Vegetation structure shapes small mammal communities in African savannas

Anne A. Loggins, Ara Monadjem, Laurence M. Kruger, Brian E. Reichert, and Robert A. McCleery*

School of Natural Resources and the Environment, University of Florida, Gainesville, Florida, USA (AAL, RAM)

Wildlife Ecology and Conservation, University of Florida, Gainesville, Florida, USA (RAM, AM)

Organization for Tropical Studies, Skukuza, South Africa (LMK)

US Geological Survey, Fort Collins Science Center, Fort Collins, Colorado, USA (BER)

Department of Biological Sciences, University of Eswatini, Private Bag 4, Kwaluseni, Eswatini (AM)

Mammal Research Institute, Department of Zoology & Entomology, University of Pretoria, Private Bag 20, Hatfield 0028, Pretoria, South Africa (AM, RAM)

Correspondent: ramccleery@ufl.edu

Disturbance by large herbivores, fires, and humans shapes the structure of savannas, altering the amount of woody vegetation and grass. Due to change in the intensity and frequency of these disturbances, savannas are shifting toward grass-dominated or shrub-dominated systems, likely altering animal communities. Small mammals are critical components of savannas, and their

distributions likely are affected by these ecosystem-wide changes in vegetative cover. We assessed the responses of small mammals to a gradient of woody cover in low-lying savannas of southeastern Africa. In Kruger National Park (South Africa) and in three nearby reserves (Eswatini), we live-trapped over two years to build multi-species occupancy models that assessed the responses of the small mammal community to grass and woody cover. Overall, whole-community occupancy increased with grass biomass. More species responded positively to woody cover than to grass biomass, but woody cover was associated with reduced occurrence of one species (*Mastomys natalensis*). Our results suggest that an increase in grass biomass enhances whole-community occupancy of small mammals, but regional diversity is likely to be higher in areas that contain patches of high grass biomass as well as patches of woody cover.

Grasslands and savannas cover 20-30% of the planet's land surface, are home to most of the world's extant megafauna, and encompass a vast diversity of life (Parr et al. 2014). Savanna ecosystems contain both woody plants (trees and shrubs) and grasses that fluctuate in dominance depending on precipitation and disturbance (Sankaran et al. 2005; Shorrocks 2007). However, savanna biodiversity is under increasing pressure from human stressors such as overgrazing, intensive agriculture, altered fire regimes, and resource extraction (Shorrocks 2007; Andersen et al. 2012; Parr et al. 2014). Browsing herbivores and fire reduce the abundance of woody species, while grazing herbivores and low fire frequency often increase the abundance of woody species, particularly in mesic savannas (Roques et al. 2001; Langevelde et al. 2003; Sankaran et al. 2008; Stevens et al. 2016; Pellegrini et al. 2017). Changes in the frequency and intensity of disturbances worldwide are homogenizing savannas, such that they are dominated by grasses or woody plants (Roques et al. 2001; Cremene et al. 2005; Andersen et al. 2012; Parr et al. 2014; Stevens et al. 2017).

Without regular disturbance, savannas often experience woody plant encroachment that may in turn suppress the growth of grasses (Eldridge et al. 2011; Stevens et al. 2017), potentially reducing plant and animal diversity (Blaum et al. 2007; Ratajczak et al. 2012; Sirami and Monadjem 2012; Stanton et al. 2018; Soto-Shoender et al. 2018). Alternatively, the loss of large trees through the harvesting of firewood or intense herbivory may decrease biodiversity by reducing woody species and creating open grasslands (Fenton et al. 1998; Birkett and Stevens-Wood 2005; Treydte et al. 2009; Asner and Levick 2012; Foster et al. 2014). Species richness and is often highest in areas where woody species and grasses co-occur rather than at either extreme of the grassland to woodland continuum (Blaum et al. 2009; Sirami and Monadjem 2012; Abu Baker and Brown 2014; Tilman et al. 2014; McCleery et al. 2018).

Small mammals play diverse roles in savannas, as seed and vegetation consumers (Miller 1994; Keesing 2000; Bergstrom 2013), prey, ecosystem engineers, and promoters of nutrient cycling (Happold 2001), as well as acting as biological indicators (Avenant 2011; Hurst et al. 2014). While we have a clearer understanding of how shifts in grass and woody components influence communities of larger mammals in African Savannas (Soto-Shoender et al. 2018), there is a need to understand how shifts in the vegetation of African savannas influence small mammals. At fine scales, many species of small mammal in African savannas are associated positively with both woody and grass cover (Kern 1981; Monadjem 1997a; Monadjem and Perrin 2003; van Deventer and Nel 2006). McCleery et al. (2018) suggested that a combination of grass and woody cover may increase species richness of small mammals in African Savannas. However, this study did not link species-level responses to community responses, nor did it investigate the relative importance of these competing plant forms (February et al. 2013).

In this study, our objectives were to understand the relative importance of grass and woody cover to small mammal species and communities in African savannas, and to evaluate the potential synergistic effects of grass and woody cover. We did this by quantifying the species occurrence of small mammal species and the whole-community (average species response) across gradients of woody and grass cover in southern African savannas. We predicted that herbivorous small mammals (*Aethomys ineptus, Lemniscomys rosalia, Micaelamys namaquensis*) and small mammals that have previously been associated with thick or tall grass (*Dendromus mystacalis, Lemniscomys rosalia, Crocidura hirta., Crocidura* spp.) would increase in occurrence with increased grass biomass, while those species that have previously been associated with shrub cover (*Aethomys ineptus*, *Mus minutoides, Elephantulus brachyrhynchus*) would increase in occurrence with increased woody cover (Table 1). Due to the predominance of

herbivorous and grass-associated small mammals in African savannas (Table 1), and the importance of grass for the diversity of larger mammals in the system (Soto-Shoender et al. 2018), we predicted that increased grass cover would increase species richness of small mammals.

Table 1.— Average adult mass (g), diet, savanna conditions (based on canopy), and favored vegetation structure of small mammals trapped in this study in South Africa and Eswatini. Small mammal community statistics from Skinner and Chimimba (2005), Long et al. (2012), and Monadjem et al. (2015). Predicted responses indicate positive responses to increased grass or woody cover.

Species	Mass	Diet	Savanna conditions	Vegetation structure[a]	Predicted response
Aethomys ineptus	78	Granivore-herbivore	mixed	↑shrub or grass cover	grass, woody
Dendromus mystacalis	8	Granivore-insectivore	open	↑tall grass	grass
Gerbilliscus leucogaster	70	Omnivore	open	↑sandy soil	
Lemniscomys rosalia	57	Herbivore-granivore	open-closed	↑tall grass	grass
Mastomys natalensis	46	Granivore-omnivore	open, disturbed	↓grass-shrub cover	
Micaelamys namaquensis	48	Herbivore-granivore	open-closed	↑rock	
Mus minutoides	6	Omnivore	open-closed, disturbed	↑shrub	woody
Saccostomus campestris	48	Granivore	open	↓grass-shrub cover	
Steatomys pratensis	23	Granivore	open	↑sandy soil	grass
Crocidura hirta.	16	Insectivore	open	↑thick grass	grass
Crocidura spp.	9	Insectivore	open	↑thick grass	grass
Elephantulus brachyrhynchus	44	Insectivore	open	↑shrub cover	woody

[a] ↑ = responds positively to increased structure, ↓ = responds negatively to increased structure

MATERIALS AND METHODS

We sampled small mammals within four protected areas in southern Africa. We used a nested study design, placing 0.25-ha study plots within 30.25-ha grids spaced a minimum of 1 km apart to account for variation both across and within landscapes. We placed grids to encompass a

gradient of vegetative cover, from landscapes dominated by woody plants to those dominated by grasses.

Study sites.--- We placed sampling grids on geologically similar areas within four protected areas in Eswatini and South Africa (McCleery et al. 2018). In Eswatini, we sampled small mammals and vegetation in Mbuluzi Game Reserve (30 km²), Mlawula Nature Reserve (165 km²), and Hlane Royal National Park (220 km²). These protected areas are located in the country's lowveld region adjacent to the Lubombo Mountains on basaltic soils. The Eswatini lowveld has a subtropical climate and a unimodal rainfall pattern with the wet season during October-March (75% of the annual rainfall) and the dry season during April-September (25% of the annual rainfall; Matondo et al. 2004). Yearly precipitation in the region ranges from 500-750 mm (Matondo et al. 2005). *Senegalia nigrescens* and *Sclerocarya birrea* were the most common trees in the savannas. The dominant species of grasses included *Themeda* spp. and *Panicum maximum*, while *Dichrostachys cinerea* was the dominant shrub (Sirami and Monadjem 2012).

In South Africa, we sampled on basaltic soils at the base of the Lubombo Mountains in Kruger National Park (19,000 km²). Rainfall at our sites averaged 610 mm annually, mostly falling between November and March (Smit et al. 2013). The most common overstory trees on the site included *Sclerocarya birrea* and *Senegalia nigrescens*, while the shrub layer was dominated by *Dichrostachys cinerea* and *Gymnosporia senegalensis* (Levick et al. 2009).

