1   *Title:* Forecasting potential routes for movement of endemic birds among important sites for

2   biodiversity in the Albertine Rift under projected climate change.

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Abstract

The ability of species to shift their distributions in response to climate change may be impeded by lack of suitable climate or habitat between species' current and future ranges. We examined the potential for climate and forest cover to limit the movement of bird species among sites of biodiversity importance in the Albertine Rift, East Africa, a biodiversity hotspot. We forecasted future distributions of suitable climate for 12 Albertine Rift endemic bird species using species distribution models based on current climate data and projections of future climate. We used these forecasts alongside contemporary forest cover and natal dispersal estimates to project potential movement of species over time. We identified potentially important pathways for the bird species to move among 30 Important Bird and Biodiversity Areas (IBAs) that are both currently forested and projected to provide suitable climate over intervening time periods. We examined the relative constraints imposed by availability of suitable climate and forest cover on future movements.

The analyses highlighted important pathways of potential dispersal lying along a north-south axis through high elevation areas of the Albertine Rift. Both forest availability and climate suitability were projected to influence bird movement through these landscapes as they are affected by future climate change. Importantly, forest cover and areas projected to contain suitable climate in future were often dissociated in space, which could limit species' responses to climate change. A lack of climatically suitable areas was a far greater impediment to projected movement among IBAs than insufficient forest cover. Although current forest cover appears sufficient to facilitate movement of bird species in this region, protecting the remaining forests in areas also projected to be climatically suitable for species to move through in the future should be a priority for adaptation management.

Keywords:

Bird dispersal, climate change adaptation, connectivity analysis, graph theory, Important Bird and Biodiversity Areas, dispersal corridors, biodiversity conservation, Maximum Entropy.

Introduction

Climate change is driving substantial shifts in species distributions and abundance patterns, and planning for these shifts is a major challenge for conservation biology (Heller and Zavaleta 2009, Parmesan 2006, Stephens, et al. 2016). Of particular concern is the possibility that sites that are currently important for supporting species of conservation concern may not retain suitable climates for these species in the future (Araujo, et al. 2004, Hannah, et al. 2007). There is growing evidence that although many individual sites will experience substantial turnover in species composition as climates change, suitable climate for most species of conservation concern will continue to be represented within networks of conservation sites (Araujo, et al. 2011, Bagchi, et al. 2013, Hole, et al. 2009). There is a strong possibility, however, that in many cases the location of suitable climate will shift to sites other than those where the species currently occur (Araujo, et al. 2011, Bagchi, et al. 2013, Baker, et al. 2015, Hole, et al. 2009). Therefore, the continued effectiveness of site networks at conserving the species for which they were designated will be dependent on the ability of these species to move between sites (Cushman, et al. 2013, Heller and Zavaleta 2009).

Given that species may have to shift their ranges in response to climate change, identifying the dispersal routes they might use between conservation sites, and detecting potential barriers, is an important conservation objective (Aben, et al. 2016, Heller and Zavaleta 2009, Lawler, et al. 2013). The need to identify priority areas for facilitating movement is particularly acute in places that combine high biodiversity and habitat heterogeneity with large and expanding human populations and anthropogenic fragmentation. The Albertine Rift of East Africa is one such region and is widely recognised as a global conservation priority (Brooks, et al. 2001, Brooks, et al. 2006, Plumptre, et al. 2007, Stattersfield, et al. 1998). Climate change is likely to drive considerable turnover in the species in the high elevation areas of the Albertine Rift, and this might particularly disadvantage upper elevation endemics (Garcia, et al. 2012, Hole, et al. 2009) while providing refuge for species for which lower elevations are projected to become climatically unsuitable (Ayebare, et

al. 2013, Garcia, et al. 2012). Climatically, the region has been projected to provide suitable habitat

for many species as they shift their ranges (Ayebare, et al. 2013, Hole, et al. 2011), but the rapid

rates of forest clearance and fragmentation in the region (Duveiller, et al. 2008, Hole, et al. 2009,

Plumptre 2002, Plumptre, et al. 2003, Plumptre, et al. 2007) may impede the ability of species to

track suitable future climate. Previous assessments of landscape connectivity in the region have

suggested that the majority of conservation sites in the region are currently well interconnected via

relatively natural habitat (Plumptre, et al. 2007) and that much of the area connecting sites is

projected to be climatically suitable for many species of conservation concern through the 21st

century (Ayebare, et al. 2013). However, explicit analyses of animal movement in the context of

future climate change and forest cover are needed to identify movement corridors that are robust to

breaks in forest cover and narrow areas of unsuitable climate. Emerging techniques for modelling

species movement based on graph theory (McRae, et al. 2008) can combine projections of habitat

suitability (Lawler, et al. 2013) and species' dispersal ability (see methods) to identify such

movement routes and can also compare the relative effects of different limiting factors (e.g. areas

with unsuitable climate and gaps in forest cover) on landscape connectivity.

In this study we investigated the potential for 12 endemic forest bird species of the Albertine

Rift to move from Important Bird and Biodiversity Areas (IBAs, BirdLife International 2014) that are

currently climatically suitable to those that are projected to be suitable in the future. IBAs are

identified using standardised criteria based on the presence of species of conservation concern and

networks of these sites provide a useful framework for evaluating the extent to which sites of

biodiversity importance might be connected under future scenarios of environmental change.

