RESPONSE OF BIRD FUNCTIONAL TRAITS TO LANDSCAPE HETEROGENEITY

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INTRODUCTION

With rapidly increasing human populations as a driving force, agricultural expansion has intensified globally (Godfray et al., 2010; Tilman et al., 2011). As agriculture expands into previously unused regions, it fragments and replaces natural habitats, shifting diverse native vegetation to exotic monocultures that support lower biodiversity (Benton et al. 2002; Díaz et al. 2000; Donald, 2004; Stoate et al., 2001). These agricultural landscapes often remain interspersed with pockets of native vegetation, forming a mosaic landscape with a variety of land uses and covers. Mosaic landscapes can be either beneficial or detrimental to the persistence species within them (Berg, 2002). Species with lower dispersal ability tend to decrease in abundance in these mosaic landscapes, while a few species with high dispersal ability may increase in relative abundance before declining if the quality of the habitat decreases (Fahrig, 2001). Understanding the presence of different species across mosaic landscapes and any traits that may be shared by species which disperse throughout these landscapes is key to predicting the responses of wildlife to changing landscapes, to understanding the possible long-term impacts of habitat fragmentation on community structures, and to developing successful conservation plans (Ibarra-Macias, 2011).

Birds are one such taxa in which the dynamic impacts of human modification of the landscape are crucial to study, as the overall abundance of birds has been shown to increase with urbanization through high populations of a few species, while the overall diversity of birds has been shown to decrease with increased urbanization (Evans et al., 2009). This relationship between urbanization and diversity is indicative of human's influence on avian community structure. The expansion of agriculture, which fragments habitat like urbanization could impact the presence of a variety of taxa, such as birds. Birds are good models to study ecological processes because they are well known, easily monitored, and diverse (de Lima, 2013; Seymour, 2015). Additionally, birds' well described range of functional traits represent various aspects of bird life histories and behavior. For example, wing length, mass, and body length provide information about birds' abilities to move through the environment. Clutch size reveal details about the reproductive success of birds, and their diet influences their resource requirements. Considering these traits in birds may help provide predictions about how certain bird traits respond to the environment and potentially if certain traits should be targeted for conservation efforts.

In this study, we examined the effects of two classes of landscape heterogeneity, compositional and configurational, on the relative occupancy of birds and whether the relationship between these two factors could be explained by a particular functional trait or functional traits. For this study, compositional landscape heterogeneity was considered simply the number of different land uses in a landscape, such as savannah or rain-fed agriculture, while

configurational landscape heterogeneity was how those land uses were broken up and organized within the landscape.

METHODS

Study area

We conducted this study during the dry season from June 2016 to July 2016 at 16 sites across the savanna lowveld of north-eastern Swaziland. We selected 16 sites that exemplified various levels of compositional and configurational landscape heterogeneity among a mosaic of protected lands, communal rangelands, cattle ranches, and commercial agriculture. The average temperature of this region is 18 ° C in July, and 26 °C in January (Goudie & Price Williams, 1983). Average annual rainfall is between 550-725 mm per year, with a majority of rainfall experienced from October to April (Goudie & Price Williams, 1983; Roques et al., 2001). Soil found in the north-eastern lowveld is vertisol on basalt or dolerite, as well as lithosols, red acidic loams, and solonedzites (Murdoch, 1970; Roques et al., 2001). These soils support *Acacia* savanna in the east and broadleaf stands in the west (Roques et al., 2001; Monadjem, 2003). We tested how bird diversity responded to compositional and configurational heterogeneity across four different spatial scales.

