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Responses of global waterbird populations to climate change vary with latitude

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

Climate change continues to pose various serious threats to biodiversity, and there is an urgent need to understand how species respond on a global scale to changing climates. A wide range of species have already been shown to respond to climate change through changes in geographical range[1], phenology[2] and abundance[3]. However, the rate and direction of these responses vary greatly among species and locations[1,2,4]. As climate-driven changes in biodiversity are expected to affect ecosystem functioning, human well-being and the dynamics of climate change itself[5], understanding how species' responses to climate change may vary globally could provide crucial evidence for a more-effective allocation of limited resources for the conservation of species and ecosystems most threatened by climate change and for assessing how climate-driven changes in biodiversity may affect human societies (see Supplementary Data for the Abstract in different languages).

Existing gaps in the geographical coverage of available evidence seriously limit our understanding of species' responses to climate change across the globe[6]. Earlier global reviews of species' responses to climate change have rarely incorporated species and studies in the tropics[7] due to the lack of ecological data[8]. Such geographical biases are even more prominent in studies investigating responses in species abundance[9], which is a major determinant of species extinction risk[10], ecosystem function and services[11]. Research on abundance responses to climate change to date has largely been conducted in Europe, North America, Australia and the Arctic[3,12–15], with a recent global study showing a link between climate warming and abundance declines in birds and mammals[9] but still largely missing the tropics. As a result, although tropical species are predicted to be more vulnerable to increasing temperature[16], there is still little empirical evidence on how responses in species abundance to climate change vary among and within species at the global scale.

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[17]. 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[18].

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

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° × 1° grid cells across latitudes, including the tropics, for a wide range of waterbird

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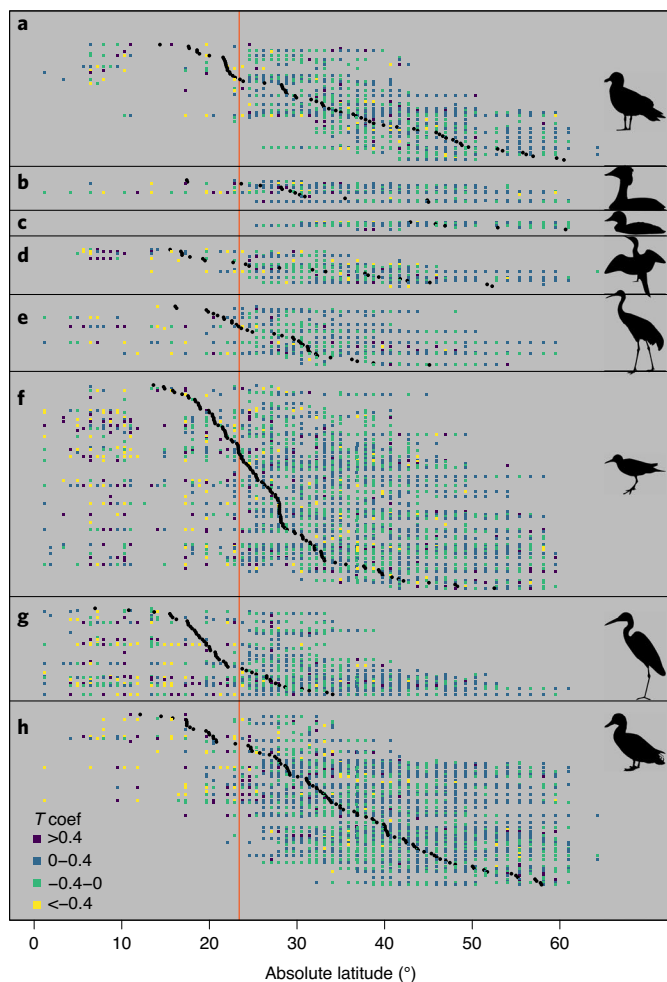
Fig. 1 | Latitudinal distribution of abundance responses to changes in temperature for each species. a–h, Each horizontal row of squares shows the absolute latitudes of 1° × 1° grid cells with estimates for each of the 390 species in coursers, gulls, terns and auks (**a**); grebes and flamingos (**b**); loons and petrels (**c**); pelicans, boobies and cormorants (**d**); rails and cranes (**e**); shorebirds (**f**); storks, ibises and herons (**g**); and waterfowl (**h**) (see Methods for definition). Black circles indicate the median absolute latitude of geographical range of each species. Grid cells in the tropical region (the area on the left of the red vertical line) tend to show more negative responses (shown in yellow). *T* coef, the rate of abundance changes with increasing temperature. Silhouettes reproduced from PhyloPic (http://phylopic.org/) under a Creative Commons licence (http://creativecommons.org/licenses/by/3.0/). Credit: **a,f**, Rebecca Groom; **b,c**, Doug Backlund (photo) (**b**) and unknown (photo) (**c**); John E. McCormack, Michael G. Harvey, Brant C. Faircloth, Nicholas G. Crawford, Travis C. Glenn, Robb T. Brumfield and T. Michael Keesay; **d,g**, Shyamal/ Wikimedia Commons; **h**, Maija Karala (image flipped horizontally).

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 midpoints 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 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 1 and 2). By contrast, for most

species there was no clear geographical pattern in abundance responses to precipitation increases, and precipitation was found to have a low importance in explaining abundance changes (the overall median $R^2 = 0.051$; Supplementary Data 1 and 2). These geographical patterns were also evident in the distribution of abundance responses averaged across all species observed within each grid cell; species generally showed more negative responses to temperature increases at lower latitudes, such as in South and Southeast Asia, and positive responses at higher latitudes (Fig. 2).

For 213 species with estimates at ten or more grid cells, we then tested hypotheses on how responses to temperature and precipitation increases and the importance of temperature and precipitation vary both among species (among each species' estimates at latitudinal range midpoints; species-level responses) and within species (among grid cells within each species; population-level responses) along latitudes. When compared among species, abundance responses to temperature increases shifted from positive at higher latitudes to negative at lower latitudes, with 69% of the tropical species showing negative responses to temperature increases (Fig. 3a, Extended Data Fig. 5a). When compared within species, although 198 (93%) of the 213 species showed more negative responses to temperature increases at lower latitudes, this within-species latitudinal pattern was significant ('significant' refers to 95% credible intervals for estimated coefficients not overlapping with zero here and throughout the Article) only in eight of the 198 species (Fig. 3b, Supplementary Data 3). The importance of temperature in explaining abundance changes also increased with latitude among species (Fig. 3c, Extended Data Fig. 5b) and within species for all 55 species with a significant within-species latitudinal pattern (Fig. 3d, Supplementary Data 3). 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.

By contrast, neither abundance responses to precipitation increases nor the importance of precipitation in explaining abundance changes showed significant latitudinal patterns among species. This does not necessarily mean that precipitation was not important; for some species in the tropics, precipitation was found to have a relatively high importance in explaining abundance changes (Fig. 4a,c, Extended Data Fig. 6 and Supplementary Data 3). Precipitation was shown to have a higher importance in explaining abundance changes in species with a wider latitudinal range (Extended Data Fig. 6b). When compared within species, five species showed a significant pattern: one species showed a decrease, three species showed an increase, and another species showed a hump-shaped curve in abundance responses to precipitation increases along latitudes (Fig. 4b and Supplementary Data 3). The importance of precipitation in explaining abundance changes showed a significant within-species latitudinal pattern for just one species (Fig. 4d and Supplementary Data 3). These conclusions were robust even when the effect of June–August precipitation was considered (Extended Data Figs. 7 and 8) and appeared to be driven largely by patterns in the Northern Hemisphere (Supplementary Figs. 1–4).

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 within-species patterns (Extended Data Fig. 3). Species in the tropics tend to live closer to their upper temperature limits[16], have a narrower temperature niche[20] and change their temperature niche at a slower rate[21], all of which indicate that tropical species are more vulnerable to increasing
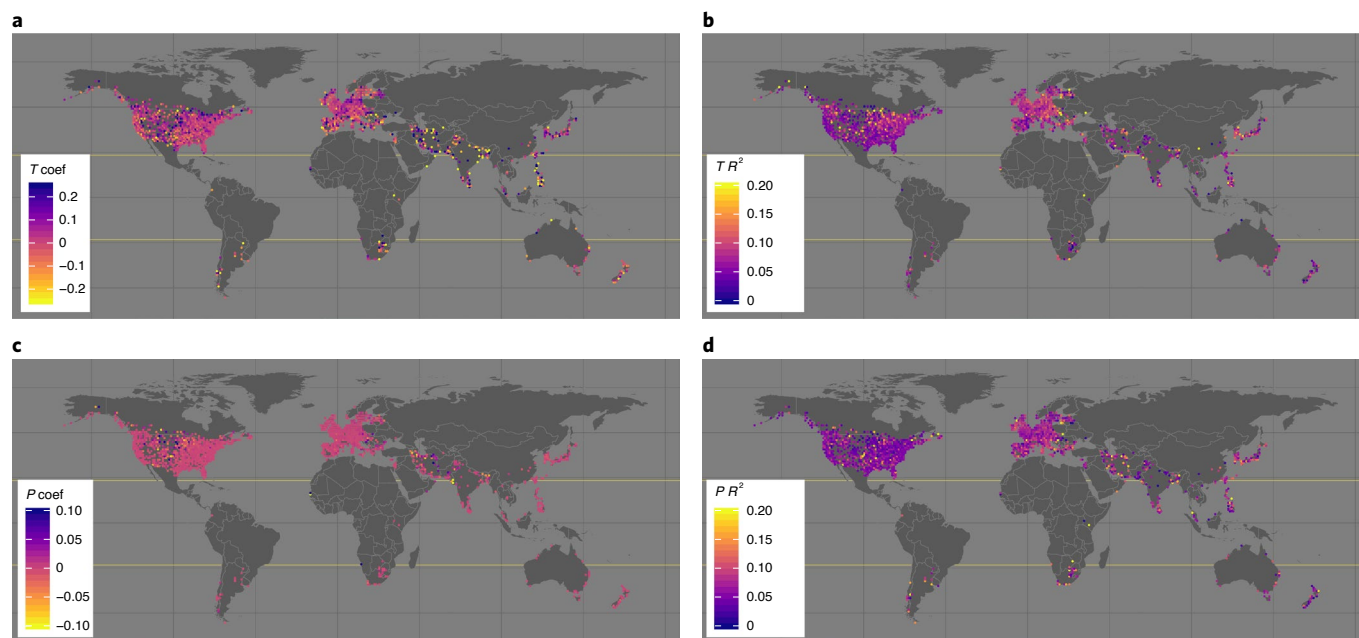
Fig. 2 | Mean abundance responses across 390 waterbird species to changes in temperature and precipitation in each 1° × 1° grid cell. a, The rate of abundance changes with increasing temperature (T coef), showing more negative responses to temperature increases at lower latitudes (shown with yellow dots) and positive responses at higher latitudes (shown with purple dots). **b**, The independent capacity of temperature in explaining abundance changes (T R^2). **c**, The rate of abundance changes with increasing precipitation (P coef). **d**, the independent capacity of precipitation in explaining abundance changes (P R^2). The region between the yellow solid lines is the tropics.