Previous analyses of African IBAs have indicated that they will remain important for bird species of

conservation concern under future climate change, but that there will potentially be substantial

turnover in the species that individual IBAs are climatically suitable for (Baker, et al. 2015, Hole, et al.

2009). In our analyses we combined species distribution modelling with two methods for assessing

connectivity (shortest paths and current flow), to identify areas that might be important for

96   movement of these species in response to climate change up to 2100. We accounted for both the

97   current distribution of forest and the projected future climate suitability of IBAs and the intervening

98   landscape. We explicitly incorporated estimates of species' dispersal ability in our analyses by

99   allowing movement between non-adjacent cells in the landscape that are within each species' natal

100   dispersal range. We used these analyses to address the following two questions: 1) Will a lack of

101   availability of areas of suitable climate or a lack of forest pose the greater barrier to species

102   movement between IBAs? 2) Which routes are projected to be most important for species

103   movement from IBAs that are currently climatically suitable to those that are projected to be

104   suitable in the future?

Methods

Study region

107   The Albertine Rift region is part of the Eastern Afromontane Biodiversity Hotspot

108   (Mittermeier, et al. 2004) and is one of the most topographically and ecologically diverse areas of

109   Africa. It supports 52% of the bird species of continental Africa, including 42 species endemic to the

110   region (Plumptre, et al. 2003 report 41 species but this increases according to revised taxonomy

111   available at www.birdlife.org/datazone/info/taxonomy). It also supports one of the highest rural

112   human populations in Africa with an average population density of 94.6 people per km^2, rising to

113   600-700 people per km^2 in some areas (Burgess, et al. 2007, Plumptre, et al. 2003).

114   This study is centred on the Albertine Rift Mountains Endemic Bird Area (EBA), which covers

115   approximately 56,000 km^2 and includes the mountains that flank the Albertine Rift Valley, from the

116   Lendu Plateau in northeast Democratic Republic of the Congo (DRC), south to the Marungu

117   Highlands also in DRC, plus the mountains of south-west Uganda, Rwanda, Burundi and extreme

118   western Tanzania (Figure 1)**.** In order to include potential future range shifts of our study species, we

119   also included areas outside the Albertine Rift Mountains EBA, including part of the adjacent Eastern

120   Zairean Lowlands EBA (Okapi Faunal Reserve and Mount Hoyo Reserve in the North, Maiko to the

121   West and the Itombwe Mountains in the South) because birds could conceivably move through or

122   establish in these adjacent regions even if they do not currently occur there.

123   *Data sets*

124   *Bird locality records*

125   The data set used in this study was compiled from field surveys to assess the biodiversity of

126   the Albertine Rift Forests undertaken between 1999 and 2007 throughout the region by the Wildlife

127   Conservation Society (A. J. Plumptre, unpublished data; Ayebare, et al. 2013). Five-minute point

128   counts were made at 250 m intervals along randomly placed transects in sectors of the forests or, in

129   the case of remote and very rugged areas, along reconnaissance walks which aimed to follow

130   specific compass directions but avoid major obstacles to the team's progress. The surveys targeted

131   the coverage of as much of the forest as possible, particularly the full altitude range found at a site.

132   Presence of armed groups in eastern Democratic Republic of Congo made it impossible to sample all

133   sites planned but this will not have affected estimates of the niche envelopes calculated for this

134   paper. At each point the ornithological team would wait for two minutes to allow birds to settle

135   down and then start the point count during which all birds seen or heard were recorded.

136   We used data from these surveys for 12 of the 42 restricted-range bird species entirely

137   confined to the Albertine Rift mountains Endemic Bird Area (Plumptre, et al. 2003, Stattersfield, et

138   al. 1998). These 12 species (listed in Table 1) were chosen as: i) representative of the broader set of

139   Albertine Rift endemics, including some which are common and widespread and others which are

140   rare (or rarely recorded) and/or which are confined to only part of the region and ii) species with

141   more than 10 locality records (those with 10 or fewer records were excluded as they could not be

142   modelled robustly). Moist montane forest is the main habitat type for all species (Table 1).

143   *Dispersal data*

144   Estimates of the mean and maximum natal dispersal distances for these species were

145   obtained from BirdLife's and IUCN's Species Information Service database (BirdLife International,

146   unpublished data). The database contains banded estimates for each genus for mean and maximum

147   natal dispersal distance, based on species-specific estimates from the literature, with data gaps filled

148   by extrapolation from close relatives. All species used in this study belonged to genera with mean

149   and maximum natal dispersal distance bands of 0-4, 5-24, or 25-49 km (Table 1). We used the mid-

150   point of the mean dispersal band and the upper limit of the maximum dispersal band as estimates of

151   mean and maximum dispersal respectively.

