

1 **Title:** Long-term changes in populations of rainforest birds in the Australia Wet Tropics

2 bioregion: a climate-driven biodiversity emergency

3

4 **Running title:** Rainforest birds on escalator to extinction

5

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16 **Abstract**

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

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

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39

40 **Introduction**

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

64

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

73 increased population fragmentation, and increased risk of extinction with upslope movement
74 into ever-smaller area [28, 29]. The high degree of specialization to narrow temperature ranges
75 that montane species typically exhibit has raised concern over their future under climate change
76 [10, 29, 30]. It is widely expected that montane species will experience further upslope shifts
77 in the future and, in the absence of broad latitudinal shifts due to the geographical features of
78 montane ecosystems, such movements will leave species with less habitable area as they
79 approach mountain peaks [29, 31]. Left with nowhere else to go, montane species are predicted
80 to become increasingly susceptible to the stochastic extinctions or declining populations [32].
81 This so-called “escalator to extinction” [33] has been predicted, and now observed, in a number
82 of places and taxa around the world [28, 34-36].

83

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

103

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

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

123

124

125

126 **Results**

127 Overall, across all 42 species over the 17 years, there has been a significant decline in local
128 abundance of rainforest birds of approximately $12 \pm 1.4\%$ ($\sim -0.2\%$ per year) (Figure 1a, Table
129 1). However, this overall trend masks complex, and often contrasting trends, within different
130 ecological subsets of the rainforest bird assemblage (Table 1). Habitat generalists increased by
131 more than 50% from 2000 to 2011 and then steadily declined until 2016 (13 species, 3.3%/year,
132 overall trend $9 \pm 4.1\%$, Figure 1b, Table 1). Local abundances of rainforest specialist species
133 have declined on average by approximately 20% (29 species, -1.7% /year, overall trend $-20 \pm$
134 1.3% , Figure 1c, Table 1). Regionally endemic species, a subset of habitat specialists, showed
135 the strongest decline with a loss of $\sim 34 \pm 1.7\%$ in local abundance (10 species, -2.4% /year,
136 Figure 1d, Table 1). Population trends of habitat generalists and specialists were significantly
137 different (trend difference 0.05 ± 0.002 , $p < 0.05$). However, these average multi-species trends
138 in ecological groupings also mask variable trends for individual species (Figure S1) and

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

142 [Appendix -](#)

143

144 https://alejandrolafuente.shinyapps.io/BirdsPopTrendAWT/?_ga=2.148260535.10245279

145 [38.1618546081-1577712465.1581926346](https://alejandrolafuente.shinyapps.io/BirdsPopTrendAWT/?_ga=2.148260535.10245279) .

146

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.**

<i>Indicator</i>	Overall			2000 - 2008			2009 - 2016		
	<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

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

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

234 So, what is driving these shifting abundance patterns? Is it the direct impacts of temperature
235 on the birds or is it an indirect effect via food resources or other biotic interactions? There is
236 little confidence in our ability to predict the potential impacts of the complex changes in biotic
237 interactions due to these marked changes in abundance and geographic shifts in distributions.
238 Upland and midland assemblages are likely coming under increased pressure due to changing
239 biotic interactions and community structure associated with the increasing abundance of lower
240 elevation species as they shift higher up the mountain. The changes shown in this study suggest
241 that, thus far, the impacts on species have been largely direct, or at least directly associated
242 with an important resource, rather than changes in competitive interactions between bird
243 species. We argue this on the basis that upland bird species have declined in their core range
244 (>850m) despite there being no significant increase in midland birds in the uplands thus far.
245 Midland birds have only declined by about 20% in the midlands despite the influx of lowland
246 species. Lowland species have increased (albeit with more recent trends of decline) and there
247 has been no noticeable change in species composition or new invading species in the lowlands

248 to date. Thus far, there is no evidence supporting “lowland attrition” of species in this system
249 [31]; however, this is not entirely surprising given that we have little knowledge of the upper
250 thermal limits of the lowland species because they already occur in the hottest part of the region
251 Shoo, Anderson (57) suggested that the elevational pattern of abundance for the Lewin’s
252 Honeyeater was directly influenced by temperature and not competitive interactions. This
253 conclusion was based on a demonstration that the elevational abundance profile of the species
254 varied as predicted by temperature in the populations on mountains on Cape York, a hotter
255 montane system, within a very different bird assemblage to that in the Wet Tropics region[57].
256 However, this does not account for other biotic interactions that might also be changing such
257 as diseases, or other non-bird competitors such as ectotherms (invertebrates mostly) that might
258 be increasing in uplands.

