

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

Aimy Cáceres*^{1,5}, Martim Melo^{1,5,6}, Jos Barlow², Ricardo Faustino de Lima^{3,7} and Michael S.L. Mills^{4,6}

¹Centro 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.

²Lancaster Environment Centre, Lancaster University, Lancaster, UK.

³Centre for Ecology, Evolution and Environmental Changes (Ce3C), Faculdade de Ciências, Universidade de Lisboa, Lisboa, Portugal.

⁴A.P. Leventis Ornithological Research Institute, University of Jos, Plateau State, Nigeria

⁵Instituto Superior de Ciências da Educação de Huíla, Rua Sarmiento Rodrigues s/n, Lubango, Angola.

⁶DST/NRF Centre of Excellence at the Percy FitzPatrick Institute, University of Cape Town, Rondebosch, South Africa.

⁷Associação Monte Pico, Monte Café, São Tomé, Democratic Republic of São Tomé and Príncipe.

* *Corresponding author*: aimycp@gmail.com

1 **Summary**

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

17

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

19

20 **Introduction**

21 Habitat loss due to human activities is the most important threat to biodiversity (Brooks et al.,
22 2002) and the main cause of population declines and species extinctions in birds (Stattersfield
23 and Capper, 2000). This is especially significant in the tropics, where almost 70 percent of global

24 biodiversity is concentrated (Bradshaw et al., 2009) and human impacts are increasing at an
25 accelerating pace (Cincotta et al., 2000). Despite primary forests being irreplaceable for
26 maintaining tropical biodiversity (Gibson et al., 2011), modified landscapes such as secondary
27 growth and agroforestry systems can also hold important biodiversity and connect core areas for
28 conservation (Schulze et al., 2004, Gove et al., 2008, Cáceres et al., 2015). Therefore, to
29 implement successful conservation strategies it is important to assess biodiversity in human-
30 modified landscapes (Chazdon et al., 2009, Gardner et al., 2009), and to identify the key factors
31 influencing biodiversity in these landscapes. This is especially the case for extinction-prone
32 species, such as those that are range-restricted or especially sensitive to human activities.

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

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

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

63

64 **Methods**

65 *Study Area*

66 Kumbira Forest is the most representative and important site for the conservation of threatened
67 endemic birds of the Angolan Central Escarpment. It holds significant populations of four of the
68 five threatened endemics of this region, namely of the Endangered Gabela Bushshrike *Laniarius*
69 *amboimensis*, Gabela Akalat *Sheppardia gabela* and Pulitzer's Longbill *Macrosphenus pulitzeri*,

70 and Near Threatened Monteiro's Bushshrike *Malaconous monteiri* (Data Deficient at the time
71 that field work was done). Gabela Akalat is the most range-restricted of the Angolan endemics
72 with an estimated range of only *c.* 650 km², although it can be locally common, as it is at
73 Kumbira. Gabela Bushshrike has a wider distribution (*c.* 1800 km²), occurring both further north
74 and south (at Gungo) of Kumbira Forest, while Pulitzer Longbill and Monteiro Bushshrike have
75 ranges of *c.* 3700 km² and 8000 km² respectively (Mills, 2010). Additionally, Kumbira is also
76 home to the endemic, although more widespread (*c.* 190000 km²), Red-crested Turaco *Tauraco*
77 *erythrolophus* (BirdLife International, 2015b).

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

Figure 1

87

88 *Bird Data*

89 MSLM sampled bird communities by means of 10 min point counts (Bibby et al., 2000) from 13
90 September 2010 to 2 October 2010, between sunrise (*c.* 0545h) and 1030h, except when weather
91 was poor (rain or strong wind). All birds seen and heard within a 50 m radius of each sample
92 point **were recorded**. Sample points were spaced **at least**>150 m apart **of each other** to avoid

93 double-counting individuals. Furthermore, points were located along existing paths in order to
94 sample as much of Kumbira Forest as possible in this three weeks expedition. Each 10 min point
95 count was divided into two 5 min periods. In order to map the presence of the five key species, a
96 pre-composed track consisting of 30 s snippets of the vocalisations of Monteiro's Bushshrike,
97 Red-crested Turaco, Gabela Bushshrike, Gabela Akalat and Pulitzer's Longbill) was played
98 between these two periods, to increase their detectability. Playback was done using an Ipod
99 (Apple, Cupertino) and RadioShack Mini Amplifier speaker (RadioShack Corporation, Fort
100 Worth), always at the same volume. Because playback violates the point count assumption that
101 birds do not approach the observer, we only use playback data for the analysis of species
102 presence. We also excluded all observations that could refer to birds that had already been
103 registered.

