Landscape heterogeneity and woody encroachment decrease mesocarnivore scavenging in a savanna agro-ecosystem

Kyle A. Lima[a], Nicola Stevens[b,c], Samantha M. Wisely[d], Robert J. Fletcher Jr[d], Ara Monadjem[e,f], James D. Austin[d], Themb'alilahlwa Mahlaba[e], Robert A. McCleery[d,f*]

[a] Department of Wildlife, Fisheries, and Conservation Biology, 5755 Nutting Hall, University of Maine, Orono, Maine 04469, United States

[b] Environmental Change Institute, School of Geography and the Environment, University of Oxford, Oxford OX1 3QY, United Kingdom

[c] Department of Botany and Zoology, Stellenbosch University, Private Bag X1, Matieland 7602, South Africa

[d] Department of Wildlife Ecology and Conservation, 110 Newins-Ziegler Hall, University of Florida, Gainesville, Florida 32611, United States

[e] Department of Biological Sciences, University of Eswatini, Private Bag 4, Kwaluseni, Eswatini

[f] Mammal Research Institute, Department of Zoology & Entomology, University of Pretoria, Private Bag 20, Hatfield, Pretoria 0028, South Africa

[*] Corresponding author:

Robert McCleery (ramccleery@ufl.edu)
University of Florida
Department of Wildlife Ecology and Conservation
314 Newins-Zeigler Hall, Gainesville, Florida 32611

Abstract

Increased agricultural intensification and extensive woody plant encroachment are having widespread effects on the functioning of grass-dominated systems at multiple spatial scales. Yet, there is little understanding of how the provisioning of biodiversity-based ecosystem services might be altered by these ongoing changes. One fundamental ecosystem service that is decreasing globally, especially in human-altered landscapes, is scavenging that regulates disease processes, alters species distributions, and influences nutrient cycling. Accordingly, our goal was to understand how facultative scavenging, particularly that of mesocarnivores, was affected by landscape heterogeneity and woody encroachment in tropical-grassy savannas within an agricultural landscape mosaic. We baited (using chicken carcasses) plots across a gradient of land-cover heterogeneity in areas with an open and closed canopy, and subsequently measured scavenging rates. We found that scavenging efficiency of mesocarnivores and other small vertebrates was dependent on environmental variation at multiple spatial scales within our savanna agro-ecosystem. Mesocarnivores removed more bait when the overstory canopy at the plot (i.e. the exact location of the bait station) was more closed; in contrast, mesocarnivore scavenging was less efficient when patches (50m x 50m area around the bait station) within the site had a higher density of shrubs. At the landscape scale, increased land-cover fragmentation resulted in decreased amounts of scavenging by mesocarnivores. This study demonstrates that a relatively transformed agro-ecosystem can support the provision of important ecosystem services and offer an important buffer against loss of ecosystem services. Our results suggest that targeted woody encroachment control, protection of large trees and management or mitigation of extreme levels of fragmentation can help maintain ecosystem service provision and biodiversity.

Key Words

Ecosystem Service; Agriculture; Africa; Eswatini; Shrub Encroachment; Landscape Heterogeneity

Introduction

Changing land-cover in grass-dominated systems is causing two clear and widespread trends: 1) the transition of grassland and savannas to agricultural landscapes (i.e., intensively utilized rangelands and croplands); and 2) extensive woody plant encroachment (Martin et al., 2014; Stevens et al., 2017; Osborne et al., 2018). These shifts alter landscapes and disrupt ecosystem services (Parr et al., 2014; Hurst et al., 2014; Veldman, 2016; Luvuno et al., 2018; Osborne et al., 2018) by creating patches of encroached grassland and savannas embedded within a matrix of intensively utilized rangelands and croplands (Martin et al., 2014; Osborne et al., 2018). These trends are particularly strong in Africa's diverse tropical-grassy savannas (Murphy et al., 2016), which provide essential ecosystem services that contribute to human livelihoods and culture (Cousins, 1999; Holechek et al. 2016; Ryan et al., 2016). Over the next century, agriculture land-uses are accepted to intensity and expand (Donald, 2004; Osborne et al., 2018) with the addition of 3.1 - 5.7 billion people to the African continent (Gerland et al., 2014; Osborne et al., 2018).

In agro-ecosystems, common metrics used to quantify the influence of land-use patterns on diversity and ecological processes often focus on the diversity or heterogeneity of the landscape. Compositional heterogeneity reflects the diversity of land-cover types, whereas configurational heterogeneity estimates the variation in the arrangement of land cover types (Duelli, 1997; Fahrig et al., 2011; Reynolds et al., 2018). These landscape patterns influence species richness, abundance, and ecological interactions (Tews et al., 2004; Neumann et al., 2016). High levels of heterogeneity can enhance biodiversity (Dunning et al., 1992; Huston, 1994; Benton et al., 2003) and support high levels of ecosystem services (Brandt, 2003; Landis, 2017); however, too much configurational heterogeneity resulting in fragmentation can reduce biodiversity and disrupt key ecosystem services (Chase et al., 2020).

These trends in African savannas have implications at multiple spatial scales (Reynolds et al., 2018; Holechek and Valdez 2018; LaScaleia et al. 2018; Stanton et al. 2020.). When landscape-scale heterogeneity is altered by new agricultural development, smaller, within patch characteristics like shrub density and canopy cover can be altered as well (Pickett and Rodgers, 1997). These structural changes can lead to variable responses from animal communities, which respond to the direct (land conversation) and indirect effects (vegetation structural) of land-cover at different scales (Tews et al., 2004; Reynolds et al., 2018; Stanton et al. 2020). However, we have little understanding of how the provision of biodiversity-based ecosystem services (services provided or enhanced by diverse biological communities) that these animal communities provide may be affected by changes currently shaping Africa’s increasingly agricultural landscapes (Hurst et al. 2014).

