



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

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## 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 CO<sub>2</sub>, 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 m<sup>2</sup> 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-m<sup>2</sup> 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 (vo), 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

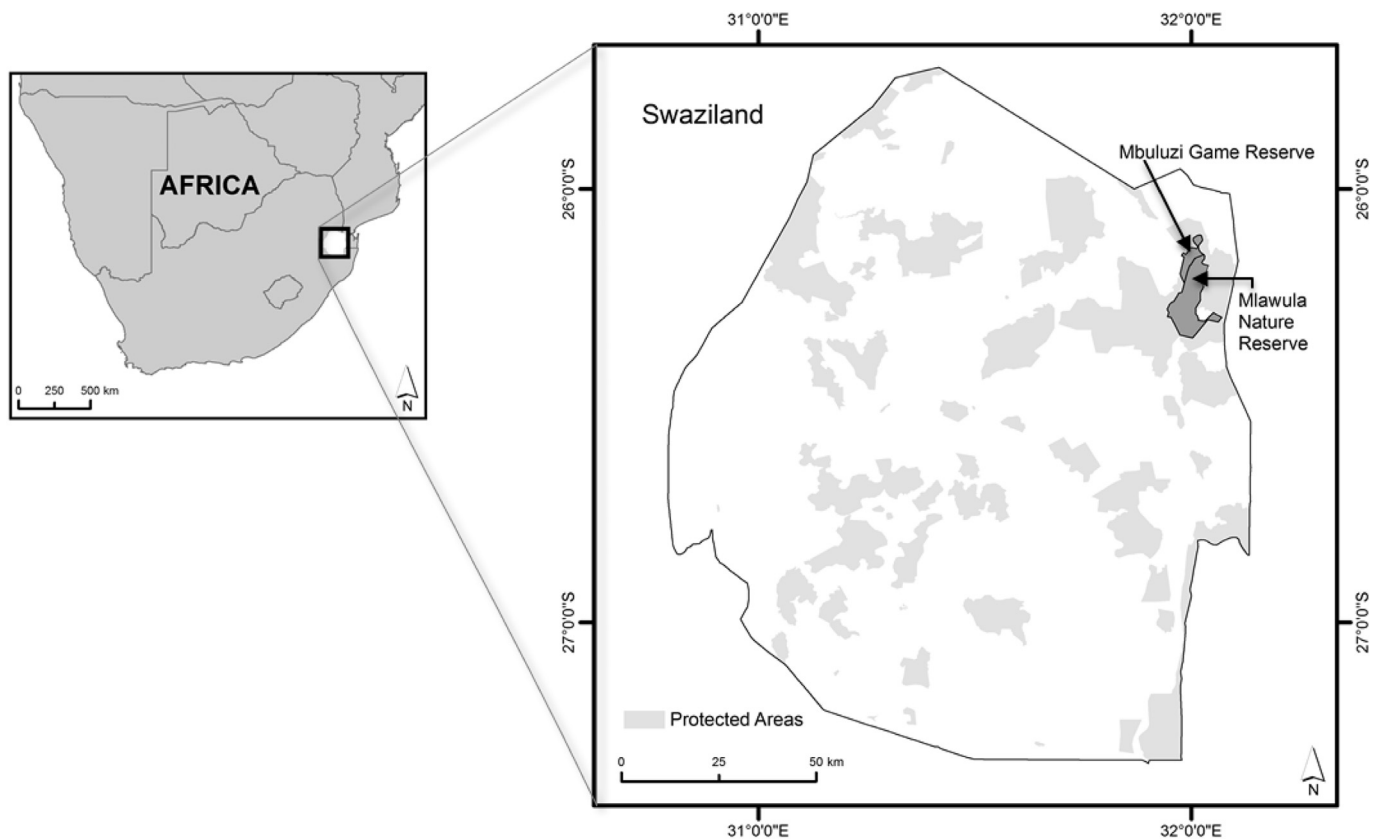


Fig. 1. Map of study area location. Insert map shows location of Swaziland within the continent of Africa (black square), while main map shows location of nature and game reserves surveyed in Swaziland, 2012–2013.

quality in African savannas (McNaughton and Georgadis, 1986; Owen-Smith, 2002; Kleynhans et al., 2011). We standardized all continuous covariates measured to mean zero and a standard deviation of 1.

### 2.3. Multi-species Bayesian hierarchical model

We constructed a Bayesian hierarchical model that estimates multi-species abundances while accounting for incomplete and variable detection probability of each species (e.g. Beesley et al., 2014). To model species-specific local abundances and species richness, we first created a matrix of 0's and 1's (0 = absent, 1 = observed), where the columns represented the species detected and the rows the plots surveyed.

Our model was constructed in a multi-species framework that specifies species-specific parameters as random effects drawn from hyperdistributions governed by hyperparameters. This formalizes the assumption that patterns in species abundances are neither equivalent nor independent but related according to distributional assumptions (i.e. random effects). This aspect of the model structure allows information to be shared among species, potentially increasing statistical power and allowing for species-specific metrics (i.e. abundance) and community-level metrics (i.e. species richness) to be estimated simultaneously. Under this framework, our estimate of abundance is considered a measure of relative abundance per species at each plot (Yamaura et al., 2011; Beesley et al., 2014). In the case of camera trapping studies, Tobler et al. (2015) defined the measure of abundance obtained from this model as the number of individuals using the area around the station, and as an indicator of site preference by one or more individuals.

Our model assumes that species-specific abundance is a latent random variable that conforms to a Poisson distribution as  $N_{i,j} \sim \text{Poisson}(\lambda_{i,j})$ , where  $\lambda_{i,j}$  is the Poisson mean for species  $i$  at plot  $j$ . Our incidence data are modeled as binomial outcomes  $y_{i,j} \sim \text{Binomial}(k, p_{i,j})$ , where  $k$  is

the number of replicate samples (i.e. days of sampling at a plot) and  $p_{i,j}$  is the probability of detecting one or more individuals of species  $i$  at plot  $j$ . We linked our abundance model to the detection model by assuming a relationship between  $p_{i,j}$  and  $N_{i,j}$  per Royle and Nichols (2003) as,  $p_{ij} = 1 - (1 - r_{ij})^{N_{ij}}$ , where  $r_{ij}$  is the detection probability on the individual scale (i.e. the average probability of any individual being detected). This equation describes the probability of detecting at least one individual as a saturating function of abundance, where  $p_{i,j} = 0$  when  $N_{i,j} = 0$  and  $p_{i,j}$  approaches an asymptote of one as  $N_{i,j}$  increases.

We accounted for the effects of temporal (i.e., *season*, *year*) and environmental factors (i.e., distance to water (*dwt*), *shrub*, *grass*, and *tree* cover) on species-specific abundances by incorporating these variables as covariates into the abundance model with a log link as:

$$\log(\lambda_{i,j}) = \beta 1_i + \beta 2_i \text{shrub}_j + \beta 3_i \text{tree}_j + \beta 4_i \text{grass}_j + \beta 5_i \text{season}_j + \beta 6_i \text{year}_j + \beta 7_i \text{dwt}_j + \beta 8_i \text{dwt} \times \text{season}_j$$

where  $\beta 1_i$  is the species-specific intercept and  $\beta 2_i$ – $\beta 8_i$ , are the species-specific regression coefficients for each covariate.

