

RESEARCH ARTICLE

The climatic drivers of long-term population changes in rainforest montane birds

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Abstract

Climate-driven biodiversity erosion is escalating at an alarming rate. The pressure imposed by climate change is exceptionally high in tropical ecosystems, where species adapted to narrow environmental ranges exhibit strong physiological constraints. Despite the observed detrimental effect of climate change on ecosystems at a global scale, our understanding of the extent to which multiple climatic drivers affect population dynamics is limited. Here, we disentangle the impact of different climatic stressors on 47 rainforest birds inhabiting the mountains of the Australian Wet Tropics using hierarchical population models. We estimate the effect of spatiotemporal changes in temperature, precipitation, heatwaves, droughts and cyclones on the population dynamics of rainforest birds between 2000 and 2016. We find a strong effect of warming and changes in rainfall patterns across the elevational-segregated bird communities, with lowland populations benefiting from increasing temperature and precipitation, while upland species show an inverse strong negative response to the same drivers. Additionally, we find a negative effect of heatwaves on lowland populations, a pattern associated with the observed distribution of these extreme events across elevations. In contrast, cyclones and droughts have a marginal effect on spatiotemporal changes in rainforest bird communities, suggesting a species-specific response unrelated to the elevational gradient. This study demonstrated the importance of unravelling the drivers of climate change impacts on population changes, providing significant insight into the mechanisms accelerating climate-induced biodiversity degradation.

KEYWORDS

Australian Wet Tropics, climate change, elevational shift, escalator to extinction, hierarchical models, population dynamics, rainforest birds, tropical rainforest

1 | INTRODUCTION

Climate change has exposed biodiversity to unprecedented conditions, significantly altering ecosystem structure and resilience in most regions (Hoegh-Guldberg et al., 2018). In the last decades, among

thousands of species spread across terrestrial, marine and freshwater systems, half to two-thirds have shifted their range in response to warming (Chen et al., 2011; Pecl et al., 2017; Pörtner et al., 2022). As a result, climate-induced distributional shifts have caused severe declines in nearly half of all studied populations (Pörtner et al., 2022).

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The degree of population loss and biodiversity erosion is highest in the tropics, where local extirpation is more common than anywhere else in the world (Pörtner et al., 2022). Within tropical ecosystems, montane species have suffered significant losses across their lower elevational limit, increasing their geographical isolation and probability of extinction (Freeman et al., 2018; Neate-Clegg et al., 2021; Pounds et al., 1999; Williams & de la Fuente, 2021).

Understanding the mechanisms behind species' responses to climate change is critical in an era of increasing biodiversity loss. Most studies have focussed on quantifying the magnitude of ecological responses to climate change by studying species' range shifts (Chen et al., 2011). Despite the important efforts of documenting how species track global warming (Freeman et al., 2021), we still lack a comprehensive understanding of the extent to which different components of climate change impact natural populations (Parmesan, 2006; Parmesan et al., 2000; Pearce-Higgins et al., 2015). By examining the mechanisms underlying climate-induced ecological responses, we can gain insights into how best to conserve and protect vulnerable species in the face of ongoing environmental changes.

In the Wet Tropics of North Queensland, Australia, rainforest bird populations have long been predicted to experience significant biodiversity loss due to climate change (Williams et al., 2003). These predictions are now coming true with extraordinary spatiotemporal shifts in bird species distributions and abundance in response to climate change in just a few decades (Williams et al., 2016; Williams & de la Fuente, 2021). Lowland species have increased their abundance by 190% at higher elevations, indicating a marked upward shift. In contrast, upland species have proportionally declined across their entire distribution, resulting in nearly 50% population loss (Williams & de la Fuente, 2021). Similarly, the populations of rainforest ringtail possums are collapsing at an alarming rate in the highlands of the region over the same period (de la Fuente & Williams, 2022), evidencing the high vulnerability of tropical upland ecosystems. The accelerated biodiversity loss in the Australian Wet Tropics rapidly translated into an urgent call for conservation actions (Williams & de la Fuente, 2021), with one-third of the studied species being incorporated into national and international priority conservation lists (Garnett & Baker, 2021). However, adequate and targeted management plans will rely on our understanding of the mechanistic drivers impacting rainforest bird populations, as conservation strategies can markedly vary depending on the nature of the climatic stressor (Garcia et al., 2014).

In this study, we unravelled the drivers of climate change impacts on rainforest birds in the Australian Wet Tropics, representing a substantial advance in our understanding of how climate change leads to population changes. We analysed the long-term population dynamics of rainforest birds and their relationship with multiple climatic stressors. We used spatially and temporally explicit climate data to develop predictors capturing regional changes in temperature and precipitation. Long-term climate change included overall changes in average temperature and precipitation patterns, while short-term climatic variables accounted for extreme weather events, such as extreme heatwaves and intense droughts. Additionally, we incorporated a dynamic vegetation index that captured the apparent forest structural damage

caused by tropical cyclones across the study area. We analysed the population dynamics using a hierarchical model, estimating spatiotemporal abundance changes while accounting for imperfect detection. We aimed to examine the hypothesis that regional warming is causing strong population changes across rainforest bird communities (Urban, 2018; Williams & de la Fuente, 2021). However, we also expected a substantial proportion of the observed population changes to be explained by a combination of multiple climatic drivers, as the effect of different climatic factors could act synergistically.

2 | MATERIALS AND METHODS

2.1 | Study area

The Wet Tropics of Queensland stretches along the northeast coast of Australia, encompassing approximately 7000 km² of mixed tropical rainforest (Figure 1). The outstanding biodiversity that characterizes the bioregion persists in large, unfragmented areas of protected rainforest in the rugged terrain dominated by mountain ranges, tablelands, foothills and a lowland coastal plain (Figure S1). The strong elevational gradient defines the biodiversity composition and ecological processes in the region (Williams et al., 1995), segregating species into three predominant communities: lowland (0–300 m), midland (300–900 m) and upland community (>900 m).