One fundamental biodiversity-based ecosystem service that is decreasing globally, especially in anthropogenically altered landscapes, is scavenging (Millennium Ecosystem Assessment, 2005; Markandya et al., 2008; DeVault et al., 2011; Mateo-Thomas et al., 2017). Efficiency of carrion removal regulates disease processes that impact wildlife and public health (Markandya et al., 2008; Jennelle et al., 2009; Chikerema et al., 2013; Lehman et al., 2017), affects the spatial distribution of species (Cortés-Avizanda et al., 2009), and influences the biogeochemical processes involved in nutrient cycling (Burkepile et al., 2006). Consumption of carrion by scavengers can also have a stabilizing effect on food web dynamics by transferring nutrients into higher trophic levels (Moleón et al., 2014; Turner et al., 2017). However, different types and scales of land-cover changes may disrupt or enhance the scavenging services offered by certain taxonomic groups (Tews et al., 2004; DeVault et al., 2011). In many anthropogenically dominated landscapes mesocarnivores are the dominant scavengers (Cancio et al., 2017, Williams et al., 2018), yet we only have a limited understanding of how patterns of land cover on different scales alter their scavenging services.

Our goal was to understand how facultative scavenging, particularly that of mesocarnivores, was affected by variability in landscape heterogeneity and woody encroachment. Within this agro-ecosystem, we predicted that higher levels of compositional heterogeneity (e.g. variability of cover types) would result in a higher removal rate, as the diversity of land-cover types would support a varied and diverse array of scavengers (Kerr and Packer, 1997; Tews et al., 2004; Moleón et al., 2014). We also predicted that as woody encroachment increased, we would see reductions in metrics of mesocarnivore scavenging as encroachment has been shown to be negatively associated with mesocarnivores' ability to detect carrion (DeVault et al., 2002; Turner et al., 2017).

Methods

Study area

Our study was located in the Lowveld region of northeastern Eswatini (formerly the Kingdom of Swaziland; Figure 1) within the Maputaland-Pondoland-Albany (MPA) center for endemism (Perera et al., 2011), an area representative of the typical anthropogenic pressures common in African savanna landscapes (Bailey et al 2016). The Eswatini lowveld consists of a mosaic of commercial agriculture, rain-fed agriculture, cattle ranches, and conservation lands that have become increasingly fragmented over time (Bailey et al. 2016; Reynolds et al., 2018). The commercial agriculture in the region is dominated by sugarcane monoculture (Esterhuizen, 2015), and rain-fed agriculture is often centered on the production of maize (Bailey et al., 2016). The region has experienced an increased loss of native savanna vegetation (Dlamini 2017) coupled with a steady increase in the amount of agricultural and urban development surrounding protected areas and savannas (Bailey et al 2016). The native vegetation is classified as basalt sweet arid lowveld (Mucina and Rutherford, 2006), with narrow strips of riparian forest (Sweet and Khumalo, 1994). Over the last 70 years, fire suppression, over grazing and possibly elevated levels of CO_2 have led to a steady increase in woody vegetation cover, predominantly by the shrub *Dichrostachys cinerea* (Roques et al., 2001; Sirami and Monadjem, 2012; McCleery et al. 2018). Climatically, the region can be characterized by dry (0 – 50mm of rain) and mild (8 – 26˚C) winters, and wet (200 –500mm of rain) and hot (15 – 33˚C) summers (Goudie and Price Williams, 1983). Soils throughout the study sites were predominantly basaltic (Goudie and Price Williams, 1983).

Site selection

To capture patterns of landscape heterogeneity within the study area, we selected 16 *a priori* savanna sites, 500 x 500m in size, based on metrics of landscape heterogeneity (Figure 1). To select these sites, we used the Reynolds et al. (2018) land cover dataset, which used a moving window analysis to quantify compositional and configurational heterogeneity within a 2-km radius of each cell. These landscape heterogeneity metrics included: Shannon diversity index of land cover types (SHDI), land cover richness (LCR), total length of edge between land cover classes (TE), total number of patches (NP), patch cohesion (COHESION), and landscape division (DIVISION). To represent compositional heterogeneity, we chose the commonly used SHDI and LCR indices, and to represent configurational heterogeneity we used the remaining landscape metrics, which represented both edge effect and connectivity processes (Cushman et al., 2008; Fletcher and Fortin, 2018). We used principal components analysis (PCA) to derive two descriptive orthogonal principal components, one representing compositional heterogeneity (*comp*), and another representing configurational heterogeneity (*config*). All cells were then ranked based on their PCA value for compositional and configurational heterogeneity. We scored sites as low (< 33%, e.g. dominated by savanna), medium (33-66%, e.g. mix of savanna and other cover types), or high (> 66%, highly variable cover types) compositional and configurational heterogeneity and stratified the 16 sites across these categories (Table 1). At all of the 16 sites, we established 6 bait plots (10 x 10m) spaced 50m apart. We split the location of these 6 plots, placing 3 in a relatively open parcel characterized by low shrub and canopy cover, and 3 in a relatively closed parcel characterized by high shrub and canopy covers (Figure 1). Paired plots were located approximately 100 - 200m apart.

Field sampling – scavenger monitoring

To determine how environmental variation influenced scavenging, we sampled during the dry season from 25 June to 26 July 2018. We created bait stations by clearing a 5m radius circle for bait presentation, which consisted of 500g (± 10g) (weighed using a 500g x 0.01g AMIR digital scale) of chicken necks. We secured the bait with wire mesh to the ground to slow consumption. Chicken is commonly used in scavenging studies (DeVault et al., 2017; Ferreras et al., 2018) and was easily accessible. To increase the detectability of the bait by scavengers via scent (Stoddart, 1980; Natusch et al., 2017) the bait was taken out of refrigeration ~24 hours prior and combined with chicken livers. We deployed bait at each plot by 16:00 and left it out for 3 nights. At the end of the 3-night sampling period we retrieved and weighed the remaining bait. To determine the proportion of mass consumed by vertebrates compared to invertebrate scavengers and desiccation, we placed three control bait piles of 500g (±10g) in open and closed patches within a site. We prevented the consumption of the bait by vertebrates by placing it inside wire mesh cages that only allowed small invertebrates to enter the wire box. After the third night, we weighed the bait to determine the amount of mass lost to desiccation and invertebrates.

To record scavenger visitation time and activity we installed a Moultrie M-40 (Birmingham, AL) game camera at each plot 4m away from the bait. All cameras were set on high passive infrared sensor (PIR) detection sensitivity and full high definition (FHD) (1920 x1080) video quality. Cameras were activated by movement and were set to record 30-second infrared video for nocturnal observations (the maximum time allowed by the camera), and 60-second videos for diurnal observations. We checked camera battery life and SD card memory between the hours of 09:00 and 11:00 each day.