temperatures at the species level. Climate-related extinctions of local populations, typically at the warmer edge of the species' geographical range, are also more frequent in the tropics, causing poleward range shifts in many species[22]. While such species-level and population-level responses to climate change have often been investigated separately to date, our results provide new empirical evidence that impacts of temperature increases on tropical ecosystems can be characterized by species-wide declines in tropical 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. 5).

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[23], indirect biotic processes (for example, changes in food availability), rather than direct abiotic processes (for example, heat stress), are reported to be more important mechanisms for climate-driven abundance changes for higher-level consumers such as birds[24,25]. For example, increases in already-high temperatures at lower latitudes can cause wetlands to dry, reducing the availability of habitats and food for waterbirds[23]. Such an indirect effect of temperature increases could have obscured the temperature–abundance relationship, especially in the tropics. Second, many of the waterbirds analysed here are migratory species, for which temperature played a higher importance in explaining abundance changes (Extended Data Fig. 5b). This does not support our hypothesis that the effects of factors at multiple locations could outweigh the effects of local climatic conditions in migratory species, but instead indicates that migratory species can

be more responsive to local temperature changes due to their higher abilities to disperse[26] and track climate niches[27]. In this study, more non-tropical species tended to be migratory compared with tropical species: 151 (96%) of 158 non-tropical species and 43 (78%) of 55 tropical species were migratory, which may explain the higher importance of local temperature in explaining the abundance of non-tropical species. Third, larger errors associated with count data can cause a lower explanatory power of variables. We may expect larger errors in the tropics, where surveyors might be less trained given the shorter history of waterbird surveys and thus be more susceptible to observation errors. Finally, other important threats, such as habitat loss and hunting, affect bird abundance, independently from, or synergistically with, climate change[28]. By testing the effect of temperature and precipitation changes on yearly abundance changes while estimating long-term growth rates, our modelling approach controlled for the consistent impacts of such threats on long-term trends in abundance (see Statistical analyses for more detail). Nevertheless, those threats can also cause yearly abundance changes, and their impacts are likely to be more severe at lower latitudes[17], potentially causing temperature to have lower importance at lower latitudes.

Contrary to our hypotheses, there was no clear latitudinal pattern in abundance responses to precipitation changes, either among or within species. Water availability, compared with ambient temperature, has been shown to be a more important driver of species richness and population size at lower latitudes[4]. Supporting this, our results showed that precipitation was more important in explaining the abundance of some tropical species compared with most species in higher latitudes, although the overall among-species pattern across latitudes was not significant (Fig. 4c). This may be explained by two reasons. First, precipitation changes can affect waterbirds at the river-basin scale (often the scale of 500–1,000 km) through effects on water flow into their wetland habitats[29]. Therefore, our analysis at the resolution of 1° grid cells (equivalent to a grain size of 96.49 km) may not have
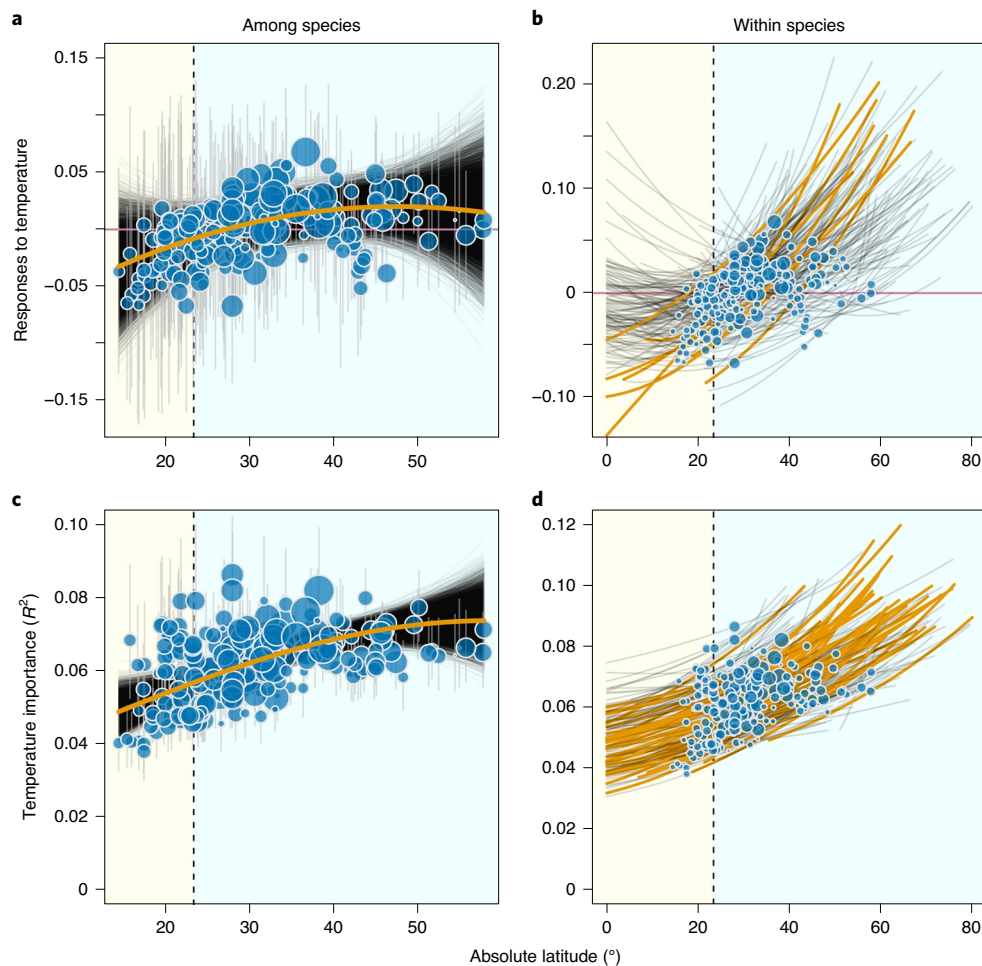
Fig. 3 | Latitudinal patterns in waterbird abundance responses to temperature increases. a,b, Abundance responses to increasing temperature at 213 species' range midpoints (**a**) and within each species (**b**). **c,d**, The importance of temperature in explaining abundance changes at species' range midpoints (**c**) and within each species (**d**). **a,c**, Orange lines, among-species patterns based on posterior median coefficients; black lines, patterns with all posterior samples; blue circles, responses at each species' range midpoints; grey lines, 95% credible intervals; circle size, the absolute latitudinal range size. **b,d**, Regression lines, within-species latitudinal patterns for each species based on posterior median coefficients (significant patterns in orange). Yellow area, the tropics.

been able to detect such a broad-scale impact of precipitation changes. Second, waterbird responses to precipitation changes can vary greatly among species (see Extended Data Fig. 3 for detail). While increased rainfall generally leads to more favourable habitat conditions for waterbirds in dry regions[23], elevated water levels associated with increased rainfall can cause the loss of shallow-water habitats, often followed by abundance decreases in certain groups, such as shorebirds[30]. Such mixed responses to precipitation changes among species may have resulted in the lack of clear latitudinal patterns, particularly among species.

