

At what scale does heterogeneity affect two meso-carnivore species with different home range sizes?

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Introduction

Landscapes are heterogeneous areas, characterized by the structure or distribution of energy, resources, and organisms, the function or interaction between those elements, and how they change through time (Turner 1989). Studies show a positive correlation between landscape heterogeneity and biodiversity, particularly in human-dominated landscapes (Tews et al. 2003) where industrial scale agricultural production and rural development are the most prominent anthropogenic influences (Foley 2005). Savannas in developing countries are experiencing increasing large-scale land conversion, creating an intricate mosaic of various land uses meshed within savanna habitat. In addition, major ecological changes over the past century have altered savannas; in particular the loss of key browsers and increased bush encroachment (Roques et al. 2001). Heterogeneity is critical for savanna systems, and the diversity they hold (Beale et al. 2013), but the scale at which heterogeneity is most influential to organisms is unclear.

Land use change generates landscape heterogeneity that can be measured via two key components: composition and configuration. Landscape configuration is the spatial arrangement of patches and is the component capturing the structural patterns seen in the landscape (Gustafson 1998). Landscape configuration, for instance, the distribution of resources among habitat patches, the amount of edge, and connectivity between patches influences how animals with different habitat requirements interact with their environment (Taylor et al. 1993). In addition to landscape configuration, landscape composition also has leverage in the landscape. Landscape composition is the diversity and relative abundance of land use types, measured using

non-spatial metrics (Dunning et al. 1992). For example, Ramesh and Downs (2013) found that servals (*Leptailurus serval*) in the Drakensberg Midlands of South Africa were more abundant in agriculture in comparison to other land use types, suggesting that different land use types provide resources that others don't.

Composition and configuration has strong implications for how animals use their surroundings and is a determinant for what resources are available to them (Pearson et al. 1999). However, organisms can respond to heterogeneity at multiple spatial and temporal scales (Turner 1989, Gehring and Swihart 2002). The broader landscape context is defined by the spatial arrangement and diversity of land use types around a habitat patch, and can be used to understand the distribution or occurrence of species and their resources in a landscape mosaic. Similarly, vegetation can be measured to understand localized heterogeneity within habitat.

Different land use types can provide better access to spatially separated resources and create additional niches where resource partitioning occurs (Tews et al. 2003). However, niches vary between species, specifically the amount of food and cover available to them. This is apparent in organisms that use different levels of their environment. For instance, arboreal or semi-arboreal organisms can access resources on the ground and within the upper levels of vegetation, while strictly terrestrial organisms are limited to resources at the ground level. Gering and Swihart (2002) found a positive correlation between the occurrence of meso-predators and their niche breadth in an agricultural matrix. However, the exact component of the landscape that best determines the distribution of species with different niche breadths, and the scale at which these effects occur is not well understood.

Meso-carnivores are a diverse guild of mammals that serve as good indices of how landscapes are used because they are highly mobile and widely ranging (Roemer et al. 2009). In

addition to their mobility, organisms within this group also use the landscape to access resources in a variety of ways and at multiple scales (Ramesh and Downs 2014). In this study we selected the black-backed jackal (*Canis mesomelas*) to investigate how heterogeneity affects a species that with a large home range size (15 – 20 km²) and broader mobility through the landscape. In contrast, the large-spotted genet (*Genetta maculata*), will serve as the focal species for investigating the influence of heterogeneity on an organism with a more localized home range (2 – 5 km²) and have more fine scale movements. Both species are widely distributed across southern Africa and have similar diets consisting of vertebrates, invertebrates, and plants.

Our aim is to understand the fundamental role of landscapes in meso-carnivore distribution and the scale at which is most influential on their occurrences for species that have different home range sizes. We hypothesize that large-scale landscape characteristics will be of greater influence to species with a broader home range, while fine-scale characteristics are more influential to species with a more localized home range. We predict that there will be higher detectability of black-backed jackals where agriculture is the dominant land use type surrounding savanna and will be strongly influenced by broader scale covariates, particularly edge. Conversely, we predict that detectability of genets will be greatly influenced by fine scale heterogeneity, specifically shrub and canopy cover.

Methods

Study area

Our study area was approximately 30 km x 100 km located in the lowveld region of Swaziland, a tropical savanna dominated by Acacia shrubs in the east and broad-leafed woodlands in the west (Figure 1). These vegetative patterns correspond to soil composition with basaltic soils in the east and granitic soils in the west. Average annual rainfall is 550-725 mm

and the average monthly temperature during the summer months 26°C and 18°C in the winter. The lowveld supports a growing human population and has experienced varying degrees of economic development, particularly commercial sugarcane production, subsistence farming, and peri-urbanisation. Conservation lands are nested within these land uses under a range of management regimes.

