taurotragus oryx*) and zebra (*Equus burchelli*) (Averbeck, 2002). The stocking densities of mammals in LMNP and the surrounding private ranchlands are not significantly different except in the ranch managed by the government (Rannestad, Danielsen, Moe, & Stokke, 2006). Both wild and domestic mammals move across the unfenced border between the protected area and the adjacent ranchlands. The park border is demarcated by concrete pillars every 200 m along the boundary. Illegal activities in the park such as grazing and poaching are managed by conducting patrols, establishing intelligence networks and satellite outposts, as well as conducting community sensitization (UWA, 2015). The park is buffered by a swamp to the south and the River Ruiz to the west within the park borders. The adjacent ranchlands are managed by limiting the herd size, bush-clearing, and improving the pasture associated with the rangeland tenure system (Kisamba-Mugerwa, Pender, & Kato, 2006). This makes LMNP a good place to study how an unfenced border between the protected and the unprotected areas influences species composition and richness and whether there is a sharp difference as seen when the border of the protected area is fenced (Hayward & Kerley, 2009). In this study, we ask (a) are there differences in plant and mammal species composition and richness on either side of the border between the protected area and the adjacent ranchlands? and (b) are there associations between the vegetation and mammal species over the same border?

Methods

Study Area

This study was conducted in the LMNP in Kiruhura District, south-western Uganda. LMNP is approximately 260 km^2 and according to Blösch (2002), it lies within the Ankole Southern climate zone at an elevation of about 1,200 m and is part of the Kagera savanna ecosystem. The area has a bimodal rainfall pattern with peaks from March to May and October to December. The average annual rainfall is about 800 mm and the mean annual temperature is 22°C.

The tropical savanna ecosystem has been modified by woody encroachment of *Acacia hockii* (Blösch, 2002). *Rhus natalensis*, *Grewia trichocarpa*, *Dichrostachys cinerea,* and *Maytenus heterophylla* are the most abundant woody species (Blösch, 2002). The most abundant wild mammals in the LMNP are zebra (*Equus quagga boehmi*), eland (*T. oryx*), impala (*Aepyceros melampus*), and waterbuck (*Kobus ellipsiprymnus defassa*) (Rannestad et al., 2006). Livestock ranching and grazing are the second most dominant land-use types in the district after wildlife conservation in LMNP. There are different rangeland tenure rights (Kisamba-Mugerwa et al., 2006) and they include

- customary communal (members within a tribe graze animals freely in the pasture land)
- individualized (exclusive-use rights of the rangeland resources of an individual are recognized by the local community)
- private (they have registered land titles with full private rights such as ranchlands)
- nonproperty (open access—anyone with access is free to use the resources as long as they have access).

The most abundant livestock in the ranchlands are Ankole cattle (*Bos taurus* L.) and goats (*Capra hircus* L.).

The protected area is owned by the government where wild animals are allowed to roam freely in the national park and the neighboring unprotected areas. Because wild animals roam freely, there is human–wildlife conflict and the government is planning to fence the protected area so as to minimize the conflict. Ranchlands are privately owned and managed for livestock production. Ranchers manage weeds (*Lantana camara*, *Ocimum gratissimum*, and *Solanum* species) and shrubs (*R. natalensis* and *Scutia myrtina*) in the ranchlands. Ranchers generally follow the resource conservation program (it ensures the maintenance of a healthy ecosystem, by managing human–wildlife conflict, law and policy enforcement, and managing wild mammals' and their habitat) managed by the Uganda Wildlife Authority, although some individuals secretly allow their livestock to graze in the park (UWA, 2015).

Sampling Design

We surveyed the eastern part of LMNP and the adjacent ranchlands (Figure 1) between June and September 2015 at the peak of the growing season for plants. We systematically created four paired blocks of $1,060 \times 1,120$ m each, running parallel to the border (Figure 2). The distance between the blocks was 1,000 m. Seventy-two plots (36 in LMNP and 36 in the ranchlands) of 20×20 m (Figure 2) were positioned 300, 420, and 540 m on either side of the border. This was designed to investigate how species composition may change relatively close to the border but also be far enough away to avoid the most obvious edge effects (Broadbent et al., 2008). This has some implications in terms of how much of the protected area is lost by having unfenced borders.

