LETTER

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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, for most ecosystems, the lack of systematically collected data at a global level limits our understanding of biodiversity changes and their local-scale drivers. Here we address this challenge by focusing on wetlands, which are among the most biodiverse and productive of any environments[1,2] and which provide 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 the strongest predictor of changes in waterbird abundance, and of conservation efforts having beneficial effects, is the effective governance of a country. In areas in which governance is on average less effective, such as western and central Asia, sub-Saharan Africa and South America, waterbird declines are particularly pronounced; a higher protected area coverage of wetland environments facilitates waterbird increases, but only in countries with more effective governance. Our findings highlight that sociopolitical instability can lead to biodiversity loss and undermine the benefit of existing conservation efforts, such as the expansion of protected area coverage. Furthermore, data deficiencies in areas with less effective governance could lead to underestimations of the extent of the current biodiversity crisis.

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 biodiversity data[10], and our current view of global biodiversity change is therefore limited to coarse-resolution patterns[11], data-rich countries[12] or protected areas[13]. This has impeded the identification of hotspots of abundance loss, and the analysis of the effects of local-scale drivers on biodiversity change at the global scale (see Supplementary Discussion; also see Supplementary Information for the Abstract in different languages).

Globally, wetlands cover more than 1,280 million hectares of coastal, inland and human-made habitats[3,14]. Despite their high levels of biological diversity and productivity[1,2] and the crucial ecosystem functions and services they provide[1,3,4], wetlands have been degraded and lost at higher rates than any other ecosystem[3]. However, the lack of appropriate data has hampered assessments of changes in wetland biodiversity at a global scale.

Here we address this by examining waterbirds as an indicator taxon for assessing the status of biodiversity in wetland ecosystems. Waterbirds have a long history of systematic monitoring, and therefore present a global dataset of abundance changes with unusually high spatial extent and resolution[15]. Modelling the global data for waterbirds enabled us to test two fundamental questions that are rarely explored in tandem; we asked where global changes in species abundance have been concentrated and what might explain changes in abundance at community, species and population levels. For the second question, we tested hypothesized predictors that were categorized into three groups: (i) anthropogenic effects (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 comprised 2,463,403 count records, covering the months of January–February for the past three decades and recording 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 the abundance of each species between 1990 and 2013 at 1° × 1° spatial resolution (Supplementary Data 1). We then summarized the changes at 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 abundance in Europe showed severe declines in other regions (Fig. 1a–c) and vice versa (see Supplementary Data 1). 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 and central Asia for waterfowl, cranes and rails (Fig. 1d–k).

We found major community-level abundance losses in areas in which biodiversity assessments have been limited, namely western and central Asia, sub-Saharan Africa and South America (Fig. 2a). On average, community-level declines were most severe in South America, which has experienced a 0.95% annual decline that equates to a 21% total decline over 25 years (Fig. 2b). The declines were also severe in western and central Asia, but predominantly occurred inland rather than in coastal regions. By contrast, Europe has experienced community-level increases in waterbird abundance, though even in regions that experienced these increases some species showed severe abundance declines (Supplementary Data 1). These geographic patterns predominantly reflected patterns in migrant species (Extended Data Fig. 2a), as non-migrants were observed only in some regions; non-migrants showed community-level declines in South America and parts of east Asia, south Asia and southeast Asia (Extended Data Fig. 2b).

Of the eight explanatory variables representing anthropogenic impacts and conservation efforts and effectiveness (see Methods),

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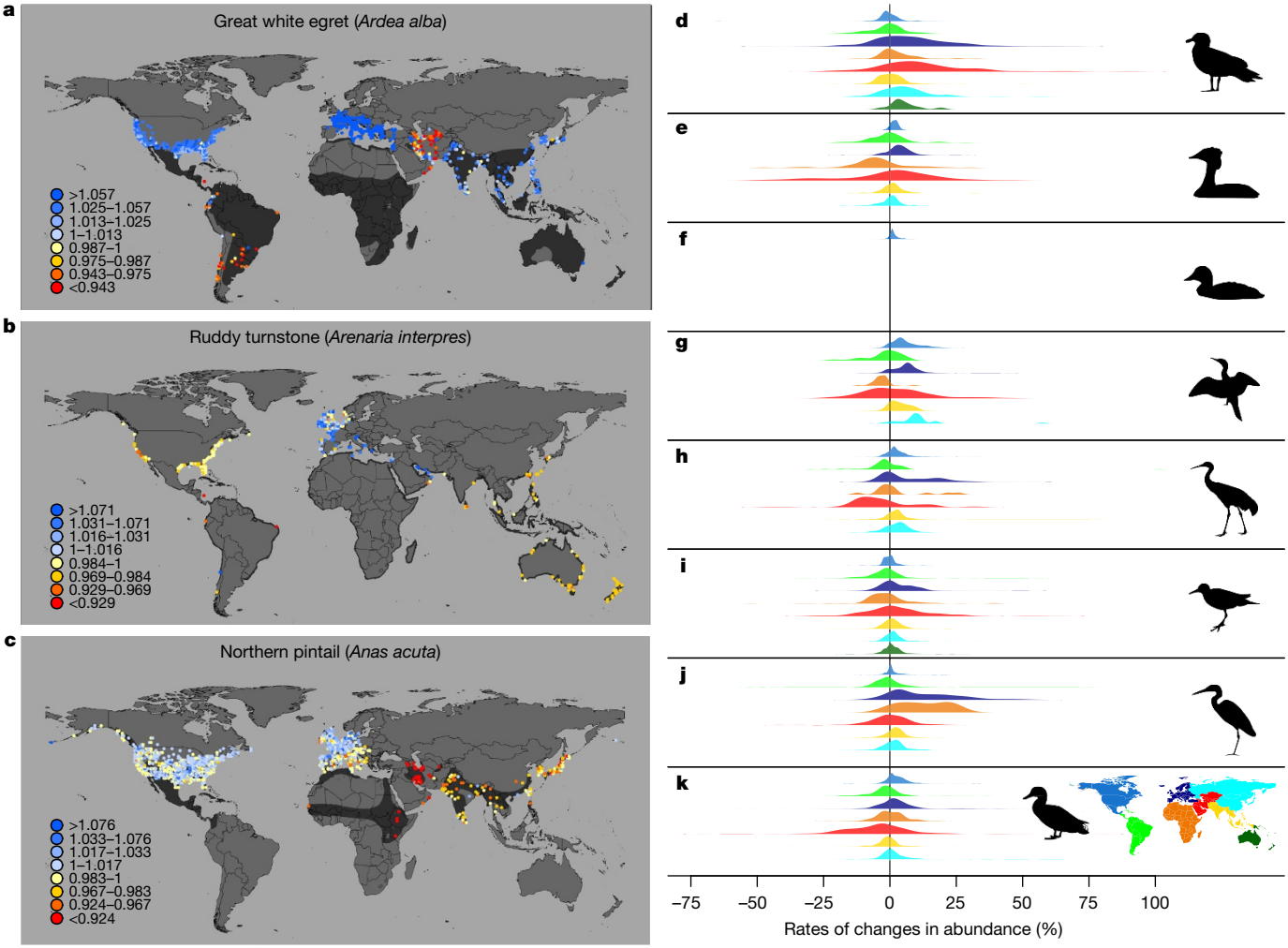

