Title: Long-term changes in populations of rainforest birds in the Australia Wet Tropics
bioregion: a climate-driven biodiversity emergency

Running title: Rainforest birds on escalator to extinction

Authors: Stephen E. Williams^{1*} & Alejandro de la Fuente¹

Stephen E. Williams Orchid Id: 0000-0002-2510-7408; ResearcherID: A-7250-2008

Alejandro de la Fuente Orchid Id: 0000-0001-9686-3844

Affiliations:

¹ Centre for Tropical Environmental Science & Sustainability, College of Science and
Engineering, James Cook University, Townsville, QLD 4811, Australia

*Correspondence to: Stephen.williams@jcu.edu.au Phone: +61 428 690280

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Abstract

Many authors have suggested that the vulnerability of montane biodiversity to climate change worldwide is significantly higher than in most other ecosystems. Despite the extensive variety of studies predicting severe impacts of climate change globally, few studies have empirically validated the predicted changes in distribution and population density . Here, we used 17 years of bird monitoring across latitudinal/elevational gradients in the rainforest of the Australian Wet Tropics World Heritage Area to assess changes in local abundance and distribution. We used relative abundance in 1977 surveys across 114 sites ranging from 0-1500m above sea level and utilised a trend analysis approach (TRIM) to investigate elevational shifts in abundance of 42 species between 2000 – 2016. The local abundance of most mid and high elevation species has declined at the lower edges of their distribution by >40% while lowland species increased by up to 190% into higher elevation areas. Upland-specialised species and regional endemics have undergone dramatic population declines of almost 50%. The “Outstanding Universal Value” of the Australian Wet Tropics World Heritage Area, one of the most irreplaceable biodiversity hotspots on Earth, is rapidly degrading. These observed impacts are likely to be similar in many tropical montane ecosystems globally.

Keywords: climate change; rainforest; birds; Australia; population declines; elevational distribution; biodiversity; species vulnerability; world heritage; escalator to extinction; montane ecosystems.

Introduction

There is widespread recognition that climate change is rapidly becoming the most significant threat to global biodiversity and natural ecosystems [1, 2]. At a global scale, estimates of total species extinctions projected over the remainder of the century vary considerably between ecosystems, taxa and methods of analysis [3]. However, in all studies, the level of predicted impacts is disturbing with potential losses of between 15-35% of all species [3, 4]. The projected impact of climate change is expected to be especially severe in mountain ecosystems with up to 84% of mountain species globally facing a high extinction risk [5-7]. Mountain regions provide a host of critical ecosystem services [8], support a disproportionate amount of the world's biological diversity and, harbour many phylogenetically unique species [5, 9-12]. Mountain regions contain roughly 87% of the world's vertebrate biodiversity [13], 54% of which is completely restricted to mountain ecosystems [13]. The global significance of montane ecosystems is heightened in the tropics [14, 15]; approximately 50% of the world's species of plants and vertebrates are believed to be endemic to 34 identified global biodiversity hotspots [16], 85% of which include large areas of tropical forest or montane cloud forest [17]. Tropical species are considered to be particularly sensitive to climate change [18-20] and the warming rates are relatively high in tropical mountains [18]. Consequently, tropical montane biodiversity is not only globally important but particularly threatened [7, 21]. Despite the global significance and high vulnerability of tropical ecosystems, there have been few studies demonstrating observed impacts of climate change in the tropics [22, 23]. The paucity of tropical studies makes it difficult to measure and predict the impacts of climate change relative to other drivers like habitat loss [24], especially given that most studies are short-term or lacking abundance data [25]. There is a need for increasing monitoring and improving understanding of the impacts of climate change in tropical montane ecosystems [12].

On mountains, biotic communities and abiotic conditions change abruptly over short distances, with greater elevational than lateral turnover in species composition [26]. Across all elevations, assemblages on mountains with high rates of past temperature change exhibit more rapid diversification, highlighting the importance of climatic fluctuations in driving the evolutionary dynamics of mountain biodiversity [12]. Globally, increasing evidence indicates that species are responding to climate change by shifting their geographical distributions [27]. These shifts often follow warming temperatures poleward and upslope [6, 10]. Montane species are of particular concern in this respect, as they are expected to experience reduced distribution area,

increased population fragmentation, and increased risk of extinction with upslope movement into ever-smaller area [28, 29]. The high degree of specialization to narrow temperature ranges that montane species typically exhibit has raised concern over their future under climate change [10, 29, 30]. It is widely expected that montane species will experience further upslope shifts in the future and, in the absence of broad latitudinal shifts due to the geographical features of montane ecosystems, such movements will leave species with less habitable area as they approach mountain peaks [29, 31]. Left with nowhere else to go, montane species are predicted to become increasingly susceptible to the stochastic extinctions or declining populations [32]. This so-called “escalator to extinction” [33] has been predicted, and now observed, in a number of places and taxa around the world [28, 34-36].

The rainforests in the Australian Wet Tropics bioregion in north-east Queensland are globally significant for high biodiversity value based on high endemism, evolutionary significance and phylogenetic distinctiveness [37-39]. These biodiversity values resulted in the region being listed as a World Heritage Area in 1988 and being described as the sixth most irreplaceable protected area globally [40] and the second most irreplaceable World Heritage Area [41]. The high endemism and relictual nature of the biodiversity within the region is largely attributed to the influence of historical fluctuations in rainforest area over the Quaternary and the restriction of rainforest to cool, moist, upland refugia [37]. This biogeographic history imposed a non-random extinction filter across the region resulting in most of the regionally-endemic species being cool-adapted upland species [42, 43]. It is this biogeographic history, with the resulting concentration of endemic species in the cool uplands, that has made the biodiversity of the region so unique but highly vulnerable to a warming climate. Predictions about the future of this biodiversity under anthropogenic climate change are grim, particularly for the upland regionally-endemic species and habitat types [5, 44-46]. In 2003, species distribution modelling of the endemic vertebrates suggested the potential for catastrophic impacts over the coming century with more than 50% of these species predicted to go extinct due to a complete loss of suitable climatic space [5]. These predictions drove a greater research effort in the region in the interim years and there have been extensive region-wide surveys of many vertebrate and invertebrate taxa [47-50].

