Drivers of bird diversity in an understudied African centre of endemism: The Angolan Central Escarpment Forest

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Summary

Natural habitats are being rapidly lost due to human activities. It is therefore vital to understand how these activities influence biodiversity so that suitable guidelines can be established for conservation. This is particularly important in understudied, high biodiversity, areas such as the Angolan Escarpment. Here we examine which habitat characteristics drive bird diversity and endemic species presence at Kumbira Forest, a key site in the Central Escarpment Forest. Bird diversity was sampled by 10 min bird point counts, whereas habitat characteristics were measured by a combination of ground-based vegetation surveys and remotely sensed data modelling of Landsat images. GLM, multi-model inference and model averaging were used to determine the most important variables driving species richness and the presence of endemics. The remote sensing variables performed poorly in predicting presence of Red-crested Turaco and Gabela Bushshrike but they contributed significantly to explain species richness and Gabela Akalat presence, both of which were associated with greater canopy cover. Liana density and elevation were also important explanatory variables in certain cases. Conservation actions at Kumbira should focus on increasing canopy cover and maintaining forest integrity (as measured by liana density), as these actions are likely to have the most positive outcomes for the avifauna.

Keywords: Angola; endemics; generalized linear model; Kumbira; model averaging

Introduction

Habitat loss due to human activities is the most important threat to biodiversity (Brooks et al., 2002) and the main cause of population declines and species extinctions in birds (Stattersfield and Capper, 2000). This is especially significant in the tropics, where almost 70 percent of global biodiversity is concentrated (Bradshaw et al., 2009) and human impacts are increasing at an accelerating pace (Cincotta et al., 2000). Despite primary forests being irreplaceable for maintaining tropical biodiversity (Gibson et al., 2011), modified landscapes such as secondary growth and agroforestry systems can also hold important biodiversity and connect core areas for conservation (Schulze et al., 2004, Gove et al., 2008, Cáceres et al., 2015). Therefore, to implement successful conservation strategies it is important to assess biodiversity in human-modified landscapes (Chazdon et al., 2009, Gardner et al., 2009), and to identify the key factors influencing biodiversity in these landscapes. This is especially the case for extinction-prone species, such as those that are range-restricted or especially sensitive to human activities.

African biodiversity is globally important but extremely understudied (Norris et al., 2010, Gardner et al., 2010, Gibson et al., 2011). This is particularly true for Angola: while it is considered one of the most biodiverse countries of Africa due its location at the confluence of five different biomes, it is very poorly known as a result of almost 30 years of armed conflict (Huntley, 1974, USAID, 2008). The Escarpment Forest constitutes one of the most important areas for biodiversity in the country, although it could not be designated as a ‘biodiversity hotspot’ due to the lack of information available at the time of the ‘hotspot’ analyses (Myers et al., 2000). In the case of birds, arguably the best-studied taxonomic group in Angola, these forests are of key conservation importance. The Escarpment Forest is an important evolutionary hotspot (Hall, 1960) where most of the endemic bird species of Angola are found, and it is the most important habitat of the Western Angola Endemic Bird Area, the only centre of bird endemism in the country. Because no protected area is located within this habitat, it has been identified as a critical conservation priority for birds, not only for Angola (Dean, 2001, BirdLife International, 2015a) but for Africa as a whole (Collar and Stuart, 1988).

By the 1960s it was estimated that 95 percent of the original forests had been converted to shade-coffee plantations, which left the high canopy trees intact (Hawkins, 1993). During the civil war (1975-2002) these plantations were abandoned, allowing forest habitats to recover (Ryan et al., 2004, Sekercioglu and Riley, 2005). The end of the war led to the migration of human populations back to rural areas like the Central Escarpment Forest, and since then slash-and-burn agriculture and logging have become major threats to these forests (Mills, 2010, Cáceres et al., 2015). It is therefore important to understand the impacts that these human activities are having on the forests, such as how they are affecting habitat characteristics, which in turn influence bird diversity and the distribution and abundance of threatened endemics.