Figure 1 | Population-level changes in waterbird abundance in each 1° × 1° grid cell between 1990 and 2013. a–c, Examples of population-level abundance changes, for *Ardea alba* (**a**), *Arenaria interpres* (**b**) and *Anas acuta* (**c**). Red, declines; blue, increases; dark grey shading, non-breeding geographical range of the species. **d–k**, Histograms of population-level changes for all species in each of the eight taxa, at all grid cells in each region shown in the inserted map (see Methods for the definition of each species group). Silhouettes reproduced from PhyloPic (http://phylopic.org/) under a Creative Commons licence (http://creativecommons.org/licenses/by/3.0/) (**d–g**, **i–k**) or Public Domain Dedication licence (http://creativecommons.org/publicdomain/zero/1.0/) (**h**). **d**, **i**, Rebecca. Groom; **e**, **f**, Doug Backlund (photo) (**e**) or Unknown (photo) (**f**), John E. McCormack, Michael. G. Harvey, Brant. C. Faircloth, Nicholas. G. Crawford, Travis. C. Glenn, Robb. T. Brumfield & T. Michael. Keesay; **g**, **j**, Shyamal/Wikimedia Commons; **k**, Maija. Karala (image flipped horizontally). Map produced from Natural Earth data v.1.4.0 (http://www.naturalearthdata.com/).

governance—defined as how effectively the authorities of a country exercise rules and enforcement mechanisms—was the strongest predictor of community-level abundance changes (Fig. 3a). Waterbird communities experienced the greatest declines in countries with less effective governance (for example, countries in western and central Asia or South America), and increased in countries in which governance was more effective (for example, countries in Europe and North America, Fig. 3b). The effects of governance also interacted with those of protected area coverage (Fig. 3a); it was only in areas with more effective governance that extensive protected area coverage was associated with community-level increases in waterbird abundances (Extended Data Fig. 3a). Community-level declines were also pronounced in areas with

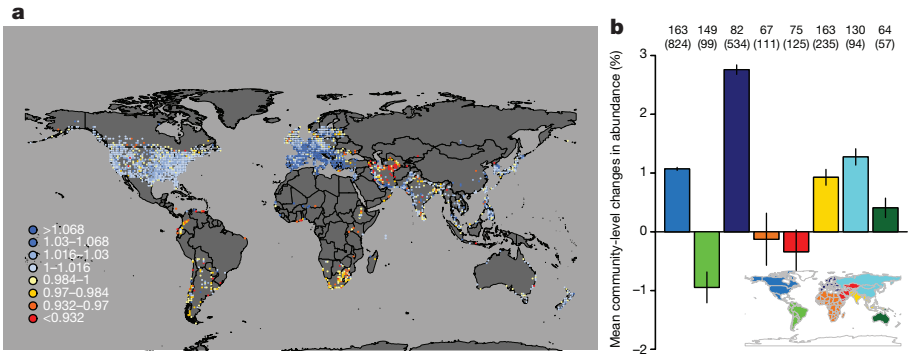

Figure 2 | Mean changes in abundance across 461 waterbird species (community-level changes) between 1990 and 2013. a, **b**, Global distribution (**a**) and mean with 95% confidence intervals (**b**) across all grid cells in each region shown in the inserted map. Numbers above bars, numbers of species observed; numbers of grid cells in parentheses. Map produced from Natural Earth data v.1.4.0 (http://www.naturalearthdata.com/).

