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

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ABSTRACT

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

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], reference number [reference number].

KEYWORDS

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

1. INTRODUCTION

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

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

Most studies on bird elevational distributions in Afrotropical mountains have focused on bird communities at relatively low elevations (~<3000 m a.s.l.) or those that occur within a single habitat type (e.g., mid-elevation to montane forests; Dulle et al., 2016; Hanz et al., 2019; Hořák et al., 2019; Neate-Clegg et al., 2020, 2021b). The literature suggests that, at these lower elevations, bird species distribution are likely to be mainly driven by biotic interactions and habitat availability and only marginally influenced by abiotic factors (Ferger et al., 2014; Hanz et al., 2019; Hořák et al., 2019; Jankowski et al., 2009, 2013; Sam et al., 2019). Indeed, abiotic factors may only become limiting for endotherms such as birds at high elevations (Jankowski et al., 2012; Spence & Tingley, 2020; Elsen et al., 2017). Unfortunately, studies conducted at lower elevations may have been unable to assess factors influencing the upper elevational limit of species, as this limit may occur beyond the upper elevational limits of the study area (Neate-Clegg et al., 2020). Similarly, these studies may have underestimated the role of biotic factors for species occurring outside of the studied forested habitat (Dulle et al., 2016). As a result, the fact that most studies on bird elevational distributions in Afrotropical mountains have focused on lower elevations and single habitat types may have limited our understanding of the respective role of biotic and abiotic factors in driving these distributions.

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

2. METHODS

2.1. Study area

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

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

2.2. Plot selection and bird surveys

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

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

2.3. Species elevational distributions and preferences

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

We characterized species elevational preferences using indicator analyses (Leach et al., 2018). More specifically, we used the point biserial (pb) correlation index r_{pb}—recommend for abundance data (De Cáceres & Legendre, 2009; De Cáceres et al., 2010)—produced by the 'multipatt' function in the R package 'indicspecies' (De Cáceres et al., 2016) to assess whether species were preferentially associated with specific elevations. Following De Cáceres & Legendre (2009) and De Cáceres et al. (2010), we used total abundance data gathered across all years for each plot. Subsequently, we used a permutation test (9999 permutations) to compare these test variables with the distribution of statistics obtained from randomly ordered data; see De Cáceres, Legendre, and Moretti (2010) for detailed explanations of these permutation tests. We used an alpha of 0.05 to determine significant associations. We considered whether species were associated with narrow elevation bands of 300 m (e.g., 2400-2700 m), or with combinations of elevational bands (e.g., 2400-2700 m and 2700-3000 m). We refer to such elevation bands as ‘preferred elevations’.

2.4. Species habitat preferences

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

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

We used generalized additive models (GAMs) to determine whether bird species abundance is influenced by climate, habitat, or competition. We first created a set of models including all predictor variables (temperature, precipitation, habitat cover, and abundance of congenerics) as well as all possible interaction terms to check for potential concurvity—a non-linear form of multicollinearity—and spatial autocorrelation. We found no significant concurvity nor autocorrelation. Given the variable numbers of predictors associated with each driver (climate, habitat, competition), we, therefore, chose to run three distinct sets of models for each driver, with no autocorrelation term. Similar to Elsen et al. (2017), we chose simple and separate models rather than more complex multi-effects models that include all variables, to allow for accurate estimations of coefficients (see also Cade, 2015).

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

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

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

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

3. RESULTS

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

3.1. Species elevational distributions

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

Twenty-seven species showed a significant (at $p < 0.05$) preference for one elevation band (20 species) and/or a combination of elevation bands (21 species; Table 1, Table S1). All but three species—White-necked Raven *Corvus albicollis*, Cape Robin-Chat *Cossypha caffra*, and Scarlet-tufted Sunbird—were significantly associated with elevation bands that span the forest-dominated parts of the study area, below the treeline at ~3600 m.

3.2 Species habitat preferences

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

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

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

We found substantial differences between the relative importance of factors at lower and upper limits. Overall, there was a higher number of species with at least one significant predictor consistent with a constraint at upper limits (32 species) than species with significant predictors consistent with a constraint at lower limits (24). There were also differences in the relative importance of the four drivers at lower and upper limits, with precipitation being the most frequent significant predictor of lower limits (for 17 species) and temperature the main predictor of upper limits (for 31 species; Figure 4).