104

105 *Environmental variables – ground variables recorded in situ*

106 Habitat characteristics were measured by AC in a circular sample plot of 10 m radius around
107 each bird sample point. The variables measured were: (1) elevation (elev) by GPS; (2) canopy
108 height (ch) as the maximum visible height of the canopy (Dallimer et al., 2009), using a Nikon
109 550 Laser rangefinder (Nikon Corporation, Tokyo); (3) canopy cover (cc) with a convex
110 spherical densiometer (Forestry Suppliers Inc., Jackson); (4) shrub cover (shrub) as the
111 percentage of vegetation cover at the shrub level (0.15-1.5m) along a 10 m transect; and (5) liana
112 density (ld) as the number of lianas along a 10 m transect. Canopy height and canopy cover were
113 the average of four measurements taken at 5 m in each cardinal direction from the sample point,

114 To estimate above-ground biomass (AGB) at each plot, we measured height and diameter
115 at breast height (DBH) of all trees with a DBH > 10 cm. Tree height was measured with a

116 clinometer and DBH with a measuring tape. AGB was calculated using a pantropical allometric
117 equation (Chave et al., 2014) that relates AGB of a tree to DBH, total height and wood density.
118 Since it was not possible to identify the species of trees to obtain specific wood densities, we
119 applied a constant wood density of 0.59 g/cm³, the average reported for trees in Africa (Henry et
120 al., 2010). Finally, biomass estimates were converted to carbon values using the fraction of 0.47
121 MgC, as recommended for tropical and subtropical regions (Paustian et al., 2006), and
122 standardized per area (MgC/ha).

123

124 *Environmental variables derived from remote sensing*

125 Spectral indices and forest cover (xfor) were calculated from Landsat 7 ETM+ satellite image
126 (WRS-2 path 181 row 68) with low cloud cover (<10%) from 18 May 2010, obtained from the
127 U.S. Geological Survey (USGS) and Earth Resources Observation & Science Center (EROS) via
128 the EarthExplorer interface (<http://earthexplorer.usgs.gov>). It was radiometric normalized and
129 atmospheric corrected using Modified Dark Object Subtraction (DOS), as proposed by Chavez
130 (1996). The empty lines of the Landsat 7 scene produced by the scan failure were treated as “no
131 data” and all sample points located in these gaps were excluded from analyses.

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

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

145

146 *Data Analysis*

147 Generalized Linear Models (GLM) (Nelder and Wedderburn, 1972) were used to evaluate bird
148 responses to environmental variables (Zuur et al., 2007) (Supplementary material, Table S1).
149 Bird responses were represented by species richness and by the presence of endemic species that
150 were recorded in over 20 percent of the point counts, namely Red-crested Turaco, Gabela Akalat
151 and Gabela Bushshrike. All variables were standardized and collinearity was assessed by
152 Spearman rank correlation coefficients, which does not assume linear relations between
153 variables. Variables with coefficients of over 0.7 were removed from the analyses (Zuur et al.,
154 2009). The variables maintained in the analyses were chosen based on their biological
155 importance and management relevance. We also assessed spatial autocorrelation using Pearson-
156 based Mantel tests (Legendre and Legendre, 1998) with 1000 permutations and mapping the
157 residuals of the best ranking models (Baddeley et al., 2005, Kühn and Dormann, 2012). All these
158 analyses were carried out for each of the response variables (species richness and the presence of
159 endemics).

160 To assess whether remote sensing variables (spectral indices and forest cover) provided
161 additional information for modelling bird diversity in Kumbira, we modelled species richness

162 and the endemic species presence using a dataset with remote sensing and ground variables.
163 Then, we identified the best models for each group of variables: (1) the “null model” (with no
164 explanatory variables); (2) only ground (hereafter “Ground Models”); (3) only remote sensing
165 (hereafter” RS Models”); and (4) ground and remote sensing (hereafter “Combined Models”).

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

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

180

181 **Results**

182 A total of 201 bird point counts were performed and 100 bird species registered. The mean
183 species richness per point count was 10.4 ± 3.4 species (mean \pm standard deviation) with a range
184 from one to 23 species. Red-crested Turaco was the most-registered endemic, recorded at 68

185 percent of the point counts (n=136), followed by Gabela Akalat (46%, n= 92) and Gabela
186 Bushshrike (21%, n=42). Monteiro Bushshrike and Pulitzer Longbill were present only in 7
187 percent (n=15) and 5 percent (n=11) of the point counts respectively. Vegetation characteristics
188 were measured for all the sample points but spectral indices (LSWI, EVI and BR) and forest
189 cover were only estimated for 132 out of 201 points due to the Landsat 7 scan failure (Figure 2).

Figure 2

190 Canopy height was strongly correlated with canopy cover ($cor=0.70$, $p-value < 0.001$)
191 and thus excluded from the analysis, as was blue-red ratio with forest cover ($cor=0.73$, $p-value <$
192 0.001) (Supplementary material, Figure S1). Both canopy cover and forest cover were retained
193 for analyses because of their importance for species richness and Gabela Akalat presence, and
194 their relevance to forest management.