Tropical biodiversity imperilled yet understudied

Our results have three major implications on the impact of climate change on global biodiversity. First, local temperature increases between December and February under ongoing climate change are likely to pose a more-negative impact on species and populations in the tropics. This provides important evidence for improving our understanding of whether tropical ecosystems have been degraded by climate change. Although climate change is not the only threat to waterbirds, impacts of other major threats, such as loss and degradation of wetlands and excessive hunting pressure, seem to be more severe in the tropics, too[17], indicating that

tropical species and populations suffer from multiple anthropogenic threats. Second, the revealed negative impact of temperature increases in the tropics suggests that existing severe biases in scientific information towards temperate regions could underestimate 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 studies on other taxa in the tropics, where most species are facing multiple threats, including climate change[8]. Finally, our other finding that abundance responds positively to temperature increases at higher latitudes highlights the possibility of global-scale poleward shifts in abundance across species and associated ecosystem functions and services. As such shifts can have serious consequences not only for biodiversity but also for human well-being, assessing latitudinal patterns in biodiversity responses to climate change at the population, species and community levels warrants further research attention.

Online content

Any methods, additional references, Nature Research reporting summaries, source data, extended data, supplementary information, acknowledgements, peer review information; details of
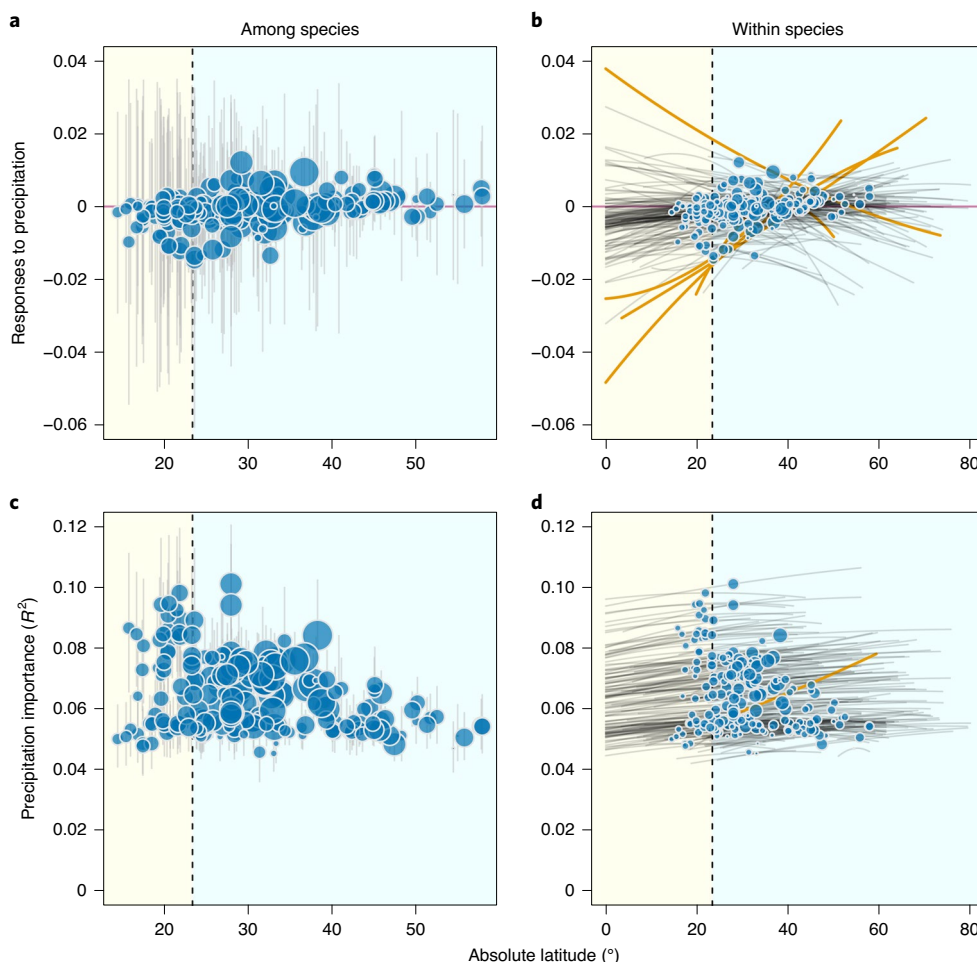
Fig. 4 | Latitudinal patterns in waterbird abundance responses to precipitation increases. a,b, Abundance responses to increasing precipitation at 213 species' range midpoints (**a**) and within each species (**b**). **c,d,** The importance of precipitation in explaining abundance changes at species' range midpoints (**c**) and within each species (**d**). **a,c,** Blue circles, responses at each species' range midpoints; grey lines, 95% credible intervals; circle size, the absolute latitudinal range size. **b,d,** Regression lines, within-species latitudinal patterns for each species based on posterior median coefficients (significant patterns in orange). Yellow area, the tropics.

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Methods

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

The IWC, launched in 1967, is a scheme for monitoring waterbird numbers, covering more than 25,000 sites in over 100 countries with more than 15,000 observers. The coordination of the IWC is divided into four regional schemes corresponding to the major migratory flyways of the world: the African–Eurasian Waterbird Census, Asian Waterbird Census, Caribbean Waterbird Census and Neotropical Waterbird Census. We did not use data from the Caribbean Waterbird Census as, having started in 2010, it provides only short-term data. The survey methodology is essentially the same across the four regional schemes. Population counts are typically carried out once every year in mid-January but may include counts between December and February. We used only the January and February counts for consistency. This means that our data from the Northern Hemisphere are for non-breeding populations while those in the Southern Hemisphere also include some breeding populations. In each country that is covered by the survey, national coordinators manage an inventory of wetland sites (hereafter, survey sites), including sites of international- or national-level recognition (for example, Ramsar sites, Flyway Network Sites, Important Bird Areas, national parks and so on). Each survey site is generally defined by boundaries so that observers know precisely which areas are to be covered in the surveys. The observers consist of a wide variety of volunteers, but national coordinators usually train them using materials produced by Wetlands International to ensure the quality of count data. Survey sites (normally up to a few km²) are typically surveyed by about two observers for up to four hours, while larger sites can require a group of observers working over several days. Most surveys are conducted on foot or from a vehicle, with boats involved in a few. The time of survey on any given day depends on the type of survey site: inland sites are normally surveyed during the morning or late afternoon, whereas coastal sites are surveyed over the high-tide period (mangrove areas and nearby mudflats are, however, covered during low tides). Surveys cover waterbirds, defined as bird species that are ecologically dependent on wetlands[31]. Counts are usually made by scanning flocks of waterbirds with a telescope or binoculars and counting each species. Zero counts are not always recorded and thus are inferred using a set of criteria (see the following for more detail). Count records, together with associated information, are submitted to the national coordinators, who compile the submitted records, check their validity and submit those records to Wetlands International. See refs. [31,32] for more details on survey methodology.

As the IWC does not cover North America, we also used data based on the CBC, which 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[33]. As described in ref. [17], each CBC consists of a record of all bird species detected within a circle (24.1 km in diameter) on a single day between 14 December and 5 January. Most circles (and most historical data) are from North America (that is, the United States and Canada). Observers join groups and survey subunits of the circle during the day using a variety of transportation methods (mostly on foot or in a car, but can include boats, skis or snowmobiles). The number of 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 used only records on waterbird species in this paper.

We compiled data from each scheme by species, except for data based on the African–Eurasian Waterbird Census, where data had already been stored by flyway for each species[32]. As data based on the Neotropical Waterbird Census are only available for 1990 onward, we used only post-1990 data for other regions as well. The latest records were in 2013. For the IWC data, we generated zero counts using an established approach[32], in which we started with a list of all species observed in each country and assumed a zero count of any species that were on the list but not recorded at a particular site on a particular day if the site was surveyed on that day, as shown by the presence of any other species' record(s), and if no multi-species code related to the species (for example, Anatinae spp. for species of the genus *Anas*) was recorded for the site–date combination. We projected all survey sites onto a Behrmann equal-area cylindrical projection and assigned them to grid cells with a grain size of 96.49 km, or approximately 1° at 30° N/S. We used only species that were observed at one or more survey sites for ten or more years since 1990; this resulted in 390 species being analysed in this study (see Supplementary Data 4 for the full list of species with the number of survey sites and 1° × 1° grid cells where each species was observed). Following ref. [17], we used the International Ornithological Congress World Bird List[34] for species groups in Fig. 1: coursers, gulls, terns and auks (Glareolidae, Laridae, Stercorariidae and Alcidae), grebes and flamingos (Podicipedidae and Phoenicopteridae), loons and petrels (Gaviidae

and Procellariidae), pelicans, boobies and cormorants (Pelecanidae, Sulidae, Fregatidae, Phalacrocoracidae and Anhingidae), rails and cranes (Rallidae, Gruidae and Aramidae), shorebirds (Burhinidae, Charadriidae, Haematopodidae, Jacanidae, Recurvirostridae, Rostratulidae and Scolopacidae), storks, ibises and herons (Ciconiidae, Threskiornithidae and Ardeidae) and waterfowl (Anatidae and Anhimidae).

Explanatory variables. To estimate responses in waterbird abundance to changes in temperature and precipitation (see Extended Data Fig. 2 for changes in mean January temperature and precipitation at all 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. Although climatic factors at different stages of species' annual cycles (that is, outside our survey (December–February) season), such as those in the breeding season for species wintering during our survey season, could affect abundance changes, we could not include such factors in our analysis due to the lack of information for most migratory species. Instead, we indirectly tested the effect of climatic factors outside our survey season by including migratory status in the latitudinal analysis (see Extended Data Fig. 4). When testing among- and within-species latitudinal patterns in abundance responses, we accounted for three species-level variables—latitudinal geographical range, migratory status and body size—that are expected to explain among-species variations in responses; data sources of those variables are shown in Extended Data Fig. 4.

