



## Vegetation structure shapes small mammal communities in African savannas

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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 livetrapped for over 2 years to build multispecies 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.

Key words: grass, occupancy modeling, rodent, shrub encroachment

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; Soto-Shoender et al. 2018; Stanton 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 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*, *L. rosalia*, *Crociodura hirta*, *Crociodura* spp.) would increase in occurrence with increased grass biomass, while those species that have previously been associated with shrub cover (*A. 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.

## 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 km<sup>2</sup>), Mlawula Nature Reserve (165 km<sup>2</sup>), and Hlane Royal National Park (220 km<sup>2</sup>). 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 to 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 km<sup>2</sup>). 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 *S. birrea*

**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 <sup>a</sup>	Predicted response
<i>Aethomys ineptus</i>	78	Granivore–herbivore	Mixed	↑Shrub or grass cover	Grass, woody
<i>Dendromus mystacalis</i>	8	Granivore–insectivore	Open	↑Tall grass	Grass
<i>Gerbilliscus leucogaster</i>	70	Omnivore	Open	↑Sandy soil	
<i>Lemniscomys rosalia</i>	57	Herbivore–granivore	Open-closed	↑Tall grass	Grass
<i>Mastomys natalensis</i>	46	Granivore–omnivore	Open, disturbed	↓Grass-shrub cover	
<i>Micaelamys namaquensis</i>	48	Herbivore–granivore	Open-closed	↑Rock	
<i>Mus minutoides</i>	6	Omnivore	Open-closed, disturbed	↑Shrub	Woody
<i>Saccostomus campestris</i>	48	Granivore	Open	↓Grass-shrub cover	
<i>Steatomys pratensis</i>	23	Granivore	Open	↑Sandy soil	Grass
<i>Crociodura hirta</i>	16	Insectivore	Open	↑Thick grass	Grass
<i>Crociodura</i> spp.	9	Insectivore	Open	↑Thick grass	Grass
<i>Elephantulus brachyrhynchus</i>	44	Insectivore	Open	↑Shrub cover	Woody

<sup>a</sup> ↑ = responds positively to increased structure; ↓ = responds negatively to increased structure.

and *S. nigrescens*, while the shrub layer was dominated by *D. 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/km<sup>2</sup> (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 to 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, 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 *L. rosalia* and *E. 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-m<sup>2</sup> plots nested in a 3 × 3 design spaced 250 m apart (90 plots in total). We baited 20 Sherman folding traps (3 × 3.5 × 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 (21 November to 1 February) and winter dry seasons (15 May to 1 August) 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 m<sup>2</sup> (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 to 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 (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 multispecies 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 ( $\Psi$ ) 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  $\psi_{ik}$  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 *Crocicidura*) in the model. We grouped small (< 12 g) *Crocicidura* 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:

$$\text{logit}(p_{ijk}) = \alpha_k + \alpha 1_k * \text{season}_i + \alpha 2_k * \text{year}_i$$



We assumed that  $\Psi$  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  $\Psi$  with the four vegetation covariates (shrub cover, tree canopy cover, grass biomass, and tree density) as random effects with hierarchical hyper-parameters using noninformative 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:

$$\begin{aligned} \text{logit}(\psi_{ik}) = & \beta_k + \beta_{1k} * \text{woodycover}_i \\ & + \beta_{2k} * \text{grassbiomass}_i \\ & + \beta_{3k} * \text{treedensity}_i \\ & + \beta_{4k} * \text{woodycover}_i * \text{grassbiomass}_i \\ & + \beta_{5k} * \text{grid}_i \end{aligned}$$

Adapting code from [Kery and Royle \(2016\)](#), we used noninformative 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 Markov Chain Monte Carlo iterations with three chains, using 12,000 samples (thin rate = 10, burn-in = 60,000). We assumed chain convergence when  $R_{\text{hat}} < 1.2$  ([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 ( $\beta_{1k}, \alpha_{1k}, \dots$ ). 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  $\Psi$  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% to 92.81% with an average of 27.35% cover across all plots and seasons. Tree density ranged from 0 to 194 trees per plot with an average of 22.56 trees per plot. Grass biomass ranged from 56.17 to 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 (*E. brachyrhynchus*), and one genus of shrew (*Crociodura*). 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 (*M. minutoides*:  $x = 16.70$ ,  $SE = 4.86$ ; *L. rosalia*:  $x = 18.40$ ,  $SE = 6.22$ ) and the wet season ( $x = 6.80$ ,  $SE = 2.69$ ;  $x = 9.70$ ,  $SE = 3.18$ , respectively). *Steatomys pratensis* was also common in the wet season ( $x = 12.20$ ,  $SE = 7.20$ ) but not in the dry season ( $x = 0.70$ ,  $SE = 0.40$ ).

