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## Elevational distribution of birds in an Eastern African montane environment as governed by temperature, precipitation, and habitat availability

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3 Title: **Elevational distribution of birds in an Eastern African montane environment as**  
4 **governed by temperature, precipitation, and habitat availability.**

5

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17 **ABSTRACT**

18 Tropical species, many of which have limited thermal tolerances and narrow ecological niches,  
19 are likely to experience elevational shifts due to climate change. However, our ability to predict  
20 these shifts is limited by a scarcity of baseline data on current distributions and a lack of  
21 understanding of drivers of species ranges. To characterize the elevational distributions of a suite  
22 of Afromontane birds, we conducted annual point counts between 2013 and 2018 at 297 plots  
23 across habitats and elevations (2,416-4,303 m) in Volcanoes National Park, Rwanda. We  
24 assessed elevational and habitat preferences via indicator analyses, and modeled abundance  
25 distributions as a function of temperature, precipitation, habitat availability, and congeneric  
26 competition. Although most of the 35 focal species were distributed across habitats and  
27 elevational ranges, 20 species particularly associated with narrow elevational range (<300 m)  
28 and 24 species were strongly associated with one to three habitat types. Abiotic factors  
29 significantly correlated with abundance distributions of 33 species (temperature 33, precipitation  
30 17), and biotic factors with distributions of 31 species (habitat 30, competition 7). Temperature  
31 and habitat availability were particularly associated with upper limits (31 and 26 species  
32 respectively vs. 10 and 6 at lower limits), whereas precipitation affected both limits similarly (17  
33 lower, 16 upper), and competition had a limited role at either limit (4 lower, 3 upper). That the  
34 elevational distribution of Afromontane birds results from a species-specific combination of  
35 biotic and abiotic factors is crucial information in our effort to predict climate change effects in  
36 this region.

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**DATA AVAILABILITY STATEMENT**

The majority of data that supports the findings of this study are available in the supplementary material of this article. Additional raw data such as GPS coordinates of bird count locations are openly available in Dryad at [http://doi.org/\[doi\]](http://doi.org/[doi]), reference number [reference number].

**KEYWORDS**

Afromontane avifauna, Albertine Rift region, altitudinal distribution, elevational niche, habitat availability, range shifts, Rwanda

## 63 1. INTRODUCTION

64 Climate change may induce shifts in the distribution of biota across elevations, latitudes, and  
65 longitudes (Lenoir & Svenning, 2015). Among tropical species, which tend to have limited  
66 thermal tolerances (Laurance et al., 2011) and narrow ecological niches (Vázquez & Stevens,  
67 2004), these distributional shifts are especially likely to occur in the form of elevational shifts  
68 given that elevational temperature gradients are stronger than latitudinal temperature gradients  
69 near the equator (Colwell et al., 2008). As a result, studies on elevational range shifts are  
70 becoming increasingly common across Afrotropical mountains, especially for birds (Dulle et al.,  
71 2016; Neate-Clegg et al., 2020; Neate-Clegg et al., 2021b). These studies show a general trend  
72 towards upslope shifts in species distribution, though the rate at which species have shifted  
73 varies considerably among regions and species; and up to a third of species have likely shifted  
74 their distribution downslope (Neate-Clegg et al., 2021b). These variations confirm that species  
75 distributions do not simply respond to changes in abiotic parameters and are likely to be  
76 influenced by a more complex set of abiotic and biotic drivers (HilleRisLambers et al., 2013).  
77 The relative importance of biotic and abiotic factors is known to vary across species and regions  
78 (Jankowski, et al., 2012; Elsen, et al., 2017). Despite the increasing number of studies on range  
79 shifts in Afrotropical mountains, we still have a limited understanding of the relative role of  
80 these factors in determining current elevational distributions in these regions, including for birds  
81 (Louthan et al., 2015; Mihoub et al., 2017; Rumpf et al., 2019).

82 Bird elevational distributions may be influenced by a host of factors (see review by  
83 Jankowski et al., 2013), of which three are particularly important: climate, habitat, and  
84 competition (Louthan et al., 2015; Elsen et al., 2017). First, they may be influenced by species  
85 climatic tolerance, i.e., the range of temperatures/precipitations for which basal metabolism can

86 be maintained, and by climatic preference, i.e., the temperature/precipitation for which species  
87 abundances peak (Carrascal et al., 2016; Sunday et al., 2012). They may also be influenced by  
88 habitat preferences, which are linked to the availability of resources such as food or potential  
89 nest sites. The availability of resources may itself be influenced by climatic factors such as  
90 temperature, precipitation, and evapotranspiration (e.g., Bhattarai & Vetaas, 2003; Hemp, 2006).  
91 Indeed, birds are known to track temporary (e.g., interannual) variations in food availability  
92 related to short-term fluctuations in precipitation (Ferber et al., 2014; Jankowski et al., 2012;  
93 Neate-Clegg et al., 2020). As a result, climate may have both a direct effect on species  
94 elevational distribution, through climatic tolerance/preference, as well as an indirect effect,  
95 through habitat preference (HilleRisLambers et al., 2013; Jankowski et al., 2013; Louthan et al.,  
96 2015). And, finally, bird elevational distributions may be determined by biotic interactions such  
97 as competition—with predation and facilitation also playing a role for certain species (see review  
98 by Jankowski et al., 2013)—though evidence for this varies across regions. For example, a study  
99 in the Andes showed that elevational distributions of a vast majority of species were related to  
100 congeneric competition (Terborgh & Weske, 1975), but this was the case for less than 12% of  
101 species in a study in the Himalayas (Elsen et al., 2017).

102       Most studies on bird elevational distributions in Afrotropical mountains have focused on  
103 bird communities at relatively low elevations ( $\sim < 3000$  m a.s.l.) or those that occur within a  
104 single habitat type (e.g., mid-elevation to montane forests; Dulle et al., 2016; Hanz et al., 2019;  
105 Hořák et al., 2019; Neate-Clegg et al., 2020, 2021b). The literature suggests that, at these lower  
106 elevations, bird species distribution are likely to be mainly driven by biotic interactions and  
107 habitat availability and only marginally influenced by abiotic factors (Ferber et al., 2014; Hanz et  
108 al., 2019; Hořák et al., 2019; Jankowski et al., 2009, 2013; Sam et al., 2019). Indeed, abiotic

109 factors may only become limiting for endotherms such as birds at high elevations (Jankowski et  
110 al., 2012; Spence & Tingley, 2020; Elsen et al., 2017). Unfortunately, studies conducted at lower  
111 elevations may have been unable to assess factors influencing the upper elevational limit of  
112 species, as this limit may occur beyond the upper elevational limits of the study area (Neate-  
113 Clegg et al., 2020). Similarly, these studies may have underestimated the role of biotic factors for  
114 species occurring outside of the studied forested habitat (Dulle et al., 2016). As a result, the fact  
115 that most studies on bird elevational distributions in Afrotropical mountains have focused on  
116 lower elevations and single habitat types may have limited our understanding of the respective  
117 role of biotic and abiotic factors in driving these distributions.

