



The combined effects of temperature and fragment area on the demographic rates of an Afrotropical bird community over 34 years

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ABSTRACT

Habitat fragmentation and climate change are two of the greatest threats to biodiversity, yet their combined impacts and potential interactions are poorly understood, particularly in the context of demographic rates. The Usambara Mountains, Tanzania, comprise a highly fragmented landscape where temperatures have increased by 0.58 °C over the last three decades. Here, we used a 34-year bird banding dataset from 14 forest fragments (0.2–908 ha) to examine the combined effects of fragment area and mean annual temperature on the demographic rates of 24 understory bird species. The population growth rates of two-thirds of species were negatively associated with at least one of the stressors, and, overall, population growth rates were 12–20% lower in the warmest year compared to the coolest year, depending on fragment size. When temperature and fragment area were combined in models of recruitment, survival, and population growth, their effects were more frequently interactive than additive, however these interactions were rarely synergistic. Independently, temperature also received more model support than fragment area and tended to have a greater impact on demographic rates across species. Despite the complexity of the interactions between fragment area and temperature, their total effects on tropical bird demographic rates were largely detrimental. The development of effective conservation strategies for montane tropical bird species needs to account for these combined impacts.

1. Introduction

Habitat loss and climate change are the two greatest threats to global biodiversity (Barlow et al., 2018; Ducatez and Shine, 2017). A large body of research has documented the adverse impacts of habitat loss and fragmentation on biodiversity (Halley et al., 2016; Pfeifer et al., 2017; Stouffer, 2020), including the independent effects of habitat area (Stouffer et al., 2011), edge (Banks-Leite et al., 2010; Pfeifer et al., 2017), and isolation (Ferraz et al., 2007), which in turn can impact species richness (Stouffer, 2020), demographic rates (Korfanta et al., 2012), and connectivity (Lees and Peres, 2009). Climate change is also having pervasive impacts on biodiversity (Parmesan, 2006). Increases in temperature over the last century have been linked to latitudinal (Chen et al., 2011; Lenoir et al., 2020) and elevational shifts of species (Freeman et al., 2018a; Neate-Clegg et al., 2021a), alteration in demographic rates of species (Neate-Clegg et al., 2021b; Srinivasan and Wilcove, 2021), as well as changes in phenology (Socolar et al., 2017)

and community structure (Stouffer et al., 2020). Despite the well-documented impacts of habitat loss and climate change on biodiversity, few studies have investigated their combined effects (Brook et al., 2008; Oliver and Morecroft, 2014).

The effects of habitat loss and climate change can combine in multiple ways (Côté et al., 2016; Oliver and Morecroft, 2014), with potentially devastating consequences (Şekercioğlu et al., 2008; Travis, 2003). Stressors could combine additively to affect biodiversity, and this is well-supported in the literature (Côté et al., 2016). Alternatively, interactions could result where the cumulative effect of multiple stressors does not equal the sum of the effects of individual stressors (Brook et al., 2008; Côté et al., 2016). Such interactions can be antagonistic, when the cumulative effect is less than the sum of the parts, although these are generally less of a problem for conservation. The more concerning interactions are synergies (Brook et al., 2008; Travis, 2003), when the negative effects of both stressors are greater than either stressor in isolation. For example, population declines caused by habitat loss can be

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exacerbated by climate change (Mac Nally et al., 2009; Mantyka-Pringle et al., 2015; McLaughlin et al., 2002), leading to higher extinction rates (Anderson et al., 2009; Şekerciöglu et al., 2008). Microclimates in fragmented forest may be less buffered against the effects of climate change, intensifying edge effects (Brook, 2008; Ewers and Banks-Leite, 2013), and a lack of climate buffer could impact demographic rates (Wolfe et al., 2015). Moreover, in fragmented landscapes climate change may increase population stochasticity, or increase area requirements leading to altered metapopulation dynamics including extirpation from smaller fragments (McLaughlin et al., 2002; Oliver and Morecroft, 2014; Opdam and Wascher, 2004). The ability of species to adapt to climate change can also be limited by habitat isolation (Opdam and Wascher, 2004; Saunders et al., 2022). For example, climate-induced upslope distributional shifts can be impeded by fragmentation (Neate-Clegg et al., 2021c), particularly if species show limited gap-crossing ability (Lees and Peres, 2009). Given the multitude of potential interactions between fragmentation and climate change, assessing their combined impacts on biodiversity is important not only heuristically but is critical for the development of effective conservation strategies in today's rapidly changing world (Laurance and Useche, 2009).

The tropics contain the vast majority of the world's biodiversity (Barlow et al., 2018), where tropical mountains, in particular, are centers of diversity and endemism (Rahbek et al., 2019) that are threatened by both habitat loss (Harris et al., 2014b; Neate-Clegg et al., 2021c; Newmark et al., 2017) and climate change (Freeman et al., 2018b; Neate-Clegg et al., 2021b). Furthermore, the high degree of ecological specialization and low dispersal ability of many tropical forest species (Salisbury et al., 2012; Sheard et al., 2020) likely makes montane tropical organisms particularly vulnerable to the combined effects of these two stressors (Şekerciöglu et al., 2008; Travis, 2003); yet, assessing the combined impacts of habitat loss and climate change requires long-term datasets, which are scarce in the tropics, especially in Africa (Sheldon, 2019). The Eastern Arc Mountains in East Africa are one of the most biologically diverse and imperiled tropical biodiversity hotspots (Mantyka-Pringle et al., 2015). Over the last several centuries, the Eastern Arc Mountains have lost 77 % of their original forest cover, with the remaining forest left highly fragmented (Newmark and McNeally, 2018).