Vegetation and Fauna Sampling

Within each 20×20 m plot, we quantified species composition of herbaceous plants (including graminoids), trees, and shrubs, as well as mammals (herbivorous and carnivorous). We recorded every tree from the seedling stage onwards in the 20×20 m plots, whereas shrubs were recorded from a central 10×10 m subplot of the main plot. Trees and shrubs were aggregated into a single category, 'woody species' in the analyses. To sample herbaceous vegetation, we established five 0.5×0.5 m subplots, four at the corners of the central 10×10 m plot and one at the center. Mammals were estimated by recording the frequency of droppings present in the entire main plot. An experienced game ranger helped in the identification of the mammal species. Not all mammals known from the area were recorded during this study. Nearly all plants were identified to species level in the field; those that we could not identify were collected and identified at Makerere herbarium.

Data Analysis

To evaluate the differences in species composition between plots outside and inside LMNP, we first quantified the main gradients in species composition using ordination methods. We used indirect ordination methods to detect the main gradients in species composition and subsequently evaluated how much of the variation along these main gradients could be attributed to whether a plot is outside or inside LMNP, and whether distance from the border explained any additional variance. We performed a Detrended Correspondence Analysis (Lepš & Šmilauer, 2003) for each of the growth forms (herbs, shrubs, and trees) separately to check the gradient length and found values of 3.08 standard deviations (*SD*) for the herbaceous species, 2.67 for woody species and 2.99 for mammal species. This indicates heterogeneity in the data and indicates that a unimodal ordination method is appropriate to analyze our data (Lepš & Šmilauer, 2003); thus, we chose Correspondence Analysis (CA; Lepš & Šmilauer, 2003). Rare species were down-weighted using the Decorana function to prevent the results of the ordination being determined by a few rare species only (Hill & Gauch, 1980). We also used a direct ordination approach (Canonical Correspondence Analyses, CCA; Lepš & Šmilauer, 2003) with land-use type (protected area or ranchlands)