Are the declines in species ranges predicted in 2003 concordant with observed spatial trends in species abundance patterns over subsequent years? Unfortunately, the answer is yes. We present quantitative evidence, based on the long-term monitoring of vertebrates across the

entire bioregion, for significant declines and shifts in the spatial distribution of populations. Field monitoring clearly demonstrates that the previously projected impacts are clearly concordant with observed shifts in species abundance. Previous analyses of the climate change impact in the region have relied on either modelled distribution changes using various IPCC emission scenarios or coarse comparisons of changes pre-2008 compared to post-2008. Here, we examine in high spatial, temporal and taxonomic detail the observed changes in the rainforest bird assemblages of the region between 2000-2016, based on the regional-scale standardised surveys from the Williams Wet Tropics monitoring program (updated from Williams, VanDerWal (47)). We use this long-term dataset to test for bird species that have undergone significant changes in local abundance and/or elevational. We predicted that bird assemblages should systematically shift upwards in elevation and that the local abundance of individual species would decline on the lower (warmer) edge of their distribution and increase at the higher (cooler) edge of their distribution [31]. We tested for trends across time in local abundance (site/elevation specific) and assemblage shifts across elevation and used an area-weighted trend to examine trends in total population size. These impacts are likely to be representative of impacts in many mountain ecosystems across the globe [7].

Results

Overall, across all 42 species over the 17 years, there has been a significant decline in local abundance of rainforest birds of approximately $12 \pm 1.4\%$ ($\sim -0.2\%$ per year) (Figure 1a, Table 1). However, this overall trend masks complex, and often contrasting trends, within different ecological subsets of the rainforest bird assemblage (Table 1). Habitat generalists increased by more than 50% from 2000 to 2011 and then steadily declined until 2016 (13 species, 3.3% /year, overall trend $9 \pm 4.1\%$, Figure 1b, Table 1). Local abundances of rainforest specialist species have declined on average by approximately 20% (29 species, -1.7% /year, overall trend $-20 \pm 1.3\%$, Figure 1c, Table 1). Regionally endemic species, a subset of habitat specialists, showed the strongest decline with a loss of $\sim 34 \pm 1.7\%$ in local abundance (10 species, -2.4% /year, Figure 1d, Table 1). Population trends of habitat generalists and specialists were significantly different (trend difference 0.05 ± 0.002 , $p < 0.05$). However, these average multi-species trends in ecological groupings also mask variable trends for individual species (Figure S1) and

assemblages in different elevational bands (Table S3). Species-specific trends in local abundance and total population size (local abundance trends weighted by area within each elevational band) are presented in the Appendix (Figure S1) ([Temporary link to interactive Appendix -](#)

https://alejandrodela Fuente.shinyapps.io/BirdsPopTrendAWT/?_ga=2.148260535.1024527938.1618546081-1577712465.1581926346 .

147 **Table 1. Multi-species indicator trends between 2000 – 2016 (overall) and separate trends pre-2009 and post-2008. Population trends were**
148 **classified following Pannekoek and van Strien (51) into one of the following categories depending on the overall multiplicative slope and**
149 **its 95% confidence interval. Strong increase/Steep decline: increase/decline significantly more than 5% per year. Moderate**
150 **increase/decline: significant increase/decline, but no more than 5% per year. Stable: no significant increase or decline, and it is certain**
151 **than trends are less than 5% per year. Uncertain: no significant increase or decline, but it is not certain if trends are less than 5% per**
152 **year.**

	Overall			2000 - 2008			2009 - 2016		
<i>Indicator</i>	<i>Slope</i>	<i>s.d.</i>	<i>Trend classification</i>	<i>Slope</i>	<i>s.d.</i>	<i>Trend classification</i>	<i>Slope</i>	<i>s.d.</i>	<i>Trend classification</i>
All species	0.998	0.001	Moderate decline	1.003	0.002	Stable	0.982	0.002	Moderate decline
Endemic species	0.976	0.001	Moderate decline	0.967	0.003	Moderate decline	0.985	0.004	Moderate decline
Lowland species	1.03	0.002	Moderate increase	1.074	0.005	Strong increase	1.008	0.005	Stable
Midland species	0.986	0.001	Moderate decline	0.992	0.003	Moderate decline	0.98	0.003	Moderate decline
Upland species	0.971	0.001	Moderate decline	0.952	0.003	Moderate decline	0.972	0.003	Moderate decline
Habitat generalists	1.033	0.002	Moderate increase	1.054	0.005	Moderate increase	0.974	0.005	Moderate decline
Rainforest specialists	0.983	0.001	Moderate decline	0.981	0.002	Moderate decline	0.986	0.002	Moderate decline

154

155 Lowland specialist species have undergone a strong and significant increase of $72 \pm 7\%$ (6
156 species, 3%/year, Figure 2a). Mid-elevation specialists declined by $21 \pm 1.4\%$ (16 species, -
157 1.9%/year, Figure 2b) and upland specialists have undergone declines of $44 \pm 4\%$ (13 species,
158 -2.9%/year, Figure 2c). Population trends for lowland specialists were significantly different
159 from the trends in both midland (trend difference 0.043 ± 0.002 , $p < 0.05$) and upland specialists
160 (trend difference 0.059 ± 0.002 , $p < 0.05$). Additionally, upland specialists have declined
161 significantly more than midland specialists (trend difference 0.015 ± 0.002 , $p < 0.05$),
162 suggesting that the pattern of decline increases with increasing elevation.

