Successful conservation of global waterbird populations depends on effective governance

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Understanding global patterns of biodiversity change is crucial for conservation research, policies and practices. However, the lack of systematically collected data at a global level has limited our understanding of biodiversity changes and their local-scale drivers in most ecosystems. We address this challenge by focusing on wetlands, which are among the most biodiverse and productive environments[1,2] providing essential ecosystem services[3,4], but are also amongst the most seriously threatened ecosystems[3,5]. Using birds as an indicator taxon of wetland biodiversity, we model time-series abundance data for 461 waterbird species at 25,769 survey sites across the globe. We show that countries' effective governance is the strongest predictor of waterbird abundance changes as well as benefits of conservation efforts. Waterbirds are declining especially where governance is, on average, less effective, such as Western/Central Asia, sub-Saharan Africa and South America. Higher protected area coverage facilitates waterbird increases, but only in countries with more effective governance. Our findings highlight that sociopolitical instability can lead to biodiversity loss and also undermine the benefit of existing conservation efforts, such as the expansion of protected area coverage. Data deficiency in areas with less effective governance could cause an underestimation of the extent of biodiversity crisis. Alternative language abstracts are in Supplementary Information.

Quantifying global patterns of biodiversity change is essential for assessing anthropogenic impacts on biodiversity, conservation priorities and the effectiveness of conservation efforts[6,7]. It has, therefore, been identified as a research priority by major international bodies[8,9]. However, most taxa have serious gaps in the spatial extent and resolution covered by available data[10], meaning our current view of global biodiversity change is limited to coarse-resolution patterns[11] or data-rich countries[12] and protected areas[13]. This has impeded the identification of hotspots of abundance losses and analysis of local-scale drivers of change at the global scale (see Supplementary Discussion).

Wetlands cover more than 1,280 million hectares of coastal, inland and human-made habitats globally[3,14]. Despite being highly biologically diverse and productive[1,2], providing a range of crucial ecosystem functions and services[1,3,4], wetlands have been degraded and lost more than any other ecosystems[3]. Yet the lack of appropriate data has hampered assessments of changes in wetland biodiversity globally.

Here we address this knowledge gap by examining waterbirds as an indicator taxon for assessing the status of biodiversity in wetland ecosystems. Waterbirds have a long history of systematic monitoring, providing a global dataset on abundance changes with unprecedented spatial extent and resolution[15]. Modelling the global data for waterbirds enabled us to test two fundamental questions that are rarely explored together: (i) where are global changes in species abundance concentrated? (ii) What explains changes in abundance at the community, species and population levels? For the second question we tested three types of hypothesised predictors: (i) anthropogenic impacts (represented by surface water change, economic and human population growth, agricultural expansion and climate change), (ii) conservation efforts and effectiveness (protected area coverage and governance), and (iii) biological characteristics of species (range size, migratory status and body size) (Extended Data Table 1). Our dataset included 2,463,403 count records in January/February for the past three decades on 461 waterbird species at 25,769 survey sites throughout the globe (Extended Data

Fig. 1). Using a hierarchical Bayesian model we estimated the global distribution of changes in each species' abundance between 1990 and 2013 at 1°×1° resolution (Supplementary Data S1). We then summarised the changes at the three levels: mean changes in abundance across all waterbird species present in each grid cell (community-level changes), mean changes across all grid cells for each species (species-level changes) and changes in each grid cell for each species (population-level changes).

In most species, population-level changes in abundance varied markedly across geographical ranges. Some species that have increased in Europe showed severe declines in other regions (Fig. 1a-c) and *vice versa* (see Supplementary Data S1 for detail). Declines were especially pronounced in Africa for grebes, flamingos, pelicans, cormorants and shorebirds, in South America for shorebirds, storks, ibises, herons, waterfowl, cranes and rails, and in Western/Central Asia for waterfowl, cranes and rails (Fig. 1d-k).

We found major community-level abundance losses in areas where the biodiversity assessments have been limited, namely Western/Central Asia, sub-Saharan Africa and South America (Fig. 2a). On average, community-level declines were most severe in South America with 0.95 % annual decline, equating to a 21% decline over 25 years (Fig. 2b). The decline was also severe, but predominantly inland, in Western/Central Asia. In contrast, Europe has experienced community-level increases. Note, however, that even in regions showing community-level increases, some species show severe abundance declines (Supplementary Data S1). These geographic patterns largely reflected patterns in migrants (Extended Data Fig. 2a). Non-migrants were observed only in some regions and showed declines in South America and part of East and South/Southeast Asia (Extended Data Fig. 2b).

Of the eight explanatory variables representing anthropogenic impacts and conservation efforts and effectiveness (see Methods), the strongest predictor of community-level abundance changes was countries' governance, i.e. how effectively the authorities of a country are exercising rules and enforcement mechanisms (Fig. 3a). Waterbird communities declined most in countries with less effective governance (e.g., Western/Central Asia and South America) and increased where it was more effective (e.g., Europe and North America, Fig. 3b). Governance also had an interactive effect with protected area coverage (Fig. 3a); extensive protected area coverage was associated with community-level increases, but only in areas with more effective governance (Extended Data Fig. 3a). Community-level declines were also pronounced in areas with higher water loss (e.g., Western/Central Asia[16], Extended Data Fig. 3b).

To ascertain the causes of community-level changes, we partitioned the effects of explanatory variables into species-level (explaining variations in species-level changes between species) and population-level effects (explaining variations in population-level changes within species) for 293 species with sufficient data. Species-level changes were explained by the governance interaction with protected area coverage, gross domestic product (GDP) growth rates and body mass (Fig. 4a). Consistent with the community-level analysis, waterbird species with a higher coverage of protected areas increased more, but only in countries with more effective governance (Fig. 4c). Species in rapidly-growing economies and small-bodied species experienced greater declines (Fig. 4b, d). Governance was also the best predictor of population-level abundance changes, and most of the species with significant governance effects showed more population-level declines in areas with less effective governance (Extended Data Fig. 4 and Supplementary Discussion). These main conclusions were robust even when considering the correlation between governance and GDP per capita, and also to other sensitivity analyses (Extended Data Figs. 5-7, Supplementary Discussion).

Although our data are not spatially complete (Extended Data Fig. 1 and Supplementary Discussion), quantifying abundance changes within each species over large geographic areas uncovered novel hotspots of threats to bird species in wetland ecosystems. Earlier attempts did not identify biodiversity loss in, for example, Western/Central Asia, mainly because relevant data were unavailable (Supplementary Discussion). This spatial overlap between general data gaps and biodiversity loss could cause an underestimation of the ongoing biodiversity crisis, and the observation highlights the need for the global monitoring of species' abundances.

Our results highlight the importance of governance, presumably environmental aspects of governance (see Methods), in explaining global patterns in waterbird abundance changes. Local and regional studies have increasingly shown the environmental consequences of ineffective governance, such as species population declines[17], deforestation[18] and agricultural expansion[19]. Ineffective governance is often associated with the lack of environmental concerns, enforcement and investments[20-22], leading to habitat loss and degradation. For example, unsustainable water management and dam construction in Western/Central Asia have caused drastic losses in permanent water over the past 30 years[16]. As a result, in Iran even some wetlands designated as protected areas have dried out[23]. Wetlands in central Argentina lack legal protection or regulations on water use, and many have shown considerable losses[24]. Ineffective hunting regulations can also explain abundance losses under ineffective governance. Political instability can weaken legal enforcement, thereby promoting unsustainable, often illegal, killing even in protected areas[25]. Numerous waterbird species are under severe hunting pressures in Iran[23] and South America[26]. As wetland loss and hunting pressure are the main threats to most taxa, the hotspots of waterbird declines identified here merit urgent attention as areas of potential loss and degradation of wetland biodiversity, its functions and services.

This study also corroborates the benefits of protected areas in improving the conservation status of waterbird species, although these benefits are applicable only to those in countries with more effective governance. Our result gives a strong scientific basis at the global scale for the argument that effective governance is critical for protected areas in achieving their goals[27]. Protected area coverage can be high even in developing countries with less effective governance (Extended Data Fig. 8). These protected areas, however, were insufficient for maintaining stable waterbird populations since 1990. Supporting this argument in wealthier regions with more effective governance, such as Western Europe, waterbirds have responded positively to the establishment of refuges and stronger legal protection under measures governed by the EU Birds Directive[28].

Although the global coverage of protected areas continues to increase, our findings indicate that ineffective governance could undermine the benefits of such conservation efforts towards improving the status of global biodiversity. Levels of governance should be considered in the processes of identifying and prioritising areas of conservation importance, and distributing future efforts in research and funding. There is also an urgent need to measure, monitor, improve, and raise awareness about environmental governance globally.

Global conservation conventions and specific agreements and frameworks could mobilise international resources and expertise to strengthen effective governance. Governance is now recognised to be essential for economic growth, social development and the eradication of poverty and hunger[4]. Efforts to better understand and improve governance as well as to find means of improving the effectiveness of specific measures when governance is weak therefore provide common ground for conservationists, social scientists, policy makers and the public for achieving sustainable development.

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Supplementary Information is linked to the online version of the paper at www.nature.com/nature.