We modeled detection probability ( $r_{i,j}$ ) as a function of temporal (i.e., *season*, *year*) and environmental covariates (i.e., visual obstruction (*vo*), *shrub*, *grass*, and *tree* cover). We added a *camera* covariate to the detection probability model that indicated whether one or two cameras were deployed per sampling plot. Thus, covariates of detection probability ( $r_{i,j}$ ) were incorporated into the detection model with a logit link as:

$$\text{logit}(r_{i,j}) = \phi 1_i + \phi 2_i \text{shrub}_j + \phi 3_i \text{tree}_j + \phi 4_i \text{grass}_j + \phi 5_i \text{vo}_j + \phi 6_i \text{camera}_j + \phi 7_i \text{season}_j + \phi 8_i \text{year}_j$$

where  $\phi 1_i$  represents the species-specific intercept and  $\phi 2_i$ – $\phi 8_i$  are the regression coefficients for each covariate.

We estimated species richness per plot ( $n_j$ ) as the sum of species

**Table 1**

Local relative abundance ( $\lambda$ ) and detection probability ( $p$ ) estimates and the direction of the effect of statistically significant covariates (for parameter values and 95% credible intervals refer to Appendix S2). Measures are for terrestrial mammals detected in camera-trapping surveys conducted in Mlawula Nature and Mbuluzi Game Reserves, Swaziland, 2012–2013. Statistical significance is based on 95% credible interval non-overlap with zero. Model fit was evaluated with the Bayesian p-value (BP) for the species model, where values between 0.05 and 0.95 indicate adequate fit and values of 0.5 indicate perfect model fit.

Species	Common name	$\lambda$ (SD)	$p$ (SD)	Covariate effects on $\lambda$	Covariate effects on $p$	BP
<i>Equus quagga</i>	Zebra	0.31 (0.23)	0.05 (0.03)	Grass (+), dwater (+)	vo (–)	0.49
<i>Connochaetes taurinus</i>	Common Wildebeest	0.23 (0.10)	0.10 (0.05)	Tree (–), grass (+), season (+)	vo (–)	0.46
<i>Kobus ellipsiprymnus</i>	Waterbuck	0.10 (0.12)	0.04 (0.04)	Shrub (–)		0.45
<i>Phacochoerus africanus</i>	Warthog	0.53 (0.16)	0.14 (0.05)	Season (+)	vo (–)	0.23
<i>Tragelaphus angasi</i>	Nyala	0.67 (0.17)	0.12 (0.04)	Grass (+), season (+)	vo (–), season (–), year (+)	0.27
<i>Aepyceros melampus</i>	Impala	0.75 (0.18)	0.08 (0.04)	Season (+), year (–)	vo (–), camera (+)	0.42
<i>Giraffa camelopardalis</i>	Giraffe	0.12 (0.12)	0.05 (0.04)	Grass (+)	Season (–)	0.56
<i>Tragelaphus strepsiceros</i>	Greater Kudu	0.72 (0.30)	0.09 (0.04)	Grass (+)	vo (–), season (–)	0.26
<i>Tragelaphus scriptus</i>	Bushbuck	0.83 (0.26)	0.07 (0.03)	Season (+)	Camera (+), season (–), year (+)	0.40
<i>Sylvicapra grimmia</i>	Common Duiker	0.92 (0.36)	0.06 (0.03)	Year (–)	Season (–)	0.59
<i>Potamochoerus larvatus</i>	Bushpig	0.22 (0.15)	0.05 (0.03)			0.36
<i>Crocuta crocuta</i>	Spotted Hyena	0.04 (0.09)	0.04 (0.04)			0.71
<i>Canis adustus</i>	Side-striped jackal	0.07 (0.10)	0.07 (0.05)	Grass (+)	vo (–)	0.46
<i>Leptailurus serval</i>	Serval	0.08 (0.11)	0.05 (0.04)			0.63
<i>Genetta maculata</i>	Rusty-spotted genet	0.68 (0.28)	0.08 (0.04)	Season (+), year (–)	vo (–), season (–)	0.45
<i>Atilax paludinosus</i>	Water Mongoose	0.04 (0.09)	0.04 (0.04)			0.58
<i>Galerella sanguinea</i>	Slender Mongoose	0.07 (0.10)	0.04 (0.04)	Grass (+)		0.53
<i>Papio ursinus</i>	Baboon	0.28 (0.13)	0.09 (0.04)	Shrub (+), grass (+)	vo (–)	0.45
<i>Chlorocebus pygerythrus</i>	Vervet Monkey	0.07 (0.09)	0.05 (0.04)			0.37
<i>Orycteropus afer</i>	Aardvark	0.09 (0.07)	0.07 (0.04)	Season (+)	vo (–)	0.57
<i>Hystrix africaeaustralis</i>	Porcupine	0.04 (0.08)	0.06 (0.04)			0.47

Parameters: shrub = mean shrub cover percentage per plot, tree = mean tree cover percentage per plot, grass = mean grass cover percentage per plot, vo = mean measure of visual obstruction per plot using robel pole, dwater = distance of center of plot to water source, camera = number of cameras (1 or 2) deployed per plot, season = season survey occurred (wet or dry season), year = year survey occurred (2012 or 2013).

with abundance greater than zero in each plot (i.e.,  $n_j = \sum_i (N_{i,j} > 0)$ ). To evaluate the relationship between species richness and grass, tree, and shrub cover, we calculated the slope between the log of  $n_i$  and the metrics of plant cover for each posterior sample of  $n_i$ , resulting in the derived posterior sample of each slope. To determine the statistical significance of species-level covariate effects on abundance and detection probabilities and trends in species-richness, we evaluated whether the credible interval of the posterior estimates overlapped zero and the position of the distribution with regards to zero to assess direction of the association. Model specifications and sample code can be found in Appendix S1 in Supporting information.

#### 2.4. Model fit evaluation

We evaluated model fit of the full model including all covariates with a Bayesian p-value (Bp, Kery, 2010). The Bayesian p-value is a posterior-predictive check that provides a measure of under- or over-dispersion of the data relative to the model (Kery, 2010). We performed this procedure by simulating the detection data (i.e. number of detections across five replicate days at each site during each year) for each Markov Chain Monte Carlo iteration. We then calculated the discrepancy between the simulated and expected values and observed and expected values with a Pearson residual as,  $[(o - e) / \sigma^2]$ , where  $o$  is either the observed or simulated number of detections,  $e$  is the expected value (i.e.  $e = kp_{i,j}$ ), and  $\sigma^2$  is the variance of  $e$  (i.e.  $\sigma^2 = kp_{i,j}(1 - p_{i,j})$ ). The simulated data are considered “perfect” because they are generated directly from the model and, thus, the resultant Pearson residual represents the fit of the model when all model assumptions are perfectly met (Kery, 2010). We then created a fit metric that is equal to one when the Pearson residual was greater for the observed data than the simulated data and is equal to zero, otherwise. The Bp was then calculated as the mean of the posterior sample of the fit metric for each species, where values between 0.05 and 0.95 indicate adequate fit and a mean of 0.5 indicates perfect model fit.