152   *Climate and environmental data*

153   We used seven environmental variables to model the distributions of the 12 study species.

154   These variables were i) mean temperature of the warmest month; ii) mean temperature of the

155   coldest month; iii) the ratio of actual to potential evapotranspiration; iv) wet season intensity; v) dry

156   season intensity; vi) slope; vii) aspect. These variables have proved optimal for modelling a wide

157   range of bird species across Africa (Hole et al, 2009). Variables (i) through (v) were obtained for the

158   period 1950 – 2000 (hereafter referred to as 20th Century) from Worldclim

159   (http://www.worldclim.org/) at 30" (arc second; approximately 1 km^2 at the equator) resolution. We

160   used a 30" resolution because it was the finest resolution available for the environmental variables

161   we used and a fine resolution is appropriate for modelling distributions in areas with high

162   topographic complexity like the Albertine Rift. Slope and aspect were taken from the Global Agro-

163   Ecological Zones database (Fischer, et al. 2008) and were selected to capture the fine scale

164   topography within the region and the resultant impacts on local climate. Projections of future

165   climate variables were obtained from three General Circulation Models (GCMs), GFDL CM2.1,

166   ECHAM5-OM and HadGEM1, over three time periods (2011-2040, 2041 – 2070 and 2071 – 2100,

167   hereafter referred to by their midpoints: 2025, 2055 and 2085) and for the A1B SRES scenario

168   (approximately equivalent to RCP 6.0 in the IPCC's Fifth Assessment Report). GCM outputs were

169   downscaled using the change factor approach (Tabor and Williams 2010, Wilby, et al. 2004) to 30".

170   *Forest cover data*

171   Land cover classification was based on the Globcover 2009 database (Arino 2010). Data were

172 obtained for the Albertine Rift region at a 30'' resolution (see Figure 2). We initially considered all

173 cells categorised in Globcover 2009 as "closed to open broad-leaved evergreen" or "semi-deciduous

174 forest and closed broad-leaved deciduous forest" (categories 40 and 50 in Globcover 2009) as

175 forested; all other cells were classified as non-forested. We then refined these maps using

176 supplemental regional satellite imagery and regional forest maps (see Ayebare, et al. 2013) to

177 reclassify plantations, often classified as natural forest by Globcover 2009, as non-forest cells.

178 ***Analytical methodology***

179 We compared the relative contributions of forest cover and climate suitability on bird movement

180 and projected potential movement routes for each of the 12 species through the multi-stage analysis

181 detailed below and summarised in Figure 2.

182   *Species distribution models and projections of suitable climate*

183   Species distribution models were developed by modelling the locality records of the 12

184 species as functions of the seven environmental variables using a commonly applied maximum

185 entropy approach, MaxEnt (Phillips, et al. 2006, Phillips and Dudík 2008). To reduce sampling bias of

186 background points we constrained the model to select background points only from within the

187 Albertine Rift EBA (Stattersfield, et al. 1998). We tested the predictive ability of each model using the

188 values obtained for the area under the curve (AUC) of a receiver operating characteristic plot

189 (Hanley and McNeil 1982), with each model calibrated on a random selection of 70% of the

190 observation data, and projection accuracy evaluated on the remaining 30%.

191   The MaxEnt model for each species was used to project the climatic suitability of each 30"

192 cell, for that species, in the 20th century (using the observed climate data) and for the three future

193 time periods (using the downscaled GCM projections for the corresponding period). Climatic

194 suitability for each cell ranged between 0 and 1, with each GCM leading to different projections of

195 climatic suitability. Hence, we used the mean of the three GCM projections for each time period as a

196 measure of the climatic suitability of a cell. We also calculated the minimum of the mean climatic

197 suitability of each cell for each pair of consecutive time periods (i.e. between (i) 20th century and

198 2025; (ii) 2025 and 2055 and; (iii) 2055 and 2085), which we used as a stringent measure of climate

199 suitability of each cell during each pair of time periods. This enabled the identification of routes

200 likely to remain climatically suitable throughout the entire period being considered.

201   *Habitat suitability*

202   Habitat suitability for the forest birds considered in this study will depend on both suitable

203 climate and forest availability. Movement among IBAs will therefore be restricted when the

204 availability of either suitable climate or forest is limited in the areas between them. In our

205 connectivity analyses we estimated the relative contributions that gaps in forest cover or suitable

206 climate might make on the movement of birds among IBAs in the future by comparing movement

207 under four limitation regimes that differed in how the habitat suitability of each grid square was

208 calculated. The four regimes were: 1) no limitation (a null model), where habitat suitability of all

209 cells was set to the maximum current climatic suitability for that species across the study region; 2)

210 climate-only limitation, where habitat suitability was set as the projected climatic suitability of each

211 cell; 3) forest-only limitation, where habitat suitability was defined purely on the basis of whether a

212 cell was either forested (habitat suitability was set to the maximum current climatic suitability for

213 that species across the study region) or not (habitat suitability was set to 0); and 4) climate-and-

214 forest co-limitation, where the habitat suitability of each cell was set to zero if it was not forested or

215 equal to the projected climatic suitability of that cell otherwise. These 30" habitat suitability cells

216 were aggregated by averaging to either a 5 x 5 km (2.5', arc minute) resolution for six poor

217 dispersing species (max dispersal 5 – 24.9 km, see Table 1) or 10 x 10 km (5') resolution for the six

218 other species with better dispersal ability (max dispersal 25 – 49.9 km). Computer run times and

219 memory requirements meant it was not possible to perform all analyses at finer resolutions for all

220   species but previous studies (Ayebare, et al. 2013, McRae, et al. 2008) suggest that connectivity

221   analyses are generally robust to such small changes in grid cell resolution.