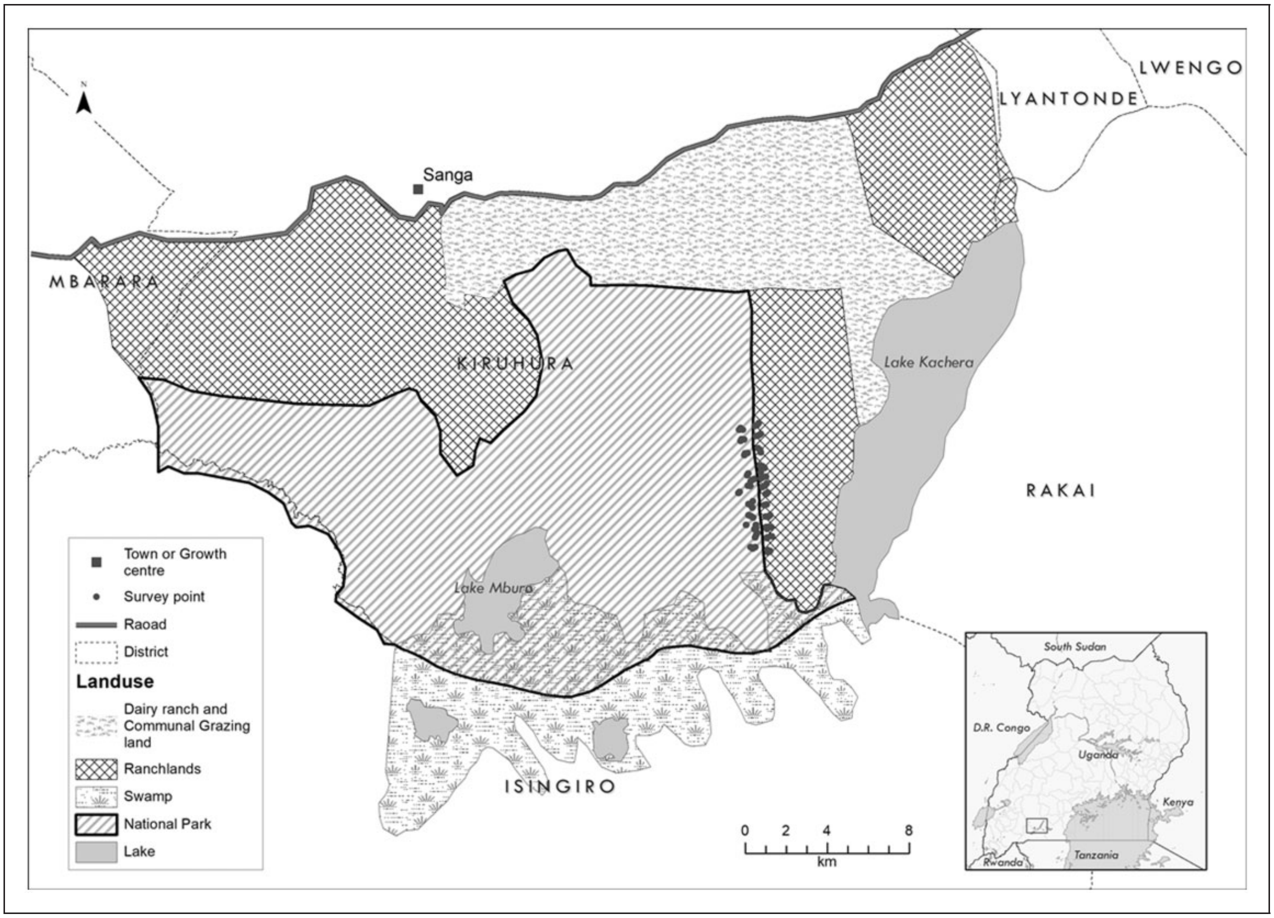

Figure 1. Map of Lake Mburo savanna ecosystem showing land-use categories. Our study focused on the eastern border of the Lake Mburo National Park and adjacent ranchlands (black dots).

as the only constraining variable to examine how much land-use type could explain the differences in species composition.

To test whether land-use type (protected area or ranchlands) could explain the main gradients in species composition and richness, we applied regression analyses with ordination site scores along the axes or species richness as a response variable. We used a random intercept mixed-effect model with a restricted maximum-likelihood algorithm and assumed a normal distribution (Zuur, Ieno, Walker, Saveliev, & Smith, 2009). Ordination scores along both Axis 1 and Axis 2 were used as response variables for each growth form separately in the mixed-effect modeling with land-use type and distance from the border as fixed factors. Land-use type was first evaluated as the sole predictor, and we then tested if distance from the border could account for any additional variation. To account for autocorrelation, the distance along the border was used as a random factor. To evaluate if the random factor was needed, we tested two preliminary models, one with the random factor and the other without, both with the two fixed factors included, following the approach suggested by Zuur et al. (2009). The best model, which is the model with the random factor, was selected based on Akaike's Information Criterion. We used this model to test the difference between LMNP and ranchlands and subsequently tested if distance explained anything additional to land-use type.

After establishing the relationship between land-use and vegetation species composition, we evaluated if mammal species composition, as represented by Axis 1 of a CA of the animal species composition, was related to herbaceous and woody species composition and richness in the same way.

Results

Species Composition and Richness

We recorded 89 herbaceous species; 80 in the LMNP and 51 in ranchlands and 59 woody taxa; 40 in LMNP and 52 in ranchlands. We found droppings of 21 mammal species; 14 in LMNP and 20 in ranchlands. Of these