Sampling landscape selection— land-cover mapping

To quantify landscape heterogeneity in our study area, we needed a classification system that delineated the dominant and ecologically distinct land cover-types. The best publically available dataset was the GlobeLand30 product (Jun et al. 2014), which is a 30 m x 30 m resolution land-cover dataset comprising eight land-cover classes of relevance to our study region. However, the dataset does not distinguish between different types of agricultural land-use and in particular no distinction is made between commercial (sugarcane) and subsistence agriculture (rain fed agriculture and grazing). This distinction is highly relevant for our study region, as well as for landscapes throughout developing world (Wright et al. 2012). Additionally, the dataset did not distinguish savanna, but rather classifies "natural" vegetation as grassland or forest. Our study region falls distinctly within the savanna biome of southern Africa, and savanna is the dominant vegetation cover in our study region. Due to these thematic issues and the lack of other fine-grained land-cover datasets with good accuracy (Jacobson et al. 2015), we developed a land-cover dataset form current satellite imagery that matched the extent of the study region and distinguished between cover classes that we deemed relevant in our landscapes (sensu Wulder and Coops 2014).

To classify our landscape we used Google Earth Engine (GEE), an open access online GIS platform for accessing and analyzing geospatial data (Google Earth Engine Team 2015). With GEE we performed supervised pixel-based classification on Landsat 8 annual TOA-corrected percentile composite imagery (Goldblatt et al. 2016). We used a classification and regression tree (CART) classifier to predict the occurrence of the land-cover types across the study area at a 50 m x 50 m resolution (Gislason et al. 2006; Goldblatt et al. 2016). To train the classifier we provided user-defined points and polygons of known land-cover. Our final training dataset consisted of over 3600 training points and 155 training polygons from five land-cover classes:

commercial agriculture, subsistence agriculture, savanna, woodland, and open water. The correct classification of training and test datasets for each land-cover class was 80.78 % for commercial agriculture, 67.92 % for subsistence agriculture, 87.04 % for savanna, 99.22 % for water and 71.65% for woodland. The overall validity of the classification was 79.15 %, and rivals that of the accuracy of the GlobalLand30 at 83.5 %. Additionally, the two datasets were qualitatively and quantitatively quite similar.

Sampling landscape selection— sampling across composition and configuration gradients

To test the effects of the different components of landscape heterogeneity on biodiversity in savanna, we stratified our sampling sites to capture independent gradients of compositional and configurational heterogeneity (Pasher et al. 2013). We used a moving window analysis to quantify compositional and configurational heterogeneity within a 2-km radius from each point on the landscape for stratification purposes. We chose this radius for stratifying our sampling as being sufficiently broad-scale to capture variation in responses amongst the more mobile taxa, but still sufficiently fine-scale to be relevant for less mobile taxa (see Ekroos et al. 2016). Within the 2-km buffer we calculated: the Shannon diversity index of land-cover types (SHDI), and total number of patches (NP). To represent compositional heterogeneity, we chose the commonly used SHDI, and to represent configurational heterogeneity we used NP, which represented connectivity processes (Cushman et al. 2008; Fahrig et al. 2011; Schindler et al. 2013). The representative metrics were correlated, so we used principal components analysis (PCA) to derive a single orthogonal principal component representing compositional heterogeneity and a single orthogonal principal component representing configurational heterogeneity. All cells were then ranked based on their PCA value for compositional and configurational heterogeneity.

With these rankings, we used stratified sampling in a partially factorial manner to sample savanna habitats embedded across gradients of compositional and configurational heterogeneity. To do so, we first identified all savanna locations at least 550 x 550 m (30.25 ha) in size (see Biodiversity Sampling below). From this sample, we randomly chose sampling locations (subject to land access approval) that were in the upper and lower quartiles of compositional and configurational heterogeneity (<25% and >75% for each combination) and supplemented this factorial sampling with locations of moderate heterogeneity (25-75% quantile). This stratification ensured that we sampled landscapes characterized by (1) both high, (2) both low, (3) high and low, and (4) moderate compositional and configurational heterogeneity. Our final selection included 15 sampled landscapes, three for each stratum, with an additional landscape added for birds. Each of these three replicates were stratified longitudinally (by creating three blocks longitudinally in the landscape) to control for potential variation across our extensive 100 km study area. Only two sampling landscapes had < 1 km minimum distance between them, and was due to logistical constraints of land access. While this design maximized the independence of sampling compositional and configurational gradients in the region, there was still a weak correlation between the compositional and configurational components in these sampled landscapes (Pearson's $r_p = 0.48$; p-value = 0.06). All analyses were conducted in R statistical software V 3.2.4 (R Core Team 2015) and Fragstats V 4.2.