222   *Connectivity analyses*

223   We used two contrasting methods to identify possible routes of species movement among

224   IBAs; "shortest paths" and "current flow". Both methods are based in graph theory (Cushman, et al.

225   2013, McRae, et al. 2008) and account for the "conductance" of each cell traversed on the route

226   between the origin and the destination. The conductance of a cell can be thought of as the inverse

227   of the cost of travelling through it (McRae, et al. 2008). The shortest path (also referred to as least-

228   cost path) between the origin and the destination follows the route with the smallest cumulative

229   cost (i.e. the sum of the costs of all cells traversed along the route is minimised). This provides an

230   estimate of the best route between the source and destination. Potential drawbacks of using

231   shortest paths are that individuals are unlikely to follow a single, optimal route (McRae, et al. 2008)

232   and several different routes might, together, allow greater movement of individuals (McRae, et al.

233   2008, Phillips, et al. 2008). Recently, methods have been developed that consider movement of

234   individuals along multiple pathways (Carroll, et al. 2012, McRae, et al. 2008, Phillips, et al. 2008).

235   One such approach, current flow, likens the movement of individuals through landscapes to the flow

236   of current through electrical circuits (Carroll, et al. 2012, McRae, et al. 2008, van Etten and Hijmans

237   2010). This approach allows for efficient calculation, for each cell, of the probability that a random

238   walker will move through it while moving from an origin to a destination. This probability provides a

239   measure of how important the cell is for movement between the origin and destination when

240   knowledge of the landscape is limited to cells that can be reached in one dispersal event.

241   To estimate the shortest paths and current flow we calculated a conductance matrix for the

242   landscape. This matrix contains information on the ability of individuals to move between each pair

243   of cells in the landscape: zero conductance indicates that it is impossible for individuals to move

244   directly between the cells while large conductance values indicate that there is little impediment to

245   movement between them. In our analyses, the conductance between pairs of cells (G_{ijk}) was defined

246   as

247      $$G_{ijk} = \frac{d_{ijk}}{-\log_e\left(\sqrt{p_{ik}\, p_{jk}}\right)}$$ (eq. 1)

248

249   where p_{ik} is the habitat suitability of each cell i for species k. The denominator is analogous to the

250   definition of cost used by Graham *et al.* (2010). The numerator, d_{ijk} is the dispersal potential of

251   species k between cells i and j and was estimated according to a truncated negative exponential

252   dispersal function so that

253      $$d_{ijk} = \begin{cases} \frac{\exp\left(-\frac{r_{ij}}{\lambda_k}\right)}{\lambda_k}, & r_{ij} < \lambda_{max_k} \\ 0, & r_{ij} > \lambda_{max_k} \end{cases}$$ (eq. 2)

254   where r_{ij} is the distance between cells i and j, and λ_k and λ_{max_k} are estimates of the mean and

255   maximum natal dispersal distances for species k respectively (see Table 1). No direct dispersal was

256   allowed between cells that were further apart than the maximum observed natal dispersal of each

257   species. This formulation allowed individuals to move directly to non-neighbouring cells within their

258   maximum natal dispersal distance without having to pass through the intervening ones. This is useful

259   because individuals are likely to be able to cross mosaic habitats and narrow areas of unsuitable

260   habitat. Note that the dispersal function above penalised movement over longer distances so that

261   skipping intermediate cells would not automatically reduce the cost of a route. This formulation of

262   dispersal constrained the distance travelled by individuals at each dispersal event. Routes that

263   traversed wide areas of unsuitable habitat, relative to the dispersal ability of the species, were

264   penalized by the dispersal function. As a result, the relative suitability of alternative routes was

265   increased. Our approach did not quantify the time it would take for a population to expand into new

266   areas.

267   The IBAs cover multiple 10 x 10 km (and 5 x 5 km) cells, so we calculated the routes between

268   the centroids of the IBA polygons. The conductance between cells within the source and destination

269   IBAs was set very high (G_{ijk} = 1000, several times higher than the highest values otherwise observed).

270   Therefore, the cost of movement between two IBAs is composed principally of the cost of

271   movement between their boundaries.

272   Once the conductance matrices had been computed, we used the gdistance package (van

273   Etten 2011) in R 3.2.3 (R Development Core Team 2015) to compute the shortest paths and the

274   current flow between each pair of IBAs, for each species and under each of the four limitation

275   regimes (null, climate-only, forest-only and climate-and-forest co-limitation). We also calculated the

276   length of the shortest path and the resistance distance of the current flow (see McRae, et al. 2008,

277   for a definition) associated with movement of each species between each pair of IBAs. We hereafter

278   refer to both the length of shortest path and the resistance distance of the current flow as path

279   length.

280   *Quantifying path importance*

281   We assumed that birds are most likely to move from IBAs that are projected to decline in

282   suitability for a species to IBAs projected to provide suitable future climate. To represent this

283   expectation, we adjusted the potential importance of the connections between each pair of IBAs to

284   account for climatic change by calculating the difference in mean climatic suitability between the

285   beginning and end of each time period within the source IBA and multiplying this by the future mean

286   suitability of each potential destination IBA. This measure of importance was set to zero for pairs

287   where the mean suitability of a source IBA remained the same or increased (i.e. there would be no

288   reason for the species to move).

