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A disconnect between upslope shifts and climate change in an Afrotropical bird community

Montague H. C. Neate-Clegg[1] | **Timothy G. O'Brien**[2] | **Felix Mulindahabi**[3] | **Çağan Hakkı Şekercioğlu**[1,4]

[1]School of Biological Sciences, University of Utah, Salt Lake City, Utah

[2]Wildlife Conservation Society, Global Programs, New York, New York

[3]Wildlife Conservation Society, Rwanda Program, Kigali, Rwanda

[4]Faculty of Sciences, Koç University, Istanbul, Turkey

Correspondence
Montague H. C. Neate-Clegg, School of Biological Sciences, University of Utah, 257 S 1400 E, Salt Lake City, UT 84112.
Email: monte.neate-clegg@utah.edu

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Abstract

Climate change threatens to push species to higher elevations and eventual extinction. Birds, in particular, are shown to be shifting upslope in the Neotropics and Southeast Asia. Yet previous studies have lacked the temporal resolution to investigate distributional dynamics over time in relation to climatic fluctuations, especially in the understudied Afrotropics. Here, we used 15 years of point-count data from across an elevational gradient (1,767–2,940 m) in Rwanda, to assess elevational shift rates and dynamics in a community of Afrotropical birds. In general, species shifted their elevations upslope by 1.9 m/year, especially at their lower elevational limits which shifted by 4.4 m/year. Importantly, these shifts occurred despite the fact that local temperature and precipitation showed little trend over the study period. Moreover, the interannual distributions of few species were associated with temperature, suggesting that temperature played little direct role in determining elevational distributions of birds. Instead, upslope shifts may be more related to incremental shifts in habitat and resources which lag behind decades of increased temperature in the region. Precipitation appeared to have more of an effect than temperature in determining interannual elevational changes, allowing species to expand their ranges in years of higher rainfall. Our results highlight the need to understand the mechanisms driving upslope shifts as they occur throughout the tropics. It will be critical for montane regions of the tropics to preserve contiguous blocks of forest across elevational gradients to allow wildlife to shift unimpeded.

KEYWORDS

Albertine Rift, elevation dynamics, precipitation, range limits, temperature

1 | INTRODUCTION

Global climate change is causing populations to move in order to track shifting climatic envelopes (Chen, Hill, Ohlemüller, Roy, & Thomas, 2011; Parmesan, 2006). Most documented shifts have been poleward movements at higher latitudes. In the understudied tropics (Harris et al., 2011), where the majority of biodiversity is found

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(Myers, Mittermeier, Mittermeier, da Fonseca, & Kent, 2000), elevational temperature gradients are much more pronounced than latitudinal gradients (Colwell, Brehm, Cardelús, Gilman, & Longino, 2008) and species are predicted to shift their distributions upslope to track rising temperature envelopes (Forero-Medina, Joppa, & Pimm, 2011; Şekercioğlu, Schneider, Fay, & Loarie, 2008). Ectotherms shift predictably to higher elevations with climate warming (Chen et al., 2009) as they are highly sensitive to temperature change (Deutsch et al., 2008; Dillon, Wang, & Huey, 2010). However, endotherms, particularly birds, have also been shown to shift upslope (Freeman & Class Freeman, 2014; Freeman, Scholer, Ruiz-Gutierrez, & Fitzpatrick, 2018; Neate-Clegg, Jones, Burdekin, Jocque, & Şekercioğlu, 2018) despite the fact that thermal physiological tolerance does not appear to limit tropical birds' elevational distributions (Freeman, 2016; Londoño, Chappell, Jankowski, & Robinson, 2017). Instead, the distributions of tropical birds seem to be constrained more by biotic interactions (Jankowski, Londoño, Robinson, & Chappell, 2012) including habitat (Jankowski et al., 2013), natural enemies (Paxton et al., 2016) and interspecific competition (Freeman, Class Freeman, & Hochachka, 2016; Jankowski, Robinson, & Levey, 2010).

If populations were to respond acutely to climatic fluctuations, then one would expect elevational ranges to shift up and down in tandem with the climate. However, if populations are constrained by biotic factors (Ferger, Schleuning, Hemp, Howell, & Böhning-Gaese, 2014) that change more slowly, such as habitat and resource availability (Elsen, Tingley, Kalyanaraman, Ramesh, & Wilcove, 2017; Jankowski et al., 2013), one would expect shift rates to be more incremental. Previous research has been constrained by a lack of temporal resolution. Studies which resurvey an elevational gradient multiple decades after initial surveys (Forero-Medina, Terborgh, Socolar, & Pimm, 2011; Freeman & Class Freeman, 2014; Freeman, Scholer, et al., 2018) may cover long time periods (during which large shifts can be detected) but cannot elucidate the interannual dynamics of distributions. Long-term, ideally annual, monitoring datasets are needed to assess elevation dynamics, but these datasets are rare in the tropics (Wormworth & Şekercioğlu, 2011).

In this study, we utilized a 15-year dataset of bird point counts along an elevational gradient in the Afrotropics to estimate changes in the distributions of bird populations over time and in relation to interannual fluctuations in temperature and precipitation. Elevational gradients in the Afrotropics are particularly understudied compared to the Neotropics (Forero-Medina, Terborgh, et al., 2011; Freeman, Scholer, et al., 2018; Neate-Clegg et al., 2018) and Southeast Asia (Boyce, Freeman, Mitchell, & Martin, 2015; Freeman & Class Freeman, 2014; Peh, 2007), making this one of the first investigations into observed shift rates in this biogeographical realm (but see Dulle et al., 2016; van der Hoek, Faida, Musemakweli, & Tuyisingize, 2020). Here, we investigated whether 51 bird species have (a) shifted their mean elevation over time, (b) shifted their elevational range limits over time, (c) shifted their elevation in relation to temperature and precipitation, and (d) whether shift rates were associated with key ecological traits.

2 | METHODS

2.1 | Study site and climate

The study took place in Nyungwe National Park (NNP) in southwestern Rwanda (2°15′–2°55′ S, 29°00′–29°30 E). NNP is located within the Albertine Rift, one of the most biodiverse regions in Africa (Plumptre et al., 2007). The park covers an area of 1,019 km^2 and spans an elevational gradient of 1,350 m (1,600–2,950 m). Together with Kibira National Park in Burundi (400 km^2), NNP forms one of the largest continuous blocks of montane forest in Africa (Vedder, Hall, Harcourt, Monfort, & Wilson, 1992). The habitat in NNP is largely undisturbed, closed-canopy rainforest, dominated by large fruiting and flowering trees. The park has a rich avifauna totaling 295 species, including 26 Albertine Rift endemics (Plumptre et al., 2007) and 15 species either threatened with extinction or near threatened (Birdlife International, 2020). Little deforestation has taken place in NNP. Between 2001 and 2011, forest loss (where forest is classified as >50% tree cover density) averaged 38.6 ha per year (Table S1) amounting to 0.42% forest loss in 11 years (data are unavailable prior to 2001), most of which occurred around the periphery of the park (Hansen et al., 2013; WCS, 2019). Additionally, there were 171 ha of forest gain between 2000 and 2012. Forest fires are a major risk to NNP (Masozera, 2007), with large burns occurring in the west of the park in 1997–1998 and 2000–2001. However, fires have not occurred around the monitoring area covered by our dataset (Mulindahabi in litt.).