#### 2.5. Bush encroachment management simulations

We used our regression model to predict average plot-level relative abundances and species richness estimates under bush encroachment management regimes with different levels of shrub and grass cover manipulation. We proposed management regimes based on historic increases of shrub cover (Sirami and Monadjem, 2012) and discussions with local managers that identified habitat interventions and classified them according to ideal outcomes, effort required and relative ease of implementation. We defined the management regimes as follows:

1) Regime 1: simulated no management action taken where average shrub cover is doubled, increasing from 32 to 64% across plots. This is a highly realist, if not conservative, estimate of shrub cover increase, as Sirami and Monadjem (2012) estimated shrub cover increased from 24% to 44% in the surrounding areas over a 10-year period. Based on our current data we estimated grass cover would decrease to 13%, and we held tree cover constant. We considered this a minimal effort management regime;

2) Regime 2: simulated an active management plan where average plant cover per plot was maintained at current levels (i.e., further growth of shrub cover was halted but not reduced), such that shrub cover = 32%, tree cover = 37%, and grass cover = 26%. Local managers consider this a realistic and feasible management regime;

And

3) Regime 3: simulated an aggressive management plan where shrub cover was reduced by half to pre-1998 levels of < 18.5% (Sirami and Monadjem, 2012). We simulated a corresponding doubling of grass cover to 53% based on our current data and again we kept tree cover constant. This was an ideal but logistically difficult regime to implement.

### 3. Results

#### 3.1. Species-specific plot-level abundance

Our plots varied substantially in shrub (range = 2.33–86.25), tree (range = 0–94.17), and grass (range = 2.00–60.04) cover percentages



with little correlation among values (all  $r^2 < 0.11$ ), suggesting adequate variation and contrast in the data. During our 1980 camera-trap nights, we recorded 21 mammal species on the sampling plots over the 2-year period (Table 1). The group with the highest number of species detected was ungulates ( $n = 12$ ), followed by carnivores ( $n = 6$ ), primates ( $n = 2$ ), rodents ( $n = 1$ ), and Tubulidentata ( $n = 1$ ). Several species had  $< 10$  detections over all surveys: serval (*Leptailurus serval*), spotted hyena (*Crocuta crocuta*), side-striped jackal (*Canis adustus*), vervet monkey (*Chlorocebus pygerythrus*), and porcupine (*Hystrix africaeustralis*). The multi-species model parameters converged satisfactorily (all GR statistics  $< 1.1$ ; maximum GR = 1.09; Appendix S2) and the Bayesian p-values indicated adequate fit for all species (range = 0.23–0.71; Table 1).

Plot-level relative abundances varied among species, through time and with habitat related covariates. Relative abundance estimates ranged from 0.04 to 0.92 (Table 1). Browsers and/or mixed feeders such as duikers (*Sylvicapra grimmia*), impalas (*Aepyceros melampus*), bushbucks (*Tragelaphus scriptus*), nyalas (*Tragelaphus angasi*), and kudus (*Tragelaphus strepsiceros*) showed the highest average relative abundance values. These species had abundance values two to six times greater than grazers such as wildebeest (*Connochaetes taurinus*), zebras (*Equus quagga*), and waterbucks (*Kobus ellipsiprymnus*). Overall, we obtained low abundance estimates for carnivores ( $\lambda < 0.10$ ), except for the rusty-spotted genet (*Genetta maculata*), whose abundance was six times higher than any other carnivore detected.

Species that showed statistically significant associations to covariates were mostly influenced by grass cover percentage and/or temporal covariates. Nine species responded to habitat covariates (Table 1; Fig. 2). Eight of these responded positively to increases in grass cover, including two browsers (giraffe and kudu) and one mixed-feeder (nyala) (Table 1; Fig. 2). Waterbuck and the Chacma baboon (*Papio ursinus*) responded negatively and positively respectively to shrub cover (Table 1; Fig. 2). While wildebeest plot-level abundance decreased with

tree cover, but increased with grass cover (Table 1; Fig. 2). Abundance of six species increased during the rainy season while values for three species were higher during the second year of sampling (Table 1). Abundance of only one species (i.e., zebra) was positively associated with distance to water sources.

### 3.2. Species-specific detection probability

We found that detection probability varied among species, through time, and with sampling related covariates. The average detection probability of each species ranged between 0.04 and 0.14 (Table 1). This represents a three-fold increase in detection between low-detection species such as water mongoose (*Atilax paludinosus*), spotted hyena, and porcupine ( $p \sim 0.04$ ) and higher-detection species such as warthog (*Phacochoerus africanus*) and nyala ( $p \geq 0.12$ ). Interestingly, there was no obvious pattern between average body mass and average detection probability of the species, as large species such as giraffe (*Giraffa camelopardalis*) and zebra had average detection probabilities (i.e.  $p \sim 0.05$ ) similar to small species such as slender mongoose (*Galerella sanguinea*), and water mongoose (i.e.  $p \sim 0.04$ ). Sampling with two cameras relative to one only significantly increased detection probability for two species (Table 1). The survey covariate describing the magnitude of visual obstruction was statistically significant for 10 species. Our model predicted that increasing visual obstruction from the lowest observed value (i.e. 0) to the highest observed value (i.e. 80) would decrease the detection probability from  $\geq 0.10$  to  $\leq 0.05$  for seven of the 10 statistically significant species with some species detection probabilities declining to near zero (e.g. nyala, zebra, wildebeest, kudu, and baboon; Fig. 3). Our results indicated that detection probability tended to be higher during the rainy season with six species demonstrating a statistically significant increase in detection during this season relative to the dry season (Table 1; Fig. 4). Furthermore, three species demonstrated an increase in detection in the second year