289   *Models of path length*

290   To quantify the potential for unsuitable climate and gaps in forest cover to limit movement

291   of each species among IBAs, we divided the path lengths under three of the limitation regimes

12

292   (climate-only, forest-only, and climate-and-forest) by the path length under the null regime, for

293   every source and destination IBA combination. We then modelled these (log-transformed) ratios

294   (shortest path and current flow distances were modelled separately) as a function of limitation

295   regime using linear mixed-effects models with species, source IBA and destination IBA entered as

296   random effects. The path importance (described in the previous section) between each pair of IBAs

297   for each species was included as a weights argument in the model.

298   *Forecasting routes for bird movement*

299   Using the results from the shortest path and current flow analyses separately, we estimated

300   the importance of a cell for each species' movements as the weighted mean (across all pairs of IBAs,

301   weighted by the importance of the IBA pair) of the number of paths traversing that cell. This

302   represents the proportion of journeys predicted to traverse that cell, and varies from 0 (no paths

303   pass through the cell) to 1 (all paths with non-zero importance pass through them). We reduced the

304   resolution of the results from the six poor-dispersing species that were modelled at a 5 x 5 km grid

305   size (*A. personata*, *B. diops*, *P. nobilis*, *K. rufocinctus*, *O. ruwenzorii* and *P. fasciiventer*) by calculating

306   the mean proportion of shortest paths (and current flow) across the four cells in each 10 x 10 km

307   grid cell. Finally, we calculated the mean of the proportion of shortest paths and (separately) current

308   flow passing through each cell across all species for each of the four limitation regimes and three

309   time periods. The finite dimensions of the study area and the locations of the IBAs mean that some

310   cells are more likely to be used for movement purely due to their location. We corrected for this,

311   both for the shortest paths and current flow methods, by subtracting the results for each cell under

312   the null limitation regime from those obtained under the other three regimes. Cells with negative

313   difference values were set to zero (i.e. these cells were considered to have no role in movement

314   among IBAs). The corrected estimates of movement from the shortest path and current flow

315   methods were then plotted separately for each time period to identify the most important dispersal

316   routes among IBAs.

Results

MaxEnt model performance

The number of locality records per species ranged from 18 for *Z. tanganjicae* to 468 for *A. personata* (median = 105.5, IQR = 150; Table 1). Model fit for individual species distribution models, assessed using AUC, ranged from 0.818 to 0.919 (median = 0.885; IQR = 0.073; Table 1), indicating good model performance for all 12 species.

Changes in climate suitability

Overall, the species distribution models projected that availability of climatically suitable habitat in the region will decline by the end of the 21st Century (Figure 3a). The models forecasted that, throughout the current century, the high elevation areas along the Albertine Rift will provide the most suitable future climate for the majority of species considered here (Figure 3a). These areas were reasonably well forested in the early 21st Century: of the area projected to be suitable for at least one species at the end of the century, about 50% was classified as forested (Figure 3b). In contrast, only 33% of the area that was projected as climatically unsuitable for all 12 species was classified as forest. The western part of the region retained the most forest cover (Figure 3b). This area included the foothills of the western cordillera of the Albertine Rift and hence was generally lower-lying and less climatically suitable for the suite of species considered here.

Connectivity analyses

Models of path lengths

The mixed-effects models suggested that climate will strongly limit the movement among IBAs of the birds of the Albertine Rift endemics considered here. This is indicated by the large increases in the path lengths of both the shortest paths (c.73 -fold increase) and current flow (c. 113-fold increase), between the null regime and climate-limitation regime (Figure 4). Restricting movement to currently forested areas, without considering climate limits, resulted in a much smaller

341   increase in path lengths compared to the null regime, although the increase was still substantial (c.

342   10-fold increase in shortest path lengths and c. 37-fold increase in current flow path lengths). The

343   combined effects of movements being restricted by both climate suitability and forest occurrence

344   led to only a slight increase in path length from that expected in the climate-only limitation regime

345   (c. 1.5-fold increase in shortest path lengths and c. 1.6-fold increase in current flow path lengths).

346   The effects of limitation regimes were consistent across the three time periods (Figure 4).

347   *Forecasts of routes for bird movement*

348   Shortest paths (Figure 5a) were less diffuse than current flow (Figure 5b) but both methods

349   predicted that movement would be concentrated in broadly similar areas under a given limitation

350   regime. Figure 5 presents the results for the central time period centred on 2055, but the results for

351   the other time periods were very similar (See Supplementary Figures S1 and S2). The extensive

352   forest cover and suitable climate along the western ridge of the rift meant that this area supported

353   the densest concentration of shortest paths and current flow under all limitation regimes, and this

354   region also encompasses several large IBAs. In particular, the areas encompassing and connecting

355   the Itombwe Mountains, eastern reaches of Kahuzi-Biega NP, Volcans NP and Ruwenzori mountains

356   had very high densities of paths regardless of analytical approach or limitation regime.