2.2 | Population data

The bird monitoring scheme in the Australian Wet Tropics was established in 1996 and expanded in 2000 to cover a total of 124 survey locations distributed across 24 independent sites (Figure 1; Table S1). Sites were established in large, unfragmented patches of rainforest away from edges and covered the elevational gradient of the four main mountain ranges in the region (Spec Uplands, Atherton Uplands, Carbine Uplands and Windsor Uplands). An intensive monitoring effort was conducted across all sites between 2000 and 2016, compiling a total of 1977 samples in 495 independent surveys (de la Fuente et al., 2023). Two observers surveyed 150 m long transects for 30 min within 2 h of sunrise. All individual birds were identified by call or observation, and the weather conditions during the survey were recorded to account for potential detection bias. Of the 54 species monitored, analyses of spatiotemporal population dynamics were possible for 47 species with robust data across sites and years (Table S2). Further details of survey methods, total species observed, sites characteristics and species traits can be found in Williams and de la Fuente (2021); Williams, VanDerWal, et al. (2010); Williams, Shoo, et al. (2010).

2.3 | Environmental data

Spatially and temporally explicit environmental variables were derived from gridded climatology data at 0.05° (~5 km) resolution, using daily

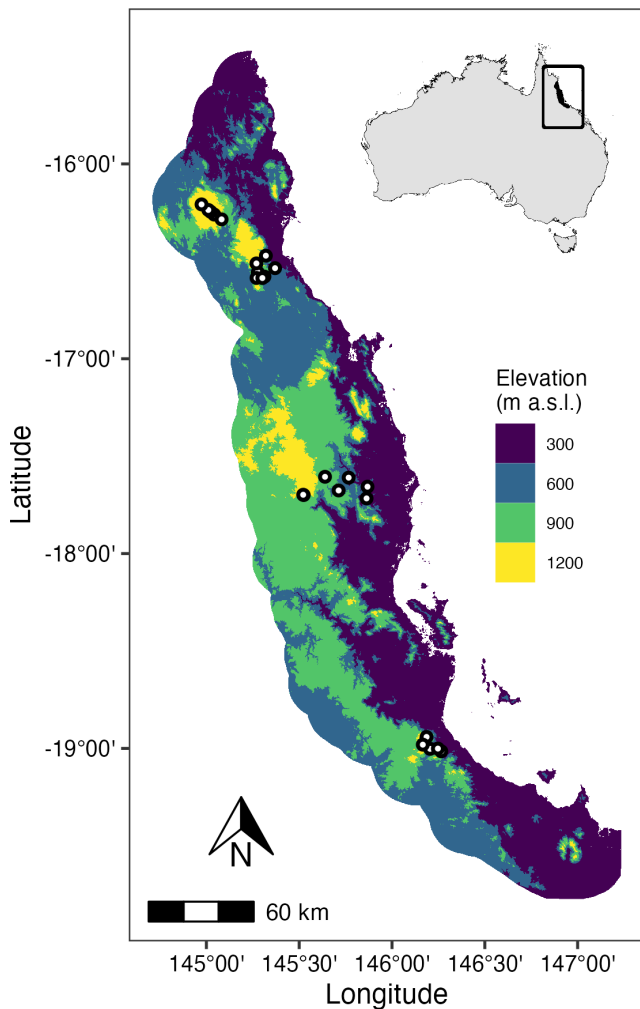


FIGURE 1 The Australian Wet Tropics World Heritage Area and its location within Australia. The colour gradient represents the main elevational bands that define species assemblages across the region. White points depict the location of the survey sites established in the four main mountain ranges of the bioregion (Table S1).

maximum and minimum temperature (Bureau of Meteorology, 2021) and daily precipitation (Frost et al., 2018) between 1965 and 2019. We used a longer climatic time series compared to the ecological data (1965–2016 vs. 2000–2016) to better capture the long-term regional climate change. The accuracy of the interpolated climatic grids was validated against observed data from regional weather stations (Cairns' airport, 3 m a.s.l., and Walkamin Research Station, 594 m a.s.l.), obtaining 96% and 99% correlation for temperature and precipitation data respectively.

We developed four climatic predictors that captured long-term climatic changes and short-term seasonal extreme events across the spatiotemporal range of the study (2000–2016; Figure S2–S6). Long-term changes in mean temperature and precipitation were obtained using a 25-year window average. Short-term seasonal climatic indices (i.e. extreme heatwaves and intense droughts) were obtained by calculating the area under the curve defined between the climatic variable

and a biologically relevant threshold (de la Fuente et al., 2021). The threshold to define the curve was derived from the 97.5th and 2.5th percentile of daily maximum temperature and monthly precipitation across the species' climatic envelope respectively. Thus, these indices represent the intensity and duration of extreme conditions (temperatures above 35°C and monthly precipitation below 10mm) at a specific site and time relative to the species' environmental range, with a high index indicating intense and prolonged exposure. In contrast, a low index indicates sites close to the lowest species exposure across its distribution at a specific time (de la Fuente et al., 2023).

In addition to the climatic predictors, we included a spatiotemporal normalized difference vegetation index (NDVI) index generated using cloud-free images from the Landsat 5 TM and Landsat 8 OLI/TIRS satellites (Foga et al., 2017; Li et al., 2010). We created annual composites of all the images within a natural year between 1987 and 2021 and extracted the median values of NDVI for each 30m pixel within the Australian Wet Tropics. A detailed explanation of how the annual composites were obtained can be found in Navarro et al. (2021). To avoid errors associated with using single pixels (e.g. pixels that fall within roads or water features), we applied a buffer of 0.01° (~1 km) around each of our study sites and calculated the median value of all the pixels within the buffer. The NDVI predictor aimed to capture the structural vegetation changes across sites impacted by tropical cyclones (Figure S2), accounting for potential cyclone-induced mortality and the recovery time of the rainforest vegetation. Short-term extreme events and NDVI fluctuation were included in the model with 1 year delay as we expected a potential immediate effect on population dynamics (observable during the following survey season).