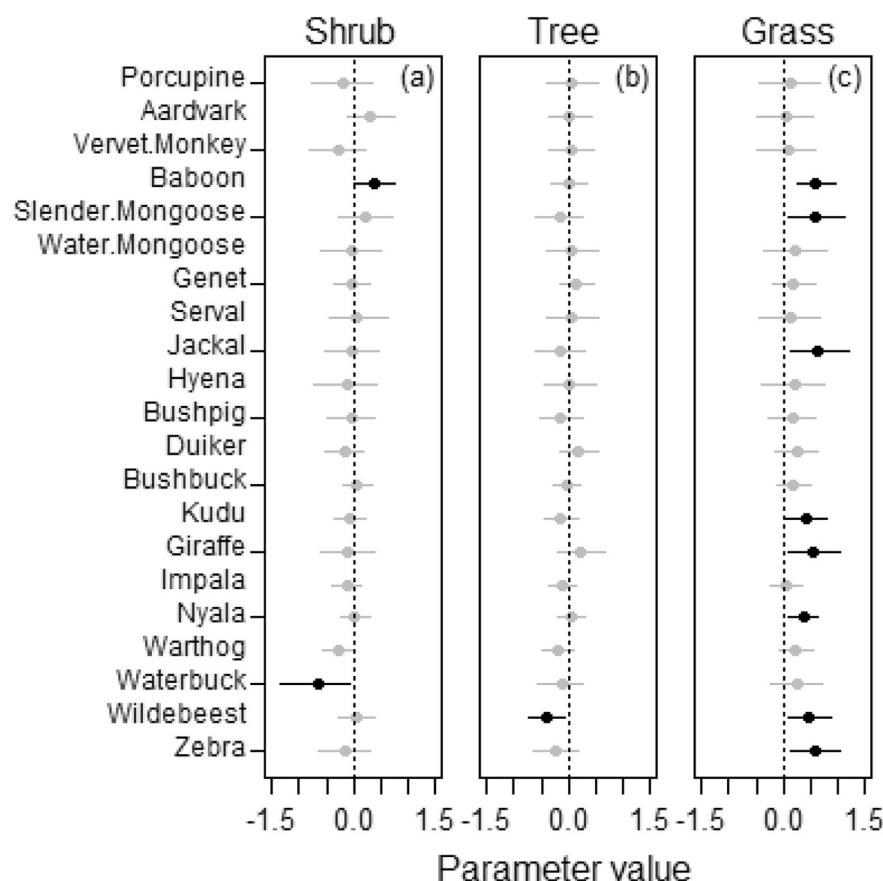


Fig. 2. Posterior summaries of the effects of shrub (a), tree (b), and grass (c) cover percentages on local relative abundances of terrestrial mammals detected in camera trap surveys in Mlawula Nature and Mbuluzi Game Reserves, Swaziland (2012–2013). Dotted vertical line represents the mean of the posterior distributions while the lines along x-axis represent 95% Bayesian credible intervals. The grey dots and lines indicate parameters that are not statistically different than zero (95% credible intervals include zero). Black dots and lines indicate statistical significance. The x-axis is the parameter value; units on the x-axis are interpreted as one unit of abundance on the log scale for every one standard deviation of the covariate.

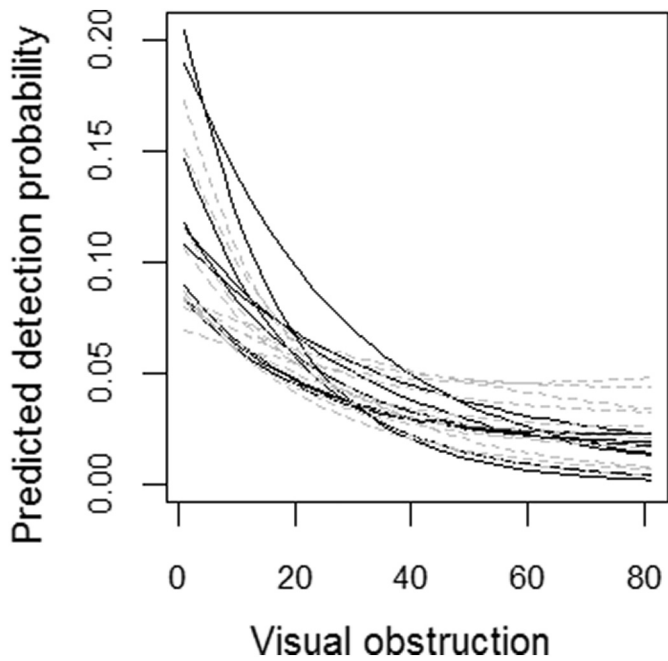


Fig. 3. Species-specific predicted detection probabilities across levels of visual obstruction. The black continuous lines are predictions for species with statistically significant relationships and the dashed grey lines are predictions for species with non-statistically significant relationships. For species-specific details of effects of visual obstruction on detection probabilities refer to Table 1.

of sampling (Table 1; Fig. 4).

3.3. Plot-level species richness

Plot-level species richness, or the number of species using a plot, varied according to vegetation cover. Species richness increased with increasing percentage grass cover (Fig. 5). Conversely, species richness per plot decreased with increasing shrub and tree cover, although this association was stronger for shrub cover (Fig. 5).

3.4. Bush encroachment management simulations

Predicted species richness and species-specific relative abundance estimates of regime 3 showed marked differences for several species between the regimes that did not involve increasing grass cover. Average relative abundances of more species were generally higher when grass cover was increased as opposed to other regimes evaluated (Fig. 6). Species such as zebras, wildebeests, nyalas, and duikers increased two-fold in the third regime when compared to regimes where shrub and tree cover were either kept at current levels or where not managed for. Similarly, average species richness per plot almost doubled when comparing regime 3 to regimes 1 and 2 (Fig. 7). The latter two regimes resulted in very similar values of predicted species richness.

4. Discussion

Our results partially support our hypothesis that bush encroached plots are used less and by a fewer number of species. Contrary to our expectations, we did not find a negative influence of shrub cover on species-specific use of plots, but grass cover positively influenced both number of species using a plot and was an important covariate

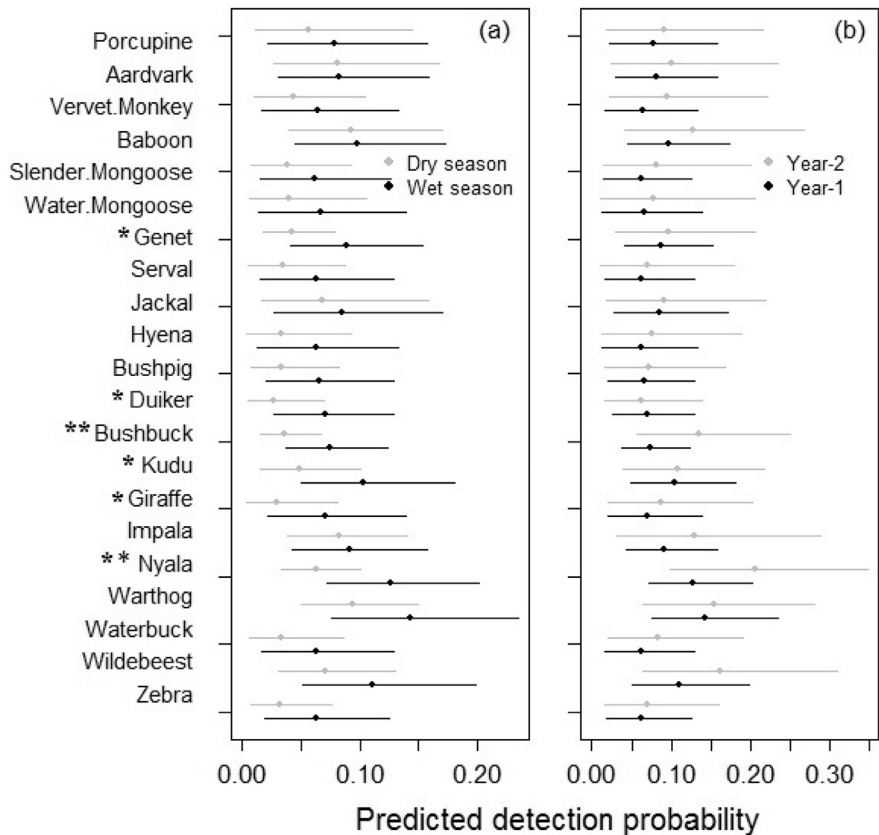


Fig. 4. Variation in species-specific predicted detection probabilities across seasons (a) and survey years (b). \* denotes species with a statistically significant relationship for season, while \*\* denotes a statistically significant relationship with both season and year.