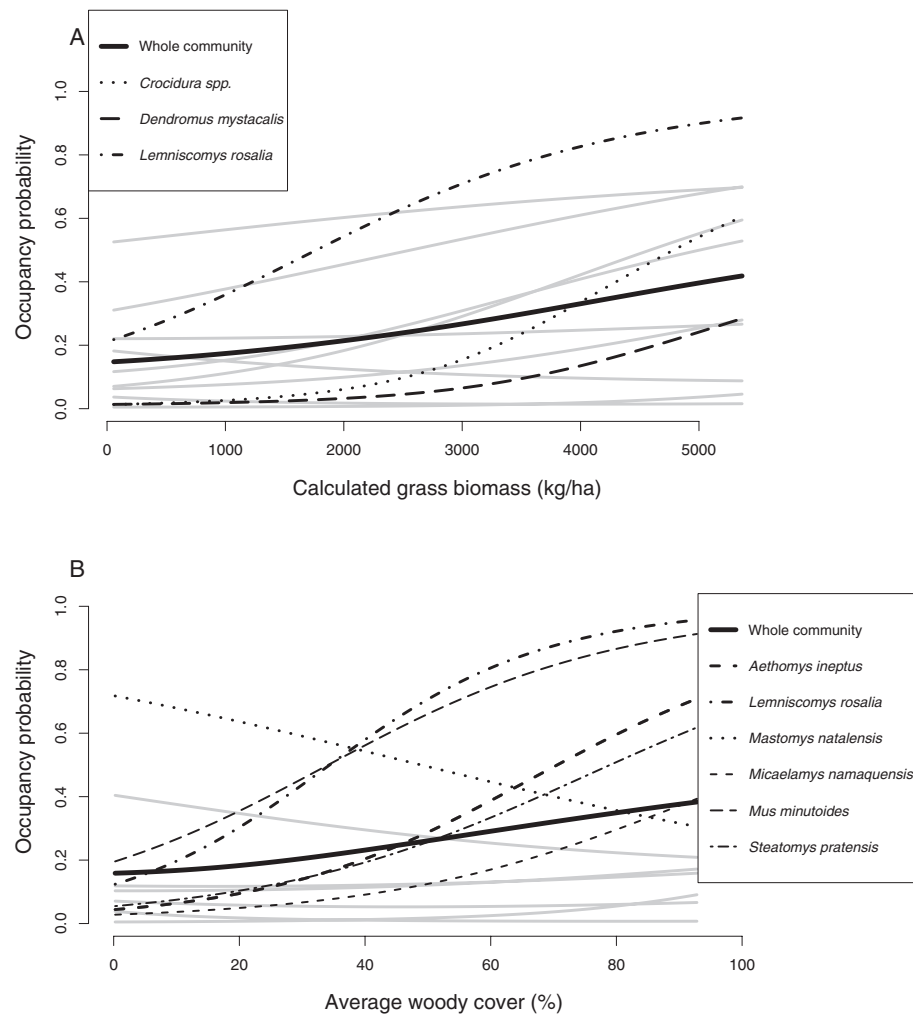
**Multispecies occupancy model: species level.**—The most commonly caught species had the highest  $\Psi$  (*L. rosalia*— $\Psi = 0.67$ , 95% CRI: 0.43, 0.87; *M. minutoides*— $\Psi = 0.63$ , 95% CRI: 0.36, 0.91; *M. natalensis*— $\Psi = 0.51$ , 95% CRI: 0.33, 0.69; [Table 2](#)) but the predicted  $\Psi$  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 *S. pratensis* had increased detection rates in the wet season.

Occupancy for three species increased as grass biomass increased (positive 95% CRI), and no species declined with increased grass biomass ([Fig. 1A](#)). The  $\Psi$  of *L. rosalia* increased steadily with grass biomass, reaching  $> 0.80$  at maximum grass biomass ([Fig. 1A](#)). The  $\Psi$  of *D. mystacalis* and *Crociodura* spp. also increased with more grass biomass, although *D. mystacalis* only reached a maximum  $\Psi$  probability of 0.20 at the highest grass biomass. Occupancy of *M. natalensis* and *A. ineptus* also tended to increase with increasing grass biomass ([Fig. 1A](#), increasing gray lines), although their 95% CRIs overlapped zero.