2.4 | Statistical analysis

We used a binomial N-mixture model to analyse the temporal variation in rainforest bird populations in response to the explicit spatiotemporal effect of climatic changes (Kéry et al., 2009; Kéry & Royle, 2020). The N-mixture model is a hierarchical model that uses replicated count data to obtain realistic ecological estimates of species abundance while accounting for imperfect detection (Royle, 2004). Thus, the hierarchical model comprises two linked components, explicitly describing the ecological and observation processes (Goldstein & de Valpine, 2022; Royle, 2004).

The ecological process assumes that abundance (N_{it}) at site i and year t follows a Poisson distribution with mean λ_{it} :

$$N_{it} \sim \text{Poisson}(\lambda_{it}).$$

The expected abundance was then modelled as the response to climate change in its multiple dimensions:

$$\log(\lambda_{it}) = \alpha + \beta_c x_{itc} + \omega_i,$$

where α defines the model's intercept, β_c represents the effect of the c -th covariate with value x_{itc} (see Section 2.3) and ω_i accounts for the unmodelled spatial variation in abundance.

The observation process assumes that detection probability ρ is represented by the observed counts (y_{jt}) sampled from the local population (N_{jt}) in each replicate j (C_{ijt}), described by a binomial distribution:

$$C_{ijt} | N_{jt} \sim \text{Binomial}(N_{jt}, p_{ijt}).$$

The expected detection probability was then modelled as the response to the weather conditions during the survey to account for adverse weather affecting bird detection (rain and wind; Robbins (1981)). Additionally, we included the date when the survey was conducted to account for seasonal variation in detection probability (linear and quadratic effect):

$$\text{logit}(p_{ijt}) = \alpha_t + \beta_d x_{ijtd} + \varepsilon_{ijt},$$

where α_t defines the intercept for detection fitted for each year, β_d represents the effect of the d -th detection covariate with value x_{ijtd} and ε_{ijt} accounts for the extra unexplained heterogeneity among surveys.

We fitted the open-population N-mixture model using Bayesian inference. Markov Chain Monte Carlo methods were used to sample the joint posterior distribution (Thompson & Brooks, 2003) using JAGS software (Plummer, 2003), called from R (R Core Team, 2021), with the *jagsUI* package (Kellner, 2021). We ran three parallel chains of 200,000 iterations each, used the first half as burn-in, and thinned the rest by one in 100 to obtain 3000 samples of the joint posterior distribution. The sampling process led to acceptable convergence of all parameters ($\hat{R} - 1 < .1$, Gelman & Hill, 2006). We examined the adequacy of the model by computing a Bayesian p -value, with values close to .5 (0.47 ± 0.036) indicating a good fit for all species modelled. We expressed the absence of prior information about the model parameter by implementing vague priors. We selected uniform distributions (-5, 5) for the effect of covariates, uniform distribution (0, 1) for the intercepts and a normal distribution for the overdispersion factor in the abundance and detection model, with a mean of 0 and precision derived from a standard deviation defined by a uniform distribution (0,100). The JAGS code is available in [Supporting Information](#).

3 | RESULTS

The climate of the Australian Wet Tropics has markedly changed during the last five decades. The annual mean temperature has linearly increased in the region at a rate of $0.013 \pm 0.002^\circ\text{C}/\text{year}$, a pattern conserved across latitude and elevation (Figure S3). Rainfall patterns showed high year-to-year variability within sites, resulting in a marginal overall long-term change ($0.07 \pm 0.11 \text{ mm}/\text{year}$; Figure S4). The derived pattern in extreme heatwaves showed marked differences across elevation but no latitude, with lowland sites showing a stronger increase in the frequency and intensity of heatwaves compared to the more stable upland sites ($0.23 \pm 0.07^\circ\text{C}/\text{year}$ for the lowlands; $0.07 \pm 0.02^\circ\text{C}/\text{year}$ for the uplands; Figure S5). A trend in intense droughts was not evident across the study area, although an overall marginal decrease was observed in lowland sites (i.e. precipitation has increased during the dry season; $-0.04 \pm 0.02 \text{ mm}/$

year; Figure S6). The NDVI time series showed the predicted 'valleys' associated with the two high-magnitude tropical cyclones that hit the eastern rainforest areas in the region in 2006 (cyclone Larry) and 2011 (cyclone Yasi), indicating substantial damages to the forest structure. However, the NDVI index suggested a full apparent vegetation recovery within a year (Figure S2).

The population dynamics of rainforest birds in the Australian Wet Tropics showed strong responses to the observed spatiotemporal climatic changes (Figure 2). The effects of climate change on population dynamics were markedly strong at the community level (Figure 2), denoting a high synchronization in the species' responses across elevation. The synchronic responses to climate change were especially significant within mountaintops and lowland communities, while species inhabiting the midlands gradually shifted in their response across the elevational gradient (Figure 2). The gradual shift in the response of midland species resulted in a weak community effect, cancelling the mean community response (Figure 2; Figure S7).