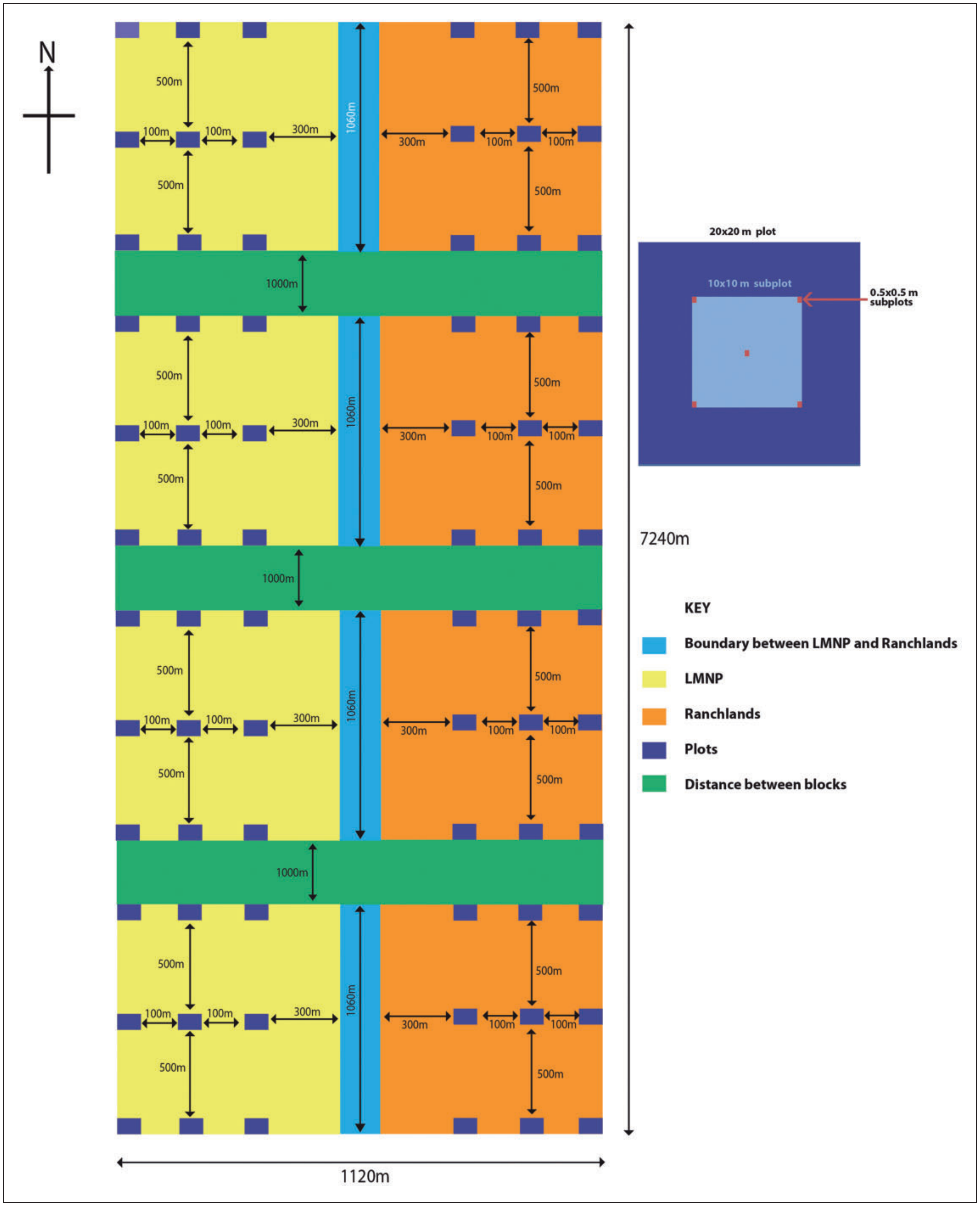

Figure 2. A graphic representation of the sampling design in the study area. Land-use types are Lake Mburo National Park and ranchlands. Four paired blocks on either side of the border were created with 18 plots of 20 × 20 m in each paired block. The plots comprised a central 10 × 10 m subplot and a further five 0.5 × 0.5 m subplots.

mammal species, Ankole cattle (*B. taurus*) and goat (*C. hircus*) are domestic and the rest are wild mammals (Online Appendix 3). Forty-one herbaceous species, 33 woody species and 13 mammal species were common to both LMNP and ranchlands. Dominant herb species were *Sporobolus africanus*, *Cynodon dactylon*, *Eragrostis tenuifolia*, *Urochloa brizantha*, and *Kyllinga bulbosa*; dominant woody species were *Teclea nobilis*, *A. hockii*, *Acacia gerrardii, R. natalensis*, and *O. gratissimum*. Dominant mammal species were zebra, eland, cattle, and impala (see Online Appendix 1 for the list of herbaceous species; Online Appendix 2 for a list of woody species, and Online Appendix 3 for a list of mammal species).

