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Responses of global waterbird populations to climate change vary with latitude

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24 Most research on climate change impacts on global biodiversity lacks the resolution to 25 detect changes in species abundance and is limited to temperate ecosystems. This limits 26 our understanding of global responses in species abundance-a determinant of 27extinction risk and ecosystem function and services-to climate change including in the 28 highly-biodiverse tropics. We address this knowledge gap by quantifying the abundance 29 response of waterbirds, an indicator taxon of wetland biodiversity, to climate change at 30 6,822 sites between 55°S and 64°N. Using 1,303,651 count records of 390 species, we 31 show that with temperature increase, the abundance of species and populations decreased at lower latitudes, particularly in the tropics, but increased at higher 32 33 latitudes. These contrasting latitudinal responses indicate potential global-scale 34 poleward shifts of species abundance under climate change. The negative responses to 35 temperature increase in tropical species are of conservation concern, as they are often 36 also threatened by other anthropogenic factors.

37

38 Climate change continues to pose various serious threats to biodiversity, and there is an 39 urgent need to understand how species respond on a global scale to changing climates. A wide 40 range of species have already been shown to respond to climate change through changes in geographical range<sup>1</sup>, phenology<sup>2</sup> and abundance<sup>3</sup>. However, the rate and direction of these 41 responses vary greatly among species and locations<sup>1, 2, 4</sup>. As climate-driven changes in 42 43 biodiversity are expected to affect ecosystem functioning, human well-being, and the dynamics of climate change itself<sup>5</sup>, understanding how species' responses to climate change 44 may vary globally could provide crucial evidence for a more effective allocation of limited 45

46 resources for the conservation of species and ecosystems most threatened by climate change, 47 and for assessing how climate-driven changes in biodiversity may affect human societies. Existing gaps in the geographical coverage of available evidence seriously limit our 48 49 understanding of species' responses to climate change across the globe<sup>6</sup>. Earlier global 50 reviews of species' responses to climate change have rarely incorporated species and studies 51 in the tropics<sup>7</sup>, due to the lack of ecological data<sup>8</sup>. Such geographical biases are even more prominent in studies investigating responses in species abundance<sup>9</sup>, which is a major 52 determinant of species extinction risk<sup>10</sup>, ecosystem function and services<sup>11</sup>. Research on 53 54 abundance responses to climate change to date has largely been conducted in Europe, North America, Australia and the Arctic<sup>3, 12-15</sup>, with a recent global study showing a link between 55 climate warming and abundance declines in birds and mammals<sup>9</sup> but still largely missing the 56 tropics. As a result, although tropical species are predicted to be more vulnerable to increasing 57 temperature<sup>16</sup>, there is still little empirical evidence on how responses in species abundance to 58 59 climate change vary among and within species at the global scale. 60 Here we address this challenge by modelling global time-series data of waterbird species

to estimate their abundance responses to changes in temperature and precipitation. The global dataset of waterbird abundance changes used is based on long-term surveys in over 100 countries and covers regions for which there is little information on climate change impacts, such as the tropics<sup>17</sup>. Waterbirds can also serve as an indicator taxon for assessing the status of biodiversity in wetland ecosystems, which have been lost at higher rates than other ecosystems, despite their high levels of biodiversity and productivity as well as the crucial ecosystem functions and services delivered<sup>18</sup>.

Using 1,303,651 count records collected since 1990 on 390 waterbird species at 6,822 68 69 sites between 55°S and 64°N (Extended Data Fig. 1) we first estimated, for each species at 70 each site, (i) the rate of abundance changes with increasing temperature and precipitation as 71 regression coefficients (responses to temperature and precipitation increases; note that the 72 actual rate and direction of temperature and precipitation changes vary spatially: Extended 73 Data Fig. 2), and (ii) the proportion of abundance changes that can be explained 74independently by temperature and precipitation changes (measured as  $R^2$ ), estimated with hierarchical partitioning<sup>19</sup> (the importance of temperature and precipitation). We then tested 75 76 multiple hypotheses that are rarely explored at the global scale (Extended Data Figs. 3 and 4), 77 to examine among- and within-species variations in responses to temperature and precipitation increases as well as the importance of temperature and precipitation across 78 latitudes. 79

## 80 Tropical species suffer from temperature increase

Applying the Gompertz model of population growth to the global waterbird dataset enabled us to estimate abundance responses to the changes in temperature and precipitation at  $1^{\circ} \times 1^{\circ}$ grid cells across latitudes, including the tropics, for a wide range of waterbird groups. Of the 390 species analysed, 144 species (36.9%) had at least one estimate in the tropics and 129 species (33.1%) had their absolute latitudinal range mid-points in the tropics (defined as tropical species; Fig. 1) although most data in the tropics were from tropical Asia (Extended Data Fig. 1).

Many species showed considerable spatial variation in abundance responses to
 temperature increases within their geographical ranges, with particularly negative responses in

90 the tropics (Fig. 1), although the importance of temperature in explaining abundance changes tended to be low across the ranges, with an overall median  $R^2$  of 0.057 (Supplementary Data 91 92 S1 and S2). In contrast, for most species there was no clear geographical pattern in abundance 93 responses to precipitation increases, and precipitation was found to have a low importance in 94 explaining abundance changes (the overall median  $R^2 = 0.051$ ; Supplementary Data S1 and 95 S2). These geographical patterns were also evident in the distribution of abundance responses 96 averaged across all species observed within each grid cell; species generally showed more 97 negative responses to temperature increases at lower latitudes, such as in South and Southeast 98 Asia, and positive responses at higher latitudes (Fig. 2).

99 For 213 species with estimates at ten or more grid cells, we then tested hypotheses on how 100 responses to temperature and precipitation increases and the importance of temperature and 101 precipitation vary both among species (among each species' estimates at latitudinal range 102 mid-points; species-level responses) and also within species (among grid cells within each 103 species; population-level responses) along latitudes. When compared among species, 104 abundance responses to temperature increases shifted from positive at higher latitudes to 105 negative at lower latitudes, with 69% of the tropical species showing negative responses to 106 temperature increases (Fig. 3a, Extended Data Fig. 5a). When compared within species, 107 although 198 (93%) out of the 213 species showed more negative responses to temperature 108 increases at lower latitudes, this within-species latitudinal pattern was significant only in eight 109 of the 198 species (Fig. 3b, Supplementary Data S3). The importance of temperature in 110 explaining abundance changes also increased with latitude among species (Fig. 3c, Extended 111 Data Fig. 5b) and within species for all 55 species with a significant within-species latitudinal 112 pattern (Fig. 3d, Supplementary Data S3). For migratory species, larger-sized species and

species with a wider latitudinal range, temperature played a higher importance in explaining
abundance changes (Extended Data Fig. 5b) although none of these seemed to explain
species-level responses to temperature increases.

116 In contrast, neither abundance responses to precipitation increases nor the importance of 117 precipitation in explaining abundance changes showed significant latitudinal patterns among 118 species. This does not necessarily mean that precipitation was not important; for some species 119 in the tropics, precipitation was found to have a relatively high importance in explaining 120 abundance changes (Fig. 4a, c, Extended Data Fig. 6 and Supplementary Data S3). 121 Precipitation was shown to have a higher importance in explaining abundance changes in 122 species with a wider latitudinal range (Extended Data Fig. 6b). When compared within 123 species, five species showed a significant pattern: one species showed a decrease, three 124 species showed an increase, and another species showed a hump-shaped curve in abundance 125 responses to precipitation increases along latitudes (Fig. 4b, Supplementary Data S3). The 126 importance of precipitation in explaining abundance changes showed a significant within-127 species latitudinal pattern for just one species (Fig. 4d, Supplementary Data S3). These 128 conclusions were robust even when the effect of Jun-Aug precipitation was considered 129 (Extended Data Figs. 7 and 8) and appeared to be driven largely by patterns in the northern 130 hemisphere (Supplementary Figs. S1-S4).

