Bird Conservation International (2017) 27:256–268. © BirdLife International, 2017
doi:10.1017/S0959270917000119

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

AIMY CÁCERES, MARTIM MELO, JOS BARLOW,
RICARDO FAUSTINO DE LIMA and MICHAEL S. L. MILLS

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 *Tauraco erythrolophus* and Gabela Bushshrike *Laniarius amboimensis* but they contributed significantly to explain species richness and Gabela Akalat *Sheppardia gabela* 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.

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% 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% 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 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.1,800 km^2), occurring both further north and south (at Gungo) of Kumbira Forest, while Pulitzer Longbill and Monteiro Bushshrike have ranges of c.3,700 km^2 and 8,000 km^2 respectively (Mills 2010). Additionally, Kumbira is also home to the endemic, although more widespread (c.190,000 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

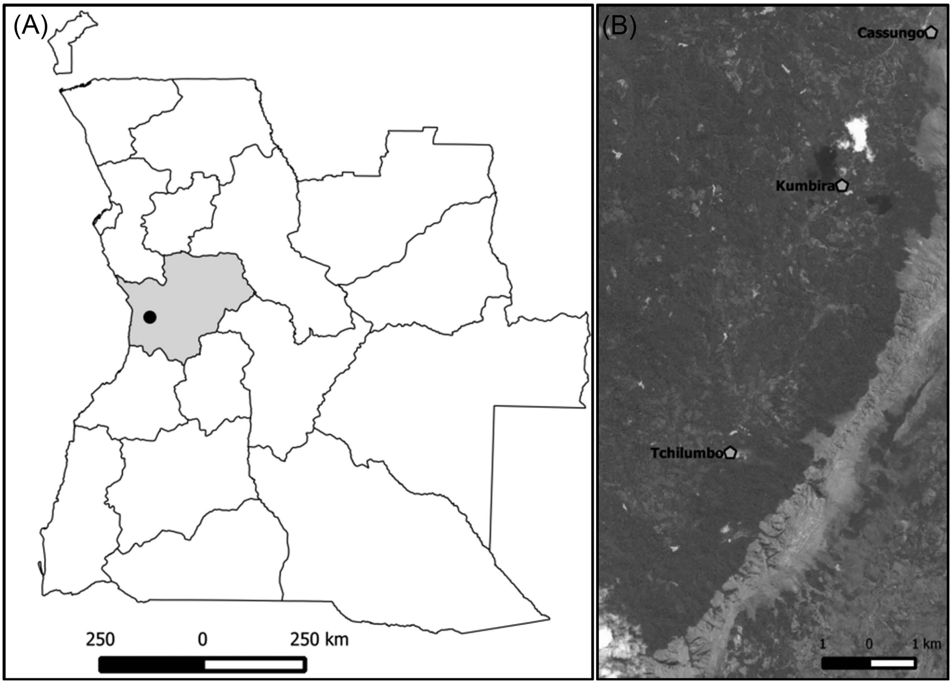

Figure 1. (A) Location of Kumbira Forest (black circle) in Kwanza Sul province (in grey), Angola. (B) Study area with the most important villages: Cassungo, Kumbira and Tchilumbo.

flat in the valley bottoms, to the steep slopes of the Njelo Mountain, with altitudes varying from c.680 to 1,160 m asl.

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 > 150 m apart from 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-week 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)

https://doi.org/10.1017/S0959270917000119 Published online by Cambridge University Press

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/cm^3, 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 and Science Center (EROS) via the EarthExplorer interface (http://earthexplorer.usgs.gov). It was radiometric normalised 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 normalised 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 normalised difference between the Blue and Red bands and represents the shadow produced by the canopy; and (3) Enhanced Vegetation Index (EVI) that optimises vegetation signal in regions with high biomass and reduces atmospheric 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

Generalised Linear Models (GLM) (Nelder and Wedderburn 1972) were used to evaluate bird responses to environmental variables (Zuur *et al.* 2007) (Table S1 in the online supplementary material). Bird responses were represented by species richness and by the presence of endemic species that were recorded in over 20% of the point counts, namely Red-crested Turaco, Gabela Akalat and Gabela Bushshrike. All variables were standardised 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 1,000 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 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, 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 coefficient 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 ± SD) with a range from one to 23 species. Red-crested Turaco was the most-registered endemic, recorded at 68% 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% ($n = 15$) and 5% ($n = 11$) 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).