The CA for herbaceous species separated plots dominated by grasses from plots dominated by forbs along Axis 1. Forbs, such as *Justicia exigua*, *Jasminum eminii*, and *Leucas martinicensis*, are found on the right-hand side, whereas grasses such as *Digitaria abyssinica* and *Digitaria velutina* are on the left side of Axis 1 (Figure 3). On Axis 2, fire and grazing-resistant species such as *Themeda triandra* and *Hyparrhenia filipendula* occur on the upper side, whereas species on the lower side are nutrient-demanding grasses, such as *Panicum maximum* and *C. dactylon*. For the woody species (Figure 4), shrub species, such as *Grewia similis, Carissa spinarum*, and *R. natalensis,* occur on the right side of Axis 1, whereas *Acacia* species, such as *A. gerrardii, A. hockii*, and *Acacia sieberiana,* occur on the left-hand side of the axis. On Axis 2, tree species, such as *T. nobilis, Olea Africana,* and *Pappea capensis,* occur on the upper side, whereas *Solanum incanum,* a shrub, occurs on the lower part. Figure 5 shows that the CA

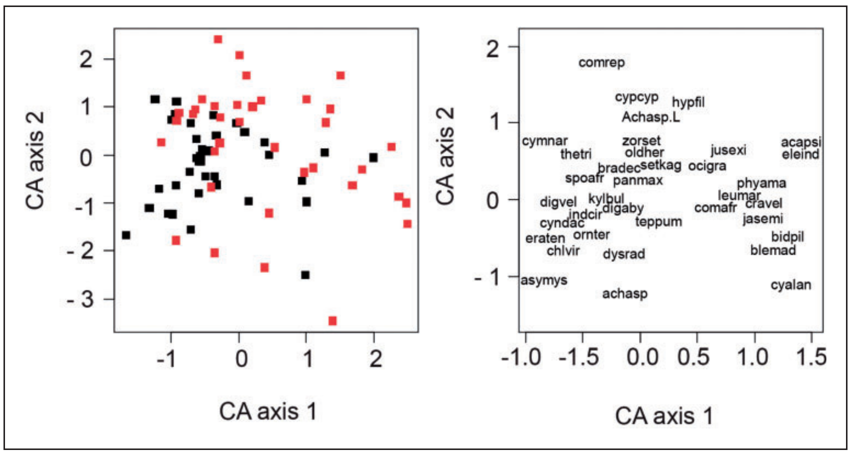

Figure 3. Correspondence Analysis of the herbaceous species composition for Lake Mburo savanna ecosystem (protected area vs. ranchlands). Red squares represent the protected area and black squares ranchlands. To keep the figure legible, species whose abundance is less than five are removed, but are included in the analysis. We abbreviated species names using the first three letters of the binomial genus name and species name, full species names are listed in Online Appendix 1

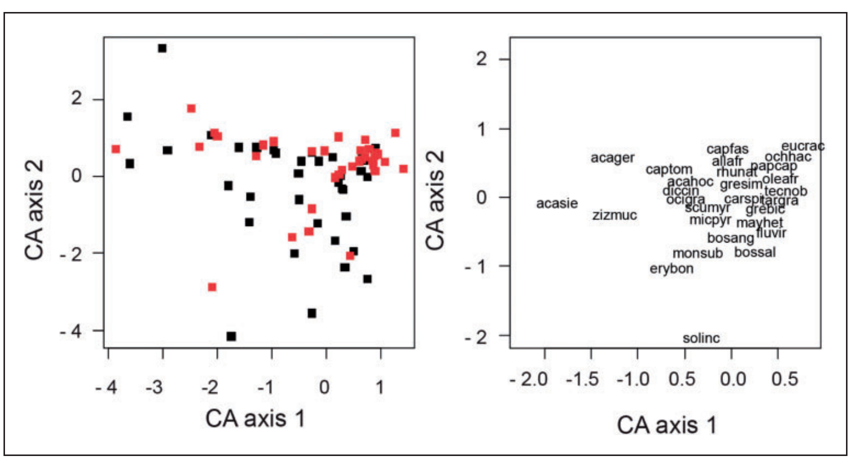

Figure 4. Correspondence analysis of the woody species composition for Lake Mburo savanna ecosystem (protected area vs. ranchlands). Red squares represent the protected area and black squares ranchlands. We abbreviated species names using the first three letters of the binomial genus name.