Statistical analyses. *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:

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

where N_{t-1}, $Temp_{t-1}$, $Prec_{t-1}$ are the abundance of the species, the relevant mean December–February temperature and precipitation at the site in year $t-1$, respectively; β_{1-3} are regression coefficients and α is the intercept. We could not test the effects of other major drivers of abundance changes, such as countries' governance and surface water change[17], due to the lack of data on yearly changes over the survey period. By estimating α as the population growth rate, this model tests the effect of temperature and precipitation on yearly changes in abundance while controlling for long-term trends in abundance. This model structure helps to avoid detecting a spurious relationship between long-term trends in abundance caused by other threats (for example, long-term declines by habitat loss) and those in temperature or precipitation (for example, long-term warming temperatures). When comparing the Akaike information criterion (AIC) between the exponential growth model ($\log(N_t) - \log(N_{t-1}) = \alpha$) and time-dependent growth model ($\log(N_t) - \log(N_{t-1}) = \alpha + \beta t$) fitted to count data at each site for each species, the exponential growth model showed a smaller AIC for 95.8% of the 79,255 time series, indicating that the preceding model structure is appropriate for our data. Taking logs and rearranging to express the model in terms of relative growth rate results in the following form:

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

and we used this form to estimate regression coefficients with linear models in R 3.4.1[36]. 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[37]; the proportion of missing values (that is, the effect of interpolation) was accounted for in the following analysis (see Latitudinal analysis). The estimated β_2 and β_3 represent site-level abundance responses to temperature and precipitation increases, respectively. Using the same model, we also estimated the site-level independent capacity of temperature and precipitation changes in explaining abundance changes (defined as the importance of temperature and precipitation) with hierarchical partitioning[19] (measured in our case as R^2) using the package hier.part[38].

As the model described in the preceding tests the effect of temperature and precipitation in the previous year (that is, year $t-1$) on abundance in the survey year (year t), we separately tested the immediate effect of temperature and precipitation in the same year (year t) as the abundance survey year. For this analysis, we used the mean temperature or precipitation in December (year $t-1$), January and February (year t) for the IWC sites, where surveys were conducted either in January or February, and mean December temperature or precipitation in year t for the CBC sites, where surveys were largely conducted in December. We compared the AIC between the models with temperature/precipitation in year t and year $t-1$ at each site for each species and used the temperature/precipitation variable in the model with a smaller AIC in the 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 ref. [17] for more detail). However, survey efforts in the CBC are known to vary through time. Following an earlier analysis[39], 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:

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

where ζ_t is the total number of survey hours per count and $\bar{\zeta}$ is the mean value of ζ_t. The parameters B and p determine a range of relationships between effort and the number of birds counted[39], and we used the values estimated for each species in our earlier study[17] (see Supplementary Data 4).

We used only survey sites with ten or more records and five or more non-zero records since 1990 for at least one species, and this resulted in 1,303,651 count records since 1990 on 390 species at 6,822 sites between 55°S and 64°N (Extended Data Fig. 1) being analysed in this study. The survey sites used in this study are inevitably biased towards certain regions, especially within the tropics, where most sites are in South and Southeast Asia (Extended Data Fig. 1). Thus, responses by waterbirds to climate change in other tropical regions still remain untested. However, note that (1) the coverage of our data in the tropics is still exceptional, considering the generally severe lack of ecological data[8,40], especially population time series[41], in the tropics, and (2) there is a known gap in previous assessments of climate change impacts on biodiversity in tropical Asia[9], and our study bridges the gap.

We aggregated the estimated site-level responses to temperature and precipitation increases as well as the importance of temperature and precipitation to 1°×1° grid cells by calculating the mean site-level estimates across all sites in each grid cell, weighted by the inverse of estimate variance at each site to account for uncertainties. The grid-cell-level estimates (Supplementary Data 2) were then used in the latitudinal analysis described in the following and for the species-level maps (Supplementary Data 1). We also calculated community-level responses (Fig. 2) by calculating the mean grid-cell-level estimates across all species observed in each grid cell, weighted by the inverse of estimate variance in each species to account for uncertainties.

Water availability in the tropics may not necessarily depend on December–February precipitation. Especially in South and Southeast Asia, where our tropical survey sites are concentrated, the summer monsoon contributes to 80% of annual rainfall[42]. Thus, we also tested the effect of precipitation during June, July and August. We first calculated mean precipitation in June, July and August in year $t-1$ for the IWC sites and in year t for the CBC sites. Then if the mean June–August precipitation was higher than the mean December–February precipitation, we compared the AIC between the model with June–August precipitation and the two models with the original precipitation variables at each site for each species, and used the precipitation variable with the smallest AIC in the final model. This allows using precipitation variables from different seasons for different sites. The estimates were then used in the following analysis for comparison with the original analysis (see Extended Data Figs. 7 and 8 for results).

Latitudinal analysis. We used absolute latitudes to test latitudinal patterns described in Extended Data Fig. 3 for the following reason. Our data include species that are distributed only in either the Northern or Southern Hemisphere (one-hemisphere species) as well as those that appear in both hemispheres (two-hemisphere species). Some of our hypotheses (for example, that for among-species patterns in abundance changes with increasing temperature, shown at the top of Extended Data Fig. 3) predict that one-hemisphere species would show a monotonic increase with raw latitudes while two-hemisphere species would show a U-shaped relationship along the raw latitudinal gradient with the lowest point at the Equator; this makes analysing those species together in the hierarchical modelling framework described in the following a complicated process. With absolute latitudes, by contrast, one-hemisphere and two-hemisphere species are both expected to show a monotonic increase, making the parameter estimation much simpler.

We tested the effects of explanatory variables on among- and within-species latitudinal variations in (1) abundance responses to temperature and precipitation changes and (2) the 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[43] under a hierarchical modelling framework to explicitly distinguish species-level effects (explaining variations in species-level responses between species) and population-level effects (explaining variations in population-level responses within species) of explanatory variables. Here we defined each species' responses at their absolute latitudinal range midpoints (for migratory species, based only on their geographical range during non-breeding season) as species-level responses, and responses within each grid cell as population-level responses.

In this model, the species effect μ_s, representing the species-level responses to temperature or precipitation increases in species s, is drawn from a normal distribution with mean of ν_s and variance of σ_ν^2; ν_s is further modelled with species-level explanatory variables:

$$\nu_s = \alpha + \beta_{B1}MIDLAT_s + \beta_{B2}MIDLAT_s^2 + \beta_{B3}LATRANGE_s$$
$$+ \beta_{B4}MIG_s + \beta_{B5}BM_s + \beta_{B6}PROPNA_s + \eta_s$$

where α is the global intercept and β_{B1-B6} represent the species-level effects. $MIDLAT_s$, $LATRANGE_s$, MIG_s, BM_s, $PROPNA_s$ are species-level explanatory variables: absolute latitudinal range midpoints, absolute latitudinal geographical range (degree), migration status (migrant or non-migrant), body mass (g, $\log_{10}$-transformed) and the mean proportion of missing values (that is, interpolated values) in count records across all sites (%) for species s, respectively. The variance inflation factor was smaller than 1.9 for all the species-level explanatory variables, indicating that multi-collinearity was not a major issue; η_s is a random term that accounts for phylogenetic dependence among species and is drawn from a multivariate normal distribution (MVN)[44,45]:

$$\eta_s \sim \mathrm{MVN}(\mathbf{0}, \delta^2 \Sigma_\lambda)$$
$$\Sigma_\lambda = \lambda\Sigma + (1-\lambda)\mathbf{I}$$

where Σ is a scaled variance–covariance matrix calculated from an ultrametric phylogenetic tree (defined in the following). By scaling Σ to a height of one, we can interpret δ^2 as the residual variance[44]. For the strength of phylogenetic signal to vary, we also incorporated Pagel's λ[46,47] into the matrix with the identity matrix $\mathbf{I}$. Here λ is a coefficient that multiplies the off-diagonal elements of Σ and a λ close to zero implies that the phylogenetic signal in the data is low, suggesting independence in the error structure of the data points, whereas a λ close to one suggests a good agreement with the Brownian Motion evolution model and thus suggests correlation in the error structure[44,47]. To incorporate uncertainties[48] in phylogenetic trees in the calculation of Σ, we used a sample of 100 trees from a comprehensive avian phylogeny[49] as the prior distribution for our analysis[44]. More specifically, one of the 100 trees was randomly drawn in each iteration and used for the calculation of Σ. In the sensitivity analysis using June–August precipitation, we limited the range of η_s to between −0.2 and 0.2, on the basis of the estimated values in the original analysis, to enhance the convergence of the models.