Field sampling – vegetation metrics

We quantified vegetation characteristics at multiple scales to understand their association with scavenging. At each savanna site we recorded vegetation structure on each of the open and closed patches within a site (Figure 1) using three 50m transects. Two transects were placed in parallel 20m apart, 10m on either side of the center of each patch. The third transect ran through the center and perpendicular to the other transects. We estimated shrub cover (*site.shrub*) using the line intercept method to average measurements from every 10m of the transect (Canfield, 1941). At every 5m interval along the transect we measured grass biomass (*site.grass*) using a disc-pasture meter (DPM) (Bransby and Tainton, 1977). DPM values were converted to estimated biomass (kg/km^2) using calibrated estimates from Zambatis et al., (2006). We estimated canopy cover of the open and closed patches (50m X 50m) within a site by recording % cover *(site.canopy*) and averaging measurements from a convex spherical densitometer every 5m along the three 50m transects (Lemmon, 1956). Additionally, to understand how overstory cover influenced mesocarnivore behavior at the scavenging bait station, we used a convex spherical densiometer to measure canopy cover at the bait station in the four cardinal directions directly over the bait at each bait plot (*plot.canopy*).

Scavenging

Scavenging efficiency, including the amount of carrion taken and how quickly it is consumed, is a critical aspect of scavenging as an ecosystem service. We estimated scavenging activity using two metrics: 1) the mass of the bait removed (*mass*); and 2) the speed at which a bait was detected (*time remaining after detection*). We considered a site scavenged by a vertebrate if bait was reduced by > 10g after adjusting for invertebrate consumption and desiccation (see above). We classified scavenging by a mesocarnivore if bait was reduced by > 10g (after adjustment) and a mesocarnivore was detected on our cameras. We also calculated the time it took for bait to be detected as an important indicator of scavenging efficiency (Moleón et al. 2015). We calculated this as the *time remaining after detection* using the camera trap data by determining the maximum number of minutes in a scavenging event (45000 min or 3 days) minus the number of minutes until a detection was recorded. A score of 0 indicated no scavenger was detected, and value near 45,000 indicated that a scavenger was detected soon after the bait was placed in the environment. Because our cameras were not configured to detect rodents and other smaller scavengers, we only calculated estimates for mesocarnivores.

Data analysis

To understand the influence of landscape heterogeneity we examined our data at three different scales: the landscape (at each site), the patch within each site (i.e. open or closed canopy), and the plot (i.e. the location of the bait station) scale. Specifically, we determined how landscape heterogeneity, site vegetation characteristics, and plot canopy cover shaped overall scavenging rates and the scavenging rates of mesocarnivores by generating three sets of models. First, to understand how scavenging service varied without regard for the type of vertebrate scavenger, we evaluated models examining the amount of bait removed (*mass*). Next, we evaluated the amount of bait removed (*mass*) and the time it took for the bait to be detected (*time remaining after detection*), at bait stations that had been scavenged by mesocarnivores. We evaluated 6 *a priori* models for each of the three sets of models. To avoid overfitting, models included single variables of landscape heterogeneity at the site scale (*comp, config)*, within site scale vegetation (*site.canopy, site.shrub, site.grass)*, and plot-scale canopy (*plot.canopy*), as well as a null model (i.e. intercept only).

We evaluated the models using generalized-linear mixed models. With count data (*mass* = number of grams removed, *time remaining after detection* = number of minutes) and non-detections (0’s) we fit our models to a zero-inflated Poisson distribution, with savanna site as a random variable, using the glmmTMB package (Magnusson et al., 2020) in R (R Core Team, 2019). Using the MuMIn package (Bartoń, 2020) for R, we compared models using AICc

(Akaike information criterion corrected for small samples) values and models weights. We considered the statistical importance of variables in models within 4 AICc units of the best model and lower than the null models. We evaluated the beta estimates of variables in these models and considered betas with 95% CI that did not include 0 to be meaningful predictors of the response variables (Burnham and Anderson, 2002).

Results

Across the 96 baited plots, an average of 92.71g of bait was removed. Vertebrates scavenged at 68 plots, (i.e. > 10g removed) with mesocarnivores responsible for scavenging at 39 of these plots. Overall, we detected 9 taxa of vertebrates that we considered to have scavenged bait (Table 2). Of these, four were mesocarnivores: large-spotted genet (*Genetta maculata*), slender mongoose (*Galerella sanguinea*), banded mongoose (*Mungos mungo*), and black-backed jackal (*Canis mesomelas*) (Table 2).

Examining the amount of bait removed from vertebrate scavenged sites, two competing models (configuration and plot.canopy) outperformed (i.e. had lower AICc) the null model; however, the beta estimates of parameters in both models had 95% CIs that included 0. At mesocarnivore scavenged sites, the best model explaining the amount of bait removed included a localized plot-scale measure of canopy cover (Table 3). The model predicted that the amount of bait removed doubled from 31 to 62g as canopy cover increased (Fig. 2) at the plot. We saw a similar but less pronounced (i.e. beta estimate included 0) pattern when we considering the relationship between all vertebrate scavenging and plot scale canopy cover (Table 3). At the landscape scale, we also found that as the complexity (measured as configuration) of the landscape was a competing model (Table 3). As the complexity of the landscape increased, the amount of bait removed at mesocarnivore scavenged plots decreased (Table 3, Fig. 3). Our model predicted a reduction in the amount of bait removed (by more than half from 83g to 30g) from the simplest to the most complex landscapes (Fig. 3). Again, we found a similar but less pronounced and meaningful pattern considering all vertebrate scavenging at the landscape scale (Table 3).

There were two competing models (site.shrub and plot.canopy) to explain the amount of time it took for mesocarnviores to locate bait piles; however, only the parameter estimate for site.shrub model did not include 0 in its 95 % CI. Mesocarnivores took longer to locate the bait on our plots (decreasing the time remaining until detection) when there was more woody encroachment (as measured by shrub cover) on the patches surrounding our plots (Table 4). On patches with negligible shrub cover, mesocarnivores detected bait in ca. 48 hours but it took them ca. 65 hours to locate the bait when shrub cover was densest (Fig. 4).