Canopy height was strongly correlated with canopy cover (cor = 0.70, $P < 0.001$) and thus excluded from the analysis, as was blue-red ratio with forest cover (cor = 0.73, $P < 0.001$) (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, $P = 0.703$) (Table S2). However, the residual plots did not show any clear pattern of the models residuals (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 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.

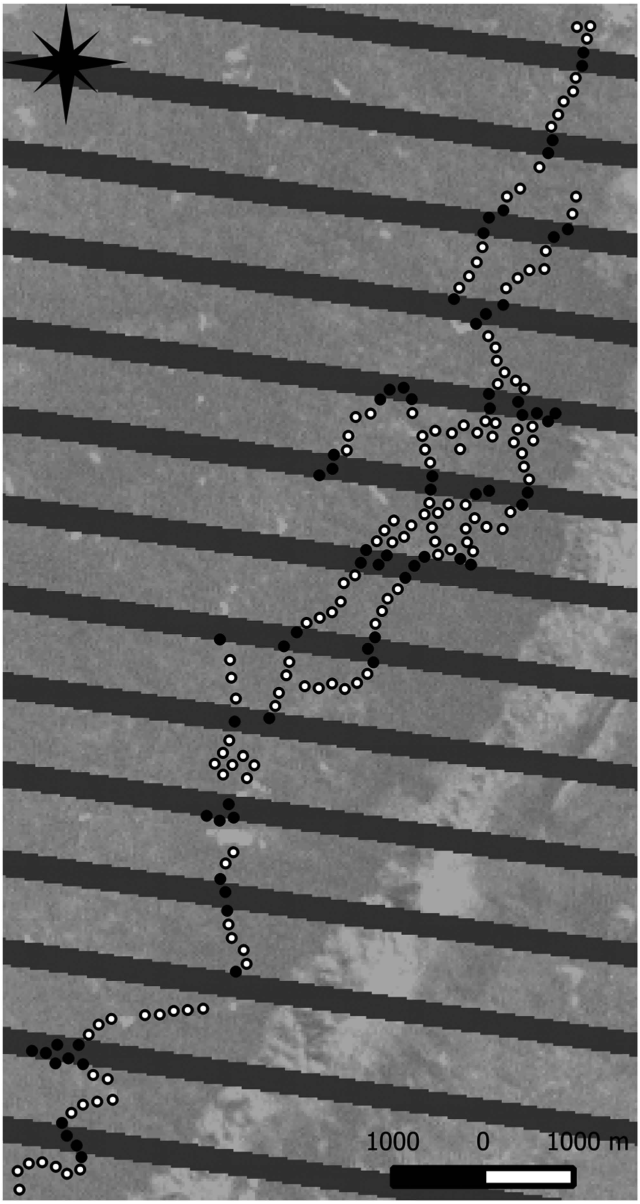

Figure 2. Landsat 7 ETM+ scene from 18 May 2010 with sample points. Dark grey strips represent the gaps created by the satellite scan failure and were treated as "no data". Vegetation characteristics were measured for all sample points (black and white circles, n=201) while spectral indices and forest cover were only estimated for 132 points (white circles) that were not affected by the scan failure.

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

https://doi.org/10.1017/S0959270917000119 Published online by Cambridge University Press

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

negative influence in Gabela Bushshrike and a positive in Red-crested Turaco (Table 2, 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 (Table S3–Table S6).