# 131 How climate affects species abundance across latitudes

Our results demonstrate that the responses in waterbird abundance to temperature increases
differ between tropical (especially Asian tropical) and non-tropical regions. At both species
and population levels, waterbird abundance generally decreased in the tropics, but increased

at higher latitudes, with increasing temperature. This supports our predictions on among- and 135 136 within-species patterns (Extended Data Fig. 3). Species in the tropics tend to live closer to their upper temperature limits<sup>16</sup>, have a narrower temperature niche<sup>20</sup> and change their 137 temperature niche at a slower rate<sup>21</sup>, all of which indicate that tropical species are more 138 139 vulnerable to increasing temperatures at the species level. Climate-related extinctions of local 140 populations, typically at the warmer edge of the species' geographical range, are also more 141 frequent in the tropics, causing poleward range shifts in many species<sup>22</sup>. While such species-142 level and population-level responses to climate change have often been investigated 143 separately to date, our results provide novel empirical evidence that impacts of temperature 144 increases on tropical ecosystems can be characterised by species-wide declines in tropical 145 species as well as population-level responses in wider-ranging species.

Temperature generally explained a small proportion of yearly abundance changes in
waterbirds, especially in tropical species and at the low-latitude range margin of species.
Despite this, our finding of negative responses to temperature increases in the tropics seems to
be robust because temperature was shown to be more important in explaining abundance
changes for grid cells in the tropics with more negative responses to temperature increases
(Supplementary Fig. S5).

The lower importance of temperature at lower latitudes might be explained by four reasons. First, the effect of temperature changes on waterbird abundance can be indirect, especially at lower latitudes. Although warmer weather conditions can directly increase the survival of waterbirds at higher latitudes<sup>23</sup>, indirect biotic processes (e.g., changes in food availability), rather than direct abiotic processes (e.g., heat stress), are reported to be more

important mechanisms for climate-driven abundance changes for higher-level consumers like 157 birds<sup>24, 25</sup>. For example, increases in already-high temperatures at lower latitudes can cause 158 wetlands to dry, reducing the availability of habitats and food for waterbirds<sup>23</sup>. Such an 159 160 indirect effect of temperature increases could have obscured the temperature-abundance 161 relationship, especially in the tropics. Second, many of the waterbirds analysed here are 162 migratory species, for which temperature played a higher importance in explaining abundance 163 changes (Extended Data Fig. 5b). This does not support our hypothesis that the effects of 164 factors at multiple locations could outweigh the effects of local climatic conditions in 165 migratory species, but instead indicates that migratory species can be more responsive to local temperature changes due to their higher abilities to disperse<sup>26</sup> and track climate niches<sup>27</sup>. In 166 167 this study more non-tropical species tended to be migratory compared to tropical species: 151 (96%) of 158 non-tropical species and 43 (78%) of 55 tropical species were migratory, which 168 169 may explain the higher importance of local temperature in explaining the abundance of non-170 tropical species. Third, larger errors associated with count data can cause a lower explanatory 171 power of variables. We may expect larger errors in the tropics, where surveyors might be less 172 trained given the shorter history of waterbird surveys and thus be more susceptible to 173 observation errors. Finally, other important threats, such as habitat loss and hunting, affect 174 bird abundance, independently from, or synergistically with, climate change<sup>28</sup>. By testing the 175 effect of temperature and precipitation changes on yearly abundance changes while estimating 176 long-term growth rates, our modelling approach controlled for the consistent impacts of such 177threats on long-term trends in abundance (see Statistical Analyses for more detail). 178 Nevertheless, those threats can also cause yearly abundance changes and their impacts are

179 likely to be more severe at lower latitudes<sup>17</sup>, potentially causing temperature to have lower
180 importance at lower latitudes.

181 Contrary to our hypotheses, there was no clear latitudinal pattern in abundance responses 182 to precipitation changes, either among or within species. Water availability, compared to 183 ambient temperature, has been shown to be a more important driver of species richness and 184 population size at lower latitudes<sup>4</sup>. Supporting this, our results showed that precipitation was 185 more important in explaining the abundance of some tropical species compared to most 186 species in higher latitudes, although the overall among-species pattern across latitudes was 187 not significant (Fig. 4c). This may be explained by the two reasons. First, precipitation 188 changes can affect waterbirds at the river basin scale (often the scale of 500 to 1,000 km) through effects on water flow into their wetland habitats<sup>29</sup>. Therefore, our analysis at the 189 190 resolution of 1° grid cells (equivalent to a grain size of 96.49 km) may not have been able to 191 detect such a broad-scale impact of precipitation changes. Second, waterbird responses to 192 precipitation changes can vary greatly among species (see Extended Data Fig. 3 for detail). 193 While increased rainfall generally leads to more favourable habitat conditions for waterbirds in dry regions<sup>23</sup>, elevated water levels associated with increased rainfall can cause the loss of 194 195 shallow-water habitats, often followed by abundance decreases in certain groups, such as 196 shorebirds<sup>30</sup>. Such mixed responses to precipitation changes among species may have resulted 197 in the lack of clear latitudinal patterns, particularly among species.

# 198 Tropical biodiversity imperilled yet understudied

199 Our results imply three major implications on the impact of climate change on global

200 biodiversity. First, local temperature increases between December and February under

201 ongoing climate change are likely to pose a more negative impact on species and populations 202 in the tropics. This provides important evidence for improving our understanding of whether 203 tropical ecosystems have been degraded by climate change. Although climate change is not 204 the only threat to waterbirds, impacts of other major threats, such as loss and degradation of 205 wetlands and excessive hunting pressure, seem to be more severe in the tropics  $too^{17}$ , 206 indicating that tropical species and populations suffer from multiple anthropogenic threats. 207 Second, the revealed negative impact of temperature increases in the tropics suggests that 208 existing severe biases in scientific information towards temperate regions could underestimate 209 the impact of climate change on species populations at the global scale. Highlighting the negative impact of climate change on tropical waterbirds should serve to inspire further 210 211 studies on other taxa in the tropics, where most species are facing multiple threats including 212 climate change<sup>8</sup>. Finally, our other finding that abundance responds positively to temperature 213 increases at higher latitudes highlights the possibility of global-scale poleward shifts in 214 abundance across species, and associated ecosystem functions and services. As such shifts can 215 have serious consequences not only for biodiversity but also for human well-being, assessing 216 latitudinal patterns in biodiversity responses to climate change at the population, species and 217 community levels warrants further research attention.

# 218 **References**

- Chen, I. C. et al., Rapid range shifts of species associated with high levels of climate
  warming. *Science* 333, 1024-1026 (2011).
- <sup>2</sup> Thackeray, S. J. et al., Phenological sensitivity to climate across taxa and trophic levels.
   *Nature* 535, 241 (2016).

- Stephens, P. A. et al., Consistent response of bird populations to climate change on two
   continents. *Science* 352, 84-87 (2016).
- Pearce-Higgins, J. W. et al., Geographical variation in species' population responses to
   changes in temperature and precipitation. *Proceedings of the Royal Society of London B:*

227 Biological Sciences 282, 20151561 (2015).

- Pecl, G. T. et al., Biodiversity redistribution under climate change: Impacts on
   ecosystems and human well-being. *Science* 355, eaai9214 (2017).
- Perez, T. M., Stroud, J. T., and Feeley, K. J., Thermal trouble in the tropics. *Science* 351, 1392-1393 (2016).
- Feeley, K. J., Stroud, J. T., Perez, T. M., and Kühn, I., Most 'global' reviews of species'
  responses to climate change are not truly global. *Diversity and Distributions* 23, 231-234
  (2017).
- Stroud, J. T. and Thompson, M. E., Looking to the past to understand the future of
  tropical conservation: The importance of collecting basic data. *Biotropica* 51, 293-299
  (2019).
- <sup>9</sup> Spooner, F. E. B., Pearson, R. G., and Freeman, R., Rapid warming is associated with
   population decline among terrestrial birds and mammals globally. *Global Change Biology* 24, 4521-4531 (2018).
- <sup>10</sup> IUCN, *IUCN Red List Categories and Criteria: Version 3.1.* (Species Survival
- 242 Commission. IUCN, Gland, Switzerland and Cambridge, UK, 2001).
- Winfree, R. et al., Abundance of common species, not species richness, drives delivery of
  a real-world ecosystem service. *Ecology Letters* 18, 626-635 (2015).
- <sup>12</sup> Bowler, D. E. et al., Cross-realm assessment of climate change impacts on species'
- abundance trends. *Nature Ecology & Evolution* **1**, 0067 (2017).

