1 **Responses of global waterbird populations to climate change vary with latitude**

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22 **Abstract**

23 While climate change continues to present a major threat to global biodiversity and

24 ecosystems, most research on climate change impacts do not have the resolution to detect

25 changes in species abundance and are often limited to temperate ecosystems. This limits our

26 understanding of global responses in species abundance—a determinant of ecosystem

27 function and services—to climate change including in the highly-biodiverse tropics. We

28 address this knowledge gap by quantifying abundance responses to climate change in

29 waterbirds, an indicator taxon of wetland biodiversity, at 6,822 sites between -55° and 64°.

30 Using 1,303,651 count records since 1990 of 390 species, we show that with temperature

31 increase, the abundance of species and populations decreased at lower latitudes, particularly

32 in the tropics, but increased at higher latitudes. These contrasting responses to temperature

33 increase according to latitude indicate potential global-scale poleward shifts of species

34 abundance under climate change, providing empirical support for predictions by earlier

35 studies. The negative responses to temperature increase in tropical species and populations

36 are of conservation concern, as they are often also threatened by other anthropogenic factors.

37 Our results suggest that existing biases in studies towards temperate regions could

38 underestimate the impact of climate change on waterbirds and other species.

39

40 **Introduction**

41 Climate change continues to pose various serious threats to biodiversity, and there is an

42 urgent need to understand how species respond to changing climates globally. A wide range

43 of species have already shown responses to climate change, such as changes in geographical

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44 range[1], phenology[2] and abundance[3]. However, the rate and direction of these responses vary

45 greatly among species and locations[1,2,4]. As climate-driven changes in biodiversity are

46 expected to affect ecosystem functioning, human well-being, and the dynamics of climate

47 change itself[5], understanding how species' responses to climate change may vary globally

48 could provide crucial evidence for a more effective allocation of limited resources on a

49 priority basis for the conservation of species and ecosystems threatened the most by climate

50 change, and for assessing how climate-driven changes in biodiversity may affect human

51 societies.

52   Existing gaps in the geographical coverage of available evidence seriously limit our

53 understanding of species' responses to climate change and its variations across the globe[6].

54 Earlier global reviews of species' responses to climate change have rarely incorporated

55 species and studies in the tropics, due to the lack of relevant information[7]. Such geographical

56 biases are even more prominent in studies investigating responses in species abundance[8,9],

57 which is a major determinant of species extinction risk[10], ecosystem function and services[11].

58 Research on abundance responses to climate change to date has largely been conducted in

59 Europe, North America and the Arctic[3,12-14], with a recent global study showing a link

60 between climate warming and abundance declines in birds and mammals[8]. As a result,

61 although tropical species are predicted to be more vulnerable to increasing temperature[15],

62 there is still little empirical evidence on how responses in species abundance to climate

63 change vary among and within species at the global scale.

64   Here we address this challenge by modelling global time-series data of waterbird species

65 to estimate their abundance responses to changes in temperature and precipitation. The global

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66   dataset of waterbird abundance changes used is based on long-term surveys in over 100

67   countries and covers regions for which there is little information on climate change impacts,

68   such as the tropics[16]. Waterbirds can also serve as an indicator taxon for assessing the status

69   of biodiversity in wetland ecosystems, which have been lost at higher rates than other

70   ecosystems, despite their high levels of biodiversity and productivity as well as the crucial

71   ecosystem functions and services delivered[17].

72   Using 1,303,651 count records collected since 1990 on 390 waterbird species at 6,822

73   sites between -55° and 64° (Figure S1) we first estimated, for each species at each site, (i) the

74   rate of abundance changes with increasing temperature and precipitation as regression

75   coefficients (responses to temperature and precipitation increases), and (ii) the proportion of

76   abundance changes that can be explained independently by temperature and precipitation

77   changes (measured as R^2), estimated with hierarchical partitioning[18] (the importance of

78   temperature and precipitation). We then tested multiple hypotheses that are rarely explored at

79   the global scale (Supplementary Tables S1 and S2), to examine among- and within-species

80   variations in responses to temperature and precipitation increases as well as the importance of

81   temperature and precipitation across latitudes.

82   **Results**

83   Applying the Gompertz model of population growth to the global waterbird dataset enabled

84   us to estimate abundance responses to the changes in temperature and precipitation at $1° \times 1°$

85   grid cells across latitudes, including the tropics, for a wide range of waterbird groups. Of the

86   390 species analysed, 144 species (36.9%) had at least one estimate in the tropics and 129

87   species (33.1%) had their absolute latitudinal range mid-points in the tropics (defined as

88   tropical species; Figure 1).

89   Many species showed considerable spatial variation in abundance responses to

90   temperature increases within their geographical ranges, with particularly negative responses

91   in the tropics (Figure 1), although the importance of temperature in explaining abundance

92   changes tended to be low across the ranges, with an overall median R^2 of 0.057

93   (Supplementary Data S1 and S2). In contrast, for most species there was no clear

94   geographical pattern in abundance responses to precipitation increases, and precipitation was

95   found to have a low importance in explaining abundance changes (the overall median $R^2 =$

96   0.051; Supplementary Data S1 and S2). These geographical patterns were also evident in the

97   distribution of abundance responses averaged across all species observed within each grid

98   cell; species generally showed more negative responses to temperature increases at lower

99   latitudes, such as in South and Southeast Asia (Figure 2).

100   For 213 species with estimates at ten or more grid cells, we then tested hypotheses on

101   how responses to temperature and precipitation increases (the rate of abundance changes with

102   increasing temperature/precipitation) and the importance of temperature and precipitation

103   (the proportion of abundance changes that can be explained by temperature/precipitation

104   changes) vary among species (among each species' estimates at latitudinal range mid-points;

105   species-level responses) and within species (among grid cells within each species;

106   population-level responses) along latitudes. When compared among species, abundance

107   responses to temperature increases were more negative in species at lower latitudes, with

108   69% of the tropical species showing negative responses to temperature increases (Figure 3a,

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109   S2a). When compared within species, although 198 (93%) out of the 213 species showed

110   more negative responses to temperature increases at lower latitudes, this within-species

111   latitudinal pattern was significant only in eight of the 198 species (Figure 3b, Supplementary

112   Data S3). The importance of temperature in explaining abundance changes also increased

113   with latitude among species (Figure 3c, S2b) and within species for all 55 species with a

114   significant within-species latitudinal pattern (Figure 3d, Supplementary Data S3). Migratory

115   species, larger-sized species and species with a wider latitudinal range showed a higher

116   importance of temperature in explaining abundance changes (Figure S2b).