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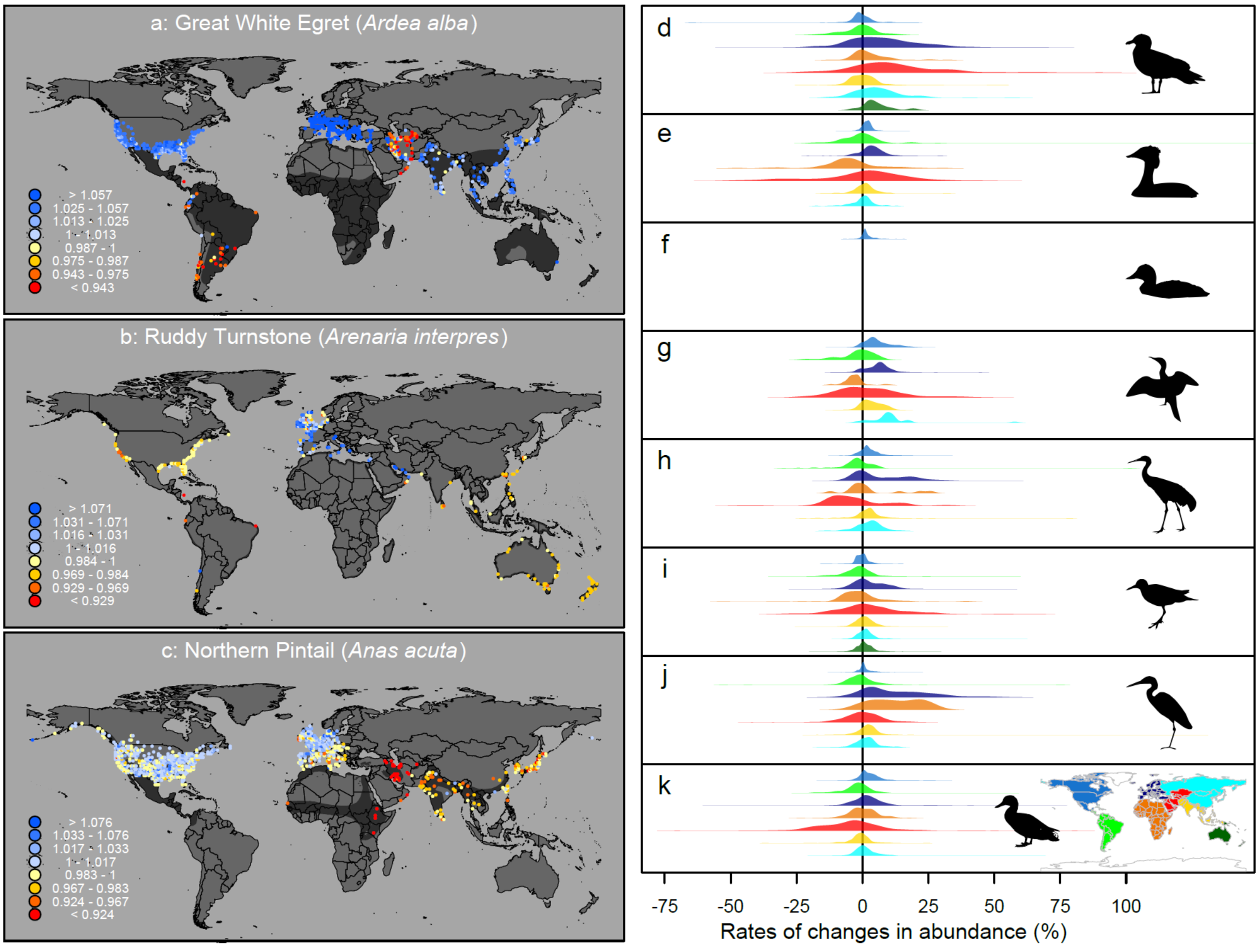

Fig. 1. Population-level changes in waterbird abundance in each 1° ×1° grid cell between 1990 and 2013. (a) *Ardea alba*, (b) *Arenaria interpres* and (c) *Anas acuta* as examples (declines in red and increases in blue). Species' geographical ranges are shaded. (d-k) Histograms show population-level changes for all species in each of the eight taxon at all grid cells in each region (regions shown in the inserted map). See Methods for the definition of each species group.

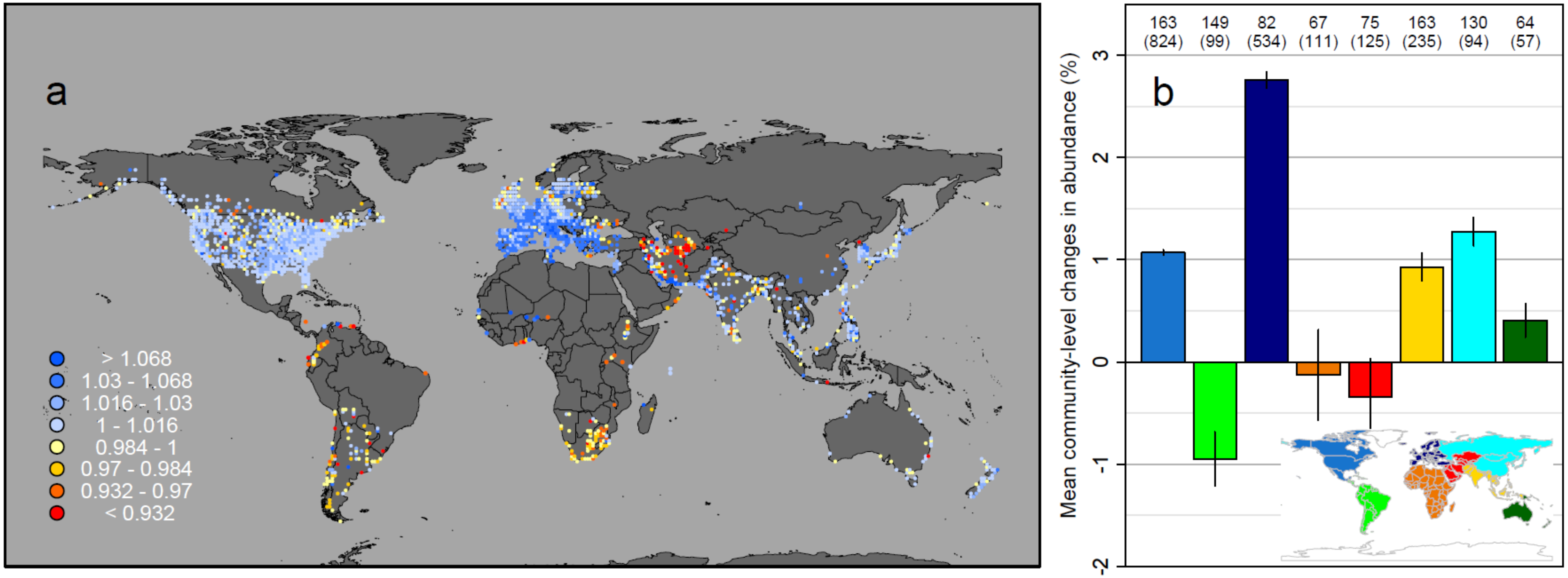

Fig. 2. Mean changes in abundance across 461 waterbird species (i.e., community-level changes) between 1990 and 2013. (a) Global distribution and (b) mean with 95% confidence intervals across all grid cells in each region (regions shown in the inserted map). The numbers of species (and grid cells in parentheses) observed are also shown above bars.

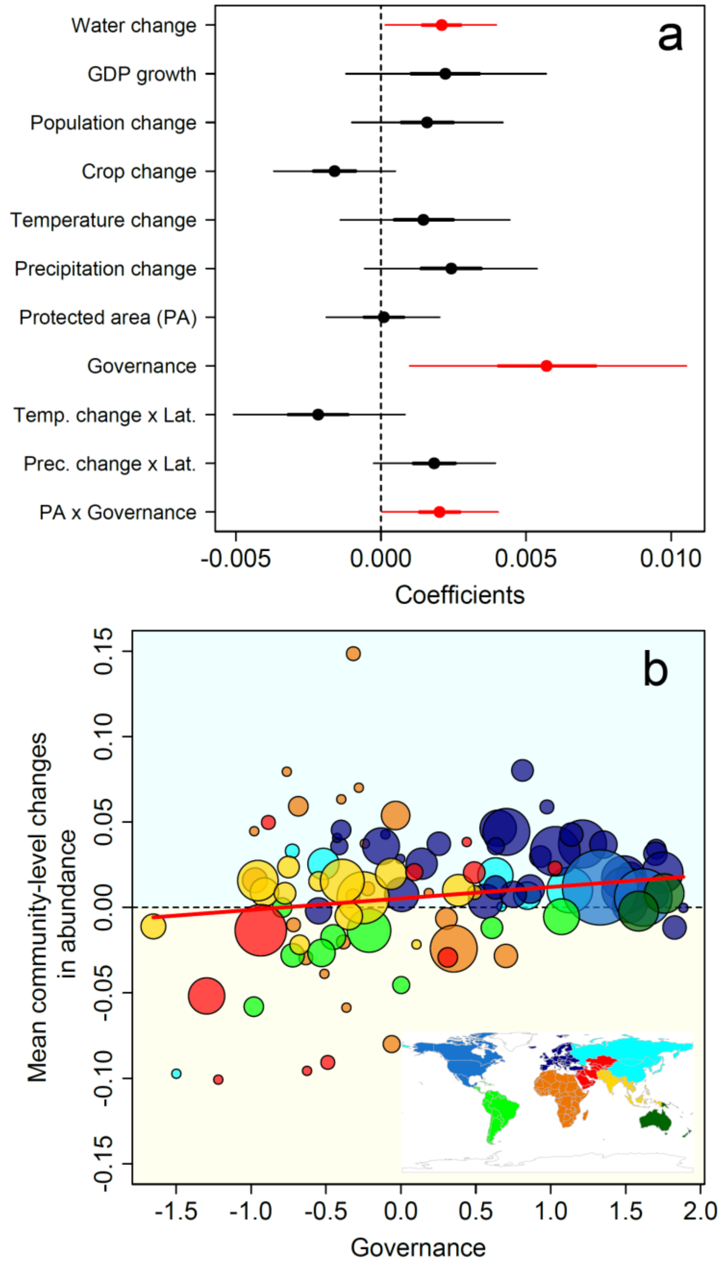

Fig. 3. Effects of predictors on community-level changes in waterbird abundance. (a) Estimated coefficients in the multivariate analysis (n=2,079). Posterior medians with 95% and 50% (thick lines) credible intervals are shown. Coefficients with 95% credible intervals not overlapping with zero are shown in red. The coefficients represent the effect size of the variables, which were standardised. (b) The relationship between community-level changes and countries' governance, where each circle represents a country and its size is related to the number of 1° ×1° grid cells with estimates, with the color indicating the region. The regression line is shown.