The most common large mammals on our sites included impalas (*Aepyceros melampus*), warthogs (*Phacochoerus africanus*), giraffes (*Giraffa camelopardalis*), zebras (*Equus quagga*) and blue wildebeest (*Connochaetes taurinus*; Soto-Shoender et al. 2018). Elephants (*Loxodonta africana)*, white rhinoceroses (*Ceratotherium simum*), and buffaloes (*Syncerus caffer*) were present on our Kruger sites but extirpated from Eswatini around 1920 (Monadjem 1998; Blanc et

al. 2003). As of 2012, Kruger supported over 16,000 elephants, an approximate density of 0.8 individuals/km² (Ferreira et al. 2012). Fire-return intervals in Kruger National Park and Mbuluzi Game Reserve were comparable with a mean of 4-5 years (Smit et al. 2013) and 3-5 years, respectively. Hlane Royal National Park and Mlawula Nature Reserve had slightly longer fire-return intervals of 5-7 and 6-9 years, respectively (McCleery et al. 2018).

The small mammal community.---There were at least 11 small mammal species present across our study sites, ranging in size from 5-100 g, from the orders Rodentia, Eulipotyphla, and Macroscelidea. These species occurred in a variety of vegetation communities ranging from open grasslands, mixed woodlands, cultivated farmlands, and rocky terrain (Kern 1981; Monadjem 1997a; Monadjem 1999; Hurst et al. 2013, 2014; Table 1), and their diets ranged from insectivorous (shrews in the family Soricidae) to omnivorous (rodents) with seasonal shifts in diet (see Table 1; Monadjem 1997b; Bergstrom 2013; Abu Baker and Brown 2014; Monadjem et al. 2015). All species were nocturnal except *Lemniscomys rosalia* and *Elephantulus brachyrhynchus*, which were largely crepuscular (Skinner and Chimimba 2005).

Data collection.---We surveyed small mammals and vegetation in each of 10 systematically placed 30.25-ha grids (six in Eswatini, four in Kruger). Within each grid there were nine 50-m² plots nested in a 3 x 3 design spaced 250 m apart (90 plots in total). We baited 20 Sherman folding traps (3 x 3.5 x 9", H. B. Sherman Traps, Inc., Tallahassee, Florida) with peanut butter and oats in each plot over four consecutive nights in the austral summer wet (November 21 - February 1) and winter dry seasons (May 15 - August 1) from November 2013 to August 2015. We identified all small mammal species and recorded their mass, sex, age (adult or juvenile), hind foot, body, and tail lengths. We fitted ear-tags on all individuals (1005-1, National Band Co., Newport, Kentucky). Home ranges of these species do not normally exceed

250 m² (Monadjem and Perrin 1998) and we did not catch any individuals on multiple plots. We therefore considered plots to be independent samples.

We measured tree density (number of woody plants > 5 m tall), shrub cover (% cover by woody plants > 0.5 m and < 5 m tall), canopy cover, and grass biomass for each plot annually in May-June (see McCleery et al. 2018). We counted every tree > 5 m tall on the plot We estimated the percentage of shrub cover along two parallel 50-m transect tapes laid across the plot using the line-intercept method (Canfield 1941). We measured canopy cover with a concave spherical densiometer every 10 m along the same transect lines (Lemmon 1956). We used a disc pasture meter, calibrated to Kruger National Park, to estimate grass biomass every 5 m along each transect (Zambatis et al. 2006). In this system, seasonal differences in canopy cover, shrub cover, and tree density are negligible between the beginning of the dry season and the beginning of the wet season (November-December). Grass biomass decreases during this period (May-June – November-December).

All animal surveys were conducted in accordance with scientific permits from South African National Parks (KRUGL1427) and approved by the University of Florida's Non-regulatory Institutional Animal Review Committee Institutional Animal Review (010-13WEC). Additionally, all research followed guidelines established by the American Society of Mammalogists (Sikes et al. 2016).

Data analysis.---We examined how variation in vegetation structure influenced the species occurrence and how vegetation gradients influenced small mammal communities. We used a multi-species occupancy modeling approach (Dorazio et al. 2006) that accounted for both the variation in occupancy among species and the inability to consistently detect all individuals within a community (MacKenzie et al. 2006). Using a hierarchical model, we estimated species-

specific effects and the whole-community effect (average species response), treating each species as a random variable within a community. This framework accounts for the variability in detection across species, improving the overall occupancy estimates (Ψ) by using the variation from both rare and common species to estimate parameters for individual species and the whole-community (Dorazio and Royle 2005). This model can also be used to measure how different environmental variables affect occupancy on species-specific and whole-community levels.

We reduced the data from the small mammal trapping within plots to binary presence-absence variables for each species, for each of the four trapping nights. We defined the probability of occupancy as ψ_{ik} for each species k at location (plot) i with detection probability defined as p_{ijk} over sampling period j. We used 11 species and one group of species (in the genus *Crocidura*) in the model. We grouped small (<12 g) *Crocidura* spp. in the same group because they are functionally similar and cannot be easily distinguished in the field.

We first built a "Null" model with grid modeled as a random effect (accounting for potential spatial autocorrelation among plots) centered on 0 but with an estimated variance from the common distribution (hyper-parameters) as a hierarchical effect. Hyper-parameters thus represented the average effect over all species. For all other random effects in the model, we estimated the mean as a hyper-parameter as well as the variance. For this base model, we also estimated how detection varied across species, and how season influenced trapping success for different species. Some species are less active in the dry season and rodent populations can fluctuate greatly from year to year (Monadjem and Perrin 2003). We included both season and year as binary variables (dry or wet, and year 1 or 2), with season as a fixed effect and year as a random effect. Detection probability p_{ijk} for species k at site i during sampling period j was modeled as:

$$logit(p_{ijk}) = \alpha_k + \alpha1_k * season_i + \alpha2_k * year_i$$

We assumed that Ψ would vary across species with vegetation structure. We averaged the data collected at each plot, generating vegetation variables representing average tree density, percentage shrub cover, percent tree canopy cover, and grass biomass (kg/ha) across plots. We modeled Ψ with the four vegetation covariates (shrub cover, tree canopy cover, grass biomass, and tree density) as random effects with hierarchical hyper-parameters using non-informative priors. We standardized the vegetation covariates so that their means fell at zero. We tested for collinearity of our vegetation covariates to control for confounding effects of correlated variables, including variables in the same model only if they had correlation coefficients below 0.6. Shrub cover and tree canopy cover were highly correlated (0.74) and were averaged into a woody cover estimate for use in the global model, which also contained grass biomass and tree density. Finally, as responses of small mammals to woody cover or grass biomass may vary depending on the quantity of each other, we also included an interaction term between grass and woody cover. We used a logit link function formulated for the global model as:

$$logit(\psi_{ik}) = \beta_k + \beta1_k * woody.cover_i$$
$$+ \beta2_k * grass.biomass_i + \beta3_k * tree.density_i$$
$$+ \beta4_k * woody.cover_i * grass.biomass_i + \beta5_k * grid_i$$

Adapting code from Kery and Royle (2016), we used non-informative priors for all parameters, building the models in JAGS 4.0 (Plummer 2003) via Program R (R Development Core Team 2016) using the R-package 'r2jags'. We ran 100,000 MCMC iterations with three chains, using 12,000 samples (thin rate = 10, burn-in = 60,000). We assumed chain convergence when Rhat < 1.2 (Gelman et al. 2013). We used the global model to determine both the species-level and whole-community responses (average species responses) to vegetation covariates.

For species-level effects, we evaluated the relevance of each vegetation parameter coefficient for each species ($\beta 1_k, \alpha 1_k \dots$). We considered responses with 95% credible intervals (*CRI*) that did not include zero to be relevant predictors. We evaluated whole-community responses by averaging the species' responses to each vegetation covariate as derived parameters (Kery and Royle 2016). Again, we considered responses with 95% *CRI* that did not overlap zero to be relevant predictors for the whole community. Using predicted gradients based on the actual range of vegetation, we evaluated the predicted Ψ of the whole community and individual species across the gradient. We also evaluated the whole-community responses to woody cover under varying levels of grass biomass (average, minimum, and maximum) to assess the interaction between woody cover and grass biomass.

RESULTS

Vegetation gradients.---Vegetation parameters (canopy cover, shrub cover, grass biomass, and tree density) differed within and across our grids (Supplementary Data SD1). Average woody cover ranged from 0.23 - 92.81% with an average of 27.35% cover across all plots and seasons. Tree density ranged from 0 - 194 trees per plot with an average of 22.56 trees per plot. Grass biomass ranged from 56.17 – 5,364.26 kg/ha with an average of 2,108.51 kg/ha.

Small mammal species.---We captured a total of 1,532 individuals of 11 species of small mammal over the sampling period, which included nine species of rodent, one macroscelidid (*Elephantulus brachyrhynchus*), and one genus of shrew (*Crocidura*). Most of the species were recorded in both regions, although we only captured *Gerbilliscus leucogaster* in Kruger and *E. brachyrhynchus* in Eswatini. Species richness varied over study plots, grids, and seasons. One generalist omnivore, *Mastomys natalensis*, was abundant across study grids with an average of

55 individuals (*SE* = 16.42) per grid in the dry and 19 (*SE* = 2.07) in the wet season. Two other generalists were captured frequently in both the dry season (*Mus minutoides*: $\bar{x}$ = 16.70, *SE* = 4.86; *Lemniscomys rosalia*: $\bar{x}$ = 18.40, *SE* = 6.22) and the wet season ($\bar{x}$ = 6.80, *SE* = 2.69; $\bar{x}$ = 9.70, *SE* = 3.18, respectively). *Steatomys pratensis* was also common in the wet season ($\bar{x}$ = 12.20, *SE* = 7.20) but not in the dry season ($\bar{x}$ = 0.70, *SE* = 0.40).