259

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

277

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

280 emissions and adapt as much as possible to minimise future impacts. Our efforts need to be
281 firmly focussed on the difficult question – what can we do? Managing habitats at the landscape
282 scale via habitat restoration, threat abatement and enhancing dispersal pathways represents one
283 avenue for local adaptation efforts to increase the resilience of biodiversity (Shoo et al. 2013,
284 [68]). The maintenance and restoration of movement pathways and corridors to facilitate
285 species movement into refugial areas will be vitally important [69], however, our results here
286 suggest that facilitating movement also warrants caution. While it is imperative that many
287 species can move into cool refugia [70], our data demonstrating the observed movement of
288 lowland, generalist species into the upland refugia, represents a potential threat to the upland
289 endemics via increased competition with more generalist species.

290

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

298

299

300 Conclusions

301 Upland bird species, of great conservation importance, are declining in abundance and
302 contracting their range to higher elevations in the montane rainforests in the Australian Wet
303 Tropics World Heritage Area in a classic example of the “escalator to extinction” [33]. These
304 species are suffering the combined, and increasing, threat of reduced distribution area, reduced
305 local population density and more fragmented and isolated populations, potentially causing a
306 loss of genetic diversity in many species; factors that increase their vulnerability to extinction
307 [69]. Low-elevation rainforest species that are often more generalist, geographically
308 widespread and locally common are increasing in abundance and range size, potentially
309 resulting in yet another negative pressure on the upland specialists and an overall
310 homogenisation of the rainforest avifauna [71]. These changes are likely to be indicative of

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

315

316 **Methods**

317 **Study area**

318 The Australian Wet Tropics bioregion is composed of mixed tropical rainforest in an area of
319 approximately 1.85 million hectares. The terrain is rugged and dominated by mountain ranges,
320 tablelands, foothills and a lowland coastal plain. The elevation varies from sea level to
321 highlands at 1000 meters, with isolated peaks reaching up to 1,620 meters [37]. Annual rainfall
322 varies between 1200-8000mm with rainforest covering most areas with annual rainfall above
323 ~1500mm.

324

325 **Data collection**

326 Rainforest birds in the Australian Wet Tropics bioregion were monitored between 1996 and
327 2016 across the region at locations ranging from 0 to 1500 meters above sea level. All
328 individuals were recorded either by call or visual observation. Each survey was based on a 30
329 minute-150 meter transect with two observers. Surveys occurred within two hours of sunrise.
330 All long-term monitoring sites were located within large, unfragmented areas of rainforest with
331 continuous forest cover over the available elevational gradient. For further details of methods,
332 species observed, site localities and species traits see Williams, VanDerWal (47), Williams,
333 Shoo (50).

334

335 Data from four mountain ranges were included in the analyses presented here (Atherton
336 Uplands, Carbine Uplands, Spec Uplands and Windsor Uplands), representing a total of 1977
337 surveys across 124 different sites. Analysis across these sites was possible based on coverage
338 of the elevational gradient and consistency and numbers of surveys over time. Years with an
339 entire elevation category missing were not included in the trend analyses (from 1996 to
340 1999). See Table S5 in supplementary information for complete breakdown of survey numbers
341 by elevation and year.

342

343 **Species included**

344 Initially, all species for which the survey technique was unsuitable (e.g. water birds) or when
345 call identification was considered unreliable due to the presence of multiple species with
346 similar calls were excluded to ensure maximum reliability in the trend analyses. This resulted
347 in a dataset of 54 species. Of these, analysis of population trends across elevation and time was
348 possible for 42 species where there was sufficient data across both elevation and years to
349 reliably analyse temporal changes in species abundance. We grouped species by habitat
350 (rainforest specialist, generalist) and elevation specialisation (lowland 0-450 m, midland 451-
351 850m, upland >850). These elevational bands were selected to have the finest scale division of
352 elevation possible with a relatively equal band width and sample size in each band. Species
353 were categorised as rainforest specialist if rainforest represented their main or core breeding
354 habitat [47]. Elevation specialisation was defined by the elevational abundance profile of each
355 species using a mean abundance for all surveys conducted between 1996-2004 within each
356 elevational band as the baseline elevation abundance profile (Table S1, Figure S1.1). Species
357 were assigned as a specialist in that elevational band when >70% of their elevational abundance
358 profile occurred within that band.