The climate in NNP is characterized by an 8.5-month wet season which lasts from the beginning of September through mid-May. Temperatures are relatively cool, ranging between an average minimum of 10.9°C and an average maximum of 19.6°C (Sun et al., 1996). At the main research station in Uwinka, a thermometer (placed under the eaves of a cabin) and a rain gauge (placed in the open) recorded daily mean temperature and total precipitation throughout the study period. From these data, we calculated yearly mean temperature (°C) and yearly total

precipitation (mm). Insufficient data were gathered in 2001 and 2011 to calculate yearly data. We used annual climate values rather than higher-resolution climate date (e.g., seasonal) because our investigation focused on interannual changes in elevation rather than seasonal movements or movements in relation to short, but extreme weather events. To include seasonal variation in climate values would potentially lead to a stronger climate signal in elevation driven by seasonality which could mask weaker interannual climate signals.

2.2 | Bird surveys

In 1997, the Projet Conservation de la Forêt Nyungwe began a bird monitoring program in NNP (Plumptre et al., 2002). The project chose 10 transects located in the northeast section of the park (seven transects in the area of Uwinka and three in the area of Gisakura; Plumptre et al., 2002) that together covered most of the elevational gradient of the park (1,767–2,940 m). Transects averaged 2.54 km in length (1.3–4.5 km) with survey sites located at 100 m intervals, totaling 264 sites. The sites were used to conduct unlimited radius point counts (Ralph, Sauer, & Droege, 1995), performed by two trained bird-monitoring technicians. Each point count comprised a 2-min settlement period followed by 10 min of surveying (Lynch, 1995) wherein all detections of birds both aural and visual were recorded. Surveys were conducted from 1997 to 2011 but no surveys were conducted in 2007. Survey effort varied over the study period, beginning with monthly surveys of each transect and ending with one-to-two surveys per year as a reduced budget precluded more extensive effort. Surveys were always evenly distributed across the year.

2.3 | Analysis

We restricted the analysis to species detected at least three times in every year (Table 1). We characterized elevational distributions with three metrics: the mean elevation (weighted by the number of detections at each site), lower limit, and upper limit. The lower and upper limits were calculated as the 2.5% and 97.5% percentiles of elevational distribution (i.e., the 95% range limits, hereafter "range limits") and were used instead of minimum and maximum values because percentiles take all of the data into account. To control for the fact that the distribution and detectability of species may vary seasonally (Loiselle & Blake, 1991), we included season in the dataset, wet vs dry, where the wet season spanned September 1–May 15 and the dry season spanned May 16–August 31. We calculated mean elevation and range limits for both seasons of each year. Some sites were surveyed more than others in early years, creating elevational bias in the mean elevation of point counts over time. Additionally, for some transects (which happened to be at higher elevations) only half the sites were surveyed in 2008 and 2009, creating elevational bias toward lower elevations in those years. To correct for these biases, we calculated the mean elevation at which sites were surveyed in a given season and year and subtracted this value from the mean and range limits of species' distributions. Thus, species' distributions were characterized relative to the mean elevation of point counts in a given year.

We regressed each of the three elevational metrics in a linear mixed model against year, yearly mean temperature and yearly total precipitation, with season (wet/dry) as a random slope effect. Including both a year covariate and climate covariates in the same model allowed us to test for both linear changes in elevational position over time as well as interannual variation in elevation in relation to climate fluctuations. We extracted the coefficients and confidence intervals of the fixed effects from the models. Coefficients were deemed significant if the confidence intervals on the coefficient did not overlap 0.

We assessed the role of ecological traits in determining elevational movements across species (Forero-Medina, Terborgh, et al., 2011; Freeman & Class Freeman, 2014; Freeman, Scholer, et al., 2018) using species-specific ecological covariates (Table 1) in linear mixed models. These ecological data were taken from BirdBase, a dataset of ecological traits for the world's birds (for a description, see Şekercioğlu et al., 2019). We initially investigated six traits but narrowed them down to three based on collinearity: natural logarithm of mass (log[mass]), habitat breadth (which was positively correlated with elevational range, Pearson's $r = .52$, and negatively correlated with elevational midpoint, Pearson's $r = -.46$) and diet breadth (species with narrow diet breadths tended to be insectivores). Habitat breadth is a count of how many different habitat types a species can be found in (14 categories such as forest, woodland, savannah, etc.) while diet breadth is a count of how many different food groups a species eats (eight categories such as invertebrates, fruit, seed, etc.). We created three full models where the coefficients for year, temperature, and precipitation from the previous analysis acted as the response variables and the ecological traits acted as the explanatory variables. We also added elevational metric (mean elevation, lower limit, or upper limit) as a fixed effect which interacted with the other three covariates. Response rates were nested within species and then within taxonomic family in the mixed models to account for phylogenetic relationships.

TABLE 1 Fifty-one Afrotropical bird species used in the analyses that were detected during point counts over 15 years in Nyungwe National Park. Every species was detected at least three times in every year. Traits marked with an asterisk were used in linear mixed models