Multi-species occupancy model: species level.--- The most commonly caught species had the highest Ψ (*Lemniscomys rosalia*— Ψ = 0.67, 95% CRI: 0.43, 0.87; *Mus minutoides*— Ψ = 0.63, 95% *CRI*: 0.36, 0.91; *Mastomys natalensis*— Ψ = 0.51, 95% *CRI*: 0.33, 0.69; Table 2) but the predicted Ψ and detection of each species varied across the plots. Species varied significantly in their occurrence as a function of vegetation gradients, especially woody and grass cover (Table 2, Fig. 1). As expected, species varied seasonally in detection probability, with increased detection for six out of 12 species during the dry season (Table 3). Only *Steatomys pratensis* had increased detection rates in the wet season.

Table 2.— The posterior probabilities for species-level occupancy means, ψ_{ik}, with standard deviation (*SD*) and 95% credible intervals (95% *CRI*). Also shown are species-specific occupancy responses to vegetation covariates (woody cover, grass) with 95% *CRI* outside zero for small mammal species trapped in Kruger National Park, South Africa, and Mbuluzi Game Reserve, Mlawula Nature Reserve, and Hlane Royal National Park, Eswatini, from Nov 2013 - June 2015.

Species	ψ_{ik}	SD	95% CRI	Responses to vegetation
Lemniscomys rosalia	0.665	0.111	(0.434, 0.869)	+ woody cover, + grass
Mus minutoides	0.627	0.145	(0.356, 0.910)	+ woody cover
Mastomys natalensis	0.511	0.092	(0.327, 0.689)	- woody cover
Crocidura hirta	0.280	0.198	(0.049, 0.797)	
Aethomys ineptus	0.256	0.154	(0.071, 0.673)	+ woody cover
Steatomys pratensis	0.233	0.098	(0.073, 0.447)	+ woody cover
Saccostomus campestris	0.124	0.088	(0.027, 0.348)	
Crocidura spp.	0.118	0.075	(0.028, 0.310)	+ grass
Micaelamys namaquensis	0.112	0.061	(0.035, 0.267)	+ woody cover
Dendromus mystacalis	0.053	0.060	(0.003, 0.205)	+ grass
Elephantulus brachyrhynchus	0.015	0.015	(0.001, 0.054)	+ woody cover
Gerbilliscus leucogaster	0.009	0.012	(0.000, 0.041)	

FIG. 1.--- The modeled occupancy probability for each species along the grass biomass gradient (A) and the average woody cover gradient (B; calculated as the average between shrub cover and canopy cover estimates) throughout the study plots in Kruger National Park, South Africa, and Mbuluzi Game Reserve, Mlawula Nature Reserve, and Hlane Royal National Park, Eswatini, from Nov 2013 – June 2015. The average community effect is displayed as a black line. Species responses with 95% CRI that do not overlap zero are shaded (see Legend) while those that do include zero are in gray. Note that the x-axes are not the same because they are different vegetation parameters.

13
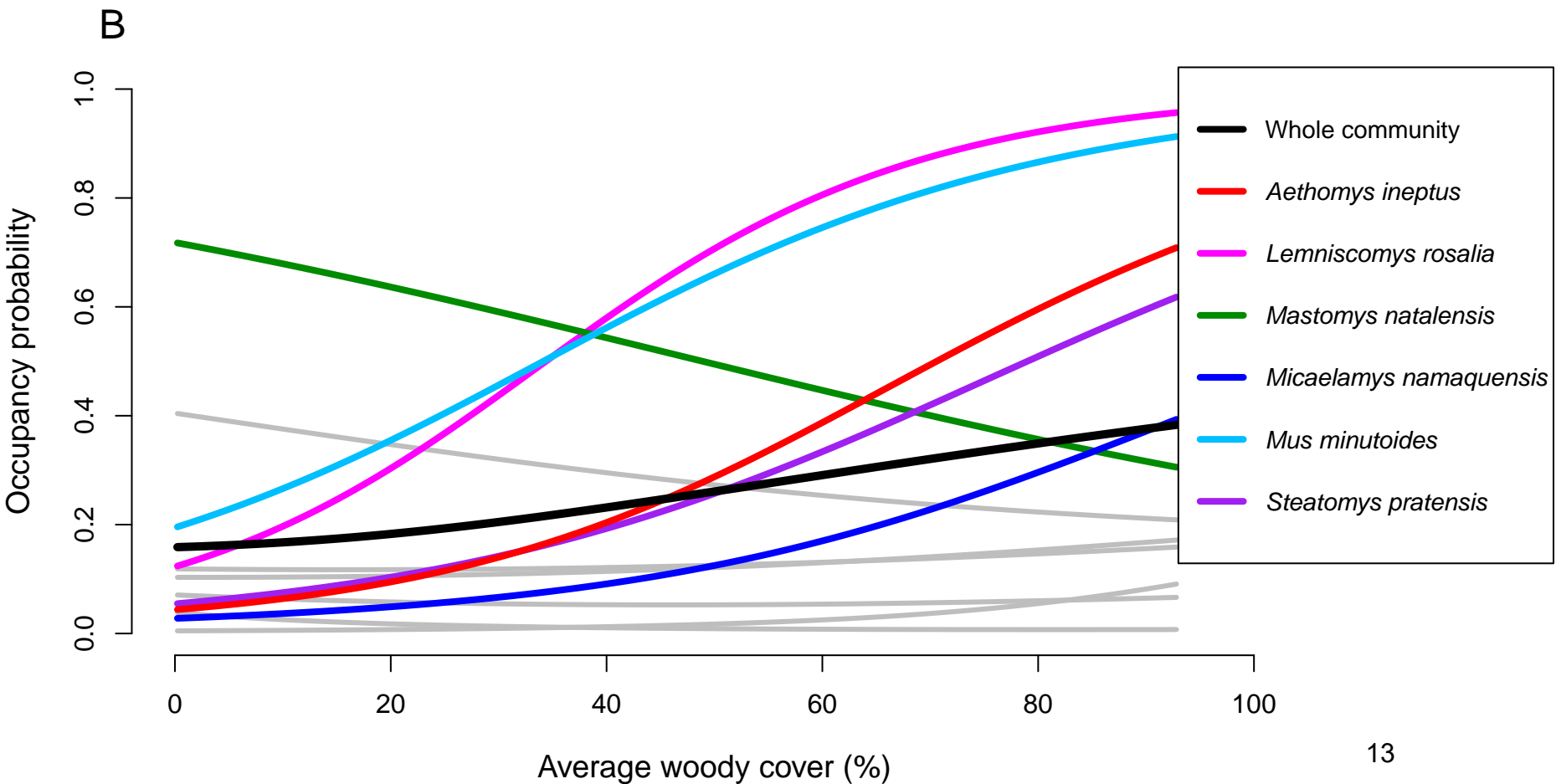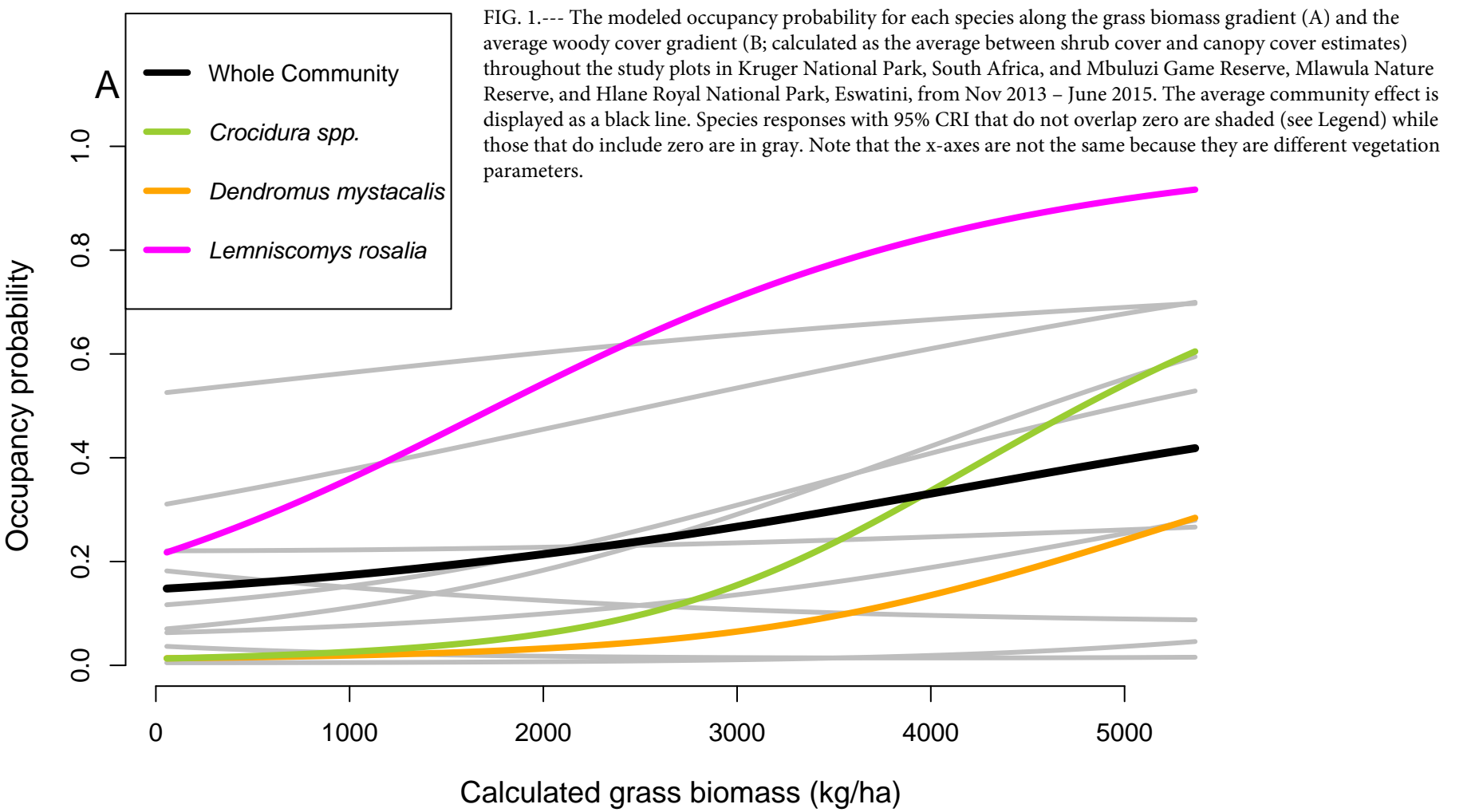
Table 3.— The posterior probabilities for species-level detection means, p_{ijk}, with standard deviation (*SD*) and 95% credible intervals (95% *CRI*). Also shown are species-specific detection responses to the Season covariate with 95% *CRI* outside zero for small mammal species trapped in Kruger National Park, South Africa, and Mbuluzi Game Reserve, Mlawula Nature Reserve, and Hlane Royal National Park, Eswatini, from Nov 2013 - June 2015.