117   In contrast, neither abundance responses to precipitation increases nor the importance of

118   precipitation in explaining abundance changes showed significant latitudinal patterns among

119   species, although, for some species in the tropics, precipitation was found to have a relatively

120   high importance in explaining abundance changes (Figure 4a, c, S3 and Supplementary Data

121   S3). Precipitation was shown to have a higher importance in explaining abundance changes in

122   species with a wider latitudinal range (Figure S3b). When compared within species, three

123   species showed a significant, one species showed a decrease and another species showed a

124   hump-shaped curve in abundance responses to precipitation increases along latitudes (Figure

125   4b, Supplementary Data S3). The importance of precipitation in explaining abundance

126   changes showed a significant within-species latitudinal pattern for just one species (Figure 4d,

127   Supplementary Data S3).

128   **Discussion**

129   Our results demonstrate the responses in waterbird abundance to temperature increases differ

130   between tropical and non-tropical regions. At both species and population levels, waterbird

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131   abundance generally decreased in the tropics, but increased at higher latitudes, with

132   increasing temperature. This supports our predictions on among- and within-species patterns

133   (Supplementary Table S1). Species in the tropics tend to live closer to their upper

134   temperature limits[15], have a narrower temperature niche[19] and change their temperature niche

135   at a slower rate[20], all of which indicate that tropical species are more vulnerable to increasing

136   temperatures at the species level. Climate-related extinctions of local populations, typically at

137   the warmer edge of the species' geographical range, are also more frequent in the tropics,

138   causing poleward range shifts in many species[21]. While such species-level and population-

139   level responses to climate change have often been investigated separately to date, our results

140   provide novel empirical evidence that impacts of temperature increases on tropical

141   ecosystems can be characterised by species-wide declines in tropical species as well as

142   population-level responses in wider-ranging species.

143   Nevertheless, we also found that temperature generally explains only a small proportion

144   of yearly abundance changes in waterbirds, especially in tropical species and at the low-

145   latitude range margin of species, possibly for four reasons. First, the effect of temperature

146   changes on waterbird abundance can be indirect especially at lower latitudes. Although

147   warmer weather conditions can directly increase the survival of waterbirds at higher

148   latitudes[22], indirect biotic processes (e.g., changes in food availability), rather than direct

149   abiotic processes (e.g., heat stress), are reported to be more important mechanisms for

150   climate-driven abundance changes, especially for higher-level consumers like birds[23,24]. For

151   example, increases in already-high temperatures at lower latitudes can cause wetlands to dry,

152   reducing the availability of habitats and food resources for waterbirds[22]. Such an indirect

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153   effect of temperature increases could have obscured the relationship between changes in

154   temperature and abundance, especially in the tropics and at the low-latitude range margins.

155   Second, many of the waterbirds analysed here are migratory species, which generally have a

156   higher dispersal ability[25] and track climate niches to a greater extent than resident species[26],

157   and thus can be more responsive to changes in local temperature; this was supported by the

158   positive effect of migratory status on the importance of temperature (Figure S2b). In this

159   study more non-tropical species tended to be migratory compared to tropical species (151

160   (96%) of 158 non-tropical species and 12 (78%) of 55 tropical species were migratory),

161   which may explain the higher importance of local temperature in explaining the abundance of

162   non-tropical species. Third, observation errors can cause a lower explanatory power of

163   variables. We may expect larger errors in the tropics, compared to temperate regions, where

164   waterbird surveys have a longer history and thus surveyors might be better trained. Finally,

165   other important threats, such as habitat loss and hunting, affect bird abundance,

166   independently from, or synergistically with, climate change[27]. By testing the effect of

167   temperature and precipitation changes on yearly abundance changes while estimating long-

168   term growth rates, our modelling approach controlled for the consistent impacts of such

169   threats on long-term trends in abundance (see *Statistical Analyses* for more detail).

170   Nevertheless, those threats can also cause yearly abundance changes and their impacts are

171   likely to be more severe at lower latitudes[16], potentially causing temperature to have lower

172   importance at lower latitudes.

173   Contrary to our hypotheses, there was no clear latitudinal pattern in abundance responses

174   to precipitation changes, either among or within species. In general water availability,

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175   compared to ambient temperature, has been shown to be a more important driver of species

176   richness and population size at lower latitudes[4,28]. Supporting this, our results showed that

177   precipitation was more important in explaining the abundance of some tropical species

178   compared to most species in higher latitudes, although the overall among-species pattern

179   across latitudes was not significant (Figure 4c). This may be explained by the following two

180   reasons. First, precipitation changes can affect waterbird species at the river basin scale (often

181   the scale of 500 to 1,000 km) through effects on water flow into their wetland habitats[29,30].

182   Therefore, our analysis at the resolution of 1° grid cells (equivalent to a grain size of 96.49

183   km) may not have been able to detect such a broad-scale impact of precipitation changes.

184   Second, waterbird responses to precipitation changes can vary greatly among species, as we

185   recognised when developing our hypotheses (Supplementary Table S1). While increased

186   rainfall generally leads to more favourable habitat conditions for waterbirds in dry regions[22,31],

187   elevated water levels associated with increased rainfall can cause the loss of shallow-water

188   habitats, often followed by abundance decreases in certain groups, such as shorebirds[32]. Such

189   mixed responses to precipitation changes among species[33] may have resulted in the lack of

190   clear latitudinal patterns, particularly among species, in this study.

191   Our results point to three major implications on the impact of climate change on global

192   biodiversity. First, despite the relatively low importance of temperature in explaining

193   waterbird abundance changes, all other things being equal, local temperature increases under

194   ongoing climate change are likely to pose a more negative impact on species and populations

195   in the tropics. This provides important evidence for the climate-driven degradation of tropical

196   ecosystems, which has recently been under debate[34,35]. Although climate change is not the

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197   only threat to waterbird species, impacts of other major threats, such as loss and degradation

198   of wetlands and excessive hunting pressure, seem to be more severe in the tropics too[16],

199   indicating that tropical species and populations suffer from multiple anthropogenic threats.

200   Second, the revealed negative impact of temperature increases in the tropics suggests that

201   existing severe biases in scientific studies and data towards temperate regions could

202   underestimate the impact of climate change on species populations at the global scale.