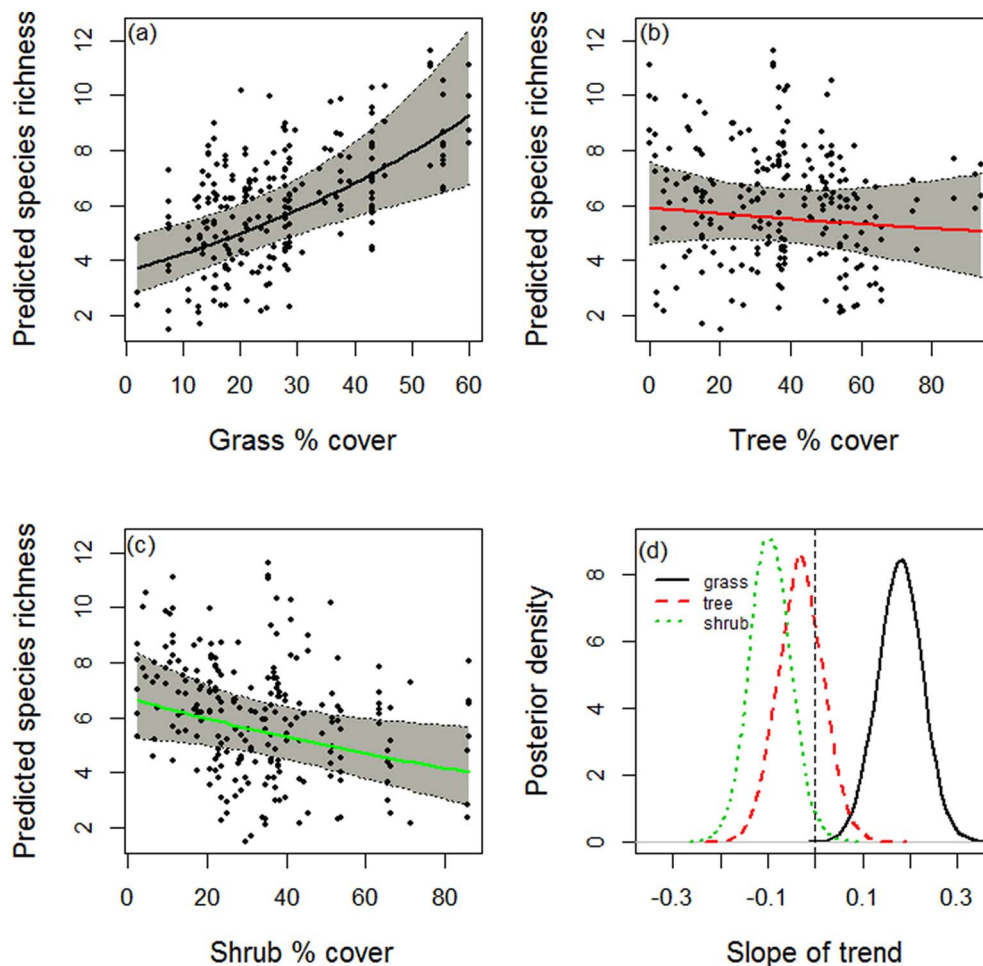


Fig. 5. Plot-specific species richness versus vegetation cover measures (mean value of vegetation type cover percentage in each plot). Estimates are for Mlawula Nature and Mbuluzi Game Reserves, Swaziland (2012–2013) obtained from Bayesian hierarchical multi-species abundance model.

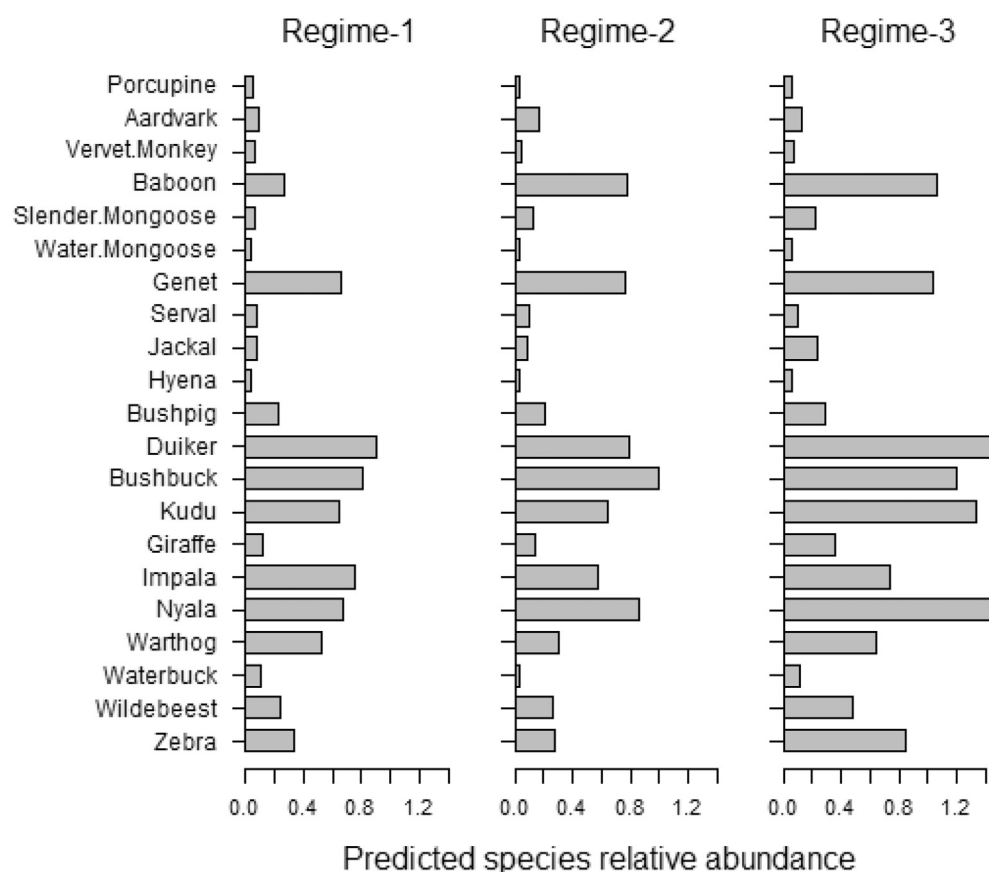
describing local abundances for almost half the species detected. Thus, our study provides further evidence for the importance of grass cover for mammals within bush encroached savannas. These findings were consistent with other research suggesting grassy patches are an important driver of mammalian species abundance (Gandiwa, 2013) and play an important role in driving savanna species diversity (Cerling et al., 1997; Bouchenak-Khelladi et al., 2009). Increased shrub cover may not directly influence mammal communities (Eldridge and Soliveres, 2014), but it may indirectly alter mammalian communities through the loss of grassy open areas. Our data suggests that within bush encroached savannas, localized patches of shrub cover do not reduce the occurrence of mammals. However, open grassy areas within these encroached savannas did increase occurrence of mammals, likely providing important resources for grazers, mixed feeders and species associated with open environments such as porcupines, armadillos (*Oryzomys ather*), and servals.