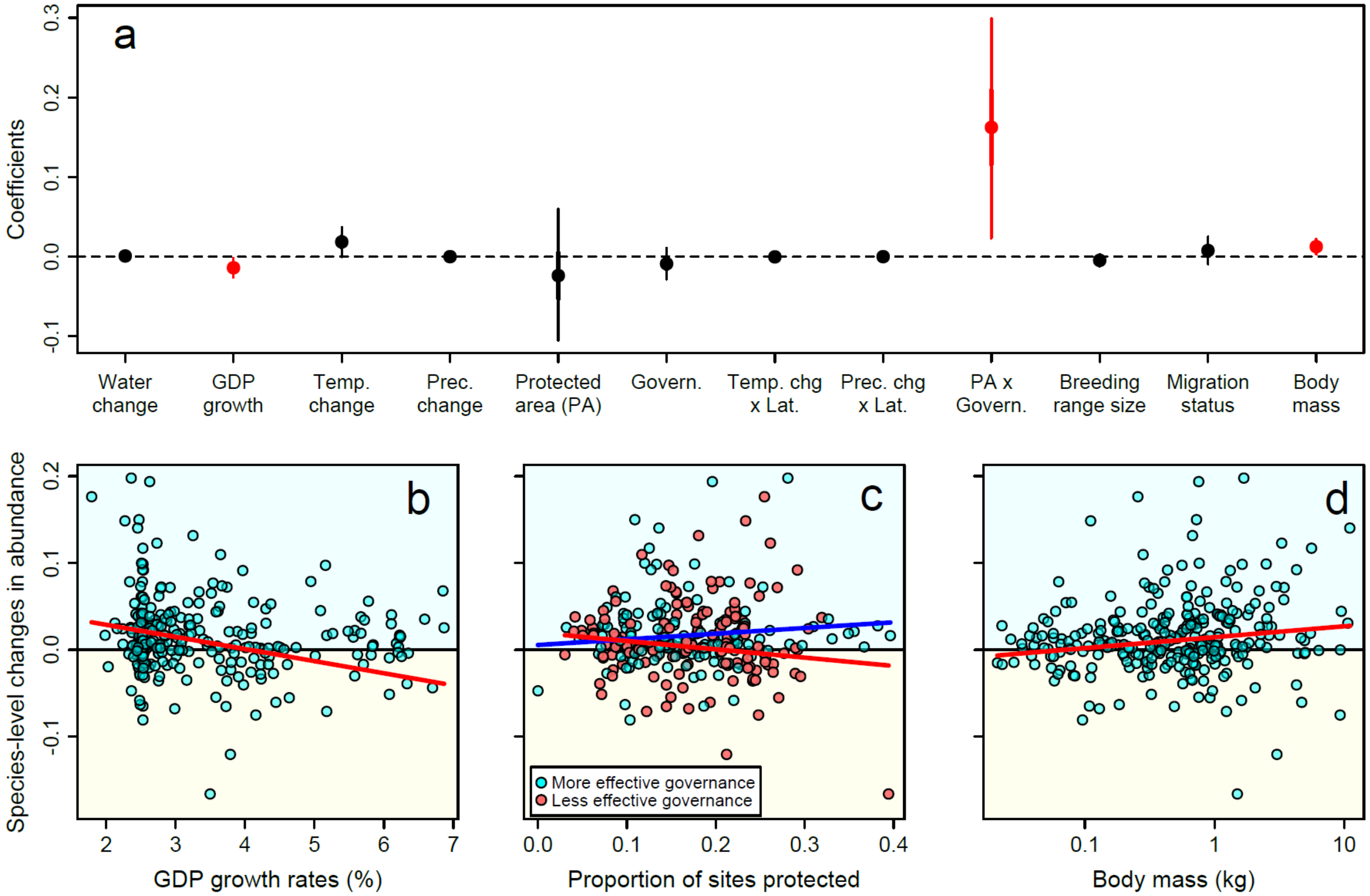

Fig. 4. Effects of predictors on species-level abundance changes in 293 waterbird species that were recorded in at least ten grid cells (see Supplementary Data S2 for details). (a) Estimated coefficients with 95% and 50% (thick lines) credible intervals (those not overlapping with zero shown in red) and the species-level relationship between abundance changes and (b) Gross Domestic Product (GDP) growth rates, (c) proportion of sites covered by protected areas, (d) body mass. Values and regression lines for species in areas with more (above median) and less (below median) effective governance are shown in blue and red, respectively, in (c).

Methods

Data

Waterbird count data

Data used in this study consisted of site-specific annual counts based on the International Waterbird Census (IWC) coordinated by Wetlands International[29] and the Christmas Bird Count (CBC) by the National Audubon Society in the USA[30].

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 further divided into four regional schemes corresponding to the major migratory flyways of the world: the African-Eurasian Waterbird Census (AEWC), Asian Waterbird Census (AWC), Caribbean Waterbird Census (CWC) and Neotropical Waterbird Census (NWC). We did not use data from the Caribbean Waterbird Census, as, having started in 2010, it only provides 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. Additional counts are also conducted in other months, particularly in July in the Southern Hemisphere, but we only used counts in January and February 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 (e.g., Ramsar sites, Important Bird Areas, national parks etc.). 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 km^2) 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. The time of survey on any given day depends on the type of survey sites: 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, which are defined as bird species that are ecologically dependent on wetlands[29]. 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 Methods 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[29,39] 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[73]. Each CBC consists of a tally of all bird species detected within 24.1 km in diameter, on a single day between 14th December and 5th January. The majority of circles (and most historical data) are from the US and Canada. Observers join groups that survey subunits of the circle during the course of 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 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.

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 within each species[31]. As data based on the Neotropical Waterbird Census are only available after 1990, we only used post-1990 data for other regions as well. The latest records were in 2013. Although the data included 487 waterbird species, we excluded species with 20 or fewer records from the analyses, and this has resulted in 461 species being analysed in this study (see Supplementary Data S2 for the full list of species). For the IWC data, we generated zero counts using an established approach[31]. In this approach, we first established 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 (e.g., 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.

When visualising the estimated abundance changes (e.g., Figs. 2b and 3b), the North and South American regions correspond to the regions covered by the CBC and NWC, respectively. The regions covered by the AEWC and AWC were further divided into a total of six regions based on socio-economic and ecological differences: Europe, Africa and Western/Central Asia (AEWC), and South/Southeast Asia, East Asia and Russia, and Oceania (AWC).

Explanatory variables

To explain variations in waterbird abundance changes over space and species, we first set up multiple hypotheses based on earlier studies and identified explanatory variables that represent those hypotheses (Extended Data Table 1). We aggregated all the explanatory variables but those on species characteristics to the same 1°×1° grid cells.

As measures of governance we used the Worldwide Governance Indicators, which summarise six broad dimensions of governance: Voice and Accountability, Political Stability and Absence of Violence, Government Effectiveness, Regulatory Quality, Rule of Law, and Control of Corruption[32]. A study of six South American countries[19] found that pro-environmental behaviours are associated with environmental aspects of governance rather than conventional dimensions of governance represented by the Worldwide Governance Indicators. At the global scale, however, the mean of the Worldwide Governance Indicators was strongly correlated with the Environmental Performance Index (EPI)[33], one of the indicators of environmental governance used in the study[19] ($r = 0.71$, $n = 180$). This indicates that the Worldwide Governance Indicators are also a good predictor of environmental aspects of governance at the global scale. Further, the EPI consists of multiple indicators, some of which are directly related to our measures of conservation efforts, such as terrestrial protected areas and species protection. We thus decided not to use the EPI in our analysis, as using it together with the coverage of protected areas in our analysis could result in redundancies.

In the World Database on Protected Areas, not every protected area has information on designation years. Thus we calculated the proportion of sites located within any protected area, assuming that it also reflects the proportion of sites covered by protected areas designated at least before 2013 (the latest survey year of count data used in this study). To examine the sensitivity of our conclusions to this assumption, we also calculated, as the most conservative approach, the proportion of sites covered only by protected areas that are known to have been designated before 1990 (the oldest survey year), and conducted the same analyses using the variable and presented the results in Extended Data Fig. 5 and Supplementary Discussion. When assessing the effectiveness of protected areas, confounding factors can mask or mimic the impacts of protected areas. We thus controlled for effects of potential drivers of abundance changes (listed in Extended Data Table 1) by including them, together with protected area coverage, in the same multivariate models.

Based on the Birdlife Data Zone (http://datazone.birdlife.org/home), the migratory status of the 461 species analysed in this study falls into four categories: full migrant, altitudinal migrant, nomadic and not a migrant. In this study we defined species categorised as full migrant or altitudinal migrant as migrants.

Other data

We derived information on generation length (in years) from the BirdLife Data Zone and the Red List category by the International Union for Conservation of Nature from the BirdLife Checklist of the Birds of the World[34] for each species. Generation length was not available in five species, for which we used the mean values across all species in the same genus. We used generation length as well as the bird species distribution maps of the world[35] for the visualisation of results (see the legend of Supplementary Data S1 for more detail). Species groups used in Fig. 1 are based on the IOC World Bird List[36]: coursers, gulls, terns and auks (Alcidae, Glareolidae, Laridae and Stercorariidae), grebes and flamingos (Phoenicopteridae and Podicipedidae), loons and petrels (Gaviidae and Procellariidae), pelicans, boobies and cormorants (Anhingidae, Fregatidae, Pelecanidae, Phalacrocoracidae and Sulidae), rails and cranes (Aramidae, Gruidae and Rallidae), shorebirds (Burhinidae, Charadriidae, Dromadidae, Haematopodidae, Ibidorhynchidae, Jacanidae, Recurvirostridae, Rostratulidae and

Scolopacidae), storks, ibises and herons (Ardeidae, Ciconiidae and Threskiornithidae), and waterfowl (Anatidae and Anhimidae).