The main aim of this study was to understand the environmental drivers influencing bird diversity at Kumbira Forest, a key site for threatened endemic birds in Angola (Mills, 2010). Because conservation planning will be most effective if it is based on regional-scale species distribution models, we first assess if variables obtained through remote sensing techniques contribute to explain bird diversity in Kumbira. Then, we use locally collected ground variables obtained through vegetation surveys to model species richness and presence of endemic birds. Finally, we propose conservation guidelines based on the results.

Methods

Study Area

Kumbira Forest is the most representative and important site for the conservation of threatened endemic birds of the Angolan Central Escarpment. It holds significant populations of four of the five threatened endemics of this region, namely of the Endangered Gabela Bushshrike *Laniarius amboimensis*, Gabela Akalat *Sheppardia gabela* and Pulitzer's Longbill *Macrosphenus pulitzeri*, and Near Threatened Monteiro's Bushshrike *Malaconous monteiri* (Data Deficient at the time that field work was done). Gabela Akalat is the most range-restricted of the Angolan endemics with an estimated range of only *c*. 650 km^2, although it can be locally common, as it is at Kumbira. Gabela Bushshrike has a wider distribution (*c*.1800 km^2), occurring both further north and south (at Gungo) of Kumbira Forest, while Pulitzer Longbill and Monteiro Bushshrike have ranges of *c*. 3700 km^2 and 8000 km^2 respectively (Mills, 2010). Additionally, Kumbira is also home to the endemic, although more widespread (*c*. 190000 km^2), Red-crested Turaco *Tauraco erythrolophus* (BirdLife International, 2015b).

Kumbira Forest is located in the municipality of Conda, in the western Angolan province of Kwanza Sul (11.107°S, 14.336°E). The exact limits of Kumbira forest are difficult to define in the west, because the forest gradually merges with dense habitats associated with the escarpment. The eastern limit is nevertheless clearly delimited by the grasslands of the Njelo Mountain, which rises to 1,688 m and runs north-east/south-west. Here we define the southern limit of the forest as 11.230°S and the northern limit as Cassungo village (11.104°S 14.311°E) (Figure 1). This forest represents an area of approximately 10 000 ha. The terrain within this area varies from relatively flat in the valley bottoms, to the steep slopes of the Njelo Mountain, with altitudes varying from *c*. 680 to 1,160 m asl.

Figure 1

Bird Data

MSLM sampled bird communities by means of 10 min point counts (Bibby et al., 2000) from 13 September 2010 to 2 October 2010, between sunrise (*c*. 0545h) and 1030h, except when weather was poor (rain or strong wind). All birds seen and heard within a 50 m radius of each sample point were recorded. Sample points were spaced at least>150 m apart of each other to avoid double-counting individuals. Furthermore, points were located along existing paths in order to sample as much of Kumbira Forest as possible in this three weeks expedition. Each 10 min point count was divided into two 5 min periods. In order to map the presence of the five key species, a pre-composed track consisting of 30 s snippets of the vocalisations of Monteiro's Bushshrike, Red-crested Turaco, Gabela Bushshrike, Gabela Akalat and Pulitzer's Longbill) was played between these two periods, to increase their detectability. Playback was done using an Ipod (Apple, Cupertino) and RadioShack Mini Amplifier speaker (RadioShack Corporation, Fort Worth), always at the same volume. Because playback violates the point count assumption that birds do not approach the observer, we only use playback data for the analysis of species presence. We also excluded all observations that could refer to birds that had already been registered.

Environmental variables – ground variables recorded in situ

Habitat characteristics were measured by AC in a circular sample plot of 10 m radius around each bird sample point. The variables measured were: (1) elevation (elev) by GPS; (2) canopy height (ch) as the maximum visible height of the canopy (Dallimer et al., 2009), using a Nikon 550 Laser rangefinder (Nikon Corporation, Tokyo); (3) canopy cover (cc) with a convex spherical densiometer (Forestry Suppliers Inc., Jackson); (4) shrub cover (shrub) as the percentage of vegetation cover at the shrub level (0.15-1.5m) along a 10 m transect; and (5) liana density (ld) as the number of lianas along a 10 m transect. Canopy height and canopy cover were the average of four measurements taken at 5 m in each cardinal direction from the sample point,

To estimate above-ground biomass (AGB) at each plot, we measured height and diameter at breast height (DBH) of all trees with a DBH > 10 cm. Tree height was measured with a clinometer and DBH with a measuring tape. AGB was calculated using a pantropical allometric equation (Chave et al., 2014) that relates AGB of a tree to DBH, total height and wood density. Since it was not possible to identify the species of trees to obtain specific wood densities, we applied a constant wood density of 0.59 g/cm3, the average reported for trees in Africa (Henry et al., 2010). Finally, biomass estimates were converted to carbon values using the fraction of 0.47 MgC, as recommended for tropical and subtropical regions (Paustian et al., 2006), and standardized per area (MgC/ha).