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

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* (*) < 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

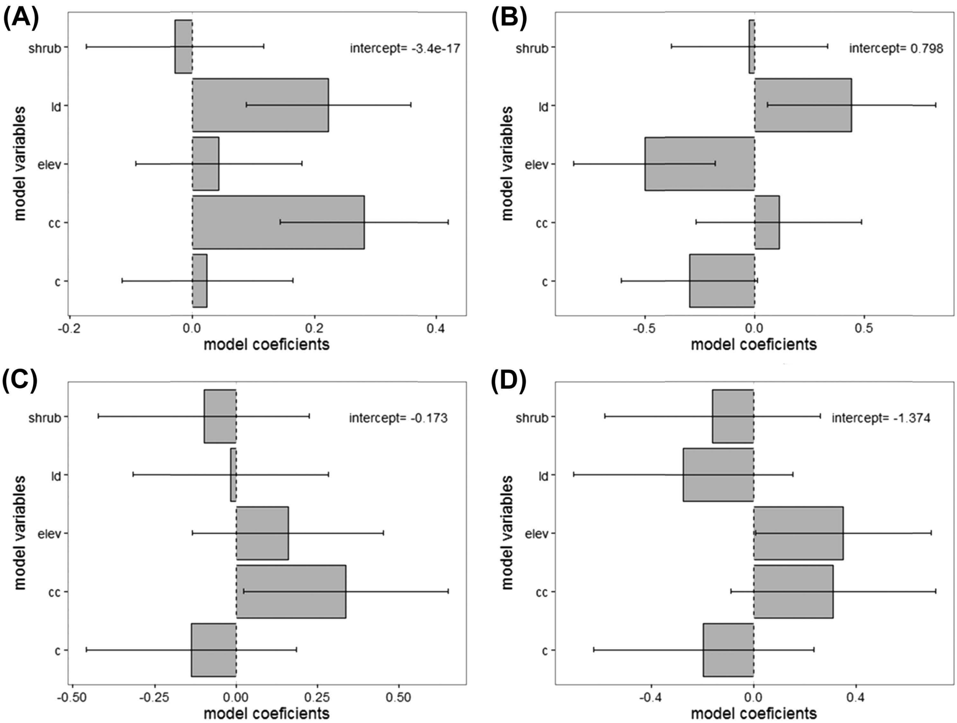

Figure 3. Model averaging coefficients estimates for ground variables (N = 201) and models with ΔAICc < 10 for (A) species richness, (B) Red-crested Turaco, (C) Gabela Akalat and (D) Gabela Bushshrike presence. All averaged coefficients are presented in grey bars and the standard errors in lines. A variable is significant when its averaged coefficients (± standard errors) do not overlap 0. The variables used were shrub – shrub cover, ld – liana density, elev – elevation, cc – canopy cover and c – carbon.

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) – as in the mosaic-like and dynamic Kumbira Forest – where spectral indices do 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, $P < 0.001$) 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 to 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, $P < 0.001$).

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.

Supplementary Material

To view supplementary material for this article, please visit https://doi.org/10.1017/S0959270917000119

Acknowledgements

Special thanks to Phil Hall, Nigel Collar, Brian Huntley, Michael Rogerson, Francisco Maiato and Fernanda Lages. Also thank you to Ricardo Solar and Paulo Cardoso for help with part of the statistics. Antonio Monteiro collaborated in estimating the spectral indexes. This scientific paper is from the Portuguese-Angolan TwinLab established between CIBIO-InBIO and ISCED/Huíla, Lubango. This research was funded by the Conservation Leadership Programme (Grant 0109710) and Mr A. P. Leventis of the A. P. Leventis Ornithological Research Institute, Jos, Nigeria. AC is funded by a PhD grant from the Portuguese Science and Technology Foundation, FCT (SFRH/BD/78778/2011). MM and RL are funded by FCT Post-Doctoral grants (SFRH/BPD/100614/2014 and SFRH/BPD/91494/2012, respectively).