Relative abundance of almost half the ungulate species increased with grass cover. These were mostly mid-sized grazers with low habitat and dietary breadths (Barthelemy et al., 2008; O'Kane et al., 2014), making them highly dependent on localized patches of grass (Schwarz et al., 2017). Without these patches of grass, encroached savannas may experience a reduced capacity to accommodate grazers because of loss of forage quantity and quality (Milton and Dean, 1995; Blaum et al., 2007a). Ungulates with higher niche breadths may benefit from a diversity of vegetation provided by encroached and non-encroached patches that offer resources for browsers and mixed feeders, especially during drier periods when resources become scarce (Owen-Smith, 2002; Hobbs and Gordon, 2010; Schwarz et al., 2017). Furthermore,

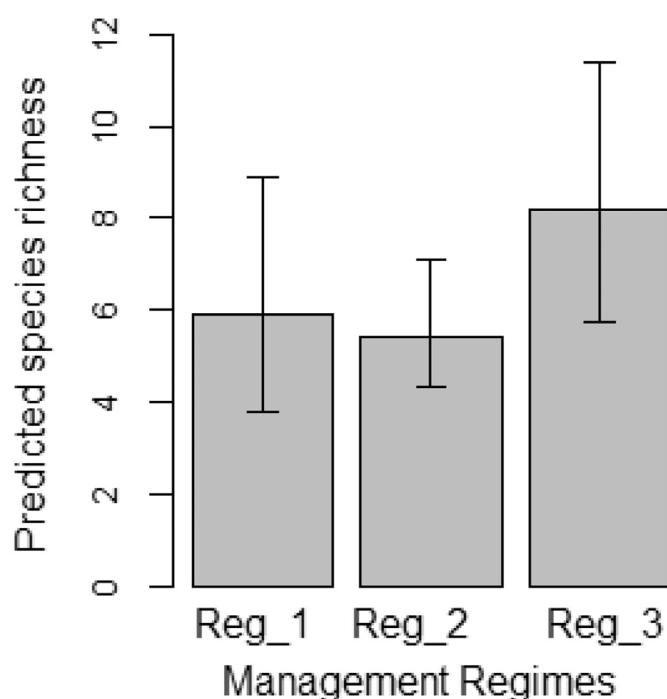
grassy areas may provide better access to woodland resources difficult to access due to bush encroachment, especially for browsers and mixed-feeders (Milton and Dean, 1995; Stafford et al., 2017). Such might be the case for browsers such as the kudu and giraffe that responded positively to grass cover. This was further supported by our simulations which showed that reducing shrub cover and increasing grass cover will also result in increased abundances of browsers and mixed-feeders.

Two ungulate species that responded negatively to shrub and tree cover (waterbuck and wildebeest respectively) also showed selectivity for grass cover. Wildebeest are dependent on high quality herbaceous plants and avoid thickets in response to ambush predators (Yoganand and Owen-Smith, 2014; Martin et al., 2015; Martin and Owen-Smith, 2016). Likewise, waterbucks select for grassy species in their diets (Kassa et al., 2007). Although zebras have been found to be less selective and move over larger areas in search of more diverse foraging opportunities (Owen-Smith and Martin, 2015), our results also show this species was strongly influenced by grass cover. Consequently, all three of these ungulates would benefit from management programs that increase grass cover.

In the case of carnivores, we found relative abundances of two of six species detected increased with localized grass cover. However, some meso-carnivores that rely on woody vegetation for cover might benefit from a combination of shrubby and grassy habitats, at least up to some specific threshold level (Blaum et al., 2007a; Blaum et al., 2007c). Like our study, Blaum et al. (2007a) documented negative effects of shrub cover on selected species in South Africa. Nonetheless, our carnivore results should be interpreted with caution due to low detection rates for some species.



**Fig. 6.** Predicted average relative abundance of terrestrial mammals detected in camera trap surveys in Mlawula Nature and Mbuluzi Game Reserves, Swaziland (2012–2013) under three different plant cover management regimes. Where: regime 1 simulates no management, action taken and as a result, shrub cover is doubled across plots; regime 2 simulates an active management plan where plant cover types are maintained to current levels (i.e., further growth of shrub cover is halted); and regime 3 simulates an aggressive management regime where actual shrub cover is reduced by half and grass cover is doubled and increased to 60% across plots.



**Fig. 7.** Predicted average plot-level species richness of terrestrial mammals detected in camera trap surveys in Mlawula Nature and Mbuluzi Game Reserves, Swaziland (2012–2013) under three different management plan regimes for the plant community. Where: regime 1 simulates no management, action taken and as a result, shrub cover is doubled across plots; regime 2 simulates an active management plan where plant cover types are maintained to current levels (i.e., further growth of shrub cover is halted); and regime 3 simulates an aggressive management regime where actual shrub cover is reduced by half and grass cover is doubled and increased to 60% across plots.

Our model allowed us to predict and quantify the direction of community composition and species-specific abundances under different plant cover management regimes. With our simulation models, we demonstrate the negative consequences for local diversity and abundances if bush encroachment continues in the area. Similarly, [Smit and Prins \(2015\)](#) found increasing shrub cover results in a shift in ungulate communities where browsers and mixed-feeders replace grazers. Our management simulations also point to a shift in the ungulate community of our study site and a reduction of ungulate diversity and abundances of most species if bush encroachment and loss of grass cover continues in the area.

Our hierarchical abundance model allowed us to account for and examine mammalian detection probabilities in a bush encroached savanna. Methods commonly used in open savannas (e.g., aerial surveys, line transects) have limited application in areas with thick vegetation such as forests, woodlands, or bush encroached savannas. These sight-based methods likely underrepresent mid-sized ungulates such as bushbuck, nyala, and duiker that are associated with dense cover and may present low detection rates ([Coates and Downs, 2007](#); [Collier et al., 2011](#)). Our results suggest we should conduct surveys during the rainy season and use visual obstruction values as an added criterion for selecting survey sites to increase detectability.

#### 4.1. Management implications/conclusions

Bush cover and biomass can be reduced through mechanical means, and fire ([Gibson, 2009](#)). Areas where shrub removal or restoration efforts are planned should be selected based on site history, soil attributes, and local acceptance and participation ([Gibson, 2009](#)). [Bai et al. \(2009\)](#) recommend identifying and targeting fast growing clusters of shrub cover to increase effectiveness of removal programs. However, our study shows that efforts to reduce shrub cover should be implemented in tandem with actions that seek to aggressively recover and



maintain grass cover across bush encroached conservation areas. For example, Schwarz et al. (2017) showed reseeding shrub-cleared sites with perennial grasses was an effective strategy to increase grass cover. Other strategies such as decreasing height of canopy cover so light can penetrate to the ground and promote grass growth should be tested (Fuhlendorf et al., 1997). These management strategies may help reduce the probability of local extirpation of species sensitive to reduced grass cover (i.e., wildebeest, waterbuck, zebra) and maximize overall species richness. Management interventions will be necessary because the wildlife species that co-evolved with C<sub>4</sub> grasses in savannas make this system particularly unique, and contribute to the maintenance of its structure and composition (Du Toit and Cumming, 1999; Augustine and McNaughton, 2004; Goheen et al., 2010). Nonetheless, our results clearly illustrate that the influence of bush encroachment is species specific. Managers should be aware that interventions focusing on shrub cover will have differential impacts per each species' requirements.

Our approach of combining camera trapping data with a hierarchical Bayesian abundance model provided us with a cost-effective, reliable method to assess habitat use across an environmental gradient. To our knowledge, no studies of this kind have been carried out in bush encroached savannas. Our relatively short sampling scheme may have limited our ability to detect all available species at a plot. However, because our sampling was consistent across an environmental gradient and we accounted for detection, it was unlikely that the general relationships described in this study would have changed with longer sampling periods.

Our results highlight the need to account for imperfect detection when examining mammal abundance and species richness patterns. Furthermore, a considerable advantage of our approach was the ability to include species with low detections. Our study is unique in that we teased apart the effects of decreasing grass cover from increasing shrub cover on mammalian habitat use and it allowed us to predict the consequences of different bush encroachment management regimes.