Statistical Analyses

Model for quantifying abundance changes

To account for missing values, large observation errors and spatial structure in the data, we used a hierarchical Bayesian spatial model and quantified population-level changes in the abundance of each species within each 1°×1° grid cell. This model is an extension of the model developed and used to quantify waterbird abundance changes in earlier studies[37,38], and based on the site effect for site i, overall year effect for year t and the cell-specific year effect for grid cell j and year t. The overall year effect β_t is assumed to be affected by the year effect in the previous two years:

$$\beta_t \sim Normal(\beta_{t-1} + r(\beta_{t-1} - \beta_{t-2}), \sigma_o^2\ ). \qquad (1)$$

Here $\sigma_o{}^2$ is the variance of the overall year effect, r ranges from 0 to 1 and determined the smoothness of the estimated curve: with $r = 0$, the overall year effect is modelled as a simple random-walk process, while other values lead to a correlated random walk with different degrees of smoothness (a larger r causes a more smoothed curve). The cell-specific year effect $\beta_{j(i),t}$ is drawn from a normal distribution with mean β_t is as follows:

$$\beta_{j(i),t} \sim Normal(\beta_t, \sigma_\beta^2\ ). \qquad (2)$$

Including the variance in the year effect $\sigma_\beta{}^2$ allows the model to account for variations in trends of population counts among grid cells. $j(i)$ indicates that grid cell j includes site i. Assuming the same population trend across all sites within each grid cell, the mean count $\mu_{i,t}$

in site i in grid cell j and year t is modelled with the cell-specific year effect $\beta_{j(i),t}$, the site effect α_i, the spatially correlated random effect $\gamma_{j(i)}$ and the overdispersion effect $\delta_{i,t}$:

$$\log(\mu_{i,t}) = \alpha_i + \beta_{j(i),t} + \gamma_{j(i)} + \delta_{i,t}. \tag{3}$$

Here, α_i and $\delta_{i,t}$ are drawn from a mean zero normal distribution with variance σ_α^2 and σ_δ^2, respectively. $\gamma_{j(i)}$ is drawn from an intrinsic Gaussian conditional autoregressive (CAR) prior distribution:

$$\gamma_{j(i)}|\gamma_k \sim Normal(\frac{\sum_{j\neq k} w_{j,k}\gamma_k}{n_j}, \frac{\sigma_\gamma^2}{n_j}), \tag{4}$$

where $w_{j,k} = 1$ if grid cells j and k are neighbors, and 0 otherwise. n_j is the total number of neighbors of grid cell j and neighbors here are defined as those grid cells directly adjacent, including those diagonal. σ_γ^2 controls the amount of variation between the random effects. The observed count $y_{i,t}$ in site i and year t is assumed to derive from a Poisson distribution with mean $\mu_{i,t}$.

We assumed constant survey efforts over time in the IWC, as regular, standardised surveys (constant methods, efforts and timing) are highly encouraged[39] (also see Supplementary Discussion). However, survey efforts in the CBC are known to vary through time. Thus using the total number of survey hours per count as the measure of survey efforts, we explicitly accounted for the effort effect for the CBC data following[40]:

$$\log(\mu_{i,t}) = \alpha_i + \beta_{j(i),t} + \gamma_{j(i)} + \delta_{i,t} + \frac{B(\left(\frac{\zeta_{i,t}}{\bar{\zeta}}\right)^p - 1)}{p}. \tag{5}$$

Here $\zeta_{i,t}$ is the total number of survey hours per count and $\bar{\zeta}$ is the mean value of $\zeta_{i,t}$. B and p are parameters determining a range of relationships between effort and the number of birds counted[40]. To test if accounting for survey efforts can change the conclusions of this paper, we also applied the model without the effort effect to the CBC data and compared the estimated rate of abundance change within each grid cell between the models for each of the 159 species with more than two grid cells. The estimated spatial patterns in abundance changes by the two models were highly correlated (median Pearson's r = 0.99, minimum r = 0.88), indicating the validity of the model without the effort effect used for the IWC data. Further discussions on the potential effects of temporal changes in survey efforts are provided in Supplementary Discussion.

We applied the models to count data of each species at the regional population level. For example, count data on Eurasian wigeon *Mareca penelope* are separately compiled as five different populations: three (northwest European, Black Sea/Mediterranean, and southwest Asian/northeast African) in the African-Eurasian Waterbird Census, one in the Asian Waterbird Census, and one in the CBC. In this case, we applied the models separately to each of the five populations. As the result, we analysed 775 regional populations of 461 species (see Supplementary Data S2 for the full list of species). For 38 regional populations where no grid cells with count records were adjacent to each other, we simply dropped the spatially correlated random effect $\gamma_{j(i)}$ from equations (3) and (5). For 32 regional populations with only one grid cell that includes more than one survey site, we dropped $\gamma_{j(i)}$ and also replaced the cell-specific year effect $\beta_{j(i),t}$ with the overall year effect β_t. For 22 regional populations with only one survey site, we applied a generalised linear model with a Poisson distribution, using observed counts as the response variable and years as the explanatory variable, and used the estimated slope as the rate of abundance change.

Using only grid cells with, on average, four or more non-zero records per site, we fitted the models to the data with the Markov chain Monte Carlo (MCMC) method in WinBUGS 1.4.3[41] and the R2WinBUGS package[42] in R 3.3.2[43]. Prior distributions of parameters were set as non-informatively as possible, so as to produce estimates similar to those generated by a maximum likelihood method. We used Gamma distributions with mean of 1 and variance of 100 for the inverses of σ_o^2, σ_β^2, σ_α^2 and σ_δ^2 and σ_γ^2, normal distributions with mean of 0 and variance of 100 for β_1, β_2 and B, a beta distribution with mean of 0.5 and variance of 0.083 ($\alpha = \beta = 1$), which is a uniform distribution, for r, and a uniform distribution on the interval [-4, 4] for p following an earlier study[44]. Each MCMC algorithm was initially run with three chains with different initial values for 300,000 iterations with the first 200,000 discarded as burn-in and the remainder thinned to one in every 20 iterations to save storage space. Model convergence was checked with R-hat values[45]. If the models did not converge with the initial conditions, we increased iterations up to 5,000,000 (with the first 1,000,000 discarded and the remainder thinned to one in every 800). We decided to remove grid cells where parameter estimates did not converge even with the increased iterations, although the number of removed cells was very small (median 2.5 grid cells in 20 out of the 775 (2.6%) regional populations).

To estimate the population-level change in abundance (since 1990) of each species in a particular grid cell, we first regressed the estimates of the cell-specific year effect $\beta_{j(i),t}$ in every posterior sample against years. To account for uncertainty in slope estimates in this regression, we derived for every posterior sample a slope estimate from a normal distribution with the mean of the estimated mean slope and standard deviation of the standard error of the slope. We then calculated the mean, median, variance and 2.5 and 97.5 percentiles of the estimated slopes from all posterior samples. We aggregated all estimates by species based on the definition by the BirdLife International[34]. We used the mean and 2.5 and 97.5 percentiles of the estimated slopes for creating species-level maps (Fig. 1a-c and Supplementary Data S1). To calculate community-level changes in abundance (Fig. 2a) and those for different migratory status (Extended Data Fig. 2), we used the mean slopes across all species, or all species in a particular group, observed in each grid cell, weighted by the inverse of slope variance in each species to account for uncertainties. To further calculate mean community-level changes in each region (Fig. 2b), we used the mean of the community-level changes across all grid cells in each region, weighted by the inverse of associated variance.

Driver analysis

We first tested correlations among the nine spatial explanatory variables in 2,079 1º×1º grid cells with abundance change estimates (Extended Data Table 2). GDP per capita and governance showed a relatively strong correlation (r = 0.76). Thus considering that GDP growth rates are another measure of economic growth, we decided to exclude GDP per capita from the main analyses but instead test its effect in a separate set of analyses where governance was replaced with GDP per capita. Here considering the hypothesised non-linear relationship between GDP per capita and species abundance changes (Extended Data Table 1), we used linear and quadratic terms of GDP per capita. We presented the results with GDP per capita in Extended Data Fig. 5 and Supplementary Discussion.

To identify factors associated with waterbird abundance changes at the community, species, and population levels, we conducted two types of analyses, both of which were implemented with WinBUGS 1.4.3 and the R2WinBUGS package in R 3.3.2.

In the first analysis, where the response variable was community-level changes in abundance within each grid cell (Fig. 2a), we used a CAR model:

$$\mu_i = \alpha + \boldsymbol{\beta X_i} + \gamma_i, \tag{6}$$

where the community-level change r_i in cell i was assumed to derive from a normal distribution with mean μ_i and variance σ_μ^2. $\boldsymbol{\beta}$ represents the vector of regression coefficients and $\boldsymbol{X_i}$ that of explanatory variables. Based on the hypotheses shown in Extended Data Table 1, we used eight explanatory variables in each grid cell: surface water change, GDP growth rates, changes in human population density, crop area, temperature, and precipitation, protected area coverage, and governance. We also tested three interaction terms between latitudes and temperature change and also latitudes and precipitation change, as population responses to temperature and precipitation can vary along the latitudes[46], and governance and protected area coverage, as governance can affect the effectiveness of conservation efforts[47]. All explanatory variables were standardised before model fitting. γ_i is the spatially-correlated random effect using an intrinsic Gaussian CAR prior distribution with variance σ_γ^2, as described in equation (4). Again prior distributions of parameters were set as non-informatively as possible; we used Gamma distributions with mean of 1 and variance of 1000 for the inverse of σ_μ^2 and σ_γ^2, normal distributions with mean of 0 and variance of 1000 for β_j, and an improper uniform distribution (i.e., a uniform distribution on an infinite interval) for the intercept α as recommended[48]. Each MCMC algorithm was run with three chains with different initial values for 1,000,000 iterations with the first 500,000 discarded as burn-in and the remainder thinned to one in every 100 iterations to save storage space. Model convergence was checked with R-hat values.