References

Anderson, D. R. and Burnham, K. P. (2002) Avoiding pitfalls when using information-theoretic methods. *J. Wildl. Manage.* 66: 912–918.

Aplin, P. (2005) Remote sensing: ecology. *Progr. Phys. Geogr.* 29: 104–113.

Baddeley, A., Turner, R., Moller, J. and Hazelton, M. (2005) Residual analysis for spatial point processes. *J, Roy. Statist. Soc. Ser. B-Statist. Methodol.* 67: 617–651.

Barton, K. (2013) MuMin: Multi-model inference. R package. Vol. 1.9.13. https://cran.r-project.org/web/packages/MuMIn/index.html

Bibby, C., Burgess, N., Hill, D. and Mustoe, S. (2000) *Bird census techniques*: London, UK: Academic Press.

BirdLife International. (2015a) Endemic Bird Area factsheet: Western Angola. http://datazone.birdlife.org/eba/factsheet/85

BirdLife International. (2015b) *IUCN Red List for birds*. http://datazone.birdlife.org/species/factsheet/red-crested-turaco-tauraco-erythrolophus

Bradshaw, C. J. A., Sodhi, N. S. and Brook, B. W. (2009) Tropical turmoil: a biodiversity tragedy in progress. *Frontiers Ecol. Environ.* 7: 79–87.

Brooks, T. M., Mittermeier, R. A., Mittermeier, C. G., Rylands, A. B., Konstant, W. R., Flick, P., Pilgrim, J. D., Oldfield, S., Magin, G. and Hilton-Taylor, C. (2002) Habitat loss and extinction in the hostspots of biodiversity. *Conserv. Biol.* 16: 909–923.

Buechley, E. R., Sekercioglu, Ç., Atickem, A., Gebremichael, G., Ndungu, J. K., Mahamued, B. A., Beyene, T., Mekonnen, T. and Lens, L. (2015) Importance of Ethiopian shade coffee farms for forest bird conservation. *Biol. Conserv.* 188: 50–60.

Burnham, K. P. and Anderson, D. R. (2002) *Model selection and multimodel inference: A practical information-theoretic approach*, New York, USA: Springer-Verlag.

Burnham, K. P. and Anderson, D. R. (2004) Understanding AIC and BIC in model selection. *Sociol. Meth. Res.* 33: 261–304.

Burnham, K. P., Anderson, D. R. and Huyvaert, K. (2011) AIC model selection and multimodel inference in behavioral ecology: some background, observations and comparisons. *Behav. Ecol. Sociobiol.* 63: 23–35.

Cáceres, A., Melo, M., Barlow, J., Cardoso, P., Maiato, F. and Mills, M. (2015) Threatened birds of the Angolan Central Escarpment: distribution and response to habitat change at Kumbira Forest. *Oryx* 49: 727–734.

Chave, J., Réjou-Mechain, M., Búrquez, A., Chidumayo, E., Colgan, M. S., Delitti, W. B. C., Duque, A., Eid, T., Fearnside, P. M., Goodman, R. C., Henry, M., Martinez-Yrizar, A., Mugasha, W. A., Muller-Landau, H., Mencuccini, M., Nelson, B. W., Ngomanda, A., Nogueira, E. M., Ortiz-Malavassi, E., Pélissier, R., Ploton, P., Ryan, C. M., Saldarriaga, J. G. and Vielledent, C. (2014) Improved allometric models to estimate aboveground biomass of tropical trees. *Global Change Biol.* 20: 3177–3190.

Chavez, P. S. (1996) Image-based atmospheric corrections revisited and improved. *Photogrammetric Engineering and Remote Sensing* 62: 1025–1036.