Binomial name	English name	Total detected	Mass (g)*	Elevational range (m)	Elevational midpoint (m)	Habitat breadth*	Dietary breadth*	Primary diet
Columba arquatrix	African olive-pigeon	424	352.75	1,800	2,300	2	3	Fruit
Turtur tympanistria	Tambourine dove	626	63.93	3,200	1,600	6	3	Omnivore
Cercococcyx montanus	Barred long-tailed cuckoo	1,633	54.00	2,800	1,400	5	1	Invertebrate
Corythaeola cristata	Great blue turaco	1,796	923.67	2,700	1,350	2	3	Fruit
Ruwenzorornis johnstoni	Rwenzori turaco	2,133	239.00	1,600	2,800	1	3	Fruit
Tauraco schuettii	Black-billed turaco	1,856	229.00	2,300	1,650	1	1	Fruit
Apaloderma vittatum	Bar-tailed trogon	378	55.00	1,400	2,300	2	1	Invertebrate
Bycanistes subcylindricus	Grey-cheeked hornbill	506	1,213.25	2,600	1,300	3	3	Fruit
Phoeniculus bollei	White-headed woodhoopoe	1,513	56.50	3,200	1,600	5	3	Invertebrate
Pogoniulus bilineatus	Yellow-rumped tinkerbird	2,691	14.80	3,000	1,500	3	2	Fruit
Oriolus percivali	Mountain oriole	1,987	37.50	920	1,990	3	2	Fruit
Batis diops	Rwenzori batis	1,180	12.38	1,700	2,450	2	1	Invertebrate
Laniarius holomelas	Albertine sooty boubou	3,191	38.00	2,385	2,192.5	4	2	Invertebrate
Terpsiphone viridis	African paradise-flycatcher	882	13.43	2,500	1,250	6	1	Invertebrate
Melaniparus fasciiventer	Stripe-breasted tit	234	14.50	1,600	2,600	2	1	Invertebrate
Graueria vittata	Grauer's warbler	964	16.33	700	1,950	3	1	Invertebrate
Oreolais ruwenzorii	Rwenzori apalis	3,650	10.25	1,550	2,325	2	1	Invertebrate
Apalis personata	Black-faced apalis	6,155	10.67	1,300	2,150	3	1	Invertebrate
Apalis jacksoni	Black-throated apalis	2,419	7.67	1,500	1,750	2	1	Invertebrate
Apalis porphyrolaema	Chestnut-throated apalis	2,441	8.75	1,800	2,500	3	1	Invertebrate
Apalis cinerea	Grey apalis	719	9.75	2,150	1,925	4	1	Invertebrate
Cisticola chubbi	Chubb's cisticola	2,776	16.00	2,500	2,100	5	1	Invertebrate
Bathmocercus rufus	Black-faced rufous-warbler	590	14.50	2,030	1,385	3	1	Invertebrate
Prinia bairdii	Banded prinia	2,769	13.48	1,500	2,250	3	1	Invertebrate
Iduna similis	Mountain yellow warbler	427	11.75	1,850	2,775	4	1	Invertebrate
Bradypterus cinnamomeus	Cinnamon bracken-warbler	2,689	18.88	2,580	2,810	4	1	Invertebrate
Psalidoprocne pristoptera	Black saw-wing	506	11.55	1,000	500	7	1	Invertebrate
Arizelocichla nigriceps	Eastern mountain greenbul	3,337	32.88	1,650	2,175	3	2	Invertebrate
Eurillas latirostris	Yellow-whiskered greenbul	6,176	28.50	2,000	1,000	5	3	Fruit
Phyllastrephus flavostriatus	Yellow-streaked greenbul	3,691	32.50	3,000	1,500	3	1	Invertebrate
Pycnonotus barbatus	Common bulbul	408	37.63	2,500	1,250	7	3	Fruit
Phylloscopus laetus	Red-faced woodland-warbler	4,122	9.63	1,620	2,310	2	1	Invertebrate
Urosphena neumanni	Neumann's warbler	1,647	14.08	1,150	1,775	2	1	Invertebrate
Sylvia atriceps	Rwenzori hill-babbler	1,186	19.05	2,300	2,050	3	3	Invertebrate
Zosterops senegalensis	African yellow white-eye	2,501	9.83	3,400	1,700	8	3	Invertebrate
Illadopsis pyrrhoptera	Mountain illadopsis	1,131	24.50	1,660	1,970	3	3	Invertebrate
Turdoides rufocinctus	Red-collared mountain-babbler	546	47.00	1,080	2,230	1	1	Invertebrate
Onychognathus walleri	Waller's starling	2,931	86.00	2,000	2,000	2	3	Fruit
Turdus abyssinicus	Abyssinian thrush	189	68.00	3,250	2,575	5	2	Invertebrate
Muscicapa adusta	African dusky flycatcher	320	11.03	3,700	1,850	4	1	Invertebrate
Melaenornis ardesiacus	Yellow-eyed black-flycatcher	430	31.10	1,000	1,800	2	1	Invertebrate
Cossypha archeri	Archer's robin-chat	1,192	23.00	2,700	2,950	3	1	Invertebrate

TABLE 1 (Continued)

Binomial name	English name	Total detected	Mass (g)*	Elevational range (m)	Elevational midpoint (m)	Habitat breadth*	Dietary breadth*	Primary diet
Pogonocichla stellata	White-starred robin	346	21.25	1,700	2,450	3	2	Invertebrate
Chamaetylas poliophrys	Red-throated alethe	545	38.33	1,700	2,150	2	1	Invertebrate
Sheppardia aequatorialis	Equatorial akalat	339	14.50	1,400	1,800	1	1	Invertebrate
Kakamega poliothorax	Grey-chested Kakamega	848	37.15	1,450	1,925	3	1	Invertebrate
Hedydipna collaris	Collared sunbird	652	7.85	2,600	1,300	7	4	Invertebrate
Cyanomitra alinae	Blue-headed sunbird	1,793	12.67	1,880	2,340	3	2	Invertebrate
Cyanomitra olivacea	Olive sunbird	302	9.05	1,850	925	4	3	Invertebrate
Cinnyris regius	Regal sunbird	3,638	6.38	1,600	2,300	2	2	Nectar
Ploceus alienus	Strange weaver	293	22.20	1,200	2,100	1	3	Invertebrate

We used stepwise AIC-based model selection to find the best model from the full model. All analyses were carried out in R version 3.2.4 (R Core Team, 2020). For linear mixed models, we used the function "lme" from the package *nlme* (Pinheiro, Bates, DebRoy, & Sarkar, 2013) and for stepwise AIC model selection, we used the function "stepAIC" from the package *MASS* (Venables & Ripley, 2013).

3 | RESULTS

Of 207 species detected, we had sufficient data to estimate the shift rates of 51 species (Table 1). These species shifted their mean elevations upslope by an average of 1.87 ± 1.41 m/year (mean ± CI; Figure 1; Table S2). Eight species significantly shifted their mean elevation upslope by an average of 8.38 ± 1.66 m/year while no species significantly shifted downslope. On average, lower elevational limits across species shifted upslope by 4.41 ± 2.02 m/year (Figure 1; Table S2). Seven species significantly shifted their lower limits upslope, by an average of 17.12 ± 8.64 m/year, compared to just one species which shifted downslope by 2.44 m/year. On average, upper elevational limits across species shifted downslope by 3.06 ± 2.54 m/year (Figure 1). Only two species significantly shifted their upper limits upslope, by an average of 14.59 ± 15.95 m/year, while three species shifted downslope by 20.80 ± 8.92 m/year. Three species expanded their range (two upslope and one downslope) while 10 species contracted their range (seven upslope and three downslope). No species shifted both range limits in one direction.

Temperature (−0.05 ± 0.05°C/year; $t = -1.99$, $p = .07$) and precipitation (+19.41 ± 39.02 mm/year; $t = 0.98$, $p = .35$) did not change significantly over time (Figure 2).