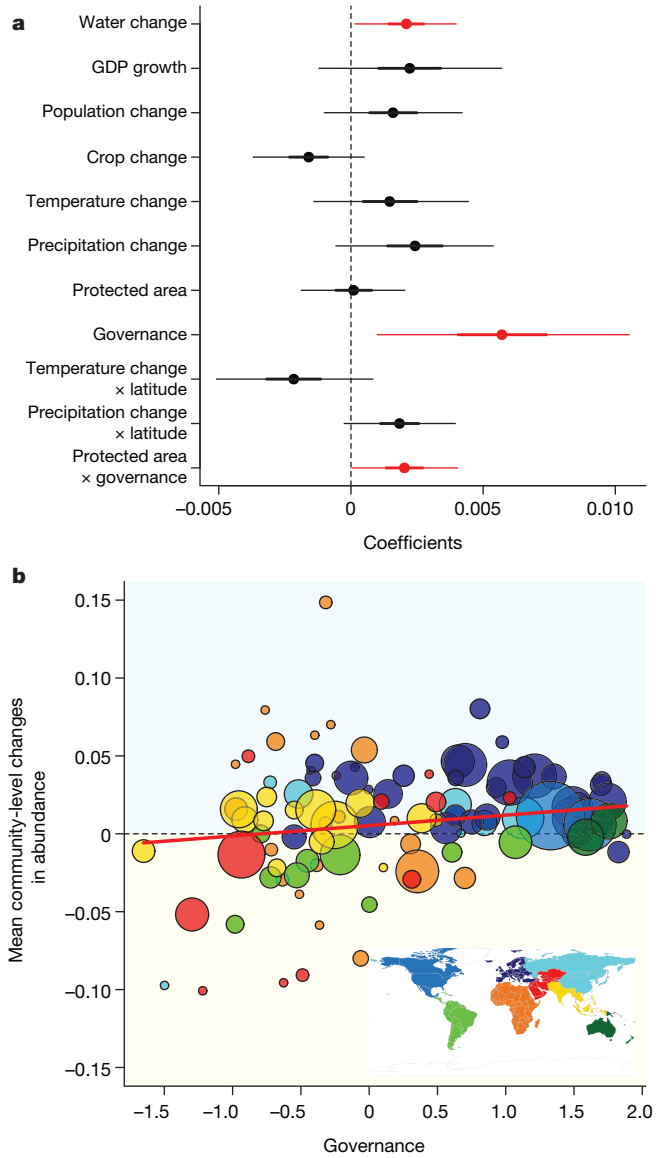

Figure 3 | Effects of predictors on community-level changes in waterbird abundance. a, Estimated coefficients in the multivariate analysis ($n = 2{,}079$). Posterior medians with 95% and 50% (thick lines) credible intervals are shown. Coefficients with 95% credible intervals that do not overlap with zero are shown in red. The coefficients represent the effect size of the standardized variables. **b**, Relationship between community-level changes and countries' governance. Each circle represents a country; circle size, the number of 1° × 1° grid cells with estimates; colour indicates the region shown in the inset map; regression line shown in red. Map produced from Natural Earth data v.1.4.0 (http://www.naturalearthdata.com/).

a higher rate of surface water loss (for example, western and central Asia[16], Extended Data Fig. 3b).

To explore the possible 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 interaction between governance and protected area coverage, by gross domestic product (GDP) growth rates and by 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 countries with rapidly growing economies, as well as 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 that were significantly affected by governance showed larger population-level declines in areas with less effective governance (Extended Data Fig. 4 and Supplementary Discussion). These conclusions were robust even when considering the correlation between governance and GDP per capita, and were also robust 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), by quantifying abundance changes within each species over large geographic areas we uncovered new hotspots of threats to bird species in wetland ecosystems. Previous studies (see Supplementary Discussion) did not identify biodiversity loss in, for example, western and central Asia, mainly because relevant data were unavailable. This spatial overlap between general data gaps and biodiversity loss could cause an underestimation of the ongoing biodiversity crisis, which highlights the need for global monitoring of species' abundances.

Our results emphasize the importance of governance—presumably the environmental aspects of governance (see Methods)—in explaining global patterns in waterbird abundance changes. Local and regional studies have increasingly highlighted 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 absence of positive attitudes to environmental protection, weakly enforced environmental legislation and low levels of investment in conservation[20–22], leading to habitat loss and degradation. For example, unsustainable water management and dam construction in western and 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]. In South America, wetlands in central Argentina lack legal protection or regulations on water use, and many have been lost[24]. Ineffective hunting regulations can also explain decreases in abundance under conditions of ineffective governance. Political instability can weaken the legal enforcement of hunting regulations and thereby promote unsustainable and often illegal killing, even in protected areas[25]; numerous waterbird species are under severe hunting pressure 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, and its concomitant functions and services.