Located in Tanzania at the northern end of the Eastern Arc Mountains, the East and West Usambara Mountains contain dozens of forest fragments embedded within an agricultural matrix. Since 1987, understory birds have been monitored across a range of these fragments (Korfanta et al., 2012), and in that time the temperature in the Usambara mountains has increased by 0.58 °C (Neate-Clegg et al., 2021b). Here, we use a 34-year capture-mark-recapture dataset to assess the combined effects of fragmentation and warming temperatures on the demographic rates of 24 understory bird species in these mountains. We examine the relationship between fragment area (as a proxy for fragmentation) and mean annual temperature on realized population growth rates, recruitment rates, and apparent survival while controlling for imperfect detectability. Our inference centers upon four main questions:

1. What are the main effects of temperature and fragment area on demographic rates?
2. How many species show additive versus interactive effects including synergies?
3. What are the combined effects of temperature and fragment area on demographic rates?
4. What is the relative importance of temperature versus area on demographic rates?

2. Methods

2.1. Study sites

This study was conducted within 14 forest fragments over 34 years

(1987–2020) in the East and West Usambara Mountains in northeast Tanzania (Fig. S1), two adjacent mountain ranges separated by a lowland valley. Of these fragments, nine (0.2–640 ha, 969–1150 m in elevation) are located in the East Usambara Mountains, and five (1.5–908 ha, 1074–1301 m in elevation) are located in the West Usambara Mountains (Table S1). Like much of the Eastern Arc Mountains, the Usambara Mountains have experienced extensive deforestation and habitat fragmentation over several centuries (Newmark et al., 2010), including a 25 % loss of forest between 1955 and 2000 (Hall et al., 2009). However, the 14 fragments in our study were isolated between 1893 and 1968. All of the fragments are entirely surrounded by a matrix consisting of small-scale agriculture, tea, and Eucalyptus plantations. Over the course of the study, there has been no additional habitat loss to the study fragments, nor change in matrix habitats, with the exception of a <2 % change in matrix habitat area (from small-scale agriculture to Eucalyptus plantations) adjacent to the largest fragment in the East Usambara Mountains (Neate-Clegg et al., 2021b). In this study we choose to focus on fragment area as a proxy for fragmentation in general, including all the processes associated with habitat loss (Banks-Leite et al., 2010; Ferraz et al., 2007). However, we also conducted an alternative analysis that considered the effects of temperature and fragment isolation on vital rates (Appendix A).

2.2. Data gathering

Bird banding was initiated in all fragments between 1987 and 1989 (Table S2). Birds were captured using mist nets that were placed in a continuous line beginning at and running perpendicular to the forest edge. Smaller forest fragments were entirely bisected by a net line, while irregularly shaped and larger fragments contained up to four net lines, with the number of nets deployed proportional to fragment area (Table S1). Nets in each fragment were operated from dawn until dusk for three consecutive days per survey period (36 h). Each survey period was conducted between July and September during the cool dry season when the weather was safer and more suitable for bird banding, and sites were visited in roughly the same order each year. Between 1987 and 2020, the total number of surveys per fragment ranged from 17 to 34 (Table S2), with a mean (\pm SE) interval between surveys of 1.69 ± 0.09 years (range: 1–7 years; Table S2). Mist nets were always erected in the same locations across years and were opened for the same amount of time each survey period, resulting in 252,792 total mist-net hours. The constancy of effort over time allows demographic parameters to be modeled over time, while differences in effort between fragments can be controlled for in the capture probabilities. All birds received standard aluminum bands (National Band and Tag Company, Newport, Kentucky, USA; I.Ö. Mekaniska AB, Bankeryd, Sweden).

We extracted mean monthly temperature data from the Climatic Research Unit (CRU), University of East Anglia (Harris et al., 2014a), which is available globally at a half-degree grid cell resolution (CRU TS v.4.05), and adequately covers our study period and areas. Although two half-degree CRU grid cells overlap the study areas in the Usambara Mountains, we selected the single grid cell (5.25 S, 38.75 E) in which mean monthly temperature data were most highly correlated with temperature logger data recorded onsite. From the CRU data, annual mean temperature was calculated for the 12 months (October–September) prior to and including the annual survey period (July–September). We chose to use annual mean temperature so as to avoid assumptions regarding the influence of extreme values or temporal windows such as breeding, fledging, molting, or dispersal (Neate-Clegg et al., 2021b). Precipitation was not included in this analysis because we found little support in a previous study for precipitation as a predictor of demographic rates of understory bird species in the two largest fragments in the study system (Neate-Clegg et al., 2021b).

2.3. Analyses

Based on the need for mark-recapture models to have sufficient capture and recapture rates, we a priori limited species to those where ≥ 50 individuals were captured and where at least 10 % of all individuals were captured two or more times. Additional species were subsequently excluded due to issues of model fit (see below). For each species, we created capture histories and modeled demographic parameters using *RMark* (Laake and Rexstad, 2006), an R package which interacts with program MARK to estimate demographic rates from capture-recapture data (Cooch and White, 2006). We investigated three key demographic parameters: apparent survival (ϕ , the probability of individuals surviving and remaining in the population), recruitment (f , the per capita rate at which new individuals join the population), and realized population growth (λ , the per capita change in population size equal to $\phi + f$). In calculating these parameters, we controlled for imperfect capture probability, p . As many fragments were not surveyed every year, we fixed p equal to 0 in years when a fragment was not surveyed.