Biodiversity sampling

In each sampling landscape we surveyed biodiversity within a 550 m x 550 m grid centered in savanna. Each grid was composed of five 50 m x 50 m plots, with one plot located in the center of the grid and one at each of the four corners, totaling 80 plots across 16 landscapes.

We surveyed birds using 10-min point counts, where every species seen or heard within a 50 m radius of the center of the plot was counted and identified. Particular attention was paid to avoid double counting the same individuals. Point counts were conducted by experienced observers (MDS, CR and AM), occurred between dawn and 3.5 hours after sunrise, and were not conducted under rainy or windy conditions. We repeated point counts on each plot over four consecutive days, resulting in a total of 320 point counts for the study. We randomized the sampling order of the plots and alternated observers between plots on consecutive days, to further reduce bias. Raptors, waterbirds, and birds transiting through the plots were excluded from the analysis.

Landscape metrics

The interpretation of the effects of principal components of configurational and compositional heterogeneity is not ecologically intuitive across different scales. To aid interpretation we chose to model the effects of individual landscape metrics on taxonomic diversity. We used Shannon diversity index of land-cover types (SHDI) as the single metric of compositional heterogeneity, as it is commonly used to represent compositional landscape diversity (Cushman et al. 2008). We calculated SHDI at four different spatial scales, with buffer radii of 1000-m, 1500-m, 2-km, and 3-km centered on each landscape. This represented a range of scales from the double the size of the grid to 1.5 times the scale at which the sample landscapes were originally classified. We also found that the total number of patches (NP) and SHDI were consistently the least correlated pair of compositional versus configurational heterogeneity metrics across all spatial scales (Pearson's rp 0.69 – 0.48). The NP was thus calculated for each spatial scale to represent configurational heterogeneity (NP). All landscape metrics were calculated in Fragstats V 4.2 using the eight neighbor rule for delineating patches (McGarigal et al. 2012).

Statistical analysis

For our 80 sampling plots we used the occupancy model of Royle and Nichols to predict the relative occurrence of each bird species based upon the likelihood of detection (time of day and identity of observer) and varying measures of heterogeneity characteristics [compositional (SHDI) and configurational (NP) heterogeneity at four different scales] for each plot (Royle, 2004). We then employed generalized linear models to test how a series of functional traits (body length, clutch size, diet, mass, wing length) predict the relative occupancy values of bird species in response to compositional and configurational heterogeneity at varying scales. For each type of relative occupancy estimate as a function of SHDI or NP at one of four spatial scales (1000-m—3-km), we ran a series of 8 candidate models comprised of one or two (minimally correlated; <0.60) bird-functional-trait predictors against a null model. Spatial autocorrelation between the sampling grids was not a concern in our dataset (Moran's I = 0.12; p-value 0.09). To determine the functional traits that best predicted the relationship between relative occupancy and

compositional or configurational heterogeneity, we compared the AICc between the different functional trait models within a specified group of heterogeneity-bird-occupancy relationships at each one of the four spatial scales. The best model at each type and scale of heterogeneity predicted occupancy had the smallest AICc, but was only considered as "best" if it showed an improvement on the null model of ≥ 2 AIC units. Models that fall within 2 AIC units of each other can be considered equivalent, hence those that fall within 2 AIC units of the null model, can be considered to have predictive capacity comparable to the null model (Burnham and Anderson, 2002). To determine the scale at which these components were most influential on biodiversity, we compared the AICc of models across all scales within a taxonomic group.

We conducted our Royle and Nichols occupancy models in the Unmarked package (Royle, 2004) and generalized linear models in R statistical software V 3.2.5 (R Core Team 2016). Bird functional trait information was taken from the Roberts Database (Hockey et al., 2005) and EltonTraits 1.0 (Wilman et al., 2014). All predictors were scaled so that model estimates were comparable.

RESULTS

A total of 26 bird species (of 86) fit parameters of the Royle and Nichols occupancy models and were considered in further analysis. Each of these species was present in at least 5% of all point-count surveys (16 of 320 surveys).