This study corroborates the observation that protected areas improve the conservation status of waterbird species, although the benefits of these protected areas are applicable only in countries with more effective governance. Our results provide strong support at the global scale for the argument that effective governance is critical for protected areas to achieve their goals[27]. Even in developing countries with less effective governance, protected area coverage can be high (Extended Data Fig. 8); however, these protected areas have been insufficient to maintain stable waterbird populations since 1990. By contrast, 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 that aim to improve 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 research and funding efforts. 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 mobilize international resources and expertise to strengthen effective

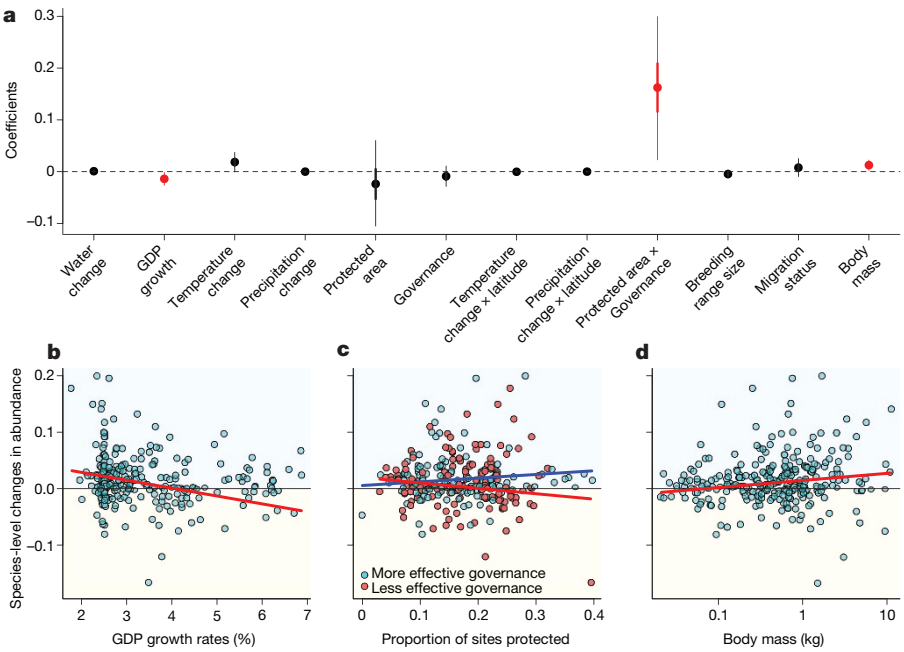

Figure 4 | Effects of predictors on species-level abundance changes in 293 waterbird species that were recorded in at least ten grid cells. **a**, Estimated coefficients with 95% and 50% (thick lines) credible intervals; those not overlapping with zero are shown in red. **b**–**d**, Relationship at the species level between abundance changes and GDP growth rates (**b**), proportion of sites covered by protected areas (**c**) and body mass (**d**). 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**. See Supplementary Data 2 for details of the 293 species.

governance. Governance is now recognized 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.

Online Content Methods, along with any additional Extended Data display items and Source Data, are available in the online version of the paper; references unique to these sections appear only in the online paper.

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1. The Ramsar Convention on Wetlands. *Wetland Ecosystem Services*. http://archive.ramsar.org/cda/en/ramsar-pubs-info-ecosystem-services/main/ramsar/1-30-103%5E24258_4000_0__ (2011).
2. Dudgeon, D. *et al.* Freshwater biodiversity: importance, threats, status and conservation challenges. *Biol. Rev. Camb. Philos. Soc.* **81,** 163–182 (2006).
3. Millennium Ecosystem Assessment. *Ecosystems and Human Well-Being: Wetlands and Water Synthesis* (World Resources Institute, 2005).
4. United Nations General Assembly. *Transforming Our World: the 2030 Agenda for Sustainable Development. Resolution Adopted by the General Assembly on 25 September 2015* (United Nations, 2015).
5. Young, H. S., McCauley, D. J., Galetti, M. & Dirzo, R. Patterns, causes, and consequences of Anthropocene defaunation. *Annu. Rev. Ecol. Evol. Syst.* **47,** 333–358 (2016).
6. Balmford, A., Green, R. E. & Jenkins, M. Measuring the changing state of nature. *Trends Ecol. Evol.* **18,** 326–330 (2003).
7. Margules, C. R. & Pressey, R. L. Systematic conservation planning. *Nature* **405,** 243–253 (2000).
8. Convention on Biological Diversity. *Decision X/2. The Strategic Plan for Biodiversity 2011–2020 and the Aichi Biodiversity Targets* (Secretariat of the Convention on Biological Diversity, 2010).
9. Intergovernmental Platform on Biodiversity and Ecosystem Services. *Generic Scoping Report for the Regional and Subregional Assessments of Biodiversity and Ecosystem Services* (Intergovernmental Platform on Biodiversity and Ecosystem Services, 2015).
10. Pimm, S. L. *et al.* The biodiversity of species and their rates of extinction, distribution, and protection. *Science* **344,** 1246752 (2014).
11. WWF. *Living Planet Report 2016. Risk and Resilience in a New Era* (WWF International, 2016).
12. Bowler, D. E. *et al.*, Cross-realm assessment of climate change impacts on species' abundance trends. *Nat. Ecol. Evol.* **1,** 0067 (2017).
13. Barnes, M. D. *et al.* Wildlife population trends in protected areas predicted by national socio-economic metrics and body size. *Nat. Commun.* **7,** 12747 (2016).
14. The Ramsar Convention on Wetlands. *Classification System for Wetland Type* http://archive.ramsar.org/cda/en/ramsar-documents-guidelines-strategic-framework-and/main/ramsar/1-31-105%5E20823_4000_0__#B (2012).
15. Boere, G. C., Galbraith, C. A. & Stroud, D. A. eds. *Waterbirds Around the World* (The Stationery Office, 2006).
16. Pekel, J.-F., Cottam, A., Gorelick, N. & Belward, A. S. High-resolution mapping of global surface water and its long-term changes. *Nature* **540,** 418–422 (2016).
17. Smith, R. J., Muir, R. D. J., Walpole, M. J., Balmford, A. & Leader-Williams, N. Governance and the loss of biodiversity. *Nature* **426,** 67–70 (2003).
18. Umemiya, C., Rametsteiner, E. & Kraxner, F. Quantifying the impacts of the quality of governance on deforestation. *Environ. Sci. Policy* **13,** 695–701 (2010).
19. Ceddia, M. G., Bardsley, N. O., Gomez-y-Paloma, S. & Sedlacek, S. Governance, agricultural intensification, and land sparing in tropical South America. *Proc. Natl Acad. Sci. USA* **111,** 7242–7247 (2014).
20. Harring, N. Understanding the effects of corruption and political trust on willingness to make economic sacrifices for environmental protection in a cross-national perspective. *Soc. Sci. Q.* **94,** 660–671 (2013).
21. Sundström, A. Covenants with broken swords: corruption and law enforcement in governance of the commons. *Glob. Environ. Change* **31,** 253–262 (2015).
22. Miller, D. C., Agrawal, A. & Timmons Roberts, J. Biodiversity, governance, and the allocation of international aid for conservation. *Conserv. Lett.* **6,** 12–20 (2013).
23. Nourani, E., Kaboli, M. & Collen, B. An assessment of threats to Anatidae in Iran. *Bird Conserv. Int.* **25,** 242–257 (2015).
24. Brandolin, P. G. & Blendinger, P. G. Effect of habitat and landscape structure on waterbird abundance in wetlands of central Argentina. *Wetl. Ecol. Manag.* **24,** 93–105 (2016).
25. Brochet, A.-L. *et al.* Preliminary assessment of the scope and scale of illegal killing and taking of birds in the Mediterranean. *Bird Conserv. Int.* **26,** 1–28 (2016).
26. Morrison, R. I. G. *et al.* Dramatic declines of semipalmated sandpipers on their major wintering areas in the Guianas, Northern South America. *Waterbirds* **35,** 120–134 (2012).
27. Lockwood, M. Good governance for terrestrial protected areas: A framework, principles and performance outcomes. *J. Environ. Manage.* **91,** 754–766 (2010).
28. Kirby, J. S. *et al.* Key conservation issues for migratory land- and waterbird species on the world's major flyways. *Bird Conserv. Int.* **18,** S49–S73 (2008).