Following Korfanta et al. (2012) and Neate-Clegg et al. (2021b), we used a two-step mark-recapture analysis. We first modeled ϕ and p using open-population Cormack-Jolly-Seber (CJS) models (Cormack, 1964; Jolly, 1965; Lebreton et al., 1992; Seber, 1965). We then used the results of the CJS models to inform the structure (see below) of Pradel models (Pradel, 1996) which, in addition to modeling ϕ and p , estimate either f or λ using a reverse-time approach. In both steps we modeled demographic parameters using linear predictor formulae with logit (ϕ and p) and log (f and λ) link functions. Beginning with the CJS models, we defined a global model of apparent survival and recapture containing eight parameters as:

$$\phi(\text{temperature} + \text{area} + \text{temperature} * \text{area} + \text{location})p(\text{area} + \text{location})$$

such that apparent survival (ϕ) varied as a function of fragment area, annual mean temperature, and their interaction, as well as a binary location indicator (East versus West Usambara Mountains) which allowed for differences in survival between the two mountain ranges (Korfanta et al., 2012; Neate-Clegg et al., 2021b). Capture probability (p) was modeled as a function of fragment area and mountain range. Fragment area (in ha) was log-transformed prior to analysis, as fragment size effects typically increase linearly on the radius scale. In addition, to facilitate interpretation of parameter estimates, we multiplied the area covariate by -1 so that larger values indicated smaller fragment area. This ensured that a negative coefficient for both temperature and area represented a negative effect on a demographic rate. Finally, both area and temperature were centered and scaled (transformed to mean = 0, SD = 1) to provide standardized coefficients comparable in units of standard deviations.

After creating a global model for each species, we constructed a reduced set of nested models (Table S3) to facilitate parsimonious multi-model selection and inference based on AIC_c (Burnham and Anderson, 2002). To account for potential overdispersion we estimated $median-\hat{c}$ using the Median- \hat{c} routine in MARK (Cooch and White, 2006). When the estimated $median-\hat{c} > 1$ with confidence intervals that did not overlap 0, we used the $median-\hat{c}$ to scale the deviance when calculating AIC_c ($QAIC_c$) (Cooch and White, 2006). The global model for ϕ contains nine nested formulae while the global model for p contains three nested formulae (Table S3). For each species we ran 40 models representing all possible parameterizations (10 ϕ by 4 p) including the global model and an unconstrained null model [$\phi(\cdot)p(\cdot)$]. Species found either only in the East or the West Usambara Mountains had a reduced set of 10 models (5 ϕ by 2 p parameterizations). We extracted the top-ranked CJS model for each species based on (Q)AIC_c. For each species, model formulae for ϕ and p from the top-ranked CJS model were used in the subsequent Pradel models.

In the Pradel models, we incorporated 10 models separately for f and

λ , where the parameter of interest was constrained by one of the 10 formulae previously applied to ϕ in the CJS models, while ϕ and p were modeled using the formulae from the top-ranked CJS model. We used this two-step approach (Korfanta et al., 2012; Neate-Clegg et al., 2021b) because varying the formulae for ϕ and p in both the f and the λ model sets would result in modeling the same parameters twice which would have different model weights between the two model sets thus hindering interpretation of results. In addition, adopting a two-step modeling approach is less unwieldy (60 models versus 400 models). After running the models, we excluded those that failed to estimate all the parameters or that had unreasonable point or error estimates (e.g., ϕ estimates of 1, standard errors of 0, or confidence intervals that converged on the limit boundaries of 0 and 1). For three species (*Modulatrix stictigula*, *Cinnyris usambaricus*, and *Linurgus olivaceus*) we were unable to run a ϕ model containing a temperature * area interaction term.

As temperatures increased significantly over time, we also performed a supplementary analysis to compare the effects of temperature with the linear effects of time (Appendix A). Temperature was somewhat interchangeable with year in competing models for several species. However, without plausible alternative hypotheses, temperature remained the most likely temporal covariate associated with demographic rates (Appendix A).

Besides fragment area, another important aspect of fragmentation that can affect birds is fragment isolation (Ferraz et al., 2007). We therefore performed a supplementary analysis that repeated the modeling approach above but replaced the area covariate with an isolation covariate (Appendix A). In this latter analysis, isolation was a poorer predictor of demographic rates than fragment area, and thus we chose to focus in the main body of the study on area rather than isolation.

2.4. Model assessment

We assessed model results in several ways. First, for each species we extracted the covariate coefficients (with their 95 % confidence intervals) from the top-ranked ϕ , f , and λ models, i.e., the model with the lowest (Q)AIC_c (hereafter “top model”). To examine the main effects, we tabulated how often temperature or area covariates appeared in the top model, as well as the sign and significance of the coefficients. To examine the combined effects of temperature and area, we determined how often temperature and area covariates co-occurred in the top model, and whether the model was additive or interactive (i.e., containing an interaction term). If both main effects were negative, and the interaction term was also negative, we defined that as a negative synergy, but if the interaction term was positive, we defined that as a negative antagonism (the reverse being true if both main effects were positive). Interactions where the main effects do not agree in sign were more difficult to categorise and were evaluated based on the overall outcome (Côté et al., 2016).

To determine the total effects of temperature and fragment area on demographic rates, we averaged predictions of λ , f , and ϕ across all models for each species, weighted by (Q)AIC_c model weights (Burnham and Anderson, 2002). This enabled us to visualize trends across temperature and area based on all models and their associated model weights. We summarized the findings across species by extracting the model-averaged estimates for each species in four scenarios: the largest fragment (908 ha) in the coolest year (25.33 °C), the largest fragment in the warmest year (26.58 °C), the smallest fragment (0.2 ha) in the coolest year, and the smallest fragment in the warmest year. We then calculated the mean and 95 % confidence intervals of the parameter estimates across species for each scenario, using bootstrapping to propagate the uncertainty in the estimates (Appendix A). We also grouped species based on disturbance sensitivity into “low” and “high” to examine whether the two groups were responding differently to fragment area and temperature (Appendix A). Finally, to assess the relative importance of temperature and area for each species across

models, we summed model weights for models containing each covariate (Burnham and Anderson, 2002). As temperature and area occur in the same number of models in the model set, we compared the summed weights of these covariates for each species.

