

Animal diversity declines with broad-scale homogenization of canopy cover in African savannas



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ABSTRACT

Savannas are increasingly threatened by anthropogenic forces that are causing broad-scale directional shifts in woody vegetation that homogenizes their structure. Yet, whether animal communities respond consistently to changes in woody vegetation in savannas, particularly in terms of the effects of spatial scale, remains poorly understood. We addressed this gap by testing for changes in birds, bats and terrestrial small mammals across a gradient of woody cover in the savannas of southeastern Africa for two years at multiple spatial scales. We found that homogenization of vegetation structure corresponded with decreases in animal richness, diversity and functional diversity. Additionally, metrics of animal diversity declined at opposing ends of a canopy cover gradient (< 10% and > 65%), where we found distinctly different animal assemblages. These patterns were consistently more pronounced on a broader grid scale (30.25 ha) when compared with the plot scale (0.25 ha). The broad-scale reductions in the diversity and functions of animals observed may be indicative of reductions in the resilience, stability and ecosystem function of tropical savannas. Our results suggest that conservation and management aimed at promoting heterogeneity at broad scales may be critical for maintaining diversity and functionality in savannas.

1. Introduction

Savannas are characterized by the co-dominance of grasses and woody vegetation, the ratio of which can vary considerably and may shift rapidly over time and space from minimal woody cover to dense thickets of up to 80% canopy cover (Higgins et al., 2000; Parr et al., 2014). Spatial variation of woody cover that appears to be important in maintaining the diversity and functionality of tropical savannas (Bond, 2008; Scholes et al., 2003; Tilman et al., 2014). However, savannas are increasingly threatened by anthropogenic forces that are causing broad-scale directional shifts in woody vegetation and homogenizing them. The suppression of fire, increased atmospheric CO₂, grazing by cattle and other processes interact to increase woody vegetation across the globe and particularly in Africa (Roques et al., 2001; Stanton et al., 2018; Wigley et al., 2010). In contrast, the loss of big trees, firewood collection, and intensive browsing act to reduce shrub and tree cover (Foster et al., 2014; Hejmanova et al., 2010; Levick et al., 2009; Mograbi et al., 2015).

These disparate and punctuated shifts in the woody vegetation of savannas are likely to have a profound influence on animal communities, altering the diversity, functionality and the structure of these communities (Sirami and Monadjem, 2012; Stanton et al., 2018; Thiollay, 2006). Some research has explored the response of selected animal communities to increasing (Blaum et al., 2007; Sirami and Monadjem, 2012; Sirami et al., 2009) or decreasing (Cumming et al., 1997; Fenton et al., 1998; Ogada et al., 2008; Skarpe et al., 2004) woody cover. However, researchers have an incomplete understanding of how animal communities change across a gradient of woody cover (Foster et al., 2014) and if responses are consistent across taxonomic groups (Stanton et al., 2018). Additionally, we do not know if animal communities respond differently to changes in woody vegetation at different spatial scales, because most studies have only examined animal communities at a local plot scale (Stanton et al., 2018). Because savanna management can impact woody cover in a variety of ways through fire management, cattle grazing, browsing and mechanical clearing (Roques et al., 2001; Staver et al., 2009; Smit et al., 2016)

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assessing the consistency and scale of animal responses to vegetation is critical to understanding and addressing the ecological consequences of these changes.

Our goal was to determine the dominant vegetation features shaping animal communities across a gradient of woody cover. To address this goal, we examined three taxonomic groups (birds, bats and terrestrial small mammals) that are closely linked with vegetation and have not been directly managed or introduced. At broad scales, we predicted measures of diversity would follow the heterogeneity hypothesis (Huston, 1979), increasing with variation in the structure of vegetation and peaking at intermediate levels of canopy cover. Hence, intermediate levels of canopy cover should allow for more heterogeneity by creating a variety of conditions within the grass, shrub and tree layers that could be exploited by different animals. Similarly, we predicted that broad scale changes in woody (shrub and canopy) vegetation would alter animal community composition. We expected communities dominated by grass adapted species in low canopy areas and distinctly different communities of woodland adapted species in high canopy areas. We expected the structural components of vegetation (e.g., canopy, shrub and grass) would be more important for shaping communities of less mobile taxonomic groups (i.e., terrestrial small mammals) at finer scales, due to their restricted mobility and close association with and utilization of specific structural components.

2. Materials and methods

2.1. Study areas

To capture a gradient of woody cover we sampled four protected areas with similar rainfall, soils, flora, and faunal communities on basaltic soils in the flat low-lying savannas of southeastern Africa (Hijmans et al., 2005; Hockey et al., 2005; Mucina and Rutherford, 2006; Skinner and Chimimba, 2005). In northeastern Swaziland we sampled within Mbuluzi Game Reserve (30 km²), Hlane Royal National Park (142 km²) and Mlawula Nature Reserve (165 km²), all of which were predominantly located on nutrient-rich shallow clay soils (Harmse, 1975). These sites had a dense grass cover (*Themda* spp., *Panicum maximum*), a substantial shrub layer dominated by *Dichrostachys cinerea* and variable tree cover dominated by *Senegalia* (*Acacia*) *nigrescens* and *Sclerocarya birrea caffra* (Sirami and Monadjem, 2012). The region has seen an increase in woody cover over the last 70 years (Roques et al., 2001). It has an average annual rainfall of between 500 and 700 mm (Hijmans et al., 2005), with most of the rain falling from

November to February.