Next for 293 species observed at ten or more grid cells, we adopted the within-subject centring approach[49] under a hierarchical modelling framework to explicitly distinguish species-level effects (explaining variations in species-level abundance changes between species) and population-level effects (explaining variations in population-level abundance changes within species) of explanatory variables. In this model the species effect μ_s, representing the species-level change in abundance of 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:

$$\nu_s = \alpha + \sum_{k=1}^{9} \beta_{Bk} \bar{x}_{k,s} + \sum_{k=10}^{12} \beta_{Bk} z_{k,s} + \eta_s, \qquad (7)$$

where α is the global intercept and β_{Bk} represents the species-level effect. $\bar{x}_{k,s}$ is the mean of spatial explanatory variable k across all grid cells where species s was recorded. Note that even if the estimated species-level abundance changes are biased due to geographical biases in available grid cells, they are correctly matched up with $\bar{x}_{k,s}$, as the calculation of both variables is based on the same set of grid cells. The spatial explanatory variables used were based on the hypotheses in Extended Data Table 1, but we dropped changes in human population density and crop area, as these were least influential in the analysis of community-level population changes and also in a preliminary analysis of this model. Thus we used the remaining six explanatory variables (surface water change, GDP growth rates, changes in temperature and precipitation, protected area coverage, and governance) and the same three interaction terms as in the community-level analysis. $z_{k,s}$ represents three explanatory variables on species characteristics described in Extended Data Table 1. η_s is a random term that accounts for phylogenetic dependence among species and is drawn from a multivariate normal distribution[50,51]:

$$\eta_s \sim MVN(\mathbf{0},\ \delta^2 \Sigma_\lambda), \tag{8}$$

$$\Sigma_\lambda \ = \ \lambda\Sigma + (1-\lambda)\mathbf{I} \tag{9}$$

where Σ is a scaled variance-covariance matrix calculated from an ultrametric phylogenetic tree. By scaling Σ to a height of one, we can interpret δ^2 as the residual variance[50]. For the strength of phylogenetic signal to vary, we also incorporated Pagel's λ[52,53] into the matrix in equation (9) with the identity matrix **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[50,53]. To incorporate uncertainties[54] in phylogenetic trees in the calculation of Σ, we used a sample of 100 trees from a comprehensive avian phylogeny[55] as the prior distribution for our analysis[50]. More specifically, one of the 100 trees was randomly drawn in each iteration and used for the calculation of Σ.

The population-level change in abundance $r_{s,i}$ 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:

$$\mu_{s,i} = \mu_s + \textstyle\sum_{j=1}^{6} \beta_{W_{s,j}}(x_{j,i} - \bar{x}_{j,s}) + \gamma_{s,i}. \tag{10}$$

Here $\beta_{Ws,j}$ represents the population-level effect for species s, explaining within-species variations in population-level abundance changes ($\mu_{s,i} - \mu_s$) by within-species variations in explanatory variables $(x_{j,i} - \bar{x}_{j,s})$, where $x_{j,i}$ is explanatory variable j in grid cell i and $\bar{x}_{j,s}$ is the mean of x_j for species s. The species-specific $\beta_{Ws,j}$ is the random effect each governed by hyper-parameters as:

$$\beta_{W_{s,j}} \sim Normal(h\beta_{W_j}, \sigma^2_{\beta_{W_j}}). \quad (11)$$

For population-level effects we used the same six explanatory variables (surface water change, GDP growth rates, changes in temperature and precipitation changes, protected area coverage and governance). $\gamma_{s,i}$ accounts for spatial autocorrelation within each species and is drawn from an intrinsic Gaussian CAR prior distribution with variance $\sigma^2_{\gamma_s}$, as in equation (4).

As non-informative prior distributions, we used a Gamma distribution with mean of 1 and variance of 100 for σ_v^2, δ^2, σ_μ^2, $\sigma^2_{\beta_{W_j}}$ and $\sigma^2_{\gamma_s}$, a uniform distribution on the interval [0, 1] for λ, normal distributions with mean of 0 and variance of 100 for α, β_{Bk}, and $h\beta_{Wj}$. Each MCMC algorithm was run with three chains with different initial values for 10,000 iterations with the first 5,000 discarded as burn-in and the remainder thinned to one in every two 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[34,55], we combined two separate species defined in the BirdLife Checklist[34] 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*.

Data Availability

The waterbird count data used in this study are collated and managed by Wetlands International and the National Audubon Society, and available on request. All the data on explanatory variables are freely available as specified in Extended Data Table 1.

Code Availability

All the R and WinBUGS codes used for the analyses are available from the corresponding author upon request.

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Extended Data Table 1. Hypotheses and explanatory variables tested for explaining the patterns in waterbird abundance changes over space and species.

Hypotheses	Drivers	Descriptions	Explanatory variables used	Data sources
Anthropogenic impacts	Surface water	Surface water provides an essential habitat for most wetland-dependent species[1], thus its decline can threaten the status of waterbirds	Mean changes (%) in surface water occurrence between 1984-1999 and 2000-2015, within 1km from each survey site	Global Surface Water[16]
	Economic growth	Economic growth poses a threat to species through habitat loss and degradation but can also improve environmental quality at a high economic level[56].	Mean country-level GDP per capita between 1990 and 2010	World Bank*
			Mean country-level GDP growth rate (annual %) between 1990 and 2010	World Bank†
	Human population growth	High species extinction risk is associated with high human population density[57] and rapid human population growth[58].	Mean changes in human population density between 1990 and 2000	Population Density Grid v3[59]
	Agricultural expansion	Farming is the biggest source of threats to bird species[60].	Changes in crop area (croplands and cropland/natural vegetation mosaics) between 2001 and 2010	Collection 5 MODIS Global Land Cover Type product[61]
	Climate change	Climate change is a strong predictor of bird abundance changes[62].	Changes in mean Dec-Feb temperature between 1985-1990 and 2005-2010	CRU TS3.10 Dataset[63]
			Changes in mean Dec-Feb precipitation between 1985-1990 and 2005-2010	CRU TS3.10 Dataset[63]
Conservation efforts and effectiveness	Protected areas	Waterbird abundance increased more rapidly in protected than in unprotected wetlands[64,65].	Proportion of sites covered by protected areas	World Database on Protected Areas[66]
	Governance	Ineffective governance in a country is associated with species population declines[17].	Mean of six country-level Worldwide Governance Indicators between 1996 and 2010	World Bank‡
Species characteristics	Geographical range size	Species with small geographical range may be more susceptible to large-scale, stochastic threats[67].	Breeding/resident geographical range size (km^2)	Birdlife Data Zone§
	Migratory status	Migratory species can be affected by conditions at multiple locations, thus tend to show population declines[68,69].	Migrant or non-migrant	Birdlife Data Zone§
	Body size	Body size is a strong predictor of bird abundance changes[70] but its association with bird extinction risk can be both positive and negative, depending on threats to the species[71]	Body mass (g)	EltonTraits 1.0[72]

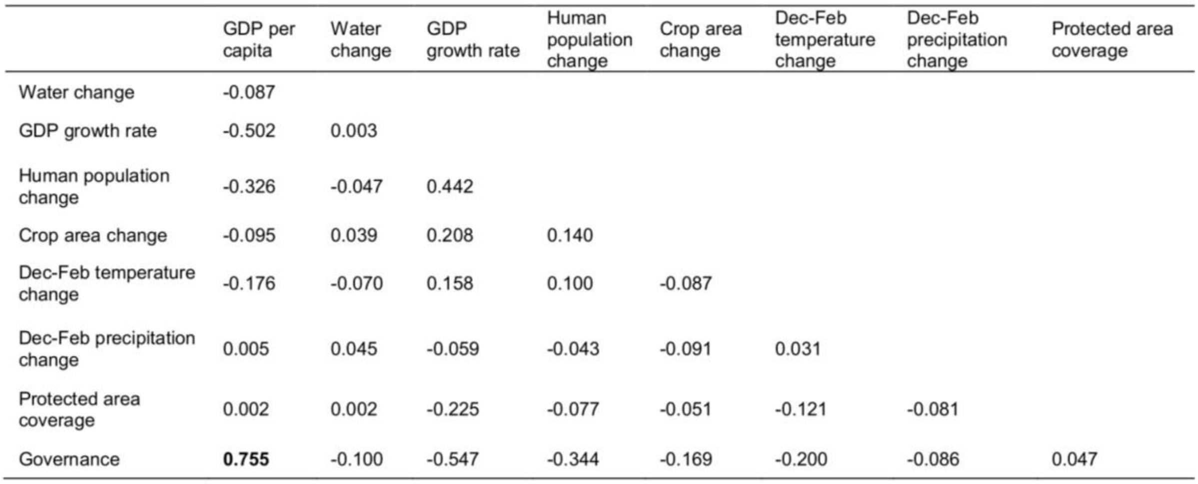
* http://data.worldbank.org/indicator/NY.GDP.PCAP.KD

† http://data.worldbank.org/indicator/NY.GDP.MKTP.KD.ZG

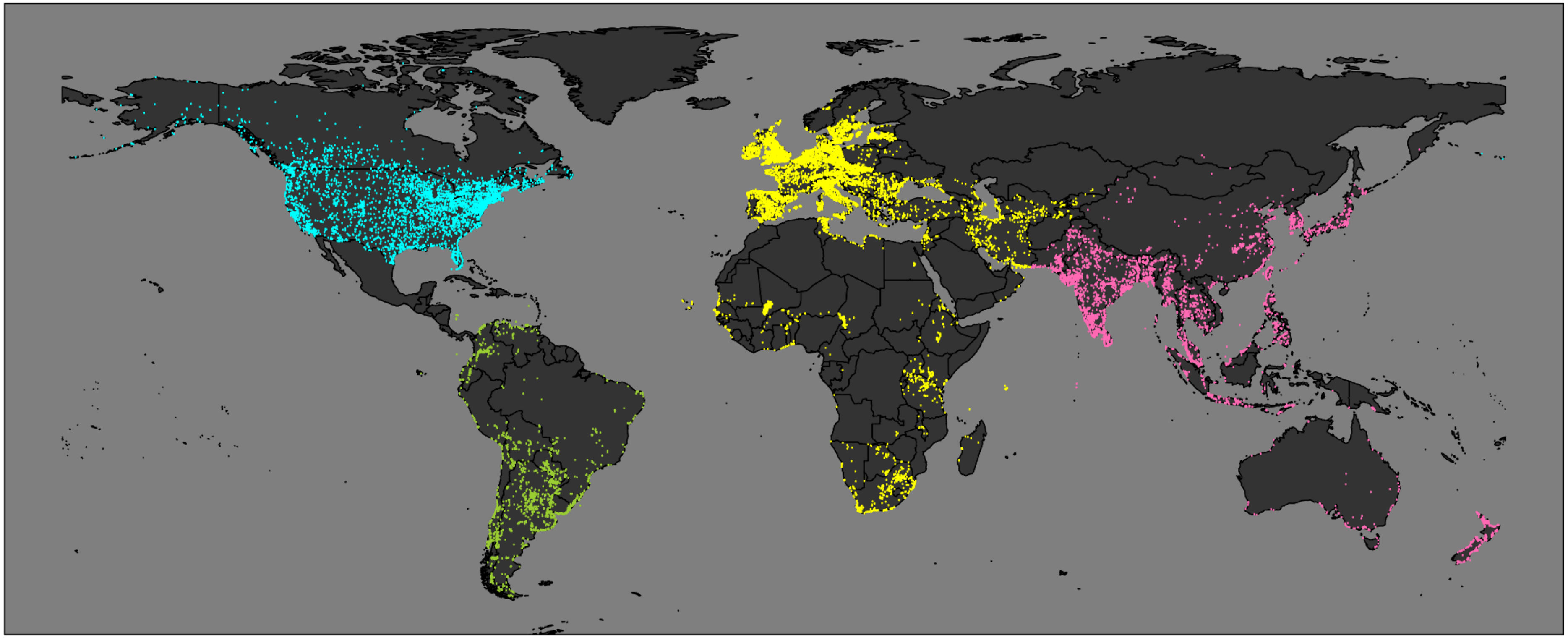
‡ http://data.worldbank.org/data-catalog/worldwide-governance-indicators