4. DISCUSSION

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

Many species showed a decline in abundance with a decrease in temperature at upper limits. This result is consistent with some literature highlighting that temperature may influence the upper limits of distributions of tropical species (Ghalambor et al., 2006; Janzen, 1967), but contrasts with other studies (e.g., Neate-Clegg et al., 2020). Contrasts with other studies may partially be explained by the fact that our study area included a much higher elevation range (>1000 m) than those included in many other studies of tropical avifauna (e.g., Campos-Cerqueira et al., 2017; Forero-Medina et al., 2011; Neate-Clegg et al., 2018; Neate-Clegg et al., 2020). And only at such high elevations may we find the low temperatures that can induce thermoregulatory costs (i.e., the energetic requirements to maintain body temperatures within critical limits) that affect survival or behavior (Londoño et al., 2017).

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

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

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

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

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

Our analyses provide baseline data on elevational distributions of Afromontane birds (similar to e.g., Kittelberger et al., 2021) that hint at elevational zonation driven by a complex and species-specific combination of biotic and abiotic factors. We note that we looked at changes in abundances within a predefined elevational range and that the elevational distribution of some species extends below the park boundaries. As such, we caution that the estimated range limits only apply within the context of VNP, and that most of our focal species are also found outside the park at lower elevations (see Table S1). Our approach was also correlative, which does not imply that drivers significantly associated with declines in species' abundances were also causal to elevational limits. Many confounding, interacting, and partially multicollinear effects could also play a role in shaping observed correlations. For example, although a test for concurvity showed no significant correlation between the four variables tested in our separate models, they may have

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

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

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

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AUTHOR CONTRIBUTIONS

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

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

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

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

Figure legends.