Historically, the lowveld was first settled 30,000 years ago but only experienced major changes to the landscape 100 years ago with an influx of cattle ranching, followed by the sugarcane industry in the 1980's. Later, roughly 2-3% of the lowveld was altered or set-aside for protected areas. Swaziland has since experienced a population increase from approximately 80,000 to around one million today, consequently generating a human-dominated matrix. The lowveld experiences an array of anthropogenic impacts, even within savanna habitat, rendering our study area as an exemplary site for exploring the effects of heterogeneity on mesomammals.

Land-use mapping

To map land use, we acquired 30 m x 30 m land-cover data from Landsat 8 data in Google Earth Engine (Figure 1). Land cover was classified into five principal land-use types: open savanna, closed savanna, riparian/forest, communal land, and agriculture. We used a moving-window analysis to quantify variation in landscape heterogeneity based on the change in landscape composition and configuration across the lowveld. Within a 2 km radius of each savanna cell on the map, we measured compositional heterogeneity using the Shannon-Weiner Index of land-cover diversity and land-cover richness. For configurational heterogeneity, we calculated the total length of edge between land uses and the total number of patches to interpret the extent of fragmentation of land-cover. Moreover, we calculated a 'largest patch' index, a metric of landscape subdivision, which quantifies the probability that two randomly selected

pixels are not located within the same patch, and a 'patch cohesion' index that quantifies the connectedness of land cover types to capture structural connectivity. These metrics were correlated; for this reason, we ran a principal component analysis (PCA) to derive a single compositional heterogeneity variable and a single configurational heterogeneity variable to guide our site selection method.

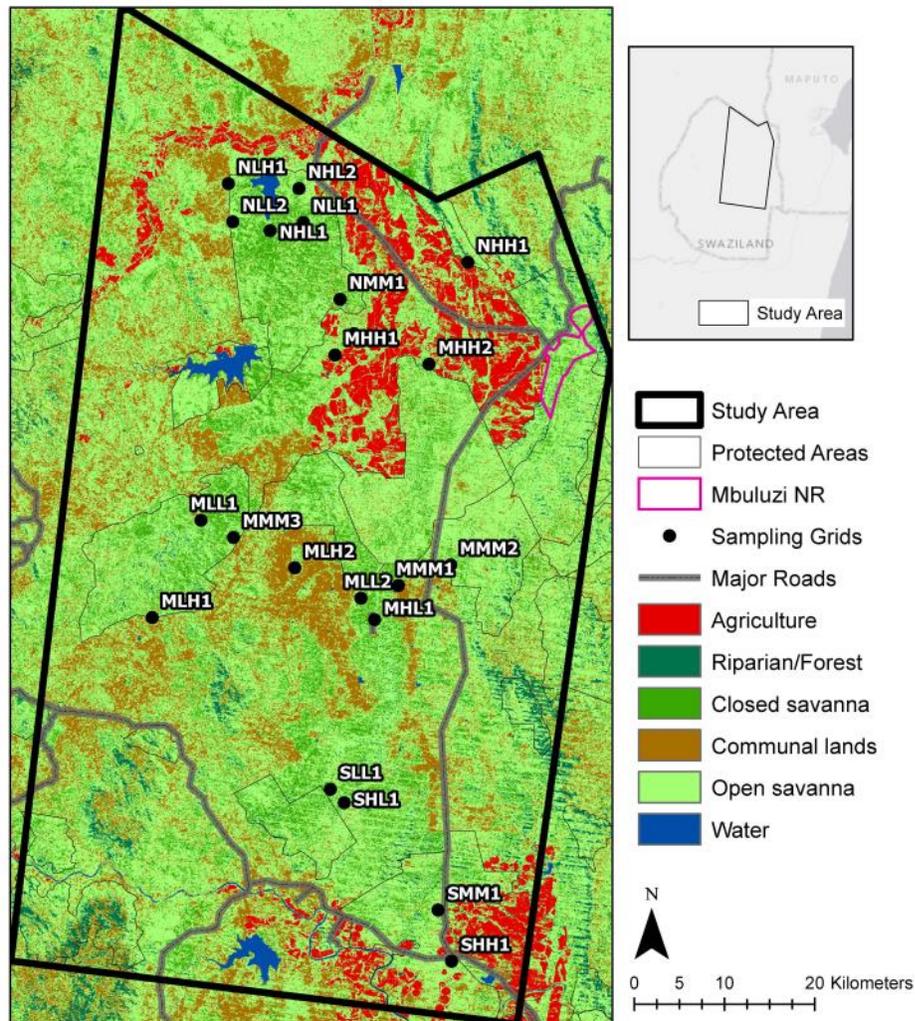


Figure 1. Map of the study site and sampling grids in the lowveld of Swaziland. The 30 m x 30 m land-use raster emphasizes large variation in the amount and arrangement of agriculture, forest, savanna, and rural homesteads.

