



The importance of grass cover for mammalian diversity and habitat associations in a bush encroached savanna



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ARTICLE INFO

Keywords:

Bayesian hierarchical abundance model
Bush encroachment
Camera trapping
Mammals
Savanna systems
Swaziland

ABSTRACT

In grasslands across the world, woody species are replacing grass cover. This bush encroachment can alter available food, cover, and space resources for most mammalian species; however, the specific responses of mammals to bush encroachment in African savannas remain largely unknown. We examined the fine-scale response of mammals across a gradient of bush encroachment using camera traps and a Bayesian hierarchical multi-species abundance model that estimates local relative abundance and species richness while accounting for imperfect detection. Additionally, we simulated species-specific relative abundances and species richness responses to differing bush encroachment management actions. Contrary to our expectations, the relative abundance of only one species showed a negative relationship to shrub cover and another to tree cover. However, the relative abundance of eight out of twenty-one species showed a positive association with grass cover. Mammal species richness increased with grass cover, decreased with shrub cover, and showed no clear pattern with increasing tree cover. Furthermore, our simulations suggest reducing and increasing shrub and grass cover respectively by 50% would increase species richness and local abundances for the mammal community of the area. Our results indicate grass cover exerts a strong influence on habitat use, relative abundances and species richness in bush encroached areas. Our study shows that mammal's positive response to grass cover is more important than potential negative impacts of increasing shrub cover. Consequently, recovering and maintaining adequate grass cover in savannas subject to bush encroachment is an indispensable condition to maximize mammalian diversity and abundances.

1. Introduction

Globally grasslands are transitioning to become dominated by woody plant species, a phenomenon often termed bush encroachment (Eldridge et al., 2011). Climate and atmospheric changes, such as altered rainfall patterns and increased atmospheric CO₂, along with changes to fire regimes and herbivory have resulted in the replacement of grass cover by woody species in grasslands across the world (Milton and Dean, 1995; Roques et al., 2001; Wigley et al., 2010). Bush encroachment has been particularly widespread in tropical savannas of southern Africa (Roques et al., 2001; Blaum et al., 2007a; Sirami and Monadjem, 2012). Some low-lying savannas of southern Africa have seen shrub cover increase 20% and grass cover decrease up to 30% over the last two decades (Sirami and Monadjem, 2012).

Bush encroachment in grasslands can impact rangeland productivity, biodiversity, community structure, and ecosystem function (Archer et al., 2001; Van Auken, 2009). The increase of bush cover may

reduce animal species diversity and carrying capacity of grasslands through the loss of forage quantity and quality (Milton and Dean, 1995; Blaum et al., 2007a; Van Auken, 2009). Increased bush cover in savannas has been linked to community shifts for several taxonomic groups such as lizards (Meik et al., 2002), birds (Sirami and Monadjem, 2012), rodents (Blaum et al., 2007b), carnivores (Blaum et al., 2007a), and ungulates (Smit and Prins, 2015). However, the consequences of bush encroachment for animal diversity and ecosystem function are still not well understood, and may be context dependent (Eldridge et al., 2011; Eldridge and Soliveres, 2014).

Mammals may be especially susceptible to bush encroachment due to their reliance on grassland resources and vegetation structure. Most large mammals in Africa are found within managed protected areas or reserves (Caro and Scholte, 2007), including reserves in Swaziland (Monadjem, 1998; Roques et al., 2001), where bush encroachment has occurred (Bailey et al., 2016). Because mammals play an essential role in maintaining the structure and composition of vegetation in savannas

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(Dalerum et al., 2008; Goheen et al., 2010; Holdo et al., 2013), there is an urgent need for a better understanding of how mammal communities are responding to bush encroachment in African protected areas.

The changes in vegetation structure and composition from bush encroachment can influence how mammals use the landscape in several ways (Van Auken, 2009). The increase of native woody species likely provides food for browsers and cover for ambush predators and prey species. However, bush cover tends to increase outward and horizontally (Bai et al., 2009) and can create impenetrable woody thickets. Thus, bush encroachment can restrict foragers to the edge of a patch and may reduce the available space for species seeking cover. Marked increases in bush cover may also negatively affect surrounding vegetation as they concentrate soil moisture and nutrients around them (Pressland, 1973; Schlesinger and Pilmanis, 1998). Specifically, woody species can suppress herbaceous species, leading to decreases in grass and herbaceous plants that many savanna mammals depend on (Teague et al., 2008; Smit and Prins, 2015). Consequently, bush encroachment has the potential to alter the distribution of mammals across the landscape (Van Auken, 2009).

Our objective was to examine the influence of localized bush encroachment on mammalian habitat use in two protected areas of southern Africa experiencing bush encroachment. We used a multi-species Bayesian hierarchical abundance model that accounts for imperfect detection (e.g. Yamaura et al., 2011; Beesley et al., 2014) to model presence/absence data obtained from camera trapping surveys across a gradient of bush encroachment. These models acknowledge heterogeneous detectability across species by modeling the observation (i.e., probability of detection) and the biological (i.e., abundance and/or occupancy) processes as separate components of the same system ((Royle and Dorazio, 2008). Methods typically used to examine habitat associations such as sign surveys (e.g., Atickem and Loe, 2013; Mamo et al., 2015; Mugume et al., 2015) ignore the potential bias in detectability. This can lead to biased estimates (MacKenzie et al., 2006) and/or to confounding the parameter of interest (occupancy or abundance) with detection (Guillera-Arroita et al., 2014).