163

164 Shifts in patterns of local abundance are species-specific and highly variable, often involving
165 complex spatio-temporal and non-monotonic trends (for example, Brown Gerygone, Figure
166 S1, Figure S1.1). However, the overall multi-species trends that summarise the observed shifts
167 in bird assemblages along the elevational gradient are what we would predict under a warming
168 climate: there have been significant upslope shifts in bird abundance patterns across the 17
169 years of this study. We demonstrated this by examining the trends in local abundance for each
170 group of elevational specialists in their original preferred elevation (baseline averaged
171 abundance at each elevation across 1996-2003) and in the adjacent elevational bands over time.
172 We predicted, for example, that lowland species should increase in the midlands, and upland
173 species should decline at lower elevations. The observed spatial shifts in elevational
174 distribution and abundance are in accord with the earlier predictions based on distribution
175 changes. Lowland specialist species have moderately increased in local abundance in the
176 lowlands (+17%). On the other hand, lowland specialists' local abundance has dramatically
177 increased into the midlands (~190% increase) (Figure 3). Midland specialist species have
178 declined in the lowlands by approximately 42%, by 22% in the midlands and are currently
179 stable in the uplands (Figure 3). Upland specialist species have declined everywhere, with a
180 catastrophic 49% decline in the lower-elevation midlands and a 33% decline in the uplands
181 (Figure 3). Detailed trends for individual species at each elevation category are in Appendix
182 (Table S3).

183

184

185 **Discussion**

186 There is a temptation for policy makers and environmental managers to consider that
 187 biodiversity within a protected area is safe, this is a dangerous, and in this case incorrect,
 188 assumption. The montane rainforest birds of the Australia Wet Tropics World Heritage Area
 189 are in danger of extinction due to the increasingly severe impacts of a changing climate. In
 190 2003, Williams et al. [52] predicted catastrophic extinction levels within the regionally
 191 endemic species of the Australian Wet Tropics World Heritage Area by the end of the 21st
 192 century. These early predictions were based on bioclimatic envelope models of the changes in
 193 species distributions with increasing temperature. However, the reliability of predictions using
 194 this simple approach is debateable , with a likelihood of overestimating the severity of impacts
 195 [53]. Therefore, a more intensive monitoring effort was conducted throughout the region,
 196 covering ~94% of the environmental space present and providing standardised estimates of
 197 local abundance for many species.

198

199 An earlier analysis using these local abundance measures of rainforest birds across elevation
 200 [45] predicted that 74% of rainforest bird species would become threatened by the end of the
 201 21st century. demonstrated a tight relationship between elevation and the assemblage structure
 202 of birds based on empirical, site-based relative abundance across the elevational gradient.
 203 Based on this relationship, they predicted that bird assemblages would systematically move
 204 upwards in elevation as the climate warmed. However, despite the development of more
 205 sophisticated modelling approaches and the availability of more field data, the qualitative
 206 outcomes of predictions remained similar to the 2003 predictions. Here, we demonstrate that
 207 these predicted trends, whether based on species distribution models or empirical abundance,
 208 were concordant with expectations. Our results here demonstrate that the rainforest bird
 209 assemblage in the Australian Wet Tropics bioregion is clearly, and consistently, moving uphill
 210 in a classic demonstration of the “escalator to extinction” [33].

211

212 Overall, we are on track for severe impacts on rainforest birds, particularly the upland
 213 specialists. Many of these species are endemic to the region and/or include species that are
 214 evolutionary distinct and/or ecologically specialised [38]. Upland bird populations have

declined since 2000 by 33% within their core range and the more marginal populations in the midlands have crashed by almost 50% (Figure 3). Midland species, although stable in the cooler uplands at this stage, have declined by >20% within their core area and >40% in the hotter lowlands. Lowland species are mostly increasing in abundance thus far with increases in abundance in the lowlands and strong increases in range and abundance into the midlands (Figure 3, Table 1).

The pattern in temporal change in abundance of rainforest birds presented in this study is consistent with observed species elevational shift worldwide [27, 34-36, 54-56]. Globally, evidence suggests a strong uphill elevational shift across different taxa, indicating that this trend could be a generality. However, some studies have pointed out some idiosyncratic results found in species-specific trends within different communities [27, 54]. According to this, our results showed that, even though the uphill distribution shift is marked across most species, some birds showed stable trends, while others showed pattern opposite than expected (e.g., *Acanthiza katherina*, figure S1). Those individual exceptions to the overall pattern highlighted potential interspecific differences in dispersal capacity, resilience, and adaptability between bird species in the Wet Tropics, whose impact in the overall community “re-shuffling” at the ecosystem level should be further studied. Overall, this study supports growing evidence to the rapid impact that climate change is having on tropical ecosystems [28] and provides the first evidence of a climate-induced elevational shift in tropical rainforest of Australia.