Composition	Configuration	n
High	High	4
High	Low	4
Low	Low	5
Low	High	3
Medium	Medium	5
Total:		21

Table 1. Combinations and number of replicates of each land-use composition and configuration treatment. Each region (North, Middle, South) contains at least one replicate of each combination.

Site Selection

To account for variability along a rainfall gradient, we stratified the study area into three regions longitudinally: North, Middle, and South. We identified 5 conditions surrounding savannas that comprise of combinations of high, low, and medium land-use composition and configuration (Table 1). Within each stratum, we randomly selected at least one area of savanna surrounded by each condition. All sampled points were restricted to be on accessible land and at least 1 kilometer apart.

Sampling design

To sample and compare communities at two scales, we used 550 m x 550 m sampling grids at each selected site. Each grid consists of five 50 m x 50 m plots at the four corners and center of the grid (Figure 2).

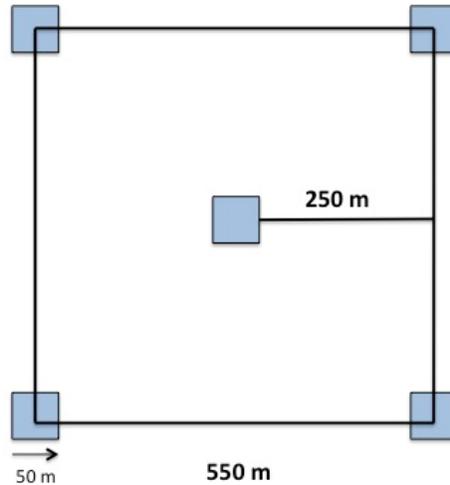


Figure 2. Grid sampling design with five 50 m x 50 m plots.

Vegetation sampling and human impact measurements

We sampled the following variables in each plot: (1) dominant tree species, (2) shrub cover, (3) canopy cover, canopy height, and canopy layer diversity, and (4) grass biomass. Canopy cover, canopy height, and grass biomass were measured with a densitometer, meter stick, and disc pasture meter every 5 m along two 50 m transects, respectively. Canopy layer diversity was measured by estimating the percentage of space occupied by woody biomass within vertical 2 m x 2 m x 2 m volumes every 10 m along two 50 m transects. To eliminate observer bias, the same individual estimated canopy layer diversity in each plot. In addition, signs of cattle, presence of termite mounds, and a human influence rating from 1-5 was noted at each plot.

Camera trap surveys

Jackal and genet distributions were surveyed across four days per plot using motion-sensor camera traps (Primos, Truth Cam 35). We placed three cameras in each plot: two were situated in the center along separate game trails with no bait and one was baited with a chicken neck and positioned in the corner of the plot. Photos were then collected and organized by grid, plot, camera, and SD card. Photos containing animals or humans were kept and the rest were

discarded. These photos were then imported into the software program Daminion (2016) and subsequently tagged by grid, plot, species, and survey method (baited or unbaited camera).

Data analysis

We used multiple linear regressions using R V. 3.2.4 (R Development Core Team 2016) to select the best candidate model to explain the variance in the response variables. We modeled the response of jackal and genet presence or absence as a function of landscape composition, landscape configuration, amount of each land-use type, and structural heterogeneity at plot and grid-level. After testing all subsets of the main effects, the best models will be selected using the Akaike information criterion (AIC) to then determine the best predictors of jackal and genet presence.

Results

We detected large-spotted genets in 14 out of the 15 grids and 42 out of 75 plots. Black-backed jackals were detected in 7 out 15 grids and in 13 out of 75 plots. Baited cameras were more influential on detection of both black-backed jackals and large-spotted genets.