357   There were important differences in projected path densities among limitation regimes.

358   Under the forest-only limitation regime, the greatest concentration of shortest paths and, in

359   particular, current flow, shifted towards the forested western part of the region (Figure 5, left

360   panels). In contrast, when climate was the sole factor limiting movement among IBAs, the highest

361   concentrations of shortest paths and current flow were situated in the centre of the region,

362   following a north-south axis along the high elevation areas of the Albertine Rift (Figure 5, middle

363   panels). When only climate was limiting, both the shortest path and current flow analyses suggested

364   that the eastern shore of Lake Kivu, running northwards from Nyungwe Forest to Volcans and

365   Virunga National Parks (NP), would be important for bird movement. However, a lack of forest in the

366 area reduced its projected importance for bird movement under the co-limitation regime (Figure 5,

367 right panels).

Discussion

369   The species distribution models projected that the high elevation areas of the Albertine Rift

370 will provide the most suitable climate for most of the species considered here. Given projected

371 climate change in the Albertine Rift and assuming no loss of the forest cover available in the early

372 21st Century, our analyses suggested that limited availability of suitable climate, rather than gaps in

373 forest cover, will impose the greatest constraints on movement among IBAs. Despite these

374 constraints, our analyses identified several movement corridors and suggested that the well-

375 forested, high-elevation areas along the western flank of the Albertine Rift will be particularly

376 important for the 12 species as they adjust their ranges in response to climate change.

377   A single important route through the central high elevation areas of the region connected a

378 large proportion of the IBAs included in our analyses. This route runs along a north-south axis from

379 the Itombwe Mountains through the high elevation areas of Kahuzi-Beiga NP, before passing

380 through the "Greater Virunga Landscape" (incorporating Volcans NP, Virunga NP, Queen Elizabeth

381 NP, Rwenzori NP and Semiliki NP among others; Plumptre, et al. 2007). The Itombwe Mountains,

382 parts of Virunga NP and the Rwenzori Mountains were particularly important locations on this route.

383 Both the Greater Virunga Landscape and the Itombwe Mountains have been previously highlighted

384 as among the most biodiverse regions in Africa (Hart, et al. 1999, Plumptre, et al. 2007), and the

385 evidence from our analyses of their potential role in maintaining the future connectivity of the

386 region provides further support for their high conservation value.

387   A previous analysis of conservation priorities in the region (but not in a climate change

388 context) highlighted six main areas as crucial for connecting the conservation site network in the

389 Albertine Rift (Plumptre, et al. 2007). The Greater Virunga Landscape was one of these areas, and, as

390 discussed above, it is also identified by our analyses. Three other areas considered by Plumptre *et al*.

16

391   (2007) also lie within the scope of this study (the other two are either too small or lie outside of the

392   region we consider). These areas are (i) between Murchison Falls and Semliki Reserves, (ii) from

393   Maiko NP through Kahuzi-Beiga NP to the Itombwe Mountains and (iii) from Mount Kabobo to the

394   Marungu Highlands at the southern extremity of the region. Under the forest-only limitation regime,

395   high densities of paths occurred through all three areas. However, the future climates along the

396   forested routes through two of these areas (i and iii) were projected to be unsuitable for the species

397   considered here, and consequently these areas were less important for bird movement under the

398   climate-only and co-limitation regimes. The highland route between eastern Kahuzi-Beiga and the

399   Itombwe mountains (area ii) is forested and the future climate is projected to be suitable for the

400   species included in this study, emphasising the likely importance of forested, high-elevation routes in

401   this region. The lower elevation forest routes identified by Plumptre *et al.* (2007) may continue to be

402   important for species that are tolerant of a wide range of climates. However, for the landscape to

403   allow movement of this suite of 12 endemic bird species under climate change, relatively continuous

404   forest must be maintained in the climatically suitable highlands of the region.

405   Although our analyses suggested that, in future, forest cover will be generally less limiting to

406   bird movement than availability of suitable climate, movement through some areas projected to be

407   climatically suitable was constrained by a lack of forest cover. The most important of these forest-

408   limited connections is along the eastern shore of Lake Kivu between Nyungwe Forest and Volcans NP

409   to its north. Under the climate-only regime, this route appeared very important and may also have

410   facilitated movement further north of Volcans NP, through Echuya Forest Reserve and Bwindi

411   Impenetrable NP to the eastern edge of Queen Elizabeth NP. However, much of the forest between

412   Nyungwe Forest and Volcans NP has been converted to *Eucalyptus* plantations. Consequently, the

413   path density along this route decreased substantially once gaps in forest cover were accounted for.