Supplementary Information is available in the online version of the paper.

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METHODS

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

Launched in 1967, the IWC is a scheme involving more than 15,000 observers that monitors waterbird numbers and covers more than 25,000 sites in over 100 countries. The IWC is divided into four regions, each of which corresponds to a major migratory flyway 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 CWC, because it started only in 2010 and therefore 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. Additional counts are conducted in other months, particularly in July in the Southern Hemisphere; for consistency, we used only counts from January and February. Our Northern Hemisphere data therefore relate to non-breeding populations, whereas those from 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) that include sites of international- or national-level recognition (for example, Ramsar 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 km^2) are typically surveyed by about two observers for up to four hours, but larger sites can require a group of observers to work 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 during high tide periods (mangrove areas and nearby mudflats are, however, surveyed 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 are thus inferred using a set of criteria (see below). Count records and associated information are submitted to the national coordinators, who compile the submitted records, check their validity and submit them to Wetlands International. Further details of survey methodology have been previously published[29,31].

As the IWC does not cover North America, we also used data from the CBC, which has been conducted annually since 1900, involves more than 70,000 observers each year and now includes over 2,400 count circles (defined as survey sites in this study)[32]. Each CBC consists of a tally of all bird species detected within a survey site (a circle 24.1 km in diameter), on a single day that falls on a date 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; they use a variety of transportation methods, mostly surveying on foot or in a car but also using 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. In this paper, we only used records describing waterbird species.

We compiled data from each scheme by species, except for data derived from the AEWC that had already been stored by flyway for each species[33]. Because data from the NWC are only available after 1990, we restricted the study to data that post-dated 1990 for all regions. The latest records were in 2013. Although the data included 487 waterbird species in total, we excluded from the analyses species with 20 or fewer records; this resulted in 461 species being analysed (see Supplementary Data 2 for the full list of species). For the IWC data, we generated zero counts using an established approach[33]. In this approach, we first established a list of all species observed in each country, and assumed a zero count for any species that was 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 or S.

When visualizing the estimated abundance changes (for example, see Figs 2b, 3b), the North and South American regions correspond to regions covered by the CBC and NWC, respectively. The regions covered by the AEWC and AWC were divided into a total of six regions on the basis of socio-economic and ecological differences. The AEWC was divided into three regions: Europe, Africa, and western and central Asia. The AWC was also divided into three regions: south and southeast Asia, east Asia and Russia, and Oceania.

Explanatory variables. To explain variations in waterbird abundance changes over space and species, we first set up multiple hypotheses on the basis of earlier studies and then identified explanatory variables that represented these hypotheses (Extended Data Table 1). We aggregated all the explanatory variables, except those relating to species characteristics, to the same $1° \times 1°$ grid cells.

As measures of governance we used the Worldwide Governance Indicators, which summarize six dimensions of governance: voice and accountability, political stability and absence of violence, government effectiveness, regulatory quality, rule of law, and control of corruption[34]. A previous study[19] of six South American countries found that pro-environmental behaviours are associated with environmental aspects of governance rather than the 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)[35], one of the indicators of environmental governance used in the aforementioned 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 (https://www.protectedplanet.net/), not every protected area has information on the year of designation. We therefore calculated the proportion of sites located within any protected area, assuming that this 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 only the proportion of sites covered by protected areas that are known to have been designated before 1990 (the oldest survey year), and conducted the same analyses using this variable (results in Extended Data Fig. 5 and Supplementary Discussion). When assessing the effectiveness of protected areas, confounding factors can mask or mimic the effects of protected areas. We 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.