Species	p_{ijk}	*SD*	95% *CRI*	Responses to season
Mastomys natalensis	0.614	0.020	(0.574, 0.654)	+ Dry
Lemniscomys rosalia	0.524	0.029	(0.467, 0.579)	
Mus minutoides	0.323	0.033	(0.260, 0.390)	+ Dry
Gerbilliscus leucogaster	0.312	0.143	(0.081, 0.621)	
Micaelamys namaquensis	0.244	0.067	(0.136, 0.398)	+ Dry
Steatomys pratensis	0.214	0.036	(0.148, 0.291)	+ Wet
Elephantulus brachyrhynchus	0.206	0.133	(0.030, 0.540)	+ Dry
Aethomys ineptus	0.181	0.071	(0.073, 0.347)	
Crocidura spp.	0.146	0.072	(0.042, 0.318)	+ Dry
Saccostomus campestris	0.106	0.050	(0.035, 0.225)	
Dendromus mystacalis	0.066	0.066	(0.005, 0.246)	+ Dry
Crocidura hirta	0.064	0.038	(0.017, 0.160)	

Occupancy for three species increased as grass biomass increased (positive 95% *CRI*), and no species declined with increased grass biomass (Fig. 1a). The Ψ of *Lemniscomys rosalia* increased steadily with grass biomass, reaching > 0.80 at maximum grass biomass (Fig. 1a). The Ψ of *Dendromus mystacalis* and *Crocidura* spp. also increased with more grass biomass, although *D. mystacalis* only reached a maximum Ψ probability of 0.20 at the highest grass biomass. Occupancy of *Mastomys natalensis* and *Aethomys ineptus* also tended to increase with increasing grass biomass (Fig. 1a, increasing gray lines), although their 95% *CRI*s overlapped zero.

The Ψ of five species increased as a function of increasing woody cover, with *Mus minutoides* and *Lemniscomys rosalia* showing the strongest positive response, increasing rapidly up to Ψ = 0.90 at the maximum levels of woody cover (Fig. 1b). *Aethomys ineptus*, *Micaelamys namaquensis*, and *Steatomys pratensis* also increased Ψ with cover, rising at average woody cover >30%. Conversely, *Mastomys natalensis* declined steadily as cover increased, decreasing from Ψ = 0.70 at the lowest levels of woody cover to Ψ = 0.30 at the highest levels of woody

14

cover. *Crocidura hirta* also tended to decline with increases in woody cover (Fig. 1b, declining grey line) but the 95% CRI included zero, indicating that cover was not a strong predictor of Ψ. Tree density had little effect on small mammal species (Supplementary Data SD2), with none of the species showing a strong response.

Only *Lemniscomys rosalia* showed a strong response to the interaction between woody cover and grass biomass, responding positively to cover when grass biomass was at its average and highest levels, but remaining at low ($\Psi = 0.20$) when grass was at its lowest level (Supplementary Data SD3).

Multi-species occupancy model: whole-community level.--- The small mammal whole-community Ψ increased as grass biomass and woody cover increased (Table 4; Fig. 2), and showed no response to tree density (Supplementary Data SD4). Yet when averaged, only grass biomass was a relevant predictor of community Ψ ($\beta = 0.57$, 95% *CRI*: 0.33, 0.83). Woody cover was a predictor of occupancy for more individual species, but when averaged the *CRI* intervals overlapped zero. Similarly, the interaction between woody cover and grass biomass was not a predictor of the whole-community response, although the average occupancy within woody cover did tend to increase with increasing grass biomass (Fig. 3).

15

FIG. 2.--- The modeled occupancy probability for the whole community along the grass biomass gradient (A) and the average woody cover gradient (B; calculated as the average between shrub cover and canopy cover estimates) throughout the study plots in Kruger National Park, South Africa, and Mbuluzi Game Reserve, Mlawula Nature Reserve, and Hlane Royal National Park, Eswatini, from Nov 2013 – June 2015. The average community effect is displayed as a black line, with 95% CRI in gray. Note that the x-axes are not the same because they are different vegetation parameters.