- <sup>13</sup> Myers-Smith, I. H. et al., Climate sensitivity of shrub growth across the tundra biome.
   Nature Climate Change 5, 887 (2015).
- Lowe, J. R. et al., Responses of coral reef wrasse assemblages to disturbance and marine
   reserve protection on the Great Barrier Reef. *Marine Biology* 166 (2019).
- <sup>15</sup> Martay, B. et al., Impacts of climate change on national biodiversity population trends.
   *Ecography* 40, 1139-1151 (2017).
- <sup>16</sup> Khaliq, I. et al., Global variation in thermal tolerances and vulnerability of endotherms to
   climate change. *Proceedings of the Royal Society B: Biological Sciences* 281, 20141097
- 255 (2014).
- Amano, T. et al., Successful conservation of global waterbird populations depends on
  effective governance. *Nature* 553, 199-202 (2018).
- Ramsar Convention on Wetlands, *Global Wetland Outlook: State of the World's Wetlands and their Services to People.* (Ramsar Convention Secretariat, Gland, Switzerland, 2018).
- <sup>19</sup> Mac Nally, R., Hierarchical partitioning as an interpretative tool in multivariate inference.
- 261 *Australian Journal of Ecology* **21**, 224-228 (1996).
- <sup>20</sup> Cadena, C. D. et al., Latitude, elevational climatic zonation and speciation in New World
   vertebrates. *Proceedings of the Royal Society B: Biological Sciences* 279, 194-201
- 264 (2012).
- <sup>265</sup> <sup>21</sup> Jezkova, T. and Wiens, J. J., Rates of change in climatic niches in plant and animal
- 266 populations are much slower than projected climate change. *Proceedings of the Royal*
- 267 Society B: Biological Sciences **283**, 20162104 (2016).
- <sup>22</sup> Wiens, J. J., Climate-related local extinctions are already widespread among plant and
   animal species. *PLOS Biology* 14, e2001104 (2016).
- 270 <sup>23</sup> Maclean, I. M. D., Rehfisch, M. M., Delany, S., and Robinson, R. A., *The effects of*
- 271 *climate change on migratory waterbirds within the African-Eurasian flyway.* (The

- Agreement on the Conservation of African-Eurasian Migratory Waterbirds Secretariat,
  Bonn, Germany, 2007).
- <sup>24</sup> Ockendon, N. et al., Mechanisms underpinning climatic impacts on natural populations:
   altered species interactions are more important than direct effects. *Global Change*
- 276 *Biology* **20**, 2221-2229 (2014).
- 277 <sup>25</sup> Cahill, A. E. et al., How does climate change cause extinction? *Proc. R. Soc. B-Biol. Sci.*278 **280** (2013).
- Angert, A. L. et al., Do species' traits predict recent shifts at expanding range edges?
   *Ecology Letters* 14, 677-689 (2011).
- <sup>27</sup> Gómez, C., Tenorio, E. A., Montoya, P., and Cadena, C. D., Niche-tracking migrants and
   niche-switching residents: evolution of climatic niches in New World warblers
- 283 (Parulidae). *Proceedings of the Royal Society B: Biological Sciences* **283**, 20152458
- 284 (2016).
- <sup>28</sup> Betts, M. G. et al., Synergistic effects of climate and land-cover change on long-term bird
   population trends of the western USA: a test of modeled predictions. *Frontiers in*
- 287 *Ecology and Evolution* **7** (2019).
- <sup>29</sup> Kingsford, R. T., Bino, G., and Porter, J. L., Continental impacts of water development
   on waterbirds, contrasting two Australian river basins: Global implications for sustainable
- 290 water use. *Global Change Biology* **23**, 4958-4969 (2017).
- <sup>30</sup> Canepuccia, A. D. et al., Waterbird response to changes in habitat area and diversity
- generated by rainfall in a SW Atlantic coastal lagoon. *Waterbirds* **30**, 541-553 (2007).

293 Methods

294 Data

295 *Waterbird count data* 

296 Data used in this study comprised site-specific annual counts based on the International 297 Waterbird Census (IWC) coordinated by Wetlands International and the Christmas Bird 298 Count (CBC) by the National Audubon Society in the USA, and were compiled in our earlier study<sup>17</sup>. Counts based on these surveys should be described as relative abundance, as we 299 300 could not account for imperfect detections in this study. However, we have referred to them 301 as abundance throughout the manuscript for simplicity. Nevertheless, these count records 302 should still be comparable among years (see section Model for estimating abundance 303 responses for more detail).

304 The IWC, launched in 1967, is a scheme for monitoring waterbird numbers, covering 305 more than 25,000 sites in over 100 countries with more than 15,000 observers. The 306 coordination of the IWC is divided into four regional schemes corresponding to the major 307 migratory flyways of the world: the African-Eurasian Waterbird Census (AEWC), Asian 308 Waterbird Census (AWC), Caribbean Waterbird Census (CWC) and Neotropical Waterbird 309 Census (NWC). We did not use data from the CWC, as, having started in 2010, it only 310 provides short-term data. The survey methodology is essentially the same across the four 311 regional schemes. Population counts are typically carried out once every year in mid-January 312 but may include counts between December to February. We only used the January and 313 February counts for consistency. This means that our data from the Northern Hemisphere are 314 for non-breeding populations while those in the Southern Hemisphere also include some 315 breeding populations. In each country that is covered by the survey, national coordinators 316 manage an inventory of wetland sites (hereafter, survey sites), including sites of international-317 or national-level recognition (e.g., Ramsar sites, Flyway Network Sites, Important Bird Areas,

318 national parks etc.). Each survey site is generally defined by boundaries so that observers 319 know precisely which areas are to be covered in the surveys. The observers consist of a wide 320 variety of volunteers, but national coordinators usually train them using materials produced 321 by Wetlands International to ensure the quality of count data. Survey sites (normally up to a 322 few km<sup>2</sup>) are typically surveyed by about two observers for up to four hours, while larger sites 323 can require a group of observers working over several days. Most surveys are conducted on 324 foot, or from a vehicle, with boats involved in a few. The time of survey on any given day 325 depends on the type of survey site: inland sites are normally surveyed during the morning or 326 late afternoon, whereas coastal sites are surveyed over the high tide period (mangrove areas 327 and nearby mudflats are, however, covered during low tides). Surveys cover waterbirds, defined as bird species that are ecologically dependent on wetlands<sup>31</sup>. Counts are usually 328 329 made by scanning flocks of waterbirds with a telescope or binoculars and counting each 330 species. Zero counts are not always recorded, and thus are inferred using a set of criteria (see 331 below for more detail). Count records, together with associated information, are submitted to 332 the national coordinators, who compile the submitted records, check their validity and submit those records to Wetlands International. See <sup>31, 32</sup> for more details on survey methodology. 333 334 As the IWC does not cover North America, we also used data based on the CBC, which 335 has been conducted annually since 1900, and now includes over 2,400 count circles (defined as survey sites in this study) and involves more than 70,000 observers each year<sup>33</sup>. As 336 described in <sup>17</sup>, each CBC consists of a record of all bird species detected within a circle (24.1 337 338 km in diameter) on a single day between 14th December and 5th January. Most circles (and 339 most historical data) are from North America (i.e., the US and Canada). Observers join groups 340 and survey subunits of the circle during the day using a variety of transportation methods 341 (mostly on foot, or in a car, but can include boats, skis, or snowmobiles). The number of 342 observers and the duration of counts can vary among circles and through time. The total

number of survey hours per count has been recorded as a covariate to account for the variable
duration of and participation in the count. We only used records on waterbird species in this
paper.