3. Results

Between 1987 and 2020 we caught 85 species including three species classified by IUCN as threatened and three species as near-threatened. Of these species, ≥ 50 individuals were caught for 36 species (Fig. S2, Table S4), for which mark-recapture model fit was adequate for 24 species (Fig. S2). Our final species set were all non-migratory year-round residents and included three near-threatened, near-endemic species: montane tiny greenbul (*Phyllastrephus albigula*), Usambara thrush (*Turdus roehli*), and Usambara double-collared sunbird (*Cinnyris usambaricus*).

3.1. Main effects of temperature and fragment area

We found demographic associations with temperature and/or area for most species (Fig. 1a), with 21 of 24 species (88 %) containing at least one of these covariates in their top-ranked population growth rate (λ) model (Fig. S3a, Tables 1, S5). Population growth rates in the top model were negatively associated with at least one of the stressors for 17 species (71 %), and positively associated with at least one stressor for six species (25 %). The temperature covariate was present in the top model for 17 species (Fig. 1a) and the coefficient was significantly negative (i.e., 95 % confidence intervals did not overlap 0) for ten species, and significantly positive for one species (Fig. S3a, Table S5). The area covariate was present in the top model for 13 species (Fig. 1a) and the coefficient was significantly negative for five species (indicating that population growth rates were lower in smaller fragments), but was not significantly positive for any species (Fig. 1a, Table S5).

For recruitment rates (f), temperature was present in the top model for 18 species (Fig. 1b), and the coefficient was significantly negative for seven species and significantly positive for three species (Fig. S3b, Table S6). The area covariate was present in the top model for 14 species (Fig. 1b), and the coefficient was significantly negative for three species and significantly positive for four species (Fig. S3b, Table S6).

For apparent survival (ϕ), temperature was present in the top model for seven species (Fig. 1c), and the coefficient was significantly negative for three species, but was not significantly positive for any species (Fig. S3c, Table S7). The area covariate was present in the top model for seven species (Fig. 1c), and the coefficient was significantly negative for

Table 1

Top capture-mark-recapture models for 24 understory bird species over 34 years in the Usambara Mountains, Tanzania. For each species, a top-ranked model was selected based on (Q)AIC_c for population growth rates (λ), recruitment rates (f), and apparent survival (ϕ). This table gives the number of species whose top model contained a particular model formula where T = temperature, A = area, T:A = temperature:area interaction, and L = location (East vs West Usambara Mountains). Models can be classified based on the main and interactive effects they contain. A “constant” model was an intercept-only model. Full top model results can be found in Tables S5–S7.

Formula	Model type	λ	f	ϕ
T + A + T:A + L	Interactive	3	4	0
T + A + T:A	Interactive	3	1	2
T + A + L	Additive	2	3	1
T + A	Additive	1	3	1
T + L	Temp only	6	6	0
T	Temp only	2	1	3
A + L	Area only	1	0	2
A	Area only	3	3	1
L		1	2	3
Constant		2	1	11

four species, but was not significantly positive for any species (Fig. S3c, Table S7).

3.2. Combined effects of temperature and fragment area

Temperature and area co-occurred in the top population growth rate model of nine species (38 %) and the interaction term was present for six of those species (Fig. S3a, Tables 1, S5). The interaction coefficient was significantly positive for three species (Fig. 1a, S3a), and significantly negative for one species (Table S5). For recruitment, temperature and area co-occurred in the top model of 11 species (46 %) and the interaction term was present for five of those species (Fig. S3b, Tables 1, S6). The interaction coefficient was significantly positive for three species (Figs. 1b, S3b), but was not significantly negative for any species (Table S5). Finally, for apparent survival, temperature and area co-occurred in the top model of four species (17 %) where an interaction term was present for two species but was significant for neither (Figs. 1c, S3c, Tables 1, S7). Thus, significant interaction terms were rarely present in our species set, but were more likely to be positive than negative. In only one case, for spot-throat (*Modulatrix stictigula*), was the interaction effect on population growth rates a negative synergy.

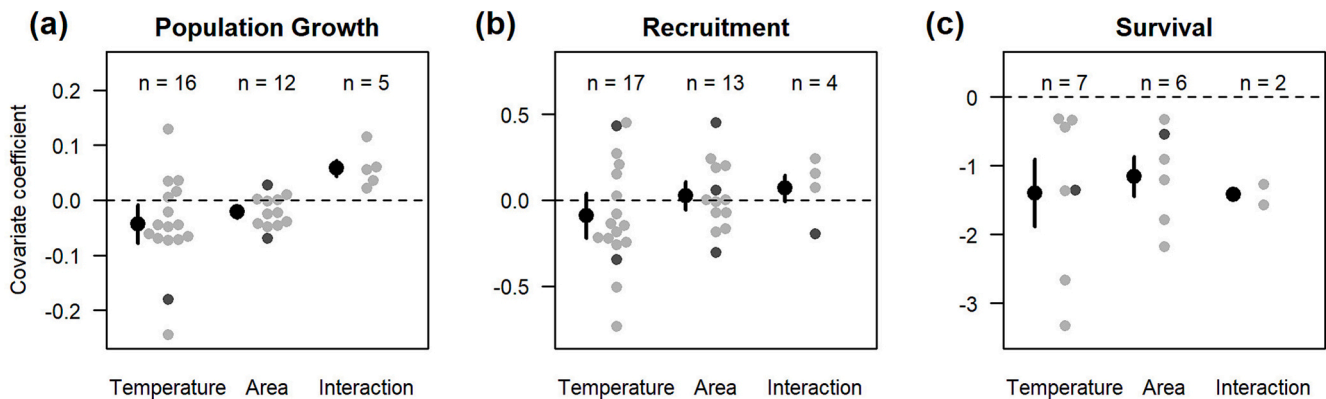


Fig. 1. The main and interactive coefficients for the effects of temperature and fragmentation on the demographic parameters of Afrotropical bird species over 34 years (1987–2020) in the Usambara Mountains, Tanzania. Plotted are the temperature, area, and interaction coefficients for each species from the top-ranked model of (a) realized population growth rate — λ , (b) recruitment rate — f , and (c) apparent survival probability — ϕ . Three near-threatened, near-endemic species are shown as darker points. Model rankings were based on (Q)AIC_c. Means and 95 % confidence intervals across species are given as black points and bars, offset from the main points. Sample sizes (n) give the number of species that contained a given covariate in their top model. Results for spot-throat are not shown because of the large size of the coefficients, but can be found in Table S5.