16
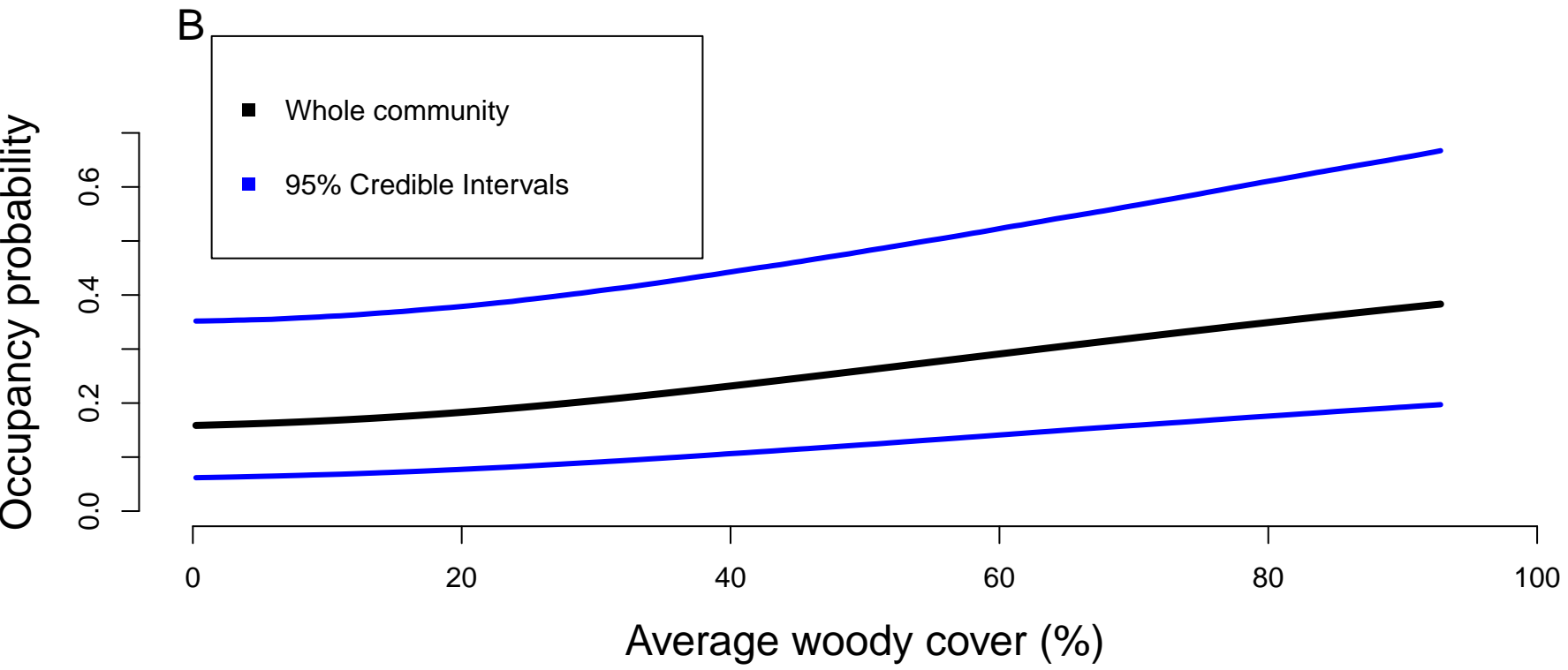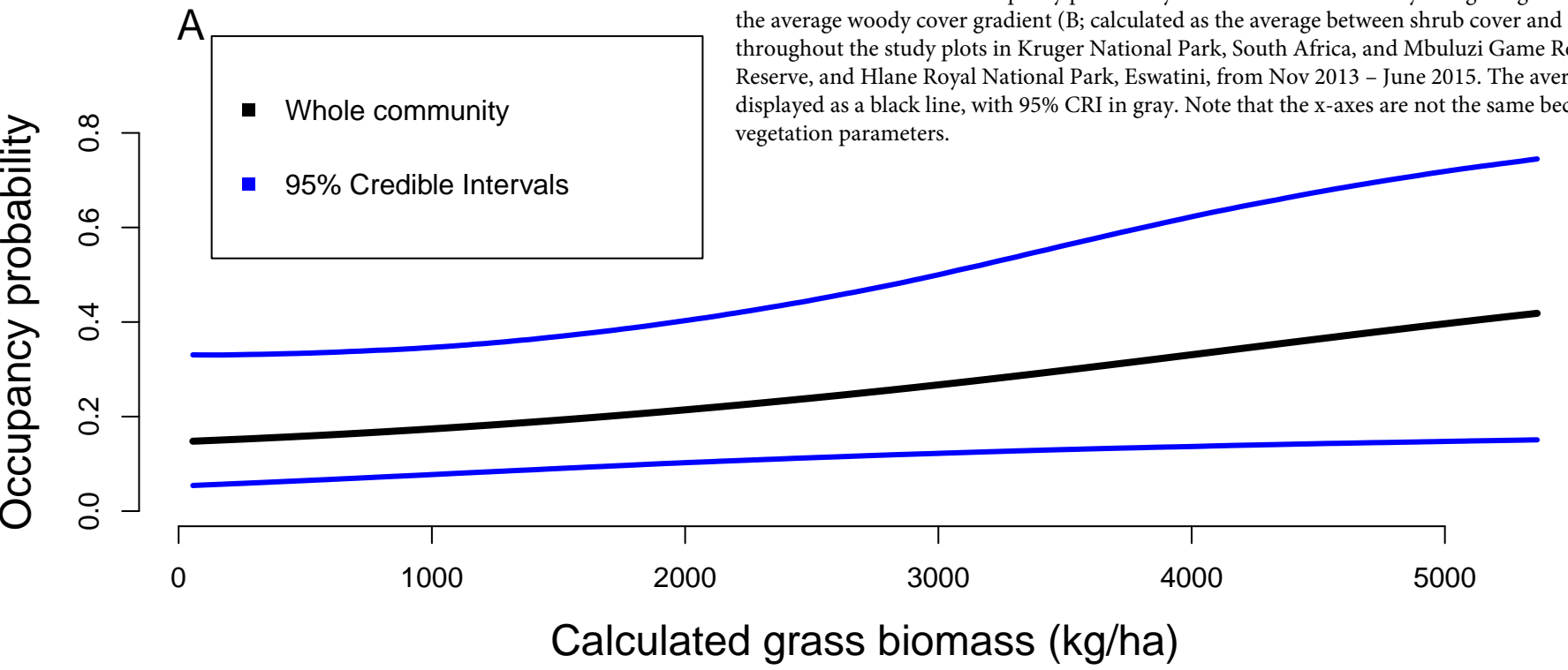
FIG. 3.--- The modeled occupancy probability for the whole community along the average woody cover gradient (calculated as the average between shrub cover and canopy cover estimates) interacting with different levels of grass biomass throughout the study plots in Kruger National Park, South Africa, and Mbuluzi Game Reserve, Mlawula Nature Reserve, and Hlane Royal National Park, Eswatini, from Nov 2013 – June 2015. The effect under average grass biomass is displayed as a black line, the minimum level of grass is dashed, and the maximum level of grass is dotted.
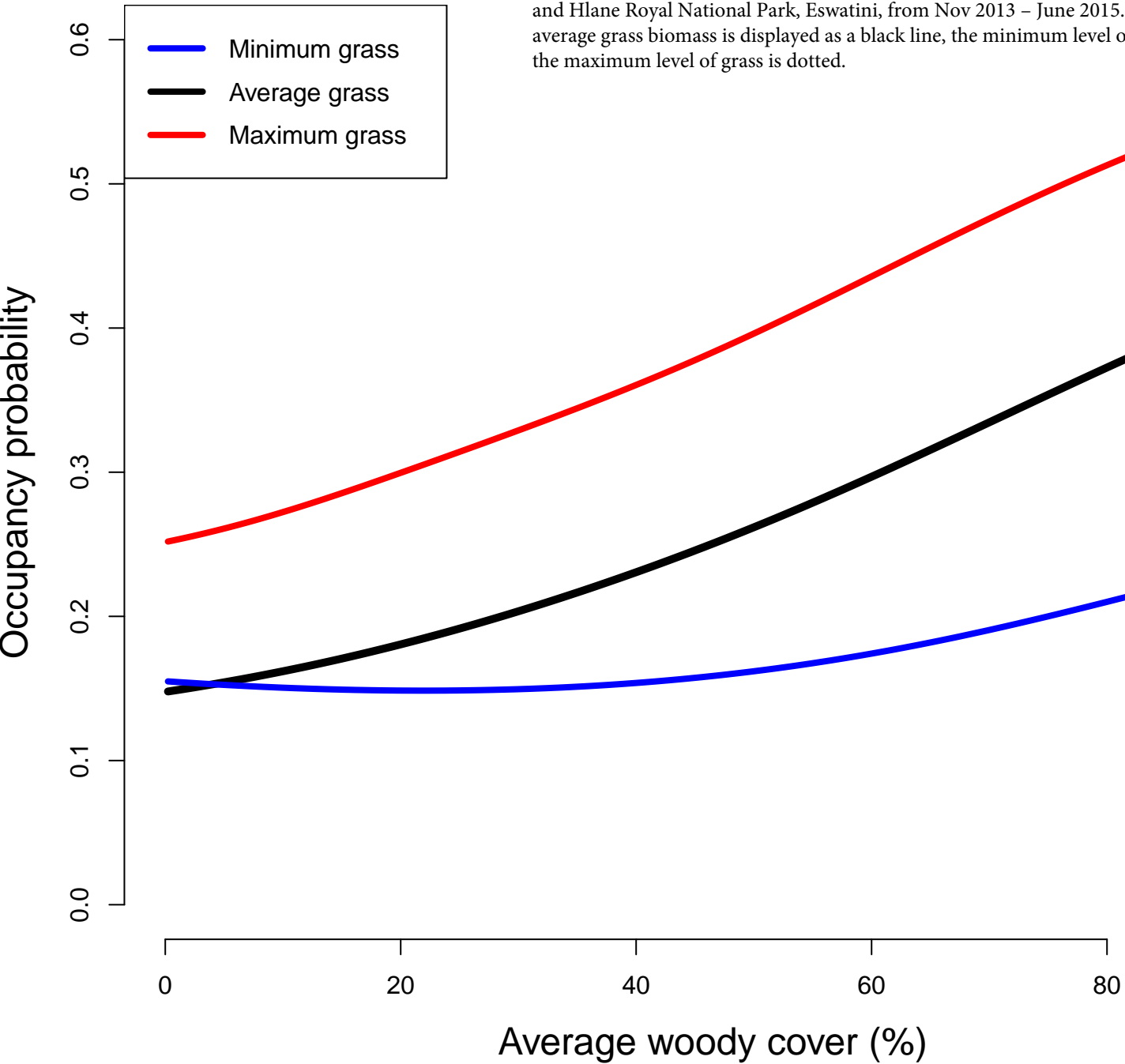
Table 4.— The posterior probabilities for the global model for the average community-level effects of vegetation covariates (standard deviation, *SD*, and 95% credible intervals, 95% *CRI*) on small mammal occupancy (β_i) and detection (α_i) for small mammal species trapped in Kruger National Park, South Africa, and Mbuluzi Game Reserve, Mlawula Nature Reserve, and Hlane Royal National Park, Eswatini, from Nov 2013 - June 2015. Response with [a] indicates 95% *CRI* that did not overlap zero.

Model type	Parameter (covariate)	Mean	*SD*	95% *CRI*
$\beta1 + \beta2 + \beta3 + \beta4 + \beta5$	$\beta2$ (grass biomass)[a]	0.323	0.142	(0.059, 0.622)
$\alpha1 + \alpha2$	$\beta1$ (average cover)	0.316	0.180	(-0.048, 0.654)
	$\beta4$ (cover-grass interaction)	0.133	0.114	(-0.101, 0.353)
	$\beta3$ (tree density)	0.007	0.103	(-0.203, 0.203)
	$\beta5$ (grid)	-0.003	0.197	(-0.406, 0.392)
	$\alpha1$ (season)	0.339	1.146	(-1.814, 2.605)
	$\alpha2$ (year)	-0.225	0.711	(-1.662, 1.170)

DISCUSSION

Changes in grass biomass influenced species occurrence and species richness. This pattern was driven by increased occurrence of three species associated with thick or tall grass (*Lemniscomys rosalia, Dendromus mystacalis, Crocidura* spp.; Table 1). However, our findings provided little evidence that herbivory or dietary preferences were associated with increased occurrence of small mammals in areas with increased grass biomass (Tables 1, 2).