Discussion

Habitat characteristics at different ecological scales can act as filters that shape the community of scavengers and the efficiency of their carrion removal (Pardo-Barquín et al., 2019). In this study, we found that scavenging efficiency was dependent on environmental factors measured at multiple scales within the savanna agro-ecosystem. This was particularly true for scavenging mesocarnivores, which experienced changes in scavenging efficiency depending on environment characteristics at the plot, site, and landscape scales. At the plot scale, more bait was removed by mesocarnivores when the scavenging location was characterized by increased overstory canopy cover, indicative of large trees surrounding the bait. At the scale of a patch of savanna (i.e. our sites), however, all mesocarnivore scavengers took longer to find the bait, and were thus less efficient when the patch had increased woody encroachment. At the landscape scale, increased fragmentation and edge decreased the amount of bait removed by mesocarnivores.

Detection and efficiency of carrion removal is controlled by the complex interaction of factors at the patch and local scales (DeVault, 2004; Arrondo et al., 2020). In this study, mesocarnivore scavengers were less efficient at detecting carrion when the shrub cover increased at the patch scale. This pattern of decreased carcass detection in areas with elevated woody cover has also been shown for avian scavengers (Bamford et al., 2009; Arrondo et al., 2020), and for mammalian scavengers in open pine forests of the southeastern United States (Turner et al., 2017). For mammals, densely vegetated habitats can truncate visual and olfactory cues, which can be an important component of carrion detection (DeVault et al., 2002; Turner et al., 2017). Conversely, the decreased efficiency that we observed could have been due to an overall decrease in mesocarnivore density in areas with more shrub cover; hence fewer animals occupying the patch may have driven the longer detection times. In this scenario, the mesocarnivore guild as a whole would have had reduced efficiency due to lower scavenger density. However, this is unlikely to be the case in our system because the most common mesocarnivores here, the large-spotted genet and slender mongoose, both appear to be more active in areas with dense shrub cover (Ramesh and Downs, 2014).

While scavenging by all species was reduced in woody encroached savanna patches, mesocarnivores were further influenced by habitat characteristics at both smaller and larger spatial scales. At the plot scale, mesocarnivores removed more bait when the bait station was placed under canopy cover. Semi-arboreal genets were the most frequent visitor to bait stations (75%) and likely drove this pattern. Genets are small mesocarnivores (< 2.5kg; Hennemann et al., 1980) that are themselves prey for other, larger avian and mammalian predators. Microsite characteristics like tree presence in a savanna patch may create foraging spaces that offer preferred habitats that are perceived to be less risky for semi-arboreal species (Coleman et al., 2014), particularly around resources that are shared by a diverse guild of mammals, including potential predators and competitors. Carcasses can create temporary “landscapes of fear” that can cause animals to practice vigilance around resources that attract predators (Frank et al., 2020). Thus, large trees likely create refuge for these mesocarnivores that allow them to increase the amount of time spent at a carcass and the amount of carrion removed. Indeed, scattered mature trees in agro-ecological systems provide critical resources for many species and are considered keystone structures in this context (Manning et al., 2006).

Landscape heterogeneity has been shown to have a strong influence on the distribution of mammals in agricultural mosaics (McCleery et al., 2018; Shapiro et al., 2020), but the response of scavengers to fragmentation and patch size is not uniform. In a cornfield-woodlot agro-ecosystem of the central United States, patch connectivity did not influence carcass detection (Olson et al., 2016). In an agricultural landscape in Japan, increased forest patch size decreased the rate of removal of carcasses by mammals (Sugiura et al., 2013). In our study, increased configuration (the result of increased edge and decreased patch size) was correlated with decreases in mesocarnivore scavenging. This reduction in scavenging may be a result of the increased edge around the bait plot. In this ecosystem, edges are typically footpaths or roads with extensive human traffic. Humans commonly persecute and hunt mammalian scavengers, which potentially reducing their foraging time around the presence of people (Smith et al., 2017). Thus, the presence of humans may magnify the effect of fragmentation (Berger-Tal et al., 2019), potentially altering mesocarnivore’s contributions to carrion removal.

Our choice of bait likely influenced the outcome of our results. We used small-sized bait to simulate small (< 1kg) carcasses on the landscape. Small-sized bait is utilized less by obligate scavengers like vultures or larger predators like jackals and leopard (*Panthera pardus*), and instead is utilized to a greater extent by facultative scavengers like suids and mesocarnivores (Moleón et al., 2015; Olson et al., 2012; Olson et al., 2016). Indeed, neither vultures nor hyenas visited our bait plots despite their presence in the area. Scavenging by facultative mammals is dependent on multiple factors such as carrion size, climate, habitat succession, and scavenging community composition, all of which interact to create an ecosystem function that can be difficult to predict (DeVault et al., 2004; Eldridge et al., 2015). In the savanna agro-ecosystem, habitat characteristics at multiple spatial scales appeared to operate as ecological filters on facultative scavengers performing this ecosystem function.

Agro-ecological landscapes can both positively and negatively affect biodiversity and ecosystem services. Too much landscape heterogeneity can reduce ecosystem function and service provisioning if it is so extensive that it leads to fragmentation (van den Berg et al., 2001). Alternatively, as we found in this study, some semi-natural rangeland and cropland matrices may support biodiversity-based ecosystem services. The potential to maintain biodiversity services within agriculture systems offers novel opportunities for the conservation of grasslands and savannas (Martin et al., 2014; Sayre et al., 2017). Understanding the scale and response of ecological processes and services within agro-ecosystem represents an opportunity to discover and implement landscape-based conservation strategies that integrate biodiversity and ecosystem functions with important anthropogenic land uses.