So, what is driving these shifting abundance patterns? Is it the direct impacts of temperature on the birds or is it an indirect effect via food resources or other biotic interactions? There is little confidence in our ability to predict the potential impacts of the complex changes in biotic interactions due to these marked changes in abundance and geographic shifts in distributions. Upland and midland assemblages are likely coming under increased pressure due to changing biotic interactions and community structure associated with the increasing abundance of lower elevation species as they shift higher up the mountain. The changes shown in this study suggest that, thus far, the impacts on species have been largely direct, or at least directly associated with an important resource, rather than changes in competitive interactions between bird species. We argue this on the basis that upland bird species have declined in their core range (>850m) despite there being no significant increase in midland birds in the uplands thus far. Midland birds have only declined by about 20% in the midlands despite the influx of lowland species. Lowland species have increased (albeit with more recent trends of decline) and there has been no noticeable change in species composition or new invading species in the lowlands

to date. Thus far, there is no evidence supporting “lowland attrition” of species in this system [31]; however, this is not entirely surprising given that we have little knowledge of the upper thermal limits of the lowland species because they already occur in the hottest part of the region Shoo, Anderson (57) suggested that the elevational pattern of abundance for the Lewin’s Honeyeater was directly influenced by temperature and not competitive interactions. This conclusion was based on a demonstration that the elevational abundance profile of the species varied as predicted by temperature in the populations on mountains on Cape York, a hotter montane system, within a very different bird assemblage to that in the Wet Tropics region[57]. However, this does not account for other biotic interactions that might also be changing such as diseases, or other non-bird competitors such as ectotherms (invertebrates mostly) that might be increasing in uplands.

There are many indirect mechanisms that could potentially exacerbate the impact that climate change will ultimately have on bird species. Increased pressure from parasites with increasing temperature [58], decreased reproductive success during prolonged dry seasons [59, 60], increased habitat and population fragmentation [61-63] and increased environmental marginality [64]. In this region, Williams, Shoo (50) hypothesised that dry season bottlenecks and changes in net primary productivity could have a strong influence on bird populations. Net primary productivity is limited by both temperature and water availability and could possibly increase in the uplands with a warming climate, potentially alleviating some of the more direct impacts of high temperatures. However, the strong declines in the abundance of upland bird species shown here suggests that any positive influence of increased net primary productivity has been swamped by the negative impacts of increasing temperature. There is existing evidence highlighting the importance of changing rainfall patterns, especially harsher dry-seasons [59, 65] and decreasing water input from cloud interception [66]. It seems most likely that the driving factor behind many of the changes demonstrated in this study are the increasing frequency and intensity of heat waves [67]. We need to increase our understanding of the impacts of extreme climatic events so we can make more robust predictions than those that rely only on changes in average conditions.

There have been clear impacts on biodiversity in almost every ecosystem and taxa across the globe due to anthropogenic climate change [2]; and now the world urgently needs to reduce

emissions and adapt as much as possible to minimise future impacts. Our efforts need to be firmly focussed on the difficult question – what can we do? Managing habitats at the landscape scale via habitat restoration, threat abatement and enhancing dispersal pathways represents one avenue for local adaptation efforts to increase the resilience of biodiversity (Shoo et al. 2013, [68]). The maintenance and restoration of movement pathways and corridors to facilitate species movement into refugial areas will be vitally important [69], however, our results here suggest that facilitating movement also warrants caution. While it is imperative that many species can move into cool refugia [70], our data demonstrating the observed movement of lowland, generalist species into the upland refugia, represents a potential threat to the upland endemics via increased competition with more generalist species.

It is clear that montane systems are of paramount importance due to their high biodiversity value, many specialists and endemics and their role as the best-available cool refugia [70] and that these biodiversity hotspots are particularly threatened by climate. It is particularly disconcerting that, even in a fully protected and well-managed system such as the Australian Wet Tropics World Heritage Area, observed impacts are significant and accelerating. Most other tropical, montane biodiversity hotspots across the globe also face additional threats such as ongoing habitat degradation, poaching and urban encroachment.

Conclusions

Upland bird species, of great conservation importance, are declining in abundance and contracting their range to higher elevations in the montane rainforests in the Australian Wet Tropics World Heritage Area in a classic example of the “escalator to extinction” [33]. These species are suffering the combined, and increasing, threat of reduced distribution area, reduced local population density and more fragmented and isolated populations, potentially causing a loss of genetic diversity in many species; factors that increase their vulnerability to extinction [69]. Low-elevation rainforest species that are often more generalist, geographically widespread and locally common are increasing in abundance and range size, potentially resulting in yet another negative pressure on the upland specialists and an overall homogenisation of the rainforest avifauna [71]. These changes are likely to be indicative of

impacts across all montane ecosystems globally, especially in important biodiversity hotspots associated with tropical mountain ecosystems. The important next step is to determine how we can slow, prevent, or adapt to these impacts to prevent the loss of the unique biodiversity of these regions around the world.

Methods

Study area

The Australian Wet Tropics bioregion is composed of mixed tropical rainforest in an area of approximately 1.85 million hectares. The terrain is rugged and dominated by mountain ranges, tablelands, foothills and a lowland coastal plain. The elevation varies from sea level to highlands at 1000 meters, with isolated peaks reaching up to 1,620 meters [37]. Annual rainfall varies between 1200-8000mm with rainforest covering most areas with annual rainfall above ~1500mm.

Data collection

Rainforest birds in the Australian Wet Tropics bioregion were monitored between 1996 and 2016 across the region at locations ranging from 0 to 1500 meters above sea level. All individuals were recorded either by call or visual observation. Each survey was based on a 30 minute-150 meter transect with two observers. Surveys occurred within two hours of sunrise. All long-term monitoring sites were located within large, unfragmented areas of rainforest with continuous forest cover over the available elevational gradient. For further details of methods, species observed, site localities and species traits see Williams, VanDerWal (47), Williams, Shoo (50).