Similarly, we found little evidence that dietary preferences were associated with the increased occurrence of the six species that increased with woody cover (Table 2). These species included a mix of herbivores, granivores, insectivores, and omnivores (Table 1). However, all the species associated with increased shrub cover (*Aethomys ineptus*, *Mus minutoides, Elephantulus brachyrhynchus*) responded positively to increased woody cover (Tables 1, 2). Three additional species also responded similarly (Table 2). *Mastomys natalensis*, however, showed a strong negative response to increased woody cover in our study, corroborating previous research (Monadjem 1997a). Increasing woody cover likely did not significantly alter species richness

18

because the strong negative response of *Mastomys natalensis* counteracted the positive responses of the six other species (Fig. 1).

Our results suggest reductions in grass cover may be detrimental to small mammal communities in savanna systems. Savannas with depauperate small mammal communities may see reductions in ecosystem functions such as nutrient cycling, seed dispersal, seed predation, and herbivory (Avenant and Cavellini 2007), possibly leading to alteration in the structure and composition of vegetation (Keesing 2000). Further, the loss of small mammals as prey will likely reduce the prevalence of small and medium-sized carnivores (e.g., servals [*Leptailurus serval*], genets [*Genetta* spp.], honey badgers [*Mellivora capensis*], African civets [*Civettictis civetta*], slender mongooses [*Galerella sanguinea*]) and many species of birds of prey, that rely heavily on small mammals as a food source (Vernon 1972; Skinner and Chimimba 2005; Williams et al. 2018)

The processes that can reduce grass cover, and hence impact small mammal communities, include reduced fire frequency (O'Connor et al. 2014), overgrazing (Roques et al. 2001; Koerner and Collins 2014), and decreased browsing (Staver et al. 2009). The trend of shrub encroachment in savanna ecosystems worldwide may also contribute to declines in grass biomass (Blaum et al. 2007; Eldridge et al. 2011; Stanton et al. 2018; Stevens et al. 2017). While grass biomass decreased between trapping sessions (May-June to November-December), our measure of grass biomass should be interpreted as peak grass biomass. To address seasonal changes like these (e.g., reduced grass biomass at the beginning of the wet season, colder temperatures during the dry season), we modeled temporal changes in the variation in detection probabilities (Table 2).

Although grass biomass was the only parameter significantly related to greater small mammal species richness, woody cover was also a predictor of occurrence for some species. Two of the three most common species (*Mus minutoides* and *Lemniscomys rosalia*) had their strongest relationships with woody cover, with considerably reduced occurrence (< 0.25) in areas with low cover (< 10 %; Fig. 1). With species responding differently to grass and woody cover on fine scale (0.25-ha plots), gamma (regional) diversity is likely to be elevated in savannas that have patches of high grass biomass and patches with extensive woody cover (duToit 2003).

The strong species-level responses of small mammals also suggest that woody cover contains important resources for some species. Seed fall can be greater under thickets of woody vegetation that are interspersed throughout a savanna (Whittington-Jones et al. 2008). Due to their nutritional content and ease of handling (Kerley and Erasmus 1991; Happold 2001), woody plants should also provide valuable food resources for a number of rodents in this study (*Mus minutoides, Mastomys natalensis, Dendromus* sp*., Saccostomus campestris, Aethomys* sp.; Miller 1994; Goheen et al. 2004). However, these small mammals had inconsistent responses to woody cover and the small mammals that responded positively had broad dietary preferences (Tables 1, 2). With no clear link between increased woody cover or grass biomass and the dietary preferences of small mammals, it appears that food resources were not the dominant driver of species occurrence and richness. Instead, woody cover and grass likely provide protective cover from predators. Protective cover from grass and shrubs can have a strong influence on the movements and distribution of many small mammals in our study (*Micaelamys namaquensis, Saccostomus campestris, Mus minutoides, Aethomys* sp*., Lemniscomys rosalia*), and its influence on spatial patterns of species richness in African savannas should be investigated further

(Whittington-Jones et al. 2008; Hagenah et al. 2009; Long et al. 2012; Banasiak and Shrader 2015).

LITERATURE CITED

Abu Baker, M. A., and J. S. Brown. 2014. Foraging in space and time structure an African small mammal community. Oecologia 175:521-535.

Andersen, A. N., J. C. Z. Woinarski, and C. L. Parr. 2012. Savanna burning for biodiversity: fire management for faunal conservation in Australian tropical savannas. Austral Ecology 37:658-667.

Asner, G. P., and S. R. Levick. 2012. Landscape-scale effects of herbivores on treefall in African savannas. Ecology Letters 15:1211-1217.

Avenant, N. 2011. The potential utility of rodents and other small mammals as indicators of

    ecosystem 'integrity' of South African grasslands. Wildlife Research 38:626-639.

Avenant, N. L., and P. Cavallini. 2007. Correlating rodent community structure with ecological

    integrity, Tussen-die-Riviere Nature Reserve, Free State province, South Africa.

    Integrative Zoology 2:212–219.

Banasiak, N., and A. M. Shrader. 2015. Similarities in perceived predation risk prevent temporal

    partitioning of food by rodents in an African grassland. Journal of Mammalogy 97:483-

    489.

Bergstrom, B. J. 2013. Would East African savanna rodents inhibit woody encroachment?

    Evidence from stable isotopes and microhistological analysis of feces. Journal of

    Mammalogy 94:436-447.

Birkett, A., and B. Stevens-Wood. 2005. Effect of low rainfall and browsing by large herbivores

    on an enclosed savannah habitat in Kenya. African Journal of Ecology 43:123-130.

Blanc, J. J., R. F. W. Barnes, G. C. Craig, C. R. Thouless, I. Douglas-Hamilton, and J. A. Hart.

    2003. African elephant status report 2002: an update from the African Elephant Database.

    Occasional Paper of the IUCN Species Survival Commission 29. International Union for

    the Conservation of Nature, Gland.

Blaum, N., E. Rossmanith, and F. Jeltsch. 2007. Land use affects rodent communities in Kalahari

    savannah rangelands. African Journal of Ecology 45:189-195.

Blaum, N., C. Seymour, E. Rossmanith, M. Schwager, and F. Jeltsch. 2009. Changes in

    arthropod diversity along a land use gradient of shrub cover in savanna rangelands:

    identification of suitable indicators. Biodiversity and Conservation 18:1187-1199.

Bond, W. J. 2008. What limits trees in C4 grasslands and savannas? Annual Review of Ecology, Evolution, and Systematics 39:641-659.

Canfield, R. H. 1941. Application of the line interception method in sampling range vegetation. Journal of Forestry 39:388-394.

Cremene, C., G. Groza, L. Rakosy, A. A. Schileyko, A. Baur, A. Erhardt, and B. Baur. 2005. Alterations of steppe-like grasslands in Eastern Europe: a threat to regional biodiversity hotspots. Conservation Biology 19:1606-1618.

Dorazio, R. M., and J. A. Royle. 2005. Estimating size and composition of biological communities by modeling the occurrence of species. Journal of the American Statistical Association 100:389-398.

Dorazio, R. M., J. A. Royle, B. Söderström, and A. Glimskär. 2006. Estimating species richness and accumulation by modeling species occurrence and detectability. Ecology 87:842-854.

Eldridge, D. J., M. A. Bowker, F. T. Maestre, E. Roger, J. F. Reynolds, and W. G. Whitford. 2011. Impacts of shrub encroachment on ecosystem structure and functioning: towards a global synthesis. Ecology Letters 14:709-722.

February, E. C., S. I. Higgins, W. J. Bond and L. Swemmer. 2013. Influence of competition and rainfall manipulation on the growth responses of savanna trees and grasses. Ecology 94: 1155-1164.

Ferreira, S., S. Freitag-Ronaldson, D. Pienaar, and H. Hendriks. 2012. Elephant management plan: Kruger National Park. Scientific Services and Kruger Park Management of SANParks. Skukuza, South Africa.

Fenton, M. B., et al. 1998. Bats and the loss of tree canopy in African woodlands. Conservation Biology 12:399-407.

Foster, C. N., P. S. Barton, and D. B. Lindenmayer. 2014. Effects of large native herbivores on other animals. Journal of Applied Ecology 51:929-938.

Gelman, A., J. B. Carlin, H. S. Stern, and D. B. Rubin. 2013. Bayesian data analysis, third edition (texts in statistical science). Chapman and Hall/CRC Press. Boca Raton, Florida.

Goheen, J. R., F. Keesing, B. F. Allan, D. Ogada, and R. S. Ostfeld. 2004. Net effects of large mammals on Acacia seedling survival in an African savanna. *Ecology*:1555-1561.

Hagenah, N., H. H. Prins, and H Olff, H. 2009. Effects of large herbivores on murid rodents in a South African savanna. Journal of Tropical Ecology 25:483-492.