118         We aimed to disentangle the respective roles of climate, habitat availability and  
119 competition on bird elevational distributions using a unique dataset collected in Volcanoes  
120 National Park, Rwanda, in the Albertine Rift region. This dataset allowed us to study the  
121 distribution of 35 bird species across a wide elevational range (2,416-4,303 m) and across a wide  
122 range of forested and open habitat types. First, we characterized species elevational distributions  
123 and preferences, as well as specific habitat preferences. Second, we assessed the possible effects  
124 of precipitation, temperature, the availability of preferred habitat types, and the abundance of  
125 congeners on bird species abundance following the correlational methods developed by Elsen  
126 et al. (2017). We expected biotic factors, habitat availability and competition, to be important at  
127 both lower and upper range limits whereas we expected abiotic factors, precipitation and  
128 temperature, to play a predominant role at upper range limits (Byrne, 2016; Elsen et al., 2017;  
129 Jankowski, et al., 2012; Neate-Clegg et al., 2018).

130

## 131 **2. METHODS**

## 132 2.1. Study area

133 We studied the avifauna of Volcanoes National Park (VNP), Rwanda (between 1°21'–1°35'S,  
134 29°22'–29°44'E; Figure 1a). This protected area, located in the biologically diverse Albertine  
135 region (Plumptre et al., 2007), encompasses a variety of mountainous habitats across an  
136 elevational gradient (Plumptre, 1991; Figure 1b): (1) bamboo (*Yushania alpina*) and mixed  
137 bamboo forests (ca. 2,500–2,800 m); (2) mixed montane forests with an often dense and  
138 *Mimulopsis*-dominated understory (ca. 2,500–2,700 m); (3) Hagenia-Hypericum woodland  
139 characterized by *Hypericum* spp. and *Hagenia abyssinica* (ca. 2,800–3,300 m); (4) patches of  
140 herbaceous vegetation with little to no tree cover (ca. 2,800–3,300 m); (5) brush ridge comprised  
141 of *Hypericum*-woodland with sparse tree cover (ca. 3,000–3,300 m); (6) Alpine meadows (ca.  
142 3,100–3,400 m); and (7) sub-Alpine zone with stands of giant lobelia (*Lobelia stuhlmannii*) and  
143 *Rubus* spp. (ca. 3,300–3,600 m). There is a rapid decrease in tree cover above 3000 m and the  
144 average treeline in VNP is considered to occur between 3600-3800 m, the limit for most  
145 Ericoideae trees and shrubs (Jacob, et al. 2015). Finally, there are (8) wetlands at varying  
146 elevations across VNP.

147 Volcanoes National Park experiences an increase in annual precipitation with elevation  
148 up to 3000-3600 m and a decrease beyond 3600 m (Figure 1d). It experiences a steady decrease  
149 in minimum temperature of the coldest month with elevation, with temperatures varying from  
150 >10°C at 2400 m to 0 °C above 4000 m (Figure 1d; data obtained for all of VNP at a 30 arc-  
151 second resolution from CHELSA; Karger et al. 2017a; Karger et al. 2017b; last modified April  
152 2020).

153

## 154 2.2. Plot selection and bird surveys



155 We selected 30 transects covering all habitat types occurring within VNP (Figure 1b). Each  
156 transect was separated by at least 1,000 m. Between 4 and 18 plots were selected at 200-m  
157 intervals along each transect, resulting in a total of 297 plots. Plots were located between 2,416  
158 and 4,303 m a.s.l. For each plot, we recorded its dominant habitat type based on field  
159 observations and derived the average annual precipitation and the minimum temperature of the  
160 coldest month from the aforementioned CHELSA data. For comparative reasons, and to  
161 understand the distribution of species outside VNP, we also counted birds at 50 plots located  
162 within ~3 km downslope from the park boundaries.

163 Two highly trained observers (FE and VM) conducted points counts twice a year between  
164 2013 to 2018, visiting each plot one month apart during a relatively dry time of the year between  
165 June and September. They recorded all birds heard or seen within a 25-m radius for 10 minutes  
166 between 6:30 and 12:00. We adopted the taxonomy presented in the IOC World Bird List  
167 Version 8.2 (Gill & Donsker, 2018). We provided descriptive statistics for all recorded species  
168 (lowest and highest records and elevational range width measured as the difference between  
169 these extremes) but excluded birds with < 3 records per year from further analyses (following  
170 e.g., Neate-Clegg et al. 2020), since their elevational distribution was unlikely to be accurate due  
171 to low sample size. We also excluded all Accipitridae, Falconidae, Apodidae, and Hirundinidae,  
172 since point counts are not adapted for these species. Finally, we excluded Grauer's Swamp  
173 Warbler *Bradypterus graueri*, the only wetland specialist remaining after applying the previous  
174 filters, as the distribution of this species was restricted to three wetlands in VNP. The remaining  
175 subset of species (hereafter 'subset') showed no significant correlations between the width of  
176 elevational ranges (see 2.3) and sample size (Spearman rho 7370.3,  $p = 0.461$ ), which may serve

177 as coarse indication that sample sizes for these species were sufficiently adequate—for example,  
178 small ranges were not the result of a low sample bias—for further analyses.

179

### 180 **2.3. Species elevational distributions and preferences**

181 We characterized species elevational distribution by calculating minimum/maximum elevation,  
182 elevation range, and weighted mean elevation (mean elevation of species records weighted by  
183 the number of individuals recorded at each elevation) for each species across all years. For the  
184 minimum and maximum elevations, we used the 2.5% and 97.5% percentiles of the elevational  
185 distribution to reduce the influence of outliers (Neate-Clegg et al., 2018, 2021b), and the range  
186 was estimated as the difference between these two limits. Next, per species, we plotted the  
187 distribution of abundances along elevation using kernel density plots created with ‘ggridges’ in R  
188 (Wilke, 2021). Finally, we visualized the elevational ranges of the subset of species in a  
189 histogram.