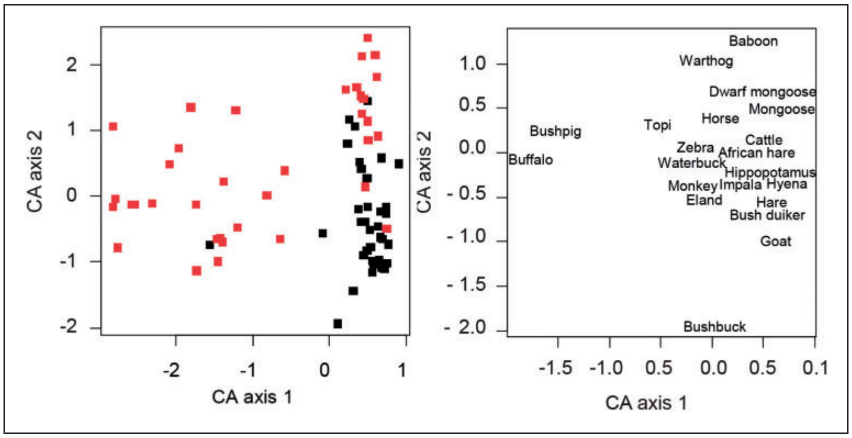

Figure 5. Correspondence analysis of the faunal species composition for Lake Mburo savanna ecosystem (protected area vs. ranchlands). Red shading represents the protected Lake Mburo National Park and black shading ranchlands.

separates buffalo and bush pig from the other species along the first axis. The buffalo has a restricted distribution and the bush pig is nocturnal. Along the second axis, baboon and warthog, which use open habitats, are separated from the solitary bushbuck and generalist herbivores that occur widely and use both the full extent of the protected area and ranchlands.

Results from the mixed-effect model (Table 1) show a statistically significant difference in the composition of herbs and mammals between the LMNP and adjacent ranchlands along Axis 1, whereas woody species composition is not significantly different. The ordination scores for Axis 2 show no statistically significant difference in herbaceous composition, whereas there are compositional differences for the woody vegetation and the mammals (Table 1). The Canonical Correspondence Analyses show that land-use type potentially can explain the variation in species composition for herbaceous vegetation (total inertia: 3.21, constrained: 0.15 with only land-use type as explanatory variable), woody vegetation (total inertia: 2.02, constrained: 0.06), and mammal species (total inertia: 1.11, constrained: 0.17). After accounting for land-use type, distance from the border did not improve the model for any of the groups (Table 1).

The regression analysis shows that the LMNP and ranchlands have similar species richness for herbaceous and woody vegetation but are different for mammal species richness (Table 1). In the model, differences in species richness are consistently nonsignificant for the herbaceous and woody vegetation, irrespective of whether the two variables were combined or separated in the analysis, whereas richness of the mammal species is significantly different (Table 1).

Association Between Vegetation and Fauna

There is a relationship between mammal composition and herbaceous composition ($t = 2.32$, $p = .024$) but no association between mammal composition and herbaceous richness ($t = -1.18$, $p = .24$). For woody vegetation, neither species composition ($t = -0.69$, $p = .50$) nor species richness ($t = -0.36$, $p = .72$) is correlated with mammal composition.

Discussion

Prior to the establishment of the protected area, livestock and wildlife grazed freely in the savanna, and thus we assume that the vegetation was similar across the whole of our study area. After defining the border in 1992, the government has attempted to prevent the protected area from being overgrazed by livestock through resource conservation programs and promoting community collaborations and awareness (UWA, 2015). The differences we find in species composition and richness across the border (but not with distance from the border after accounting for land-use type) suggest that the border is having an effect. However, this effect and its success may be dependent on the socioeconomic situation in the region, and people's attitudes such as their perception of species and aesthetics as well as their behavior, which is determined by their personal situation such as skills and wealth, psychological factors such as motivation, and value-based factors such as social norms (Winterbach, Winterbach, Somers, & Hayward, 2013). The eastern part of LMNP is mostly inhabited by pastoralists whose attitudes and behavior are important for the conservation of wild mammals. Traditionally and culturally, pastoralists in the region do not eat wild meat and therefore when animals cross onto their ranches or private land they are not poached. Before the creation of LMNP, pastoralists herded livestock in the game reserves alongside wild mammals, and so they are familiar with having wild animals on their private land. There are few predators of the livestock that