203   Highlighting the negative impact of climate change on tropical waterbirds should serve to

204   inspire further studies on other taxa in the tropics. Finally, our finding of contrasting

205   abundance responses to temperature increases according to latitude highlights the possibility

206   of global-scale poleward shifts in abundance across species, and associated ecosystem

207   functions and services. As such shifts can have serious consequences not only for biodiversity

208   but also for human well-being, assessing latitudinal patterns in biodiversity responses to

209   climate change at the population, species and community levels warrants further research

210   attention.

211   **Methods**

212   **Data**

213   *Waterbird count data*

214   Data used in this study comprised site-specific annual counts based on the International

215   Waterbird Census (IWC) coordinated by Wetlands International and the Christmas Bird

216   Count (CBC) by the National Audubon Society in the USA, and were compiled in our earlier

217   study[16]. Note that counts based on these surveys should be described as relative abundance,

218   as we could not account for imperfect detections in this study. However, we have referred to

219   them as abundance throughout the manuscript for simplicity. Nevertheless, these count

220   records should still be comparable among years (see section *Model for estimating abundance*

221   *responses* for more detail).

222   The IWC, launched in 1967, is a scheme for monitoring waterbird numbers, covering

223   more than 25,000 sites in over 100 countries with more than 15,000 observers. The

224   coordination of the IWC is divided into four regional schemes corresponding to the major

225   migratory flyways of the world: the African-Eurasian Waterbird Census (AEWC), Asian

226   Waterbird Census (AWC), Caribbean Waterbird Census (CWC) and Neotropical Waterbird

227   Census (NWC). We did not use data from the CWC, as, having started in 2010, it only

228   provides short-term data. The survey methodology is essentially the same across the four

229   regional schemes. Population counts are typically carried out once every year in mid-January

230   but may include counts between December to February. Additional counts are also conducted

231   in other months, particularly in July in the Southern Hemisphere, but we only used the

232   January and February counts for consistency. This means that our data from the Northern

233   Hemisphere are for non-breeding populations while those in the Southern Hemisphere also

234   include some breeding populations. In each country that is covered by the survey, national

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235   coordinators manage an inventory of wetland sites (hereafter, survey sites), including sites of

236   international- or national-level recognition (e.g., Ramsar sites, Flyway Network Sites,

237   Important Bird Areas, national parks etc.). Each survey site is generally defined by

238   boundaries so that observers know precisely which areas are to be covered in the surveys.

239   The observers consist of a wide variety of volunteers, but national coordinators usually train

240   them using materials produced by Wetlands International to ensure the quality of count data.

241   Survey sites (normally up to a few km^2) are typically surveyed by about two observers for up

242   to four hours, while larger sites can require a group of observers working over several days.

243   Most surveys are conducted on foot, or from a vehicle, with boats involved in a few. The time

244   of survey on any given day depends on the type of survey site: inland sites are normally

245   surveyed during the morning or late afternoon, whereas coastal sites are surveyed over the

246   high tide period (mangrove areas and nearby mudflats are, however, covered during low

247   tides). Surveys cover waterbirds, defined as bird species that are ecologically dependent on

248   wetlands[36]. Counts are usually made by scanning flocks of waterbirds with a telescope or

249   binoculars and counting each species. Zero counts are not always recorded, and thus are

250   inferred using a set of criteria (see below for more detail). Count records, together with

251   associated information, are submitted to the national coordinators, who compile the submitted

252   records, check their validity and submit those records to Wetlands International. See [36,37] for

253   more details on survey methodology.

254   As the IWC does not cover North America, we also used data based on the CBC, which

255   has been conducted annually since 1900, and now includes over 2,400 count circles (defined

256   as survey sites in this study) and involves more than 70,000 observers each year[38]. Each CBC

257   consists of a tally of all bird species detected within 24.1 km in diameter, on a single day

258   between 14th December and 5th January. The majority of circles (and most historical data)

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259   are from the US and Canada. Observers join groups that survey subunits of the circle during

260   the course of the day using a variety of transportation methods (mostly on foot, or in a car,

261   but can include boats, skis, or snowmobiles). The number of observers and the duration of

262   counts vary among circles and through time. The total number of survey hours per count has

263   been recorded as a covariate to account for the variable duration of and participation in the

264   count. We only used records on waterbird species in this paper.

265   We compiled data from each scheme by species, except for data based on the African-

266   Eurasian Waterbird Census, where data had already been stored by flyway for each species[37].

267   As data based on the Neotropical Waterbird Census are only available for 1990 onward, we

268   only used post-1990 data for other regions as well. The latest records were in 2013. For the

269   IWC data, we generated zero counts using an established approach[37], in which we started

270   with a list of all species observed in each country and assumed a zero count of any species

271   that were on the list but not recorded at a particular site on a particular day if the site was

272   surveyed on that day, as shown by the presence of any other species' record(s), and if no

273   multi-species code related to the species (e.g., Anatinae spp. for species of the genus *Anas*)

274   was recorded for the site-date combination. We projected all survey sites onto a Behrmann

275   equal-area cylindrical projection and assigned them to grid cells with a grain size of 96.49 km,

276   or approximately 1º at 30º N/S. We only used species that were observed at one or more

277   survey sites for ten or more years since 1990, and this has resulted in 390 species being

278   analysed in this study (see Supplementary Data S4 for the full list of species). Species groups

279   used in Fig. 1 are based on the International Ornithological Congress World Bird List[39]:

280   coursers, gulls, terns and auks (Alcidae, Glareolidae, Laridae and Stercorariidae), grebes and

281   flamingos (Phoenicopteridae and Podicipedidae), loons and petrels (Gaviidae and

282   Procellariidae), pelicans, boobies and cormorants (Anhingidae, Fregatidae, Pelecanidae,

283   Phalacrocoracidae and Sulidae), rails and cranes (Aramidae, Gruidae and Rallidae),

284   shorebirds (Burhinidae, Charadriidae, Haematopodidae, Jacanidae, Recurvirostridae,

285   Rostratulidae and Scolopacidae), storks, ibises and herons (Ardeidae, Ciconiidae and

286   Threskiornithidae), and waterfowl (Anatidae and Anhimidae).

287

288   *Explanatory variables*

289   To estimate responses in waterbird abundance to changes in temperature and precipitation,

290   we used monthly mean temperature and precipitation total in the CRU TS v. 4.01 database [40],

291   by assigning each site to the 0.5° climatic grid cell including the site. When testing among-

292   and within-species latitudinal patterns in abundance responses, we also accounted for three

293   species-level variables—latitudinal geographical range, migratory status and body size—that

294   are expected to explain among-species variations in responses: data sources of those variables

295   are shown in Supplementary Table S2.