190 We characterized species elevational preferences using indicator analyses (Leach et al.,  
191 2018). More specifically, we used the point biserial (pb) correlation index  $r_{pb}$ —recommended for  
192 abundance data (De Cáceres & Legendre, 2009; De Cáceres et al., 2010)—produced by the  
193 ‘multipatt’ function in the R package ‘indicspecies’ (De Cáceres et al., 2016) to assess whether  
194 species were preferentially associated with specific elevations. Following De Cáceres &  
195 Legendre (2009) and De Cáceres et al. (2010), we used total abundance data gathered across all  
196 years for each plot. Subsequently, we used a permutation test (9999 permutations) to compare  
197 these test variables with the distribution of statistics obtained from randomly ordered data; see  
198 De Cáceres, Legendre, and Moretti (2010) for detailed explanations of these permutation tests.  
199 We used an alpha of 0.05 to determine significant associations. We considered whether species

200 were associated with narrow elevation bands of 300 m (e.g., 2400-2700 m), or with combinations  
201 of elevational bands (e.g., 2400-2700 m and 2700-3000 m). We refer to such elevation bands as  
202 ‘preferred elevations’.

203

#### 204 **2.4. Species habitat preferences**

205 We determined whether species were preferentially associated with one specific habitat type or a  
206 combination of habitat types. For this, we classified each plot as one of the seven habitats listed  
207 in *Study area*, based on field observations made during bird point counts. As sub-Alpine and  
208 Alpine vegetation types were difficult to distinguish in the field, we merged these two categories  
209 for this analysis. To determine habitat preferences, we used the same correlation indices  
210 specified above, but applied to the six habitat types instead of elevation bands. We refer to these  
211 habitats as ‘indicator habitats’.

212

#### 213 **2.4. Role of climate, habitat, and competition as drivers of species distributions**

214 We used generalized additive models (GAMs) to determine whether bird species abundance is  
215 influenced by climate, habitat, or competition. We first created a set of models including all  
216 predictor variables (temperature, precipitation, habitat cover, and abundance of congenics) as  
217 well as all possible interaction terms to check for potential concavity—a non-linear form of  
218 multicollinearity—and spatial autocorrelation. We found no significant concavity nor  
219 autocorrelation. Given the variable numbers of predictors associated with each driver (climate,  
220 habitat, competition), we, therefore, chose to run three distinct sets of models for each driver,  
221 with no autocorrelation term. Similar to Elsen et al. (2017), we chose simple and separate models

222 rather than more complex multi-effects models that include all variables, to allow for accurate  
223 estimations of coefficients (see also Cade, 2015).

224 For the climate model, we included average annual precipitation, the minimum  
225 temperature of the coldest month, and an interaction term as predictor variables. We included the  
226 interaction term to obtain more accurate coefficients for individual terms while accounting for  
227 dependent effects, but we refrain from further discussion of these interaction effects given we  
228 have no a priori hypotheses for interaction effects and the often multimodal and complex nature  
229 of these effects hinders straightforward interpretation.

230 For the habitat model, we included the absolute ( $m^2$ ) cover of preferred habitat types (15  
231 m resolution data obtained with permission from Akayezu et al., 2019) across circular buffers  
232 around bird point count plots (hereafter ‘buffer plots’) as predictor variable. We first chose  
233 buffers with a radius of 100 m, as this is a known threshold in gap-crossing movements of  
234 tropical forest birds (Ibarra-Macias, 2011). However, as the territorial or home-range sizes of  
235 many bird species may be much larger than 100 m, we also created these habitat models with the  
236 area ( $m^2$ ) of preferred habitat as measured across 500 m circular buffers. Little is known about  
237 the movement ecology or home-range sizes of most of our focal species, but we chose 500 m for  
238 these buffers given that this distance is on par with the maximum home-range sizes of other  
239 Afrotropical species (see e.g., Habel et al., 2018). When available for a species, we included all  
240 preferred habitat types as predictor variables. For species that lacked indicator habitats, we used  
241 a more general classification of habitat preference (forest or open habitat) based on the  
242 Handbook of the Birds of the World (Del Hoyo et al., 2016; assessed in February 2019), and  
243 accordingly used the total amount of forest or open habitat as predictor variables.

244 Finally, for the competition model, we included the abundance of each congeneric  
245 species as a predictor variable. We included the abundance of only one congeneric per model,  
246 which implied that we created multiple models for species that co-occur in the study area with  
247 multiple congeners.

248 We created models with a zero-inflated Poisson (or binomial family structure when  
249 records were of single individuals), using the ‘mgcv’ package in R (Wood, 2016). We used  
250 smooth functions for significant variables using mgcv’s *plot.gam* function to visualize the shape  
251 of the relationship. We subsequently compared these shapes to the elevational distribution of the  
252 relevant predictor variables (e.g., those plotted in Figure 1c, d) to determine whether variables  
253 were likely to play a role in determining lower or upper limits.

254

### 255 **3. RESULTS**

256 We recorded 132 species in VNP, of which we retained 35 for further statistical analyses  
257 (highlighted as ‘subset’ in Table S1).

#### 258 **3.1. Species elevational distributions**

259 Kernel density plots show the elevational distributions of bird species and provide visual  
260 evidence of substantial interspecific variation in the elevational distribution of species in VNP  
261 (Figure 2). Across all species in the subset, the range of elevations varied substantially between  
262 species (Figure 3), from ~556 m for Yellow-whiskered Greenbul *Eurillas latirostris* to ~1605 m  
263 for Scarlet-tufted Sunbird *Nectarinia johnstoni* (Table S1).

264 Twenty-seven species showed a significant (at  $p < 0.05$ ) preference for one elevation  
265 band (20 species) and/or a combination of elevation bands (21 species; Table 1, Table S1). All  
266 but three species—White-necked Raven *Corvus albicollis*, Cape Robin-Chat *Cossypha caffra*,

267 and Scarlet-tufted Sunbird—were significantly associated with elevation bands that span the  
268 forest-dominated parts of the study area, below the treeline at ~3600 m.

269

### 270 **3.2 Species habitat preferences**

271 We found that 24 species showed a significant preference for one habitat type (10) and/or a  
272 combination of a maximum of three (14) habitat types ( $p < 0.05$ ; Table S1). Of these, many  
273 species were associated with forested habitats (4 species with bamboo, 12 with mixed forest, 6  
274 with Hagenia-Hypericum) whereas fewer species were associated with open habitats dominated  
275 by herbaceous (7), meadow (4), brush ridge (6), and (sub) Alpine vegetation (3). Two species  
276 were associated were associated with wetlands and at least one other habitat type.