Environmental variables derived from remote sensing

Spectral indices and forest cover (xfor) were calculated from Landsat 7 ETM+ satellite image (WRS-2 path 181 row 68) with low cloud cover (<10%) from 18 May 2010, obtained from the U.S. Geological Survey (USGS) and Earth Resources Observation & Science Center (EROS) via the EarthExplorer interface (http://earthexplorer.usgs.gov). It was radiometric normalized and atmospheric corrected using Modified Dark Object Subtraction (DOS), as proposed by Chavez (1996). The empty lines of the Landsat 7 scene produced by the scan failure were treated as "no data" and all sample points located in these gaps were excluded from analyses.

The following spectral indices were calculated for a 50 m radius circular plot around each bird sample point: (1) Land Surface Water Index (LSWI), calculated as the normalized proportion between Near Infrared (NIR) and Short Wave Infrared (SWIR), represents the amount of moisture present in the leaves and soil (Xiao et al., 2002); (2) Blue-Red ratio Index (BR) that is the normalized difference between the Blue and Red bands and represents the shadow produced by the canopy; and (3) Enhanced Vegetation Index (EVI) that optimizes vegetation signal in regions with high biomass and reduces atmosphere influences (Huete et al., 2002).

A forest cover map was created using supervised classification with Maximum Likelihood Algorithm (MLA) (Jensen, 2005). The scene was classified in “Forest” and “Non-Forest” with Regions of Interest chosen based on field knowledge of the study area. Accuracy of the forest class was assessed by comparing the resulting classification with Google Earth high resolution images. Based on this information we estimated the forest cover percent in a 50 m radius circular plot around each bird sample point.

Data Analysis

Generalized Linear Models (GLM) (Nelder and Wedderburn, 1972) were used to evaluate bird responses to environmental variables (Zuur et al., 2007) (Supplementary material, Table S1). Bird responses were represented by species richness and by the presence of endemic species that were recorded in over 20 percent of the point counts, namely Red-crested Turaco, Gabela Akalat and Gabela Bushshrike. All variables were standardized and collinearity was assessed by Spearman rank correlation coefficients, which does not assume linear relations between variables. Variables with coefficients of over 0.7 were removed from the analyses (Zuur et al., 2009). The variables maintained in the analyses were chosen based on their biological importance and management relevance. We also assessed spatial autocorrelation using Pearson-based Mantel tests (Legendre and Legendre, 1998) with 1000 permutations and mapping the residuals of the best ranking models (Baddeley et al., 2005, Kühn and Dormann, 2012). All these analyses were carried out for each of the response variables (species richness and the presence of endemics).

To assess whether remote sensing variables (spectral indices and forest cover) provided additional information for modelling bird diversity in Kumbira, we modelled species richness and the endemic species presence using a dataset with remote sensing and ground variables. Then, we identified the best models for each group of variables: (1) the “null model” (with no explanatory variables); (2) only ground (hereafter “Ground Models”); (3) only remote sensing (hereafter” RS Models”); and (4) ground and remote sensing (hereafter “Combined Models”).

Only sample points that had both spectral indices and forest cover estimates were used in the analyses – those affected by Landsat 7 scan failure were excluded. Model performance was evaluated using Akaike´s Information Criterion with small sample size correction (AICc), Akaike weights (ω) and evidence ratio (Hurvich and Tsai, 1989, Anderson and Burnham, 2002, Burnham and Anderson, 2002, Burnham and Anderson, 2004).