The population-level responses to temperature or precipitation increases $r_{s,i}$ of species s in grid cell i was then assumed to derive from a normal distribution with mean $\mu_{s,i}$ and variance σ_μ^2, where $\mu_{s,i}$ is modelled using the species effect μ_s:

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

Here $\beta_{w_{s,1-3}}$ represents the population-level effect of absolute latitudes $LAT_{s,i}$ (in the form of linear and quadratic terms, to test nonlinear patterns) and the mean proportion of missing values (that is, 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 latitudinal geographical range of each species $LATRANGE_s$, so that the estimated effects of absolute latitudes are comparable among species with varying latitudinal range size. The species-specific $\beta_{w_{s,1-3}}$ is the random effect each governed by hyper-parameters as:

$$\beta_{W_{s,j}} \sim \mathrm{Normal}\left(h\beta_{W_j}, \sigma_{\beta_{W_j}}^2\right)$$

The term $\gamma_{s,i}$ accounts for spatial autocorrelation within each species and is drawn from an intrinsic Gaussian conditional autoregressive prior distribution with variance $\sigma_{\gamma_s}^2$:

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

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

We tested latitudinal patterns in the importance of temperature and precipitation using essentially the same model but the population-level importance of temperature or precipitation $imp_{s,i}$ of species s in grid cell i was assumed to derive from a beta distribution 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:

$$\mathrm{logit}(c_{s,i}) = \mu_s + \beta_{w_{s,1}}\frac{LAT_{s,i} - MIDLAT_s}{LATRANGE_s}$$

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

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

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

As latitudinal patterns might be different between two hemispheres, we also conducted the same latitudinal analysis separately for (1) narrowly defined

Southern Hemisphere species (49 species with maximum range latitude <0) and (2) all the other 164 species as "Northern Hemisphere" species (see Supplementary Figs. 1–4 for results).

The models were implemented with OpenBUGS 3.2.3[50] and the R2OpenBUGS package[51] in R 3.4.1[36]. Following ref. [17], as non-informative prior distributions, we used a Gamma distribution with mean of 1 and variance of 100 for φ_i and the inverse of σ_ν^2, δ^2, σ_μ^2, $\sigma_{\beta_{Wj}}^2$ and $\sigma_{\gamma_s}^2$, uniform distribution on the interval [0, 1] for λ, normal distributions with mean of 0 and variance of 100 for α, β_{Bk} and $h\beta_{Wj}$. We ran each Markov chain Monte Carlo 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.

Due to differences in the definition of species between the two sources used[49,52], we followed ref. [17] and combined two separate species defined in the BirdLife Checklist[52] into one in four cases for this species-level analysis: Kentish plover *Charadrius alexandrinus* and snowy plover *C. nivosus*, common snipe *Gallinago gallinago* and Wilson's snipe *G. delicata*, European herring gull *Larus argentatus* and Arctic herring gull *L. smithsonianus*, and common moorhen *Gallinula chloropus* and common gallinule *G. galeata*. *Larus glaucoides 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 IWC nor CBC necessarily targets seabird species.

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

Reporting Summary. Further information on research design is available in the Nature Research Reporting Summary linked to this article.

Data availability
The waterbird count data used in this study are collated and managed by Wetlands International and the National Audubon Society, and are available from Wetlands International at: http://iwc.wetlands.org/. The estimated abundance responses to temperature and precipitation as well as the importance of temperature and precipitation for each grid cell for each species are available as Supplementary Data 2. All the data on explanatory variables are freely available as specified in Extended Data Fig. 4.

Code availability
All the R codes used for the analyses are available as Supplementary Data 5–7.

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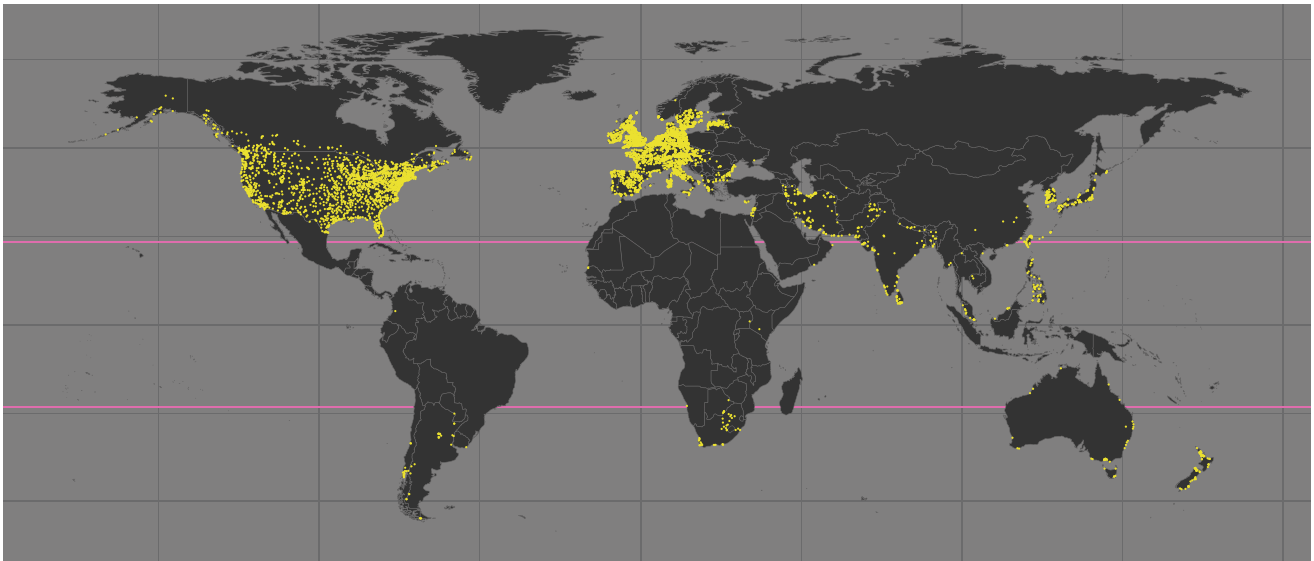
Author contributions

Competing interests

The authors declare no competing interests.

Additional information

Supplementary information is available for this paper at https://doi.org/10.1038/s41558-020-0872-3.
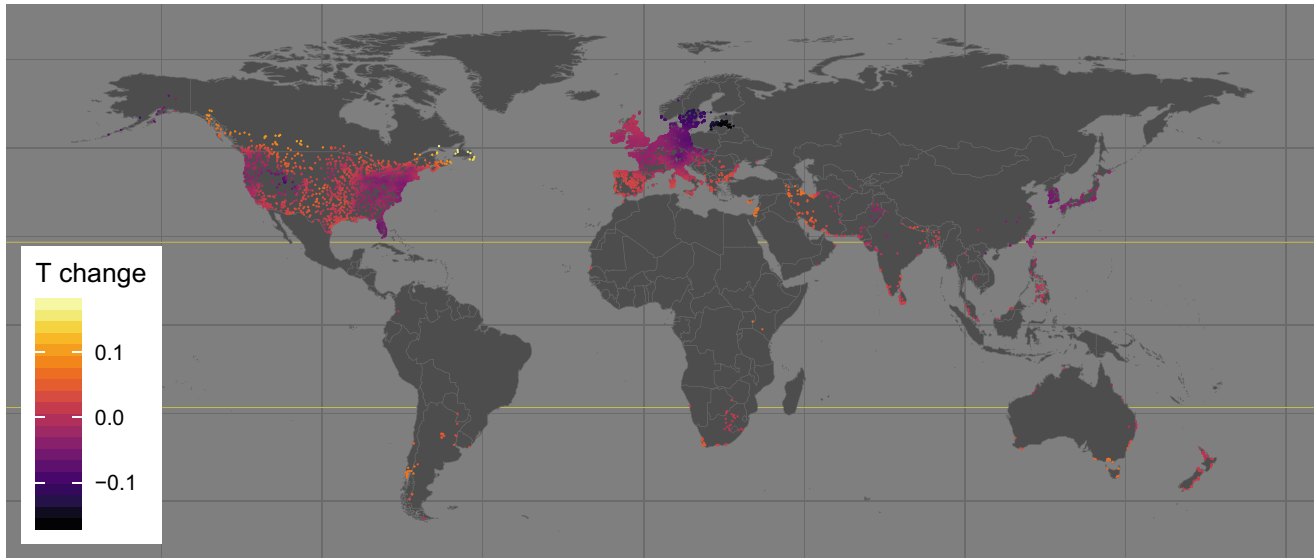
Correspondence and requests for materials should be addressed to T.A.

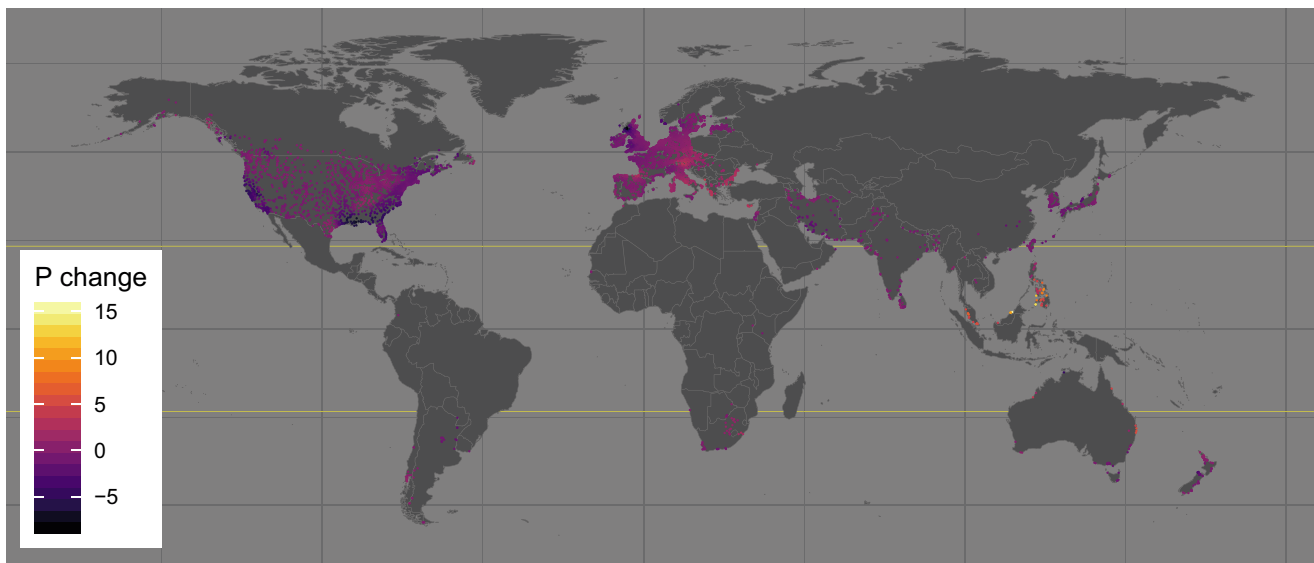**Reprints and permissions information** is available at www.nature.com/reprints.