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

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

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

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

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

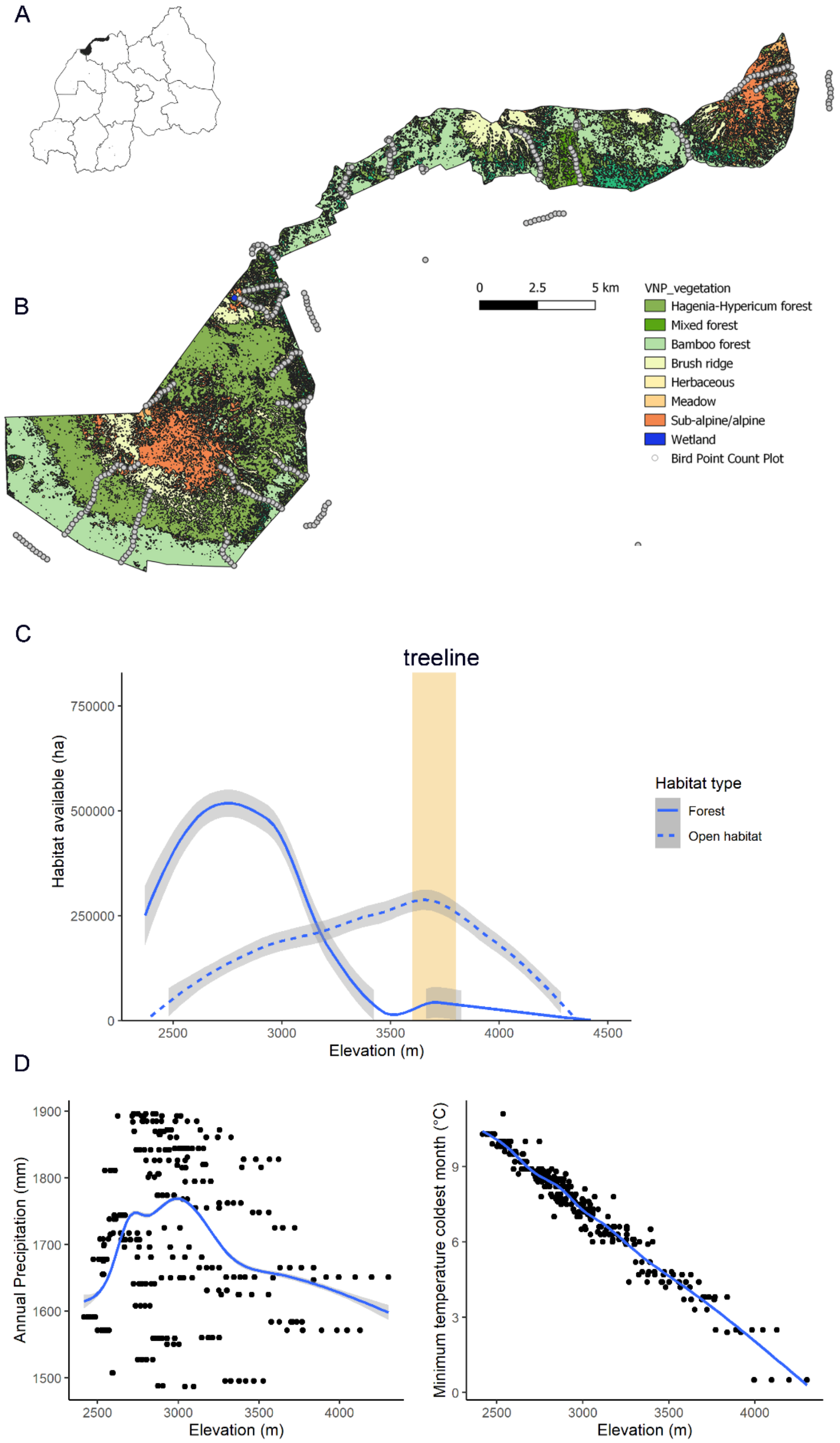
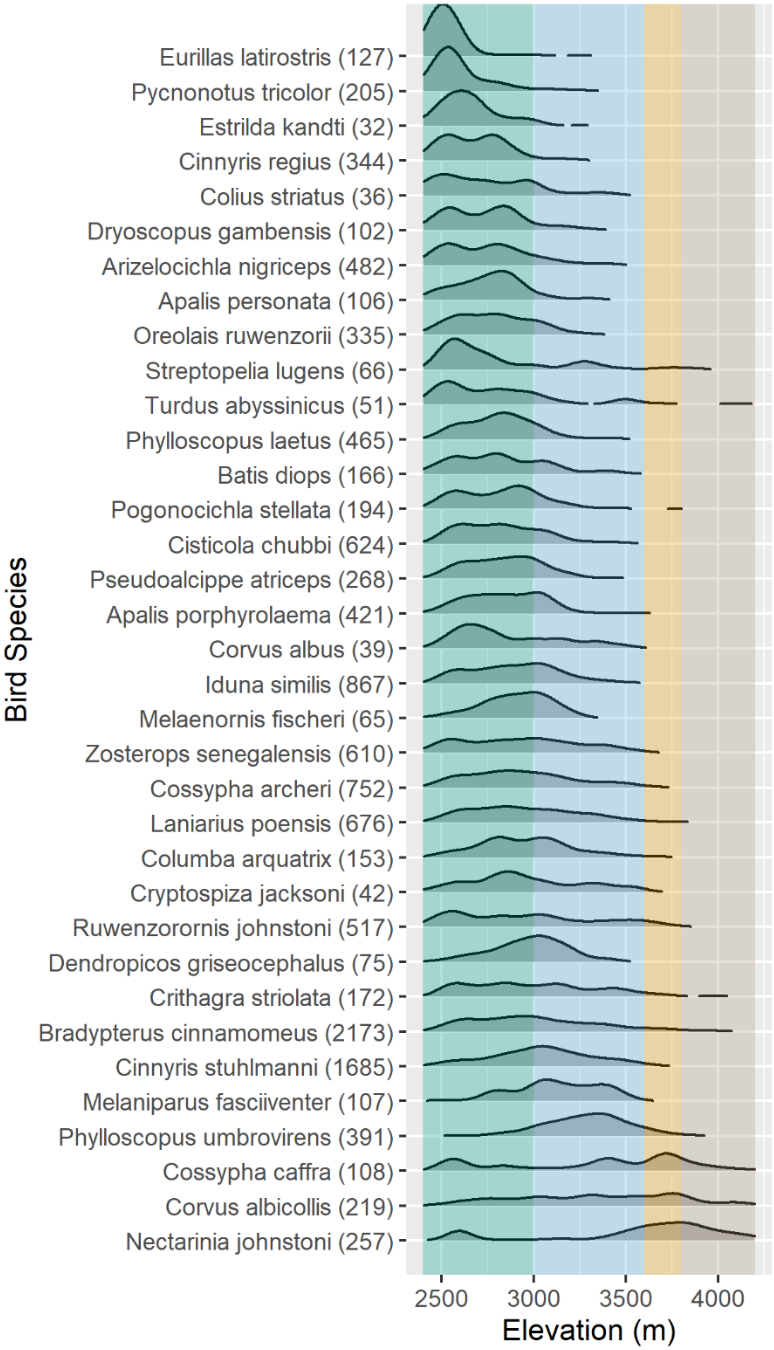