195

196 *Spatial autocorrelation*

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

202

203 *Effects of remote sensing variables*

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

Table 1

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

209

210 *Role of habitat characteristics in determining bird diversity in Kumbira*

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

Table 2

Figure 3

217

218 **Discussion**

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

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

230 2008) – like the mosaic like and dynamic Kumbira Forest – where spectral indices not always
231 directly relate to wildlife presence or abundance (Nagendra, 2001). Furthermore, the approach
232 was also limited by the lack of adequate Landsat images **due high cloud cover in the study area**
233 for most of the year.

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

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

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

252 **Canopy cover was important for species richness and the presence of threatened**
253 **endemics.** Canopy cover is indirectly related to habitat disturbance and affect the presence of
254 birds, especially forest specialists (Mammides et al., 2015). This can explain its influence in
255 Gabela Bushshrike and especially Gabela Akalat. In other areas of Africa, the presence of
256 threatened endemic forest birds is also related to canopy cover and structure (Dallimer and King,
257 2007, Dallimer et al., 2012, de Lima et al., 2013, Mammides et al., 2015). Canopy cover was
258 also highly correlated with canopy height, therefore the endemics might also be affected by
259 canopy height and other aspects of mature forests including canopy structure and understorey
260 humidity.

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

268

269 *Conservation Implications*

270 Our study provides some important insights into the conservation of one of Africa's critical
271 priority areas for bird conservation. Many of the results indicate that conservation efforts should
272 focus on the maintenance of canopy cover by protecting the remaining forest. For example,
273 canopy cover affects both overall species richness and the Gabela Akalat presence. The
274 endangered Gabela Akalat is the key priority for conservation at Kumbira because is the most

275 range-restricted of the Angolan endemics with an estimated suitable range of only *c.* 650 km²
276 (Mills, 2010). As a result, this species is particularly sensitive to forest loss and depends in the
277 maintenance of canopy cover at Kumbira for its survival.

278 Protecting high quality mature forest in the region is challenging as the extent and
279 condition of forests are threatened by slash-and-burn agriculture and logging of high canopy
280 trees for timber (Mills, 2010, Cáceres et al., 2015). Protected areas are widely used in
281 conservation, but at present no area of the Angolan Central Escarpment Forest has formal
282 protection status. A proposal for the establishment of a *c.* 50 km² strict nature reserve was put
283 forward in the past (Huntley and Matos, 1994) but has yet to be implemented. Alternative
284 approaches to protected areas could involve local populations. These include increasing forest
285 cover through reforestation initiatives, with native tree species. Such action has recently been
286 initiated in Kumbira with the establishment of an experimental nursery as part of a project
287 funded by the Conservation Leadership Programme. Wildlife friendly agriculture may also be
288 beneficial (Gove et al., 2008, Buechley et al., 2015). In this context, we recommend prioritising
289 research into the economic viability of recovering the abandoned shade coffee plantations and on
290 the impacts such action could have on biodiversity, together with the evaluation of other more
291 biodiversity-friendly agricultural practices.

292 Any conservation actions require good baseline data on the occurrence of the most
293 important species. For most species, our study demonstrates the importance of basing this on
294 good quality data from ground surveys, complemented by remote sensing variables. However, it
295 is encouraging that the presence of the most endangered species, the Gabela Akalat, can be
296 predicted by remote sensing variables, as this provides hope that large-scale mapping can be
297 used to identify priority areas. However, the models we present here had very low explanatory

298 power, indicating the role of unmeasured factors such as landscape context and resource
299 availability. Some of these may be resolved by using newer and more refined remotely sensed
300 measures, which would also provide a basis to examine other areas of the Angolan Central
301 Escarpment Forest, such as the forest of Bango-Seles 25 km to the South. In addition, future
302 research should aim at including other taxa such as plants, amphibians and insects that may be
303 more sensitive to human disturbance and may not reflect the patterns of bird diversity (Kremen
304 et al., 2008). This information is critically important to enable the effective conservation and
305 sustainable planning that are required to protect the unique biological richness of this region.

306

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320

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476 **TABLES**

477 **Table 1.** Best models generated for each group of variables (N null, G ground, RS remote sensing, and G+RS combined) for species
 478 richness and the presence of Red-crested Turaco, Gabela Akalat and Gabela Bushshrike. The rank of each model is included (from
 479 256 possible models), followed by the variables included in each model, the model log-likelihood (logLik), the number of parameters
 480 (K), the Akaike's Information Criterion with small sample size correction (AICc), AIC differences ($\Delta AICc$), Akaike weights (ω) and
 481 evidence ratio. The variables used were EVI – enhanced vegetation index, LSWI – land-surface water index, xfor – forest cover, c –
 482 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	$\Delta AICc$	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 $\Delta AICc < 10$ 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