The fourth protected area was Kruger National Park (KNP; Fig. 1), established in 1926 and, located in the low-lying savanna region of northeastern South Africa and part of the Great Limpopo Transfrontier Park (GLTP). The GLTP, established in 2002, covers an area of approximately 35,000 km² (Spenceley, 2006), of which, 19,000 km² is covered by KNP. Our study area was located in the Nhlowa Southern Basalt Supersite, southeastern KNP, and dominated by two tree species, *Sclerocarya birrea caffra* and *Senegalia nigrescens*. The area was characterized by shallow nutrient-rich clay soils (Smit et al., 2013) with a *Themeda* spp. dominated grass layer and a variable shrub layer dominated by *Dichrostachys cinerea* and *Gymnosporia senegalensis*. The site has experience a considerable loss in woody cover over the last 70 years (Eckhardt et al., 2000). Rainfall averages 610 mm annually, mostly falling between November and March (Smit et al., 2013).

The composition of ungulate communities varied somewhat between the four sites but impala (*Aepyceros melampus*), blue wildebeest (*Connochaetes taurinus*) and plains zebra (*Equus quagga burchellii*) were common on all them. All the sites had populations of megaherbivores [southern giraffe (*Giraffa giraffa*) and hippopotamus (*Hippopotamus amphibious*)] as well as the large predators [spotted hyena (*Crocuta crocuta*) and leopard (*Panthera pardus*)]. Additionally, our sites in Kruger National park were occasionally visited by white rhinoceros (*Ceratotherium simum*) and lion (*Panthera leo*). Elephants were extirpated from both areas around the turn of the 20th century (Blanc et al., 2003), returning to Kruger National Park but remaining absent on the other sites (Whyte et al., 2003).

Fires occurred frequently in Kruger National Park and Mbuluzi Game Reserve with mean fire return intervals 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-interval of 5–7 and 6–9 years, respectively. Our study sites in Kruger National Park and Mbuluzi Nature Reserve were both burnt towards the end of the dry season (late June–August) in 2011 and 2014. Similarly, our site in Mlawula Nature Reserve was burnt during the same time frame in 2012 and partial in 2014. We recorded no fires on our site in Hlane Royal National Park from 2011 to the end of the study.

2.2. Study design

We intentionally selected animal communities that were not actively managed or hunted (birds, bats and terrestrial small mammals), allowing us to assume that changes in animal communities were a

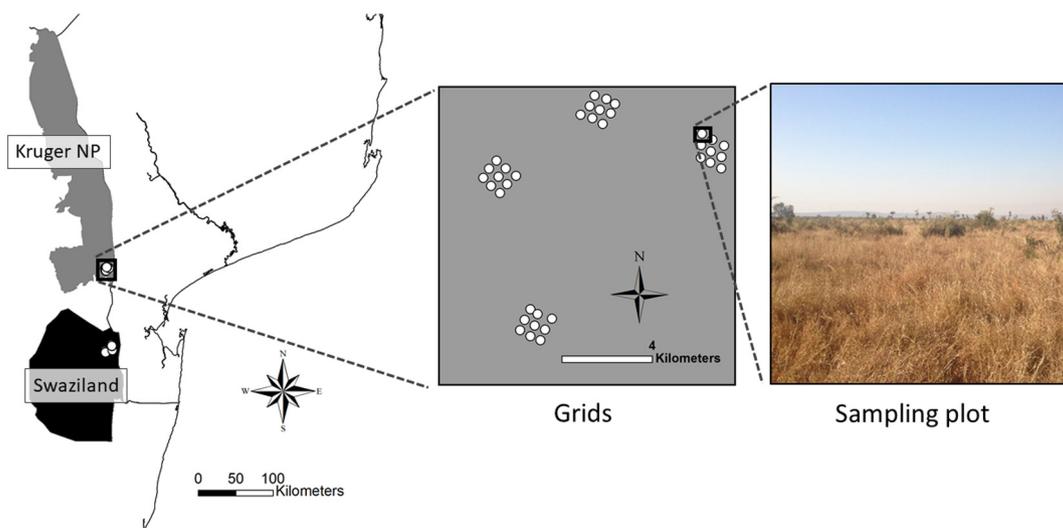


Fig. 1. Depiction of sampling plots (50 m × 50 m) in grids (30.25 ha) on study sites in n Mbuluzi Game Reserve, Hlane Royal National Park and Mlawula Nature Reserve in Swaziland and Kruger National Park, South Africa.

function of environmental rather than direct human influences. We sampled vegetation and animal communities on a total of 90 50 × 50 m plots aggregated into 10 3 × 3 grids (30.25 ha) with 250 m spacing between plots (Fig. 1). This broader scale (grid scale) allowed us to examine community level changes at a scale rarely explored by field studies or experimental exclosures in African savannas (Ogada et al., 2008). We placed four grids (36 plots) in KNP and 2 grids (18 plots) each in Mbuluzi Game Reserve, Hlane Royal National Park and Mlawula Nature Reserve. We placed grids strategically to capture the range of canopy and shrub cover available on each site. All grids were separated by > 1 km. We sampled the vegetation structure at the end of every growing season (May–August) and sampled birds, small mammals, and bats during two wet (November–February) seasons, and birds and small mammals during two dry seasons (May–August). 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 Animal Review Committee Institutional Animal Review (010-13WEC).