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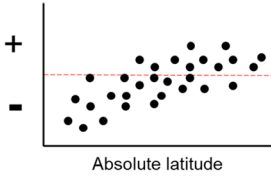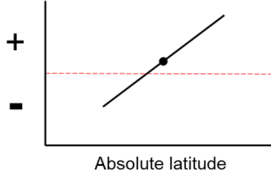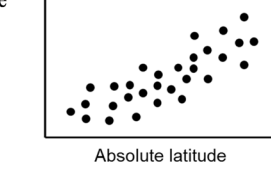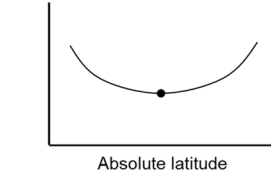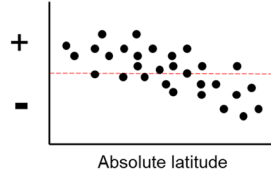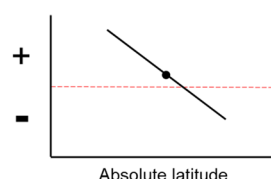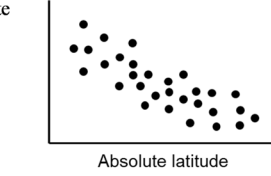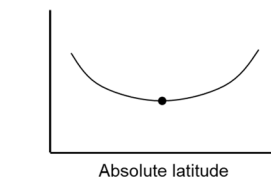
a. Annual rate of January temperature change (1990 − 2013)

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

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

Hypotheses	Expected latitudinal patterns (each dot represents the range mid-point of each species, with solid lines showing within-species patterns; dotted lines represent zero, i.e., no response). Note that latitudes are absolute values; see Methods for more detail.		Supporting evidence
Abundance changes with increasing temperature · Among species	Monotonic increase with absolute latitudes, with negative responses in species at lower latitudes		At lower latitudes, where temporal variation in temperature is lower, bird species tend to have a narrower thermoneutral zone (TNZ; the range of temperatures within which the metabolism of an endotherm is lowest and almost independent of ambient temperature) and are thus more likely to experience a thermal mismatch under climate change (maximum ambient temperature exceeds upper TNZ limit)[16, 65]
· Within species	Monotonic increase with absolute latitudes, with negative responses in populations at lower latitudes and positive responses in populations at higher latitudes		Populations at higher latitudes benefit from, and those at lower latitudes are negatively affected by, temperature increase[66], if all populations have the same fitness curve with the optimal climatic niche at the latitudinal midpoint of its range[67]
Importance of temperature in explaining abundance changes · Among species	Monotonic increase with absolute latitudes		Species-richness patterns at high latitudes are often limited by ambient energy (correlated with temperature) and at low latitudes by moisture availability[68]. If species richness represents the summation of individual population response, the same is applicable to species-level responses in abundance[4].
· Within species	Higher at both range edges		If climatic factors limit species distributions[69], they are expected to be more important determinants of species abundance at range edges[70].
Abundance changes with increasing precipitation · Among species	Monotonic decrease, with negative responses in species at higher latitudes		Increase in Dec-Feb precipitation (and associated increase in water level, decrease in habitat heterogeneity, and increased thermoregulatory cost under wet weather) is observed to negatively affect waterbird abundance at higher latitudes (e.g., Europe[71,72] and Argentina[30]) while higher precipitation increases the availability of wetlands and vegetation in dry parts of the tropics (e.g., the Sahel region[73,23]) although effects may depend on each species' ecology[23].
· Within species	Monotonic decrease, with negative responses in populations at higher latitudes		Within-species patterns are expected to be similar to among-species patterns, especially for wide-ranging species.
Importance of precipitation in explaining abundance changes · Among species	Monotonic decrease with absolute latitudes		Species-richness patterns at high latitudes are often limited by ambient energy and at low latitudes by moisture availability (correlated with precipitation)[68]. Assuming that species richness represents the summation of individual population response, the same is applicable to species-level responses in abundance[4].
· Within species	Higher at both range edges		If climatic factors limit species distributions[69], they are expected to be more important determinants of species abundance at range edges[70].

Extended Data Fig. 3 | Hypotheses tested for explaining among- and within-species latitudinal variations in waterbird abundance responses to temperature and precipitation changes. Supporting evidence includes information from refs. [65-73].

Hypotheses	Expected patterns	Variables used	Data sources
Latitudinal geographical range	· 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)[74]. · 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)[74].	Differences between maximum and minimum absolute latitudes of geographical range	BirdLife Data Zone*
Migratory status	· 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)[26]. · Migratory species generally have a higher dispersal ability[26] and track climate niches to a greater extent than resident species[27], thus can be more responsive to changes in local temperature and precipitation (i.e., the importance of temperature and precipitation is higher). · 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)[75]. · 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)[76].	Migrant or non-migrant	BirdLife Data Zone*
Body size	· 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)[26]. · 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)[26].	Body mass (g)	Elton Traits 1.0[77]

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

Extended Data Fig. 4 | Additional hypotheses tested for explaining among-species variations in waterbird abundance responses to temperature and precipitation changes. Information regarding expected patterns include refs. [26,27,74–76]; ref. [77] was used as a data source.