§ http://datazone.birdlife.org/home

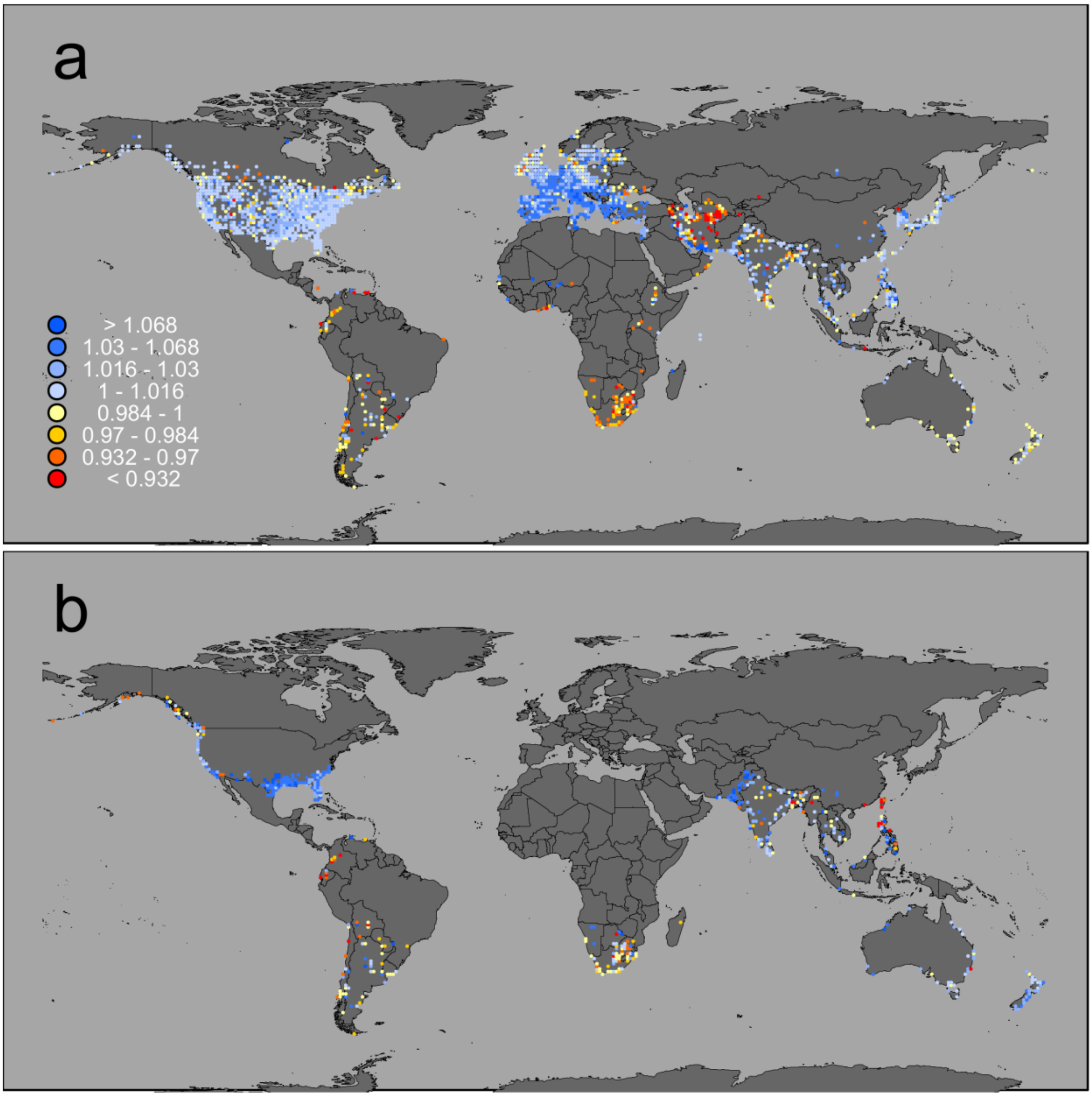
Extended Data Table 2. Correlation matrix (Spearman's rank correlation) of nine potential predictors of waterbird abundance changes (n=2,079). Gross domestic product (GDP) per capita is $\log_{10}$-transformed values. Strong correlation (|*r*| > 0.7) are shown in bold.



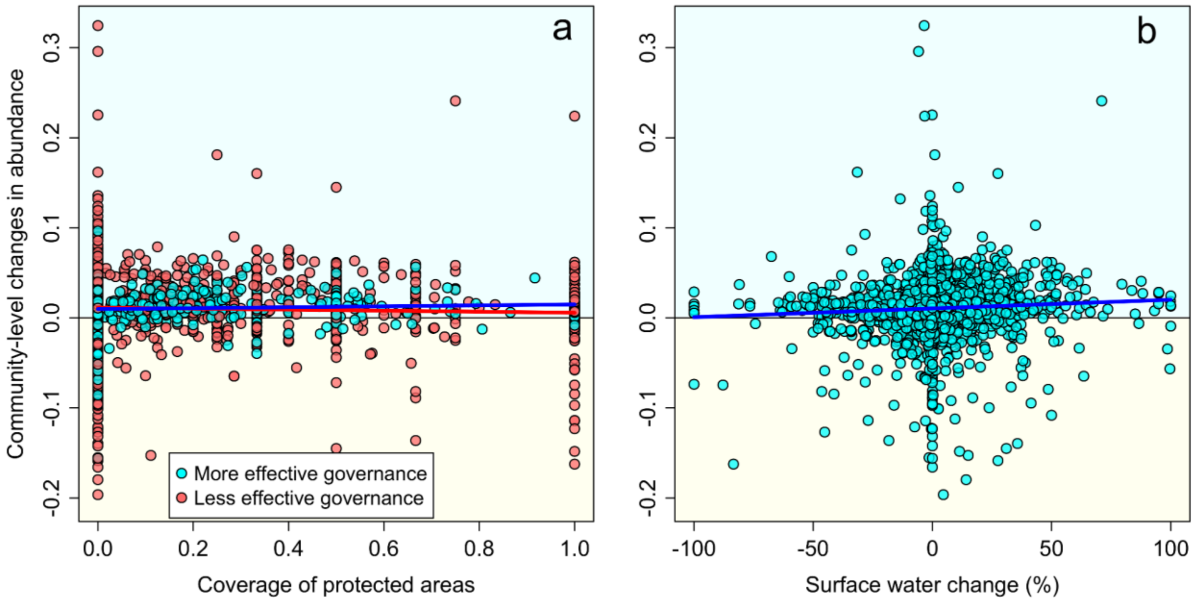
	GDP per capita	Water change	GDP growth rate	Human population change	Crop area change	Dec-Feb temperature change	Dec-Feb precipitation change	Protected area coverage
Water change	-0.087							
GDP growth rate	-0.502	0.003						
Human population change	-0.326	-0.047	0.442					
Crop area change	-0.095	0.039	0.208	0.140				
Dec-Feb temperature change	-0.176	-0.070	0.158	0.100	-0.087			
Dec-Feb precipitation change	0.005	0.045	-0.059	-0.043	-0.091	0.031		
Protected area coverage	0.002	0.002	-0.225	-0.077	-0.051	-0.121	-0.081	
Governance	**0.755**	-0.100	-0.547	-0.344	-0.169	-0.200	-0.086	0.047