2.2.1. Vegetation sampling

We measured the three major structural components of savanna vegetation: grass biomass, shrub cover and canopy cover. To do this, we established two 50 m transects 10 m on either side of the center of each plot. Every 5 m along these transects we measured the biomass of grass (and other herbaceous) material using a disc pasture meter (Bransby and Tainton, 1977). We used previously calibrated estimates to convert raw scores to estimated biomass (kg/km²) (Zambatis et al., 2006). Every 10 m along the transects, we used the line intercept method (Canfield, 1941) to determine the proportion covered with shrubs (woody vegetation between 0.5 m and 5 m in height). Finally, we estimated canopy cover using a concave spherical densiometer (Forestry-Suppliers, Jackson MS) every 10 m along the transects (Lemmon, 1956). For each of these three measures (grass biomass, shrub cover and canopy cover) and an index of heterogeneity (derived from all three measures; see below), we calculated the mean at two scales: plot level (fine scale, $n = 90$) and grid level (broad scale, $n = 10$).

2.2.2. Sampling animal communities

To survey birds, we conducted 10-min point counts at each plot, counting all birds detected within 50 m. We recorded the observer, date, time, and wind speed on a Beaufort scale, twice each morning. We visited each point four times during each season, with the wet season corresponding to the breeding seasons for most terrestrial birds in our study. We rotated three observers among grids and surveyed between 30 min before sunrise and 5 h after. We did not survey when it was raining or wind speeds were > 20 km/h. We randomly sampled grids and plots in a different sequence during each visit. We conducted counts during the wet season from November 21 to January 31 during 2013 and 2014. We conducted dry season counts from May 1 to June 30 during 2014 and 2016. We excluded raptors, waterbirds, shorebirds and nocturnal birds because these species all select habitat at a larger scale than the size of our sampling plots.

We sampled bats during two wet seasons (November 21 to January 31 during 2014 and 2015), when bats in the region are more active and diverse (Monadjem and Reside, 2008). We used Anabat Express detectors (Titely Electronics, Ballina, Australia) in 'monitor' mode to record the calls of free-flying bats. We activated each detector to record from 30 min. before sunset to 30 min. after sunrise. We fixed the detectors at approximately 1.5 m above the ground away from overhanging vegetation. We sampled for two nights each season and experienced equipment failure on approximately 15% of nights so a proportion of sites only recorded 1 night of calls. To adjust for this issue, we used the average number of echolocation calls recorded at each plot during each season.

We examined the echolocation calls recorded with the program ANALOOK (Chris Corben, version 4.8, <http://www.hoarybat.com>) and

developed species filters (or 'acoustic species groups' where calls of different species overlapped). The bat community of north-eastern Swaziland and KNP has been relatively well surveyed (Monadjem and Reside, 2008; Shapiro and Monadjem, 2016) and we used a recently developed call library to set the parameters of the filters (Monadjem et al., 2017). We combined these filters using the scan function in ANALOOK, allowing us to sample the entire data set once. Additionally, to reduce bias in relative abundance measures we used a correction factor based on detection distance of different species of bats in our region (Monadjem et al., 2017). Different bat species can produce echolocation calls that vary greatly in intensity, influencing the distance at which they can be recorded by detectors (Adams et al., 2012), by applying this correction factor we adjusted bat activity measures based on documented call strength intensities (Monadjem et al., 2017). The two species of Pteropodidae (*Epomophorus wahlbergi* and *E. crypturus*) known from the region (Shapiro and Monadjem, 2016) do not echolocate and therefore were not included here.

We surveyed terrestrial small mammals (hereafter "small mammals") on each plot with 20 Sherman folding traps (3 × 3.5 × 9", Tallahassee, FL, USA) in a 4 × 5 formation with 10 m spacing. We identified small mammals to species for rodents, or genus for shrews (*Crociodura*). For each individual, we recorded its mass, sex, and age (adult or juvenile), and measured the length of the hindfoot, body, and tail. We ear-tagged each new individual and recorded recaptures (1005-1, National band Co., Newport, KY, USA). We trapped small mammals during the wet session from November 21 to January 31 during 2013 and 2014. We conducted dry session trapping from May 1 to June 30 during 2014 and 2015.

2.3. Analysis of vegetation

We calculated the plot level means and variance for shrub cover, canopy cover and grass biomass and z-transformed them so they were on a comparable scale. Then we summed the standardized variances to create a heterogeneity index at each plot (Li and Reynolds, 1995; Reynolds et al., 2018). We presented the means and ranges of our measures of vegetation structure (i.e., shrub cover, canopy cover, grass biomass, heterogeneity index) at both spatial scales.