Implications

Scavenging services are decreasing in human-dominated systems throughout the globe (Millennium Ecosystem Assessment, 2005; Markandya et al., 2008; DeVault et al., 2011; Mateo-Thomas et al., 2017). We demonstrate that with the appropriate conditions and habitat management at local, patch and landscape scales, this service may be maintained within agricultural landscape mosaics. Highlighting the need to maintain large savanna trees (Dean et al., 1999), on our finest scale, we found open canopies were associated with decreased scavenging efficiency. Alternately, increased woody encroachment of smaller shrubs at the larger patch scale decreased time to detection of the bait. At the landscape scale, fragmentation decreased the amount of bait removed. In many grass-dominated systems, scavenging services are likely to suffer from woody encroachment (Holechek and Valdez, 2018; Stevens et al., 2017), and expanding anthropogenic land covers that facilitate habitat fragmentation (Bink et al 2009. Bailey et al 2016). Accordingly, to help maintain ecosystem service provision and biodiversity, our results suggest the need for targeted woody encroachment control and planning and restoration of landscapes with extreme levels of fragmentation.

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LITERATURE CITED

Arrondo, E., Morales-Reyes, Z., Moleón, M., Cortés-Avizanda, A., Donázar, J.A., Sánchez-Zapata, J.A., 2019. Rewilding traditional grazing areas affects scavenger assemblages and carcass consumption patterns. Basic and Applied Ecology 41, 56–66.

Atauri, J.A., de Lucio, J.V., 2001. The role of landscape structure in species richness distribution of birds, amphibians, reptiles and lepidopterans in Mediterranean landscapes. Landscape Ecology 16, 147–159.

Bailey, K.M., McCleery, R.A., Binford, M.W., Zweig, C., 2016. Land-cover change within and around protected areas in a biodiversity hotspot. Journal of Land Use Science 11, 154–176.

Bamford, A. J., Monadjem, A., Hardy, I. C., 2009. An effect of vegetation structure on carcass exploitation by vultures in an African savanna. Ostrich 80, 135–137.

Bartoń, K., 2020. Multi-Model Inference. URL: https://cran.r-project.org/web/packages/MuMIn/MuMIn.pdf

Benton, T.G., Vickery, J.A., Wilson, J.D., 2003. Farmland biodiversity: is habitat heterogeneity the key? Trends in Ecology and Evolution 18, 182–188.

Berger-Tal, O., Saltz, D., 2019. Invisible barriers: anthropogenic impacts on inter- and intra-specific interactions as drivers of landscape-independent fragmentation. Philosophical Transactions of the Royal Society B 374(1781), 20180049.

Brink, A. B., Eva, H. D., 2009. Monitoring 25 years of land cover change dynamics in Africa: A sample based remote sensing approach. Applied Geography, *29*(4), 501-512.

Blaum, N., Rossmanith, E., Fleissner, G., Jeltsch, F., 2007a. The conflicting importance of shrubby landscape structures for the reproductive success of the yellow mongoose (Cynictis penicillata). Journal of Mammalogy 88, 194–200.

Blaum, N., Rossmanith, E., Popp, A., Jeltsch, F., 2007b. Shrub encroachment affects mammalian carnivore abundance and species richness in semiarid rangelands. Acta Oecologica, 31, 86–92.

Blaum, N., Rossmanith, E., Schwager, M., Jeltsch, F., 2007c. Responses of mammalian carnivores to land use in arid savanna rangelands. Basic and Applied Ecology 8, 552–564.

Brandt, J., 2003. Multifunctional landscapes–perspectives for the future. Journal of Environmental Sciences 15, 187–192.

Bransby, D.I., Tainton, N.M., 1977. The disc pasture meter: Possible applications in grazing management. Proceedings of the Annual Congresses of the Grassland Society of Southern Africa 12(1), 115–118.

Burnham, K. P., Anderson, D. R., 2002. Model selection and inference: a practical information – theoretic approach, 2nd ed. Springer, New York.

Burkepile, D.E., Parker, J.D., Woodson, C.B., Mills, H.J., Kubanek, J., Sobecky, P.A., Hay, M.E., 2006. Chemically mediated competition between microbes and animals: microbes as consumers in food webs. Ecology 87, 2821–2831.

Cancio, I., González-Robles, A., Bastida, J.M., Isla, J., Manzaneda, A.J., Salido, T., Rey, P.J., 2017. Landscape degradation affects red fox (*Vulpes vulpes*) diet and its ecosystem services in the threatened Ziziphus lotus scrubland habitats of semiarid Spain. Journal of Arid Environments 145, 24–34.

Canfield, R.H., 1941. Application of the line interception method in sampling range vegetation. Journal of Forestry 39(4) 388–394.

Chase, J.M., Blowes, S.A., Knight, T.M., Gerstner, K., May, F., (2020). Ecosystem decay exacerbates biodiversity loss with habitat loss. Nature 584, 238–243.

Chikerema, S.M., Matope, G., Pfukenyi, D.M., 2013. Awareness and attitude toward zoonoses with particular reference to anthrax among cattle owners in selected rural communities of Zimbabwe. Vector-borne and Zoonotic Diseases 13, 243–249.

Coleman, B.T., Hill, R.A., 2014. Living in a landscape of fear: the impact of predation, resource availability and habitat structure on primate range use. Animal Behaviour 88, 165–173.

Cousins, B., 1999. Invisible Capital: The Contribution of Communal Rangelands to Rural Livelihoods in South Africa. Development Southern Africa 16, 299–318.

Cortés-Avizanda, A., Selva, N., Carrete, M., Donázar, J.A., 2009. Effects of carrion resources on herbivore spatial distribution are mediated by facultative scavengers. Basic and Applied Ecology 10, 265–272.

Cushman, S.A., McGarigal, K., Neel, M.C., 2008. Parsimony in landscape metrics: Strength, universality, and consistency. Ecological Indicators 8, 691–703.

Dean, W.R.J., Milton, S.J., Jeltsch, F., 1999. Large trees, fertile islands, and birds in arid savanna. Journal of Arid Environments, 41(1), 61–78.

DeVault, T.L., Rhodes, O.E., 2002. Identification of vertebrate scavengers of small mammal carcasses in a forested landscape. Acta Theriologica 47(2), 185–192.

DeVault, T.L., Brisbin Jr, L., 2004. Factors influencing the acquisition of rodent carrion by vertebrate scavengers and decomposers. Canadian Journal of Zoology. 82, 502–509.

DeVault, T.L., Olson, Z.H., Beasley, J.C., Rhodes, O.E., 2011. Mesopredators dominate competition for carrion in an agricultural landscape. Basic and Applied Ecology 12, 268–274.