Long-term changes in rainforest bird populations were strongly driven by gradual regional warming, with 72% of all rainforest birds showing a significant response to the increase in mean annual temperature (Table 1). The observed increase in temperature across the bioregion induced a highly symmetric response across the elevational gradient. Communities inhabiting rainforests below 600m showed a strong positive effect to an increase in temperature, while mountaintop species showed an inverse, marked negative response to warming (Figure 2a). A similar pattern was observed for the impact of changes in rainfall patterns (Figure 2b), with communities inhabiting more seasonally drier lowland areas showing a positive response to an increase in precipitation, while communities restricted to wetter upland forests showed a negative response. Short-term extreme events showed a weaker effect on bird population dynamics (Table 1; Figure 2c-e). However, lowland birds revealed an overall negative response to heatwaves (Figure 2c), suggesting that despite the positive influence of long-term warming, lowland species could be susceptible to the observed increase in the frequency of extreme temperatures in the region. The response of rainforest birds to changes in NDVI and drought intensity showed great uncertainty among communities (Figure 2d,e). Thus, the local effect of cyclones and rainfall patterns during the dry season (Figure S2; Figure S6) suggested a marginal effect on the overall observed changes in rainforest bird communities across elevation.

The variability in detection probability for rainforest birds was largely captured by the weather conditions during the survey. Species showed a decrease in detectability with an increase in rain and wind, as expected for survey methods relying on animal vocalization (Figure S8). Additionally, the date variables showed strong but heterogeneous responses among species (Figure S8), indicating that the time of the season when detection was maximized was species specific.

4 | DISCUSSION

Climate change is eroding the bird community of the Australian Wet Tropics at an accelerating rate. Our results indicate, with high

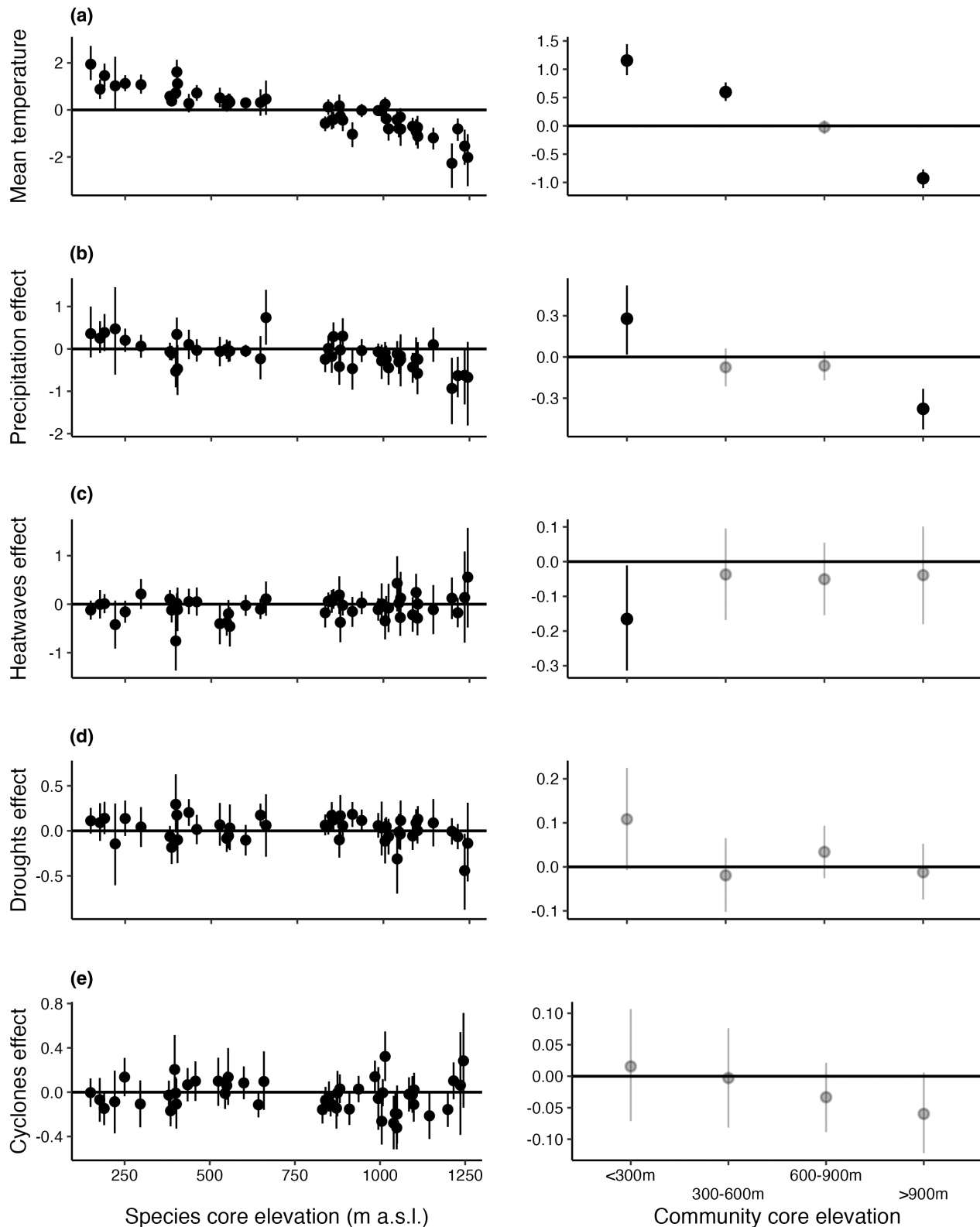


FIGURE 2 Rainforest bird communities' response to climate change in the Australian Wet Tropics. Values represent the posterior mean and 95% credible interval of the effect of the climatic variables on 47 bird species across the elevational gradient (left) and across the elevational-segregated communities (right). Panels (a) to (e) represent the response of rainforest birds to changes in mean temperature, precipitation, heatwaves, droughts, and cyclones, respectively.

confidence, that rainforest bird abundances have changed in response to a substantial increase in temperature, followed by changes in precipitation patterns and an increase in extreme heatwaves in

the lowlands. Contrastingly, cyclones and intense droughts have a marginal effect on population dynamics at the community level. By separating the effects of multiple climatic stressors on the rainforest

TABLE 1 Summary response of 47 rainforest bird species to multiple climatic drivers in the Australian Wet Tropics. The overall response refers to the percentage of species sharing a positive/negative slope (posterior mean). The significant response refers to the percentage of species sharing a positive/negative slope with a 95% CRI not overlapping zero.