We modeled local abundance, species richness estimates, and detection probabilities as a function of habitat and temporal covariates to better understand the influence of vegetation cover associated to bush encroachment (i.e., shrub cover) on mammals use of bush encroached savannas. We predicted that mammals would show reduced use of bush encroached sites (i.e., plots with more shrub than grass cover) due to the loss of food and reduced accessibility to resources. Specifically, we expected the number of species and species-specific abundances would be negatively associated with shrub cover on localized plots. Finally, we modeled predicted average species richness and species-specific relative abundances under different regimes of shrub cover management, where we expected to see an increase in species-specific relative abundances and species richness under regimes with more intense shrub thinning.

2. Methods

2.1. Study area

We conducted this study in Mlawula Nature Reserve and Mbuluzi Game Reserve, which cover 17,400 and 2400 ha, respectively, and are found in the low-lying savanna of northeastern Swaziland (Fig. 1). The vegetation communities are characterized as basalt sweet arid lowveld (Mucina and Rutherford, 2006) with patches of riparian forest (Sweet and Khumalo, 1994). The dominant large trees are *Acacia nigrescens* and *Sclerocarya birrea* and the grasses are *Themeda triandra* and *Panicum maximum* (Gertenbach and Potgieter, 1975; Roques et al., 2001). The dominant shrub species that have encroached our sites are both native, *Dichrostachys cinerea* and *Ziziphus mucronata* (Roques et al., 2001). During the past three decades, researchers have documented an increase in shrub cover, along with decreases in grass cover in the area (Roques et al., 2001; Sirami and Monadjem, 2012; Bailey et al., 2016).

Both reserves have used fire and clearing to manage bush encroachment but at the time of our study, Mbuluzi's management efforts were more concerted.

The protected areas are part of the > 60,000 ha. Lubombo conservancy. The region outside of the conservancy is surrounded by a matrix of sugar cane fields, commercial cattle ranches, and populated homesteads (Bailey et al., 2016). Although the reserves are fenced, there is some connectivity between them for most mammals. Only a few large predators may be found at low densities in these reserves, particularly some spotted hyena (*Crocuta crocuta*) and an occasional leopard (*Panthera pardus*). Thus, wildlife immigration and emigration and most potential top-down effects on mammalian species in these sites were limited. Roads and traffic were also limited within these reserves and their impact on mammal habitat use was most likely minimal.

2.2. Data collection

We established nine research grids along a gradient of grass, shrub (woody vegetation < 2 m in height), and tree cover (woody vegetation > 2 m in height) across our study site. We captured a gradient of shrub cover occurring across both reserves. Each grid was sub-divided into nine sampling plots of 50 m² with 250 m between plots. This resulted in 81 plots. We conducted camera trap surveys and vegetation sampling at each plot during the rainy (December to February) and dry (June to August) seasons for two years (2012 and 2013).

We used two camera traps ([Primos Truth Cam 35], Primos Hunting, St. Flora, Mississippi) per plot during all surveys except for one survey period (summer 2012), in which we only deployed one camera trap per survey due to logistical constraints. We did not sample all grids each year, but we sampled each grid at least once during the study period. We divided the plots in half and placed the cameras on opposite sides of the plot in areas selected to capture the most mammal activity (i.e. game trails) facing roads or animal paths. We tied the motion detection cameras to a tree 40–60 cm above ground with a clear view of at least 10 m in front of the camera. We cleared the area in the line of sight of the camera of any obstructing features or vegetation. During each sampling period, we deployed both camera traps for a period of 5 days and nights in their selected spots at each plot, resulting in five, 24-hour sampling occasions per survey period for each camera. There are usually trade-offs when designing occupancy based studies (Bailey et al., 2007), mostly due to logistics and economic considerations. In our case, we made the decision to sample across a wider range of plot types with fewer sampling occasions because our main interest was in examining plot use patterns across an environmental gradient.

We sampled the structure and cover of vegetation once a year at 13 points within each of the plots, averaging values to obtain one measure of each variable per plot. The center of the vegetation surveys coincided with the center of the camera-trapping plot and extended outwards from this point. We measured percent grass, and shrub cover by placing a 1-m² circular plot at each point, and used Daubenmire (1959) cover classes. We measured tree cover using the line intercept method (Canfield, 1941) and measured visual obstruction (*v_o*), a metric representing vegetation height and vertical density, using a Robel pole (Vermeire et al., 2002).

Additionally, we measured distance from the center of each plot to surface water using a vector layer of water obtained from the South African Department of Water Affairs and Forestry based on 2003 Land Sat images in ARCGIS 10.2® (ESRI, 2013). We joined the vector layer with the center of each plot with the surface water layer. Some of these water sources were ephemeral and may only influence mammal use of plots during the dry season when surface water is scarce. To account for this potential seasonal effect of water availability, we included an interaction term between season and distance to water as a covariate in the abundance model. We included temporal covariates to account for potential inter-annual or seasonal variation. For example, ungulates have been shown to track seasonal shifts in resource abundance and

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