To assess the environmental variables driving bird diversity at Kumbira Forest, GLMs were constructed with the larger dataset that included only the ground variables of all the sample points (N=201). An adjusted coefficient of determination was used (R^2) to assess the predictive power of the models. Model averaging was performed to obtain coefficients estimates for all models with a AICc difference (ΔAICc) smaller than 10 (Burnham and Anderson, 2002, Burnham et al., 2011). Plotting of coefficients estimates and standard errors were used to identify key variables, and their relative variable importance (RVI) was also calculated. All analyses were performed using R 3.2.0 software (R Core Team, 2015) and the packages Vegan 2.0-9 (Oksanen et al., 2012) and MuMIn 1.9.13 (Barton, 2013).

Results

A total of 201 bird point counts were performed and 100 bird species registered. The mean species richness per point count was 10.4 ± 3.4 species (mean ± standard deviation) with a range from one to 23 species. Red-crested Turaco was the most-registered endemic, recorded at 68 percent of the point counts (n=136), followed by Gabela Akalat (46%, n= 92) and Gabela Bushshrike (21%, n=42). Monteiro Bushshrike and Pulitzer Longbill were present only in 7 percent (n=15) and 5 percent (n=11) of the point counts respectively. Vegetation characteristics were measured for all the sample points but spectral indices (LSWI, EVI and BR) and forest cover were only estimated for 132 out of 201 points due to the Landsat 7 scan failure (Figure 2).

Figure 2

Canopy height was strongly correlated with canopy cover (cor=0.70, *p-value* < *0.001*) and thus excluded from the analysis, as was blue-red ratio with forest cover (cor=0.73, *p-value* < *0.001*) (Supplementary material, Figure S1). Both canopy cover and forest cover were retained for analyses because of their importance for species richness and Gabela Akalat presence, and their relevance to forest management.

Spatial autocorrelation

Only the Mantel test for the presence of Red-crested Turaco showed a weak but significant degree of spatial correlation (r=0.04, P=0.032) while in the other response variables the test was not significant (species richness r = -0.05, P = 0.951; Gabela Akalat r = 0.007, P = 0.147; Gabela Bushshrike r = -0.02, P = 0.703) (Supplementary material, Table S2). However, the residual plots did not show any clear pattern of the models residuals (Supplementary material, Figure S2).

Effects of remote sensing variables

Only in the case of species richness, Combined Models greatly outperformed both RS Models and Ground Models, as shown by the high evidence ratios (29.2 and 118.4 respectively, Table 1). RS Models were good in predicting the presence of Gabela Akalat and performed even better

Table 1

when combined with ground variables. Nevertheless, RS Models performed poorly for the presence of Red-crested Turaco and Gabela Bushshrike, as they ranked below the null models.

Role of habitat characteristics in determining bird diversity in Kumbira

Canopy cover positively influenced species richness and the presence of Gabela Akalat, while liana density positively influenced species richness and Red-crested Turaco presence. Elevation had a negative influence in Gabela Bushshrike and a positive in Red-crested Turaco (Table2, Figure 3). Despite the influence of these variables on the models, they still presented high levels of unexplained variation as shown by the low values of their adjusted coefficients of determination (Supplementary material, Table S3 - Table S6).

Table 2

Figure 3

Discussion

The use of remotely sensed data is becoming more widespread in conservation planning. Spectral indices and classification maps are often used to infer habitat suitability and examine environmental drivers of biodiversity (Huete et al., 2002, Pettorelli et al., 2005). However, we demonstrate here that the utility of this approach is rather limited and species specific for the Angolan Central Escarpment. For example, RS models performed very poorly in explaining the presence of Red-crested Turaco and Gabela Bushshrike, being even outperformed by null models.

The limited predictive performance of models based on Landsat imagery is not entirely surprising. While Landsat imagery can be used well over long temporal and large spatial scales (Kerr and Ostrovsky, 2003, Wang et al., 2010), it is less useful for biodiversity studies conducted at smaller scales and in more complex environments (Aplin, 2005, Nagendra and Rocchini,

2008) – like the mosaic like and dynamic Kumbira Forest – where spectral indices not always directly relate to wildlife presence or abundance (Nagendra, 2001). Furthermore, the approach was also limited by the lack of adequate Landsat images due high cloud cover in the study area for most of the year.