Functional traits and relative occupancy

Two candidate models fell within 2 AICc values of the best AICc for models examining the relationship between functional traits and relative occupancy of birds as a function of compositional heterogeneity (SHDI) at 1500-m. Wing length ($b = -0.14259$, $SE = 0.05137$, $t = -2.776$, $p = 0.0113^*$, Figure 1.a) and mass ($b = -0.12589$, $SE = 0.05340$, $t = -2.357$, $p = 0.0282^*$, Figure 2.a) were both found to be significant predictors in this relationship. Candidate models of these two predictors at the spatial scale of 2-km also fell within 2 AICc values of the best AICc for models examining the relationship between functional traits and relative occupancy of birds as a function of compositional heterogeneity (SHDI). Wing length ($b = -0.13339$, $SE = 0.05031$, $t = -2.651$, $p = 0.0149^*$, Figure 1.b) and mass ($b = -0.11448$, $SE = 0.05248$, $t = -2.182$, $p = 0.0407^*$, Figure 2.b) were also found to be significant predictors of this relationship at the 2-km spatial scale. No other candidate models were greater than 2 AICc values above the null model for any functional traits predicting the occupancy-based response of birds to compositional or configurational heterogeneity at any spatial scale.
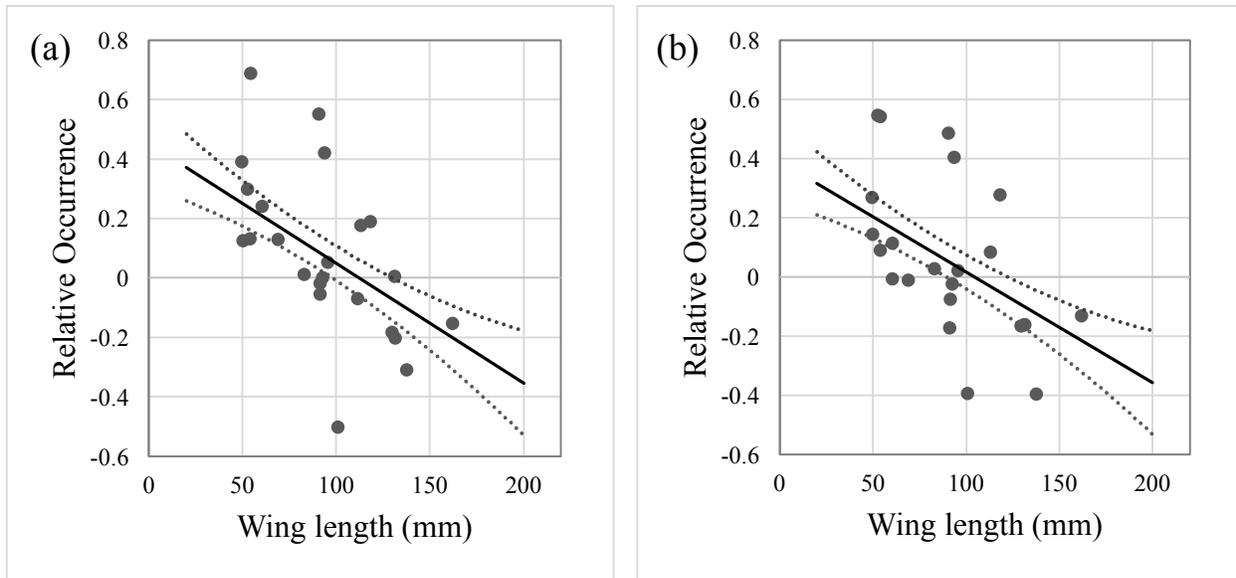
Figure 1. The relative occurrence of bird species as a function of compositional heterogeneity at (a) 1500-m and (b) 2-km, predicted by the wing length (mm) of each species (solid line) ± standard error (SE; dotted lines). Individual points represent the determined relative occurrence and average wing length of individual species.
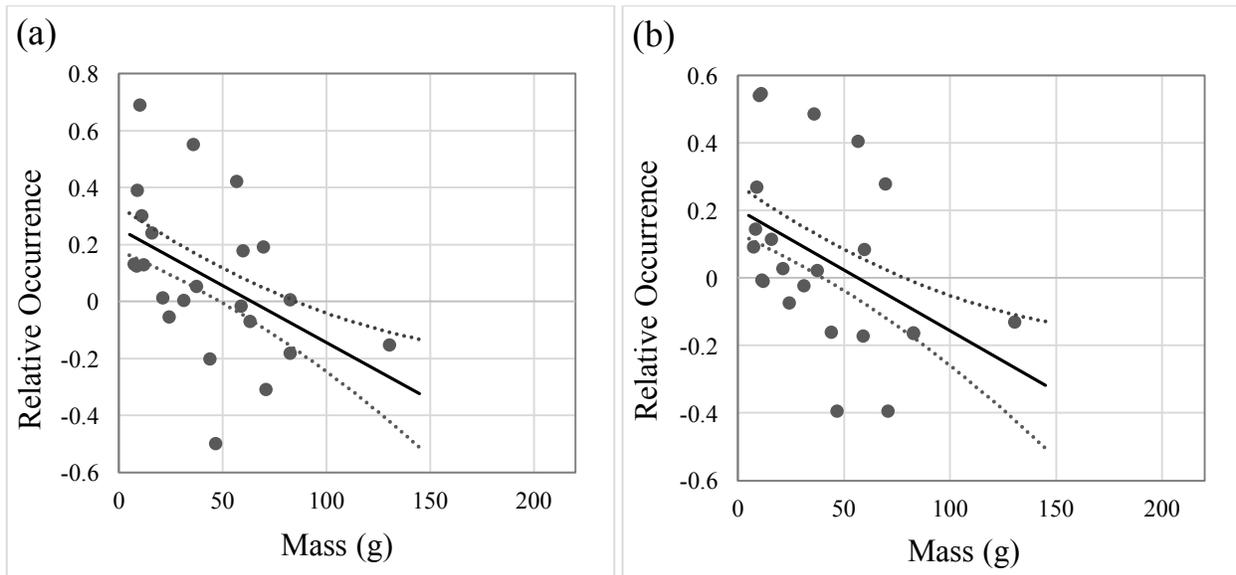