359

360 **Population indices and trends**

361 Overall population indices and trends for all 42 species were modelled using the rtrim package
362 [72], an R-package based on the TRIM software (*Trends and Indices for Monitoring data*.
363 TRIM v. 3.54. [73]). TRIM is designed to analyse time-series of counts and produce unbiased
364 yearly indices and standard errors using log-linear models. The programme also estimates the
365 dispersion factor, correcting for over-dispersion, and takes account of serial correlation
366 between counts at the same site in different years [73]. This method has proved to be robust in
367 trend calculation with missing years [74-77]. We used model 2 in rtrim, which assumed all
368 years as possible changing points in the population trend [78]. Overall trends for each species
369 were calculated with both unweighted data and data weighted by the geographic area within
370 each of the elevational bands. The weighted trends give an estimate of the changes in the
371 species total population size as it takes into account the area within each elevational band as
372 well as local abundance changes. Given that the difference in results using weighted and
373 unweighted data was very marginal (Figure S1) and our primary focus here was to examine
374 site-specific changes in local abundance and elevational distribution shifts in abundance, we
375 have only presented in the results section the unweighted trends. Area-weighted trends of total
376 population size are included in the Appendix (Figure S1b).

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

389

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

393

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

399

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406

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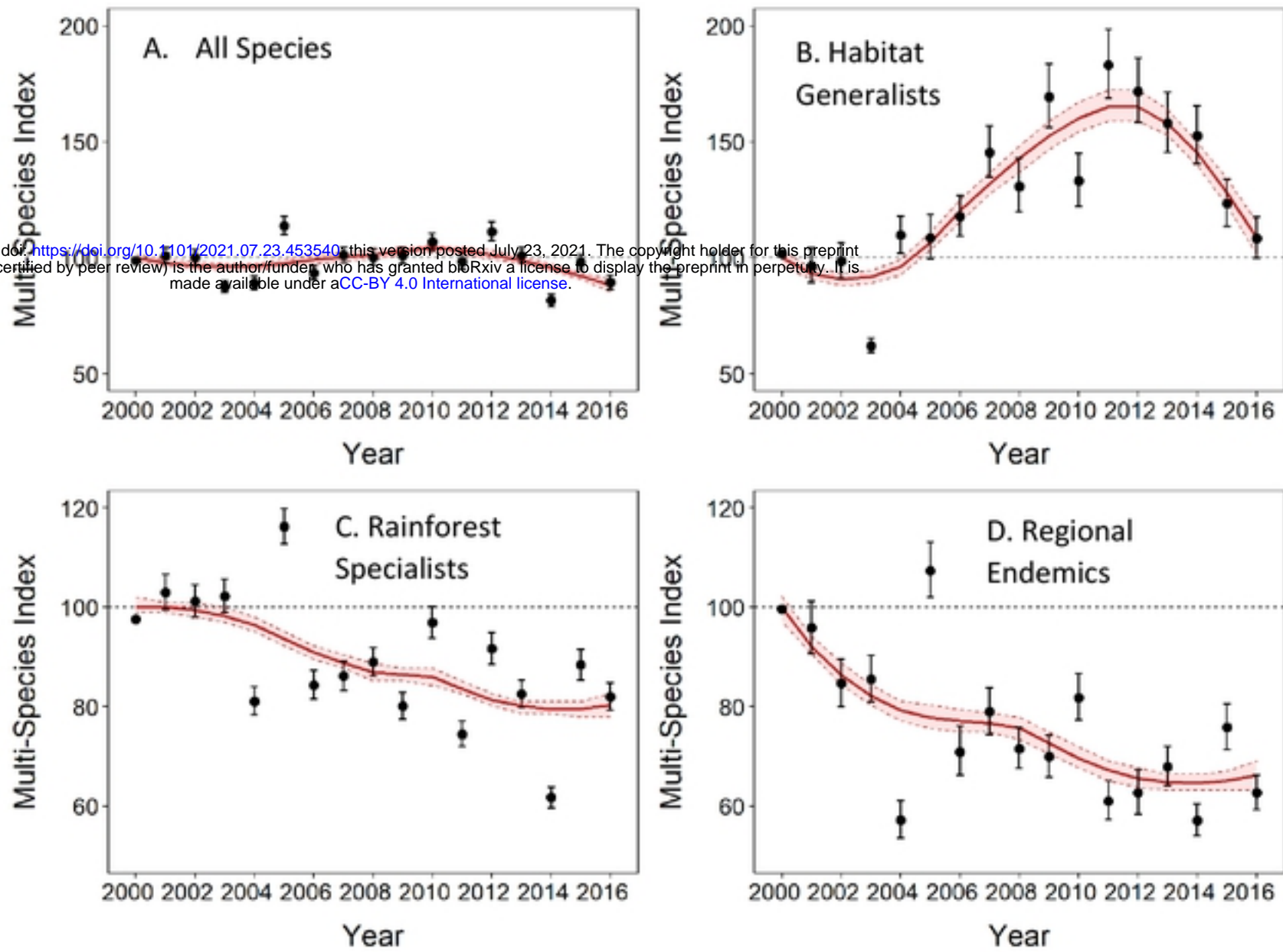
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1 **Figure 1. Trends in local abundance from 2000 to 2016 based on the multi-species**
 2 **indicators for a) all species, b) habitat generalists, c) regional endemic species and d)**
 3 **rainforest specialists. Values are the multi-species index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