Happold, D. C. D. 2001. Ecology of African small mammals: recent research and perspectives. Pp. 375-414 in African small mammals. Proceedings of the 8th International Symposium on African Small Mammals, Paris, France, 5-9 July 1999 (C. Denys, L. Granjon, and A. Poulet, eds.). IRD Editions. Paris, France.

Hurst, Z. M. et al. 2013. Dynamic edge effects in small mammal communities across a conservation-agricultural interface in Swaziland. PLoS One, 8(9): e74520. doi:10.1371/journal.pone.0074520.

Hurst, Z. M., R. A. McCleery, B. A. Collier, N. J. Silvy, P. J. Taylor, and A. Monadjem. 2014. Linking changes in small mammal communities to ecosystem functions in an agricultural landscape. Mammalian Biology 79:17-23.

Keesing, F. 2000. Cryptic consumers and the ecology of an African savanna. BioScience 50: 205-215.

Kerley, C. I. H., and T. Erasmus. 1991. What do mice select for in seeds? Oecologia 86:261-267.

Kern, N. G. 1981. The influence of fire on small mammals of the Kruger National Park. Koedoe 24:125-157.

Kery, M., and J. A. Royle. 2016. Applied hierarchical modeling in ecology: analysis of

    distribution, abundance and species richness in R and BUGS. Academic Press.

    Cambridge, Massachusetts.

Koerner, S. E., and S. L. Collins. 2014. Interactive effects of grazing, drought, and fire on

    grassland plant communities in North America and South Africa. Ecology 95:98-109.

Langevelde, F. V., et al. 2003. Effects of fire and herbivory on the stability of savanna

    ecosystems. Ecology 84:337-350.

Lemmon, P. E. 1956. A spherical densiometer for estimating forest overstory density. Forest

    Science 2:314-320.

Levick, S. R., G. P. Asner, T. Kennedy-Bowdoin, and D. E. Knapp. 2009. The relative influence

    of fire and herbivory on savanna three-dimensional vegetation structure. Biological

    Conservation 142:1693-1700.

Long, A. K., et al. 2012. Multi-scale habitat selection of *Mus minutoides* in the Lowveld of

    Swaziland. African Journal of Ecology 51:493-500.

MacKenzie, D. I., J. D. Nichols, J. A. Royle, K. H. Pollock, L. L. Bailey, and J. E. Hines.

    2006. Occupancy estimation and modeling: inferring patterns and dynamics of species

    occurrence. Academic Press. Cambridge, Massachusetts.

Matondo, J. I., G. Peter, and K. M. Msibi. 2004. Evaluation of the impact of climate change on

    hydrology and water resources in Swaziland: part 1. Physics and Chemistry of the Earth,

    Parts A/B/C 29:1181-1191.

Matondo, J. I., G. Peter, and K. M. Msibi. 2005. Managing water under climate change for peace

    and prosperity in Swaziland. Physics and Chemistry of the Earth, Parts A/B/C 30: 943-

    949.

McCleery, R. M, A. Monadjem, B. Baiser, R. Fletcher, K. Vickers, and L. Kruger. 2018. Animal diversity declines with broad-scale homogenization of canopy cover in African savannas. Biological Conservation 226:54-62.

Miller, M. F. 1994. Seed predation by nocturnal rodents in an African savanna ecosystem. South African Journal of Zoology 29(4):262-266.

Monadjem, A. 1997*a*. Habitat preferences and biomasses of small mammals in Swaziland. African Journal of Ecology 35:64-72.

Monadjem, A. 1997*b*. Stomach contents of 19 species of small mammals from Swaziland. South African Journal of Zoology 32:23-26.

Monadjem, A. 1998. Mammals of Swaziland. Conservation Trust of Swaziland. Mbabane, Swaziland.

Monadjem, A. 1999. Population dynamics of *Mus minutoides* and *Steatomys pratensis* (Muridae: Rodentia) in a subtropical grassland in Swaziland. African Journal of Ecology 37:202-210.

Monadjem, A., and M. R. Perrin. 1998. The effect of supplementary food on the home range of the multimammate mouse, *Mastomys natalensis*. South African Journal of Ecology 28:1-3.

Monadjem, A., and M. R. Perrin. 2003. Population fluctuations and community structure of small mammals in a Swaziland grassland over a three-year period. African Zoology 38:127-137.

Monadjem, A., P. J. Taylor, C. Denys, and F. P. D. Cotterill. 2015. Rodents of Sub-Saharan Africa: a biogeographic and taxonomic synthesis. Walter de Gruyter. Berlin, Germany.

O'Connor, T. G., J. R. Puttick, and M. T. Hoffman. 2014. Bush encroachment in southern

      Africa: changes and causes. African Journal of Range and Forage Science 31:67-88.

Parr, C. L., C. E. R. Lehmann, W. J. Bond, W. A. Hoffman, and A. N. Andersen. 2014. Tropical

      grassy biomes: misunderstood, neglected, and under threat. Trends in Ecology and

      Evolution 29:205-213.

Pellegrini, A. F. A., R. M. Pringle, N. Govender, and L. O. Hedin. 2017. Woody plant biomass

      and carbon exchange depend on elephant-fire interactions across a productivity gradient

      in African savanna. Journal of Ecology 105:111-121.

Plummer, M. 2003. JAGS: A program for analysis of Bayesian graphical models using Gibbs

      sampling. 3rd International Workshop on Distributed Statistical Computing (DSC 2003).

      Vienna, Austria.

R Development Core Team. 2016. R: a language and environment for statistical computing. R

      Foundation for Statistical Computing. Vienna, Austria.dwww.R-project.org/.

Ratajczak, Z., J. B. Nippert, and S. L. Collins. 2012. Woody encroachment decreases diversity

      across North American grasslands and savannas. Ecology 93:697-703.

Roques, K. G., T. G. O'Connor, and A. R. Watkinson. 2001. Dynamics of shrub encroachment in

      an African savanna: relative influences of fire, herbivory, rainfall and density

      dependence. Journal of Applied Ecology 38:268-280.

Sankaran, M., J. Ratnam, and N. Hanan. 2008. Woody cover in African savannas: the role of

      resources, fire and herbivory. Global Ecology and Biogeography 17:236–245.

Sankaran, M., et al. 2005. Determinants of woody cover in African savannas. Nature 438:846-

      849.

Shorrocks, B. 2007. The biology of African savannahs. Oxford University Press. New York, New York.

Sikes, R. S., and the Animal Care and Use Committee of the American Society of Mammalogists. 2016. 2016 Guidelines of the American Society of Mammalogists for the use of wild mammals in research and education. Journal of Mammalogy 97:663-688.

Sirami, C., and A. Monadjem. 2012. Changes in bird communities in Swaziland savannas between 1998 and 2008 owing to shrub encroachment. Diversity and Distributions 18:390-400.

Smit, I. P. J., C. F. Smit, N. Govender, M. van der Linde, and S. MacFadyen. 2013. Rainfall, geology and landscape position generate large-scale spatiotemporal fire pattern heterogeneity in an African savanna. Ecography 36:447-459.

Smit, I. P. J., and 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(9), e0137857. doi:10.1371/journal.pone.0137857.

Skinner, J. D., and C. T. Chimimba. 2005. The mammals of the Southern African Subregion. Cambridge University Press. Cambridge, United Kingdom.

Soto-Shoender, J. R., R. A. McCleery, A. Monadjem, and D.C. Gwinn. 2018. The importance of grass cover for mammalian diversity and habitat associations in a bush encroached savanna. Biological Conservation 221:127-136.

Stanton, R., W. W. Boone, J. Soto-Shoender, R. J. Fletcher, N. Blaum, and R. A. McCleery. 2018. Shrub encroachment and vertebrate diversity: a global meta-analysis. Global Ecology and Biogeography 27: 368-379 .

Staver, A. C., W. J. Bond, W. D. Stock, S. J. Van Rensburg, and M. S. Waldram. 2009. Browsing and fire interact to suppress tree density in an African savanna. Ecological Applications 19:1909-1919.

Stevens, N., B. F. N. Erasmus, S. Archibald, and W. J. Bond. 2016. Woody encroachment over 70 years in South African savannahs: overgrazing, global change or extinction aftershock? Philosophical Transactions of the Royal Society B: Biological Sciences 371:20150437.

Stevens, N., C. E. R. Lehmann, B. P. Murphy, and G. Durigan. 2017. Savanna woody encroachment is widespread across three continents. Global Change Biology 23:235-244.

Tilman, D., F. Isbell, and J. M. Cowles. 2014. Biodiversity and ecosystem functioning. Afnnual Review of Ecology, Evolution, and Systematics 45:471-493.

Treydte, A. C., C. C. Grant, and F. Jeltsch. 2009. Tree size and herbivory determine below-canopy grass quality and species composition in savannahs. Biodiversity and Conservation 18:3989-4002.

van Deventer, M., and J. A. J. Nel. 2006. Habitat, food, and small mammal community structure in Namaqualand. Koedoe 49:99-109.

Vernon, C. J. 1972. An analysis of owl pellets collected in southern Africa. Ostrich 43:109-124.