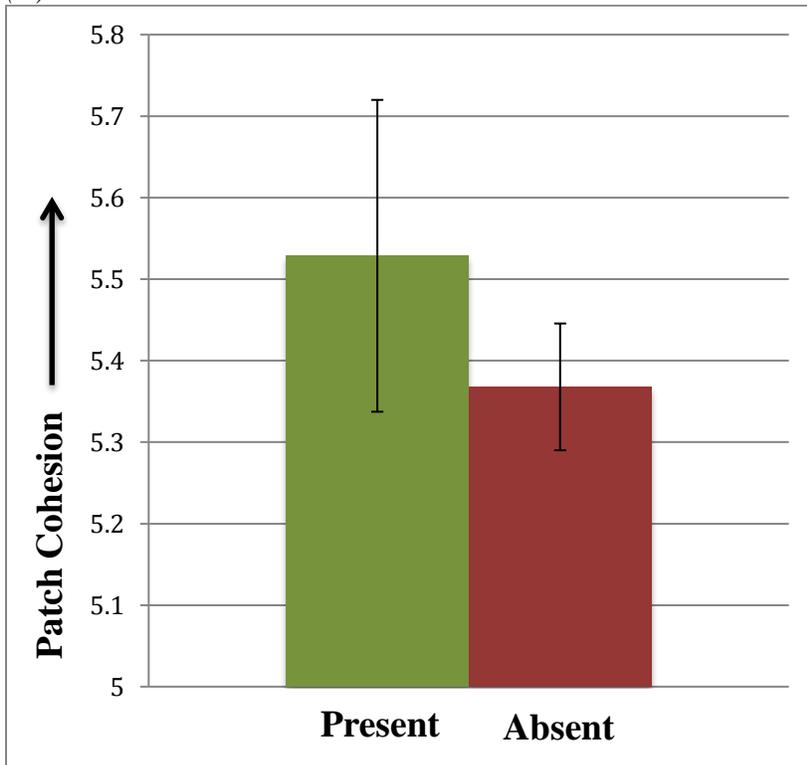
Black-backed Jackal

We found that the presence of black-backed jackals within plots was positively influenced by patch cohesion (AIC = 65.3119, NULL AIC = 70.4753)—a measure of connectivity (Figure 2 (A)). Structural heterogeneity of vegetation across the plot and across the grid was not significant in influencing the presence of jackals.

Large-spotted Genet

Genets were negatively influenced by the average grass biomass within plots (AIC = 93.2489, NULL AIC = 102.3238) (Figure 2 (B)). Landscape-level heterogeneity and grid-level heterogeneity were not influential in the presence of genets within plots.

(A)



(B)

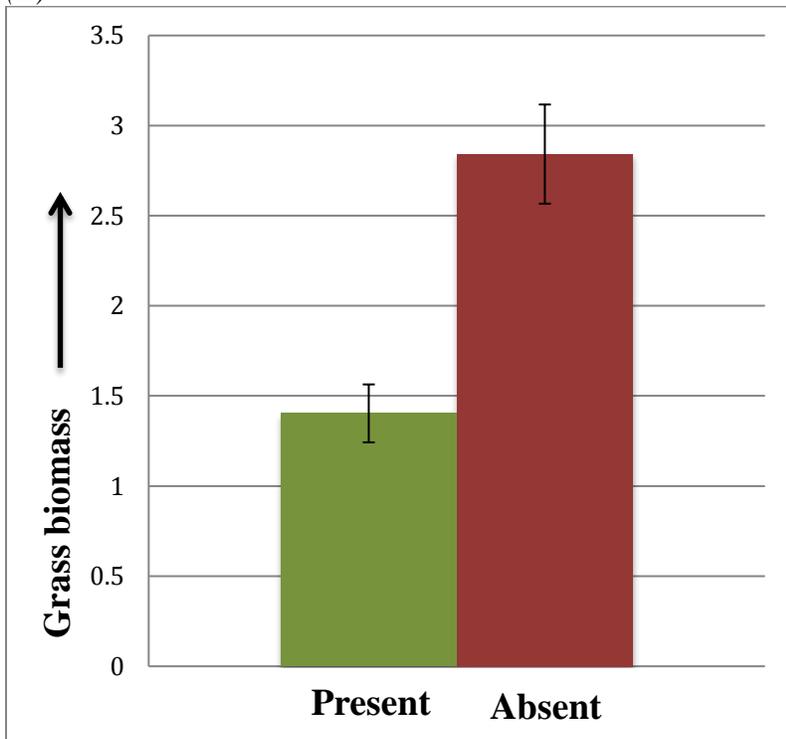


Figure 2. (A) Presence and absence of black-backed jackals in response to patch cohesion. (B) Presence and absence of large-spotted genet in response to average grass biomass.

Discussion

Our results show that jackals and genets have individual responses to heterogeneity at different scales. This should be taken into consideration when research is conducted on the response of specific species to heterogeneity.

Black-backed jackals

Our results suggest that black-backed jackals are strongly influenced by connectivity between patches. Connectivity is a measure of landscape configuration, indicating that the distribution of jackals is influenced by landscape-level heterogeneity versus compositional heterogeneity (relative abundance or diversity of land use types such as agriculture or human settlement). Structural heterogeneity of vegetation at the plot-level and grid-level were not significant in swaying the distribution of jackals, signifying that covariates at the finer scale are not as principal in their presence as landscape-level covariates are.

Large-spotted genets

Genet distribution was predominantly influenced by average grass biomass within the plot, suggesting that fine-scale vegetation covariates are imperative on their presence within the plot. Average grass biomass in plots where genets were absent was almost double the amount of average grass biomass within plots where genets were present—a striking difference.

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