2.4. Diversity metrics

To evaluate the response of animal communities across a gradient of woody cover, we generated three complementary metrics for each taxonomic group at plot and grid scales, species richness, species diversity, and functional diversity. We estimated species richness, species diversity and functional diversity for each sampling session at the plot scale; at the grid scale we aggregated all the detections on the nine plots for each grid. Using detections of birds, small mammals and bats, we estimated the species richness (number of species) on each plot and grid using the Chao estimator (Chao, 1987) to correct for potentially rare species that were missed. We used the same data to estimate Shannon Index (H'), a common measure of community diversity that accounts for species richness with evenness (Krebs, 1999). We estimated richness and Shannon's diversity using the Vegan package (Oksanen et al., 2016) on the R platform v 3.3.1 (R Core Development Team, 2016).

To measure functional diversity, we compiled functional traits for birds, bats and small mammals from published sources (Hockey et al., 2005; Monadjem et al., 2010; Monadjem et al., 2015; Wilman et al., 2014). For each taxonomic group we included traits for morphology, diet, foraging locations, nesting or roost sites, and reproductive characteristics (Appendix A). We measured functional diversity from compiled traits using the functional dispersion metric, FDis, (Laliberte and Legendre, 2010) in the FD package in R. We computed Gower distance matrices (Gower, 1971) for each sampling unit (i.e., grid or plot) by species matrix that contained relative abundances for small mammals, birds and bats. We chose the FDis metric because it tends to be

uncorrelated with species richness, is not strongly influenced by outliers, and it can be calculated using any distance or dissimilarity measure (Laliberte and Legendre, 2010). To remove potential bias associated with decreasing variance surrounding functional diversity measurements as species richness increases (Swenson, 2014), we compared observed FDis values to null distributions of FDis by calculating standard effect size (SES) of FDis (Eq. (1)). To generate null distributions of FDis values, we shuffled the names of the species in our trait data matrices and generated 999 random FDis values for each of our sampling units (Swenson, 2014). We then subtracted the mean of each null distribution from the observed FDis value for each sampling unit and divided this by the standard deviation of the null distribution to generate SES FDis values.

$$SES = \frac{\text{Observed} - \overline{\text{null}}}{sd(\text{null})} \quad (1)$$

Positive SES FDis indicate higher functional diversity than expected compared to the null distribution, whereas negative SES FDis values indicate lower functional diversity compared to the null distribution (Swenson, 2014).

2.5. Animal response to vegetation

To examine the linkages between vegetation and metrics of faunal diversity for all three taxonomic groups, we created models that included the scaled (z-score) average mean and variance of shrub cover, canopy cover and grass biomass, and the heterogeneity index. We also included the potential for curvilinear responses by including a quadratic term for shrubs, canopy and biomass. We examined all variables for multicollinearity by first constructing a correlation matrix. Finding strong associations ($r > 0.70$) between some variables on the plot (heterogeneity index and the variance of canopy cover and shrub cover) and grid (mean canopy cover, mean shrub cover and heterogeneity index; mean and variance of grass biomass; variance in canopy and variance in shrub) scales we developed model that did not include these variables in the same models. We evaluated sets of 24 a priori models at the plot and 15 a priori models at the grid scale (Appendix S1). Additionally, we evaluated variance inflation of variables in each model using the vif command in the car package for R and found no variables with variance inflation terms < 2.7 , except for quadratic terms ($X + X^2$) in curvilinear models, which when centered (all variables z-scored) have no adverse consequences on model performance and interpretation (Robinson and Schumacker, 2009).

We fitted estimates of diversity metrics to each model using a generalized linear mixed model fit to Poisson (richness) or normal distributions (Shannon index, functional diversity) with sampling session (year and season) set as a random intercept. Using spatial correlograms with non-parametric bootstrapping (Bjornstad and Falck, 2001), we checked for and found no evidence of spatial dependence in the residuals of our best fitting models, for each diversity metric for the three taxonomic groups within grids (Beale et al., 2010). We ranked models based on their Akaike Information Criterion corrected for small sample size (AICc) and considered models that were < 2 AICc units of the best model to be competing models. We evaluated the model fit of the competing models using a pseudo R^2 and evaluated the parameters in each of these models. We considered model parameters with β estimates and 95% CI that did not include 0 to be relevant predictors. After evaluating taxonomic level responses, we combined the three taxonomic groups together by scaling (z-score) their diversity metrics. We evaluated the combined responses of faunal richness, diversity and functional diversity to measures of vegetation structure that had relevant and consistent signals in single taxa models. We included each sampling season for each taxon as a random variable and evaluated model parsimony (change in AICc), model fit (R^2), and the 95% CI of model parameters. We conducted our analysis using the packages

Vegan, ncf, lme4 (Bates, 2010), AICcModavg, and ape (Paradis et al., 2004) in R.