Chazdon, R. L., Peres, C. A., Dent, D., Sheil, D., Lugo, A. E., Lamd, D., Stork, N. E. and Miller, S. E. (2009) The potential for species conservation in tropical secondary forests. *Conserv. Biol.* 23: 1406–1417.

Cincotta, R., Wisnewski, J. and Engelman, R. (2000) Human population in the biodiversity hotspots. *Nature* 404: 990–992.

Collar, N. J. and Stuart, S. N. (1988) *Key forests for threatened birds in Africa*: Cambridge, UK: International Council for Bird Preservation.

Dallimer, M. and King, T. (2007) Habitat preferences of the forest birds on the island of Príncipe, Gulf of Guinea. *Afr. J. Ecol.* 46: 258–266.

Dallimer, M., King, T. and Atkinson, R. J. (2009) Pervasive threats within a protected area: conserving the endemic birds of São Tomé, West Africa. *Anim. Conserv.* 12: 209–219.

Dallimer, M., Parnell, M., Bicknell, J. E. and Melo, M. (2012) The importance of novel and agricultural habitats for the avifauna of an oceanic island. *J. Nat. Conserv.* 20: 191–199.

de Lima, R., Dallimer, M., Atkinson, P. W. and Barlow, J. (2013) Biodiversity and land-use change: understanding the complex responses of an endemic-rich bird assemblage. *Divers. Distrib.* 19: 411–422.

Dean, W. R. J. (2001) Angola. Pp. 71–91 in L. D. C. Fishpool and M. I. Evans, eds. *Important Birds Areas in Africa and associated islands: Priority sites for conservation*. Newbury and Cambridge, UK: Pisces Publications and BirdLife International.

Gardner, T., Barlow, J., Chazdon, R., Ewers, R., Harvey, C., Peres, C. and Sodhi, N. (2009) Prospects for tropical forest biodiversity in a human-modified world. *Ecol. Lett.* 12: 561–582.

Gardner, T., Barlow, J., Sodhi, N. and Peres, C. (2010) A multi-region assessment of tropical forest biodiversity in a human-modified world. *Biol. Conserv.* 143: 2293–2300.

Gibson, L., Ming Lee, T., Pin Koh, L., Brook, B. W., Gardner, T. A., Barlow, J., Peres, C. A., Bradshaw, C. J. A., Laurance, W. F., Lovejoy, T. E. and Sodhi, N. S. (2011) Primary forests are irreplaceable for sustaining tropical biodiversity. *Nature* 478: 378–381.

Gove, A., Hylander, K., Nemomisa, S. and Shimelis, A. (2008) Ethiopian coffee cultivation—Implications for bird conservation and environmental certification. *Conserv. Lett.* 1: 208–216.

Hall, B. P. (1960) The faunistic importance of the scarp in Angola. *Ibis* 102: 420–442.

Hawkins, F. (1993) An integrated biodiversity conservation project under development: the ICBP Angola scarp project. Pp. 279–284 in R. Wilson, ed. *Proceedings of the 8th Pan-African Ornithological Congress*. Tervuren, Belgium: Annales Musée Royal de l'Afrique Centrale (Zoologie).

Henry, M., Besnard, A., Asante, W. A., Eshun, J., Adu-Bredu, S., Valentini, R., Bernoux, M. and Saint-André, L. (2010) Wood density, phytomass variations withing and among trees, and allometric equations in a tropical rainforest of Africa. *For. Ecol. Manage.* 260: 1375–1388.

Huete, A., Didan, K., Miura, T., Rodriguez, E. P., Gao, X. and Ferreira, L. G. (2002)

Overview of the radiometric and biophysical performance of the MODIS vegetation indices. *Remote Sensing Environ.* 83: 195–213.

Huntley, B. J. (1974) Outlines of wildlife conservation in Angola. *J. South Afr. Wildl. Manage. Assoc.* 4: 157–166.