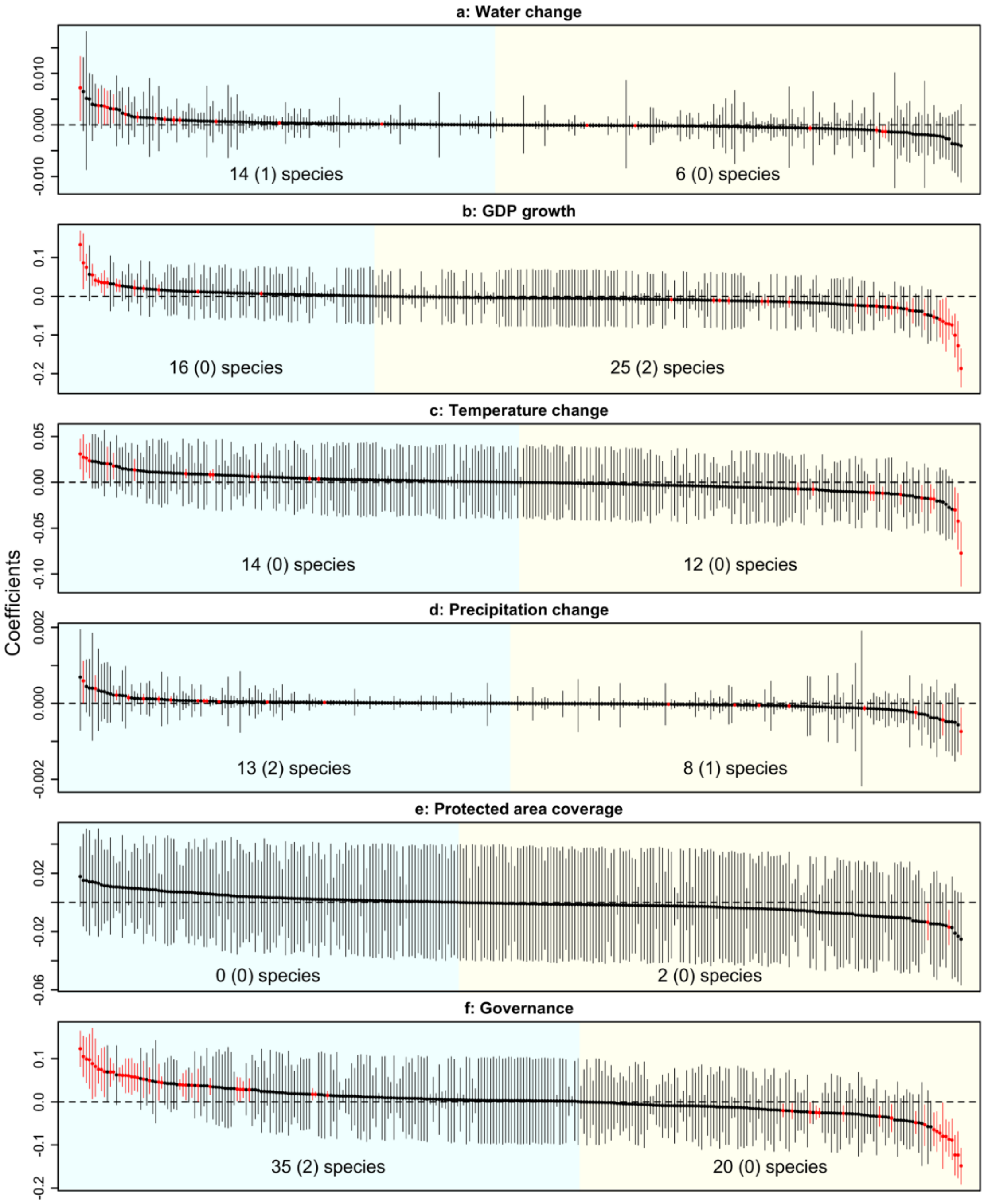
Extended Data Fig. 1. The distribution of all the 25,769 survey sites used in the analyses. Sites for the International Waterbird Census are shown in yellow (African-Eurasian Waterbird Census), pink (Asian Waterbird Census) and green (Neotropical Waterbird Census) and those for the Christmas Bird Count are in cyan.



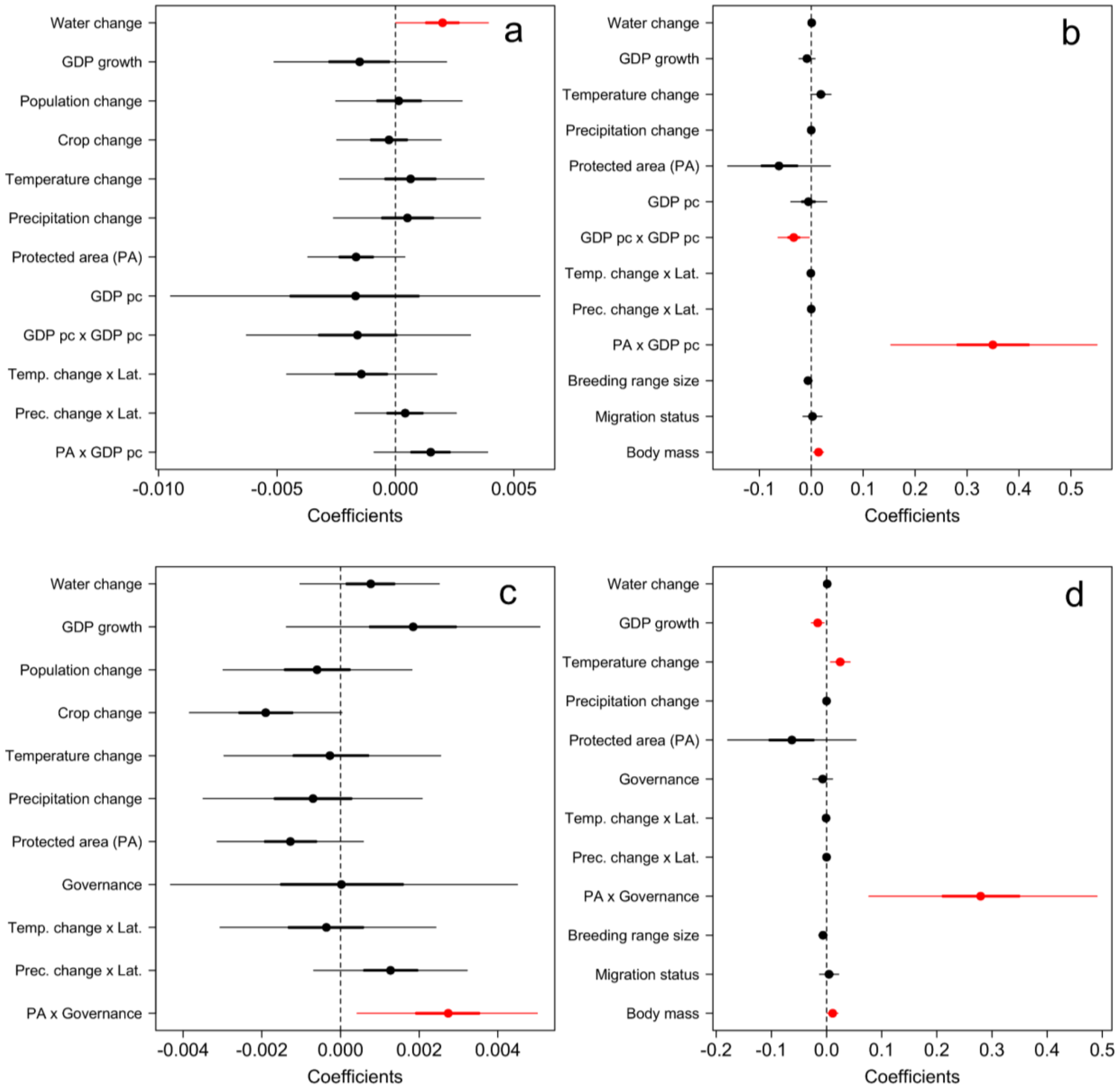
Extended Data Fig. 2. Global distribution of mean annual changes in abundance across (a) 373 migratory and (b) 88 non-migratory waterbird species (i.e., community-level changes). Migratory status of each species is from the BirdLife Data Zone (see Methods for more detail).



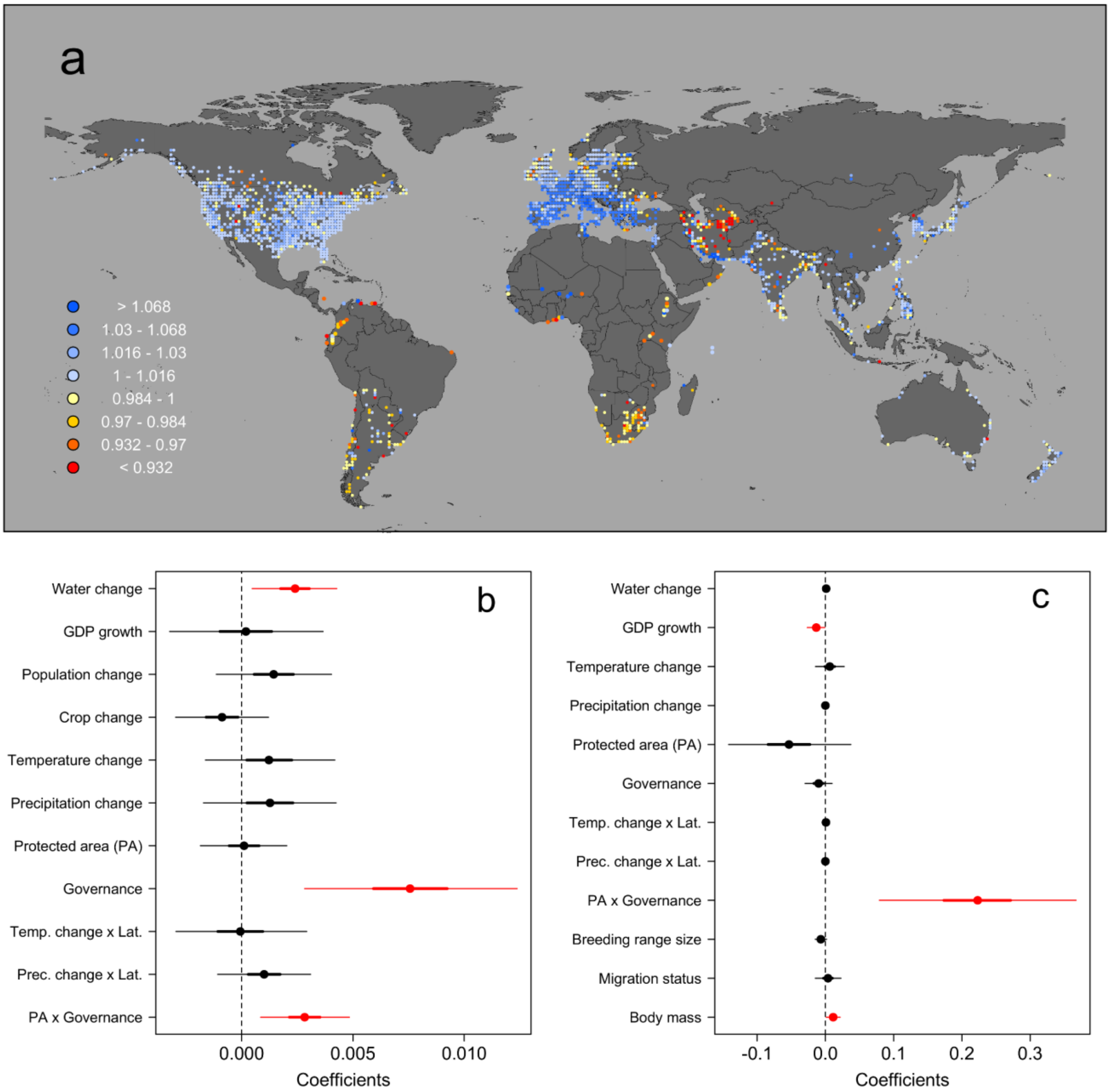
Extended Data Fig. 3. Relationships between community-level changes in abundance and (a) the proportion of sites covered by protected areas and (b) surface water change (n=2,079). Regression lines based on the estimated coefficients in Fig. 3a are also shown; values and regression lines for species in areas with more and less effective governance are shown in blue and red, respectively.