Climatic driver	Overall response (%)		Significant response (%)		
	Negative	Positive	Negative	Positive	Total
Mean temperature	24 (51%)	23 (49%)	18 (38%)	16 (34%)	34 (72%)
Precipitation	34 (72%)	13 (28%)	9 (19%)	1 (2%)	10 (21%)
Heatwaves	26 (55%)	21 (45%)	3 (6%)	0 (0%)	3 (6%)
Droughts	18 (38%)	29 (62%)	1 (2%)	5 (11%)	6 (13%)
Cyclones	30 (64%)	17 (36%)	7 (15%)	1 (2%)	8 (17%)

bird community of the Australian Wet Tropics, our results provide a substantial advance in understanding the mechanisms behind climate-induced biodiversity erosion.

The steady increase in temperature in the bioregion (0.673–0.731°C between 1965 and 2019) aligns with the observed global trends (Hoegh-Guldberg et al., 2018) and regional forecasts (Suppiah et al., 2007). In line with early predictions (Shoo et al., 2005; Williams et al., 2003), our results indicate that the rapid increase in average temperature in the Australian Wet Tropics strongly affects bird communities (Figure 2a). Bird populations show a clear pattern of an ‘escalator to extinction’ (Marris, 2007; Urban, 2018), where lowland species benefit from an early increase in temperature as they expand into higher elevations (Williams & de la Fuente, 2021). Contrastingly, upland-restricted species experience a niche contraction that leads to marked population declines (Williams & de la Fuente, 2021), leaving mountaintop species restricted to a smaller area with a higher risk of extinction (Pörtner et al., 2022; Urban, 2018). These results concur with the overwhelming evidence worldwide, with 50% of all studied populations showing a decline attributable to an increase in temperature, with extirpations becoming more common (55%) in tropical ecosystems (Pörtner et al., 2022).

Aligning with regional climate forecasts (Suppiah et al., 2007), rainfall has shown marked oscillations during the last decades in the Australian Wet Tropics. Our results suggest a tight association between long-term rainfall changes and population dynamics, potentially revealing the bottom-up effect that rainfall could impose on bird populations through primary productivity (Williams, Shoo, et al., 2010). For example, Schuur (2003) suggests that changes in rainfall and temperature could induce contrasting patterns in productivity in tropical montane ecosystems. Thus, an increase in rainfall could reduce primary productivity in the uplands due to water saturation while increasing productivity in the lowlands due to a reduction in water stress (Clark et al., 2001; Girardin et al., 2010; Schuur & Matson, 2001). This pattern matches the prediction of Albrecht's curve (Albrecht, 1957), with forest productivity increasing from the seasonally drier lowlands to a maximum at intermediate precipitation levels in the midlands and then declining in the wetter uplands. The potential decrease in productivity with precipitation in the highlands of the regions could thus be related to the decline in soil fertility as precipitation exceeds potential evapotranspiration (Cramer & Hoffman, 2015; Huston, 2012). The expected relationship between rainfall and primary productivity in tropical mountains aligns with the inverse response to precipitation shown by lowland and

mountaintop bird communities in this study (Figure 2b). Moreover, van de Weg et al. (2014) suggest that the relationship between gross primary productivity and rainfall is unrelated to drought intensity, potentially explaining the weaker link between droughts and bird population dynamics across the elevational gradient (Figure 2d). Thus, combined, the strong impact of long-term rainfall and the marginal effect of drought intensity on rainforest birds reinforces the expected association between primary productivity and population dynamics in tropical mountains (Williams, Shoo, et al., 2010).

The rising number of hot days leads to more intense and frequent extreme heatwaves in the Australian Wet Tropics, which are responsible for severe population declines of tropical montane vertebrates in the region (de la Fuente & Williams, 2022). Heatwaves are becoming widespread at lower elevations, aligning with the predicted early emergence of extreme temperatures in tropical ecosystems due to the low interannual temperature variability (Hoegh-Guldberg et al., 2018). The effect of heatwaves shows high inter-specific variability across populations, but community averages indicate an overall negative effect on lowland species (Figure 2c). These results suggest that extreme heatwaves could be causing rapid population declines in lowland communities near their upper thermal limit. Interestingly, our results highlight the contrasting effects of long-term and short-term temperature changes on rainforest bird communities. On the one hand, lowland species could benefit from long-term warming due to an upward habitat expansion (de la Fuente et al., 2022). On the other hand, extreme heatwaves could cause direct population declines, affecting the year-to-year population fluctuation. Lowland species' sensitivity to extreme temperatures could result in an overall lowland biotic attrition (Colwell et al., 2008), with no species available to fill the emptying niches in lowland rainforests.

NDVI dynamics had a marginal effect on bird communities during the study period, suggesting a species-specific response unrelated to elevation. In this regard, the observed negative response to an increase in NDVI shown by some species could be related to forest gap preference (Schemske & Brokaw, 1981). This pattern is well exemplified by species such as the spangled drongo (*Dicrurus bracteatus*; NDVI mean effect (95% credible interval) = -0.28 (-0.52 , -0.03)), which avoids dense and interior rainforest, as their feeding strategy and breeding behaviour are strongly linked to clearings (Briggs, 2016; Higgins et al., 2006). Thus, the observed fast vegetation recovery after cyclones (Figure S2) could explain the negative influence of NDVI on species that benefit from forest gaps,

highlighting the impact of cyclone-induced gap dynamics on the bird community structure (Schemske & Brokaw, 1981).