3.3. Total effects of temperature and fragment area

Due to the generally negative effects of temperature, population growth rates across species averaged lower in warmer years than in cooler years (Fig. 2b). In the largest fragment, population growth rates averaged 20 % lower in the warmest year (0.88, CI: 0.84–0.94) compared to the coolest year (1.10, CI: 1.05–1.15), while in the smallest fragment they averaged 12 % lower (0.91, CI: 0.86–0.97; 1.03, CI: 0.98–1.08). However, there was little difference in population growth rates between the largest and smallest fragments. Recruitment rates showed contrasting patterns depending on fragment size, with 32 % lower rates in the warmest year (0.26, CI: 0.16–0.37) compared to the

coolest year (0.38, CI: 0.28–0.47) in the largest fragment, but similar rates in the smallest fragment (0.38, CI: 0.28–0.48; 0.38, CI: 0.28–0.49). By comparison, apparent survival showed an additive effect of temperature and area, with highest survival in the “large cool” (0.75, CI: 0.67–0.82), followed by “small cool” (0.66, CI: 0.59–0.74), “large warm” (0.62, CI: 0.56–0.69), and “small warm” (0.53, CI: 0.46–0.61). However, these cross-species patterns varied by disturbance sensitivity (Appendix A).

At the species level, the negative effect of temperature on population growth rates tended to be of greater magnitude than the negative effect of fragment area (Figs. S4–S6). Importantly, population growth rates were predicted to be <1.0 (indicating population declines) during the