DeVault, T.L., Seamans, T.W., Linnell, K.E., Sparks, D.W., Beasley, J.C., 2017. Scavenger removal of bird carcasses at simulated wind turbines: Does carcass type matter? Ecosphere 8, e01994.

Dlamini, W. M. (2017). Mapping forest and woodland loss in Swaziland: 1990–2015. Remote Sensing Applications: Society and Environment *5*, 45-53.

Donald, P.F., 2004. Biodiversity impacts of some agricultural commodity production systems. Conservation Biology 18, 17–38.

Duelli, P., 1997. Biodiversity evaluation in agricultural landscapes: an approach at two different scales. Agriculture, Ecosystems, and Environment 62, 81–91.

Dunning, J.B., Danielson, B.J., Pulliam, H.R., 1992. Ecological processes that affect populations in complex landscapes. Oikos 65, 169–175.

Eldridge, D.J., Soliveres, S., 2015. Are shrubs really a sign of declining ecosystem function? Disentangling the myths and truths of woody encroachment in Australia. Australian Journal of Botany 62(7), 594–608.

Esterhuizen, D., 2015. The supply and demand of sugar in Swaziland. United States Department of Agriculture, Foreign Agricultural Service. GAIN Report.

Fahrig, L., Baudry, J., Brotons, L., Burel, F.G., Crist, T.O., Fuller, R.J., Sirami, C., Siriwardena, G.M., Martin, J.L., 2011. Functional landscape heterogeneity and animal biodiversity in agricultural landscapes. Ecology Letters 14, 101–112.

Ferreras, P., Díaz-Ruiz, F., Monterroso, P., 2018. Improving mesocarnivore detectability with lures in camera-trapping studies. Wildlife Research 45, 505–517.

Frank, S.C., Blaalid, R., Mayer, M., Zedrosser, A., Steyaert, S.M.J.G., 2020. Fear the reaper: ungulate carcasses may generate an ephemeral landscape of fear for rodents. Royal Society Open Science 7(6), 191644.

Gerland, P., Raftery, A.E., Sevcikova, H., Li, N., Gu, D., Spoorenberg, T., Alkema, L., Fosdick, B.K., Chunn, J., Lalic, N., Bay, G., Buettner, T., Heilig, G.K., Wilmoth, J., 2014. World population stabilization unlikely this century. Science 346, 234–237.

Goudie, A.S., Price Williams, D., 1983. The Atlas of Swaziland. Swaziland National Trust Commission, Mbabane.

Hennemann, W.W., Konecny, M.J., 1980. Oxygen consumption in Large Spotted Genets, Genetta tigrina. Journal of Mammalogy 61(4), 747–750.

Holechek, J. L., Cibils, A. F., Bengaly, K., Kinyamario, J. I., 2017. Human population growth, African pastoralism, and rangelands: a perspective. Rangeland Ecology & Management, 70(3), 273-280.

Holechek, J., Valdez, R. 2018. Wildlife conservation on the rangelands of eastern and southern Africa: past, present, and future. Rangeland Ecology & Management 71(2), 245-258.

Hurst, Z. M., McCleery, R. A., Collier, B. A., Silvy, N. J., Taylor, P. J., Monadjem, A. 2014. Linking changes in small mammal communities to ecosystem functions in an agricultural landscape. Mammalian Biology, *79*(1), 17-23.

Huston, M.A., 1994. Biological diversity: The coexistence of species on changing landscapes. Cambridge University Press.

Jennelle, C.S., Samuel, M.D., Nolden, C.A., Berkley, E.A., 2009. Deer carcass decomposition and potential scavenger exposure to chronic wasting disease. Journal of Wildlife Management 73, 655–662.

Kerr, J.T., Packer, L., 1997. Habitat heterogeneity as a determinant of mammal species richness in high-energy regions. Nature 385, 252–254.

Landis, D.A., 2017. Designing agricultural landscapes for biodiversity-based ecosystem services. Basic and Applied Ecology 18, 1–12.

LaScaleia, M. C., Reynolds, C., Magagula, C. N., Roets, F., McCleery, R. A. 2018. Dung beetle richness decreases with increasing landscape structural heterogeneity in an African savanna-agricultural mosaic. Insect Conservation and Diversity 11(4), 396-406.

Lehman, M.W., Craig, A.S., Malama, C., Kapina-Kany'anga, M., Malenga, P., Munsaka, F., Muwowo, S., Shadomy, S., Marx, M.A., 2017. Role of food insecurity in outbreak of anthrax infections among humans and hippopotamuses living in a game reserve area, rural Zambia. Emerging Infectious Diseases 23, 1471–1477.

Lemmon, P.E., 1956. A Spherical Densiometer For Estimating Forest Overstory Density. Forest Science 2(4), 314–320.

Luvuno, L., Biggs, R., Stevens, N., Esler, K., 2018. Woody encroachment as a social-ecological regime shift. Sustainability 10, 2221.

Magnusson, A., Skuag, H., Nielson, A., Berg, C., Kristensen, K., Maechler, M., van Bentham, K., Bolker, B., Sadat, N., Lüdecke, D., Lenth, R., O'Brien, J., Brooks, M., 2020. Generalized Linear Mixed Models using Template Model Builder. URL: https://cran.r-project.org/web/packages/glmmTMB/glmmTMB.pdf

Manning, A.D., Fischer, J., Lindenmayer, D.B., 2006. Scattered trees are keystone structures–implications for conservation. Biological conservation 132(3), 311–321.

Markandya, A., Taylor, T., Longo, A., Murty, M.N., Murty, S., Dhavala, K., 2008. Counting the cost of vulture decline: An appraisal of the human health and other benefits of vultures in India. Ecological Economics 67, 194–204.

Martin, L.J., Quinn, J.E., Ellis, E.C., Shaw, M.R., Dorning, M.A., Hallett, L.M., Heller, N.E., Hobbs, R.J., Kraft, C.E., Law, E., 2014. Conservation opportunities across the world's anthromes. Diversity and Distributions 20, 745–755.

Mateo-Thomas, P., Olea, P.P., Moleón, M., Selva, N., Sanchez-Zapata, J.A., 2017. Both rare and common species support ecosystem services in scavenger communities. Global Ecology and Biogeography 26, 1459–1470.