This study demonstrates the importance of unravelling the drivers of climate change impacts on communities (Pearce-Higgins et al., 2015), providing significant insight into the mechanisms accelerating climate-induced biodiversity degradation (Parmesan, 2006; Parmesan et al., 2000). The climate-driven biodiversity emergency is alarming in the Australian Wet Tropics World Heritage Area (de la Fuente & Williams, 2022; Williams & de la Fuente, 2021), a fully protected and well-managed ecosystem. The response of rainforest birds to environmental changes shown in this study is not unique. Our results align with the observed impacts of climate change across many regions and taxa (Brawn et al., 2017; Chen et al., 2011; Couet et al., 2022; Freeman et al., 2018, 2021; Neate-Clegg et al., 2018, 2021), suggesting a widespread pattern of biodiversity impoverishment in montane ecosystems worldwide (La Sorte & Jetz, 2010). Near-term warming reduction in the following decades might now be beyond reach (Pörtner et al., 2022), threatening the imminent extirpation of mountaintop communities (Colwell et al., 2008; Freeman et al., 2018). The ubiquitous pattern of ecosystem erosion worldwide is particularly concerning in tropical mountains, as they hold a disproportionate amount of global biodiversity (Quintero & Jetz, 2018) and host unique ecosystem services (Korner & Spehn, 2019).

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CONFLICT OF INTEREST STATEMENT

The authors declare no conflict of interest.

DATA AVAILABILITY STATEMENT

The data that support the findings of this study are openly available in Dryad at <https://doi.org/10.5061/dryad.hx3ffbgjj>. The JAGS code to recreate the models is included in [Supporting Information](#).

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REFERENCES

- Albrecht, W. A. (1957). Soil fertility and biotic geography. *Geographical Review*, 47(1), 86–105. <https://doi.org/10.2307/212191>
- Brawn, J. D., Benson, T. J., Stager, M., Sly, N. D., & Tarwater, C. E. (2017). Impacts of changing rainfall regime on the demography of tropical birds. *Nature Climate Change*, 7(2), 133–136. <https://doi.org/10.1038/nclimate3183>
- Briggs, A. (2016). Breeding behaviour in the spangled Drongo “*Dicrurus bracteatus*”. *Australian Field Ornithology*, 33, 83–89. <https://doi.org/10.20938/af033083089>
- Bureau of Meteorology. (2021). *Climate data online*. http://www.bom.gov.au/climate/averages/tables/cw_031108.shtml
- 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 warming. *Science*, 333(6045), 1024–1026. <https://doi.org/10.1126/science.1206432>
- Clark, D. A., Brown, S., Kicklighter, D. W., Chambers, J. Q., Thomlinson, J. R., Ni, J., & Holland, E. A. (2001). Net primary production in tropical forests: An evaluation and synthesis of existing field data. *Ecological Applications*, 11(2), 371–384. [https://doi.org/10.1890/1051-0761\(2001\)011\[0371:NPPITF\]2.0.CO;2](https://doi.org/10.1890/1051-0761(2001)011[0371:NPPITF]2.0.CO;2)
- 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(5899), 258–261. <https://doi.org/10.1126/science.1162547>
- Couet, J., Marjakangas, E.-L., Santangeli, A., Kålås, J. A., Lindström, Å., & Lehtikoinen, A. (2022). Short-lived species move uphill faster under climate change. *Oecologia*, 198(4), 877–888. <https://doi.org/10.1007/s00442-021-05094-4>
- Cramer, M. D., & Hoffman, M. T. (2015). The consequences of precipitation seasonality for Mediterranean-ecosystem vegetation of South Africa. *PLoS One*, 10(12), e0144512. <https://doi.org/10.1371/journal.pone.0144512>
- de la Fuente, A., Hirsch, B. T., Cernusak, L. A., & Williams, S. E. (2021). Predicting species abundance by implementing the ecological niche theory. *Ecography*, 44(11), 1723–1730. <https://doi.org/10.1111/ecog.05776>
- de la Fuente, A., Krockenberger, A., Hirsch, B. T., Cernusak, L. A., & Williams, S. E. (2022). Predicted alteration of vertebrate communities in response to climate-induced elevational shifts. *Diversity and Distributions*, 28, 1180–1190. <https://doi.org/10.1111/ddi.13514>
- de la Fuente, A., Navarro, A., & Williams, S. (2023). The climatic drivers of long-term population changes in rainforest montane birds. <https://doi.org/10.5061/dryad.hx3ffbgjj>
- de la Fuente, A., & Williams, S. (2022). Climate change threatens the future of rainforest ringtail possums by 2050. *Diversity and Distributions*, 00, 1–11. <https://doi.org/10.1111/ddi.13652>
- Foga, S., Scaramuzza, P. L., Guo, S., Zhu, Z., Dilley, R. D., Beckmann, T., Schmidt, G. L., Dwyer, J. L., Hughes, M. J., & Laue, B. (2017). Cloud detection algorithm comparison and validation for operational Landsat data products. *Remote Sensing of Environment*, 194, 379–390. <https://doi.org/10.1016/j.rse.2017.03.026>
- Freeman, B. G., Scholer, M., Ruiz-Gutierrez, V., & Fitzpatrick, J. (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(47), 11982–11987. <https://doi.org/10.1073/pnas.1804224115>
- Freeman, B. G., Song, Y., Feeley, K. J., & Zhu, K. (2021). Montane species track rising temperatures better in the tropics than in the temperate zone. *Ecology Letters*, 24(8), 1697–1708. <https://doi.org/10.1111/ele.13762>
- Frost, A., Ramchurn, A., & Smith, A. (2018). *The Australian landscape water balance model*. Bureau of Meteorology. https://awo.bom.gov.au/assets/notes/publications/AWRA-Lv7_Model_Description_Report.pdf
- García, R. A., Cabeza, M., Rahbek, C., & Araújo, M. B. (2014). Multiple dimensions of climate change and their implications for biodiversity. *Science*, 344(6183), 1247579. <https://doi.org/10.1126/science.1247579>