Figure 6. Some of the fauna and vegetation found in Lake Mburo National Park and neighboring ranchlands. Credit of pictures: Antonia Nyamukuru.

is the main livelihood of the pastoralists in LMNP, which helps promote a positive attitude of the people. The situation would be different for cultivators that are faced with crop-raiding animals.

The unfenced border of Naibunga Wildlife Conservancy, Kenya, was demarcated in 1999, and a study by Mureithi et al. (2016) found that the conservation areas had a different herbaceous species composition compared with the adjacent grazing areas. Herbaceous species that are resistant to grazing and disturbance, such as *C. dactylon*, *K. bulbosa*, and *E. tenuifolia* (Mureithi et al., 2016; Muthukumar, Udaiyan, & Shanmughavel, 2004; Sun & Liddle, 1993), had their optimum in the ranchlands, suggesting that the ranchlands are overgrazed and that grazing intensity drives the change in species composition. The fact that herbaceous species generally have a much shorter life cycle than woody species is probably the reason why herbaceous vegetation shows such a clear difference in species composition in the relatively short time since the protected area border demarcation.

An alternative explanation for differences in composition between LMNP and ranchlands could be the presence of termites since they are among the major drivers of vegetation change in the savanna (Moe, Mobæk, & Narmo, 2009; Okullo & Moe, 2012). Since the species composition on termite mounds is different from the adjacent areas without termite mounds (Okullo & Moe, 2012) and species associated with termite mounds such as *C. dactylon*, *P. maximum, J. eminii, J. exigua*, and *Commelina africana* are distributed across both land-use types (protected area and ranchlands), termites are not likely to be driving the vegetation changes seen in the study area. We also note that some species such as *S. africanus, C. dactylon*, and *K. bulbosa* are associated with the ranchlands rather than the

Table 1. Estimates of the Mixed-Effect Model With Random Factors for Vegetation and Mammal Composition and Species Richness for Lake Mburo Savanna Ecosystem in Uganda.

	t		*p*	
Fixed effect	Axis 1	Axis 2	Axis 1	Axis 2
Herbaceous composition				
Land-use type	2.57	−0.1	**.01**	.92
and Distance from the border	0.99	−1.77	.32	.08
Herbaceous richness				
Land-use type	1.19		.23	
and Distance from the border	−1.92		.06	
Woody composition				
Land-use type	0.76	1.99	.42	**.05**
and Distance from the border	0.66	0.6	.5	.55
Woody richness				
Land-use type	0.29		.77	
and Distance from the border	−0.62		.53	
Mammal composition				
Land-use type	−6.54	3.33	**<.01**	**<.01**
and Distance from the border	−1.6	<−0.01	.11	.99
Mammal richness				
Land-use type	−1.95		**.05**	
and Distance from the border	−1.21		.22	

Note. Land-use type (protected area vs. ranchlands) was tested as a sole explanatory variable and distance from the border refers to its marginal significance (after accounting for land-use type). Bold values indicate significant difference.

protected area (Figure 3) implying that land-use type influences species composition.

Woody vegetation has responded less obviously to the border establishment. Woody species in the savanna live for a long time and, in an ecosystem with heavy grazing, it is also likely that the grazers are keeping the system at a steady state with negligible changes in vegetation (Staver, Bond, Stock, Van Rensburg, & Waldram, 2009). Therefore, the composition of the woody species in our system is likely to be a legacy of the more or less uniform ecosystem that existed before the border was created. The woody species in both the protected area and ranchlands are likely to be equally affected by browsing by the free-ranging zebra and eland (Goheen, Young, Keesing, & Palmer, 2007; Sankaran, Augustine, & Ratnam, 2013). In addition, pastoralism seems to have less effect on woody species in the landscape. Paré, Tigabu, Savadogo, Odén, and Ouadba, (2010); Nacoulma et al. (2011); and Schmidt et al. (2016) found that pastoral land-use adjacent to protected areas may not necessarily lead to loss of diversity in woody species. However, the effect depends on the disturbance; for example, Kiruki, van der Zanden, Gikuma-Njuru, and Verburg (2017) found that agriculture, charcoal production, and land-use intensity are the main causes of vegetation change in Kitui dry woodlands in Kenya.