Huntley, B. J. and Matos, E. M. (1994) Botanical diversity and its conservation in Angola. *Strelitzia* 1: 53–74.

Hurvich, C. M. and Tsai, C.-L. (1989) Regression and time series model selection in small samples. *Biometrika* 79: 297–307.

Jensen, J. R. (2005) *Introductory digital image processing: A remote sensing perspective*. Upper Saddle River, NJ: Prentice Hall.

Kerr, J. T. and Ostrovsky, M. (2003) From space to species: ecological applications for remote sensing. *Trends Ecol. Evol.* 18: 299–305.

Kremen, C., Cameron, A., Moilanen, A., Phillips, S. J., Thomas, C. D., Beentje, H., Dransfield, J., Fisher, B. L., Glaw, F., Good, T. C., Harper, G. J., Hijmans, R. J., Lees, D. C., Louis, E., Nussbaum, R. A., Raxworthy, C. J., Razafimpahanana, A., Schatz, G. E., Vences, M., Vieites, D. R., Wright, P. C. and Zjhra, M. L. (2008) Aligning conservation priorities across taxa in Madagascar with high-resolution planning tools. *Science* 320: 222–226.

Kühn, I. and Dormann, C. F. (2012) Less than eight (and a half) mis-conceptions of spatial analysis. *J. Biogeogr.* 39: 995–998.

Legendre, P. and Legendre, L. (1998) *Numerical ecology*, Amsterdam, The Netherlands: Elsevier Scientific Publising Company.

Mammides, C., Schleuning, M., Bohning-Gaese, K., Schaab, G., Farwing, N., Kadis, C. and Coulson, T. (2015) The indirect effects of habitat disturbance on bird communities in a tropical African forest. *Biodivers. Conserv.* 24: 3083–3107.

Mills, M. (2010) Angola's central scarp forests: patterns of bird diversity and conservation threats. *Biodivers. Conserv.* 19: 1883–1903.

Myers, N., Mittermeier, R. A., Mittermeier, C. G., da Fonseca, G. A. B. and Kent, J. (2000) Biodiversity hotspots for conservation priorities. *Nature* 403: 853–858.

Nagendra, H. (2001) Using remote sensing to assess biodiversity. *Internatn. J. Remote Sensing* 22: 2377–2400.

Nagendra, H. and Rocchini, D. (2008) High resolution satellite imagery for tropical biodiversity studies: the devil is in the detail. *Biodivers. Conserv.* 17: 3431–3442.

Nelder, J. A. and Wedderburn, R. W. M. (1972) Generalized Linear Models. *J. Roy. Statist. Soc. Ser. A (General)* 135: 370–384.

Norris, K., Asase, A., Collen, B., Gockowski, J., Mason, J., Phalan, B. and Wade, A. (2010) Biodiversity in a forest-agriculture mosaic - The changing face of West African rainforests. *Biol. Conserv.* 143: 2341–2350.

Oksanen, J., Blanchet, G. F., Kindt, R., Legendre, P., Minchin, P. R., O'Hara, R. B., Simpson, G. L., Solymos, P., Stevens, H. H. and Wagner, H. (2012) *Vegan: Community Ecology Package*. R package version 2.0-5. https://cran.r-project.org/web/packages/vegan/index.html

Paustian, K., Ravindranath, N. H. and Van Amstel, A. (2006) Agriculture, forestry and other land use. Pp. 448 in H. S. Eggleston, L. Buendia, K. Miwa, T. Ngara and K. Tanabe, eds. *2006 IPCC guidelines for national greenhouse gas inventories*. Tokyo, Japan: National Greenhouse Gas Inventories Programme.

Pettorelli, N., Olav Vik, J., Mysterud, A., Gaillard, J.-M., Tucker, C. J. and Stenseth, N. C. (2005) Using the satellite-derived NDVI to assess ecological responses to environmental change. *Trends Ecol. Evol.* 20: 503–510.