- Garnett, S. T., & Baker, G. B. (2021). *The action plan for Australian birds 2020*. <https://doi.org/10.1071/9781486311910>
- Gelman, A., & Hill, J. (2006). *Data analysis using regression and multi-level/hierarchical models*. Cambridge University Press. <https://doi.org/10.1017/CBO9780511790942>
- Girardin, C. A. J., Malhi, Y., Aragão, L. E. O. C., Mamani, M., Huaraca Huasco, W., Durand, L., Feeley, K. J., Rapp, J., Silva-Espejo, J. E., Silman, M., Salinas, N., & Whittaker, R. J. (2010). Net primary productivity allocation and cycling of carbon along a tropical forest elevational transect in the Peruvian Andes. *Global Change Biology*, 16(12), 3176–3192. <https://doi.org/10.1111/j.1365-2486.2010.02235.x>
- Goldstein, B. R., & de Valpine, P. (2022). Comparing N-mixture models and GLMMs for relative abundance estimation in a citizen science dataset. *Scientific Reports*, 12(1), 12276. <https://doi.org/10.1038/s41598-022-16368-z>
- Higgins, P. J., Peter, J. M., & Cowling, S. J. (2006). *Handbook of Australian, New Zealand & Antarctic birds, Vol. 7: Boatbill to Starlings* (P. J. Higgins, Ed.). Oxford University Press.
- Hoegh-Guldberg, O., Jacob, D., Bindi, M., Brown, S., Camilloni, I., Diedhiou, A., Djalante, R., Ebi, K., Engelbrecht, F., & Guiot, J. (2018). *Impacts of 1.5 C global warming on natural and human systems. Global warming of 1.5 C. an IPCC special report*. <https://www.ipcc.ch/sr15/chapter/chapter-3/>
- Huston, M. A. (2012). Precipitation, soils, NPP, and biodiversity: Resurrection of Albrecht's curve. *Ecological Monographs*, 82(3), 277–296. <https://doi.org/10.1890/11-1927.1>
- Kellner, K. (2021). *jagsUI: A wrapper around 'rjags' to streamline 'JAGS' analyses*. R package (Version 1.5.2). <https://CRAN.R-project.org/package=jagsUI>
- Kéry, M., Dorazio, R. M., Soldaat, L., Van Strien, A., Zuiderwijk, A., & Royle, J. A. (2009). Trend estimation in populations with imperfect detection. *Journal of Applied Ecology*, 46(6), 1163–1172. <https://doi.org/10.1111/j.1365-2664.2009.01724.x>
- Kéry, M., & Royle, J. A. (2020). *Applied hierarchical modeling in ecology: Analysis of distribution, abundance and species richness in R and BUGS: Vol. 2: Dynamic and advanced models*. Academic Press.
- Korner, C., & Spehn, E. M. (2019). *Mountain biodiversity: A global assessment* (Vol. 7). Routledge.
- La Sorte, F. A., & Jetz, W. (2010). Projected range contractions of montane biodiversity under global warming. *Proceedings of the Royal Society B: Biological Sciences*, 277(1699), 3401–3410. <https://doi.org/10.1098/rspb.2010.0612>
- Li, F., Jupp, D. L. B., Reddy, S., Lymburner, L., Mueller, N., Tan, P., & Islam, A. (2010). An evaluation of the use of atmospheric and BRDF correction to standardize Landsat data. *IEEE Journal of Selected Topics in Applied Earth Observations and Remote Sensing*, 3(3), 257–270. <https://doi.org/10.1109/JSTARS.2010.2042281>
- Marris, E. (2007). The escalator effect. *Nature Reports Climate Change*, 1, 94–96. <https://doi.org/10.1038/climate.2007.70>
- Navarro, A., Young, M., Macreadie, P. I., Nicholson, E., & Ierodiaconou, D. (2021). Mangrove and saltmarsh distribution mapping and land cover change assessment for south-eastern Australia from 1991 to 2015. *Remote Sensing*, 13(8), 1450. <https://www.mdpi.com/2072-4292/13/8/1450>
- 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(5), 805–815. <https://doi.org/10.1111/btp.12596>
- Neate-Clegg, M. H. C., Stanley, T. R., Şekercioğlu, Ç. H., & Newmark, W. D. (2021). Temperature-associated decreases in demographic rates of Afrotropical bird species over 30 years. *Global Change Biology*, 27(10), 2254–2268. <https://doi.org/10.1111/gcb.15567>
- Parmesan, C. (2006). Ecological and evolutionary responses to recent climate change. *Annual Review of Ecology, Evolution, and Systematics*, 37, 637–669. <https://doi.org/10.1146/annurev.ecolsys.37.091305.110100>
- Parmesan, C., Root, T. L., & Willig, M. R. (2000). Impacts of extreme weather and climate on terrestrial biota. *Bulletin of the American Meteorological Society*, 81(3), 443–450. [https://doi.org/10.1175/1520-0477\(2000\)081<0443:IOEWAC>2.3.CO;2](https://doi.org/10.1175/1520-0477(2000)081<0443:IOEWAC>2.3.CO;2)
- Pearce-Higgins, J. W., Eglinton, S. M., Martay, B., & Chamberlain, D. E. (2015). Drivers of climate change impacts on bird communities. *Journal of Animal Ecology*, 84(4), 943–954. <https://doi.org/10.1111/1365-2656.12364>
- Pecl, G. T., Araújo, M. B., Bell, J. D., Blanchard, J., Bonebrake, T. C., Chen, I.-C., Clark, T. D., Colwell, R. K., Danielsen, F., Evengård, B., Falconi, L., Ferrier, S., Frusher, S., Garcia, R. A., Griffis, R. B., Hobday, A. J., Janion-Scheepers, C., Jarzyna, M. A., Jennings, S., ... Williams, S. E. (2017). Biodiversity redistribution under climate change: Impacts on ecosystems and human well-being. *Science*, 355(6332), eaai9214. <https://doi.org/10.1126/science.aai9214>
- Plummer, M. (2003). JAGS: A program for analysis of Bayesian graphical models using Gibbs sampling. *Proceedings of the 3rd international workshop on distributed statistical computing*.
- Pörtner, H. O., Roberts, D. C., Adams, H., Adler, C., Aldunce, P., Ali, E., Begum, R. A., Betts, R., Kerr, R. B., & Biesbroek, R. (2022). *Climate change 2022: Impacts, adaptation and vulnerability*. <https://edepot.wur.nl/565644>
- Pounds, J. A., Fogden, M. P. L., & Campbell, J. H. (1999). Biological response to climate change on a tropical mountain. *Nature*, 398(6728), 611–615. <https://doi.org/10.1038/19297>
- Quintero, I., & Jetz, W. (2018). Global elevational diversity and diversification of birds. *Nature*, 555(7695), 246–250. <https://doi.org/10.1038/nature25794>
- R Core Team. (2021). *R: A language and environment for statistical computing*. R Foundation for Statistical Computing. <http://www.R-project.org>
- Robbins, C. S. (1981). Bird activity levels related to weather. *Studies in Avian Biology*, 6, 301–310.
- Royle, J. A. (2004). N-mixture models for estimating population size from spatially replicated counts. *Biometrics*, 60(1), 108–115. <https://doi.org/10.1111/j.0006-341X.2004.00142.x>
- Schemske, D. W., & Brokaw, N. (1981). Treefalls and the distribution of understory birds in a tropical forest. *Ecology*, 62(4), 938–945. <https://doi.org/10.2307/1936992>
- Schuur, E. A. (2003). Productivity and global climate revisited: The sensitivity of tropical forest growth to precipitation. *Ecology*, 84(5), 1165–1170. [https://doi.org/10.1890/0012-9658\(2003\)084\[1165:PAGCR T\]2.0.CO;2](https://doi.org/10.1890/0012-9658(2003)084[1165:PAGCR T]2.0.CO;2)
- Schuur, E. A., & Matson, P. A. (2001). Net primary productivity and nutrient cycling across a mesic to wet precipitation gradient in Hawaiian montane forest. *Oecologia*, 128(3), 431–442. <https://doi.org/10.1007/s004420100671>
- Shoo, L. P., Williams, S. E., & Hero, J.-M. (2005). Climate warming and the rainforest birds of the Australian Wet Tropics: Using abundance data as a sensitive predictor of change in total population size. *Biological Conservation*, 125(3), 335–343. <https://doi.org/10.1016/j.biocon.2005.04.003>
- Suppiah, R., Macadam, I., & Whetton, P. (2007). *Climate change projections for the tropical rainforest region of North Queensland* [Unpublished report to the Marine and Tropical Sciences Research Facility]. Reef and Rainforest Research Centre Limited. <http://rrrc.org.au/wp-content/uploads/2014/06/25ii1-Climate-Projections.pdf>
- Thompson, J. M. T., & Brooks, S. P. (2003). Bayesian computation: A statistical revolution. *Philosophical Transactions of the Royal Society of London. Series A: Mathematical, Physical and Engineering Sciences*, 361(1813), 2681–2697. <https://doi.org/10.1098/rsta.2003.1263>
- Urban, M. C. (2018). Escalator to extinction. *Proceedings of the National Academy of Sciences of the United States of America*, 115(47), 11871–11873. <https://doi.org/10.1073/pnas.1817416115>
- van de Weg, M. J., Meir, P., Williams, M., Girardin, C., Malhi, Y., Silva-Espejo, J., & Grace, J. (2014). Gross primary productivity of a high