Whittington-Jones, G. M., R. T. F. Bernard, and D. M. Parker. 2008. Bushclumps as refugia for small mammals in two Eastern Cape conservation areas. African Zoology 43:273-276.

Williams, S. T., N. Maree, P. Taylor, S. R. Belmain, M. Keith, L. H. Swanepoel .2018. Predation by small mammalian carnivores in rural agro-ecosystems: An undervalued ecosystem service?. Ecosystem Services 30:362-371.

Zambatis, N., P. J. K. Zacharias, C. D. Morris, and J. F. Derry. 2006. Re-evaluation of the disc

    pasture meter calibration for the Kruger National Park, South Africa. African Journal of

    Range and Forage Science 23:85-97.
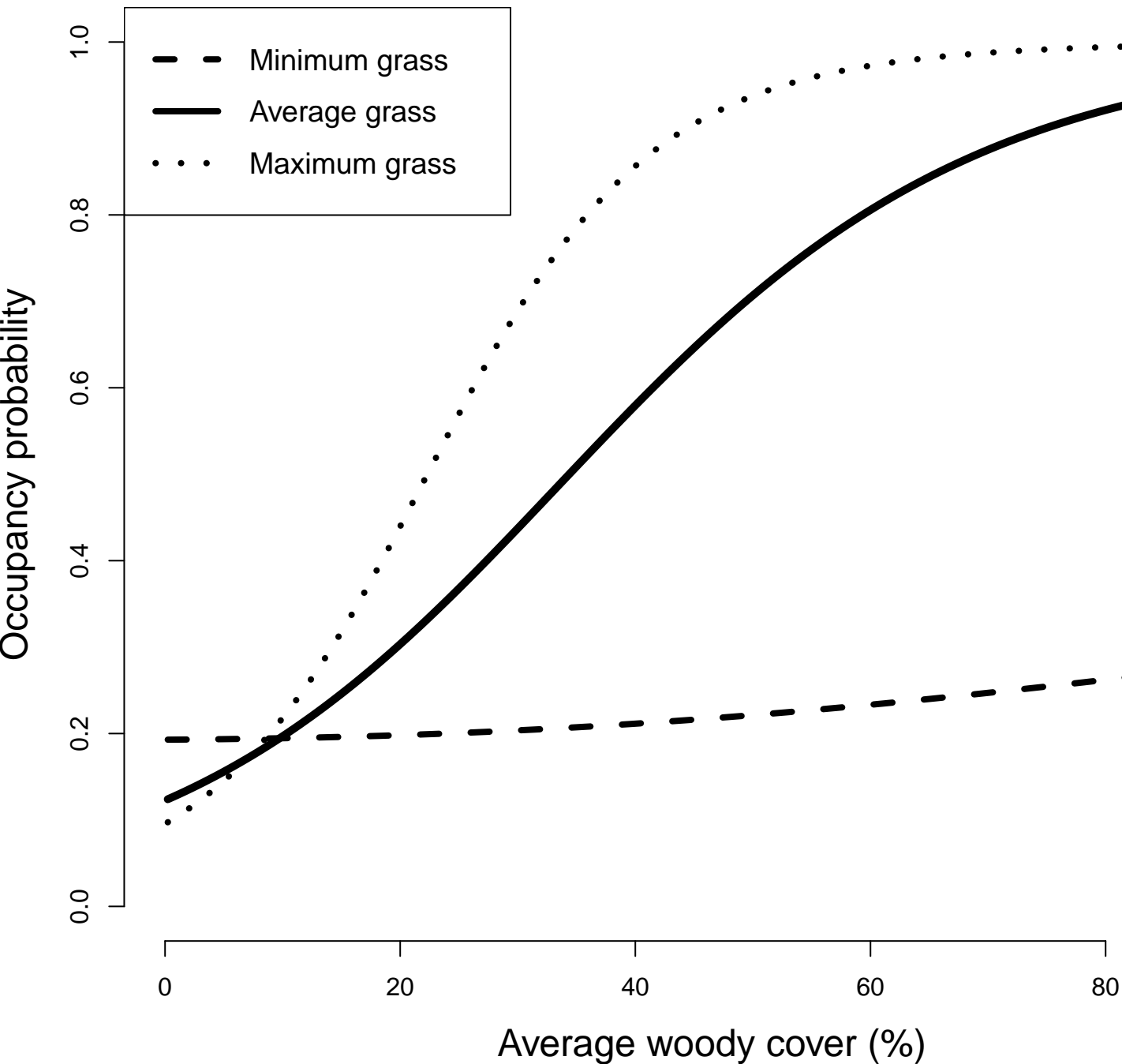
Supplementary Data

Supplementary Data SD1.---Average shrub cover, tree canopy cover, tree density, and grass biomass levels and standard deviations (SD) per study grid from vegetation sampled in Kruger National Park, South Africa, and Mbuluzi Game Reserve, Mlawula Nature Reserve, and Hlane Royal National Park, Eswatini, from Nov 2013 - June 2015.

Grid	Shrub Cover (%) Mean	SD	Canopy Cover (%) Mean	SD	Tree Density Mean	SD	Grass Biomass (kg/ha) Mean	SD
1	4.635	2.166	8.719	8.380	6.000	5.388	3125.312	898.876
2	6.908	4.787	2.490	3.748	0.111	0.319	2879.631	596.853
3	3.791	3.113	4.815	5.234	4.889	6.351	2609.174	1289.742
4	7.060	3.836	5.493	5.391	3.444	2.443	2058.060	1185.823
5	31.783	18.497	36.024	18.039	26.778	19.775	1513.266	1029.037
6	41.112	27.707	58.390	25.581	33.111	16.668	1486.461	1101.067
7	40.800	19.222	39.799	30.212	59.333	69.389	2044.234	1630.365
8	41.822	16.185	43.864	18.940	51.111	30.974	2126.560	1054.927
9	32.856	14.744	52.024	15.944	22.889	9.386	1617.686	443.683
10	39.378	20.226	45.316	19.305	18.000	10.583	1624.756	424.553

Supplementary Data SD2.---The modeled occupancy probability for each species along the tree density gradient throughout the study plots in Kruger National Park, South Africa, and Mbuluzi Game Reserve, Mlawula Nature Reserve, and Hlane Royal National Park, Eswatini, from Nov 2013 - June 2015. The average community effect is displayed as a black line. Species responses are in grey and all have 95% CRI that overlap zero
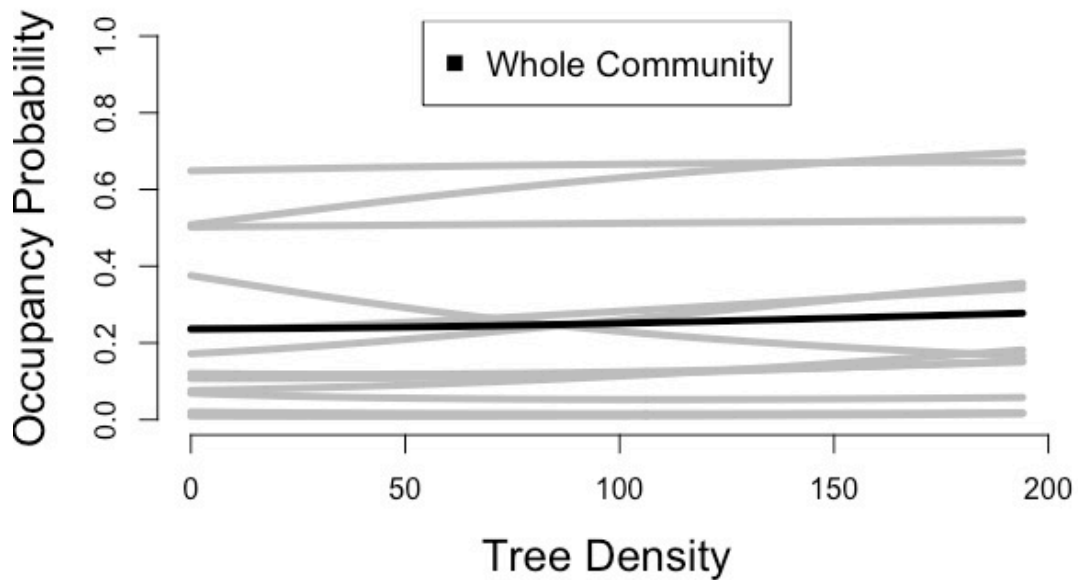
Supplementary Data SD3.---The modeled occupancy probability for Lemniscomys rosalia along the average woody cover gradient (calculated as the average between shrub cover and canopy cover estimates) interacting with different levels of grass biomass throughout the study plots in Kruger National Park, South Africa, and Mbuluzi Game Reserve, Mlawula Nature Reserve, and Hlane Royal National Park, Eswatini, from Nov 2013 – June 2015. The effect under average grass biomass is displayed as a black line, with the minimum level of grass in blue, and the maximum level of grass in red.

Supplementary Data SD4.---The modeled occupancy probability for the whole community along the tree density gradient (trees per 0.25-ha plot) throughout the study plots in Kruger National Park, South Africa, and Mbuluzi Game Reserve, Mlawula Nature Reserve, and Hlane Royal National Park, Eswatini, from Nov 2013 – June 2015. The average community effect is displayed as a black line, with 95% CRI in blue.