277

### 278 **3.2. Role of climate, habitat, and competition as drivers of species distributions**

279 For all 35 species in the subset, we detected a significant negative effect of at least one of the  
280 four drivers at range limits, consistent with our hypotheses of range limitations (Table S2, Table  
281 S3, Figure 4, Figure 5). Abiotic climatic factors were significant predictors of range limits of 33  
282 species (temperature for 33 species and precipitation for 17 species), and biotic factors of 31  
283 species (habitat at 100 m radius for 26 species, habitat at 500 m radius for 30 species, and  
284 competition for 7 species). Habitat availability as measured across 100 m-radius circular buffers  
285 was a comparably similar, albeit slightly weaker, predictor of species limits as habitat  
286 availability measured across 500 m-radius buffers.

287 We found substantial differences between the relative importance of factors at lower and  
288 upper limits. Overall, there was a higher number of species with at least one significant predictor  
289 consistent with a constraint at upper limits (32 species) than species with significant predictors

290 consistent with a constraint at lower limits (24). There were also differences in the relative  
291 importance of the four drivers at lower and upper limits, with precipitation being the most  
292 frequent significant predictor of lower limits (for 17 species) and temperature the main predictor  
293 of upper limits (for 31 species; Figure 4).

294

#### 295 **4. DISCUSSION**

296 The spatial distribution of birds in Volcanoes National Park (VNP) is characterized by distinct  
297 elevational zonation. Although elevational ranges were broader than those of birds in some other  
298 tropical montane regions (e.g., average range widths of ~200 m in the northern Andes, Ocampo-  
299 Peñuela, & Pimm, 2015), they were consistent with ranges observed for birds in montane regions  
300 (White & Bennett, 2015). Moreover, results from indicator analyses hint at preferences for  
301 specific elevational ranges for most species, in agreement with the hypothesis that tropical  
302 species have narrow thermal tolerance (Terborgh & Weske, 1975). Our results suggest that these  
303 elevational distributions are likely to be influenced by at least one of the four following drivers:  
304 temperature, precipitation, habitat availability, and competition; this was the case for all 35 focal  
305 bird species in this study. Yet, though different drivers were likely to be limiting at lower and  
306 upper range limits, we did not find support for the broad hypothesis that biotic factors are  
307 limiting at both lower and upper elevations whereas abiotic factors are more limiting at upper  
308 limits. Instead, we found more complexity, in that 1) habitat availability and temperature were  
309 most limiting at upper limits, 2) precipitation was most limiting at lower limits, and 3)  
310 competition was limiting for only a few species at either range limit.

311 Many species showed a decline in abundance with a decrease in temperature at upper  
312 limits. This result is consistent with some literature highlighting that temperature may influence  
313 the upper limits of distributions of tropical species (Ghalambor et al., 2006; Janzen, 1967), but

314 contrasts with other studies (e.g., Neate-Clegg et al., 2020). Contrasts with other studies may  
315 partially be explained by the fact that our study area included a much higher elevation range  
316 (>1000 m) than those included in many other studies of tropical avifauna (e.g., Campos-  
317 Cerqueira et al., 2017; Forero-Medina et al., 2011; Neate-Clegg et al., 2018; Neate-Clegg et al.,  
318 2020). And only at such high elevations may we find the low temperatures that can induce  
319 thermoregulatory costs (i.e., the energetic requirements to maintain body temperatures within  
320 critical limits) that affect survival or behavior (Londoño et al., 2017).

321         However, and more likely, declines in abundance at certain temperatures or levels of  
322 precipitation may also stem from indirect effects of climate on habitat quality or food availability  
323 *within* habitat types (Ferber et al., 2014; Jankowski et al., 2012; Santillán, et al., 2018). For  
324 example, avian communities are known to be shaped by habitat structure, which is, in turn,  
325 correlated with elevation and associated environmental factors (Hořák et al., 2019). This would  
326 also explain the possible role that precipitation could play in defining both upper (too much  
327 precipitation) and lower (too little precipitation) limits for some species. We found that  
328 precipitation was a particularly important predictor of lower range limits in our study area,  
329 though we note that this stems partially from a decline in precipitation towards lower elevations  
330 that may be particular to our study area and the studied southern slopes of the Virunga Massif.  
331 Yet, though the role of precipitation may be site-specific, largely indirect and mediated via  
332 habitat and resource availability (Neate-Clegg et al., 2020), and can be challenging to interpret  
333 due to the largely non-linear relationship of precipitation with elevation (see Figure 1c), it is  
334 clear that precipitation is a factor that needs to be included in studies that aim to track species  
335 range distributions or that aim to model future suitable habitat under climate scenarios—



336 especially as the effects of precipitation and temperature are often interacting and future shifts in  
337 both factors as a result of climate change may be discordant (McCain & Colwell, 2011).

338 By encompassing a wide range of elevation and habitat types, our study confirmed that  
339 habitat availability is also likely to be a significant driver of species distributions (Elsen et al.,  
340 2017). It confirms that habitat availability may be limiting for many species at upper limits, in  
341 particular for forest-associated species which cannot occur above the treeline, as was previously  
342 shown for temperate montane birds (Altamirano et al., 2020). Indeed, most of the species in our  
343 study with habitat as a potential driver of upper limits were forest associated and limited by the  
344 decline in forest availability at or near the treeline ecotone. And of the few (5) species with a  
345 possible effect of habitat at lower limits, four may be considered generalist species that favor  
346 largely or partially open habitats (Cape Robin-Chat, Scarlet-tufted Sunbird, White-necked  
347 Raven, Chubb's Cisticola *Cisticola chubbi*; the first three are also associated with open habitat at  
348 relatively high elevations above the treeline).

349 The overall slightly weaker effect of habitat as a predictor as compared to temperature  
350 (this study and Elsen et al., 2017) could be due to the rather general habitat preferences of many  
351 species in our study (only a third of species had one indicator habitat) or specific characteristics  
352 of our study area such as the presence of tall vegetation (e.g., Ericaceae, Lobelia) above  
353 elevations where tree cover becomes scarce. Moreover, that we did not detect a strong effect of  
354 habitat availability at lower elevations may be because the lower limits of our study area are  
355 found at relatively high elevations well above the lower limits of species' distributions of  
356 especially forest associated species. For some of the species included in the present study,  
357 declines in abundances as a result of declines in habitat availability may only become apparent at  
358 lower elevations, outside VNP.

