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# 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 $CO_2$, 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; Hejcmanova 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 $km^2$), Hlane Royal National Park (142 $km^2$) and Mlawula Nature Reserve (165 $km^2$), 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 $km^2$ (Spenceley, 2006), of which, 19,000 $km^2$ is covered by KNP. Our study area was located in the Nhlowa Southern Basalt Supersite, southeastern KNP, and dominated by two tree species, *Sclerocarrya 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 Malwula 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

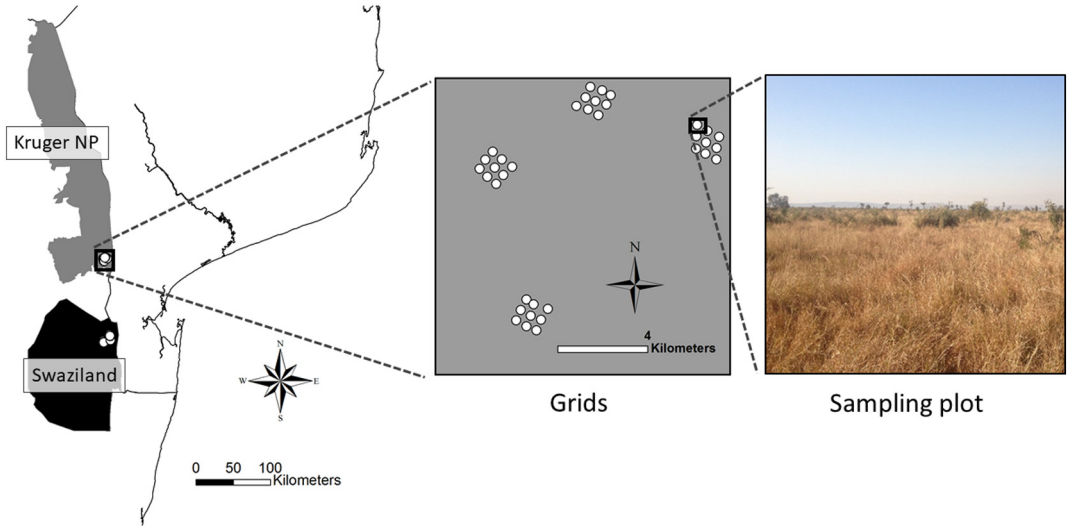


**Fig. 1.** Depiction of sampling plots (50 m × 50 m) in grids (30.25 ha) on study sites in n Mbuluzi Game Reserve, Hlane Royal National Park and Mlawula Nature Reserve in Swaziland and Kruger National Park, South Africa.