346 We compiled data from each scheme by species, except for data based on the AEWC, where data had already been stored by flyway for each species<sup>32</sup>. As data based on the NWC 347 348 are only available for 1990 onward, we only used post-1990 data for other regions as well. 349 The latest records were in 2013. For the IWC data, we generated zero counts using an established approach<sup>32</sup>, in which we started with a list of all species observed in each country 350 351 and assumed a zero count of any species that were on the list but not recorded at a particular 352 site on a particular day if the site was surveyed on that day, as shown by the presence of any 353 other species' record(s), and if no multi-species code related to the species (e.g., Anatinae spp. 354 for species of the genus Anas) was recorded for the site-date combination. We projected all 355 survey sites onto a Behrmann equal-area cylindrical projection and assigned them to grid cells 356 with a grain size of 96.49 km, or approximately 1° at 30° N/S. We only used species that were 357 observed at one or more survey sites for ten or more years since 1990; this resulted in 390 358 species being analysed in this study (see Supplementary Data S4 for the full list of species with the number of survey sites and  $1^{\circ} \times 1^{\circ}$  grid cells where each species was observed). 359 Following <sup>17</sup> we used the International Ornithological Congress World Bird List<sup>34</sup> for species 360 361 groups in Fig. 1: coursers, gulls, terns and auks (Glareolidae, Laridae, Stercorariidae and 362 Alcidae), grebes and flamingos (Podicipedidae and Phoenicopteridae), loons and petrels 363 (Gaviidae and Procellariidae), pelicans, boobies and cormorants (Pelecanidae, Sulidae, Fregatidae, Phalacrocoracidae, Anhingidae), rails and cranes (Rallidae, Gruidae and 364 365 Aramidae), shorebirds (Burhinidae, Charadriidae, Haematopodidae, Jacanidae, 366 Recurvirostridae, Rostratulidae and Scolopacidae), storks, ibises and herons (Ciconiidae, Threskiornithidae and Ardeidae), and waterfowl (Anatidae and Anhimidae). 367

368

# 369 *Explanatory variables*

370 To estimate responses in waterbird abundance to changes in temperature and precipitation 371 (see Extended Data Fig. 2 for changes in mean January temperature and precipitation at all 372 survey sites), we used monthly mean temperature and precipitation total in the CRU TS v. 4.01 database  $^{35}$ , by assigning each site to the 0.5° climatic grid cell including the site. 373 374 Although climatic factors at different stages of species' annual cycles (i.e., outside our survey 375 (December-February) season), such as those in the breeding season for species wintering 376 during our survey season, could affect abundance changes, we could not include such factors 377 in our analysis due to the lack of information for most migratory species. Instead we 378 indirectly tested the effect of climatic factors outside our survey season by including 379 migratory status in the latitudinal analysis (see Extended Data Fig. 4). When testing among-380 and within-species latitudinal patterns in abundance responses, we accounted for three 381 species-level variables-latitudinal geographical range, migratory status and body size-that 382 are expected to explain among-species variations in responses; data sources of those variables 383 are shown in Extended Data Fig. 4.

384

# 385 Statistical Analyses

# 386 *Model for estimating abundance responses*

We first estimated, for each species at each survey site, the rate of abundance changes with increasing temperature and precipitation as regression coefficients (defined as abundance responses to temperature or precipitation increases) by applying the Gompertz model of population growth to count records:

391 
$$N_{t} = N_{t-1} exp(\alpha + \beta_{1} \log N_{t-1} + \beta_{2} Temp_{t-1} + \beta_{3} Prec_{t-1}),$$

392 where N<sub>t-1</sub>, Temp<sub>t-1</sub>, Prec<sub>t-1</sub> are the abundance of the species, the relevant mean Dec-Feb 393 temperature and precipitation at the site in year t - 1, respectively.  $\beta_{1-3}$  are regression 394 coefficients and  $\alpha$  is the intercept. We could not test the effects of other major drivers of 395 abundance changes, such as countries' governance and surface water change<sup>17</sup>, due to the lack 396 of data on yearly changes over the survey period. By estimating  $\alpha$  as the population growth 397 rate, this model tests the effect of temperature and precipitation on yearly changes in 398 abundance while controlling for long-term trends in abundance. This model structure helps to 399 avoid detecting a spurious relationship between long-term trends in abundance caused by 400 other threats (e.g., long-term declines by habitat loss) and those in temperature or 401 precipitation (e.g., long-term warming temperatures). When comparing the AIC between the 402 exponential growth model  $(\log(N_t) - \log(N_{t-1}) = \alpha)$  and time-dependent growth model  $(\log(N_t) - \log(N_{t-1})) = \alpha$  $-\log(N_{t-1}) = \alpha + \beta t$  fitted to count data at each site for each species, the exponential growth 403 404 model showed a smaller AIC for 95.8% of the 79,255 time-series, indicating that the model 405 structure above is appropriate for our data. Taking logs and rearranging to express the model 406 in terms of relative growth rate results in the following form:

407 
$$\log N_t - \log N_{t-1} = \alpha + \beta_1 \log N_{t-1} + \beta_2 Temp_{t-1} + \beta_3 Prec_{t-1},$$

and we used this form to estimate regression coefficients with linear models in R 3.4.1<sup>36</sup>. As this model does not allow missing values, any missing values between the first and last survey years at each site for each species were replaced by linear interpolation using the package zoo<sup>37</sup>; the proportion of missing values (i.e., the effect of interpolation) was accounted for in the following analysis (see *Latitudinal analysis*). The estimated  $\beta_2$  and  $\beta_3$  represent site-level abundance responses to temperature and precipitation increases, respectively. Using the same 414 model we also estimated the site-level independent capacity of temperature and precipitation 415 changes in explaining abundance changes (defined as the importance of temperature and 416 precipitation) with hierarchical partitioning<sup>19</sup> (measured in our case as R<sup>2</sup>) using the package 417 hier.part<sup>38</sup>.

418 As the model described above tests the effect of temperature and precipitation in the 419 previous year (i.e., year t-1) on abundance in the survey year (year t), we separately tested the 420 immediate effect of temperature and precipitation in the same year (year t) as the abundance 421 survey year. For this analysis we used the mean temperature or precipitation in December 422 (year *t*-1), January and February (year *t*) for the IWC sites, where surveys were conducted 423 either in January or February, and mean Dec temperature or precipitation in year t for the 424 CBC sites, where surveys were largely conducted in December. We compared the AIC 425 between the models with temperature/precipitation in year *t* and year *t*-1 at each site for each 426 species and used the temperature/precipitation variable in the model with a smaller AIC in the 427 final model.

We assumed constant survey efforts over time for the IWC, because regular and standardized surveys with constant methods, efforts and timing are strongly encouraged in this scheme (see Supplementary Discussion in<sup>17</sup> for more detail). However, survey efforts in the CBC are known to vary through time. Following an earlier analysis<sup>39</sup> we thus accounted for the survey effort effect for the CBC data by using the total number of survey hours per count as the measure of survey efforts:

434 
$$\log N_t - \log N_{t-1} = \alpha + \beta_1 \log N_{t-1} + \beta_2 Temp_{t-1} + \beta_3 Prec_{t-1} + \frac{B((\frac{\zeta_t}{\zeta})^p - 1)}{p},$$

435	where $\zeta_t$ is the total number of survey hours per count and $\overline{\zeta}$ is the mean value of $\zeta_t$ . The
436	parameters B and p determine a range of relationships between effort and the number of birds
437	counted <sup>39</sup> and we used the values estimated for each species in our earlier study <sup>17</sup> (see
438	Supplementary Data S4).
439	We only used survey sites with ten or more records and five or more non-zero records
440	since 1990 for at least one species, and this resulted in 1,303,651 count records since 1990 on
441	390 species at 6,822 sites between -55° and 64° (Extended Data Fig. 1) being analysed in this
442	study. The survey sites used in this study are inevitably biased towards certain regions,
443	especially within the tropics, where most sites are in South and Southeast Asia (Extended
444	Data Fig. 1). Thus, responses by waterbirds to climate change in other tropical regions still
445	remain untested. However, note that (i) the coverage of our data in the tropics is still
446	exceptional, considering the generally severe lack of ecological data <sup>8, 40</sup> , especially population
447	time-series <sup>41</sup> , in the tropics, and (ii) there is a known gap in previous assessments of climate
448	change impacts on biodiversity in tropical Asia9 and our study bridges the gap.
449	We aggregated the estimated site-level responses to temperature and precipitation
450	increases as well as the importance of temperature and precipitation to $1^{\circ} \times 1^{\circ}$ grid cells by
451	calculating the mean site-level estimates across all sites in each grid cell, weighted by the
452	inverse of estimate variance at each site to account for uncertainties. The grid cell-level
453	estimates (Supplementary Data S2) were then used in the latitudinal analysis described below
454	and for the species-level maps (Supplementary Data S1). We also calculated community-level
455	responses (Fig. 2) by calculating the mean grid cell-level estimates across all species observed
456	in each grid cell, weighted by the inverse of estimate variance in each species to account for
457	uncertainties.