Figure 2. The relative occurrence of bird species as a function of compositional heterogeneity at (a) 1500-m and (b) 2-km, predicted by the mass (g) of each species (solid line) ± standard error (SE; dotted lines). Points represent the determined relative occurrence and average mass of individual species.

These results indicate that larger birds, those with a longer wing length and those with a higher mass, have decreasing relative occupancy as compositional heterogeneity increases at the 1500-m and 2-km scales. Conversely birds with smaller wing lengths and masses tend to increase in relative occupancy as compositional heterogeneity increases at the 1500-m and 2-km scales.

DISCUSSION

The results achieve our goal of determining what traits predict birds' occupancy-based relationship with compositional landscape heterogeneity. These traits, mass and wing length, we found predict the relationship at two of the four scales (1500-m and 2-km). We found that birds' response to compositional heterogeneity (SHDI) and not configurational heterogeneity (NP) was significantly predicted by wing length and by mass at two of the four spatial scales. The lack of predictors for birds' occupancy-based relationship with configurational heterogeneity suggests that this measure may not be appropriate for describing birds' response to landscape fragmentation.

The implications of this study are that larger birds will have a greater relative occupancy in areas with lower compositional heterogeneity and that as compositional heterogeneity increases the occupancy of birds longer wing lengths and higher masses with decrease. It is important to note that this study was conducted using passerine species. This negative relationship with size-based functional traits and compositional heterogeneity was found even when excluding all of the largest bird species, such as raptors and waterbirds, as these species tend to select on broader scales than those considered in this study (Bellrose, 1968; Peery, 2000). We predict that this relationship will be even more pronounced in larger bird taxa and should be considered in future studies. Our study supports that integrative conservation for birds moving forward will require the maintenance of both expansive protected areas for larger species and diverse mosaics of land uses for smaller species.

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