Remote sensing variables did provide a good approximation for some ground variables. For example, forest cover (remote sensing) was correlated with canopy cover (vegetation survey) (cor=0.6, *p-value*<0.001) and positively influenced bird species richness and Gabela Akalat presence. This is encouraging, as variables derived from remote sensing are easier, faster and cheaper to collect than most field-collected ground data, and they can be extrapolated across a larger area to assess the presence of key species.

The poor performance of remote sensing variables for Red-crested Turaco and Gabela Bushshrike can be related with satellite imagery resolution and scale issues. Despite the 30 m resolution of Landsat imagery, the variables obtained from them do not seem to detect the characteristics affecting these birds. These species territories might include more of the mosaic-like landscape of Kumbira, where small spatial changes might not to be detected by the Landsat images.

Environmental variables collected in situ – elevation, canopy cover, shrub cover, liana density and carbon – seem to be good predictors of bird diversity in Kumbira but even the best models had high levels of unexplained variation and the variables presented a low explanatory power. This can be related with the lack of statistical power due to the low detectability of some endemics (present just in 20% of the sample points), or the failure of the vegetation surveys to record the habitat characteristics that are driving bird diversity.

Canopy cover was important for species richness and the presence of threatened endemics. Canopy cover is indirectly related to habitat disturbance and affect the presence of birds, especially forest specialists (Mammides et al., 2015). This can explain its influence in Gabela Bushshrike and especially Gabela Akalat. In other areas of Africa, the presence of threatened endemic forest birds is also related to canopy cover and structure (Dallimer and King, 2007, Dallimer et al., 2012, de Lima et al., 2013, Mammides et al., 2015). Canopy cover was also highly correlated with canopy height, therefore the endemics might also be affected by canopy height and other aspects of mature forests including canopy structure and understorey humidity.

Liana density was also an important variable. Lianas usually increase in gap areas or as part of the successional process of secondary growth (Schnitzer and Bongers, 2002). However, due to the history of human disturbance in Kumbira (transformation of natural forest to shade coffee plantation), it is possible that liana presence here is indicative of older and more natural forest – as lianas can only grow if there are trees in the first place – rather than areas frequently disturbed mainly by slash-and-burn agriculture. This is supported by the positive associations between liana density and canopy height (cor=0.37, p-value<0.001).t.

Conservation Implications

Our study provides some important insights into the conservation of one of Africa's critical priority areas for bird conservation. Many of the results indicate that conservation efforts should focus on the maintenance of canopy cover by protecting the remaining forest. For example, canopy cover affects both overall species richness and the Gabela Akalat presence. The endangered Gabela Akalat is the key priority for conservation at Kumbira because is the most range-restricted of the Angolan endemics with an estimated suitable range of only *c*. 650 km^2 (Mills, 2010). As a result, this species is particularly sensitive to forest loss and depends in the maintenance of canopy cover at Kumbira for its survival.

Protecting high quality mature forest in the region is challenging as the extent and condition of forests are threatened by slash-and-burn agriculture and logging of high canopy trees for timber (Mills, 2010, Cáceres et al., 2015). Protected areas are widely used in conservation, but at present no area of the Angolan Central Escarpment Forest has formal protection status. A proposal for the establishment of a *c*. 50 km^2 strict nature reserve was put forward in the past (Huntley and Matos, 1994) but has yet to be implemented. Alternative approaches to protected areas could involve local populations. These include increasing forest cover through reforestation initiatives, with native tree species. Such action has recently been initiated in Kumbira with the establishment of an experimental nursery as part of a project funded by the Conservation Leadership Programme. Wildlife friendly agriculture may also be beneficial (Gove et al., 2008, Buechley et al., 2015). In this context, we recommend prioritising research into the economic viability of recovering the abandoned shade coffee plantations and on the impacts such action could have on biodiversity, together with the evaluation of other more biodiversity-friendly agricultural practices.