Data from four mountain ranges were included in the analyses presented here (Atherton Uplands, Carbine Uplands, Spec Uplands and Windsor Uplands), representing a total of 1977 surveys across 124 different sites. Analysis across these sites was possible based on coverage of the elevational gradient and consistency and numbers of surveys over time. Years with an entire elevation category missing were not included in the trend analyses (from 1996 to 1999). See Table S5 in supplementary information for complete breakdown of survey numbers by elevation and year.

Species included

Initially, all species for which the survey technique was unsuitable (e.g. water birds) or when call identification was considered unreliable due to the presence of multiple species with similar calls were excluded to ensure maximum reliability in the trend analyses. This resulted in a dataset of 54 species. Of these, analysis of population trends across elevation and time was possible for 42 species where there was sufficient data across both elevation and years to reliably analyse temporal changes in species abundance. We grouped species by habitat (rainforest specialist, generalist) and elevation specialisation (lowland 0-450 m, midland 451-850m, upland >850). These elevational bands were selected to have the finest scale division of elevation possible with a relatively equal band width and sample size in each band. Species were categorised as rainforest specialist if rainforest represented their main or core breeding habitat [47]. Elevation specialisation was defined by the elevational abundance profile of each species using a mean abundance for all surveys conducted between 1996-2004 within each elevational band as the baseline elevation abundance profile (Table S1, Figure S1.1). Species were assigned as a specialist in that elevational band when >70% of their elevational abundance profile occurred within that band.

Population indices and trends

Overall population indices and trends for all 42 species were modelled using the rtrim package [72], an R-package based on the TRIM software (*Trends and Indices for Monitoring data*. TRIM v. 3.54. [73]). TRIM is designed to analyse time-series of counts and produce unbiased yearly indices and standard errors using log-linear models. The programme also estimates the dispersion factor, correcting for over-dispersion, and takes account of serial correlation between counts at the same site in different years [73]. This method has proved to be robust in trend calculation with missing years [74-77]. We used model 2 in rtrim, which assumed all years as possible changing points in the population trend [78]. Overall trends for each species were calculated with both unweighted data and data weighted by the geographic area within each of the elevational bands. The weighted trends give an estimate of the changes in the species total population size as it takes into account the area within each elevational band as well as local abundance changes. Given that the difference in results using weighted and unweighted data was very marginal (Figure S1) and our primary focus here was to examine site-specific changes in local abundance and elevational distribution shifts in abundance, we have only presented in the results section the unweighted trends. Area-weighted trends of total population size are included in the Appendix (Figure S1b).

Individual species indices produced by TRIM were combined into multi-species indicators for each predefined group. Multi-species indicators were calculated using the MSI-tool in R [79]. This tool uses species-specific annual indices and their standard errors provided by TRIM to calculate annual multispecies indicator with confidence interval, accounting for sampling error, using the Monte Carlo simulation method. This method calculates a mean and a SE from 1000 simulated multi-species indicators and back-transforms these to an index scale, then repeats the process 10000 times. Those indicators are considered a measure of biodiversity change, where a reduction in index mean will occur if more species are declining than increasing and vice versa [75, 80]. We tested for significant differences between the multi-species indicators using the TREND_DIFF-function, based on a Monte Carlo procedure (1000 iterations) and report the average difference with SE in the multiplicative trends and the significance of this difference.

Additionally, we explored the influence of changing trends over the study period by separately examining the trends prior to, and after, 2008 (the midpoint of the time-series). This enables some consideration of how the trends would have been observed over shorter time periods.

Finally, to examine the population changes of each species within each elevational band, we estimated the local trends for each species along the elevational gradient. Multi-species trends in each elevation category were combined for each of the elevation specialist species groups. Differences within groups were tested using the TREND_DIFF-function. R (version 3.6.2) was used in all the analyses [81].