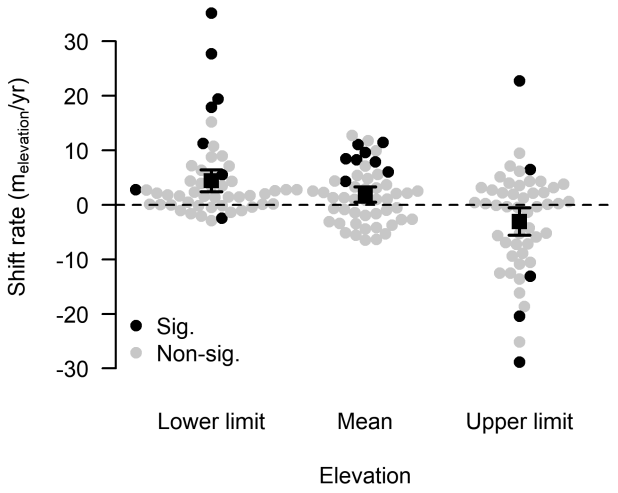


FIGURE 1 Shift rates in the mean elevation, and lower and upper range limits (95% limits) of 51 Afrotropical bird species over 15 years in Nyungwe National Park, Rwanda. Also displayed are the mean and 95% confidence intervals (black squares and bars) of the shift rates across species

Temperature tended to have little association with species' elevations (Table S2), except at lower elevational limits, which shifted downslope in warmer years (−14.22 ± 11.57 m/°C). Six species showed a significant negative association with temperature (Figure 3a), shifting their lower limits downslope in warmer years. Precipitation had a contrasting association with range limits (Table S2) whereby increased precipitation was associated with downslope shifts in lower limits (−0.32 ± 0.24 $m_{elevation}/cm_{rain}$) but upslope shifts in upper limits (+0.42 ± 0.21 $m_{elevation}/cm_{rain}$; Figure 3b).

After stepwise AIC-based model selection, the model of year coefficients with the lowest AIC contained two explanatory variables: log(mass) and elevational metric. Yearly shift rates were negatively associated with mass

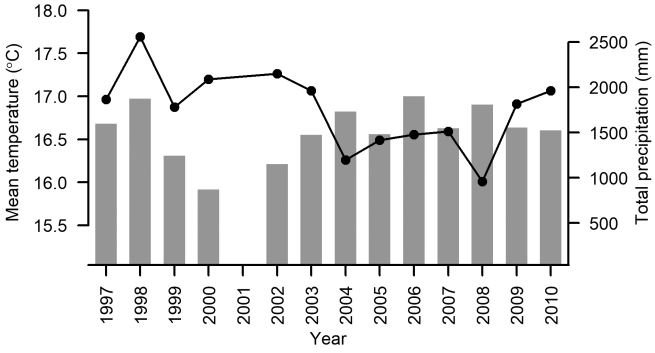


FIGURE 2 The dynamics of yearly mean temperature (°C) and total precipitation (mm) between 1997 and 2010 in Nyungwe National Park, Rwanda. Insufficient data were available for 2001 and 2011

(Table S3) such that smaller-bodied species tended to shift their lower limits upslope while large-bodied species tended to shift their upper limits downslope (Figure 4a). Elevational response rates to temperature were again associated with log(mass) but this relationship depended on the elevational metric (Table S3). Larger-bodied species tended to expand their upper and lower limits in years of higher temperature (Figure 4b). Finally, elevational response rates to precipitation were associated with dietary breadth, depending on the elevational metric (Table S3). Species with more specialized diets tended to expand their upper and lower limits in years of high precipitation (Figure 4c).

4 | DISCUSSION

Tropical bird communities have been documented shifting upslope in Southeast Asia (Freeman & Class Freeman, 2014) and the Neotropics (Forero-Medina, Joppa, & Pimm, 2011; Freeman, Scholer, et al., 2018; Neate-Clegg et al., 2018) but few studies have focused on Afrotropical birds (Dulle et al., 2016; van der Hoek et al., 2020). In this study, we found that a bird community within the Albertine Rift shifted its mean elevation upslope by 1.87 m per year, a rate slightly greater than that found in similar studies (Forero-Medina, Terborgh, et al., 2011; Freeman, Scholer, et al., 2018) and amounting to 28 m over the 15-year study period. Only 16% of species showed a significant shift in mean elevation (Figure 1) but all of these shifted upslope (by an average of 126 m over 15 years), which is the expected direction under climate warming (Şekercioğlu et al., 2008). Across species, the shift rate was much greater for lower elevational limits (Figure 1), which moved upslope by an average of 66 m over 15 years, with 14% of species significantly shifting their lower limits upslope. Freeman, Scholer, et al. (2018) also found the shift rates of lower limits to be greater than that of mean elevations.

Shifts in the lower elevational limits of tropical birds could be linked to changes in land use at lower elevations (Harris et al., 2014; Neate-Clegg et al., 2018). Yet there has been minimal deforestation (0.42%) within NNP between 2001 and 2011 (Table S1) and most of this occurred around the fringes of the park (Hansen et al., 2013; WCS, 2019), far from the transects. We thus do not believe that deforestation contributed to the observed trends. Similarly, although forest fires did affect the western arm of the park in the late 1990s and early 2000s, they did not occur near the transects and burnt areas were distributed over higher elevations of the park (Mulindahabi in litt.) so should not have reduced abundance at lower elevations. We have no