359 Finally, our findings contrast with earlier suggestions that congeneric competition is an  
360 important driver of elevational zonation among tropical birds (Terborgh & Weske, 1975;  
361 Freeman et al., 2019) and instead align with studies that found only scarce evidence for  
362 congeneric competition among montane bird communities (Barve & Dhondt, 2017; Dehn &  
363 Christiansen, 2001; Elsen et al., 2017; Jankowski et al. 2010). We found that all congeneric  
364 species overlapped to some extent in their elevational ranges (see ranges in Table S1) and it is  
365 likely that other forms of niche partitioning (e.g., regarding diets or the location of reproductive  
366 sites) account for these levels of sympatry (Elsen et al., 2017). Yet, there were some species for  
367 which congeneric competition could play a role, notably warblers of the genus *Phylloscopus*, a  
368 finding in line with e.g., Elsen et al. (2017). And we acknowledge that there could be other forms  
369 of biotic interactions not considered in this study that play a role in shaping elevational  
370 distributions, such as habitat avoidance, facilitation, or predation (Jankowski et al., 2012). For  
371 example, birds that nest or roost in tree cavities could be limited in their distribution by nest  
372 substrates, and preliminary studies in VNP show that cavity density drops rapidly above 3300-  
373 3400 m. These elevations coincide with the upper elevational limit for cavity-nesting species  
374 such as Olive Woodpecker *Dendropicos griseocephalus*.

375 Our analyses provide baseline data on elevational distributions of Afromontane birds  
376 (similar to e.g., Kittelberger et al., 2021) that hint at elevational zonation driven by a complex  
377 and species-specific combination of biotic and abiotic factors. We note that we looked at changes  
378 in abundances within a predefined elevational range and that the elevational distribution of some  
379 species extends below the park boundaries. As such, we caution that the estimated range limits  
380 only apply within the context of VNP, and that most of our focal species are also found outside  
381 the park at lower elevations (see Table S1). Our approach was also correlative, which does not

382 imply that drivers significantly associated with declines in species' abundances were also causal  
383 to elevational limits. Many confounding, interacting, and partially multicollinear effects could  
384 also play a role in shaping observed correlations. For example, although a test for concurvity  
385 showed no significant correlation between the four variables tested in our separate models, they  
386 may have

387         For example, habitat availability seemed a limiting factor at upper limits for the Stripe-  
388 breasted Tit *Melaniparus fasciiventer* but this could also be linked to a more specific resource  
389 such as the availability of the tree cavities for nest sites. These tree cavities are, in turn, known to  
390 be products of interactions between temperature, precipitation, habitat type, and the presence of  
391 certain keystone species such as the also mentioned Olive Woodpecker (Remm & Löhmus,  
392 2011).

393         Despite these caveats of our correlative methods, it is apparent that temperature seems  
394 particularly important in determining elevational distributions in our study area, though we also  
395 found precipitation and habitat availability to be potential predictors of elevational distributions  
396 of many species. This is important when considering possible effects of future climate change,  
397 which in our study area may come in the form of increased temperatures, increased variability in  
398 annual precipitation patterns (IPCC, 2013a,b; Ngoma et al., 2021), and upslope shifts in  
399 vegetation (Ponce-Reyes et al., 2017; Ayebare et al., 2018; Bagchi et al., 2018). Indeed, our  
400 study confirms the need to include variables other than temperature, precipitation in particular, in  
401 projections and explanations of shifts of animal distributions (Tingley et al., 2012; Neate-Clegg  
402 et al., 2020). Future changes in precipitation and temperature may have contrasting effects on  
403 animal distributions and may further interact in the way they impact factors such as food  
404 resource availability.

405           Next steps would be to consider interactions between drivers of elevational distributions  
406 and to monitor temporal and spatial shifts in elevational distributions, for which we need to  
407 commit to long-term monitoring. Only with such long-term data can we effectively guide our  
408 efforts to forecast and mitigate climate change effects on Afromontane bird species. Meanwhile,  
409 we may look at management strategies available to mitigate possible negative climate change  
410 effects on birds in our study area. Such strategies do little to counter effects at high elevations,  
411 but we can look at ways to provide additional habitat to birds at elevations below current park  
412 boundaries. After all, about a third of all species recorded in our study were found up to the  
413 lowest edges of the park (Table S1), and abiotic conditions do not seem to be limiting the lower  
414 tails of distributions of most species. Thus, downslope addition of habitat may provide the  
415 opportunity for downslope range shifts of certain species and may overall provide more space for  
416 bird populations, especially of forest-associated species, which could provide some buffering  
417 from negative climate change effects.

418

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423

#### 424 **AUTHOR CONTRIBUTIONS**

425 EF and VM performed the majority of the fieldwork with contributions by YVDH and DT;  
426 YVDH analyzed the data, YVDH and CS wrote the manuscript, and all authors commented on

427 the final draft and approved the final manuscript. We thank two anonymous reviewers for their  
428 comments on an earlier version of this manuscript.

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466 **Table 1. The number of species (out of 35) significantly ( $p < 0.05$ ) associated with a**  
 467 **particular narrow (300 m) or broader (>300 m) elevational band.**  
 468

Elevation (m)	Total
2400-2700	7
2700-3000	3
3000-3300	6
3300-3600	1
3600-3900	3
Total	20
2400-3000	6
2400-3300	5
2400-3600	3
2700-3300	4
3600-4200	2
Total	21

469

470 **Figure legends.**

471 **Figure 1. Study area and bird point count locations relative to elevation, vegetation cover,**  
472 **mean annual temperature.** A. Map of location Volcanoes National Park (VNP) in northern  
473 Rwanda. B. Map of vegetation cover of VNP and the location of bird point count plots. C. Loess  
474 plot of the distribution of open habitat and forest habitat along elevation (Grey shaded area =  $\pm$   
475 SE). The vertical yellow column shows the approximate location of the treeline at 3600-3800 m.  
476 D. Graphs showing the annual precipitation (mm) and mean temperatures ( $^{\circ}$ C) across elevations;  
477 dots correspond to values at bird point count plots and the line and grey shaded area represent a  
478 visualization of a default loess regression (span = 0.75)  $\pm$  SE. Loess regressions in panels C and  
479 D are conducted using the `geom_smooth()` command in R's 'ggplot2' package (Wickham, 2006).