414   It should be recognised that the inference that bird movement will be constrained more by

415   climate than by forest cover, is dependent on there being no further forest loss in the region,

416   especially along the high ground flanking the west of the Albertine Rift Valley where suitable climate

417   and forest cover coincide. Forest cover and suitable projected climate overlap little beyond the

418   western ridge of the Albertine Rift, and hence, loss of these high-elevation forests could greatly

419   impede bird movement across the region. However, the high human population density and

420   prevalence of armed conflict have driven rapid and extensive forest loss across the region, especially

421   outside protected areas (Duveiller, et al. 2008, Hanson, et al. 2009, Kanyamibwa 1998, Plumptre, et

422   al. 2003). Areas that our analyses highlighted as especially important for bird movement along the

423   western Albertine rift, like Virunga NP and the Itombwe Mountains, have also suffered recent

424   deforestation (Hanson, et al. 2009, Hart, et al. 1999, McNeely 2003, Plumptre, et al. 2003). In

425   addition, human responses to climate change in the region may well lead to changes in where

426   people live, where they cultivate land, and how they generate energy, all of which could have

427   substantial impacts on deforestation. Such indirect impacts of climate change may prove to be as

428   significant as direct impacts (Segan, et al. 2015). It is unclear how much further forest destruction

429   the region can undergo before forest becomes more of a limiting factor than climate in the response

430   of the endemic forest birds to climate change. Ideally, we would have incorporated projections of

431   forest loss (which are available for some tropical areas, e.g. Soares-Filho, et al. 2006) into our

432   analyses. Projections of deforestation would have allowed us to identify movement corridors that

433   are likely to remain forested and suggest areas that could be prioritised for additional protection.

434   Unfortunately, reliable projections of deforestation are currently unavailable for the region, largely

435   because human activity is likely to be the primary driver but is also highly uncertain (Ayebare, et al.

436   2013). What is almost certain however, is that incorporating future deforestation scenarios in our

437   models would have increased the projected constraints on future range shifts by the bird species we

438   considered.

439   The use of methods from graph theory to model animal movement, as we do in this study,

440   provides a powerful tool for ecologists and conservation biologists (Lawler, et al. 2013, McRae, et al.

441   2008). Nevertheless, such approaches are inevitably simplifications of complex ecological processes

442 (Moilanen 2011, Sawyer, et al. 2011). In particular, our analyses ignored variation within populations

443 in dispersal ability, behaviour and habitat requirements and the capacity for populations to adapt

444 evolutionarily in response to environmental change (Baguette and Van Dyck 2007, Hawkes 2009,

445 Nussey, et al. 2005). It is unclear how such simplifications might affect the analyses. One criticism of

446 some movement analyses has been their inability to allow individuals to cross even relatively small

447 sections of unsuitable habitat (Moilanen 2011). Although the data we used to parameterise the

448 dispersal functions in our analyses were relatively crude and ignored variation among individuals,

449 their inclusion in the modelling framework enhanced biological realism by allowing small patches of

450 suitable habitat to serve as stepping stones to areas that might sustain viable populations. This

451 approach could be developed further, perhaps in combination with more extensive dispersal

452 information. Another parameter that is very difficult to measure is the scale at which individuals

453 perceive and respond to the landscape they are moving through. In this study, we compared two

454 methods that make contrasting assumptions about perception. Shortest paths assume a perfect

455 knowledge of the landscape (so individuals always take the most direct route) while current-flow

456 paths assume individuals have no knowledge of the wider landscape beyond their next move (so

457 individuals take a more circuitous route). Although the current-flow method resulted in more diffuse

458 movement routes than the shortest path method, both highlighted the same areas as most

459 important and suggested similar differences among limitation regimes. Thus, it appears that our

460 main conclusions were not sensitive to assumptions about bird perception.

461 More refined forest classification data and climate projections would also have improved

462 our analyses. We used forest classification data based on satellite images (Arino 2010) that provide

463 consistent classifications across large spatial scales (Sawyer, et al. 2011). However, the bird species

464 considered here probably have more specialised habitat preferences than can be defined using

465 current remotely-sensed images. Although we augmented the forest classification data from

466 GlobCover 2009 (Arino 2010) by reclassifying known plantations as unsuitable habitat, our models

467 undoubtedly allowed movement through unsuitable forest and prevented movement through

468 suitable forests. Similar concerns could be raised about the projections of future climate from the

469 species distribution models, because although they provide an efficient means of estimating

470 conductance across large landscapes for multiple species (Lawler, et al. 2013), they undoubtedly

471 include errors. Such errors will shift the projected movement corridors and could also alter the

472 estimates of path lengths. In particular, if the distribution of suitable future climate is less restricted

473 than is projected by our species distribution models, the relative contribution of forest cover to

474 movement of these species could increase.

475 Overall, our analyses suggest that there are corridors of both suitable climate and forest

476 cover within the Albertine Rift region that will permit the region's endemic forest bird species to

477 move in response to future climate change. However, corridors defined by considering either climate

478 or forest cover alone may prove inappropriate or inadequate, and so, both should be considered in

479 conservation planning. Although movement of birds in our models was far more limited by the

480 availability of suitable climate than by forest cover, this assumed no loss of current forest cover,

481 which is unrealistically optimistic. Therefore, although the existence of movement corridors that

482 endemic birds might use to respond to shifting climate provides hope for conservation adaptation to

483 climate change in the Albertine Rift, implementing a landscape-scale conservation strategy to cope

484 with climate change faces considerable challenges in this biodiversity hotspot.

485 **Acknowledgements**

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599

Tables

Table 1: Restricted-range bird species endemic to the Albertine Rift included in the analysis, indicating their 2016 IUCN Red List category (LC: Least Concern; NT: Near Threatened), mean and maximum dispersal distance bands (representing the mean for each genus or, where indicated with asterisks, for each family) and preferred habitat. The number of point localities where the species was observed and used in the species distribution models and the predictive performance of the models (measured by AUC) are also presented.