458 Water availability in the tropics may not necessarily depend on Dec-Feb precipitation. 459 Especially in South and Southeast Asia, where our tropical survey sites are concentrated, the summer monsoon contributes to 80% of annual rainfall<sup>42</sup>. Thus we also tested the effect of 460 461 precipitation during June, July and August. We first calculated mean precipitation in June, 462 July and August in year *t*-1 for the IWC sites and in year *t* for the CBC sites. Then if the mean 463 Jun-Aug precipitation was higher than the mean Dec-Feb precipitation, we compared the AIC 464 between the model with Jun-Aug precipitation and the two models with the original 465 precipitation variables at each site for each species, and used the precipitation variable with 466 the smallest AIC in the final model. This allows using precipitation variables from different 467 seasons for different sites. The estimates were then used in the following analysis for 468 comparison with the original analysis (see Extended Data Figs. 7 and 8 for results). 469

## 470 Latitudinal analysis

471 We used absolute latitudes to test latitudinal patterns described in Extended Data Fig. 3 for 472 the following reason. Our data include species that are distributed only in either the northern 473 or southern hemisphere (one-hemisphere species) as well as those that appear in both the 474 hemispheres (two-hemisphere species). Some of our hypotheses (e.g., that for among-species 475 patterns in abundance changes with increasing temperature, shown at the top of Extended 476 Data Fig. 3) predict that one-hemisphere species would show a monotonic increase with raw 477 latitudes while two-hemisphere species would show a U-shaped relationship along the raw 478 latitudinal gradient with the lowest point at the equator; this makes analysing those species 479 together in the hierarchical modelling framework described below a complicated process. 480 With absolute latitudes, in contrast, one-hemisphere and two-hemisphere species are both 481 expected to show a monotonic increase, making the parameter estimation much simpler.

482 We tested the effects of explanatory variables on among- and within-species latitudinal 483 variations in (i) abundance responses to temperature and precipitation changes and (ii) the 484 importance of temperature and precipitation. For this analysis we used only 213 species with estimates at ten or more grid cells. We adopted the within-subject centring approach<sup>43</sup> under a 485 486 hierarchical modelling framework to explicitly distinguish species-level effects (explaining 487 variations in species-level responses between species) and population-level effects 488 (explaining variations in population-level responses within species) of explanatory variables. 489 Here we defined each species responses at their absolute latitudinal range mid-points (for 490 migratory species, based only on their geographical range during non-breeding season) as 491 species-level responses, and responses within each grid cell as population-level responses.

In this model the species effect  $\mu_s$ , representing the species-level responses to temperature or precipitation increases in species *s*, is drawn from a normal distribution with mean of  $v_s$  and variance of  $\sigma_{v}^2$ .  $v_s$  is further modelled with species-level explanatory variables:

495  $v_{s} = \alpha + \beta_{B1}MIDLAT_{s} + \beta_{B2}MIDLAT_{s}^{2} + \beta_{B3}LATRANGE_{s} + \beta_{B4}MIG_{s} + \beta_{5}BM_{Bs} +$ 496  $\beta_{B6}PROPNA_{s} + \eta_{s},$ 

497 where  $\alpha$  is the global intercept and  $\beta_{B1-B6}$  represent the species-level effects. *MIDLAT*<sub>s</sub>, 498 LATRANGEs, MIGs, BMs, PROPNAs are species-level explanatory variables; absolute 499 latitudinal range mid-points, absolute latitudinal geographical range (degree), migration status 500 (migrant or non-migrant), body mass (g, log10-transformed) and the mean proportion of 501 missing values (i.e., interpolated values) in count records across all sites (%) for species s, 502 respectively. The variance inflation factor was smaller than 1.9 for all the species-level 503 explanatory variables, indicating that multi-collinearity was not a major issue.  $\eta_s$  is a random 504 term that accounts for phylogenetic dependence among species and is drawn from a multivariate normal distribution<sup>44, 45</sup>: 505

506 
$$\eta_s \sim MVN(\mathbf{0}, \ \delta^2 \Sigma_{\lambda}),$$

507 
$$\Sigma_{\lambda} = \lambda \Sigma + (1 - \lambda)\mathbf{I}$$

508 where  $\Sigma$  is a scaled variance-covariance matrix calculated from an ultrametric phylogenetic 509 tree (defined below). By scaling  $\Sigma$  to a height of one, we can interpret  $\delta^2$  as the residual variance<sup>44</sup>. For the strength of phylogenetic signal to vary, we also incorporated Pagel's  $\lambda^{46, 47}$ 510 511 into the matrix with the identity matrix I. Here  $\lambda$  is a coefficient that multiplies the off-512 diagonal elements of  $\Sigma$  and a  $\lambda$  close to zero implies that the phylogenetic signal in the data is 513 low, suggesting independence in the error structure of the data points, whereas a  $\lambda$  close to 514 one suggests a good agreement with the Brownian Motion evolution model and thus suggests correlation in the error structure<sup>44, 47</sup>. To incorporate uncertainties<sup>48</sup> in phylogenetic trees in 515 516 the calculation of  $\Sigma$ , we used a sample of 100 trees from a comprehensive avian phylogeny<sup>49</sup> as the prior distribution for our analysis<sup>44</sup>. More specifically, one of the 100 trees was 517 randomly drawn in each iteration and used for the calculation of  $\Sigma$ . In the sensitivity analysis 518 519 using Jun-Aug precipitation we limited the range of  $\eta_s$  to between -0.2 and 0.2, based on the 520 estimated values in the original analysis, in order to enhance the convergence of the models. 521 The population-level responses to temperature or precipitation increases  $r_{s,i}$  of species s in 522 grid cell *i* was then assumed to derive from a normal distribution with mean  $\mu_{s,i}$  and variance  $\sigma_{\mu}^2$ , where  $\mu_{s,i}$  is modelled using the species effect  $\mu_s$ : 523

524 
$$\mu_{s,i} = \mu_s + \beta_{w_{s,i}} \frac{LAT_{s,i} - MIDLAT_s}{LATRANGE_s} + \beta_{w_{s,2}} \left(\frac{LAT_{s,i} - MIDLAT_s}{LATRANGE_s}\right)^2 + \beta_{w_{s,3}} pNA_{s,i} + \gamma_{s,i}$$

Here  $\beta_{Ws, I-3}$  represents the population-level effect of absolute latitudes  $LAT_{s,i}$  (in the form of linear and quadratic terms, to test non-linear patterns) and the mean proportion of missing values (i.e., interpolated values) in count records across all sites  $pNA_{s,i}$  (%) of grid cell *i* for species *s*. Here within-species variations in population-level responses ( $\mu_{s,i} - \mu_s$ ) are explained by within-species variations in absolute latitudes ( $LAT_{s,i} - MIDLAT_s$ ), divided by the absolute 530 latitudinal geographical range of each species *LATRANGEs*, so that the estimated effects of

absolute latitudes are comparable among species with varying latitudinal range size. The

532 species-specific  $\beta_{W_{S}, 1-3}$  is the random effect each governed by hyper-parameters as:

533 
$$\beta_{W_{s,j}} \sim Normal(h\beta_{W_j}, \sigma_{\beta_{W_i}}^2).$$

534  $\gamma_{s,i}$  accounts for spatial autocorrelation within each species and is drawn from an intrinsic 535 Gaussian conditional autoregressive (CAR) prior distribution with variance  $\sigma_{\gamma_c}^2$ :

536 
$$\gamma_{s,i}|\gamma_{s,k} \sim Normal(\frac{\sum_{i \neq k} w_{i,k} \gamma_{s,k}}{n_i}, \frac{\sigma_{\gamma s}^2}{n_i}),$$

537 where  $w_{i,k} = 1$  if grid cells *i* and *k* are neighbours, and 0 otherwise.  $n_i$  is the total number of 538 neighbours of grid cell *i* and neighbours here are defined as those grid cells directly adjacent, 539 including those diagonal.  $\sigma_{ys}^2$  controls the amount of variation between the random effects.