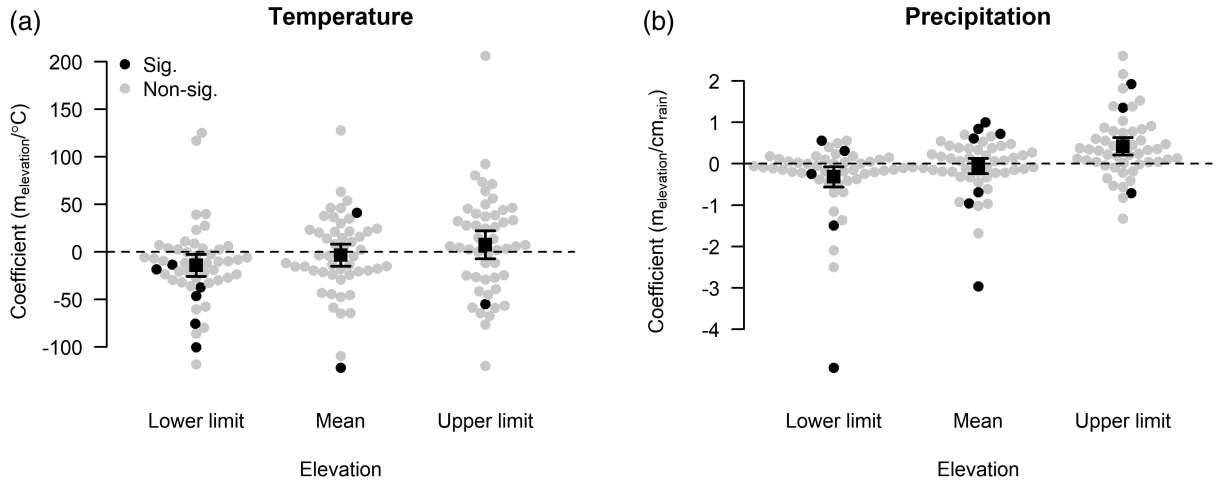


FIGURE 3 Response rates of mean elevation and range limits to temperature and precipitation for 51 Afrotropical bird species over 15 years in Nyungwe National Park, Rwanda. Plots show the effect of (a) yearly mean temperature and (b) yearly total precipitation on the three elevational metrics. Also displayed are the mean and 95% confidence intervals (black squares and bars) of the response rates across species

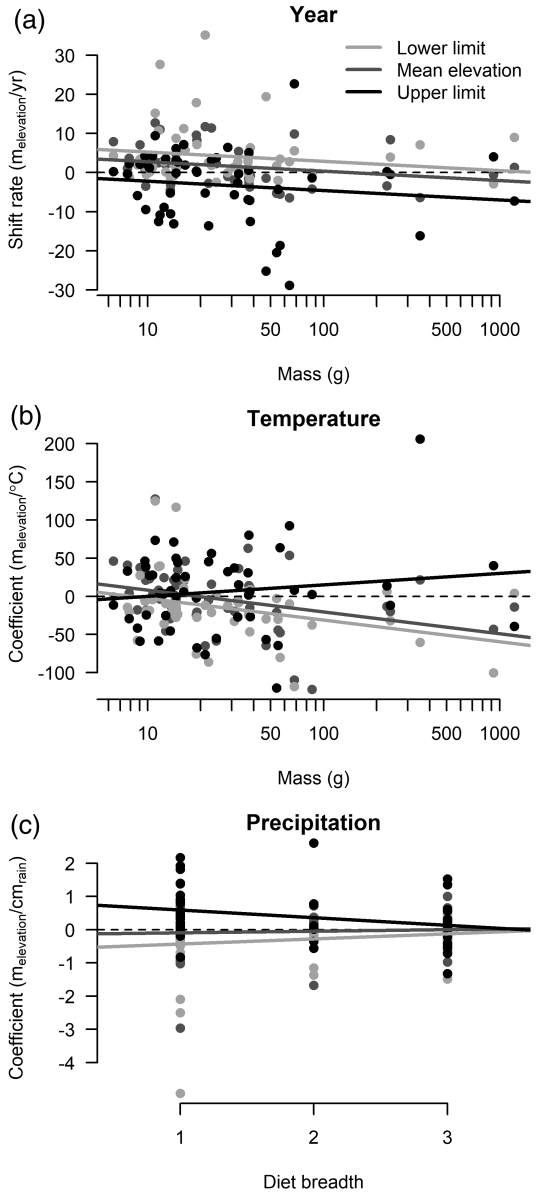


FIGURE 4 The associations between species-specific ecological traits and elevational movements for 51 Afrotropical bird species over 15 years in Nyungwe National Park, Rwanda. Plot (a) shows the relationship between mass and elevational shift rate over time. Plot (b) shows the relationship between mass and elevational responses to yearly mean temperature. Plot (c) shows the relationship between diet breadth and elevational responses to yearly total precipitation

evidence to suggest that the fires affected bird densities on our transects.

At species' range boundaries we found that lower limits moved upslope, as predicted, but that upper limits did not. NNP does not exceed 3,000 m in elevation, with the highest survey site at 2,940 m and the vast majority of the park below 2,600 m. It is therefore probable that many species cannot expand their upper limits any higher. As lower limits push upslope while upper limits cannot, elevational ranges will contract as is already the case for several species. If this process continues it could lead to mountaintop extinctions (Freeman, Scholer, et al., 2018; Şekercioğlu et al., 2008; Wormworth & Şekercioğlu, 2011).

While several studies have revealed upslope shifts (Forero-Medina, Terborgh, et al., 2011; Freeman & Class Freeman, 2014; Freeman, Lee-Yaw, Sunday, & Hargreaves, 2018; Neate-Clegg et al., 2018), our results are notable as the bird community appears to be shifting despite the fact that temperatures did not increase over the study period (Figure 2). Instead, our results may reflect longer-term changes in temperature, mediated by incremental changes in habitat or other biotic interactions (Jankowski et al., 2012). Using temperature data for the region (2.25 S 29.25 E) from the Climatic Research Unit (CRU, 2019) we found that temperatures have increased by 0.015°C per year since 1950 (Figure S1), amounting to an increase of 0.93°C in 62 years (1950–2011). This steady warming could have caused suitable habitats (Feeley et al., 2011; Morueta-Holmea et al., 2015) or food sources (Ferger et al., 2014) to shift upslope. Forests are slow to shift in response to temperature increases and could therefore be buffered against interannual fluctuations in climate but responsive to gradual changes over time (Dullinger, Dirnböck, & Grabherr, 2004; Feeley et al., 2011). Elevational shifts in birds have also been shown to lag behind the speed of climate change (Forero-Medina, Terborgh, et al., 2011). It is worth noting, however, that we have few climate data from NNP before 1997 (Sun et al., 1996) and the CRU data do not correlate well with the local temperature (Pearson's $r = .18$) and precipitation (Pearson's $r = .17$) data. Thus, we can only say that temperatures have increased over the last 62 years in the general region.

If temperature played a direct role in determining elevational distributions, we would expect it to be associated with the elevations of many species. However, there was little relationship between yearly mean temperature and species' elevational distributions (Figure 3a), except at species' lower range limits. Here, species moved downslope in years of increased temperature, counter to expectations (Şekercioğlu et al., 2008). One explanation could be that warmer temperatures favor food availability, resulting in increased production of fruits or insects. For example, increased temperatures could lead to the gain of invertebrates from lower elevations (Colwell et al., 2008), providing additional foraging opportunities to insectivorous birds, beyond their usual realized niche (Jankowski et al., 2012). Conversely, increased temperatures could lower food availability for specialists, forcing populations to expand to find more food (Ippi, Cerón, Alvarez,

Aráoz, & Blendinger, 2018). Yet, these explanations would still be indirect effects of temperature (Ferger et al., 2014), and elsewhere, temperature has not been identified as a direct constraint on the range limits of tropical birds (Freeman, 2016; Londoño et al., 2017).