296

297   **Statistical Analyses**

298   *Model for estimating abundance responses*

299   We first estimated for each species at each survey site the rate of abundance changes with

300   increasing temperature and precipitation as regression coefficients (defined as abundance

301   responses to temperature or precipitation increases) by applying the Gompertz model of

302   population growth to count records:

303    $$N_t = N_{t-1} exp(\alpha + \beta_1 \log N_{t-1} + \beta_2 Temp_{t-1} + \beta_3 Prec_{t-1}),$$

304   where N_t, $Temp_t$, $Prec_t$ are the abundance of the species, the relevant mean Dec-Feb

305   temperature and precipitation at the site in year t, respectively. β_{1-3} are regression coefficients

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306   and α is the intercept. By estimating α as the population growth rate, this model tests the

307   effect of temperature and precipitation on yearly changes in abundance while controlling for

308   long-term trends in abundance. This model structure helps to avoid detecting a spurious

309   relationship between long-term trends in abundance caused by other threats (e.g., long-term

310   declines by habitat loss) and those in temperature or precipitation (e.g., long-term warming

311   temperatures). Taking logs and rearranging to express in terms of relative growth rate result

312   in the following form:

313    $$\log N_t - \log N_{t-1} = \alpha + \beta_1 \log N_{t-1} + \beta_2 Temp_{t-1} + \beta_3 Prec_{t-1},$$

314   and we used this form to estimate regression coefficients with linear models in R 3.4.1[41]. As

315   this model does not allow missing values, any missing values between the first and last

316   survey years at each site for each species were replaced by linear interpolation using the

317   package zoo[42]; the proportion of missing values (i.e., the effect of interpolation) was

318   accounted for in the following analysis (see *Latitudinal analysis*). The estimated β_2 and β_3

319   represent site-level abundance responses to temperature and precipitation increases,

320   respectively. Using the same model we also estimated the site-level independent capacity of

321   temperature and precipitation changes in explaining abundance changes (defined as the

322   importance of temperature and precipitation) with hierarchical partitioning[18] (measured in our

323   case as R^2) using the package hier.part[43].

324   As the model described above tests the effect of temperature and precipitation in the

325   previous year (i.e., year *t-1*) on abundance in the survey year (year *t*), we also separately

326   tested the immediate effect of temperature and precipitation in the same year (year *t*) as the

327   abundance survey year. For this analysis we used mean temperature and precipitation in

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328   December (year *t-1*), January and February (year *t*) for the IWC sites, where surveys were

329   conducted either in January or February, and mean Dec temperature and precipitation in year

330   *t* for the CBC sites, where surveys were largely conducted in December. We compared AIC

331   of the two models at each site for each species and used the coefficients in the model with a

332   smaller AIC.

333   We assumed constant survey efforts over time for the IWC, because regular and

334   standardized surveys with constant methods, efforts and timing are strongly encouraged in

335   this scheme (see Supplementary Discussion in[16] for more detail). However, survey efforts in

336   the CBC are known to vary through time. Following a previously published analysis[44] we

337   thus accounted for the survey effort effect for the CBC data by using the total number of

338   survey hours per count as the measure of survey efforts:

339    $$\log N_t - \log N_{t-1} = \alpha + \beta_1 \log N_{t-1} + \beta_2 Temp_{t-1} + \beta_3 Prec_{t-1} + \frac{B\left(\left(\frac{\zeta_t}{\bar{\zeta}}\right)^p - 1\right)}{p},$$

340   where ζ_t is the total number of survey hours per count and $\bar{\zeta}$ is the mean value of ζ_t. The

341   parameters B and p determine a range of relationships between effort and the number of birds

342   counted[44] and we used the values estimated for each species in our earlier study[16] (see

343   Supplementary Data S4).

344   We only used survey sites with ten or more records and five or more non-zero records

345   since 1990 for at least one species, and this has resulted in 1,303,651 count records since

346   1990 on 390 species at 6,822 sites between -55° and 64° (Supplementary Figure S1) being

347   analysed in this study. We aggregated the estimated site-level responses to temperature and

348   precipitation increases as well as the importance of temperature and precipitation to 1°×1°

349   grid cells by calculating the mean site-level estimates across all sites in each grid cell,

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350   weighted by the inverse of estimate variance at each site to account for uncertainties. The grid

351   cell-level estimates (Supplementary Data S2) were then used in the latitudinal analysis

352   described below and for the species-level maps (Supplementary Data S1). We also calculated

353   community-level responses (Figure 2) by calculating the mean grid cell-level estimates across

354   all species observed in each grid cell, weighted by the inverse of estimate variance in each

355   species to account for uncertainties.

356

357   *Latitudinal analysis*

358   We used absolute latitudes to test latitudinal patterns described in Supplementary Table S1

359   for the following reason. Our data include species that are distributed only in either the

360   northern or southern hemisphere (one-hemisphere species) as well as those that appear in

361   both the hemispheres (two-hemisphere species). Some of our hypotheses (e.g., that for

362   among-species patterns in abundance changes with increasing temperature, shown at the top

363   of Supplementary Table S1) predict that one-hemisphere species would show a monotonic

364   increase with raw latitudes while two-hemisphere species would show a U-shaped

365   relationship along the raw latitudinal gradient with the lowest point at the equator; this makes

366   analysing those species together in the hierarchical modelling framework described below a

367   complicated process. With absolute latitudes, in contrast, one-hemisphere and two-

368   hemisphere species are both expected to show a monotonic increase, making the parameter

369   estimation much simpler.

370   To explain among- and within-species latitudinal variations in abundance responses to

371   temperature and precipitation changes as well as the importance of temperature and

372   precipitation for 213 species with estimates at ten or more grid cells, we adopted the within-

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373   subject centring approach[45] under a hierarchical modelling framework to explicitly

374   distinguish species-level effects (explaining variations in species-level responses between

375   species) and population-level effects (explaining variations in population-level responses

376   within species) of explanatory variables. Here we defined each species responses at their

377   absolute latitudinal range mid-points as species-level responses, and responses within each

378   grid cell as population-level responses.