540 We tested latitudinal patterns in the importance of temperature and precipitation using 541 essentially the same model but the population-level importance of temperature or 542 precipitation *imp<sub>s,i</sub>* of species *s* in grid cell *i* was assumed to derive from a beta distribution 543 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:

544 
$$logit(c_{s,i}) = \mu_s + \beta_{w_{s,1}} \frac{LAT_{s,i} - MIDLAT_s}{LATRANGE_s} + \beta_{w_{s,2}} \left(\frac{LAT_{s,i} - MIDLAT_s}{LATRANGE_s}\right)^2 + \beta_{w_{s,3}} pNA_{s,i} + \gamma_{s,i},$$

545 
$$\alpha_i = c_{s,i}\varphi_i,$$

546 
$$\beta_i = (1 - c_{s,i})\varphi_i$$

As latitudinal patterns might be different between two hemispheres, we also conducted the same latitudinal analysis separately for (i) narrowly-defined southern-hemisphere species (49 species with maximum range latitude < 0), and (ii) all the other 164 species as "northernhemisphere" species (see Supplementary Figs. S1-S4 for results).

551 The models were implemented with OpenBUGS 3.2.3<sup>50</sup> and the R2OpenBUGS package<sup>51</sup>

552 in R 3.4.1<sup>36</sup>. Following <sup>17</sup>, as non-informative prior distributions, we used a Gamma

distribution with mean of 1 and variance of 100 for  $\varphi_i$  and the inverse of  $\sigma_{v}^2$ ,  $\delta^2$ ,  $\sigma_{\mu}^2$ ,  $\sigma_{\beta_{W_j}}^2$ and  $\sigma_{\gamma_s}^2$ , a uniform distribution on the interval [0, 1] for  $\lambda$ , normal distributions with mean of 0 and variance of 100 for  $\alpha$ ,  $\beta_{Bk}$ , and  $h\beta_{Wj}$ . We ran each MCMC algorithm with three chains with different initial values for 30,000 iterations with the first 10,000 discarded as burn-in and the remainder thinned to one in every four iterations to save storage space. Model convergence was checked with R-hat values.

559 Due to differences in the definition of species between the two sources used<sup>49, 52</sup>, we

560 followed <sup>17</sup> and combined two separate species defined in the BirdLife Checklist<sup>52</sup> into one in

561 four cases for this species-level analysis: Kentish plover *Charadrius alexandrinus* and snowy

562 plover C. nivosus, common snipe Gallinago gallinago and Wilson's snipe G. delicata,

563 European herring gull Larus argentatus and Arctic herring gull L. smithsonianus, and

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

565 *thayeri* was excluded from the latitudinal analysis as it is not included in either database. We

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

567 IWC nor CBC necessarily targets seabird species.

We also used R packages ape<sup>53</sup>, data.table<sup>54</sup>, dplyr<sup>55</sup>, ggplot2<sup>56</sup>, gridExtra<sup>57</sup>, mapdata<sup>58</sup>,
plyr<sup>59</sup>, png<sup>60</sup>, RcolorBrewer<sup>61</sup>, rgdal<sup>62</sup>, raster<sup>63</sup> and viridis<sup>64</sup>.

570

#### 571 Data Availability

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

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

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

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

576	for each species are available as Supplementary Data S2. All the data on explanatory variables				
577	are freely available as specified in Extended Data Fig. 4.				
578					
579	Code Availability				
580	All the R codes used for the analyses are available as Supplementary Data S5-7.				
581					
582	References				
583	31	Delany, S., Guidance on waterbird monitoring methodology: field protocol for waterbird			
584		counting. (Wetlands International, Wageningen, 2010).			
585	32	van Roomen, M., van Winden, E., and van Turnhout, C., Analyzing population trends at			
586		the flyway level for bird populations covered by the African Eurasian Waterbird			
587		Agreement: details of a methodology. (SOVON Dutch Centre for Field Ornithology,			
588		Nijmegen, the Netherlands, 2011).			
589	33	LeBaron, G. S., The 115th Christmas Bird Count. (National Audubon Society, New			
590		York. Available at: https://www.audubon.org/news/the-115th-christmas-bird-count-0,			
591		2015).			
592	34	Gill, F. and Donsker, D. eds., IOC World Bird List (v 5.1). (Available at:			
593		http://www.worldbirdnames.org/, 2015).			
594	35	Harris, I., Jones, P. D., Osborn, T. J., and Lister, D. H., Updated high-resolution grids of			
595		monthly climatic observations - the CRU TS3.10 Dataset. International Journal of			
596		<i>Climatology</i> <b>34</b> , 623-642 (2014).			
597	36	R Core Team, R: A language and environment for statistical computing. (R Foundation			
598		for Statistical Computing, Vienna, Austria (http://www.R-project.org/), 2017).			

- <sup>37</sup> Zeileis, A. and Grothendieck, G., zoo: S3 infrastructure for regular and irregular time
  series. *Journal of Statistical Software* 14, 1-27 (2005).
- Walsh, C. and Nally, R. M., *hier.part: hierarchical partitioning. R package version 1.0-4.*(https://CRAN.R-project.org/package=hier.part, 2013).
- <sup>39</sup> Link, W. A. and Sauer, J. R., Seasonal components of avian population change: joint
   analysis of two large-scale monitoring programs. *Ecology* 88, 49-55 (2007).
- <sup>40</sup> Stroud, J. T. and Feeley, K. J., Neglect of the tropics is widespread in ecology and
- evolution: A comment on Clarke et al. *Trends in Ecology and Evolution* **32**, 626-628
- 607 (2017).
- <sup>41</sup> Amano, T. and Sutherland, W. J., Four barriers to the global understanding of
- 609 biodiversity conservation: wealth, language, geographical location and security.

610 *Proceedings of the Royal Society B: Biological Sciences* **280**, 20122649 (2013).

- <sup>42</sup> Turner, A. G. and Annamalai, H., Climate change and the South Asian summer monsoon.
   *Nature Climate Change* 2, 587-595 (2012).
- <sup>43</sup> van de Pol, M. and Wright, J., A simple method for distinguishing within- versus
- 614 between-subject effects using mixed models. *Animal Behaviour* **77**, 753-758 (2009).
- <sup>44</sup> de Villemereuil, P., Wells, J., Edwards, R., and Blomberg, S., Bayesian models for
- 616 comparative analysis integrating phylogenetic uncertainty. *BMC Evolutionary Biology*
- 617 **12**, 102 (2012).
- <sup>45</sup> Abadi, F. et al., Importance of accounting for phylogenetic dependence in multi-species
   mark-recapture studies. *Ecological Modelling* 273, 236-241 (2014).
- <sup>46</sup> Pagel, M., Inferring the historical patterns of biological evolution. *Nature* 401, 877-884
  (1999).
- <sup>47</sup> Freckleton, R. P., Harvey, P. H., and Pagel, M., Phylogenetic analysis and comparative
- data: A test and review of evidence. *American Naturalist* **160**, 712-726 (2002).

- <sup>48</sup> Donoghue, M. J. and Ackerly, D. D., Phylogenetic uncertainties and sensitivity analyses
- 625 in comparative biology. *Philosophical Transactions of the Royal Society of London B:*

626 *Biological Sciences* **351**, 1241-1249 (1996).

- <sup>49</sup> Jetz, W. et al., The global diversity of birds in space and time. *Nature* 491, 444-448
  (2012).
- <sup>50</sup> Spiegelhalter, D., Thomas, A., Best, N., and Lunn, D., *OpenBUGS user manual version 3.2.3.* (http://www.openbugs.net/Manuals/Manual.html, 2014).
- <sup>51</sup> Sturtz, S., Ligges, U., and Gelman, A., R2WinBUGS: a package for running WinBUGS
  from R. *Journal of Statistical Software* 12, 1-16 (2005).
- <sup>52</sup> BirdLife International. *The BirdLife checklist of the birds of the world: Version 7*
- 634 (Downloaded from
- http://www.birdlife.org/datazone/userfiles/file/Species/Taxonomy/BirdLife\_Checklist\_V
  ersion\_70.zip. 2014).
- <sup>53</sup> Paradis, E., Claude, J., and Strimmer, K., APE: analyses of phylogenetics and evolution
   in R language. *Bioinformatics* 20, 289-290 (2004).
- <sup>54</sup> Dowle, M. and Srinivasan, A., *data.table: extension of 'data.frame'. R package version*
- 640 *1.10.4-3.* (https://CRAN.R-project.org/package=data.table, 2017).
- <sup>55</sup> Wickham, H., Francois, R., Henry, L., and Muller, K., *dplyr: a grammar of data*
- 642 *manipulation. R package version 0.7.4.* (https://CRAN.R-project.org/package=dplyr,
- 643 2017).
- <sup>56</sup> Wickham, H., *ggplot2: elegant graphics for data analysis*. (Springer-Verlag New York,
  2016).
- <sup>646</sup><sup>57</sup> Auguie, B., gridExtra: miscellaneous functions for "grid" graphics. R package version
- 647 2.3. (https://CRAN.R-project.org/package=gridExtra, 2017).