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

Millennium Ecosystem Assessment, 2005. Ecosystems and human well-being: synthesis. Washington, DC: Island Press.

Moleón, M., Sanchez-Zapata, J.A., Selva, N., Donazar, J.A., Owen-Smith, N., 2014. Interspecific interactions linking predation and scavenging in terrestrial vertebrate assemblages. Biological Reviews 89, 1042–1054.

Moleón, M., Sanchez-Zapata, J.A., Sebastián-González, E., Owen-Smith, N., 2015. Carcass size shapes the structure and functioning of an African scavenging assemblage. Oikos 124, 1391–1403.

Mucina, L., Rutherford, M., 2006. The vegetation of South Africa, Lesotho and Swaziland. Strelitzia 19. South African National Biodiversity Institute, Pretoria.

Murphy, B.P., Andersen, A.N., Parr, C.L., 2016. The underestimated biodiversity of tropical grassy biomes. Philosophical Transactions of the Royal Society B: Biological Sciences 371, 20150319.

Natusch, D.J.D., Lyons, J.A., Shine, R., 2017. How do predators and scavengers locate resource hotspots within a tropical forest? Austral Ecology 42, 742–749.

Neumann, J., Griffiths, G.H., Hoodless, A., Holloway, G.J., 2016. The compositional and configurational heterogeneity of matrix habitats shape woodland carabid communities in wooded-agricultural landscapes. Landscape Ecology 31, 301315.

Olson, Z.H., Beasley, J.C., DeVault, T.L., Rhodes Jr, O.E., 2012. Scavenger community response to the removal of a dominant scavenger. Oikos 121, 77–84.

Olson, Z.H., Beasley, J.C., and Rhodes Jr, O.E., 2016. Carcass type affects local scavenger guilds more than habitat connectivity. PlosOne 11, e0147798.

Osborne, C.P., Charles-Dominique, T., Stevens, N., Bond, W.J., Midgley, G., Lehmann, C.E.R., 2018. Human impacts in African savannas are mediated by plant functional traits. New Phytologist 220, 10–24.

Pardo-Barquín, E., Mateo-Tomás, P., Olea, P.P., 2019. Habitat characteristics from local to landscape scales combine to shape vertebrate scavenging communities. Basic and Applied Ecology 34, 126-139.

Parr, C.L., Lehmann, C.E., Bond, W.J., Hoffmann, W.A., Andersen, A.N., 2014. Tropical grassy biomes: Misunderstood, neglected, and under threat. Trends in Ecology & Evolution 29, 205–213.

Perera, S.J., Ratnayake-Perera, D., Procheş, Ş., 2011. Vertebrate distributions indicate a greater Maputaland- Pondoland-Albany region of endemism. South African Journal of Science 107.

Pickett, S.T., Rogers, K. H. 1997. Patch dynamics: the transformation of landscape structure and function, in: Bissonette J.A (eds.) Wildlife and landscape ecology. Springer, New York, NY. pp. 101-127.

Ramesh, T., Downs, C. T. 2014. Modelling large spotted genet (*Genetta tigrina*) and slender mongoose (*Galerella sanguinea*) occupancy in a heterogeneous landscape of South Africa. Mammalian Biology, 79(5), 331-337.

Reynolds, C., Fletcher Jr, R.J., Carneiro, C.M., Jennings, N., Ke, A., LaScaleia, M.C., Lukhele, M.B., Mamba, M.L., Sibiya, M.D., Austin, J.D., Magagula, C.N., Mahlaba, T., Monadjem, A., Wisely, S.M., McCleery, R.A., 2018. Inconsistent effects of landscape heterogeneity and land-use on animal diversity in an agricultural mosaic: A multi-scale and multi-taxon investigation. Landscape Ecology 33, 241–255.

Ryan, C.M., Pritchard, R., McNicol, I., Owen, M., Fisher, J.A., Lehmann, C., 2016. Ecosystem services from southern African woodlands and their future under global change. Philosophical Transactions of the Royal Society B: Biological Sciences 371, 20150312.

R Core Team (2019). R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. URL: https://www.R-project.org/

Roques, K.G., O’Connor, T.G., Watkinson, A.R., 2001. Dynamics of shrub encroachment in an African savanna: relative influences of fire, herbivory, rainfall and density dependence. Journal of Applied Ecology 38, 268–280.

Sayre, N.F., Davis, D.K., Bestelmeyer, B., Williamson, J.C., 2017. Rangelands: Where anthromes meet their limits. Land 6, 31.

Shapiro, J.T., Monadjem, A., Röder, T., McCleery, R.A., 2020. Response of bat activity to land cover and land use in savannas is scale-, season-, and guild-specific. Biological Conservation 241, 108245.

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

Smith, J.A., Suraci, J.P., Clinchy, M., Crawford, A., Roberts, D., Zanette, L.Y., Wilmers, C.C., 2017. Fear of the human ‘super predator’ reduces feeding time in large carnivores. Proceedings of the Royal Society B: Biological Sciences 284(1857), 20170433.

Stanton, R. A., Fletcher, R. J., Sibiya, M., Monadjem, A., McCleery, R. A. 2020. The effects of shrub encroachment on bird occupancy vary with land use in an African savanna. Animal Conservation. URL: https://doi.org/10.1111/acv.12620

Stanton, R.L., Morrissey, C.A., Clark, R.G., 2018. Analysis of trends and agricultural drivers of farmland bird declines in North America: A review. Agriculture, Ecosystems & Environment 254, 244–254.

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

Stoddart, D.M., 1980. Some responses of a free living community of rodents to the odors of predators. In: Müller-Schwarze, D., Silverstein, R.M., (eds) Chemical Signals. Springer, Boston, MA.

Sugiura, S., Tanaka, R., Taki, H., Kanzaki, N., 2013. Differential responses of scavenging arthropods and vertebrates to forest loss maintain ecosystem function in a heterogeneous landscape. Biological Conservation 159, 206–213.

Sweet, R.J., Khumalo, S., 1994. Range resources and grazing potentials in Swaziland. Ministry of Agriculture and Cooperatives/United Nations Development Programme, Mbabane.

Tews, J., Brose, U., Grimm, V., Tielbörger, K., Wichmann, M.C., Schwager, M., Jeltsch, F., 2004. Animal species diversity driven by habitat heterogeneity/diversity: The importance of keystone structures. Journal of Biogeography 31, 79–92.