379   In this model the species effect μ_s, representing the species-level responses to temperature

380   or precipitation increases in species s, is drawn from a normal distribution with mean of v_s

381   and variance of σ_v^2. v_s is further modelled with species-level explanatory variables:

382   $$v_s = \alpha + \beta_{B1}MIDLAT_s + \beta_{B2}MIDLAT_s^2 + \beta_{B3}LATRANGE_s + \beta_{B4}MIG_s + \beta_5 BM_{Bs} +$$

383   $$\beta_{B6}PROPNA_s + \eta_s,$$

384   where α is the global intercept and β_{B1-B6} represent the species-level effects. $MIDLAT_s$,

385   $LATRANGE_s$, MIG_s, BM_s, $PROPNA_s$ are species-level explanatory variables; absolute

386   latitudinal range mid-points, absolute latitudinal geographical range (degree), migration

387   status (migrant or non-migrant), body mass (g, $\log_{10}$-transformed) and the mean proportion of

388   missing values (i.e., interpolated values) in count records across all sites (%) for species s,

389   respectively. η_s is a random term that accounts for phylogenetic dependence among species

390   and is drawn from a multivariate normal distribution[46,47]:

391   $$\eta_s \sim MVN(\mathbf{0},\ \delta^2 \Sigma_\lambda),$$

392   $$\Sigma_\lambda = \lambda\Sigma + (1-\lambda)\mathbf{I},$$

393   where Σ is a scaled variance-covariance matrix calculated from an ultrametric phylogenetic

394   tree (defined below). By scaling Σ to a height of one, we can interpret δ^2 as the residual

395   variance[46]. For the strength of phylogenetic signal to vary, we also incorporated Pagel's λ[48,49]

18

396   into the matrix with the identity matrix **I**. Here λ is a coefficient that multiplies the off-

397   diagonal elements of Σ and a λ close to zero implies that the phylogenetic signal in the data is

398   low, suggesting independence in the error structure of the data points, whereas a λ close to

399   one suggests a good agreement with the Brownian Motion evolution model and thus suggests

400   correlation in the error structure[46,49]. To incorporate uncertainties[50] in phylogenetic trees in

401   the calculation of Σ, we used a sample of 100 trees from a comprehensive avian phylogeny[51]

402   as the prior distribution for our analysis[46]. More specifically, one of the 100 trees was

403   randomly drawn in each iteration and used for the calculation of Σ.

404   The population-level responses to temperature or precipitation increases $r_{s,i}$ of species s in

405   grid cell i was then assumed to derive from a normal distribution with mean $\mu_{s,i}$ and variance

406   σ_μ^2, where $\mu_{s,i}$ is modelled using the species effect μ_s:

407
$$\mu_{s,i} = \mu_s + \beta_{w_{s,1}} \frac{LAT_{s,i} - MIDLAT_s}{LATRANGE_s} + \beta_{w_{s,2}} \left(\frac{LAT_{s,i} - MIDLAT_s}{LATRANGE_s}\right)^2 + \beta_{w_{s,3}} pNA_{s,i} + \gamma_{s,i}.$$

408   Here $\beta_{Ws,1-3}$ represents the population-level effect of absolute latitudes $LAT_{s,i}$ (in the form of

409   linear and quadratic terms, to test non-linear patterns) and the mean proportion of missing

410   values (i.e., interpolated values) in count records across all sites $pNA_{s,i}$ (%) of grid cell i for

411   species s. Here within-species variations in population-level responses ($\mu_{s,i} - \mu_s$) are

412   explained by within-species variations in absolute latitudes ($LAT_{s,i} - MIDLAT_s$), divided by

413   the absolute latitudinal geographical range of each species $LATRANGE_s$, so that the estimated

414   effects of absolute latitudes are comparable among species with varying latitudinal range size.

415   The species-specific $\beta_{Ws,1-3}$ is the random effect each governed by hyper-parameters as:

416
$$\beta_{W_{s,j}} \sim Normal(h\beta_{W_j}, \sigma^2_{\beta_{W_j}}).$$

417    $\gamma_{s,i}$ accounts for spatial autocorrelation within each species and is drawn from an intrinsic

418   Gaussian conditional autoregressive (CAR) prior distribution with variance $\sigma^2_{\gamma_s}$:

19

419
$$\gamma_{s,i}|\gamma_{s,k} \sim Normal\left(\frac{\sum_{i \neq k} w_{i,k}\gamma_{s,k}}{n_i}, \frac{\sigma_{\gamma_s}^2}{n_i}\right),$$

420 where $w_{i,k} = 1$ if grid cells i and k are neighbours, and 0 otherwise. n_i is the total number of

421 neighbours of grid cell i and neighbours here are defined as those grid cells directly adjacent,

422 including those diagonal. $\sigma_{\gamma_s}^2$ controls the amount of variation between the random effects.

423 We tested latitudinal patterns in the importance of temperature and precipitation using

424 essentially the same model but the population-level importance of temperature or

425 precipitation $imp_{s,i}$ of species s in grid cell i was assumed to derive from a beta distribution

426 with mean $c_{s,i}$ and variance $\frac{\alpha_i \beta_i}{(\alpha_i + \beta_i)^2 (\alpha_i + \beta_i + 1)}$ with a logit link function:

427
$$logit(c_{s,i}) = \mu_s + \beta_{w_{s,1}}\frac{LAT_{s,i} - MIDLAT_s}{LATRANGE_s} + \beta_{w_{s,2}}\left(\frac{LAT_{s,i} - MIDLAT_s}{LATRANGE_s}\right)^2 + \beta_{w_{s,3}}pNA_{s,i} + \gamma_{s,i},$$

428
$$\alpha_i = c_{s,i}\varphi_i,$$

429
$$\beta_i = (1 - c_{s,i})\varphi_i.$$

430 The models were implemented with OpenBUGS 3.2.3[52] and the R2OpenBUGS package[53]

431 in R 3.4.1[41]. As non-informative prior distributions, we used a Gamma distribution with mean

432 of 1 and variance of 100 for φ_i and the inverse of σ_v^2, δ^2, σ_μ^2, $\sigma_{\beta_{W_j}}^2$ and $\sigma_{\gamma_s}^2$, a uniform

433 distribution on the interval [0, 1] for λ, normal distributions with mean of 0 and variance of

434 100 for α, β_{Bk}, and $h\beta_{Wj}$. Each MCMC algorithm was run with three chains with different

435 initial values for 30,000 iterations with the first 10,000 discarded as burn-in and the

436 remainder thinned to one in every four iterations to save storage space. Model convergence

437 was checked with R-hat values.