- <sup>58</sup> Brownrigg, R., mapdata: extra map databases. R package version 2.3.0.
- 649 (https://CRAN.R-project.org/package=mapdata, 2018).
- <sup>59</sup> Wickham, H., The split-apply-combine strategy for data analysis. *Journal of Statistical*Software 40, 1-29 (2011).
- <sup>60</sup> Urbanek, S., png: read and write PNG images. R package version 0.1-7.
- 653 (https://CRAN.R-project.org/package=png, 2013).
- <sup>61</sup> Neuwirth, E., *RColorBrewer: ColorBrewer Palettes. R package version 1.1-2.*
- 655 (https://CRAN.R-project.org/package=RColorBrewer, 2014).
- <sup>62</sup> Bivand, R., Keitt, T., and Rowlingson, B., rgdal: bindings for the geospatial data
- 657 abstraction library. R package version 1.2-8. (https://CRAN.R-
- 658 project.org/package=rgdal, 2017).
- <sup>63</sup> Hijmans, R. J., *raster: geographic data analysis and modeling. R package version 2.6-7.* (https://CRAN.R-project.org/package=raster, 2017).
- <sup>64</sup> Garnier, S., viridis: default color maps from 'matplotlib'. R package version 0.5.1.
- 662 (https://CRAN.R-project.org/package=viridis, 2018).
- <sup>65</sup> Nadeau, C. P., Urban, M. C., and Bridle, J. R., Climates past, present, and yet-to-come
- shape climate change vulnerabilities. *Trends in Ecology & Evolution* **32**, 786-800 (2017).
- <sup>66</sup> Breed, G. A., Stichter, S., and Crone, E. E., Climate-driven changes in northeastern US
  <sup>66</sup> butterfly communities. *Nature Climate Change* 3, 142-145 (2012).
- <sup>67</sup> Valladares, F. et al., The effects of phenotypic plasticity and local adaptation on forecasts
- of species range shifts under climate change. *Ecology Letters* **17**, 1351-1364 (2014).
- <sup>68</sup> Hawkins, B. A. et al., Energy, water, and broad-scale geographic patterns of species
- 670 richness. *Ecology* **84**, 3105-3117 (2003).

671	69	Sexton, J. P., McIntyre, P. J., Angert, A. L., and Rice, K. J., Evolution and ecology of
672		species range limits. Annual Review of Ecology, Evolution, and Systematics 40, 415-436
673		(2009).
674	70	Mills, S. C. et al., European butterfly populations vary in sensitivity to weather across
675		their geographical ranges. Global Ecology and Biogeography 26, 1374-1385 (2017).
676	71	Johnston, A. et al., Observed and predicted effects of climate change on species
677		abundance in protected areas. Nature Climate Change 3, 1055-1061 (2013).
678	72	Faragó, S. and Hangya, K., Effects of water level on waterbird abundance and diversity
679		along the middle section of the Danube River. Hydrobiologia 697, 15-21 (2012).
680	73	Kleijn, D. et al., Waterbirds increase more rapidly in Ramsar-designated wetlands than in
681		unprotected wetlands. Journal of Applied Ecology 51, 289-298 (2014).
682	74	Slatyer, R. A., Hirst, M., and Sexton, J. P., Niche breadth predicts geographical range
683		size: a general ecological pattern. Ecology Letters 16, 1104-1114 (2013).
684	75	Estrada, A., Morales-Castilla, I., Caplat, P., and Early, R., Usefulness of species traits in
685		predicting range shifts. Trends in Ecology and Evolution 31, 190-203 (2016).
686	76	Dhanjal-Adams, K. L. et al., Distinguishing local and global correlates of population
687		change in migratory species. Diversity and Distributions 25, 797-808 (2019).
688	77	Wilman, H. et al., EltonTraits 1.0: Species-level foraging attributes of the world's birds
689		and mammals. <i>Ecology</i> <b>95</b> , 2027-2027 (2014).
690		

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# 710 **Author contributions**

- 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.
- collected and prepared data for the analyses. T.A. analysed the data and wrote the paper. All
- authors discussed the results and commented on the manuscript at all stages.

# 714 **Competing interests**

715 The authors declare no competing interests.

# 716 Additional information

- **Extended data** is available for this paper.
- **Supplementary information** is available for this paper.
- **Correspondence and requests for materials** should be addressed to T.A.
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722 Fig. 1. Latitudinal distribution of abundance responses to changes in temperature (T coef: the rate of abundance changes with increasing temperature) for each species. Each 723 724 horizontal row of squares shows the absolute latitudes of  $1^{\circ} \times 1^{\circ}$  grid cells with estimates for 725 each of the 390 species in (a) coursers, gulls, terns and auks, (b) grebes and flamingos, (c) 726 loons and petrels, (d) pelicans, boobies and cormorants, (e) rails and cranes, (f) shorebirds, (g) 727 storks, ibises and herons, and (h) waterfowl (see Methods for definition). Black circles 728 indicate the median absolute latitude of geographical range of each species. Grid cells in the 729 tropical region (the area on the left of the red vertical line) tend to show more negative 730 responses (shown in yellow). Silhouettes reproduced from PhyloPic (http://phylopic.org/) under a Creative Commons licence (http://creativecommons.org/licenses/by/3.0/) (a-d, f-h) 731 732 or Public Domain Dedication licence (http://creativecommons.org/publicdomain/zero/1.0/) 733 (e). a, f, Rebecca. Groom; b, c, Doug Backlund (photo) (b) or Unknown (photo) (c), John E. 734 McCormack, Michael. G. Harvey, Brant. C. Faircloth, Nicholas. G. Crawford, Travis. C. 735 Glenn, Robb. T. Brumfield & T. Michael. Keesay; d, g, Shyamal/Wikimedia Commons; h, 736 Maija Karala (image flipped horizontally).





738 Fig. 2. Mean abundance responses across 390 waterbird species to changes in temperature and precipitation in each 1° × 1° grid cell. (a) The rate of abundance changes 739 740 with increasing temperature (T coef), showing more negative responses to temperature 741increases at lower latitudes (shown with yellow dots) and positive responses at higher 742 latitudes (shown with purple dots), (b) the independent capacity of temperature in explaining 743 abundance changes (T R-squared), (c) the rate of abundance changes with increasing 744 precipitation (P coef) and (d) the independent capacity of precipitation in explaining 745 abundance changes (P R-squared). The region between the yellow solid lines is the tropics.





747 Fig. 3. Latitudinal patterns in waterbird abundance responses to temperature increases. 748 (a) Abundance responses to increasing temperature at 213 species' range mid-points and (b) 749 within each species, (c) the importance of temperature in explaining abundance changes at 750 species' range mid-points and (d) within each species. In (a) and (c), orange lines: among-751 species patterns based on posterior median coefficients; black lines: patterns with all posterior 752 samples; blue circles: responses at each species' range mid-points; grey lines: 95% credible 753 intervals; circle size: the absolute latitudinal range size. In (b) and (d) regression lines: within-754species latitudinal patterns for each species based on posterior median coefficients (significant 755 patterns in orange). Yellow area: the tropics.



757 758 (a) Abundance responses to increasing precipitation at 213 species' range mid-points and (b) 759 within each species, (c) the importance of precipitation in explaining abundance changes at 760 species' range mid-points and (d) within each species. In (a) and (c), orange lines: among-761 species patterns based on posterior median coefficients; black lines: patterns with all posterior 762 samples; blue circles: responses at each species' range mid-points; grey lines: 95% credible 763 intervals; circle size: the absolute latitudinal range size. In (b) and (d) regression lines: within-764species latitudinal patterns for each species based on posterior median coefficients (significant 765 patterns in orange). Yellow area: the tropics.