2.6. Community composition

Measuring animal diversity is important for understanding how communities respond across a gradient of woody cover; however, these measures cannot identify shifts in community composition. To assess faunal community shifts we conducted partial distance-based redundancy analysis, db-RDA (Laliberte and Legendre, 2010). We conducted separate tests for each taxonomic group at each scale. We used Wisconsin transformation and Bray-Curtis distance (McArdle and Anderson, 2001) on sampling unit by species matrices and conducted partial dbRDA using the “capscale” function in the Vegan package in R. We tested the influence of measures of vegetation structure that had relevant and consistent signals in single taxa models (canopy cover, shrub cover, and our heterogeneity index) on community composition, while partialling out the effect of year, season, and grid for plot scale analyses. We conducted a permutation test to assess the significance of the constraining variables using the ‘anova.cca’ function in the Vegan package.

3. Results

Throughout our surveys, we recorded 155 species of birds, 14 species of small mammals, and nine species (or species groups) of bats. Of all these species, just one bird (Southern white-crowned shrike, *Eurocephalus anguitimens*), and one mammal (African bush squirrel, *Paraxerus cepapi*) were not available as part of the regional species pool at all sites. Both species were only recorded once in KNP. None of the birds or mammals (bats and small mammals) in this study were regionally endemic (Monadjem et al., 2010; Monadjem et al., 2015; Wilman et al., 2014) or considered critically endangered, endangered, threatened or vulnerable by the IUCN (International Union for Conservation of Nature) southern African red data lists (Taylor et al., 2015; Child et al., 2016).

Our measures of canopy cover ($\bar{x} = 31\%$; Plot [0–99]; Grid [0–78]), shrub cover ($\bar{x} = 23\%$; Plot [0–95]; Grid [3–58]), grass biomass ($\bar{x} = 1645 \text{ kg/km}^2$; Plot [100–5419]; Grid [348–3867]) and our heterogeneity index ($\bar{x} = 0$; Plot [–3.1–10.4]; Grid [–2.4–3.5]) captured a broad range of structural conditions at both plot and grid scales.

All of our animal communities showed strong responses to variation in vegetation structure. Across the three taxonomic groups and the two scales, heterogeneity and measures of canopy cover were the most consistent explanatory variables for variation in richness and diversity (Table 1, Appendices S1, S2). Variation in richness and diversity of birds, bats, and small mammals was most commonly explained by a positive association with vegetation heterogeneity, a curvilinear association with mean canopy cover, and a positive or curvilinear association with mean shrub cover (Table 1, Appendices S1, S2). Variation in diversity metrics were also explained by mean grass biomass, with some taxonomic groups being positively associated (small mammals), and others negatively associated (bats, birds). Variation in functional diversity more than the other metrics appeared to change by taxon and scale (Table 1, Appendices S1, S2).

To interpret overall effects of a gradient of woody cover on diversity across taxa, we created composite models of the three taxonomic groups: birds, bats, and small mammals. These models emphasized the consistency of animal communities' response to woody vegetation and heterogeneity across diversity metrics and on both scales (Appendices S2, S3). However, these models consistently fit the data better and showed stronger responses to vegetation on the broader grid scale (Fig. 2, Appendices S2, S3). Measures of model fit (R^2) of the best models at the grid scale (Richness = 0.452, Diversity = 0.625, Functional Diversity = 0.463) were approximately double those on the finer plot scale (Richness = 0.248, Diversity = 0.292, Functional