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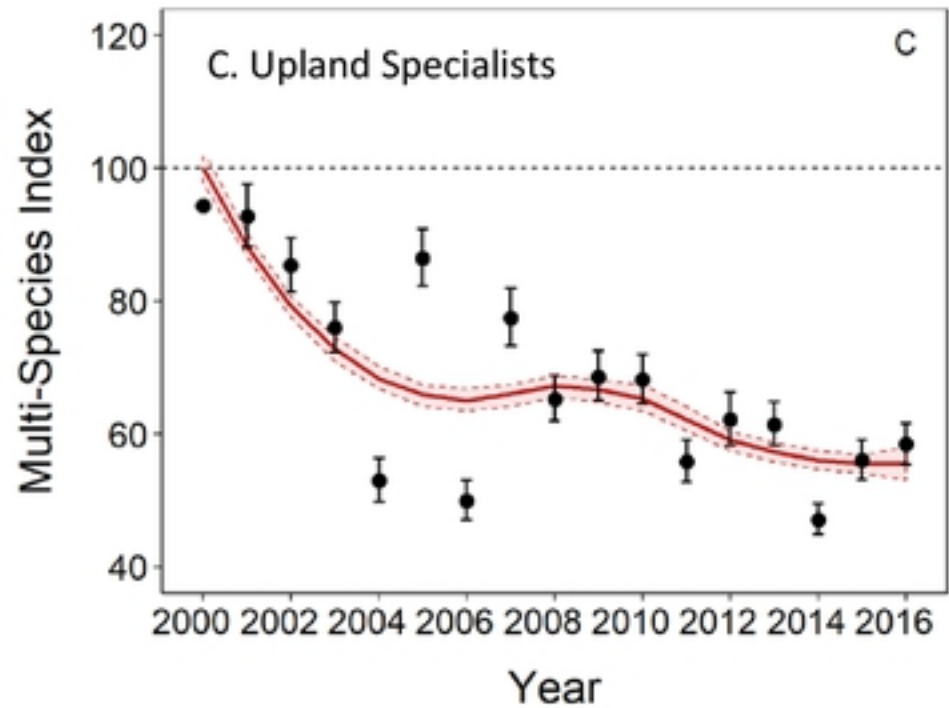