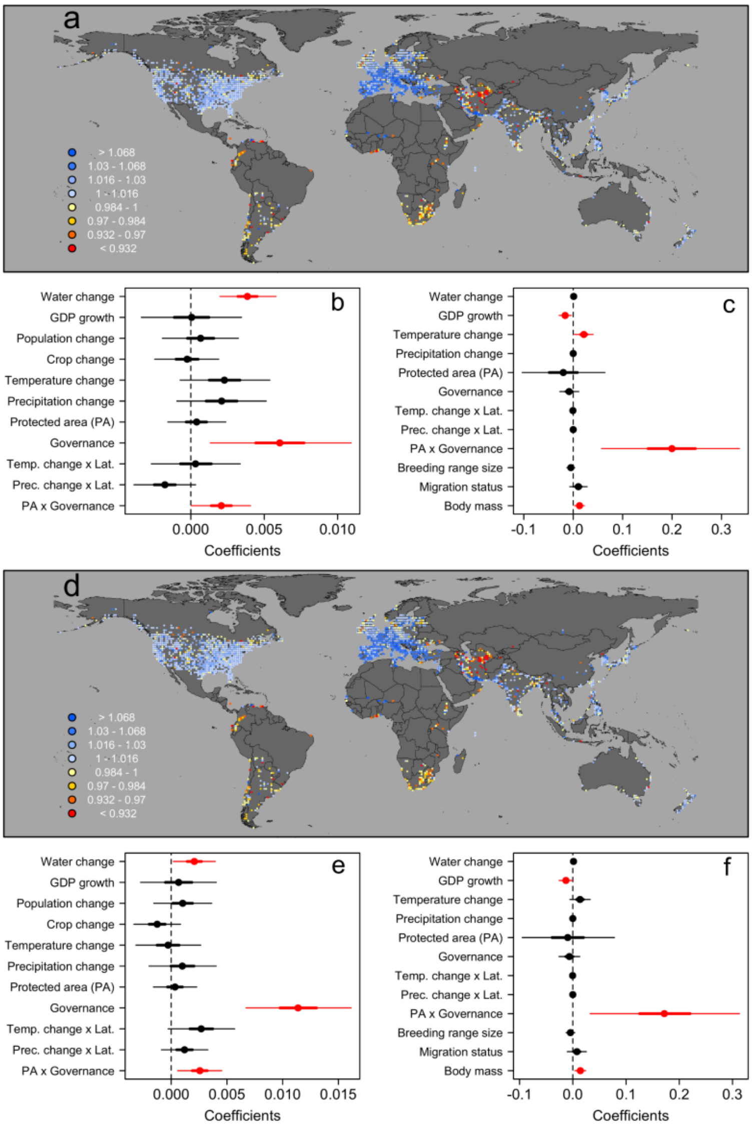
Extended Data Fig. 4. Effects of five hypothesised predictors (see Extended Data Table 1 for more detail) on population-level changes in abundance. In each panel, the medians and 95% credible intervals of the estimated coefficients for 293 species are shown in order of decreasing positive effect size from the left (those with 95% credible intervals not overlapping with zero shown in red). The numbers of species with significant positive and negative coefficients are also shown, with the number of non-migratory species in parentheses.



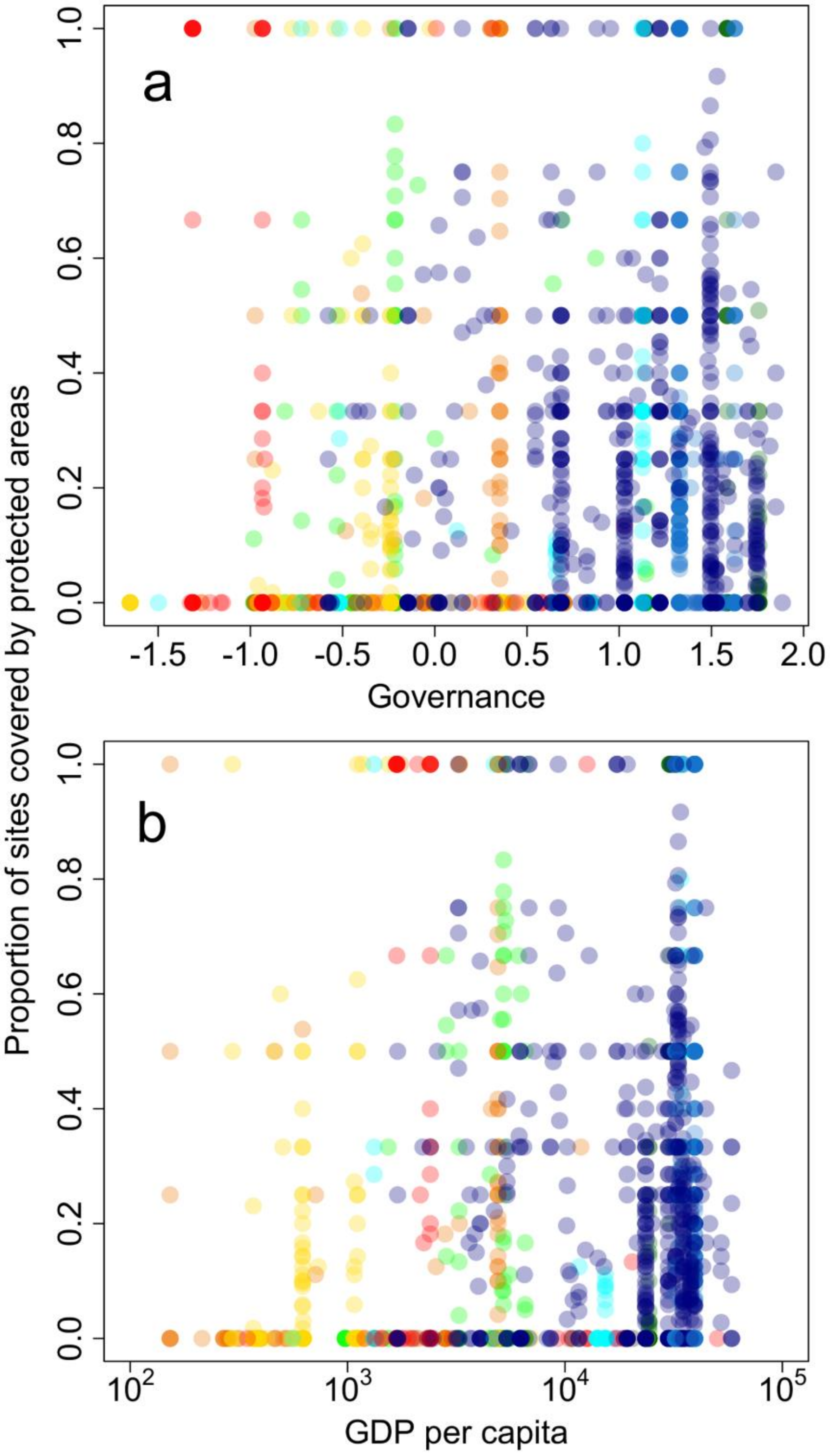
Extended Data Fig. 5. Sensitivity of results to the correlation between governance and gross domestic product (GDP) per capita and designation years of protected areas. Estimated coefficients in the multivariate analysis of (a) community-level (n=2,079) and (b) species-level changes in abundance (based on 293 species; see Supplementary Data S2 for the number of grid cells in each species), where governance was replaced with linear and quadratic terms of GDP per capita, and (c) community-level (n=2,079) and (d) species-level changes in abundance (based on 293 species; see Supplementary Data S2 for the number of grid cells in each species), where only protected areas known to have been designated before 1990 (the first survey year in our dataset) were used in the most conservative approach. Posterior medians with 95% and 50% (thick lines) credible intervals are shown. Coefficients with 95% credible intervals not overlapping with zero are shown in red.



Extended Data Fig. 6. Sensitivity of the results to the inclusion of seabird species. (a) Global distribution of mean annual changes in abundance across 447 waterbird species excluding the 14 seabird species between 1990 and 2013. Estimated coefficients in the multivariate analysis of (b) community-level (n=2,079) and (c) species-level changes in abundance, where the 14 seabird species were excluded (i.e., based on 447 species; see Supplementary Data S2 for the number of grid cells in each species). Posterior medians with 95% and 50% (thick lines) credible intervals are shown. Coefficients with 95% credible intervals not overlapping with zero are shown in red.



Extended Data Fig. 7. Sensitivity of the results to the choice of Christmas Bird Count (CBC) survey sites for the analyses. (a) Global distribution of mean annual changes in abundance across 461 waterbird species between 1990 and 2013 after excluding 41 CBC grid cells with neither landscape-scale wetland areas nor local-scale surface water occurrences (within 1km of all the survey sites included). Estimated coefficients in the multivariate analysis of (b) community-level (n=2,038) and (c) species-level changes in abundance (based on 293 species), where 41 CBC grid cells with neither landscape-scale wetland areas nor local-scale surface water occurrences (within 1km of all the survey sites) were excluded. (d) Global distribution of mean annual changes in abundance across 461 waterbird species between 1990 and 2013 after excluding eight CBC grid cells where the proportion of urban areas was over 0.3. Estimated coefficients in the multivariate analysis of (e) community-level (n=2,071) and (f) species-level changes in abundance (based on 293 species), where eight CBC grid cells with a proportion of urban areas of over 0.3 were excluded. Posterior medians with 95% and 50% (thick lines) credible intervals are shown. Coefficients with 95% credible intervals not overlapping with zero are shown in red.



Extended Data Fig. 8. Relationships between the proportion of sites covered by protected areas and (a) governance and (b) gross domestic product (GDP) per capita. Colors indicate regions: blue: North America, green: South America, navy: Europe, orange: Africa, red: Western/Central Asia, yellow: South/Southeast Asia, cyan: East Asia and Russia, and dark green: Oceania.