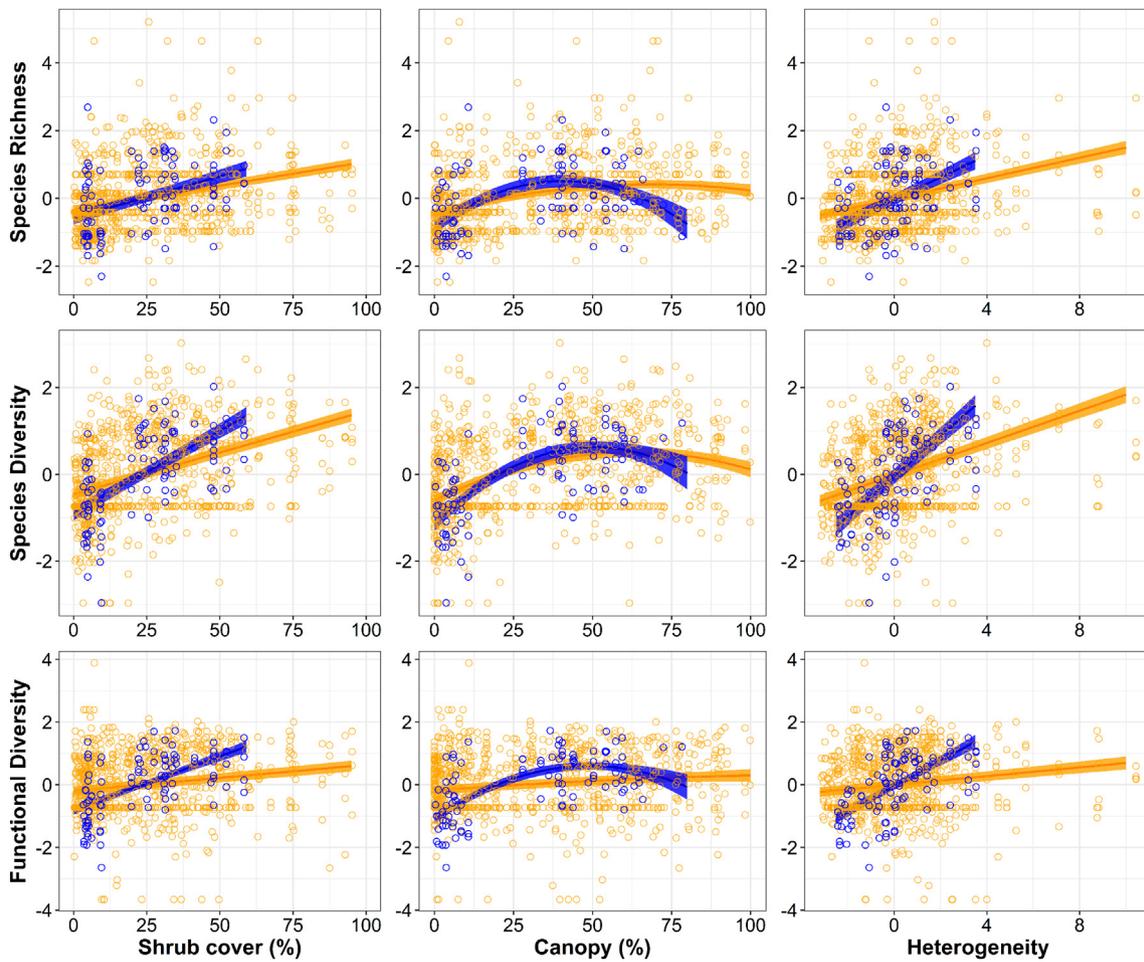


Fig. 2. Predicted response of species richness, species diversity and functional diversity to shrub cover, canopy cover and an index of heterogeneity from composites model that combined measure of birds, bats and small mammals. Lines represent predicted responses and SEs and circles represent data points. Blue indicates grid scale (30.25 ha) and orange indicates plot scale (50 m × 50 m). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

Diversity = 0.225). Parameter estimates (β) of standardized vegetation measures were consistently higher at the grid scale (Fig. 2), suggesting an increased biological response of animal communities to vegetation structure changes at this scale. A curvilinear response of canopy cover

was consistently the most parsimonious model (i.e. lowest AIC) of animal communities' responses to vegetation (Appendix S3). Metrics of diversity began to decrease with canopy cover between 41% and 51% at the grid scale. Decreases in these diversity metrics as a function of

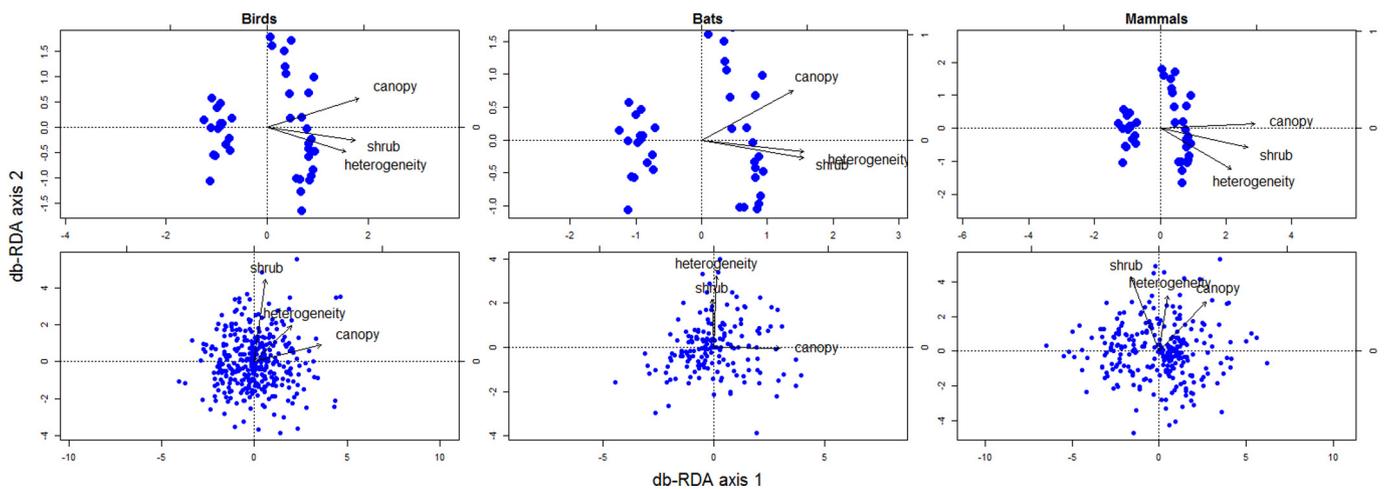


Fig. 3. Distance-based redundancy (db-RDA) plots showing the relationship between bird, bat, and mammals communities and shrub cover, canopy cover, and heterogeneity index. The constraining variables describe 22%, 29%, and 10% of the variation for birds, bats, and small mammals at the grid-scale (top row) while describing < 1% of the variation at the plot-scale (bottom row) for all taxa.