Turner, K.L., Abernethy, E.F., Conner, L.M., Rhodes, O.E., Beasley, J.C., 2017. Abiotic and biotic factors modulate carrion fate and vertebrate scavenging communities. Ecology 98, 2413–2424.

van den Berg, L.J.L., Bullock, J.M., Clarke, R.T., Langston, R.H.W., Rose, R.J., 2001. Territory selection by the Dartford warbler (Sylvia undata) in Dorset, England: the role of vegetation type, habitat fragmentation and population size. Biological Conservation 101, 217–228.

Veldman, J.W., 2016. Clarifying the confusion: Old-growth savannahs and tropical ecosystem degradation. Philosophical Transactions of the Royal Society B: Biological Sciences 371, 20150306.

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

Zambatis, N., Zacharias, P.J.K., Morris, C.D., Derry, J.F., 2006. Re-evaluation of the disc pasture meter calibration for the Kruger National Park, South Africa. African Journal of Range & Forage Science 23(2), 85–97.

Table 1. Stratification of sampled sites based on observed quantiles of landscape composition *comp*) and configuration (*config*) at 2 km. Both compositional and configurational metrics were derived from separate PCAs, wherein for composition, Shannon diversity and land cover richness was used. For configuration, edge length, number of patches, patch cohesion and landscape division index was used. We then stratified values from the first principal component into three quantile categories for sampling (< 33%, 34-66%, and >67%).

	< 33% comp	**34-66% comp**	**> 67% comp**
< 33% config	2	2	2
34-66% config	2	1	2
> 67% config	2	0	3

Table 2. The 9 vertebrate taxa that scavenged bait and were recorded by camera traps, and the number of sites (n = 16) that the corresponding taxa were found to have scavenged from. All data were recorded in 2018 from the lowveld region of northwestern Eswatini, Africa.

Species	**Sites scavenged**
Large-spotted genet (*Genetta tigrina*)	13 (81%)
Slender mongoose (*Galerella sanguinea*)	7 (44%)
Rodentia spp.	7 (44%)
Warthog (*Phacochoerus aethiopicus*)	4 (25%)
Banded mongoose (*Mungos mungo*)	2 (13%)
Black-backed jackal (*Canus mesomelas*)	1 (6%)
Side-striped jackal (*Canis adustus*)	1 (6%)
Serval (*Felis serval*)	1 (6%)
Common dwarf mongoose (*Helogale parvula*)	1 (6%)

Table 3. Comparison of two sets of models: 1) All, the amount of bait removed during scavenging trials on sites where > 10g of bait was removed and 2) Carnivore, > 10g of bait removed and a mesocarnivore was detected. Comparisons were based on the number of parameters (K), differences in AICc (ΔAICc) scores and model weights (*W*$_i$). Models evaluated variation in vegetation within a site (grass biomass, shrub cover, canopy over), canopy cover at the bait station (plot) and the composition and configuration of the surrounding landscape at a 2km scale. Scaled beta estimates (*β*) of models better than the null model are presented and bolded if 95% CI did not include 0.

Dependent Variable	**Model**	**K**	**ΔAIC_c**	**W_i**	***β*** **(95%CI)**
All	configuration	4	0	0.260	-0.21 (-0.46-0.04)
	plot.canopy	4	0.28	0.226	0.11 (-0.03- 0.25)
	null	3	0.35	0.219	
	site.shrub	4	2.46	0.076	
	site.grass	4	2.49	0.075	
	site.canopy	4	2.57	0.072	
	composition	4	2.57	0.072	
Carnivore	plot.canopy	4	0	0.463	**0.26 (0.03- 0.50)**
	configuration	4	1.15	0.260	**-0.32 (-0.62--0.02)**
	null	3	2.74	0.118	
	site.shrub	4	4.85	0.041	
	composition	4	4.9	0.040	
	site.grass	4	4.92	0.040	

site.canopy	4	4.96	0.039

Table 4. Comparison of models investigating variation in the time to the first detection of a mesocarnivore at the bait station. Comparisons were based on the number of parameters (K), differences in AICc (ΔAICc) scores and model weights (W_i). Models evaluated variation of vegetation within a site (grass biomass, shrub cover, canopy over), canopy cover at the bait station (plot) and the composition and configuration of the surrounding landscape at a 2km scale. Scaled beta estimates (*β*) of models better than the null model are presented and bolded if 95% CI did not include 0. Positive *β's* indicated a shorter time to detection.

Dependent Variable	**Model**	**K**	**ΔAICc**	W_i	***β* (95%CI)**
Carnivore	site.shrub	4	0	0.560	**-0.23 (-0.47--0.05)**
	plot.canopy	4	3.11	0.118	-0.13(-0.29- 0.02)
	null	3	3.45	0.100	
	site.grass	4	3.58	0.094	
	site.canopy	4	4.38	0.063	
	configuration	4	5.66	0.033	
	composition	4	5.67	0.033	

Figure Captions

Figure 1. Field sampling sites and experimental design conducted in the lowveld of northwestern Eswatini during 2018. With each of the 16 savanna sites we placed 3 bait plots in a closed patch of savanna (high shrub and canopy cover) and an open patch of savanna (low shrub and canopy cover) for a total of 6 plots per site.

Figure 2. The predicted values (bold line), 95% CIs (shaded areas), and raw data (open circles) of the weight of bait removed by mesocarnivores as a function of canopy cover at the plot scale in the Loweld of Eswatini in 2018.

Figure 3. The predicted values (bold line), 95% CIs (shaded areas), and raw data (open circles) of the weight of bait removed at the bait location by mesocarnivores as a function of the landscape configuration. Data was collected in the Loweld of Eswatini in 2018.

Figure 4. The predicted values (bold line), 95% CIs (shaded areas), and raw data (open circles) of the time it took mesocarnivores to detect bait as a function of shrub cover within a site. Time remaining after detection was measured as the maximum number of minutes in a scavenging event (45000 min) minus the number of minutes until a detection was recorded. A score of 0 indicated a mesocarnivore was not detected, and values near 45,000 indicated that they were detected soon after the bait was placed in the environment. Data was collected in the Loweld of Eswatini in 2018.