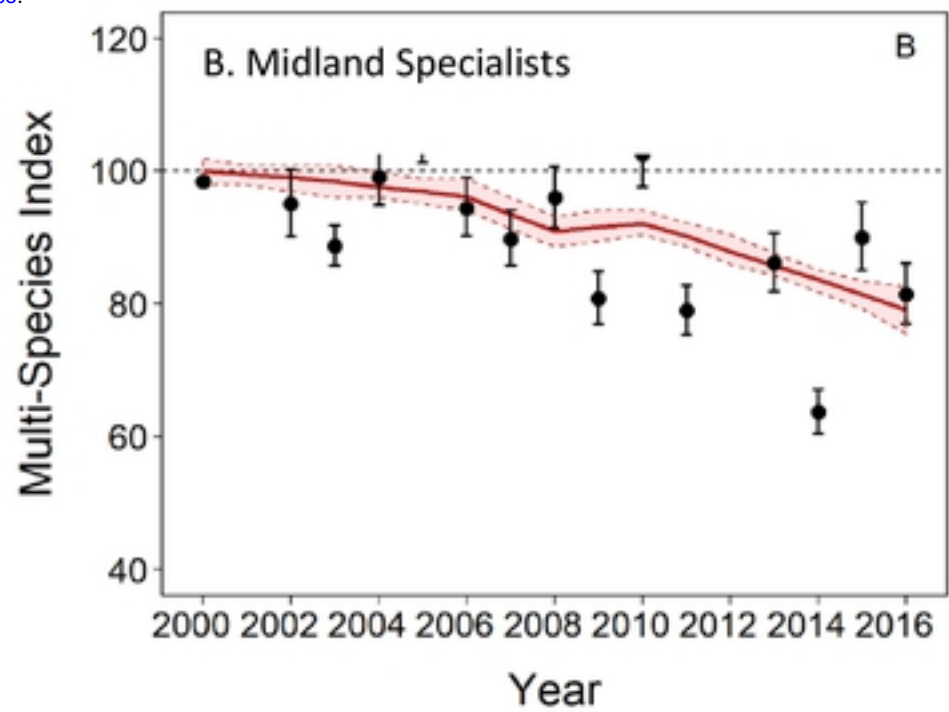
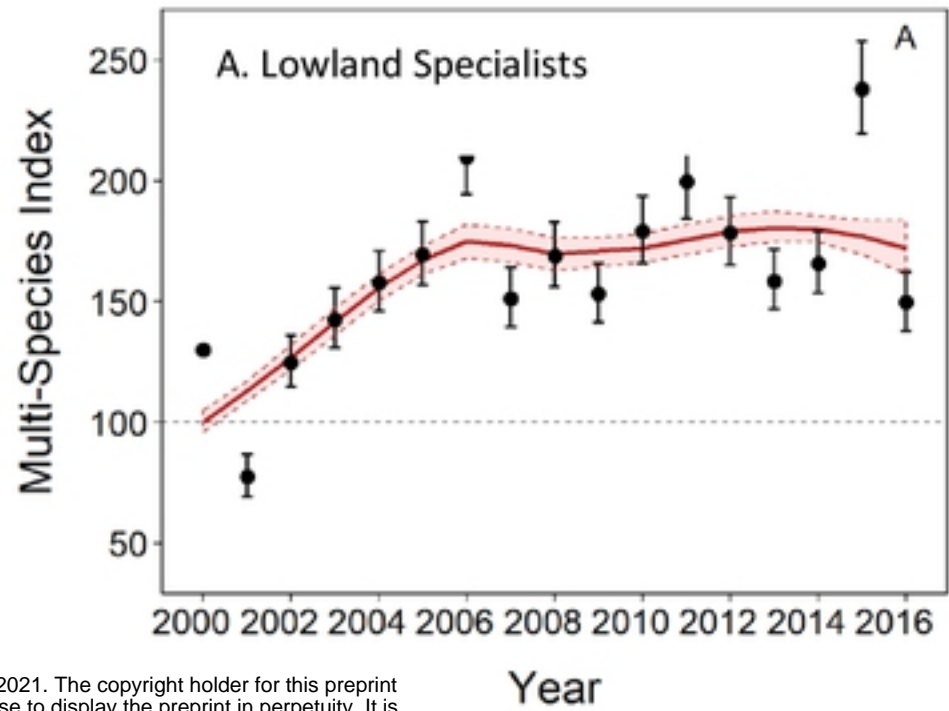