More species showed a significant association with yearly total precipitation (Figure 3b), with ranges tending to expand upslope and downslope in wetter years. Precipitation increases with elevation in the Albertine Rift (McCain & Colwell, 2011), so an increase in rainfall would cause precipitation envelopes to move downslope. This fact may explain downslope expansion but it does not explain upslope expansion. High rainfall is positively associated with food availability (Brown & Sherry, 2006; Studds & Marra, 2007; Williams & Middleton, 2008) so it may be that wetter years allow populations to expand into suboptimal habitats, widening their realized niche (Jankowski et al., 2012). This hypothesis is supported by the fact that dietary specialists (generally insectivores) were more likely than generalists to expand their range in wetter years (Figure 4c). Precipitation has not shown a clear trend in Rwanda, even since 1950 (Figure S1; CRU, 2019), and the effects of climate change on precipitation regimes are hard to predict (Hawkins & Sutton, 2011), so the future effect of rainfall on bird distributions in NNP is uncertain.

Body mass was negatively associated with upslope shift rates (Figure 4a). Bergmann's rule states that smaller-bodied species tend to be found in warmer environments (Bergmann, 1847; Blackburn, Gaston, & Loder, 1999; Blackburn & Ruggiero, 2001). If higher elevations became warmer, they could also become more suitable for small-bodied species. Yet, if temperatures did not increase over the study period, this phenomenon would only occur as an indirect effect of temperature (Blackburn et al., 1999). For example, if body size at lower elevations is generally constrained by greater competition, then upslope shifts in a bird community would lead to smaller-bodied species colonizing higher elevations. Larger-bodied species tended to expand their ranges in warmer years. The five species above 100 g in weight are all frugivores (three turacos, a hornbill and a pigeon) so it is possible that they expanded their ranges in relation to fruit availability. The relationship between temperature and fruit production in tropical forests varies, depending on the complex interaction of temperature, irradiance, and precipitation (Potts, Watts, Langergraber, & Mitani, 2020; Wright & Calderon, 2006), but recent evidence suggests increased temperature lowers fruit production (Potts et al., 2020) and this may push frugivores to expand both their diet (Sun & Moermond, 1997) and their elevational range. Clearly, a more mechanistic understanding of elevational distributions is required in order to understand interannual variation in elevational position. It will also be important to understand the population dynamics underpinning elevational range shifts and whether climate change is allowing, or forcing, species to expand and contract their ranges.

As temperatures continue to rise throughout the tropics, montane birds may become increasingly imperiled, facing extinction as the area available in suitable environments dwindles (Freeman, Scholer, et al., 2018; Şekercioğlu, Primack, & Wormworth, 2012). In this study, we have found a disconnect between elevational range shifts and climate change, showing that many species have moved upslope, particularly at their lower limits, despite the fact that temperatures did not increase over the study period. These shifts have led to range contractions and portend future extirpation (Freeman, Scholer, et al., 2018). The fact that birds appeared to move their distributions in directions counter to the interannual movement of climate envelopes diminishes the role of temperature and precipitation as direct determinants of elevational position. This result places more emphasis on habitat conservation. If bird populations are indeed more constrained by biotic interaction than by direct changes in temperature and precipitation, conservation scientists should focus on preserving ecosystem processes that maintain biotic interactions (Franklin, 1993).

The birds of the Albertine Rift face an uncertain future. If population shifts lag behind climate change, it may take these species longer than predicted to reach extinction thresholds, buying humanity more time to tackle global climate change and prevent mountaintop extinctions. However, should global warming slow down or halt, a lagged response may mean a slower recovery for imperiled species. NNP is relatively undisturbed which is important as other forms of anthropogenic change such as habitat fragmentation likely exacerbate the effects of climate change (Harris et al., 2014; Neate-Clegg et al., 2018; Travis, 2003) by preventing dispersal across landscapes (Lees & Peres, 2009). However, anthropogenic forest fires pose a great risk to NNP (Masozera, 2007) and climate change increases that risk (Liu, Stanturf, & Goodrick, 2010). Although fires have not yet occurred around the study transects, they have affected other parts of the park and burnt areas are slow to regenerate. Accelerating the recovery and regeneration of burnt forest by planting trees and removing *Pteridium* ferns (Masozera, 2007; Shono, Cadaweng, & Durst, 2007) is an important action that could increase the forest's resilience to climate change (Timpane-Padgham, Beechie, & Klinger, 2017). It is critical that NNP and other montane parks continue to maintain the contiguity of forests across elevational gradients to allow animal and plant populations to plastically alter their elevations.

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CONFLICT OF INTEREST

The authors declare no potential conflict of interest.

AUTHOR CONTRIBUTIONS

Montague H. C. Neate-Clegg: Conceived and designed the study. **Timothy G. O'Brien** and **Felix Mulindahabi**: Managed the field seasons, collated, and curated the data. **Montague H. C. Neate-Clegg**: Conducted the analysis and wrote the manuscript with input from Timothy G. O'Brien and Çağan Hakkı Şekercioğlu. **Çağan Hakkı Şekercioğlu**: Supervised the project and provided intellectual insight. All authors reviewed versions of the manuscript.

DATA AVAILABILITY STATEMENT

In this study, we provide model coefficients for the effect of year, temperature, and precipitation on species' mean elevation and upper and lower elevational range limits (Table S2). The raw data on which these estimates are based are available from the authors (and the Wildlife Conservation Society) upon request.

ETHICS STATEMENT

All data collection in this study was remote (point counts) with no physical contact with birds.

ORCID

Montague H. C. Neate-Clegg https://orcid.org/0000-0001-9753-6765

REFERENCES

Bergmann, C. (1847). Über die verhältnisse der wärmeökonomie der thiere zu ihrer grösse. In *Gottinger Studien* (Vol. *3*, pp. 595–708).

Birdlife International. (2020). BirdLife Data Zone. Retrieved from http://datazone.birdlife.org/species.

Blackburn, T. M., Gaston, K. J., & Loder, N. (1999). Geographic gradients in body size: A clarification of Bergmann's rule. *Diversity and Distributions*, *5*, 165–174.

Blackburn, T. M., & Ruggiero, A. (2001). Latitude, elevation and body mass variation in Andean passerine birds. *Global Ecology and Biogeography*, *10*, 245–259.

Boyce, A. J., Freeman, B. G., Mitchell, A. E., & Martin, T. E. (2015). Clutch size declines with elevation in tropical birds. *The Auk*, *132*, 424–432.

Brown, D. R., & Sherry, T. W. (2006). Food supply controls the body condition of a migrant bird wintering in the tropics. *Oecologia*, *149*, 22–32.

Chen, I.-C., Hill, J. K., Ohlemüller, R., Roy, D. B., & Thomas, C. D. (2011). Rapid range shifts of species associated with high levels of climate change. *Science*, *333*, 1024–1026.