Table 1

Estimates with 95% CI that did not include 0 from best competing models examining the relationship between bird, small mammal and bats and 3 diversity metrics, species richness, species diversity (H') and functional diversity. Models considered diversity metrics as a function of a heterogeneity index and means (m) and variances (v) of grass biomass (*Grass*), canopy cover (*Canopy*) and shrub cover (*Shrub*). Models included quadratic terms for curvilinear effects (*curve*). Plus and minus signs indicate the direction of the relationships.

Metric	Birds		Small mammals		Bats	
	Plot	Grid	Plot	Grid	Plot	Grid
Richness	Grass (v) + Canopy curve Grass(m) –	Heterogeneity +	Heterogeneity + Grass (m) + Canopy(m) +	Heterogeneity +	Heterogeneity + Canopy curve Shrub (m) + Canopy (v) + Grass (m) –	Canopy curve
Diversity	Grass (v) + Canopy curve Grass (m) –	Heterogeneity +	Shrub (m) + Canopy (m) +	Heterogeneity + Canopy (v) + Canopy curve Grass (v) +	Heterogeneity + Canopy curve Shrub (m) ² –	Shrub curve
Function	Grass (m) +	Heterogeneity + Grass (m) –	Shrub curve	Canopy curve Grass (m) +	Heterogeneity + Canopy curve Shrub (v) +	Shrub curve Heterogeneity

canopy cover were more variable at the plot scale (Fig. 2). A positive relationship between heterogeneity and metrics of diversity and richness provided the best model fits (R^2) for composite measures on both scales. A positive relationship with shrub cover was the best fitting and most parsimonious model of functional diversity for composite models at a plot scale (Fig. 2, Appendix S4).

3.1. Community composition

Distance-based redundancy analysis (db-RDA) showed that components of vegetation structure that consistently influenced species composition (i.e., heterogeneity, shrub cover, canopy cover) described < 1% of the variation in community composition for all three taxonomic groups at the plot scale (Fig. 3, Appendix S4). At the broader grid scale, vegetation structure accounted for variation in the composition of small mammal (adjusted $R^2 = 0.1$), bird (adjusted $R^2 = 0.22$), and bat (adjusted $R^2 = 0.29$) communities. For all three taxonomic groups, the first db-RDA axis at the broader grid scale was positively correlated with canopy cover, shrub cover, and heterogeneity (Fig. 3). These axes accounted for 24%, 31%, and 13% of the variation (unadjusted) in community composition for birds, bats, and small mammals, respectively (Fig. 3). Permutation tests indicated that the first db-RDA axes for each taxonomic group was statistically significant ($P < 0.05$; Appendix S4).

4. Discussion

Our results show that the broad scale homogenization of vegetation structure in the savannas of southeastern Africa has major consequences for animal communities. The structural heterogeneity of vegetation has been an organizing principle for conservation in African savannas (du Toit et al., 2003) and is broadly recognized as a driver of animal diversity (Tews et al., 2004). Consistent with our predictions, we found reductions in the variation of vegetation structure corresponded to reductions in animal diversity. Animal diversity also declined at opposing ends of the canopy cover (< 10% or > 65%) gradient. This pattern was likely due to the lack of niche space available in environments with extensive or minimal canopy cover. While the extremes of canopy cover showed similar reductions in diversity, on broader scales this resulted in the creation of distinctly different assemblages of bats, birds and small mammals.

There are numerous anthropogenic and natural drivers of woody

vegetation in tropical savannas. Observed increases of woody vegetation can be caused by increased CO₂ and precipitation, edaphic properties, reductions in fire, loss of megaherbivores and intense grazing (Roques et al., 2001; Sankaran et al., 2008; Stanton et al., 2018; Stevens et al., 2016; Wigley et al., 2010). In this study, at the broader grid scale, animal diversity decreased once canopy cover was > 50% (3 of 10 grids). This may be a growing threat to animal diversity across tropical savannas (Stevens et al., 2017), particularly in mesic savannas with > 700 mm rain, which require disturbance for the persistence of grasses in the system (Sankaran et al., 2008). However, most of the increases in the woody vegetation in African savannas have been manifested in the shrub layer (Stevens et al., 2016) and we found the diversity of most taxonomic groups, at the broader scale, increased or did not change with shrub cover. At a finer scale, some metrics for small mammals and bats showed decreased diversity in areas of thick shrub cover. These results were consistent with a recent meta-analysis suggesting that mammal communities are more likely to respond negatively to an increasing shrub layer compared with other taxonomic groups (Stanton et al., 2018).