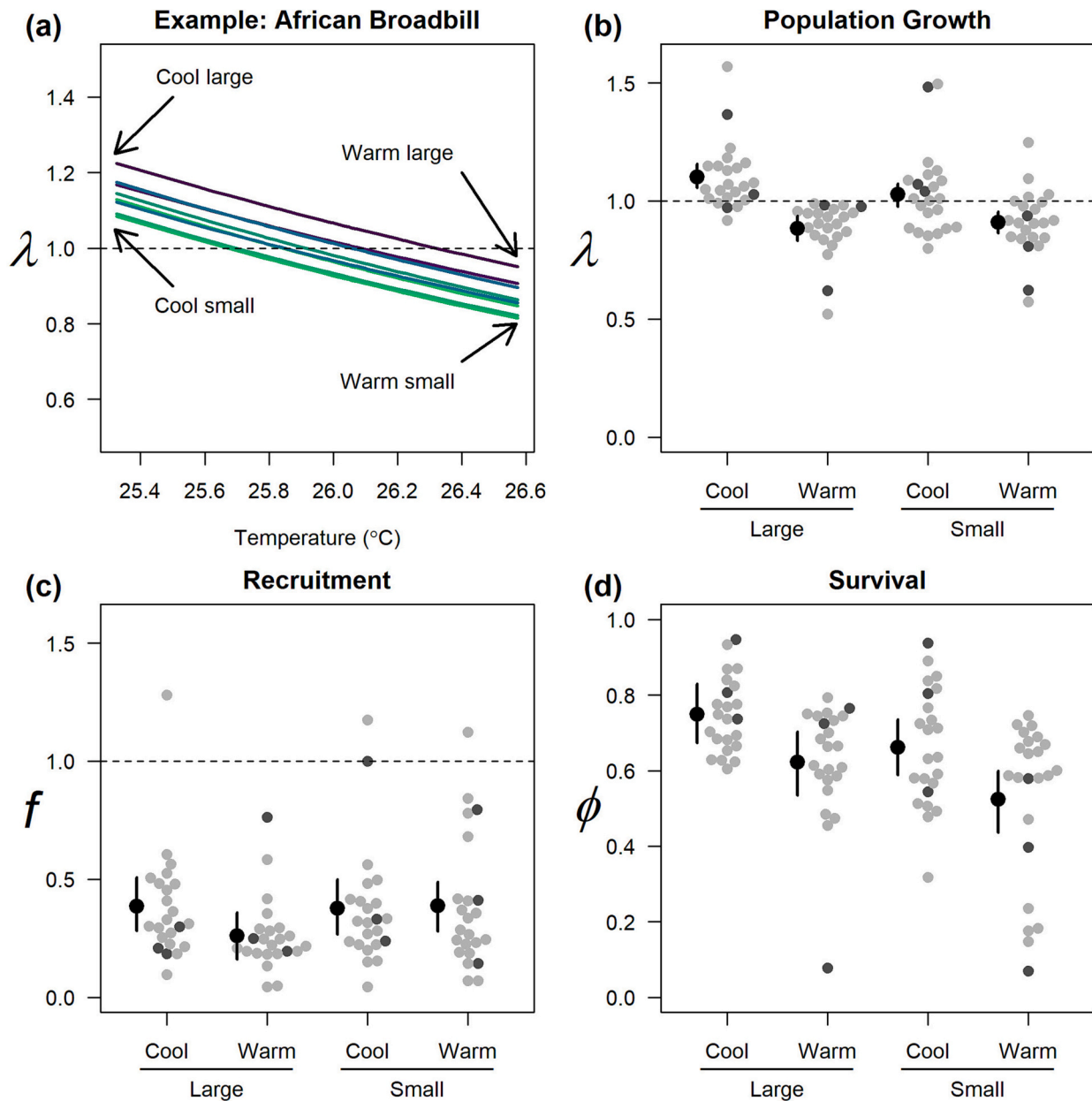


Fig. 2. The total effects of temperature and fragmentation on the demographic parameters of Afrotropical bird species over 34 years (1987–2020) in the Usambara Mountains, Tanzania. Predicted values of demographic rates (a) were estimated for each species (African Broadbill in this example; similar plots for all species can be found in Figs. S4–S6) using model averaging over all models and across the full range of observed temperatures and fragment sizes (purple for larger fragments, green for smaller fragments). From these predictions, estimates of (b) realized population growth rate, λ , (c) recruitment rate, f , and (d) apparent survival probability, ϕ , were extracted for four scenarios: the coolest year in the largest fragment (908 ha), the coolest year in the smallest fragment (0.2 ha), the warmest year in the largest fragment, and the warmest year in the smallest fragment. Predictions for each species (small points), with averages (plus 95 % confidence intervals) based on bootstrapping (Appendix A). Three near-threatened, near-endemic species are shown as darker points. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

warmest years of the study in at least one fragment for all species, and across all fragments for 19 species (79 %; Fig. S4). For species exhibiting important interactions, population growth rates often decreased with temperature in larger fragments but increased with temperature in smaller fragments — a pattern mirrored in recruitment rates (Fig. S5). The population growth rates of only one species, spot-throat, showed a negative synergistic interaction between temperature and area (Table S5) where the negative effect of temperature on population growth rates became more pronounced in smaller fragments (Fig. S4). A similar interaction was also shown for the recruitment rate of the spot-throat (Fig. S5). In the montane tiny greenbul, recruitment rates decreased with increasing temperature in smaller fragments but did not change in larger fragments (Fig. S5).

3.4. Relative importance of temperature and fragment area

For population growth rates, temperature had a higher summed model weight than area for 12 species (50 %; Fig. 3a). By comparison, area had a higher summed weight than temperature for seven species (29 %; Fig. 3a), with the remaining species showing roughly equal weight. A similar pattern was found for recruitment rates: temperature had a higher summed weight than area for 12 species (50 %) while area had a higher summed weight for eight species (33 %; Fig. 3b). Across apparent survival models, the summed weights of both variables tended to be low (Fig. 3c).

4. Discussion

4.1. General effects of temperature and fragment area

The main effects of habitat loss and climate change on biodiversity are well documented, but the ways in which these stressors interact and their relative importance have received little attention (Brook et al., 2008; Oliver and Morecroft, 2014). In the Usambara Mountains of Tanzania, we found that over two-thirds of our focal species showed negative demographic associations with at least one of the two stressors (Table 1). Regardless of fragment area, our models predicted that population growth rates for most species would be <1.0 (i.e., population decline) at temperatures observed in the warmest study years (Fig. S4), and these temperatures are indicative of steady warming rather than unusually hot years (Neate-Clegg et al., 2021b). The negative association between temperature and demographic rates (Fig. 1a) corroborates previous work in the Usambara Mountains (Neate-Clegg et al., 2021b),

as well as studies around the globe (Dybala et al., 2013; Srinivasan and Wilcove, 2021; Woodworth et al., 2018) — although there is a paucity of such community-level demographic studies in the tropics (Sheldon, 2019).

For several species, population growth rates were also negatively associated with fragment area (Fig. 1b), meaning that populations tended to decrease in smaller fragments (Fig. S4). This pattern was expected, based on extensive literature documenting the negative effects of fragmentation on biodiversity (Newmark and McNeally, 2018; Pfeifer et al., 2017; Stouffer, 2020) although, again, few studies have assessed the effects of fragmentation on demographic rates using mark-recapture models. Importantly, species affected by temperature in this study were not necessarily the same as those affected by fragment area. By generally examining these stressors separately, scientists may have underestimated the proportion of species negatively affected by anthropogenic change (Saunders et al., 2022). However, the effects of fragment area on population growth rates appeared to be small in magnitude compared to the effects of temperature, despite the relatively large range of fragment sizes. Furthermore, fragment area received comparatively less support than temperature across competing models (Fig. 3), and there was no cross-species effect of fragment area. Thus, in these fragments that have been isolated for decades, even small increases in temperature appear to trump the effects of fragment area. One caveat is that we chose to use fragment area as a proxy for fragmentation in general, and it is possible that more nuanced factors are at play (Banks-Leite et al., 2010; Ferraz et al., 2007). However, we found even less consistent support for fragment isolation as a predictor of demographic rates (Appendix A). Future studies with a higher sample size of fragments may be able to tease apart different mechanisms.

4.2. Combined effects of temperature and fragment area

We found that the population growth rates of 38 % of our focal species (nine species total) were affected by both temperature and fragment area (Table 1, Fig. S3a), including five of the more disturbance-sensitive species and the near-threatened Usambara double-collared sunbird. The consequence of this combination was that population growth rates across species were lowest in the warmest study years (Fig. 2b), and, for more disturbance-sensitive species, lowest in the smallest fragments (Fig. S7b). These more disturbance sensitive species should be a focus of conservation attention due to their sensitivity to these combined threats. However, the combined effects of temperature and area in smaller fragments were less detrimental than either stressor