Future research should focus on evaluating management interventions designed to increase grass cover in bush encroached savannas. It is also important to determine the mechanisms underlying the species-specific and community-wide negative responses of mammals to loss of grass cover. Two potential mechanisms are a reduction of food quality or decreased space and/or access to resources due to thorny clumps of shrub cover.

Finally, our study was carried out in two of the many smaller reserves and game ranches found across southern Africa and our results might have been influenced by the surrounding landscape and the potentially restricted movement of mammals. Thus, our finding may not be directly transferable to larger protected areas where mammalian movement is not as restricted. We suggest similar research be implemented across a wider range of savanna systems (e.g., larger systems such as Kruger National Park) to test whether our findings are consistent.

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## Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.biocon.2018.02.028>.

## References

- Archer, S., Boutton, T.W., Hibard, K.A., 2001. Trees in grasslands: biogeochemical consequences of woody plant expansion. In: Schulze, M., Heimann, S., Harrison, E., Holland, J., Lloyd, I. (Eds.), *Global Biogeochemical Cycles in the Climate System*. Academic Press, San Diego, California, pp. 115–138.
- Atickem, A., Loe, L.E., 2013. Livestock-wildlife conflicts in the Ethiopian highlands: assessing the dietary and spatial overlap between mountain nyala and cattle. *Afr. J. Ecol.* 52, 343–351.
- Augustine, D.J., McNaughton, S.J., 2004. Regulation of shrub dynamics by native browsing ungulates on East African rangeland. *J. Appl. Ecol.* 41, 45–58.
- Bai, E., Boutton, T.W., Wu, X.B., Liu, F., Archer, S.R., 2009. Landscape-scale vegetation dynamics inferred from spatial patterns of soil  $\delta^{13}C$  in a subtropical savanna parkland. *J. Geophys. Res.* 114.
- Bailey, L.L., Hines, J.E., Nichols, J.D., MacKenzie, D.I., 2007. Sampling design tradeoffs in occupancy studies with imperfect detection: examples and software. *Ecol. Appl.* 17, 281–290.
- Bailey, K.M., McCreery, R.A., Binford, M.W., Zweig, C., 2016. Land-cover change within and around protected areas in a biodiversity hotspot. *J. Land Use Sci.* 11, 154–176.
- Barthelemy, K., Roland, L., Brice, S., 2008. Diet and food preference of the waterbuck (*Kobus ellipsiprymnus defassa*) in the Pendjari National Park, Benin. *Afr. J. Ecol.* 46, 303–310.
- Beesley, L.S., Gwinn, D.C., Price, A., King, A.J., Gawne, B., Koehn, J.D., Nielsen, D.L., 2014. Juvenile fish response to wetland inundation: how antecedent conditions can inform environmental flow policies for native fish. *J. Appl. Ecol.* 51, 1613–1621.
- Blaum, N., Rossmanith, E., Popp, A., Jeltsch, F., 2007a. Woody encroachment affects mammalian carnivore abundance and species richness in semiarid rangelands. *Acta Oecol.* 31, 86–92.
- Blaum, N., Rossmanith, E., Popp, A., Jeltsch, F., 2007b. Land use affects rodent communities in Kalahari savanna rangelands. *Afr. J. Ecol.* 45, 189–195.
- Blaum, N., Rossmanith, E., Fleissner, G., Jeltsch, F., 2007c. The conflicting importance of shrubby landscape structures for the reproductive success of the yellow mongoose (*Cynictis penicillata*). *J. Mammal.* 88, 194–200.
- Bouchenak-Khelladi, Y., Anthony Verboom, G., Hodgkinson, T.R., Salamin, N., Francois, O., Ni Chonghaile, G., Savolainen, V., 2009. The origins and diversification of C<sub>4</sub> grasses and savanna-adapted ungulates. *Glob. Chang. Biol.* 15, 2397–2417.
- Canfield, R.H., 1941. Application of the line interception method in sampling range vegetation. *J. For.* 39, 388–394.
- Caro, T., Scholte, P., 2007. When protection falters. *Afr. J. Ecol.* 45, 233–235.
- Cerling, T.E., Harris, J.M., Macfadden, B.J., Leakey, M.G., Quade, J., Eisenmann, V., Ehleringer, J.R., 1997. Global vegetation changes through the Miocene/Pliocene boundary. *Nature* 389, 153–158.
- Coates, G.D., Downs, C.T., 2007. Population estimates of bushbuck (*Tragelaphus scriptus*) in valley thicket and coastal bushveld-grassland habitat. *S. Afr. J. Wildl. Res.* 37, 91–95.
- Collier, B.A., McCreery, R.A., Clahouh, K.W., Roques, K.G., Monadjem, A., 2011. Detection probabilities of ungulates in the eastern Swaziland lowveld. *S. Afr. J. Wildl. Res.* 41, 61–67.
- Dalerum, F., Somers, M.J., Kunkel, K.E., Cameron, E.Z., 2008. The potential for large carnivores to act as biodiversity surrogates in southern Africa. *Biodivers. Conserv.* 17, 2939–2949.
- Daubenmire, R.F., 1959. A tree-coverage method of vegetational analysis. *Northwest Sci.* 33, 43–64.
- Du Toit, J.T., Cumming, D.H.M., 1999. Functional significance of ungulate diversity in African savannas and the ecological implications of the spread of pastoralism. *Biodivers. Conserv.* 8, 1643–1661.
- Eldridge, D.J., Soliveres, S., 2014. Are shrubs really a sign of a declining ecosystem function? Disentangling the myths and truths of woody encroachment in Australia. *Aust. J. Bot.* 62, 594–608.
- Eldridge, D.J., Bowker, M.A., Maestre, F.T., Roger, E., Reynolds, J.F., Whitford, W.G., 2011. Impacts of shrub encroachment on ecosystem structure and functioning: towards a global synthesis. *Ecol. Lett.* 14, 709–722.
- ESRI, 2013. ArcGIS Desktop: Release 10. Environmental Systems Research Institute, Redlands, CA.
- Fuhlendorf, S.D., Smeins, F.E., Taylor, C.A., 1997. Browsing and tree size influences on Ashe juniper understory. *J. Range Manag.* 50, 507–512.
- Gandiwa, E., 2013. Vegetation factors influencing density and distribution of wild large herbivores in a southern African savanna. *Afr. J. Ecol.* 52, 274–283.
- Gertenbach, W.P.D., Potgieter, A.L.F., 1975. Veldbrandnavorsing in die knoppiesdoring-maroeelaveld van die sentrale distrik, Kruger Nasionale Park. (Unpublished burning trial report for the South African National Parks Board, Pretoria).
- Gibson, D.J., 2009. Grasses and Grassland Ecology, 1st edition. Oxford University Press, New York.
- Goheen, J.R., Palmer, T.M., Keesing, F., Riginos, C., Young, T.P., 2010. Large herbivores facilitate savanna tree establishment via diverse and indirect pathways. *J. Anim. Ecol.* 79 (2), 372–382.
- Guillera-Arroita, G., Lahoz-Monfort, J.J., MacKenzie, D.I., Wintle, B.A., McCarthy, M.A., 2014. Ignoring imperfect detection in biological surveys is dangerous: a response to 'fitting and interpreting occupancy models'. *PLoS One* 9, e99571. <http://dx.doi.org/10.1371/journal.pone.0099571>.
- Hobbs, N.T., Gordon, L.J., 2010. How does landscape heterogeneity shape dynamics of large herbivore populations? In: Owen-Smith, N. (Ed.), *Dynamics of Large Herbivore Populations in Changing Environments, towards Appropriate Models*. Wiley-Blackwell, John Wiley and Sons Ltd, pp. 141–164.
- Holdo, R.M., Holt, R.D., Fryxell, J.M., 2013. Herbivore-vegetation feedbacks can expand