Chen, I.-C., Shiu, H.-J., Benedick, S., Holloway, J. D., Chey, V. K., Barlow, H. S., ... Thomas, C. D. (2009). Elevation increases in moth assemblages over 42years on a tropical mountain. *Proceedings of the National Academy of Sciences of the United States of America*, *106*, 1479–1483.

Colwell, R. K., Brehm, G., Cardelús, C. L., Gilman, A. C., & Longino, J. T. (2008). Global warming, elevational range shifts, and lowland biotic attrition in the wet tropics. *Science*, *322*, 258–261.

CRU. (2019). Climatic Research Unit, University of East Anglia. Retrieved from www.cru.uea.ac.uk.

Deutsch, C. A., Tewksbury, J. J., Huey, R. B., Sheldon, K. S., Ghalambor, C. K., Haak, D. C., & Martin, P. R. (2008). Impacts of climate warming on terrestrial ectotherms across latitude. *Proceedings of the National Academy of Sciences of the United States of America*, *105*, 6668–6672.

Dillon, M. E., Wang, G., & Huey, R. B. (2010). Global metabolic impacts of recent climate warming. *Nature*, *467*, 704–706.

Dulle, H. I., Ferger, S. W., Cordeiro, N. J., Howell, K. M., Schleuning, M., Böhning-Gaese, K., & Hof, C. (2016). Changes in abundances of forest understorey birds on Africa's highest mountain suggest subtle effects of climate change. *Diversity and Distributions*, *22*, 288–299.

Dullinger, S., Dirnböck, T., & Grabherr, G. (2004). Modelling climate change-driven treeline shifts: Relative effects of temperature increase, dispersal and invasibility. *Journal of Ecology*, *92*, 241–252.

Elsen, P. R., Tingley, M. W., Kalyanaraman, R., Ramesh, K., & Wilcove, D. S. (2017). The role of competition, ecotones, and temperature in the elevational distribution of Himalayan birds. *Ecology*, *98*, 337–348.

Feeley, K. J., Silman, M. R., Bush, M. B., Farfan, W., Cabrera, K. G., Malhi, Y., ... Saatchi, S. (2011). Upslope migration of Andean trees. *Journal of Biogeography*, *38*, 783–791.

Ferger, S. W., Schleuning, M., Hemp, A., Howell, K. M., & Böhning-Gaese, K. (2014). Food resources and vegetation structure mediate climatic effects on species richness of birds. *Global Ecology and Biogeography*, *23*, 541–549.

Forero-Medina, G., Joppa, L., & Pimm, S. L. (2011). Constraints to species' elevational range shifts as climate changes. *Conservation Biology*, *25*, 163–171.

Forero-Medina, G., Terborgh, J., Socolar, S. J., & Pimm, S. L. (2011). Elevational ranges of birds on a tropical montane gradient lag behind warming temperatures. *PLoS One*, *6*, 1–5.

Franklin, J. F. (1993). Preserving biodiversity: Species, ecosystems, or landscapes? *Ecological Applications*, *3*, 202–220.

Freeman, B. G. (2016). Thermal tolerances to cold do not predict upper elevational limits in New Guinean montane birds. *Diversity and Distributions*, *22*, 309–317.

Freeman, B. G., & Class Freeman, A. M. (2014). Rapid upslope shifts in New Guinean birds illustrate strong distributional responses of tropical montane species to global warming. *Proceedings of the National Academy of Sciences of the United States of America*, *111*, 4490–4494.

Freeman, B. G., Class Freeman, A. M., & Hochachka, W. M. (2016). Asymmetric interspecific aggression in New Guinean songbirds that replace one another along an elevational gradient. *Ibis*, *158*, 726–737.

Freeman, B. G., Lee-Yaw, J. A., Sunday, J. M., & Hargreaves, A. L. (2018). Expanding, shifting and shrinking: The impact of global warming on species' elevational distributions. *Global Ecology and Biogeography*, *27*, 1268–1276.

Freeman, B. G., Scholer, M. N., Ruiz-Gutierrez, V., & Fitzpatrick, J. W. (2018). Climate change causes upslope shifts and mountaintop extirpations in a tropical bird community. *Proceedings of the National Academy of Sciences of the United States of America*, *115*, 11982–11987.

Hansen, M. C., Potapov, P. V., Moore, R., Hancher, M., Turubanova, S. A., Tyukavina, A., ... Townshend, J. R. G. (2013). High-resolution global maps of 21st-Century forest cover change. *Science*, *342*(6160), 850–853. http://dx.doi.org/10.1126/science.1244693.

Harris, J. B. C., Dwi Putra, D., Gregory, S. D., Brook, B. W., Prawiradilaga, D. M., Sodhi, N. S., ... Fordham, D. A. (2014). Rapid deforestation threatens mid-elevational endemic birds but climate change is most important at higher elevations. *Diversity and Distributions*, *20*, 773–785.

Harris, J. B. C., Şekercioğlu, Ç. H., Sodhi, N. S., Fordham, D. A., Paton, D. C., & Brook, B. W. (2011). The tropical frontier in avian climate impact research. *Ibis*, *153*, 877–882.

Hawkins, E., & Sutton, R. (2011). The potential to narrow uncertainty in projections of regional precipitation change. *Climate Dynamics*, *37*, 407–418. Retrieved from http://link.springer.com/10.1007/s00382-010-0810-6

Ippi, S., Cerón, G., Alvarez, L. M., Aráoz, R., & Blendinger, P. G. (2018). Relationships among territory size, body size, and food availability in a specialist river duck. *Emu*, *118*, 293–303.

Jankowski, J. E., Londoño, G. A., Robinson, S. K., & Chappell, M. A. (2012). Exploring the role of physiology and biotic interactions in determining elevational ranges of tropical animals. *Ecography*, *36*, 1–12.

Jankowski, J. E., Merkord, C. L., Rios, W. F., Cabrera, K. G., Revilla, N. S., & Silman, M. R. (2013). The relationship of tropical bird communities to tree species composition and vegetation structure along an Andean elevational gradient. *Journal of Biogeography*, *40*, 950–962.

Jankowski, J. E., Robinson, S. K., & Levey, D. J. (2010). Squeezed at the top: Interspecific aggression may constrain elevational ranges in tropical birds. *Ecology*, *91*, 1877–1884.

Lees, A. C., & Peres, C. A. (2009). Gap-crossing movements predict species occupancy in Amazonian forest fragments. *Oikos*, *118*, 280–290.

Liu, Y., Stanturf, J., & Goodrick, S. (2010). Trends in global wildfire potential in a changing climate. *Forest Ecology and Management*, *259*, 685–697 Elsevier.