a. Responses to temperature

b. Importance of temperature
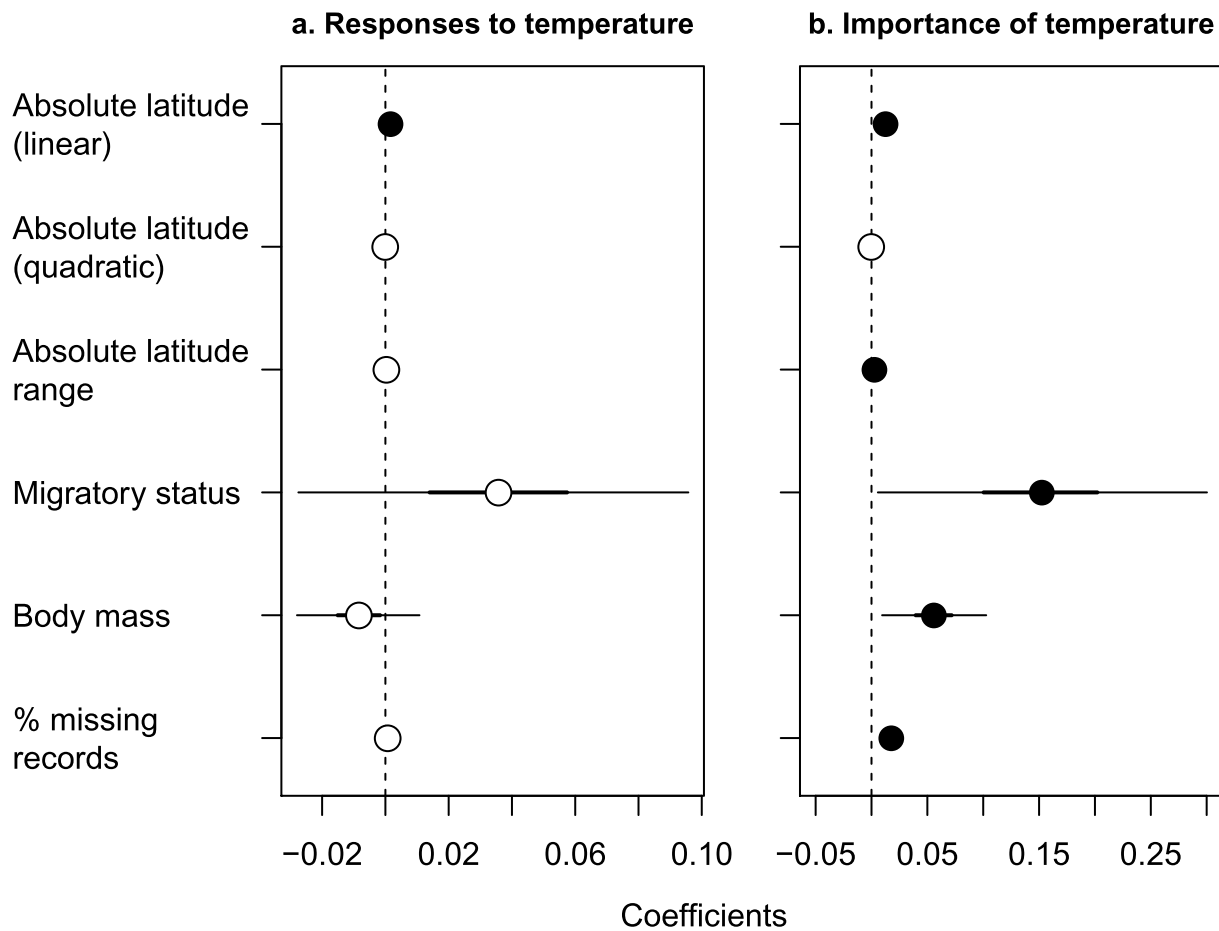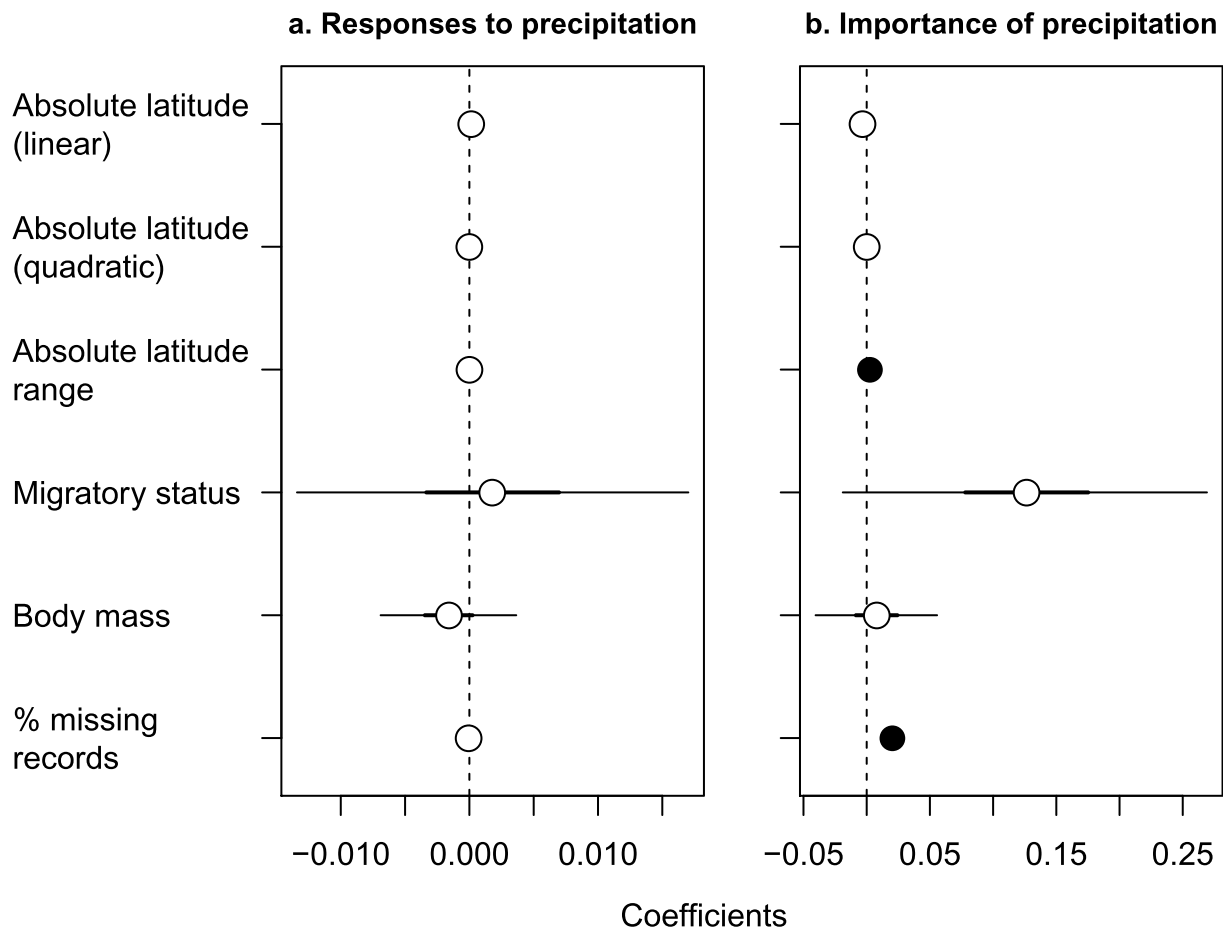
Coefficients

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.

a. Responses to precipitation

b. Importance of precipitation
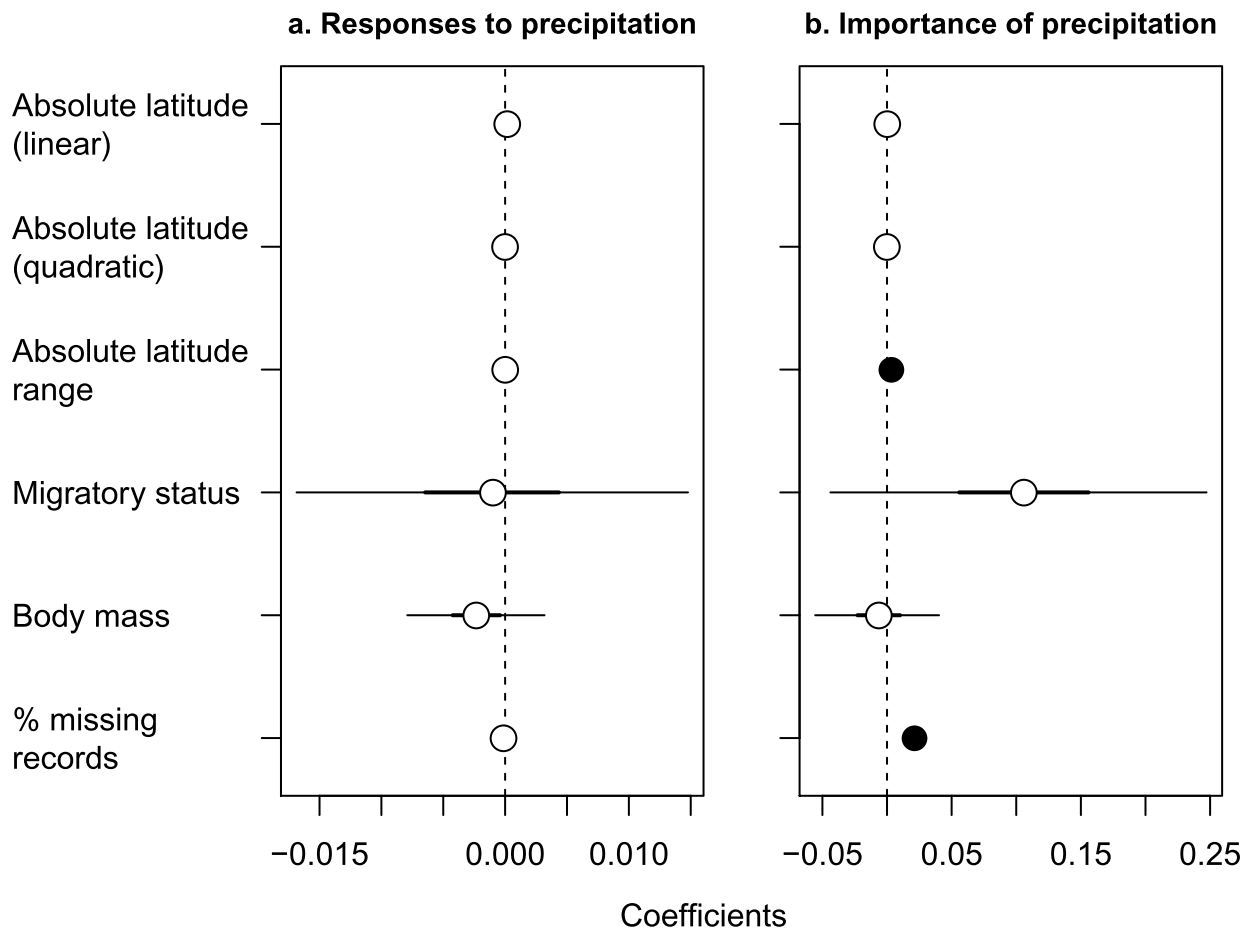
Coefficients

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.