Species	Red List category	Mean dispersal band (km)	Max dispersal band (km)	Preferred Habitat	No. of point localities observed	Test AUC
Alethe poliophrys	LC	5-24*	25-49*	Moist montane forest	95	0.820
Apalis personata	LC	5-24	5-24	Moist montane forest	468	0.865
Batis diops	LC	0-4	0-4	Moist and dry montane forest	162	0.904
Pternistis nobilis	LC	5-24	5-24	Moist montane forest and shrubland	24	0.911
Hemitesia neumanni	LC	5-24	25-49	Moist montane forest	101	0.892
Kupeornis rufocinctus	NT	0-4	5-24	Moist montane forest	25	0.865
Nectarinia alinae	LC	5-24	25-49	Moist montane forest	110	0.818
Nectarinia purpureiventris	LC	5-24	25-49	Moist montane forest	121	0.872

Species	Status			Habitat		
Nectarinia regia	LC	5-24	25-49	Moist montane forest	300	0.919
Oreolais ruwenzorii	LC	0-4*	5-24*	Moist Montane Forest	448	0.887
Parus fasciiventer	LC	0-4	5-24	Moist Montane Forest	54	0.885
Zoothera tanganjicae	NT	5-24	25-49	Moist Montane Forest	18	0.884

607

Figures Legends

609 **Figure 1:** Map of the Albertine Rift study region with the locations of the 30 IBAs considered. The

610 abbreviation "NP" stands for National Park. Elevation (background shading), large lakes (blue fill and

611 text) and international borders (dotted and dashed lines) are also indicated.

612 **Figure 2:** Schematic outline of the analysis. White boxes and black arrows indicate steps that were

613 used to address both questions while grey boxes and lines indicate steps only used to address

614 question 1 and blue boxes and arrows indicate steps only used to address question 2. See the text

615 for more details.

616 **Figure 3:** Maps of the Albertine Rift presenting (a) summed projected climate suitability for the 12

617 bird species for the time periods centred on 2025, 2055 and 2085 and (b) early 21st century forest

618 cover based on Globcover 2009 (Arino 2010) and adjusted to account for known plantations. Dark

619 blue lines indicate IBA boundaries.

620 **Figure 4**: A comparison of path lengths resulting from the three limitation regimes using (a) shortest

621 paths and (b) current flow to model movement of 12 Albertine Rift endemic bird species in the time

622 period centred on 2055 (there was little variation among time periods in path lengths). Points

623 represent the mean ratio of path lengths (dimensionless) under each regime to the path length

624 under the null regime (i.e. no limitation by either forest or climate). Larger values indicate greater

625 limitation. Error bars represent the standard-errors of the mean.

626 **Figure 5:** Maps of (a) shortest paths and (b) current flow summed across all pairs of IBAs and species

627 for the three limitation regimes in the time period centred on 2055 (similar results were obtained for

628 the other time periods). For each species and method, we calculated the proportion of paths that

629 ran through each cell under each limitation regime. We subtracted the proportion of paths

630 traversing cells under the null limitation regime from each of the other three limitation regimes. We

631 then averaged these proportions across species to get a measure of the proportion of paths across

632   all 12 species that traversed each cell. White areas indicate cells with no paths. Black polygons

633   indicate the IBA boundaries.

634   **Figure S1:** Maps of shortest paths summed across all pairs of IBAs and species for the three

635   limitation regimes presented separately for all three time periods considered. For each species and

636   method, we calculated the proportion of paths that ran through each cell. The proportion of paths

637   has been corrected by subtracting the proportion of paths traversing cells under the null limitation

638   regime. The corrected proportions were then averaged across species to get a measure of the

639   proportion of paths across all 12 species that traversed each cell. White areas indicate cells

640   traversed by no paths. Black polygons indicate the IBA boundaries.

641   **Figure S2:** The proportion of current flow, from all pairs of IBAs and species, traversing each cell

642   under the three limitation regimes for all three time periods. For each species, method and

643   limitation regime, we calculated the proportion of paths that ran through each cell. The proportion

644   of paths was corrected by subtracting the proportion of paths traversing cells under the null

645   limitation regime. Cells that were not used by any species between any pair of IBAs get values of 0

646   (white). The black polygons indicate the IBA boundaries.

647   **Figure S3:** Maps of 2055 shortest paths for each species and limitation regime separately, summed

648   across all pairs of IBAs. For each species and method, we calculated the proportion of paths that ran

649   through each cell. The proportion of paths has been corrected by subtracting the proportion of paths

650   traversing cells under the null limitation regime. The data from all species are presented on the same

651   common scale. White areas had no paths passing through them. Black polygons indicate the IBA

652   boundaries.

653   **Figure S4:** Maps of 2055 current flow for each species and limitation regime separately, summed

654   across all pairs of IBAs. For each species and method, we calculated the proportion of paths that ran

655   through each cell. The proportion of paths was corrected by subtracting the proportion of paths

656   traversing cells under the null limitation regime. The data from all species are presented on a

657   common scale. White areas had no paths passing through them. Black polygons indicate the IBA

658   boundaries.