- the range of savanna persistence: insights from a simple theoretical model. *Oikos* 122 (3), 441–453.
- Kassa, B., Libois, R., Sinsin, B., 2007. Diet and food preference of the waterbuck (*Kobus ellipsiprymnus defassa*) in the Pendjari National Park. *Afr. J. Ecol.* 46, 303–310.
- Kery, M., 2010. Introduction to WinBUGS for Ecologists: Bayesian Approach to Regression, ANOVA, Mixed Models and Related Analyses. Academic Press, Burlington USA.
- Kleynhans, E.J., Jolles, A.E., Bos, M.R.E., Olff, H., 2011. Resource partitioning along multiple niche dimensions in differently sized African savanna grazers. *Oikos* 120, 591–600.
- MacKenzie, D.I., Nichols, J.D., Royle, J.A., Pollock, K.H., Bailey, L.L., Hines, J.E., 2006. Occupancy Estimation and Modeling. Elsevier, Amsterdam, The Netherlands.
- Mamo, Y., Asefa, A., Mengesha, G., 2015. Habitat use of ungulates in Bale Mountains National Park, Ethiopia. *Afr. J. Ecol.* 53, 512–520.
- Martin, J., Owen-Smith, N., 2016. Habitat selectivity influences the reactive responses of African ungulates to encounters with lions. *Anim. Behav.* 116, 163–170.
- Martin, J., Benhamou, S., Yoganand, K., Owen-Smith, N., 2015. Coping with spatial heterogeneity and temporal variability in resources and risks: adaptive movement behaviour by a large grazing herbivore. *PLoS One* 10 (2). <http://dx.doi.org/10.1371/journal.pone.0118461>.
- McNaughton, S.J., Georgadis, N.J., 1986. Ecology of African grazing and browsing mammals. *Annu. Rev. Ecol. Syst.* 17, 39–65.
- Meik, J.M., Jeo, R.M., Mendelson III, J.R., Jenks, K.E., 2002. Effects of bush encroachment on an assemblage of diurnal lizard species in central Namibia. *Biol. Conserv.* 106, 29–36.
- Milton, S.J., Dean, W.R.J., 1995. South Africa's arid and semiarid rangelands: why are they changing and can they be restored? *Environ. Monit. Assess.* 37, 245–264.
- Monadjem, A., 1998. Distributional patterns and conservation status of mammals of Swaziland, southern Africa. *Koedoe* 41, 45–59.
- Mucina, L., Rutherford, M.C., 2006. The Vegetation of South Africa, Lesotho and Swaziland. South African National Biodiversity Institute, Pretoria.
- Mugume, S., Isabirye-Basuta, G., Otali, E., Reyna-Hurtado, R., Chapman, C.A., 2015. How do human activities influence the status and distribution of terrestrial mammals in forest reserves? *J. Mammal.* 96, 998–1004.
- O'Kane, C.A.J., Page, B.R., MacDonald, D.W., 2014. Differing influences of resource availability on the demographics and habitat selection of wildebeest compared with impala. *J. Trop. Ecol.* 30, 189–198.
- Owen-Smith, N., 2002. Adaptive Herbivore Ecology: From Resources to Populations in Variable Environments. Cambridge University Press, United Kingdom (374 pp).
- Owen-Smith, N., Martin, J., 2015. Identifying space use at foraging arena scale within the home ranges of large herbivores. *PLoS One* 10 (6). <http://dx.doi.org/10.1371/journal.pone.0128821>.
- Pressland, A.J., 1973. Rainfall partitioning by an arid woodland (*Acacia anura* F. Muell.) in southwestern Queensland. *Aust. J. Bot.* 21, 235–245.
- Roques, K.G., O'Connor, T.G., Watkinson, A.R., 2001. Dynamics of woody encroachment in an African savanna: relative influence of fire, herbivory, rainfall and density dependence. *J. Appl. Ecol.* 38, 268–280.
- Royle, J.A., Dorazio, R.M., 2008. Hierarchical Modeling and Inference in Ecology. Academic Press, Amsterdam, The Netherlands.
- Royle, J.A., Nichols, J.D., 2003. Estimating abundance from repeated presence-absence data or point counts. *Ecology* 84, 777–790.
- Schlesinger, W.H., Pilmanis, A.M., 1998. *Biogeochemistry* 42, 169–187.
- Schwarz, K., Finckh, M., Stolter, C., 2017. Influence of differently managed bush-encroached sites on the large herbivore distribution in the Namibian Savannah. *Afr. J. Ecol.* <http://dx.doi.org/10.1111/aje.12451>.
- Sirami, C., Monadjem, A., 2012. Changes in bird communities in Swaziland savannas between 1998 and 2008 owing to woody encroachment. *Divers. Distrib.* 18, 390–400.
- Smit, I.P.J., Prins, H.H.T., 2015. Predicting the effects of woody encroachment on mammal communities, grazing biomass and fire frequency in African savannas. *PLoS One* 10, e0137857. <http://dx.doi.org/10.1371/journal.pone.0137857>.
- Stafford, W., Birch, C., Etter, H., Blanchard, R., Mudavanhu, S., Angelstam, P., Blignaut, J., Ferreira, L., Marais, C., 2017. The economics of landscape restoration: benefits of controlling bush encroachment and invasive plant species in South Africa and Namibia. *Ecosyst. Serv.* 27, 193–202.
- Sweet, R.J., Khumalo, S., 1994. Range resources and grazing potentials in Swaziland. In: FAO Report. Mbabane, Ministry of Agriculture and Co-operatives.
- Teague, W.R., Ansley, R.J., Pinchak, W.E., Dowhower, S.L., Gerrard, S.A., Waggoner, J.A., 2008. Interannual herbaceous biomass response to increasing honey mesquite cover on two soils. *Rangel. Ecol. Manag.* 61, 496–508.
- Tobler, M.W., Zuniga Hartley, A., Carrillo-Percecastegui, S.E., Powell, G.V.N., 2015. Spatiotemporal hierarchical modelling of species richness and occupancy using camera trap data. *J. Appl. Ecol.* 52, 413–421.
- Van Auken, O.W., 2009. Causes and consequences of woody plant encroachment into Western North American grasslands. *J. Environ. Manag.* 90, 2931–2942.
- Vermeire, L.T., Ganguli, A.C., Gillen, R.L., 2002. A robust model for estimating standing crop across vegetation types. *J. Range Manag.* 55, 494–497.
- Wigley, B.J., Bond, W.J., Hoffman, M.T., 2010. Thicket expansion in a South African savanna under divergent land use: local vs. global drivers? *Glob. Chang. Biol.* 16, 964–976.
- Yamaura, Y., Royle, A., Kuboi, J., Tada, T., Ikeno, S., Makino, S., 2011. Modelling community dynamics based on species-level abundance models from detection/non-detection data. *J. Appl. Ecol.* 48, 67–75.
- Yoganand, K., Owen-Smith, N., 2014. Restricted habitat use by an African savanna herbivore through the seasonal cycle: key resources concept expanded. *Ecography* 37, 969–982.