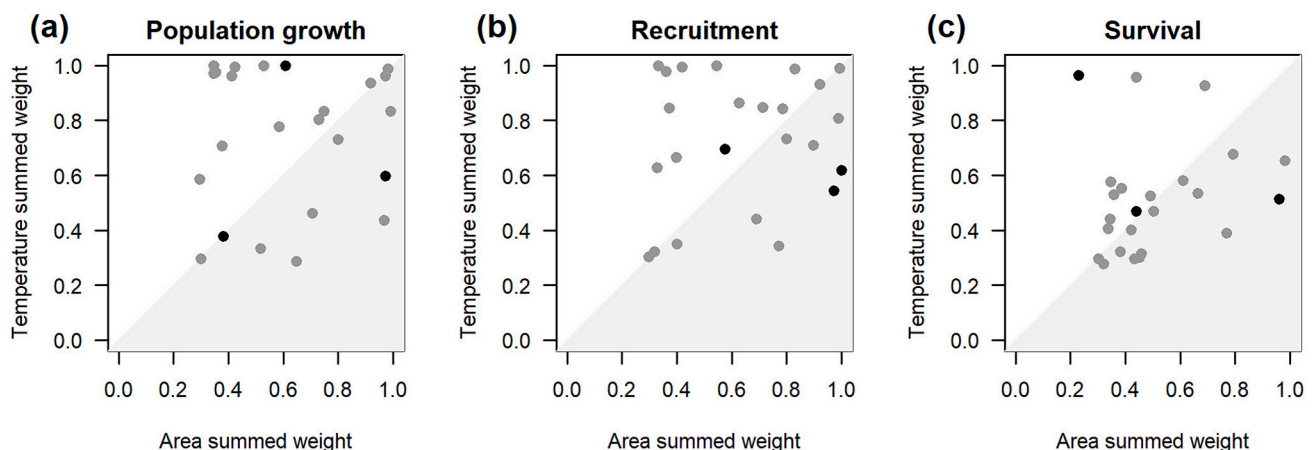


Fig. 3. The relative importance of temperature and fragmentation in the demographic models of Afrotropical bird species over 34 years (1987–2020) in the Usambara Mountains, Tanzania. For (a) realized population growth, (b) recruitment, and (c) apparent survival, the parameters were modeled as a function of temperature and area over several models. The model weights of models containing each covariate were then summed for each species. Three near-threatened, near-endemic species are shown as darker points. In the white segments, temperature had higher summed weight than area; while in the gray segments, area had a higher summed weight.

individually (Fig. 2b). This could be because increasing temperatures and fragmentation are competing risks to birds, i.e., if one stressor substantially reduces a demographic rate, that rate may no longer be sensitive to the other stressor (Folt et al., 1999). Our results over three decades are similar to those found in the Himalayas (Srinivasan and Wilcove, 2021) where declines in apparent survival of high elevation species over 8 years were found in primary forest but not in logged forest.

Of the species with both temperature and fragment area in their top population growth rate model, a third were additive models compared to two-thirds that were interactive models. Within these interactive models, we expected the interactions to be negative synergies, where the negative effect of temperature on population growth rates was more pronounced in smaller fragments (Mac Nally et al., 2009; McLaughlin et al., 2002; Travis, 2003). However, the interactions we found tended to be more nuanced, with the effect of temperature often negative in larger fragments but positive in smaller fragments (Fig. S4). The species showing these conflicting interactions, such as Shelley's greenbul (*Ariazelocichla masukuensis*), tend to be edge-tolerant, moderate dispersers, and common in small forest fragments (Korfanta et al., 2012). These species may be more likely to benefit from anthropogenic change, potentially contributing to biotic homogenization across fragments (de Castro Solar et al., 2015). By contrast, the only species exhibiting a negative synergy in its top population growth rate model was the spot-throat (*Modularix stictigula*), a true interior specialist with negligible gap-crossing ability (Newmark et al., 2010). Population growth rates of spot-throat decreased across study fragments, and more so in smaller fragments during warm years (Fig. S4), demonstrating the synergistic effects of temperature and fragment area on this sensitive species. Indeed, spot-throats are now present in only the three largest fragments of this study, and their disappearance from small fragments led to poor model convergence which excluded the species from subsequent analyses (but see Table S7). It is possible that increasing temperatures are hastening the loss of this species from smaller fragments (Mac Nally et al., 2009; Mantyka-Pringle et al., 2015; McLaughlin et al., 2002), perhaps mediated by changes in microclimate which are less buffered in smaller fragments (Ewers and Banks-Leite, 2013). As a comparison, demographic rates of manakins in Costa Rica were found to be more sensitive to climatic fluctuations in young second growth forest than mature forest (Wolfe et al., 2015).

The lack of evidence for negative synergistic effects in this study could be an artefact of our set of focal species. The often-complex demographic models require large numbers of captures and high recapture rates across fragments. Only a fraction of species in the Usambara Mountains met these criteria, and those species tended to be the most common and therefore potentially the most tolerant of anthropogenic change. By contrast, the species most sensitive to synergies between climate change and fragmentation may be those too rare to sample. Importantly, monitoring in these study fragments began in 1987, decades after the isolation of the fragments (the latest being 1968, but all small fragments were created by 1936). In the intervening decades, baselines will have shifted, and much of the extinction debt owed in these small fragments would likely have been paid (Halley et al., 2016; Stouffer, 2020), especially without secondary growth to facilitate recolonization (Stouffer et al., 2011). Those sensitive species that remained would often be present at very low densities, precluding sample sizes sufficient for this study (Fig. S2, Table S4). As a result, our inference could be biased toward those species that are generally less sensitive to fragmentation.

Our results may indicate that the threats of fragmentation and climate change have acted sequentially in the Usambara Mountains. Initially, following the fragmentation event, the species most sensitive to fragmentation are likely to be lost (Stouffer et al., 2011). Consequently, decades later, at the inception of this study, the persisting species may have been less sensitive to fragmentation, but then have had to contend with increasing temperatures. This reasoning would also help to explain

why fragment area tended to have lower model support (Fig. 3) and less of an effect than temperature on demographic rates (Figs. 1, 2). Although our study is unusual due to its very long-term data on “old” fragments, studies that have monitored birds since the creation of forest fragments would be well-placed to assess the combined impacts of climate change and fragmentation at the inception of isolation, and may indeed find more negative synergies compared to this study.