The  $\Psi$  of five species increased as a function of increasing woody cover, with *M. minutoides* and *L. rosalia* showing the strongest positive response, increasing rapidly up to  $\Psi = 0.90$  at the maximum levels of woody cover ([Fig. 1B](#)). *Aethomys ineptus*, *M. namaquensis*, and *S. pratensis* also increased  $\Psi$  with cover, rising at average woody cover  $> 30\%$ . Conversely, *M. natalensis* declined steadily as cover increased, decreasing from  $\Psi = 0.70$  at the lowest levels of woody cover to  $\Psi = 0.30$  at the highest levels of woody cover. *Crociodura hirta* also tended to decline with increases in woody cover ([Fig. 1B](#), declining gray line) but the 95% CRI included zero, indicating that cover

**Table 2.**—The posterior probabilities for species-level occupancy means,  $\psi_{ik}$ , with *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 November 2013 to June 2015.

Species	$\psi_{ik}$	<i>SD</i>	95% <i>CRI</i>	Responses to vegetation
<i>Lemniscomys rosalia</i>	0.665	0.111	(0.434, 0.869)	+ Woody cover, + grass
<i>Mus minutoides</i>	0.627	0.145	(0.356, 0.910)	+ Woody cover
<i>Mastomys natalensis</i>	0.511	0.092	(0.327, 0.689)	– Woody cover
<i>Crocidura hirta</i>	0.280	0.198	(0.049, 0.797)	
<i>Aethomys ineptus</i>	0.256	0.154	(0.071, 0.673)	+ Woody cover
<i>Steatomys pratensis</i>	0.233	0.098	(0.073, 0.447)	+ Woody cover
<i>Saccostomus campestris</i>	0.124	0.088	(0.027, 0.348)	
<i>Crocidura</i> spp.	0.118	0.075	(0.028, 0.310)	+ Grass
<i>Micaelamys namaquensis</i>	0.112	0.061	(0.035, 0.267)	+ Woody cover
<i>Dendromus mystacalis</i>	0.053	0.060	(0.003, 0.205)	+ Grass
<i>Elephantulus brachyrhynchus</i>	0.015	0.015	(0.001, 0.054)	+ Woody cover
<i>Gerbilliscus leucogaster</i>	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 November 2013 to June 2015. The average community effect is displayed as a black line. Species responses with 95% credible intervals (*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.

was not a strong predictor of  $\Psi$ . Tree density had little effect on small mammal species (Supplementary Data SD2), with none of the species showing a strong response.

Only *L. 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 low ( $\Psi = 0.20$ ) when grass was at its lowest level (Supplementary Data SD3).

**Multispecies occupancy model: whole-community level.**—The small mammal whole-community  $\Psi$  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  $\Psi$  ( $\beta = 0.57$ , 95% *CRI*: 0.33, 0.83). Woody cover was a predictor of occupancy for more individual species, but when averaged for the community response the *CRI* 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).

**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 (*L. rosalia*, *D. 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 and 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 (*A. ineptus*, *M. minutoides*, *E. brachyrhynchus*) responded positively to increased woody cover (Tables 1 and 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 because the strong negative response of *M. natalensis* counteracted the positive responses of the six other species (Fig. 1).

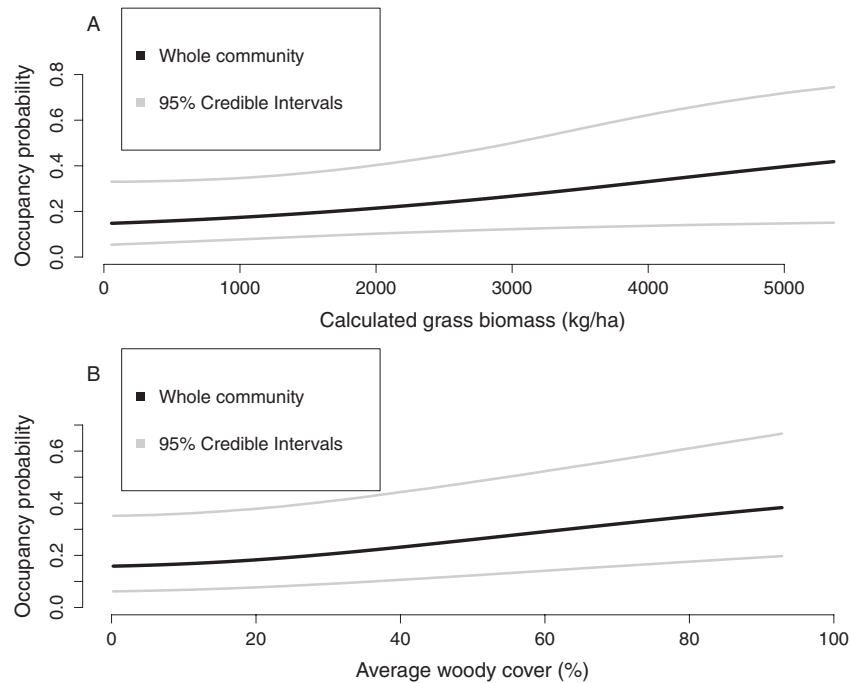
Our results suggest reductions in grass cover may be detrimental to small mammal communities in savanna systems. Savannas with depauperate small mammal communities may see reductions in ecosystem functions such as nutrient cycling, seed dispersal, seed predation, and herbivory (Avenant and Cavallini 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