On the basis of information from 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 that were 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 assessed by the International Union for Conservation of Nature from the BirdLife Checklist of the Birds of the World[36], for each species. Generation length was not available for 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 global distribution maps[37] for the visualization of results (see Supplementary Data 1 for more detail). Species groups used in Fig. 1 are based on the International Ornithological Congress World Bird List[38]: 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 $1° \times 1°$ grid cell. This model is an extension of a model developed and used to quantify waterbird abundance changes in previous studies[39,40]; it is 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:

$$\beta_t \sim \text{normal}(\beta_{t-1} + r(\beta_{t-1} - \beta_{t-2}), \sigma_o^2)$$

Here σ_o^2 is the variance of the overall year effect, and r ranges from 0 to 1 and determines the smoothness of the estimated curve. With $r = 0$, the overall year effect is modelled as a simple random-walk process, whereas 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 as follows:

$$\beta_{j(i),t} \sim \text{normal}(\beta_t, \sigma_\beta^2)$$

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

$$\log(\mu_{i,t}) = \alpha_i + \beta_{j(i),t} + \gamma_{j(i)} + \delta_{i,t} \quad (1)$$

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. The variable $\gamma_{j(i)}$ is drawn from an intrinsic Gaussian conditional autoregressive (CAR) prior distribution:

$$\gamma_{j(i)}|\gamma_k \sim \text{normal}\left(\frac{\sum_{j\neq k} w_{j,k}\gamma_k}{n_j}, \frac{\sigma_\gamma^2}{n_j}\right) \quad (2)$$

where $w_{j,k}=1$ if grid cells j and k are neighbours, and 0 otherwise. The variable n_j is the total number of neighbours of grid cell j; neighbours are grid cells directly adjacent to grid cell j, and include cells that are diagonally adjacent. The amount of variation between the random effects is controlled by σ_γ^2. 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 for the IWC, because regular and standardized surveys with constant methods, efforts and timing are strongly encouraged in this scheme[31] (see Supplementary Discussion). However, survey efforts in the CBC are known to vary through time. By 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 a previously published analysis[41]:

$$\log(\mu_{i,t}) = \alpha_i + \beta_{j(i),t} + \gamma_{j(i)} + \delta_{i,t} + \frac{B\left(\left(\frac{\zeta_{i,t}}{\bar{\zeta}}\right)^p - 1\right)}{p} \quad (3)$$

Here $\zeta_{i,t}$ is the total number of survey hours per count and $\bar{\zeta}$ is the mean value of $\zeta_{i,t}$. The parameters B and p determine a range of relationships between effort and the number of birds counted[41]. To test whether accounting for survey efforts changes the conclusions of this paper, we also applied the model without the effort effect to the CBC data, and compared the two models in terms of their estimated rate of abundance change within each grid cell for each of the 159 species with more than two grid cells. The estimated spatial patterns in abundance changes in each of the two models were highly correlated (median Pearson's $r=0.99$, minimum $r=0.88$), which indicates that the model without the effort effect that was used for the IWC data is valid. Further discussions on the potential effects of temporal changes in survey efforts are provided in the Supplementary Discussion.

We applied the models to count data for each species at a regional population level. For example, count data for the Eurasian wigeon *Mareca penelope* are separately compiled as five populations: three (northwest European, Black Sea–Mediterranean and southwest Asian–northeast African) in the AEWC, one in the AWC 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 2 for the full list of species). For 38 regional populations in which no grid cells with count records were adjacent to one other, we dropped the spatially correlated random effect $\gamma_{j(i)}$ from equations (1) and (3). For 32 regional populations with only one grid cell that included 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 generalized 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 that had 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 v.1.4.3[42] and the R2WinBUGS package[43] in R v.3.3.2[44]. Prior distributions of parameters were set as non-informatively as possible, to produce estimates similar to those generated by a maximum likelihood method. We used gamma distributions with a mean of 1 and variance of 100 for the inverses of σ_o^2, σ_β^2, σ_α^2, σ_δ^2 and σ_γ^2, normal distributions with a mean of 0 and variance of 100 for β_1, β_2 and B, a beta distribution with a 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 a previous study[45]. 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 twenty iterations to save storage space. Model convergence was checked with R hat values[46]. 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 in which parameter estimates did not converge even with the increased iterations, although the number of removed cells was very small (median of 2.5 grid cells in 20 out of the 775 (2.6%) regional populations).

To estimate the population-level change in abundance since 1990 for 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 s.d. of the standard error of the slope. We then calculated the mean, median, variance and 2.5th and 97.5th percentiles of the estimated slopes from all posterior samples. We aggregated all estimates by species on the basis of definitions from BirdLife International[36]. We used the mean and 2.5th and 97.5th percentiles of the estimated slopes for creating species-level maps (Fig. 1a–c and Supplementary Data 1). To calculate community-level changes in abundance (Fig. 2a) and community-level changes for species with different migratory statuses (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 $1°\times1°$ grid cells that had abundance change estimates (Extended Data Table 2). GDP per capita and governance were relatively strongly correlated ($r=0.76$) with one another. Thus, considering that GDP growth rates are another measure of economic growth, we decided to exclude GDP per capita from the main analyses; instead, we tested its effect in a separate set of analyses in which governance was replaced with GDP per capita. In these analyses, considering the hypothesized nonlinear relationship between GDP per capita and species abundance changes (Extended Data Table 1), we used linear and quadratic terms of GDP per capita. We present the results of these analyses that use 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 v.1.4.3 and the R2WinBUGS package in R v.3.3.2.