438 Due to differences in the definition of species between the two sources used[51,54], we

439 combined two separate species defined in the BirdLife Checklist[54] into one in four cases for

440 this species-level analysis: Kentish plover *Charadrius alexandrinus* and snowy plover *C.*

441 *nivosus*, common snipe *Gallinago gallinago* and Wilson's snipe *G. delicata*, European

20

442   herring gull *Larus argentatus* and Arctic herring gull *L. smithsonianus*, and common

443   moorhen *Gallinula chloropus* and common gallinule *G. galeata*. *Larus glaucoides thayeri*

444   was excluded from the latitudinal analysis as it is not included in either database. We also

445   excluded from the analysis eight seabird species in Alcidae and Sulidae as neither the IWC

446   nor CBC necessarily targets seabird species.

447   We also used R packages ape[55], data.table[56], dplyr[57], ggplot2[58], gridExtra[59], mapdata[60],

448   plyr[61], png[62], RcolorBrewer[63], rgdal[64], raster[65] and viridis[66].

449

450   **Data Availability**

451   The waterbird count data used in this study are collated and managed by Wetlands

452   International and the National Audubon Society, and are available from Wetlands

453   International at: http://iwc.wetlands.org/. The estimated abundance responses to temperature

454   and precipitation as well as the importance of temperature and precipitation for each grid cell

455   for each species are available as Supplementary Data S2. All the data on explanatory

456   variables are freely available as specified in Supplementary Table S2.

457

458   **Code Availability**

459   All the R codes used for the analyses are available as Supplementary Data S5-7.

460

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613

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630   **Author contributions**

631   T.A. designed the study. T.A., T.S., H.S.W., B.S., S.N., T.M., T.L., D.B. and N.L.M.

632   collected and prepared data for the analyses. T.A. analysed the data and wrote the paper. All

633   authors discussed the results and commented on the manuscript at all stages.

634   **Competing interests**

635   The authors declare no competing interests.

636   **Additional information**

637   **Supplementary information** is available for this paper.

638   **Correspondence and requests for materials** should be addressed to T.A.
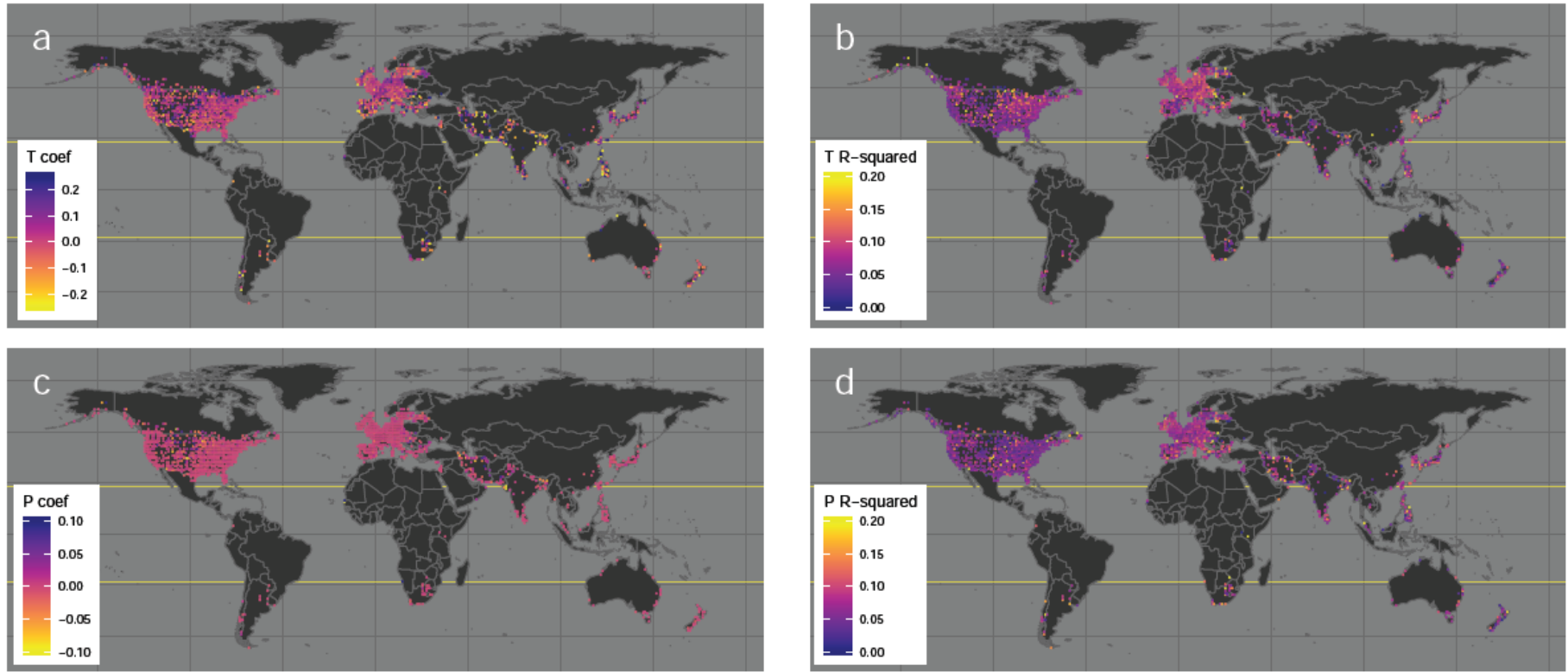
639   (t.amano@uq.edu.au)