R Core Team. (2015) *R: A language and environment for statistical computing*. Vienna, Austria: R Foundation for Statistical Computing.

Ryan, P. G., Sinclair, I., Cohen, C., Mills, M., Spottiswoode, C. and Cassidy, R. (2004) The conservation status and vocalizations of threatened birds from the scarp forest of the Western Angola Endemic Area. *Bird Conserv. Internatn.* 14: 247–260.

Schnitzer, S. A. and Bongers, F. (2002) The ecology of lianas and their role in forests. *Trends Ecol. Evol.* 17: 223–230.

Schulze, C. H., Waltert, M., Kessler, P. J. A., Pitopang, R., Shahabuddin Dorthe, V., Mühlenberg, M., Gradstein, S. R., Leuschner, C., Steffan-Dewenter, I. and Tscharntke, T. (2004) Biodiversity indicator groups of Tropical land-use systems: comparing plants, birds, and insects. *Ecol. Applic.* 14: 1321–1333.

Sekercioglu, Ç. and Riley, A. (2005) A brief survey of the birds in Kumbira Forest, Gabela, Angola. *Ostrich* 76: 111–117.

Stattersfield, A. and Capper, D. (2000) *Threatened birds of the world*. Barcelona: Lynx Edicions.

USAID (2008) *Biodiversity and tropical forest asssessment for Angola*. Available at: http://pdf.usaid.gov/pdf_docs/Pnadl906.pdf

Wang, K., Franklin, S. E., Guo, X. and Cattet, M. (2010) Remote sensing of ecology, biodiversity and conservation: a review from the perspective of remote sensing specialists. *Sensors* 10: 9647–9667.

Xiao, X., Boles, S., Frolking, S., Salas, W., Moore III, B., Li, C., He, L. and Zhao, R. (2002) Observation of flooding and rica transplatting of paddy rice fields at the site to landscape scales in China using vegetation sensor data. *Internatn. J. Remote Sensing* 23: 3009–3022.

Zuur, A. F., Ieno, E. N. and Smith, G. M. (2007) *Analysing ecological data*, New York, USA: Springer-Verlag.

Zuur, A. F., Ieno, E. N., Walker, N. J., Saveliev, A. A. and Smith, G. M. (2009) *Mixed effects models and extensions in ecology with R*. New York, USA: Springer-Verlag.

AIMY CÁCERES[1,2,6*], MARTIM MELO[2,6,7], JOS BARLOW[3], RICARDO FAUSTINO DE LIMA[4,8], MICHAEL S. L. MILLS[5,6]

[1]*Escuela de Ingeniería Ambiental, Facultad de Ingeniería, Universidad San Ignacio de Loyola, Av. La Fontana 550, La Molina, Lima – Perú.*

[2]*Centro de Investigação em Biodiversidade e Recursos Genéticos, Universidade do Porto, InBIO Laboratório Associado, Campus Agrário de Vairão, Rua Padre Armando Quintas, 4485-661 Vairão, Portugal.*

[3]*Lancaster Environment Centre, Lancaster University, Lancaster, UK.*

[4]*Centre for Ecology, Evolution and Environmental Changes (Ce3C), Faculdade de Ciências, Universidade de Lisboa, Lisboa, Portugal.*

[5]*A.P. Leventis Ornithological Research Institute, University of Jos, Plateau State, Nigeria.*

[6]*Instituto Superior de Ciências da Educação de Huíla, Rua Sarmento Rodrigues s/n, Lubango, Angola.*

[7]*DST/NRF Centre of Excellence at the Percy FitzPatrick Institute, University of Cape Town, Rondebosch, South Africa.*

[8]*Associação Monte Pico, Monte Café, São Tomé, Democratic Republic of São Tomé and Príncipe.*

**Author for correspondence; e-mail: aimycp@gmail.com*

Received 25 April 2016; revision accepted 4 February 2017;
Published online 27 February 2017