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

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

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; β represents the vector of regression coefficients and $\boldsymbol{X_i}$ the vector of explanatory variables. On the basis of 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 tested interaction terms between latitude and temperature change, and latitude and precipitation change, as population responses to temperature and precipitation can vary by latitude[47]. We also tested a third interaction term between governance and protected area coverage, because governance can affect the effectiveness of conservation efforts[48]. All explanatory variables were standardized before model fitting. The spatially-correlated random effect γ_i used an intrinsic Gaussian CAR prior distribution with variance σ_γ^2, as described in equation (2). Prior distributions of parameters were set as non-informatively as possible; we used gamma distributions with a mean of 1 and variance of 1,000 for the inverse of σ_μ^2 and σ_γ^2, normal distributions with a mean of 0 and variance of 1,000 for β_j, and an improper uniform distribution (a uniform distribution on an infinite interval) for the intercept α, as recommended by a previous study[49]. 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 in ten or more grid cells, we adopted the within-subject centring approach[50] 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 a mean of ν_s and variance of σ_ν^2. The variable ν_s is further modelled with species-level explanatory variables:

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

where α is the global intercept and β_{Bk} represents the species-level effect. The mean of spatial explanatory variable k across all grid cells where species s was recorded is represented by $\bar{x}_{k,s}$. Even if the estimated species-level abundance changes are biased owing to geographical biases in available grid cells, they match up with $\bar{x}_{k,s}$ because the calculation of both variables is performed on the same set of grid cells. The spatial explanatory variables used were derived from the hypotheses in Extended Data Table 1; 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 species-level model. We therefore used the remaining six explanatory variables (surface water change, GDP growth rates, changes in temperature, changes in precipitation, protected area coverage and governance) and the same three interaction terms as used in the community-level analysis. The term $z_{k,s}$ represents three explanatory variables in species characteristics, described in Extended Data Table 1. The random term η_s accounts for phylogenetic dependence among species and is drawn from a multivariate normal distribution (MVN)[51,52]:

$$\begin{aligned} \eta_s &\sim \mathrm{MVN}(0,\ \delta^2\Sigma_\lambda) \\ \Sigma_\lambda &= \lambda\Sigma + (1-\lambda)I \end{aligned} \tag{4}$$

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[51]. To enable the strength of phylogenetic signal to vary, we also incorporated Pagel's λ[53,54] into the matrix in equation (4) with the identity matrix I. Here λ is a coefficient that multiplies the off-diagonal elements of Σ; a λ close to zero implies that the phylogenetic signal in the data is low, which suggests independence in the error structure of the data points, whereas a λ that is close to one suggests a good agreement with the Brownian motion evolution model and thus suggests correlation in the error structure[51,54]. To incorporate uncertainties[55] in phylogenetic trees in the calculation of Σ, we used a sample of 100 trees from a comprehensive avian phylogeny[56] as the prior distribution for our analysis[51]. 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:

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

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 ($x_{j,i} - \bar{x}_{j,s}$); here, $x_{j,i}$ is the 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 governed by hyper-parameters as:

$$\beta_{W_{s,j}} \sim \mathrm{normal}(h\beta_{Wj}, \sigma^2_{\beta_{Wj}})$$

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

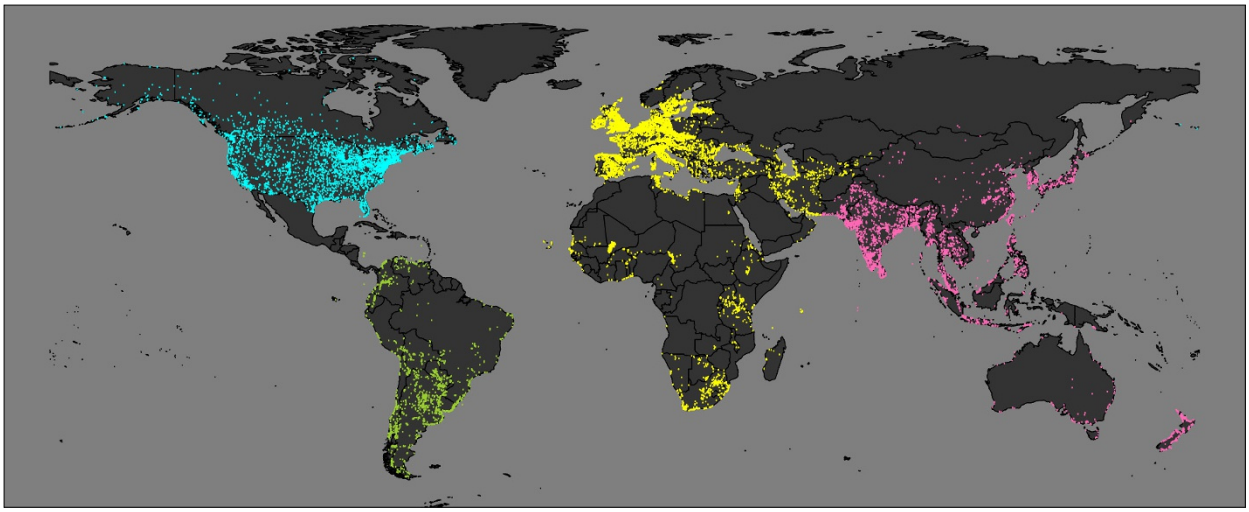
As non-informative prior distributions, we used a gamma distribution with a mean of 1 and variance of 100 for σ_ν^2, δ^2, σ_μ^2, $\sigma^2_{\beta_{Wj}}$ and $\sigma^2_{\gamma_s}$, uniform distribution on the interval [0, 1] for λ, normal distributions with a mean of 0 and variance of 100 for α, β_{Bk}, 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. Owing to differences in the definition of species between the two sources used[36,56], in four cases we combined two separate species defined in the BirdLife Checklist[36] into one for the species-level analysis. These were the 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*.