480

481 **Figure 2. Kernel density distributions of 35 bird species across elevation in Volcanoes**  
482 **National Park, Rwanda.**

483 **Figure 3. Elevational range widths of 35 bird species recorded in Volcanoes National Park,**  
484 **Rwanda.** Elevational range widths are the difference between the 2.5% and the 97.5%  
485 percentiles of the elevational distribution, e.g., a width of 300 m indicates that a species was  
486 recorded across a  $\sim$ 300 m elevational range. The sample size is given in parentheses behind the  
487 species name. Vertical shading refers to: green, the approximate location of a forest-dominated  
488 zone (<3000 m a.s.l.); blue, the transition zone from forest to open habitat ( $\sim$ 3000-3600 m);  
489 yellow, the treeline ecotone (3600-3800 m); gray, the open Alpine zone (> 3800 m). s

490 **Figure 4. Number of species whose Generalized Additive Models showed a significant**  
491 **negative association of abundance with temperature, precipitation, habitat, or competition**  
492 **at elevational limits.** The sum of these numbers do not equal the total number of bird species (n  
493 = 35) considered for these analyses as many species had multiple significant predictors of  
494 abundance. For the bar related to habitat, we used the habitat availability as measured across 500  
495 m-radius circular buffers around bird point count plots.

496 **Figure 5. Examples of plots of component smooth functions that make up generalized**  
497 **additive models.** These effects are significant when the shaded area (95% confidence interval)  
498 does not overlap with zero. For Red-faced Woodland Warbler *Phylloscopus laetus*, this implies a  
499 negative trend in abundances at low temperatures, corresponding to upper elevational limits; for  
500 Rwenzori Hill Babbler *Pseudoalcippe atriceps* there are negative trends at low amounts of  
501 precipitation, which for this species correspond to both its lower and upper elevational limits; for  
502 White-starred Robin *Pogonocichla stellata* there is a negative effect on abundance at low  
503 amounts of bamboo—here we plot abundance against bamboo availability in a 100 m-radius  
504 circular buffer—, a scenario which occurs at its upper elevational limits; and high abundances of  
505 the congeneric Brown Woodland Warbler *Phylloscopus umbrovirens* pose a possible constraint  
506 on the abundances of the Red-faced Woodland Warbler at the latter species' upper limits.

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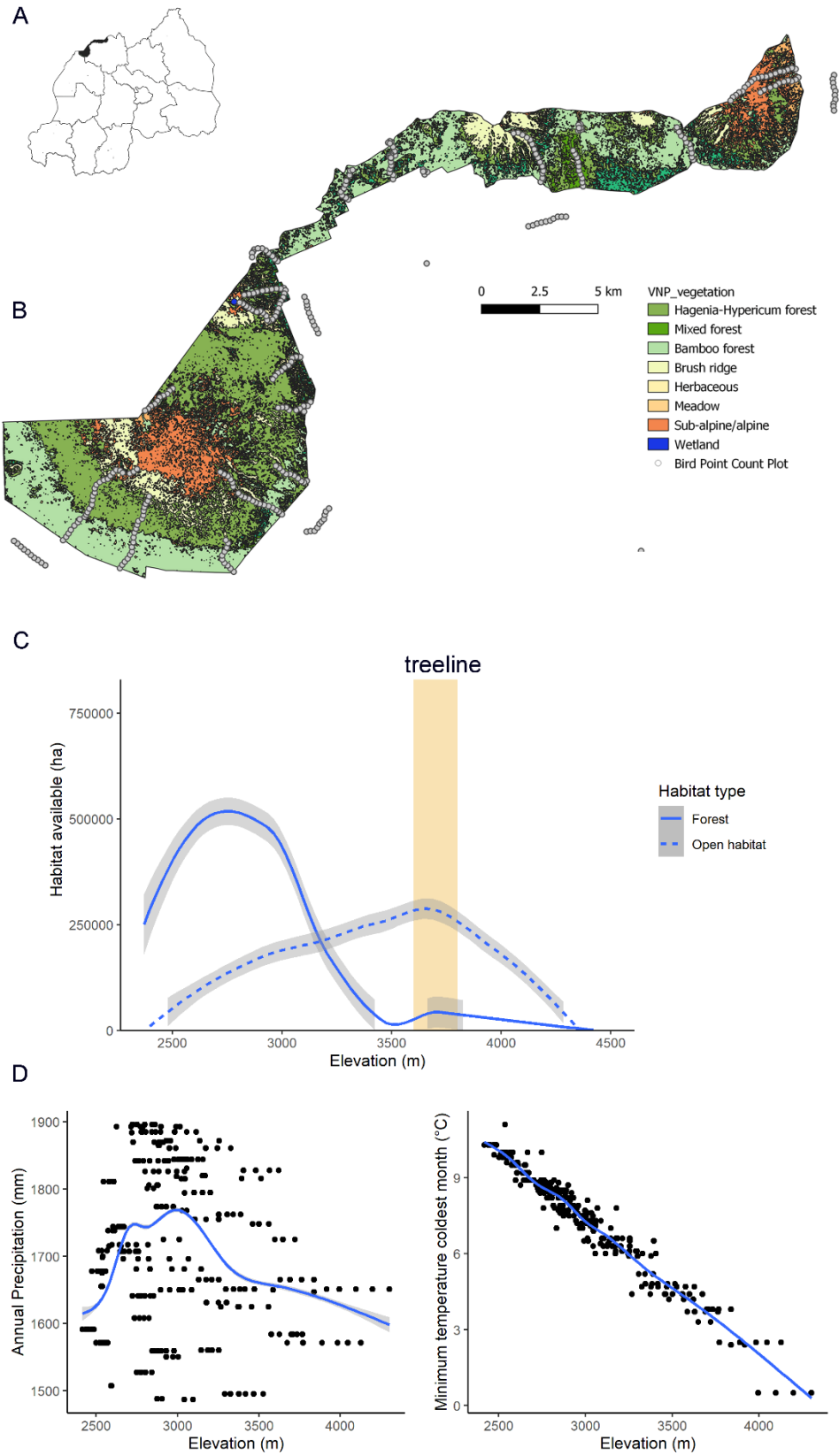
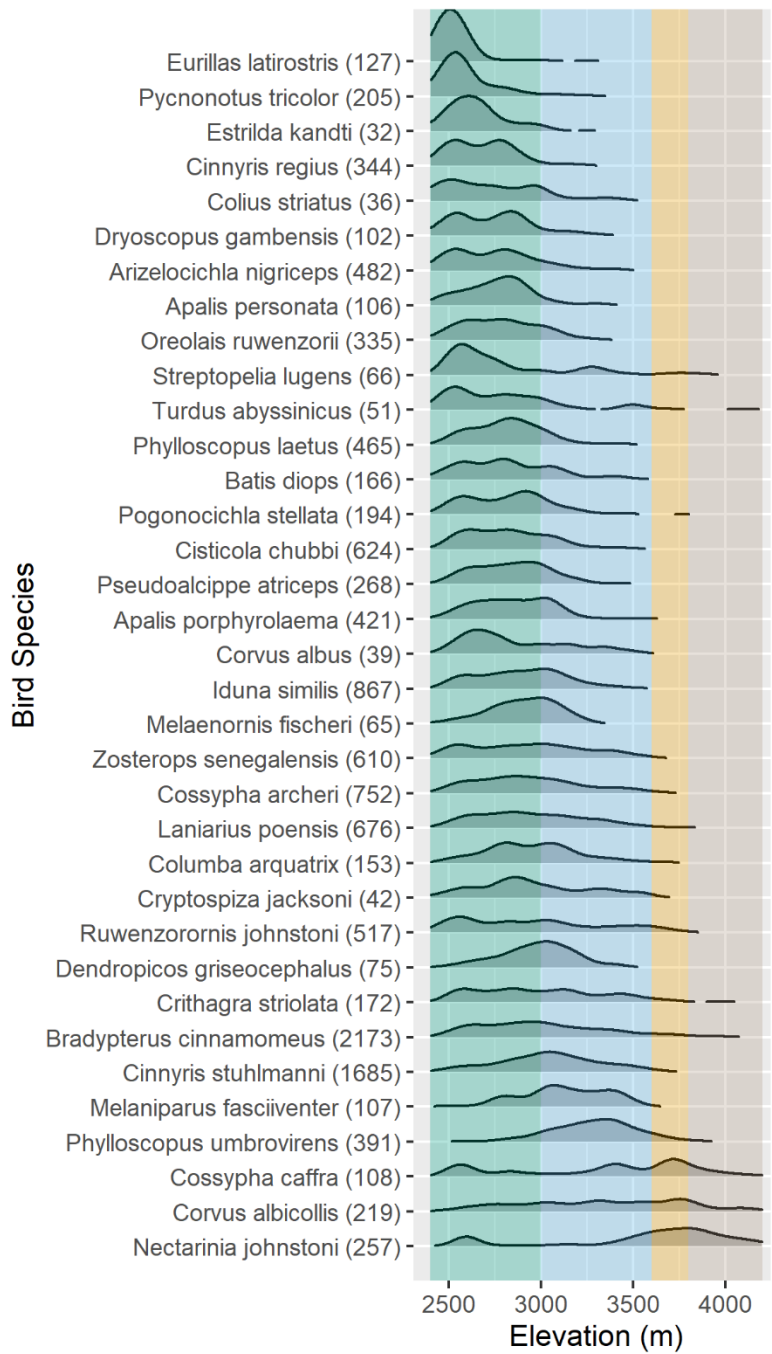