We found the lowest levels of animal diversity at the broader grid scale in areas with minimal shrub cover, canopy cover and variation (heterogeneity) in vegetation structure (Fig. 2). In savannas this type of homogenization and loss of woody vegetation can be a function of over grazing, removal of big trees and fire wood collection (Birkett and Stevens-Wood, 2005; Hejmanova et al., 2010; Mograbi et al., 2015; Thiollay, 2006). However, in this study the most likely driver of limited woody cover was the presence of elephants and their synergetic effects with fire. While elephants were extirpated from all our study areas around the same time (circa 1900; Blanc et al., 2003), woody cover has been increasing on the elephant free sites for at least 70 years (Roques et al., 2001) and decreasing on the recolonized site for approximately the same amount of time (Eckhardt et al., 2000). Large trees are generally considered to be immune to fire given their large size and thick bark (Bond and Wilgen, 1996; Lawes et al., 2011; Moncrieff et al., 2008); however, bark stripping from elephant feeding can kill trees outright and leave them vulnerable to mortality from fires (Moncrieff et al., 2008). Therefore, high densities of resident elephants can have a marked influence on the structure of savanna vegetation through their reduction of woody cover (Asner and Levick, 2012; Ben-Shahar, 1993; Kuiper and Parker, 2014). Furthermore, the loss of woody vegetation and reductions in heterogeneity on our sites in Kruger National Park have been directly tied to the presence (and residence time) of

elephants (Asner and Levick, 2012; Levick et al., 2009).

There is a lack of consensus that elephant-altered vegetation can reduce animal diversity (Guldemond et al., 2017; Kuiper and Parker, 2014); however, there is a suite of research findings suggesting the elephant induced loss of woody vegetation has led to declines in animal diversity (Cumming et al., 1997; Fenton et al., 1998; Ogada et al., 2008; Western, 1989). Alternatively, it may be possible that differences in vegetation were a function of subtle differences in the rainfall, soils or the composition of the non-elephant mammalian herbivores community (Sankaran et al., 2008). However, there were only minimal differences in the soils and rainfall across our sites and our data from three different protected areas without elephants suggest that subtle differences in the composition of non-elephant herbivores did not have a meaningful influence on woody vegetation. There was also no indication that the pool of animal species differed among our research sites. In fact, we found that bat, bird, and small mammal communities were indistinguishable at fine scales (Fig. 3). Finally, we saw no evidence that the patterns described in this study were a function of large predators. Had large predators influenced animal communities, the suppression of large predators (i.e. lions) on the elephant free sites should have decreased the diversity of birds, bats and small mammals through the release of meso-predators (Crooks and Soulé, 1999) or other related processes (Estes et al., 2011).

Variation in vegetation structure at fine scales is typical of savannas (Parr et al., 2014) and may explain why animal communities did not show the magnitude of responses at the fine-scale seen at larger scales. Due to their lack of mobility and well-known responses to fine-scale vegetation structure (Price, 1978), we expected non-volant small mammals to show a stronger response at a fine scale. Perhaps reductions in landscape diversity, heterogeneity, and cover hindered their movements into smaller patches of potential habitat (Fahrig, 2001). Alternatively, birds and bats regularly moved in and out of our 50 × 50 m plots and, as expected, responded strongly to changes in vegetation at broader scales (Belisle et al., 2001; Law and Dickman, 1998; Wiens, 1989). At these broader scales, there was consistency between measures of diversity and changes in community composition that were not found at finer scales. Plot-level variation in animal communities was possibly driven by grass biomass (Appendices S1–S3), composition of the vegetation, or other factors that were not measured as a part of this study.

4.1. Management implications

The broad-scale reductions of diversity and animal functions observed here may be indicative of reductions in the resilience and stability of savannas (Elmqvist et al., 2003; Peterson et al., 1998). As functional diversity declines we expect corresponding reductions and in ecosystem functions and processes (Elmqvist et al., 2003; Gagic et al., 2015; Loreau et al., 2001). Reductions in functions from altered animal communities may make it even more difficult to preserve favorable conditions for biodiversity in the planet's already stressed tropical savannas (Parr et al., 2014).

Our results emphasize that heterogeneity at relatively broad scales supports higher biodiversity relative to more homogenized areas. Efforts to maintain and restore savannas that have been homogenized from an increased canopy include the mechanical removal of trees and shrubs to reduce woody vegetation, allowing for an open canopy and increased grass cover (Smit, 2005; Isaacs et al., 2013). Such mechanical thinning should target fast growing species, particularly where they occur in clusters (Bai et al., 2009) and seed the resulting bare patches with native grass seeds (Schwarz et al., 2017; Soto-Shoender et al., 2018). Managers may also use frequent high-intensity fires as a stand-alone method for controlling woody plants (Smit et al., 2016) or couple prescribed fires with thinning or browsing (Smit, 2004; Staver et al., 2009). Most importantly, efforts to reduce canopy cover through thinning, fire and browsing all require sustained management efforts to

ensure any long-term benefits (Smit, 2004).

Alternatively, savannas that have been homogenized due to the loss of woody vegetation are likely to benefit from a reduction in browsers such as impala and goats, that have been shown to limit recruitment and growth of trees (Moe et al., 2009), and from reductions in intensity and frequency of fire (Staver et al., 2009; Smit et al., 2016). Additionally, numerous options, such as creating habitat corridors, removing surface water, translocations, contraception, and disturbance stimuli have been proposed to reduce elephant activity, but none have been broadly implemented (Van Aarde and Jackson, 2007; Ferreira et al., 2012; Asner et al., 2016). Managers' options to reduce elephant activity may be constrained by costs and political realities or they may choose to accept decreased canopy cover and reduced biodiversity in some areas for the benefit of tourists, public opinion and planet's dwindling elephant population (Owen-Smith et al., 2006).

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