**Table 3.**—The posterior probabilities for species-level detection means,  $p_{ijk}$ , with *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 November 2013 to June 2015.

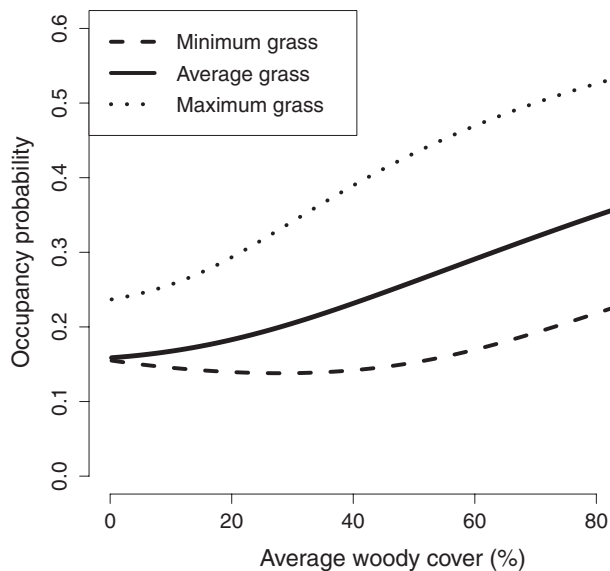
Species	$P_{ijk}$	<i>SD</i>	95% <i>CRI</i>	Responses to season
<i>Mastomys natalensis</i>	0.614	0.020	(0.574, 0.654)	+ Dry
<i>Lemniscomys rosalia</i>	0.524	0.029	(0.467, 0.579)	
<i>Mus minutoides</i>	0.323	0.033	(0.260, 0.390)	+ Dry
<i>Gerbilliscus leucogaster</i>	0.312	0.143	(0.081, 0.621)	
<i>Micaelamys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

**Table 4.**—The posterior probabilities for the global model for the average community-level effects of vegetation covariates (*SD* and 95% credible intervals, 95% *CRI*) on small mammal occupancy ( $\beta_i$ ) and detection ( $\alpha_i$ ) 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 November 2013 to June 2015. Response with <sup>a</sup> indicates 95% *CRI* that did not overlap zero.

Model type	Parameter (covariate)	Mean	<i>SD</i>	95% <i>CRI</i>
$\beta1 + \beta2 + \beta3 + \beta4 + \beta5$	$\beta2$ (grass biomass) <sup>a</sup>	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)



**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 November 2013 to June 2015. The average community effect is displayed as a black line, with 95% credible intervals (CRI) in gray. Note that the x-axes are not the same because they are different vegetation parameters.



**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 November 2013 to 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.

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 birds of prey, which 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 (Blum et al. 2007; Eldridge et al. 2011; Stevens et al. 2017; Stanton et al. 2018). 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 (*M. minutoides* and *L. 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 et al. 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 (*M. minutoides*, *M. 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 and 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 (*M. namaquensis*, *S. campestris*, *M. minutoides*, *Aethomys* sp., *L. 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).

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#### SUPPLEMENTARY DATA

Supplementary data are available at *Journal of Mammalogy* online.

**Supplementary Data SD1.**—Average shrub cover, tree canopy cover, tree density (trees per 0.25-ha plot), and grass biomass levels and *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 November 2013 to June 2015.

**Supplementary Data SD2.**—The modeled occupancy probability for each species 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 November 2013 to June 2015. The average community effect is displayed as a black line. Species responses are in gray and all have 95% credible intervals (*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 November 2013 to 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 November 2013 to June 2015. The average community effect is displayed as a black line, with 95% credible intervals (*CRI*) in blue.

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