640
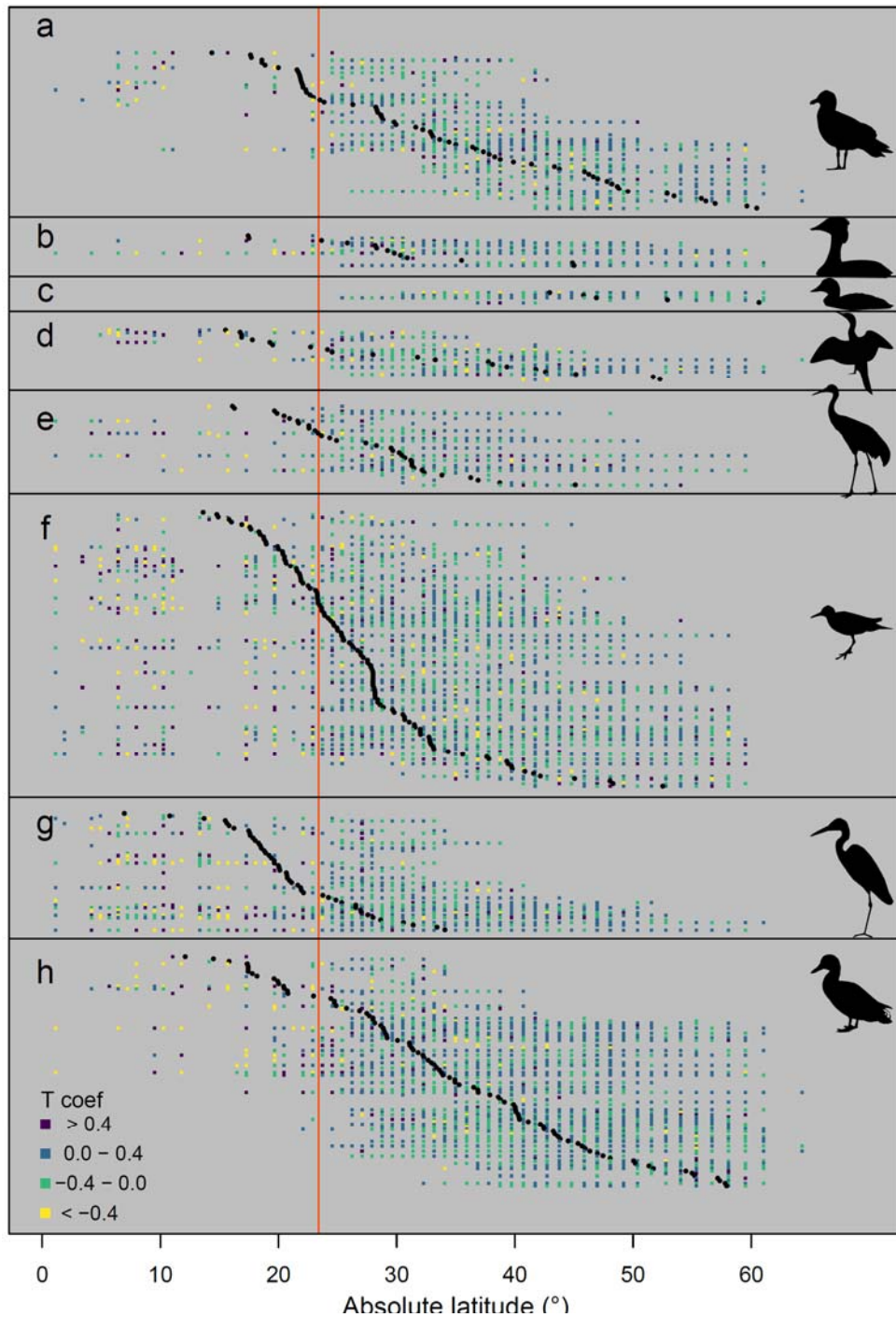
Fig. 1. Latitudinal distribution of abundance responses to changes in temperature (the rate of abundance changes with increasing temperature) for each species. Each horizontal row of squares shows the absolute latitudes of $1° \times 1°$ grid cells with estimates for each of the 390 species in (a) coursers, gulls, terns and auks, (b) grebes and flamingos, (c) loons and petrels, (d) pelicans, boobies and cormorants, (e) rails and cranes, (f) shorebirds, (g) storks, ibises and herons, and (h) waterfowl (see Methods for the definition of each species group). Black circles indicate the latitudinal range mid-point (i.e., median absolute latitude of geographical range) of each species. The area on the left of the red vertical line (absolute latitude < 23.4°) represents the tropical region.