Our results suggest that the unfenced border is creating clear differences in species composition across the border, and although a more targeted comparison of fenced and unfenced areas is needed to evaluate the size of the effect, these results indicate that unfenced borders can be efficient in conserving biodiversity in protected areas. Assuming the whole area was more uniform 23 years ago and subject to similar levels of pressure from domesticated animals, their subsequent exclusion from the protected area is likely to have caused the differences we see today. The successfulness of the unfenced border can be attributed to the management practice and rangeland tenure rights in the region. Ranchers manage their ranchlands by improving the pastures and clearing bushes to create open space for grazing livestock (UWA, 2015), which makes ranchlands a better grazing area than the protected area. The rangeland tenure system in the Lake Mburo savanna ecosystem also limits the mobility of a pastoralist's livestock to rangeland resources within their own community (Kisamba-Mugerwa et al., 2006).

Wild mammals, however, roam freely in the Lake Mburo savanna ecosystem causing potential human–wildlife conflict outside the protected area. Such conflicts encompass competition for pasture, predation of livestock, injury to people, and crop damage by animals such as bush pigs, buffalo, and baboons, especially in agricultural lands (Kagoro-Rugunda, 2004; Tweheyo et al., 2012).

We noted a cross-border association between the composition of the herbaceous vegetation and mammals in our study area. The most likely explanation for this correlation is that the mammals affect the vegetation with the different composition and stocking levels being reflected by differences in the vegetation across the border. Although we did not test the direction of the association between the herbaceous vegetation and the mammals, herbivores are known to have an effect on the savanna vegetation (Holdo, 2007; Holdo, Holt, & Fryxell, 2013; Porensky, Bucher, Veblen, Treydte, & Young, 2013).

Given the challenges associated with fenced borders, such as interrupted gene flow, limited plant dispersal, restricted free-ranging of species outside of the protected area to forage resources, and the costs of erecting and maintaining a fence (Boone & Hobbs, 2004; Caughley, 1994; Lindsey et al., 2012; Saccheri et al., 1998), our results suggest that an unfenced border is a feasible and easy way to maintain and achieve ecological benefits.

Implications for Conservation

Although unfenced, the LMNP shows a difference in herbaceous and mammal species composition compared with neighboring ranchlands. This suggests that the unfenced border of the protected area can be effective in conserving vegetation and mammals in the park. Unfenced borders facilitate the free movement of species and dispersal agents for plants that are sensitive to barriers (Higgins, Lavorel, & Revilla, 2003). On the other hand, unfenced borders also have their negative aspects such as hunting of animals that cross the borders to graze and browse in the neighboring landscapes. However, the negative aspects of unfenced borders can be reduced by promoting community-based conservation. Future studies should consider other land-use types neighboring the protected area with different tenure rights so that we can form a clearer understanding of the effectiveness of unfenced borders for conservation. In addition, studies are needed that can directly compare unfenced borders of protected areas with fenced areas, including an evaluation of the costs of patrolling an unfenced border.

Acknowledgments

The authors thank Uganda Wildlife Authority for providing permission to Lake Mburo National Park. Fred Matovu, Patrick Bodo, Sebastian Walaita, Wilson Kyera, and Rose Kentaro helped during fieldwork. Protase Rwaburindore supported in plant identification. Uganda National Council for Science and Technology provided the research permit (NS 511). We are also grateful for helpful comments from Cathy R. Jenks and an anonymous reviewer.

Declaration of Conflicting Interests

The author(s) declared no potential conflicts of interest with respect to the research, authorship, and/or publication of this article.

Funding

The author(s) disclosed receipt of the following financial support for the research, authorship, and/or publication of this article: The authors received financial support from the Norwegian Programme for Capacity Building in Higher Education and Research for Development (NORHED) project (UGA-13/0019) under the NORAD programme.

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Supplemental material

Supplemental material is available for this article online.

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