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7 **Figure 2. Trends in local abundance**
 8 **from 2000 to 2016 based on multi-**
 9 **species indicators for A) lowland**
 10 **specialists, B) midland specialists**
 11 **and C) uplands specialists. Values**
 12 **represent multi-species index with**
 13 **SE (error bars). The overall**
 14 **smoothed trend is represented by the**
 15 **line with shaded area showing the**

16 **95% CI for the smoothed trend.**
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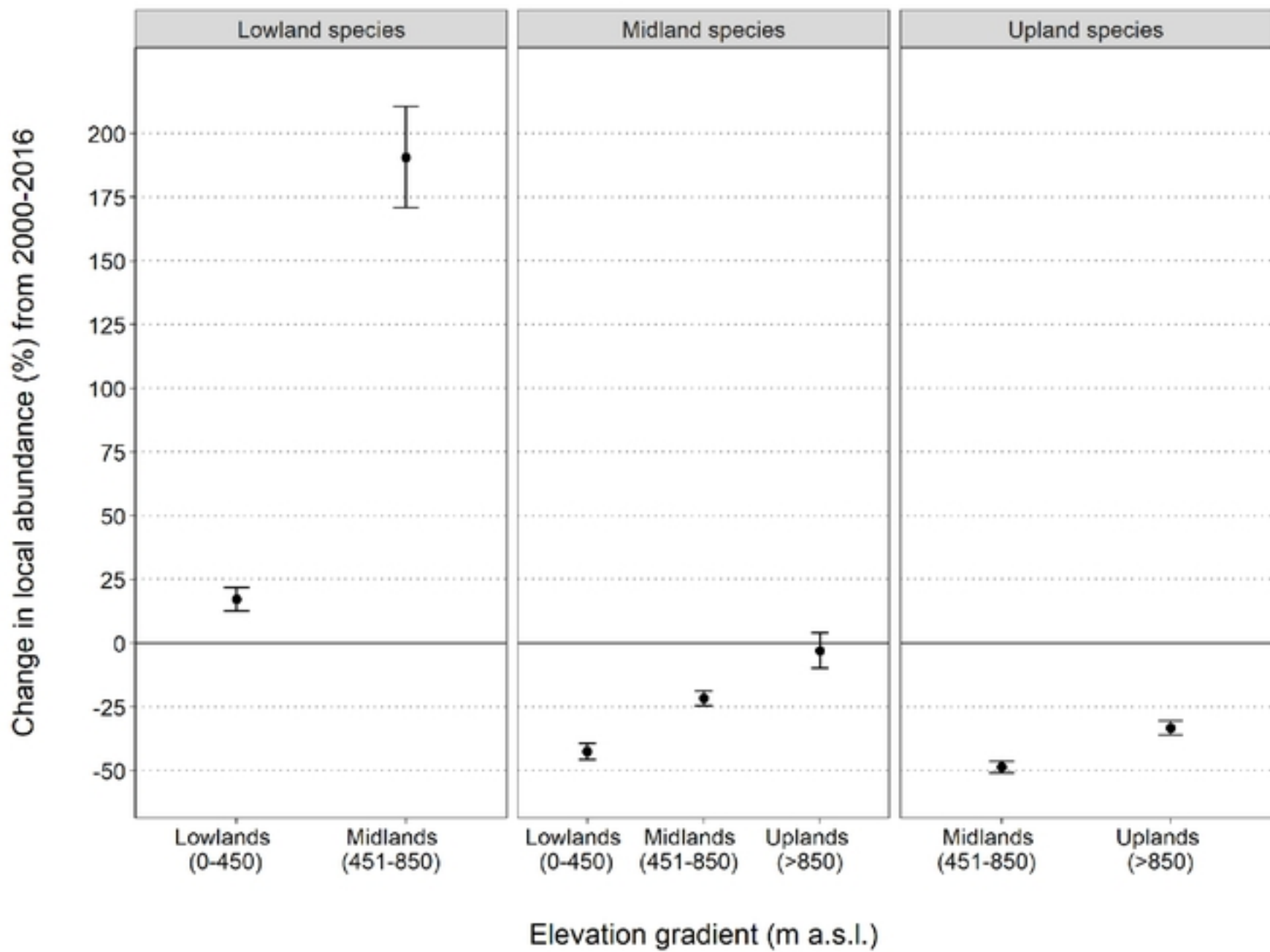
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24 **Figure 3. Elevational shifts in local abundance patterns in bird assemblages between 2000**
25 **to 2016 across the elevational gradient. Baseline population set to 0 with values above the**
26 **baseline representing an increase in local population 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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