Fig. 2. Mean abundance responses across 390 waterbird species to changes in temperature and precipitation in each 1° × 1° grid cell. The rate of abundance changes with increasing temperature (a), the independent capacity of temperature in explaining abundance changes (b), the rate of abundance changes with increasing precipitation (c) and the independent capacity of precipitation in explaining abundance changes (d). The region between the yellow solid lines is the tropics.
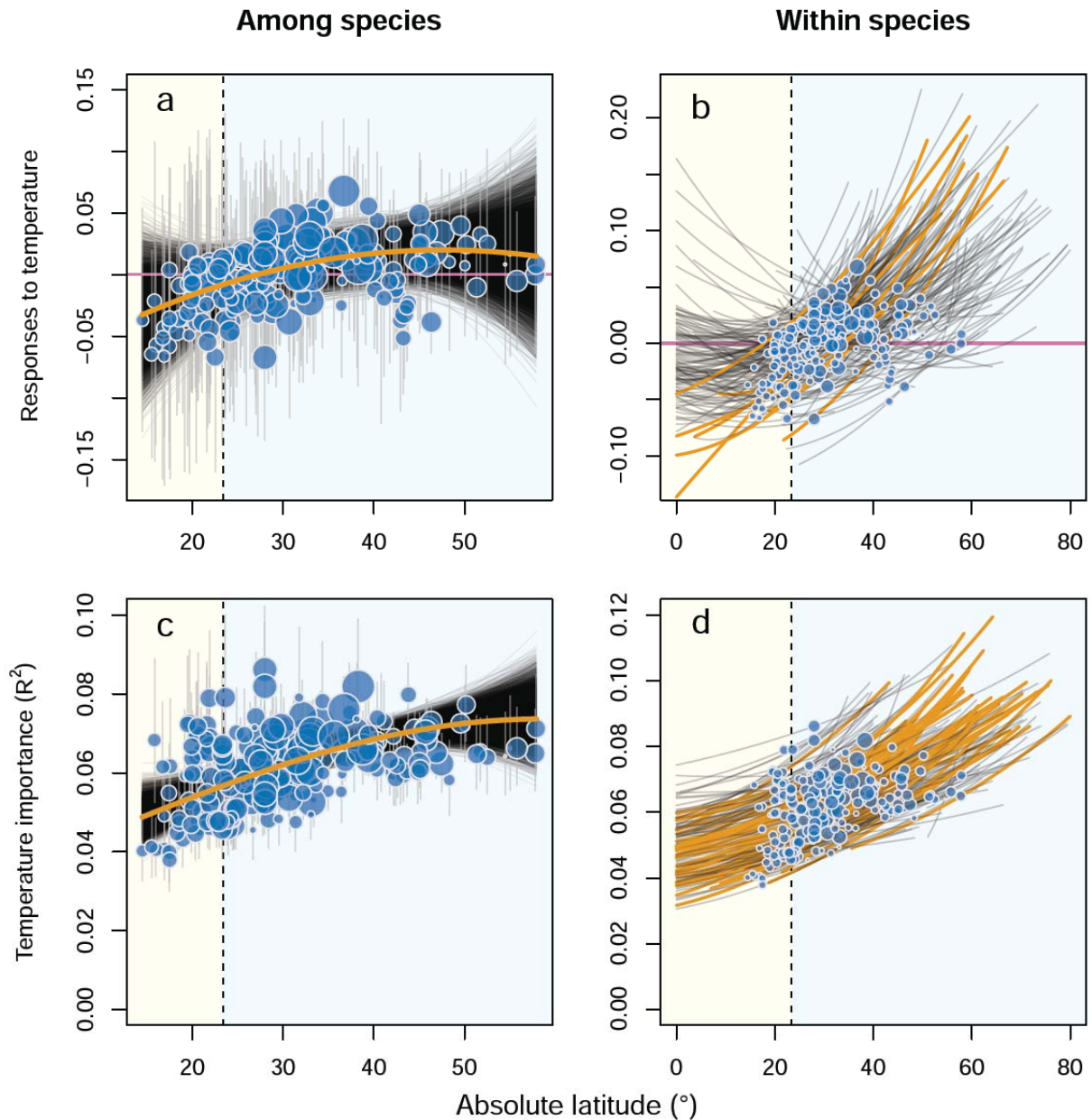
Fig. 3. Latitudinal patterns in waterbird abundance responses to temperature increases.
The rate of abundance changes with increasing temperature at each species' range mid-points
(a) and within each species (b), the independent capacity of temperature in explaining
abundance changes at each species' range mid-points (c) and within each species (d). In (a)
and (c) orange lines represent the among-species latitudinal patterns based on posterior
median coefficients with black lines showing patterns based on all posterior samples. Blue
circles indicate the estimated responses at each species' range mid-points (also shown in (b)
and (d)) with grey vertical lines showing 95% credible intervals; circle size, the absolute
latitudinal range size. In (b) and (d) regression lines show the estimated within-species
latitudinal patterns for each species based on posterior median coefficients; orange lines
represent significant patterns. The yellow area (absolute latitude < 23.4°) represents the
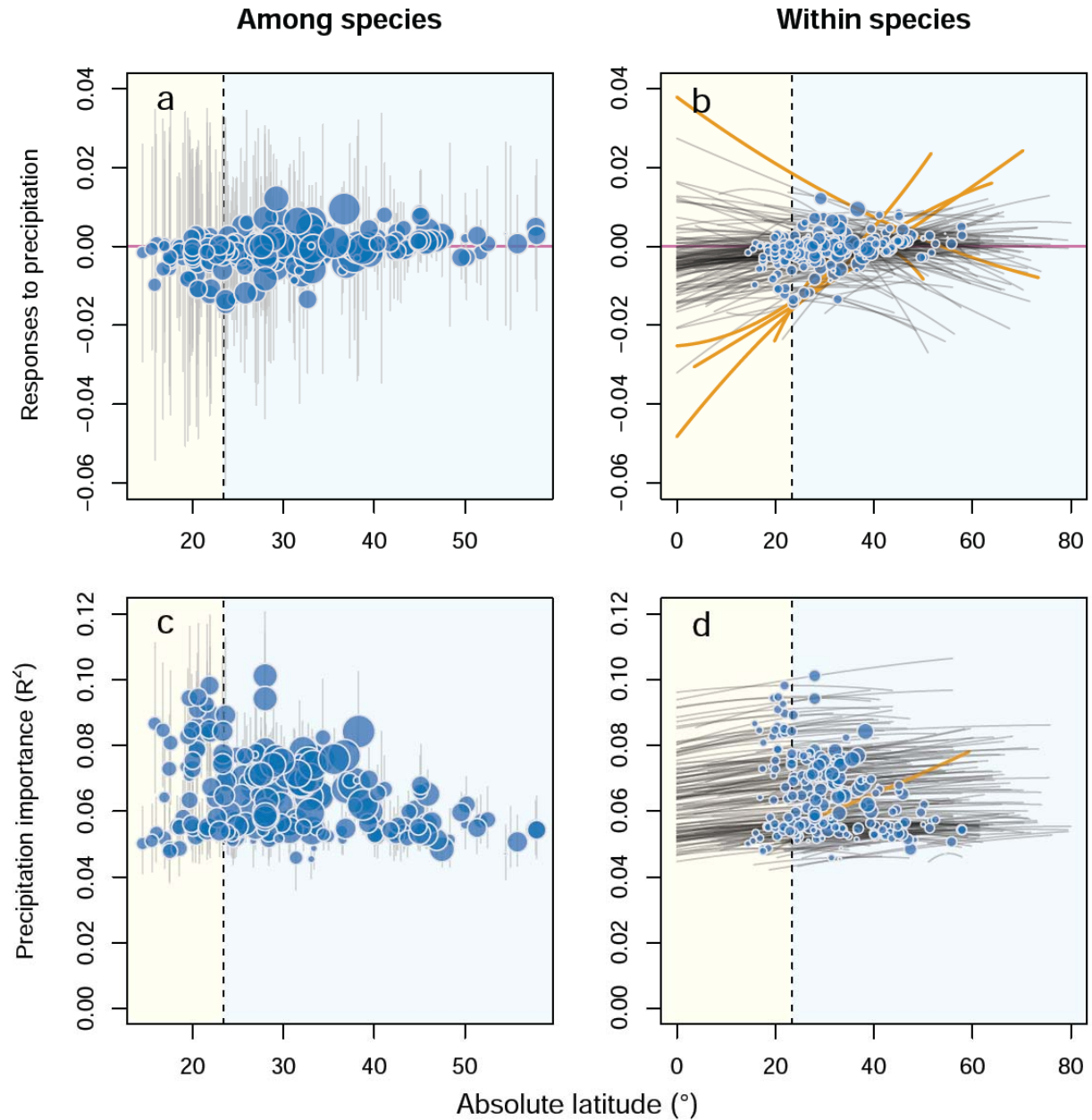tropical region.

Fig. 4. Latitudinal patterns in waterbird abundance responses to precipitation increases.
The rate of abundance changes with increasing precipitation for each species' range mid-points (a) and within each species (b), the independent capacity of precipitation in explaining abundance changes at each species' range mid-points (c) and within each species (d). In (a) and (c) orange lines represent the among-species latitudinal patterns based on posterior median coefficients with black lines showing patterns based on all posterior samples. Blue circles indicate the estimated responses at each species' range mid-points (also shown in (b) and (d)) with grey vertical lines showing 95% credible intervals; circle size, the absolute latitudinal range size. In (b) and (d) regression lines show the estimated within-species latitudinal patterns for each species based on posterior median coefficients; orange lines represent significant patterns. The yellow area (absolute latitude < 23.4°) represents the tropical region.