Loiselle, B. A., & Blake, J. G. (1991). Temporal variation in birds and fruits along an elevational gradient in Costa Rica. *Ecology*, *72*, 180–193.

Londoño, G. A., Chappell, M. A., Jankowski, J. E., & Robinson, S. K. (2017). Do thermoregulatory costs limit altitude distributions of Andean forest birds? *Functional Ecology*, *31*, 204–215.

Lynch, J. F. (1995). Effects of point count duration, time-of-day, and aural stimuli on detectability of migratory and resident bird species in Quintana Roo, Mexico. In C. J. Ralph, J. R. Sauer, & S. Droege (Eds.), *Monitoring bird populations by point counts* (pp. 1–6). Albany, CA: Pacific Southwest Research Station.

Masozera, A. B. (2007). *Post-fire regeneration in Nyungwe National Park*. Kigali, Rwanda: Wildlife Conservation Society.

McCain, C. M., & Colwell, R. K. (2011). Assessing the threat to montane biodiversity from discordant shifts in temperature and precipitation in a changing climate. *Ecology Letters*, *14*, 1236–1245.

Morueta-Holmea, N., Engemann, K., Sandoval-Acuña, P., Jonas, J. D., Segnitz, R. M., & Svenning, J.-C. (2015). Strong upslope shifts in Chimborazo's vegetation over two centuries since Humboldt. *Proceedings of the National Academy of Sciences of the United States of America*, *112*, 12741–12745.

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

Neate-Clegg, M. H. C., Jones, S. E. I., Burdekin, O., Jocque, M., & Şekercioğlu, Ç. H. (2018). Elevational changes in the avian community of a Mesoamerican cloud forest park. *Biotropica*, *50*, 805–815.

Parmesan, C. (2006). Ecological and evolutionary responses to recent climate change. *Annual Review of Ecology, Evolution, and Systematics*, *37*, 637–669.

Paxton, E. H., Camp, R. J., Gorresen, P. M., Crampton, L. H., Leonard, D. L., Jr., & Vanderwerf, E. A. (2016). Collapsing avian community on a Hawaiian Island. *Science Advances*, *2*, 1–8.

Peh, K. S. H. (2007). Potential effects of climate change on elevational distributions of tropical birds in Southeast Asia. *The Condor*, *109*, 437–441.

Pinheiro, J., Bates, D., DebRoy, S., Sarkar, D. (2013). nlme: Linear and nonlinear mixed effects models.

Plumptre, A. J., Davenport, T. R. B., Behangana, M., Kityo, R., Eilu, G., Ssegawa, P., ... Moyer, D. (2007). The biodiversity of the Albertine Rift. *Biological Conservation*, *134*, 178–194.

Plumptre, A. J., Masozera, M., Fashing, P. J., McNeilage, A., Ewango, C., Kaplin, B. A., Liengola, I.. (2002). Biodiversity surveys of the Nyungwe Forest Reserve in S.W. Rwanda. Bronx, NY: Wildlife Conservation Society.

Potts, K. B., Watts, D. P., Langergraber, K. E., & Mitani, J. C. (2020). Long-term trends in fruit production in a tropical forest at Ngogo, Kibale National Park, Uganda. *Biotropica 52*, 521–532.

R Core Team. (2020). *R: A language and environment for statistical computing*. Vienna, Austria: R Foundation for Statistical Computing.

Ralph, C. J., Sauer, J. R., & Droege, S. (1995). *Monitoring bird populations by point counts*, In General Technical Report, Albany, CA: U.S. Department of Agriculture, Forest Service, Pacific Southwest Research Station.

Şekercioğlu, Ç. H., Mendenhall, C. D., Oviedo-Brenes, F., Horns, J. J., Ehrlich, P. R., & Daily, G. C. (2019). Long-term declines in bird populations in tropical agricultural countryside. *Proceedings of the National Academy of Sciences of the United States of America*, *116*, 9903–9912.

Şekercioğlu, Ç. H., Primack, R. B., & Wormworth, J. (2012). The effects of climate change on tropical birds. *Biological Conservation*, *148*, 1–18.

Şekercioğlu, Ç. H., Schneider, S. H., Fay, J. P., & Loarie, S. R. (2008). Climate change, elevational range shifts, and bird extinctions. *Conservation Biology*, *22*, 140–150.

Shono, K., Cadaweng, E. A., & Durst, P. B. (2007). Application of assisted natural regeneration to restore degraded tropical forestlands. *Restoration Ecology*, *15*, 620–626.

Studds, C. E., & Marra, P. P. (2007). Linking fluctuations in rainfall to nonbreeding season performance in a long-distance migratory bird, *Setophaga ruticilla*. *Climate Research*, *35*, 115–122.

Sun, C., Kaplin, B. A., Kristensen, K. A., Munyaligoga, V., Mvukiyumwami, J., Kajondo, K. K., & Moermond, T. C. (1996). Tree phenology in a tropical montane forest in Rwanda. *Biotropica*, *28*, 668.

Sun, C., & Moermond, T. C. (1997). Foraging ecology of three sympatric turacos in a montane forest in Rwanda. *Auk*, *114*, 396–404.

Timpane-Padgham, B. L., Beechie, T., & Klinger, T. (2017). A systematic review of ecological attributes that confer resilience to climate change in environmental restoration. *PLoS One*, *12*, e0173812.

Travis, J. M. J. (2003). Climate change and habitat destruction: A deadly anthropogenic cocktail. *Proceedings of the Royal Society B: Biological Sciences*, *270*, 467–473.

van der Hoek, Y., Faida, E., Musemakweli, V., & Tuyisingize, D. (2020). Living the high life: Remarkable high-elevation records of birds in an east African mountain range. *Ecology*, *101*, 1–4.

Vedder, A., Hall, J., Harcourt, A., Monfort, A., & Wilson, R. (1992). Burundi and Rwanda. In J. A. Sayer, C. S. Harcourt, & N. M. Collins (Eds.), *The Conservation Atlas of Tropical Forests: Africa* (pp. 102–109). New York, NY: IUCN.

Venables, W. N., & Ripley, B. D. (2013). *Modern applied statistics with S*. New York, NY: Springer-Verlag.

WCS. (2019). Nature's strongholds impact platform.

Williams, S. E., & Middleton, J. (2008). Climatic seasonality, resource bottlenecks, and abundance of rainforest birds: Implications for global climate change. *Diversity and Distributions*, *14*, 69–77.

Wormworth, J., & Şekercioğlu, Ç. H. (2011). *Winged sentinels: Birds and climate change*. New York, NY: Cambridge University Press.

Wright, S. J., & Calderon, O. (2006). Seasonal, El Nino and longer term changes in flower and seed production in a moist tropical forest. *Ecology Letters*, *9*, 35–44.

SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section at the end of this article.

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