- elevation tropical montane cloud Forest. *Ecosystems*, 17(5), 751–764. <https://doi.org/10.1007/s10021-014-9758-4>
- Williams, S., Bolitho, E. E., & Fox, S. (2003). Climate change in Australian tropical rainforests: An impending environmental catastrophe. *Proceedings of the Royal Society of London. Series B: Biological Sciences*, 270(1527), 1887–1892. <https://doi.org/10.1098/rspb.2003.2464>
- Williams, S., & de la Fuente, A. (2021). Long-term changes in populations of rainforest birds in the Australia wet tropics bioregion: A climate-driven biodiversity emergency. *PLoS One*, 16(12), e0254307. <https://doi.org/10.1371/journal.pone.0254307>
- Williams, S., Falconi, L., Moritz, C., & Fenker Antunes, J. (2016). *State of wet tropics report 2015–2016: Ancient, endemic, rare and threatened vertebrates of the wet tropics*. <https://www.wet tropics.gov.au/site/user-assets/docs/sowt2015-16b5-lres.pdf>
- Williams, S., Pearson, R., & Walsh, P. (1995). Distributions and biodiversity of the terrestrial vertebrates of Australia's wet tropics: A review of current knowledge. *Pacific Conservation Biology*, 2(4), 327–362. <https://doi.org/10.1071/PC960327>
- Williams, S., VanDerWal, J., Isaac, J., Shoo, L. P., Storlie, C., Fox, S., Bolitho, E. E., Moritz, C., Hoskin, C. J., & Williams, Y. M. (2010). Distributions, life-history specialization, and phylogeny of the rain forest vertebrates in the Australian Wet Tropics. *Ecology*, 91(8), 2493. <https://doi.org/10.1890/09-1069.1>
- Williams, S. E., Shoo, L. P., Henriod, R., & Pearson, R. G. (2010). Elevational gradients in species abundance, assemblage structure and energy use of rainforest birds in the Australian Wet Tropics bioregion. *Austral Ecology*, 35(6), 650–664. <https://doi.org/10.1111/j.1442-9993.2009.02073.x>

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