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406

References

1. IPCC CC. Mitigation of climate change. Contribution of working group III to the fifth assessment report of the intergovernmental panel on climate change. 2014.
2. Pecl G, Araújo M, Bell J, Blanchard J, Bonebrake T, Chen I-C, et al. Biodiversity redistribution under climate change: Impacts on ecosystems and human well-being. *Science*. 2017;355(6332):eaai9214.
3. Urban M. Climate change. Accelerating extinction risk from climate change. *Science*. 2015;348(6234):571-3. Epub 2015/05/02. doi: 10.1126/science.aaa4984. PubMed PMID: 25931559.
4. Thomas C, Cameron A, Green R, Bakkenes M, Beaumont L, Collingham Y, et al. Extinction risk from climate change. *Nature*. 2004;427(6970):145-8.
5. Williams SE, Bolitho EE, Fox S. Climate change in Australian tropical rainforests: an impending environmental catastrophe. *Proceedings of the Royal Society of London Series B: Biological Sciences*. 2003;270(1527):1887-92.
6. Mamantov MA, Gibson-Reinemer DK, Linck EB, Sheldon KS. Climate-driven range shifts of montane species vary with elevation. *Global Ecology and Biogeography*. 2021. doi: <https://doi.org/10.1111/geb.13246>.
7. Manes S, Costello MJ, Beckett H, Debnath A, Devenish-Nelson E, Grey K-A, et al. Endemism increases species' climate change risk in areas of global biodiversity importance. *Biological Conservation*. 2021:109070.
8. Korner C, Spehn EM. Mountain biodiversity: a global assessment: Routledge; 2019.
9. Lomolino MV. Elevation gradients of species-density: historical and prospective views. *Global Ecology and biogeography*. 2001;10(1):3-13.
10. La Sorte F, Jetz W. Projected range contractions of montane biodiversity under global warming. *Proceedings of the Royal Society B: Biological Sciences*. 2010;277(1699):3401-10.
11. Jetz W, Rahbek C, Colwell RK. The coincidence of rarity and richness and the potential signature of history in centres of endemism. *Ecology Letters*. 2004;7(12):1180-91.
12. Quintero I, Jetz W. Global elevational diversity and diversification of birds. *Nature*. 2018;555(7695):246-50. doi: 10.1038/nature25794.
13. Rahbek C, Borregaard MK, Colwell RK, Dalsgaard B, Holt BG, Morueta-Holme N, et al. Humboldt's enigma: What causes global patterns of mountain biodiversity? *Science*. 2019;365(6458):1108-13.
14. Grenyer R, Orme CDL, Jackson SF, Thomas GH, Davies RG, Davies TJ, et al. Global distribution and conservation of rare and threatened vertebrates. *Nature*. 2006;444(7115):93-6.
15. Buckley LB, Jetz W. Linking global turnover of species and environments. *Proceedings of the National Academy of Sciences*. 2008;105(46):17836-41.
16. Myers N, Mittermeier RA, Mittermeier CG, Da Fonseca GA, Kent J. Biodiversity hotspots for conservation priorities. *Nature*. 2000;403(6772):853-8.
17. Bubb P, May IA, Miles L, Sayer J. Cloud forest agenda. 2004.
18. Perez TM, Stroud JT, Feeley KJ. Thermal trouble in the tropics. *Science*. 2016;351(6280):1392-3. doi: 10.1126/science.aaf3343.
19. Deutsch C, Tewksbury J, Huey R, Sheldon K, Ghalambor C, Haak D, et al. Impacts of climate warming on terrestrial ectotherms across latitude. *Proceedings of the National Academy of Sciences*. 2008;105(18):6668-72.
20. Wright SJ, Muller-Landau HC, Schipper J. The future of tropical species on a warmer planet. *Conservation biology*. 2009;23(6):1418-26.
21. Nogués-Bravo D, Araújo MB, Errea M, Martinez-Rica J. Exposure of global mountain systems to climate warming during the 21st Century. *Global environmental change*. 2007;17(3-4):420-8.
22. Harris J, Sekercioglu C, Sodhi N, Fordham D, Paton D, Brook B. The tropical frontier in avian climate impact research. *Ibis-Journal of the British Ornithologists Union*. 2011;153(4):877.
23. Urban MC. Accelerating extinction risk from climate change. *Science*. 2015;348(6234):571-3.

24. Sodhi N, Sekercioglu C, Barlow J, Robinson S. Conservation of tropical birds: John Wiley & Sons; 2011.
25. Brook B, Sodhi N, Bradshaw C. Synergies among extinction drivers under global change. *Trends in ecology & evolution*. 2008;23(8):453-60.
26. Terborgh J. Distribution on environmental gradients: theory and a preliminary interpretation of distributional patterns in the avifauna of the Cordillera Vilcabamba, Peru. *Ecology*. 1971;52(1):23-40.
27. Chen I-C, Hill JK, Ohlemüller R, Roy DB, Thomas CD. Rapid range shifts of species associated with high levels of climate warming. *Science*. 2011;333(6045):1024-6.
28. Şekerciöğlü Ç, Schneider S, Fay J, Loarie S. Climate change, elevational range shifts, and bird extinctions. *Conservation biology*. 2008;22(1):140-50.
29. Şekerciöğlü Ç, Primack R, Wormworth J. The effects of climate change on tropical birds. *Biological Conservation*. 2012;148(1):1-18. doi: <https://doi.org/10.1016/j.biocon.2011.10.019>.
30. Laurance WF, Uuseche DC, Shoo LP, Herzog SK, Kessler M, Escobar F, et al. Global warming, elevational ranges and the vulnerability of tropical biota. *Biological Conservation*. 2011;144(1):548-57.
31. Colwell R, Brehm G, Cardelús C, Gilman A, Longino J. Global Warming, Elevational Range Shifts, and Lowland Biotic Attrition in the Wet Tropics. *Science*. 2008;322(5899):258-61. doi: 10.1126/science.1162547.
32. Lande R. Risks of population extinction from demographic and environmental stochasticity and random catastrophes. *The American Naturalist*. 1993;142(6):911-27.
33. Marris E. The escalator effect. *Nature Reports Climate Change*. 2007;1:94-6.
34. Freeman B, Freeman A. 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*. 2014;111(12):4490-4.
35. Morueta-Holme N, Engemann K, Sandoval-Acuña P, Jonas J, Segnitz R, Svenning J. Strong upslope shifts in Chimborazo's vegetation over two centuries since Humboldt. *Proceedings of the National Academy of Sciences*. 2015;112(41):12741-5. doi: 10.1073/pnas.1509938112.
36. Freeman B, Scholer M, Ruiz-Gutierrez V, Fitzpatrick J. Climate change causes upslope shifts and mountaintop extirpations in a tropical bird community. *Proceedings of the National Academy of Sciences*. 2018;115(47):11982-7.
37. Nix H, Switzer MA. Rainforest animals: atlas of vertebrates endemic to Australia's wet tropics: Australian National Parks and Wildlife Service; 1991.
38. Williams S, Falconi L, Moritz C, Fenker Antunes J. State of Wet Tropics Report 2015-2016: ancient, endemic, rare and threatened vertebrates of the wet tropics. 2016.
39. Authority WTM. State of Wet Tropics report 2017—2018: 30 years of World Heritage in the Wet Tropics—reflections and aspirations (Wet Tropics Management Authority, Cairns). 2018.
40. Le Saout S, Hoffmann M, Shi Y, Hughes A, Bernard C, Brooks T, et al. Protected areas and effective biodiversity conservation. *Science*. 2013;342(6160):803-5.
41. Bertzky B, Shi Y, Hughes A, Engels B, Ali M, Badman T. Terrestrial Biodiversity and the World Heritage List: identifying broad gaps and potential candidate sites for inclusion in the natural World Heritage network. IUCN, Gland, Switzerland and UNEP-WCMC, Cambridge, UK. 2013.
42. Williams SE, Pearson RG. Historical rainforest contractions, localized extinctions and patterns of vertebrate endemism in the rainforests of Australia's wet tropics. *Proceedings of the Royal Society of London Series B: Biological Sciences*. 1997;264(1382):709-16.
43. Williams SE. Patterns of Mammalian Species Richness in the Australian Tropical Rainforests: Are Extinctions during Historical Contractions of the Rainforest the Primary Determinants of Current Regional Patterns in Biodiversity? *Wildlife Research*. 1997;24(5):513-30. doi: <https://doi.org/10.1071/WR96040>.