a. Responses to temperature

b. Importance of temperature

Coefficients
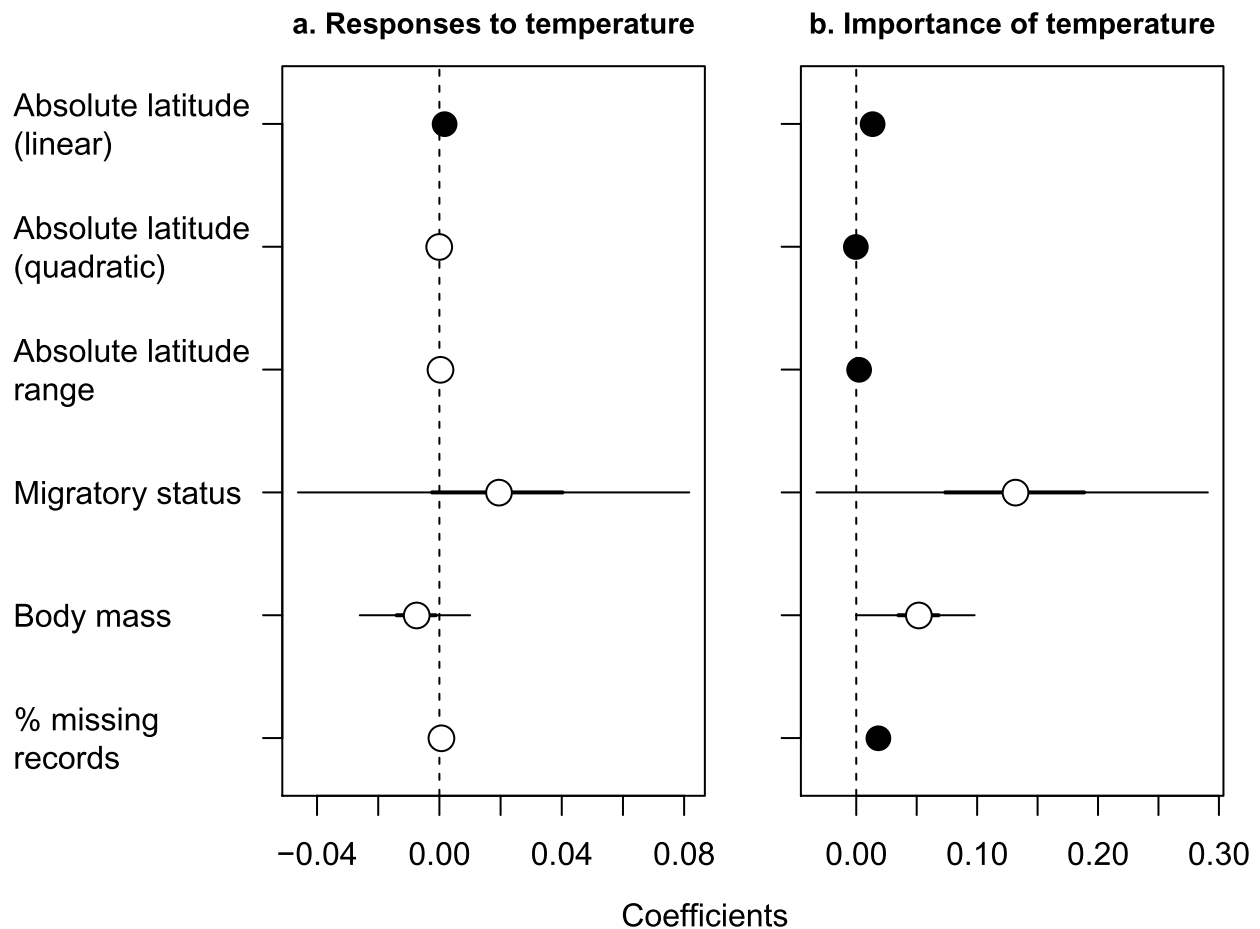
Extended Data Fig. 7 | Sensitivity of the results on responses to temperatures to the choice of precipitation seasons. Effects of species-level predictors on waterbird abundance responses to temperature changes when using precipitation during June, July and August in the model (see Statistical Analyses for more detail). 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 positive while that for *Absolute latitude (quadratic)* in (**b**) is negative.

a. Responses to precipitation

b. Importance of precipitation

Coefficients

Extended Data Fig. 8 | Sensitivity of the results on responses to precipitations to the choice of precipitation seasons. Effects of species-level predictors on waterbird abundance responses to precipitation changes when using precipitation during June, July and August in the model (see Statistical Analyses for more detail). 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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Reporting Summary

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Statistics

For all statistical analyses, confirm that the following items are present in the figure legend, table legend, main text, or Methods section.

n/a	Confirmed	
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☐	☒	A statement on whether measurements were taken from distinct samples or whether the same sample was measured repeatedly
☐	☒	The statistical test(s) used AND whether they are one- or two-sided *Only common tests should be described solely by name; describe more complex techniques in the Methods section.*
☐	☒	A description of all covariates tested
☐	☒	A description of any assumptions or corrections, such as tests of normality and adjustment for multiple comparisons
☐	☒	A full description of the statistical parameters including central tendency (e.g. means) or other basic estimates (e.g. regression coefficient) AND variation (e.g. standard deviation) or associated estimates of uncertainty (e.g. confidence intervals)
☒	☐	For null hypothesis testing, the test statistic (e.g. *F*, *t*, *r*) with confidence intervals, effect sizes, degrees of freedom and *P* value noted *Give P values as exact values whenever suitable.*
☐	☒	For Bayesian analysis, information on the choice of priors and Markov chain Monte Carlo settings
☒	☐	For hierarchical and complex designs, identification of the appropriate level for tests and full reporting of outcomes
☐	☒	Estimates of effect sizes (e.g. Cohen's *d*, Pearson's *r*), indicating how they were calculated

Our web collection on statistics for biologists contains articles on many of the points above.

Software and code

Policy information about availability of computer code

Data collection	No software was used for data collection.
Data analysis	R3.4.1 and OpenBUGS 3.2.3 were used for data analysis. All the R codes used for the analyses are available as Supplementary Data S5-7.

For manuscripts utilizing custom algorithms or software that are central to the research but not yet described in published literature, software must be made available to editors/reviewers. We strongly encourage code deposition in a community repository (e.g. GitHub). See the Nature Research guidelines for submitting code & software for further information.

Data

Policy information about availability of data

All manuscripts must include a data availability statement. This statement should provide the following information, where applicable:
- Accession codes, unique identifiers, or web links for publicly available datasets
- A list of figures that have associated raw data
- A description of any restrictions on data availability

The waterbird count data used in this study are collated and managed by Wetlands International and the National Audubon Society, and are available from Wetlands International at: http://iwc.wetlands.org/. The estimated abundance responses to temperature and precipitation as well as the importance of temperature and precipitation for each grid cell for each species are available as Supplementary Data S2. All the data on explanatory variables are freely available as specified in Supplementary Table S2.

Field-specific reporting

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☐ Life sciences   ☐ Behavioural & social sciences   ☒ Ecological, evolutionary & environmental sciences

Ecological, evolutionary & environmental sciences study design

All studies must disclose on these points even when the disclosure is negative.

Study description	Data used in this study comprised site-specific annual counts based on the International Waterbird Census coordinated by Wetlands International and the Christmas Bird Count by the National Audubon Society in the USA. We used 1,303,651 count records collected since 1990 on 390 waterbird species at 6,822 sites between -55° and 64°.
Research sample	We used existing datasets on global waterbird populations as described above.
Sampling strategy	The sample size in this study was not pre-determined but essentially driven by the availability of data. For the first part of our analysis ("Model for estimating abundance responses"), we used as many available count records as possible, which determined the sample size. We only used species that were observed at one or more survey sites for ten or more years since 1990, and this has resulted in 390 species being analysed in this study (see Supplementary Data S4 for the full list of species with the number of survey sites and 1° × 1° grid cells where each species was observed). The 390 species cover a wide range of waterbird species groups inhabiting a variety of habitats, thus should represent the spatial and temporal dynamics of global waterbird communities. For the second part of our analysis ("Latitudinal analysis"), we only used 213 species with estimates at ten or more grid cells. We believe 213 species are sufficient to test the effect of six species-level predictors. Ten or more grid cells should also be sufficient to test the effect of three population-level predictors within each species.
Data collection	The waterbird data were collected by a number of observers through the International Waterbird Census and the Christmas Bird Count. The full description of data collection procedures can be found in the method section ("Waterbird count data"). The data on explanatory variables were derived by TA, HSW and BS from existing data sources described in Supplementary Table S2.
Timing and spatial scale	The waterbird data were collected at 6,822 sites across the globe (see Supplementary Figure S1 for the map) between 1990 and 2013. The survey was essentially conducted every year, which should be sufficient to test the relationship between climate and yearly abundance changes. The proportion of missing values in count records is shown in Supplementary Data S2.
Data exclusions	We only used species that were observed at one or more survey sites for ten or more years since 1990 and excluded the other species, and this has resulted in 390 species being analysed in this study. For the latitudinal analysis, we excluded species with estimates at nine or less grid cells as well as eight seabird species in Alcidae and Sulidae (as neither the IWC nor CBC necessarily targets seabird species) and Larus glaucoides thayeri (as it is included in neither of the two databases used in this study).
Reproducibility	Our study is not based on experiments. We provided data sources and R codes for reproducibility.
Randomization	In the analyses we used as many species and survey sites as possible, based on the criteria described above. Nevertheless, our survey sites could still be biased towards, e.g., Europe and North America, where monitoring has been active. Therefore in the latitudinal analyses, we used CAR models to account for spatial autocorrelation, which is expected to reduce the effect of such spatial biases in data.
Blinding	Blinding is not relevant to our study as we did not use any experiments.

Did the study involve field work?   ☐ Yes   ☒ No

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Materials & experimental systems

n/a	Involved in the study
☒	☐ Antibodies
☒	☐ Eukaryotic cell lines
☒	☐ Palaeontology
☐	☒ Animals and other organisms
☒	☐ Human research participants
☒	☐ Clinical data

Methods

n/a	Involved in the study
☒	☐ ChIP-seq
☒	☐ Flow cytometry
☒	☐ MRI-based neuroimaging

Animals and other organisms

Policy information about [studies involving animals](#); [ARRIVE guidelines](#) recommended for reporting animal research

Laboratory animals	This study did not involve laboratory animals.
Wild animals	We used observation data on 390 waterbird species (detail shown in Supplementary Data S4). Sex and age were not recorded in the surveys.
Field-collected samples	This study did not involve samples collected from the field.
Ethics oversight	No ethical approval was required because this study is based on observation data and the observations were conducted far enough to avoid impacts on species, such as disturbance.

Note that full information on the approval of the study protocol must also be provided in the manuscript.