4.3. Recruitment and apparent survival

For most species in this study, changes in population growth rates were associated largely with changes in recruitment rates, with covariates in the top population growth rate models corresponding to covariates in the top recruitment models (Fig. S3). By contrast, apparent survival was less sensitive to fragment area and temperature, with models containing these stressors receiving low support (Fig. 3c), although temperature and area did appear to have additive effects on survival across species (Fig. 2c). This result follows from other studies demonstrating the greater sensitivity of recruitment rates (Brawn et al., 2017; Neate-Clegg et al., 2021b). Recruitment of new individuals can result from the birth and survival of offspring as well as immigration from other sites. In general, tropical interior understory birds tend to have very low dispersal ability (Lees and Peres, 2009; Sheard et al., 2020) and high site fidelity (Habel et al., 2016), and this includes many of the focal species in this study (Newmark and McNeally, 2018). Recruitment rates are therefore more likely indicative of birth rates and juvenile survival, and these appear to be lower in warmer years for sensitive species. However, there were a number of less disturbance-sensitive species – which tend to have moderate dispersal ability – that showed high recruitment rates in smaller fragments during warmer years (Fig. S7c). For these species, recruitment rates are likely to also include immigration from other fragments. As such, we may be seeing source-sink dynamics acting across the fragments (Runge et al., 2006), where the populations in smaller fragments are rescued by immigration from larger fragments (Stouffer et al., 2011). Warmer years may also produce more abundant resources such as fruit or flowers in smaller fragments – which comprise mainly “edge” habitat – attracting edge-tolerant species (Neate-Clegg et al., 2016; Wright and Calderon, 2006). Thus, species-level differences in recruitment rates in smaller fragments – mediated by differences in dispersal ability – could be contributing to the overall antagonistic effects of temperature and area on population growth rates.

4.4. Near-endemic species

Of particular conservation concern are the three near-threatened, near-endemic species in our species set that are restricted to the Usambara Mountains in addition to some neighboring mountain ranges. Of the three species, Usambara double-collared sunbird was the most negatively affected by temperature, driven by the negative association between temperature and apparent survival (Figs. S4, S6). Usambara thrush, by contrast, was relatively unaffected by temperature, and was instead more sensitive to fragmentation (Figs. S4–S6). Montane tiny greenbul presented an interesting case of relative stability in population growth rates (Fig. S4), despite a negative effect of fragment area on apparent survival (Fig. S6), and an interaction between temperature and fragment area for recruitment rates where rates were more negatively affected by temperature in smaller fragments (Fig. S5). Thus, even among these three near-threatened species, responses to anthropogenic threats can be diverse. The thrush, a terrestrial insectivore, may be more sensitive to fragmentation due to edge effects (Stouffer, 2020), while the sunbird, a tiny nectarivore, may be more sensitive to changes in flower production or physiological stress. Finally, the interaction effect for montane tiny greenbul could reflect the fact that low recruitment in large fragments is balanced by high survival – with both rates buffered against temperature increases – but that recruitment rates in smaller

fragments, despite being high to begin with, are more sensitive to temperature increases due possibly to strong edge effects that limit the habitat quality and resource availability of small fragments. Together, the findings for these species highlight the need to understand nuanced, species-specific responses to anthropogenic change when conservation planning.

Although the remaining species in this study are currently listed as Least Concern, conservation planners should still focus efforts toward ameliorating the effects of climate change and fragmentation before populations reach the stage of being threatened, and this is especially true for species such as spot-throat that are imperiled by both stressors simultaneously.

5. Conclusion

Across 24 Afrotropical bird species we found that the majority were negatively affected by increasing temperatures and, to a lesser degree, decreasing fragment area. However, the ways in which temperature and area combined to impact demographic rates were diverse. Assessing either of these anthropogenic threats in isolation provides an incomplete picture which hinders both our understanding and the development of effective conservation strategies. We know that understory birds in the Usambara Mountains are shifting their elevational ranges upslope with increasing temperatures, but that fragmentation appears to be inhibiting this process (Neate-Clegg et al., 2021c). This study adds to that picture by showing that these same species are facing population declines due to both temperature and fragmentation. Together, these studies demonstrate the vulnerability of Afromontane birds to the combined effects of climate change and fragmentation, vulnerability that is likely prevalent elsewhere in the tropics (Harris et al., 2014a; Mantyka-Pringle et al., 2015; Srinivasan and Wilcove, 2021). Reforestation of linkages among the largest forest fragments could help to reduce both of these threats (Newmark et al., 2017) and thus enhance the capacity of Afromontane birds to resist the combined effects of climate change and fragmentation.

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Ethics statement

All bird banding conformed to the Bander's Code of Ethics (USGS) and the Code of Ethics on Animal Research (BTO). Research permits were granted by the Tanzania Wildlife Research Institute and Tanzania Commission for Science and Technology.

CRedit authorship contribution statement

Montague H.C. Neate-Clegg: Conceptualization, Methodology, Software, Formal analysis, Investigation, Writing – original draft, Visualization, Project administration. **Matthew A. Etersson:** Methodology, Writing – review & editing. **Morgan W. Tingley:** Methodology, Writing – review & editing, Visualization, Supervision. **William D. Newmark:** Conceptualization, Methodology, Investigation, Resources, Data curation, Supervision, Project administration, Funding acquisition.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence

the work reported in this paper. The views expressed in this article are those of the authors and do not necessarily represent the views or policies of the USEPA. Any mention of trade names, products, or services does not imply an endorsement by the USEPA.

Data availability

Data will be made available on request.

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Appendix A. Supporting Information

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