44. Hilbert D, Bradford M, Parker T, Westcott D. Golden bowerbird (*Prionodura newtonia*) habitat in past, present and future climates: predicted extinction of a vertebrate in tropical highlands due to global warming. *Biological Conservation*. 2004;116(3):367-77.
45. Shoo L, Williams S, Hero J. 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*. 2005;125(3):335-43.
46. Shoo L, Williams S, Hero J. Potential decoupling of trends in distribution area and population size of species with climate change. *Global Change Biology*. 2005;11(9):1469-76.
47. Williams S, VanDerWal J, Isaac J, Shoo L, Storlie C, Fox S, et al. Distributions, life-history specialization, and phylogeny of the rain forest vertebrates in the Australian Wet Tropics: Ecological Archives E091-181. *Ecology*. 2010;91(8):2493-.
48. Staunton K, Nakamura A, Burwell C, Robson S, Williams S. Elevational distribution of flightless ground beetles in the tropical rainforests of north-eastern Australia. *PloS one*. 2016;11(5).
49. Staunton K, Robson S, Burwell C, Reside A, Williams S. Projected distributions and diversity of flightless ground beetles within the Australian Wet Tropics and their environmental correlates. *PloS one*. 2014;9(2).
50. Williams SE, Shoo LP, Henriod R, Pearson RG. Elevational gradients in species abundance, assemblage structure and energy use of rainforest birds in the Australian Wet Tropics bioregion. *Austral Ecology*. 2010;35(6):650-64.
51. Pannekoek J, van Strien A. TRIM 3 Manual (trends and indices for monitoring data). 2005.
52. Williams SE, Bolitho EE, Fox S. Climate change in Australian tropical rainforests: an impending environmental catastrophe. *P Roy Soc B-Biol Sci*. 2003;270(1527):1887-92. doi: doi:10.1098/rspb.2003.2464.
53. Araújo MB, Whittaker RJ, Ladle RJ, Erhard M. Reducing uncertainty in projections of extinction risk from climate change. *Global Ecology and Biogeography*. 2005;14(6):529-38. doi: 10.1111/j.1466-822X.2005.00182.x.
54. Tingley M, Koo M, Moritz C, Rush A, Beissinger S. The push and pull of climate change causes heterogeneous shifts in avian elevational ranges. *Global Change Biology*. 2012;18(11):3279-90.
55. Tiberti R, Mangiacotti M, Bennati R. The upward elevational shifts of pond breeding amphibians following climate warming. *Biological Conservation*. 2021;253:108911.
56. Menéndez R, González-Megías A, Jay-Robert P, Marquéz-Ferrando R. Climate change and elevational range shifts: Evidence from dung beetles in two European mountain ranges. *Global Ecology and Biogeography*. 2014;23(6):646-57.
57. Shoo L, Anderson A, Williams S. On the isolated population of Lewin's Honeyeater (*Meliphaga lewinii* amphochlora) from the McIlwraith Range uplands, Cape York Peninsula, Australia: estimates of population size and distribution. *Emu - Austral Ornithology*. 2009;109(4):288-93. doi: 10.1071/MU08062.
58. Zamora-Vilchis I, Williams SE, Johnson CN. Environmental temperature affects prevalence of blood parasites of birds on an elevation gradient: implications for disease in a warming climate. *PloS one*. 2012;7(6):e39208-e. Epub 2012/06/19. doi: 10.1371/journal.pone.0039208. PubMed PMID: 22723966.
59. Williams SE, Middleton J. Climatic seasonality, resource bottlenecks, and abundance of rainforest birds: implications for global climate change. *Diversity and Distributions*. 2008;14(1):69-77. doi: 10.1111/j.1472-4642.2007.00418.x.
60. Frith C, Frith D. Seasonality of insect abundance in an Australian upland tropical rainforest. *Australian Journal of Ecology*. 1985;10(3):237-48. doi: 10.1111/j.1442-9993.1985.tb00886.x.
61. Laurance W, Lovejoy T, Vasconcelos H, Bruna E, Didham R, Stouffer P, et al. Ecosystem Decay of Amazonian Forest Fragments: a 22-Year Investigation. *Conservation Biology*. 2002;16(3):605-18. doi: 10.1046/j.1523-1739.2002.01025.x.