A
B
0
2.5
5 km
VNP_vegetation
Hagenia-Hypericum forest
Mixed forest
Bamboo forest
Brush ridge
Herbaceous
Meadow
Sub-alpine/alpine
Wetland
Bird Point Count Plot
C
treeline
Habitat available (ha)
750000
500000
250000
0
2500
3000
3500
4000
4500
Elevation (m)
Habitat type
Forest
Open habitat
D
Annual Precipitation (mm)
1900
1800
1700
1600
1500
2500
3000
3500
4000
Elevation (m)
Minimum temperature coldest month (°C)
9
6
3
0
2500
3000
3500
4000
Elevation (m)

Figure 1.



Eurillas latirostris (127)
Pycnonotus tricolor (205)
Estrilda kandti (32)
Cinnyris regius (344)
Colius striatus (36)
Dryoscopus gambensis (102)
Arizelocichla nigriceps (482)
Apalis personata (106)
Oreolais ruwenzorii (335)
Streptopelia lugens (66)
Turdus abyssinicus (51)
Phylloscopus laetus (465)
Batis diops (166)
Pogonocichla stellata (194)
Cisticola chubbi (624)
Pseudoalcippe atriceps (268)
Apalis porphyrolaema (421)
Corvus albus (39)
Iduna similis (867)
Melaenornis fischeri (65)
Zosterops senegalensis (610)
Cossypha archeri (752)
Laniarius poensis (676)
Columba arquatrix (153)
Cryptospiza jacksoni (42)
Ruwenzorornis johnstoni (517)
Dendropicos griseocephalus (75)
Crithagra striolata (172)
Bradypterus cinnamomeus (2173)
Cinnyris stuhlmanni (1685)
Melaniparus fasciiventer (107)
Phylloscopus umbrovirens (391)
Cossypha caffra (108)
Corvus albicollis (219)
Nectarinia johnstoni (257)
Bird Species
2500
3000
3500
4000
Elevation (m)

Figure 2.

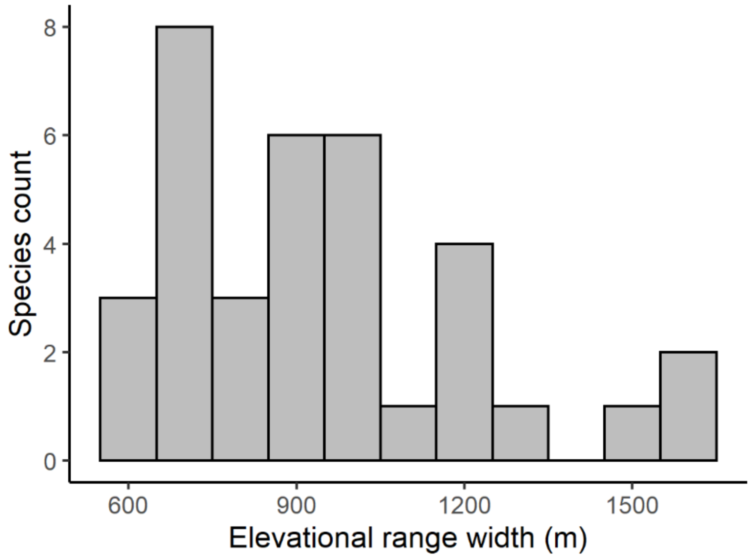

Species count
8
6
4
2
0
600
900
1200
1500
Elevational range width (m)

Figure 3.