767 Extended Data Fig. 1. Distribution of the 6,822 survey sites used in the analyses. The area

between pale pink lines represents the tropical region.



a. Annual rate of January temperature change (1990 - 2013)

b. Annual rate of January precipitation change (1990 - 2013)



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- 771 Extended Data Fig. 2. Annual rates of changes in January mean temperature and
- 772 precipitation at the 6,822 survey sites used in the analyses. The area between yellow lines
- represents the tropical region.



775 Extended Data Fig. 3. Hypotheses tested for explaining among- and within-species

- 776 latitudinal variations in waterbird abundance responses to temperature and
- 777 precipitation changes.

Hypotheses	Expected patterns	Variables used	Data sources
Latitudinal geographical range	<ul> <li>Species with a narrower latitudinal range have narrower temperature niche, thus more vulnerable to temperature increases (i.e., the rate of abundance changes with increasing temperature is more negative)<sup>74</sup>.</li> <li>Species with a narrower latitudinal range have narrower temperature niche, thus their abundance is affected more by temperature changes (i.e., the importance of temperature is higher)<sup>74</sup>.</li> </ul>	Differences between maximum and minimum absolute latitudes of geographical range	BirdLife Data Zone <sup>*</sup>
Migratory status	<ul> <li>Resident species can be more negatively affected by temperature increases, due to their limited dispersal ability (i.e., the rate of abundance changes with increasing temperature is more negative)<sup>26</sup>.</li> <li>Migratory species generally have a higher dispersal ability<sup>26</sup> and track climate niches to a greater extent than resident species<sup>27</sup>, thus can be more responsive to changes in local temperature and precipitation (i.e., the importance of temperature and precipitation is higher).</li> <li>Migratory species often show fidelity to breeding and non-breeding sites between years, thus may be less responsive to changes in local temperature and precipitation (i.e., the importance of temperature and precipitation is lower)<sup>75</sup>.</li> <li>Migratory species can also be affected by conditions at multiple locations (e.g., climatic factors and threats at different migratory stages), thus local climatic conditions may play a limited role in explaining their abundance (i.e., the importance of temperature and precipitation is lower)<sup>76</sup>.</li> </ul>	Migrant or non-migrant	BirdLife Data Zone*
Body size	<ul> <li>Smaller-sized species can be more negatively affected by increasing temperature, due to their limited dispersal ability (i.e., the rate of abundance changes with increasing temperature is more negative)<sup>26</sup>.</li> <li>Larger-sized species have a higher dispersal ability, thus may be more responsive to changes in local temperature and precipitation (i.e., the importance of temperature and precipitation is higher)<sup>26</sup>.</li> </ul>	Body mass (g)	Elton Traits 1.0 <sup>77</sup>

778 \* http://datazone.birdlife.org/home

779 Extended Data Fig. 4. Additional hypotheses tested for explaining among-species

variations in waterbird abundance responses to temperature and precipitation changes.



### 782 Extended Data Fig. 5. Effects of species-level predictors on waterbird abundance

**responses to temperature changes.** The estimated coefficients with 95% and 50% (thick lines) credible intervals of six explanatory variables for explaining among-species variations in the rate of abundance changes with increasing temperature (a) and the importance of temperature in explaining abundance changes (b). Filled circles indicate variables with 95% credible intervals not overlapping with zero. Only 213 species for which there were estimates at ten or more grid cells were analysed. Note that the estimated coefficients for *Absolute latitude (linear)* in both (a) and (b) and for *Absolute latitude range* in (b) are all positive.



## 791 Extended Data Fig. 6. Effects of species-level predictors on waterbird abundance

responses to precipitation changes. The estimated coefficients with 95% and 50% (thick lines) credible intervals of six explanatory variables for explaining among-species variations in the rate of abundance changes with increasing precipitation (a) and the importance of precipitation in explaining abundance changes (b). Filled circles indicate variables with 95% credible intervals not overlapping with zero. Only 213 species for which there were estimates at ten or more grid cells were analysed. Note that the estimated coefficient for *Absolute latitude range* in (b) is positive.



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801 choice of precipitation seasons. Effects of species-level predictors on waterbird abundance 802 responses to temperature changes when using precipitation during June, July and August in 803 the model (see Statistical Analyses for more detail). The estimated coefficients with 95% and 804 50% (thick lines) credible intervals of six explanatory variables for explaining among-species 805 variations in the rate of abundance changes with increasing temperature (a) and the 806 importance of temperature in explaining abundance changes (b). Filled circles indicate 807 variables with 95% credible intervals not overlapping with zero. Only 213 species for which 808 there were estimates at ten or more grid cells were analysed. Note that the estimated 809 coefficients for Absolute latitude (linear) in both (a) and (b) and for Absolute latitude range in

Extended Data Fig. 7. Sensitivity of the results on responses to temperatures to the

810 (b) are positive while that for *Absolute latitude (quadratic)* in (b) is negative.



### 812 Extended Data Fig. 8. Sensitivity of the results on responses to precipitations to the

813 choice of precipitation seasons. Effects of species-level predictors on waterbird abundance 814 responses to precipitation changes when using precipitation during June, July and August in 815 the model (see Statistical Analyses for more detail). The estimated coefficients with 95% and 816 50% (thick lines) credible intervals of six explanatory variables for explaining among-species 817 variations in the rate of abundance changes with increasing precipitation (a) and the 818 importance of precipitation in explaining abundance changes (b). Filled circles indicate 819 variables with 95% credible intervals not overlapping with zero. Only 213 species for which 820 there were estimates at ten or more grid cells were analysed. Note that the estimated 821 coefficient for Absolute latitude range in (b) is positive.

# **Supplementary Information**

# Responses of global waterbird populations to climate change vary with latitude

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**Supplementary Fig. S1. Effects of species-level predictors on waterbird abundance responses to temperature changes at the northern hemisphere**. The estimated coefficients with 95% and 50% (thick lines) credible intervals of six explanatory variables for explaining among-species variations in the rate of abundance changes with increasing temperature (a) and the importance of temperature in explaining abundance changes (b). Filled circles indicate variables with 95% credible intervals not overlapping with zero. Only 164 northern hemisphere species were analysed (see **Statistical Analysis** for more details). Note that the estimated coefficients for *Absolute latitude (linear)* in both (a) and (b) and for *Absolute latitude range* and % *missing records* in (b) are all positive.



**Supplementary Fig. S2. Effects of species-level predictors on waterbird abundance responses to precipitation changes at the northern hemisphere**. The estimated coefficients with 95% and 50% (thick lines) credible intervals of six explanatory variables for explaining among-species variations in the rate of abundance changes with increasing precipitation (a) and the importance of precipitation in explaining abundance changes (b). Filled circles indicate variables with 95% credible intervals not overlapping with zero. Only 164 northern hemisphere species were analysed (see **Statistical Analysis** for more details). Note that the estimated coefficient for *Absolute latitude range* in (b) is positive.



**Supplementary Fig. S3. Effects of species-level predictors on waterbird abundance responses to temperature changes at the southern hemisphere**. The estimated coefficients with 95% and 50% (thick lines) credible intervals of six explanatory variables for explaining among-species variations in the rate of abundance changes with increasing temperature (a) and the importance of temperature in explaining abundance changes (b). Filled circles indicate variables with 95% credible intervals not overlapping with zero. Only 49 southern hemisphere species were analysed (see **Statistical Analysis** for more details).



**Supplementary Fig. S4. Effects of species-level predictors on waterbird abundance responses to precipitation changes at the southern hemisphere**. The estimated coefficients with 95% and 50% (thick lines) credible intervals of six explanatory variables for explaining among-species variations in the rate of abundance changes with increasing precipitation (a) and the importance of precipitation in explaining abundance changes (b). Filled circles indicate variables with 95% credible intervals not overlapping with zero. Only 49 southern hemisphere species were analysed (see **Statistical Analysis** for more details).



Supplementary Fig. S5. Grid cell-level relationship between abundance responses to temperature and temperature importance. Each dot represents estimates for each species within each  $1^{\circ} \times 1^{\circ}$  grid cell. Grid cells in the tropical region (absolute latitude < 23.4) are shown in red.