62. Laurance W. Rainforest fragmentation and the structure of small mammal communities in tropical Queensland. *Biological Conservation*. 1994;69(1):23-32. doi: [https://doi.org/10.1016/0006-3207\(94\)90325-5](https://doi.org/10.1016/0006-3207(94)90325-5).
63. Laurance W. Ecological Correlates of Extinction Proneness in Australian Tropical Rain Forest Mammals. *Conservation Biology*. 1991;5(1):79-89. doi: 10.1111/j.1523-1739.1991.tb00390.x.
64. Cuervo J, Møller A. Temporal Variation in Population Size of European Bird Species: Effects of Latitude and Marginality of Distribution. *Plos One*. 2013;8(10):e77654. doi: 10.1371/journal.pone.0077654.
65. Suppiah R, Hennessy K, Whetton P, McInnes K, Macadam I, Bathols J, et al. Australian climate change projections derived from simulations performed for the IPCC 4th Assessment Report. *Aust Meteorol Mag*. 2007;56:131-52.
66. McJannet D, Wallace J, Reddell P. Precipitation interception in Australian tropical rainforests: II. Altitudinal gradients of cloud interception, stemflow, throughfall and interception. *Hydrological Processes*. 2007;21(13):1703-18. doi: 10.1002/hyp.6346.
67. Meade J, VanDerWal J, Storlie C, Williams S, Gourret A, Krockenberger A, et al. Substantial reduction in thermo-suitable microhabitat for a rainforest marsupial under climate change. *Biology Letters*. 2018;14(12):20180189. doi: doi:10.1098/rsbl.2018.0189.
68. Williams S, Hobday A, Falconi L, Hero J, Holbrook N, Capon S, et al. Research priorities for natural ecosystems in a changing global climate. *Global change biology*. 2020;26(2):410-6.
69. Williams SE, Shoo LP, Isaac JL, Hoffmann AA, Langham G. Towards an integrated framework for assessing the vulnerability of species to climate change. *PLoS Biol*. 2008;6(12):e325.
70. Shoo L, Storlie C, Vanderwal J, Little J, Williams S. Targeted protection and restoration to conserve tropical biodiversity in a warming world. *Global Change Biology*. 2011;17(1):186-93. doi: 10.1111/j.1365-2486.2010.02218.x.
71. Clavel J, Julliard R, Devictor V. Worldwide decline of specialist species: toward a global functional homogenization? *Frontiers in Ecology and the Environment*. 2011;9(4):222-8. doi: 10.1890/080216.
72. Bogaart P, Van der Loo M, Pannekoek J. rtrim: Trends and indices for monitoring data. 1 ed. R package version 2016.
73. Pannekoek J, van Strien A. TRIM (Trends And Indices For Monitoring Data). . 3.54 ed: Voorburg: Statistics Netherlands.; 2006.
74. Bowler DE, Heldbjerg H, Fox AD, de Jong M, Böhning-Gaese K. Long-term declines of European insectivorous bird populations and potential causes. *Conservation Biology*. 2019;33(5):1120-30.
75. Gregory R, Skorpilova J, Vorisek P, Butler S. An analysis of trends, uncertainty and species selection shows contrasting trends of widespread forest and farmland birds in Europe. *Ecological Indicators*. 2019;103:676-87. doi: <https://doi.org/10.1016/j.ecolind.2019.04.064>.
76. Kamp J, Frank C, Trautmann S, Busch M, Dröschmeister R, Flade M, et al. Population trends of common breeding birds in Germany 1990–2018. *Journal of Ornithology*. 2021;162(1):1-15.
77. Gómez-Catasús J, Pérez-Granados C, Barrero A, Bota G, Giralt D, López-Iborra GM, et al. European population trends and current conservation status of an endangered steppe-bird species: the Dupont's lark *Chersophilus duponti*. *PeerJ*. 2018;6:e5627.
78. Pannekoek J, van Strien A, Bogaart P. rtrim by example.: Voorburg: Statistics Netherlands.; 2018. Available from: http://cran.wustl.edu/web/packages/rtrim/vignettes/Skylark_example.html.
79. Soldaat L, Pannekoek J, Verweij R, van Turnhout C, van Strien A. A Monte Carlo method to account for sampling error in multi-species indicators. *Ecological Indicators*. 2017;81:340-7. doi: <https://doi.org/10.1016/j.ecolind.2017.05.033>.
80. Gregory R, van Strien A. Wild bird indicators: using composite population trends of birds as measures of environmental health. *Ornithological Science*. 2010;9(1):3-22. doi: 10.2326/osj.9.3.
81. R Core Team. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria 2019.

1 **Figure 1. Trends in local abundance from 2000 to 2016 based on the multi-species**
2 **indicators for a) all species, b) habitat generalists, c) regional endemic species and d)**
3 **rainforest specialists. Values are the multi-species index with SE (error bars) with the**
4 **smoothed trend line with 95% CI (shaded area).**

5

6

Figure 2. Trends in local abundance from 2000 to 2016 based on multi-species indicators for A) lowland specialists, B) midland specialists and C) uplands specialists. Values represent multi-species index with SE (error bars). The overall smoothed trend is represented by the line with shaded area showing the 95% CI for the smoothed trend.

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24 **Figure 3. Elevational shifts in local abundance patterns in bird assemblages between 2000**
25 **to 2016 across the elevational gradient. Baseline population set to 0 with values above the**
26 **baseline representing an increase in local population abundance and values below the**
27 **baseline representing a decline. Values represent the change in local abundance over the**
28 **full time period based on the mean multiplicative slope of the multi-species trend with its**
29 **SE (error bars). See the full abundance trends over time for each combination of**
30 **elevational band and species group in Appendix (Figure S4, Table S4).**

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