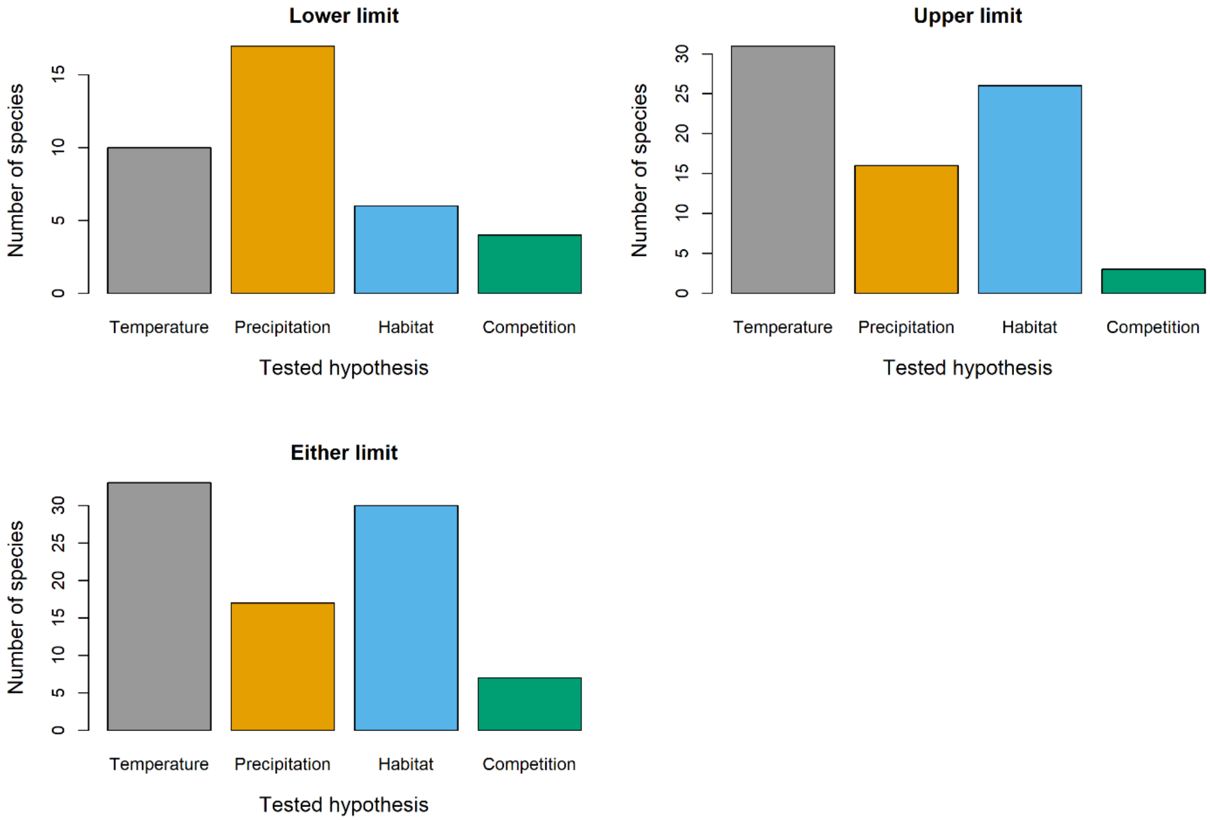

Lower limit
Number of species
0
5
10
15
Temperature
Precipitation
Habitat
Competition
Tested hypothesis
Upper limit
Number of species
0
5
10
15
20
25
30
Temperature
Precipitation
Habitat
Competition
Tested hypothesis
Either limit
Number of species
0
5
10
15
20
25
30
Temperature
Precipitation
Habitat
Competition
Tested hypothesis

Figure 4.