Figure 1.





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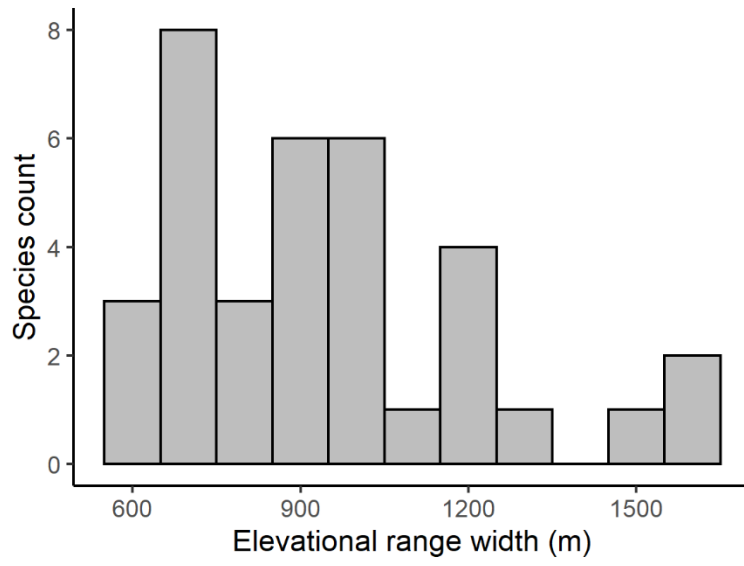
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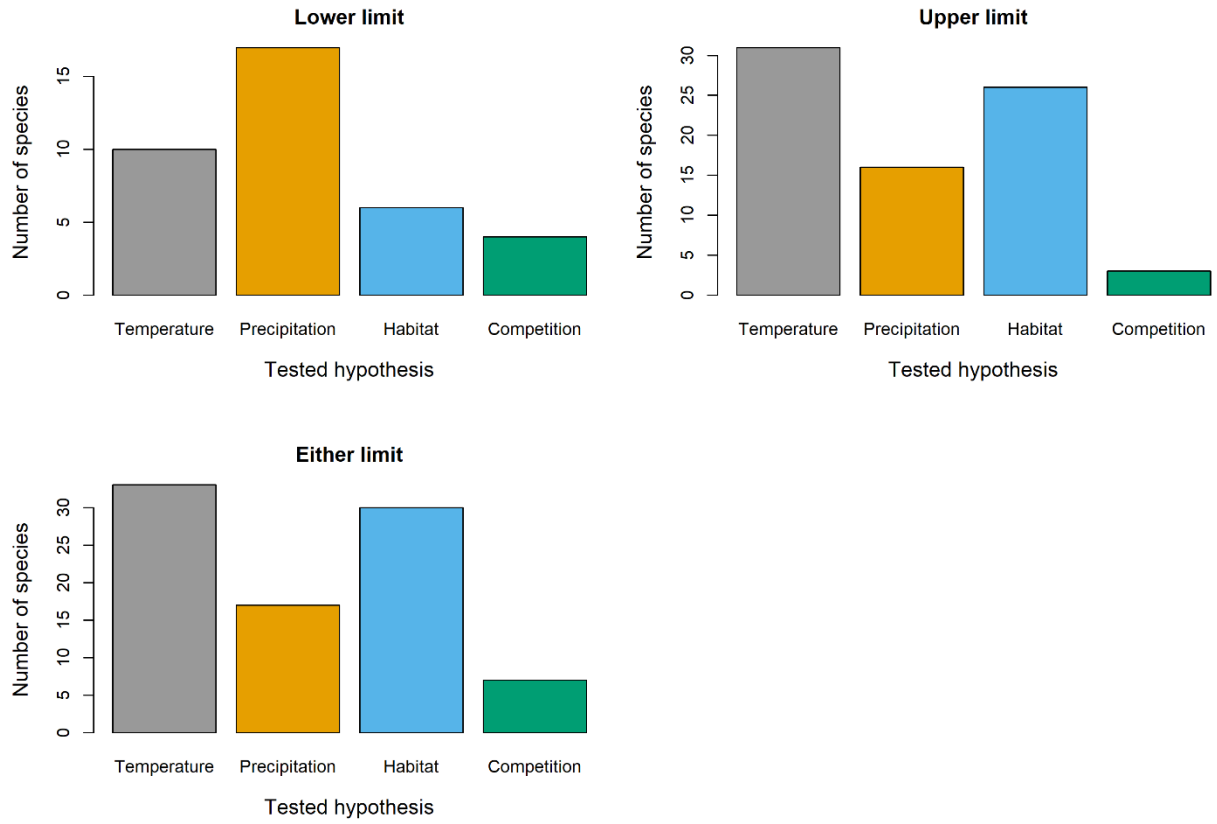
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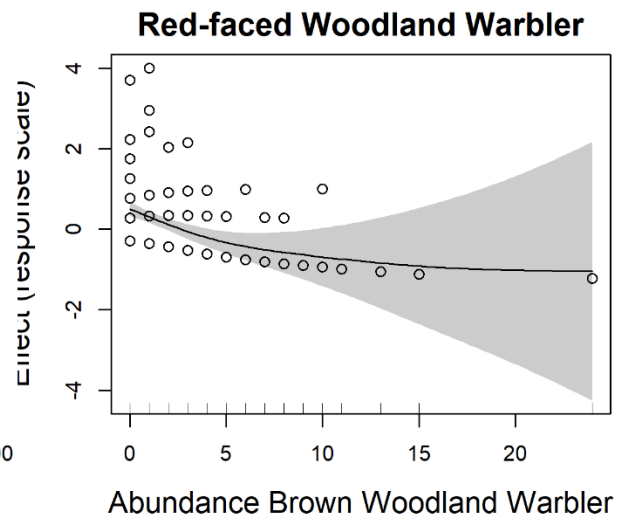
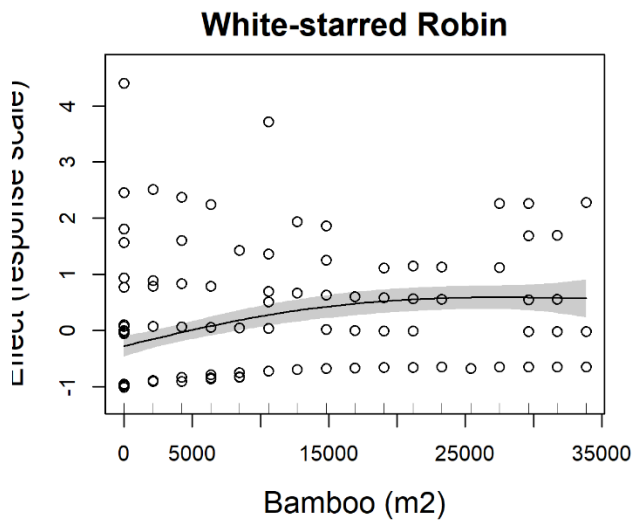
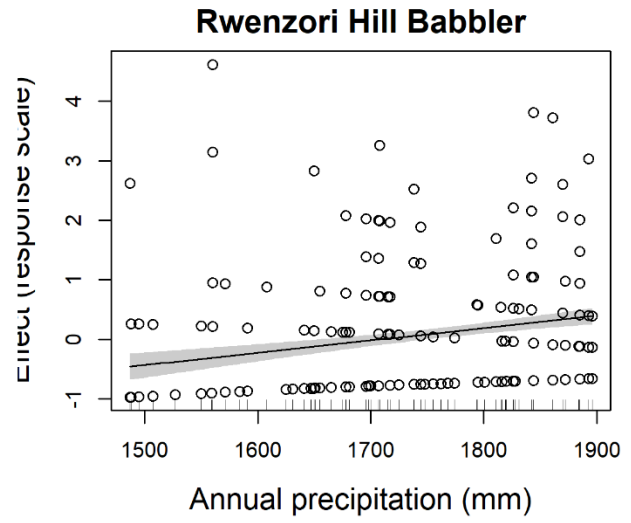
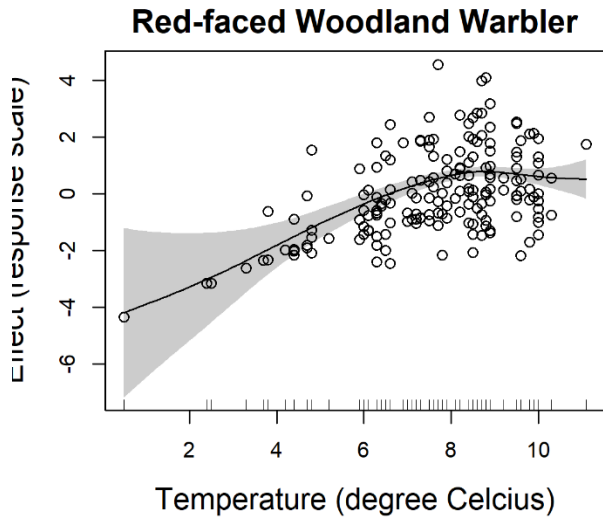
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540 Figure 5.

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794 **Supporting Information**

795 Table S1. Overview of 132 bird species recorded in Volcanoes National Park, Rwanda, and their  
796 elevational distributions, elevational and habitat preferences, and whether the study area  
797 contained congeneric species. Included are also miscellaneous data on dietary guild, the  
798 inclusion of each species in statistical analyses ('subset'), and the status as Albertine Rift  
799 Endemic (ARE) or globally threatened species (following IUCN categories), and the presence of  
800 a given species in plots in the ~3 km 'buffer' downslope from the park's boundaries.

801 Table S2. Interpretation of Generalized Additive Models for 35 bird species with at least one  
802 significant negative relationship between abundance one of the biotic (habitat availability,  
803 competition) or abiotic (temperature, precipitation) at lower or upper range limits.

804 Table S3. Overview of raw output of Generalized Additive Models of abundance for 35 bird  
805 species.

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