Any conservation actions require good baseline data on the occurrence of the most important species. For most species, our study demonstrates the importance of basing this on good quality data from ground surveys, complemented by remote sensing variables. However, it is encouraging that the presence of the most endangered species, the Gabela Akalat, can be predicted by remote sensing variables, as this provides hope that large-scale mapping can be used to identify priority areas. However, the models we present here had very low explanatory power, indicating the role of unmeasured factors such as landscape context and resource availability. Some of these may be resolved by using newer and more refined remotely sensed measures, which would also provide a basis to examine other areas of the Angolan Central Escarpment Forest, such as the forest of Bango-Seles 25 km to the South. In addition, future research should aim at including other taxa such as plants, amphibians and insects that may be more sensitive to human disturbance and may not reflect the patterns of bird diversity (Kremen et al., 2008). This information is critically important to enable the effective conservation and sustainable planning that are required to protect the unique biological richness of this region.

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TABLES

Table 1. Best models generated for each group of variables (N null, G ground, RS remote sensing, and G+RS combined) for species richness and the presence of Red-crested Turaco, Gabela Akalat and Gabela Bushshrike. The rank of each model is included (from 256 possible models), followed by the variables included in each model, the model log-likelihood (logLik), the number of parameters (K), the Akaike´s Information Criterion with small sample size correction (AICc), AIC differences (ΔAICc), Akaike weights (ω) and evidence ratio. The variables used were EVI – enhanced vegetation index, LSWI – land-surface water index, xfor – forest cover, c – carbon, cc – canopy cover, elev – elevation, ld – liana density and shrub – shrub cover.

Response Variable	Variable groups	Model rank #	Variables in model	logLik	K	AICc	ΔAICc	ω	Evidence ratio
Species Richness	G+RS	1	ld, xfor	-174.53	3	357.38	0.00	0.1113	
	RS	56	xfor	-178.97	2	364.13	6.75	0.0038	29.2
	G	97	cc, ld	-179.31	3	366.93	9.55	0.0009	118.4
	N	246		-186.80	1	377.69	20.31	0.0000	25714.8
Red-crested Turaco	G	1	elev, ld	-82.66	3	171.50	0.00	0.0319	
	G+RS	3	c, elev, ld, xfor	-80.78	5	172.03	0.53	0.0245	1.3
	N	26		-85.95	1	173.93	2.42	0.0095	3.4
	RS	41	xfor	-85.35	2	174.79	3.28	0.0062	5.2
Gabela Akalat	G+RS	1	c, EVI, xfor	-84.15	4	176.61	0.00	0.0490	
	RS	3	xfor	-86.71	2	177.51	0.90	0.0312	1.6
	G	38	c, cc	-87.14	3	180.46	3.85	0.0071	6.9
	N	87		-89.97	1	181.98	5.37	0.0033	14.7
Gabela Bushshrike	G	1	elev, ld	-65.88	3	137.95	0.00	0.0528	
	G+RS	2	elev, ld, xfor	-64.97	4	138.25	0.30	0.0455	1.2
	N	70		-70.75	1	143.52	5.57	0.0033	16.2
	RS	111	xfor	-70.42	2	144.93	6.98	0.0016	32.7

Table 2. Relative variable importance (RVI) and averaged coefficients estimates obtained from generalised linear models with ground variables (c – carbon, cc – canopy cover, elev – elevation, ld – liana density, shrub – shrub cover) for species richness and the presence of Red-crested Turaco, Gabela Akalat and Gabela Bushshrike. Only models with ΔAICc<10 were included in the analysis. The grey shading highlights variables with the highest relative importance values (>0.5) and the asterisks indicate significance levels for *p-value* (*)<0.05, (**)<0.01, and (***)<0.001.

	Species Richness		Red-crested Turaco		Gabela Akalat		Gabela Bushshrike	
	RVI	Coef.	RVI	Coef.	RVI	Coef.	RVI	Coef.
c	0.268	0.025	0.679	-0.298	0.349	-0.138	0.362	-0.1951
cc	1.000	**0.282*** **	0.307	0.110	0.798	**0.338***	0.554	0.3127
elev	0.299	0.044	0.992	**-0.503****	0.388	0.159	0.729	**0.3512***
ld	0.992	**0.223****	0.883	**0.443***	0.267	-0.016	0.474	-0.276
shrub	0.271	-0.029	0.268	-0.024	0.308	-0.098	0.334	-0.1591