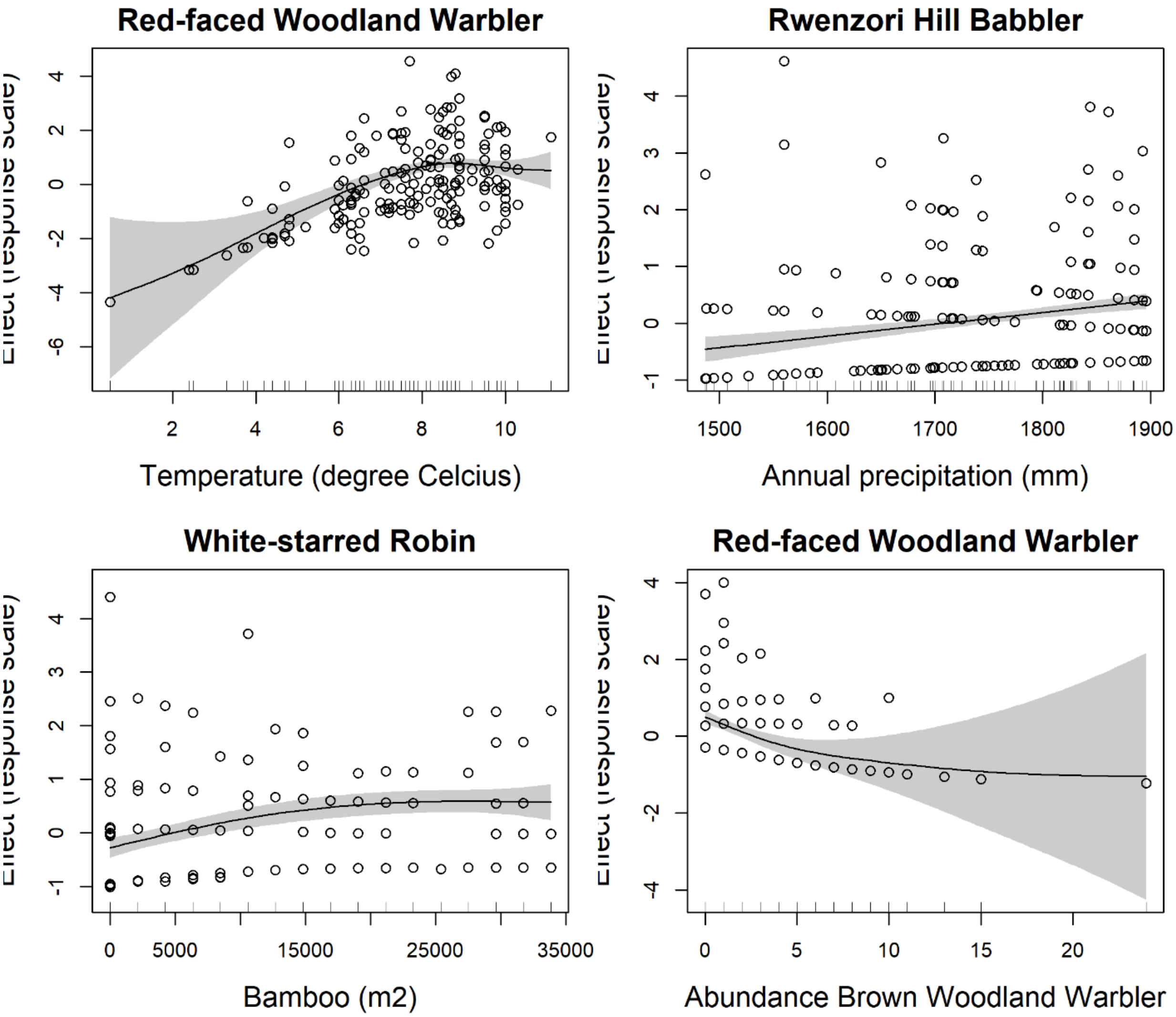

Red-faced Woodland Warbler
Temperature (degree Celcius)
2
4
6
8
10
4
2
0
-2
-4
-6
Rwenzori Hill Babbler
Annual precipitation (mm)
1500
1600
1700
1800
1900
4
3
2
1
0
-1
White-starred Robin
Bamboo (m2)
0
5000
15000
25000
35000
4
3
2
1
0
-1
Red-faced Woodland Warbler
Abundance Brown Woodland Warbler
0
5
10
15
20
4
2
0
-2
-4

Figure 5.

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Supporting Information

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

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

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