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

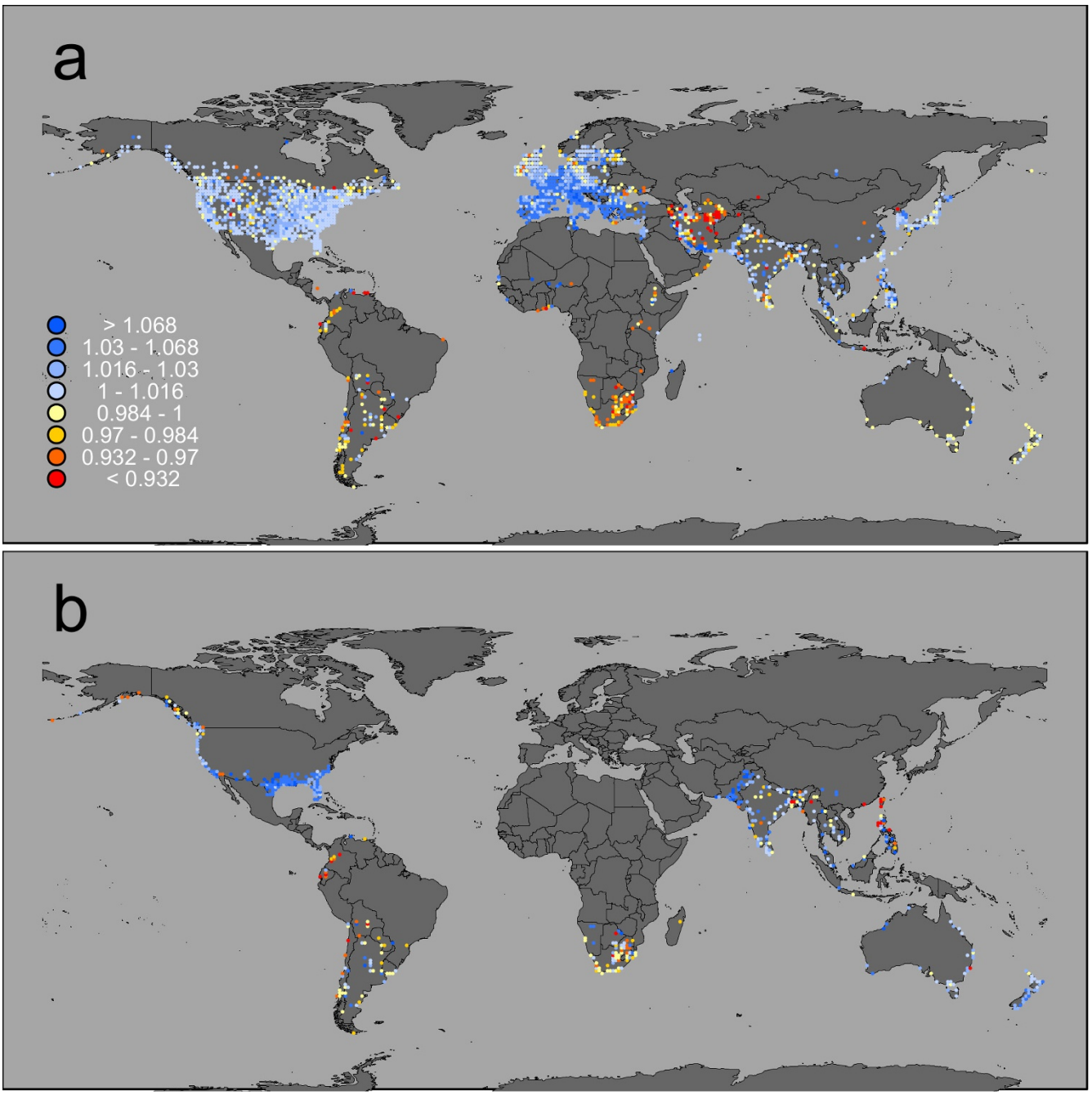
Data availability. The waterbird count data used in this study are collated and managed by Wetlands International and the National Audubon Society, and are available on request. All maps in figures are derived from the Natural Earth dataset (v.1.4.0) at 1:110 m scale (http://www.naturalearthdata.com/downloads/110m-cultural-vectors/110m-admin-0-countries/). All the data that pertain to explanatory variables are freely available, as specified in Extended Data Table 1. Supplementary Data 1 is available at https://doi.org/10.6084/m9.figshare.5669827. Supplementary Data 2 is available in the online version of the paper.

29. Delany, S. *Guidance on Waterbird Monitoring Methodology: Field Protocol for Waterbird Counting* (Wetlands International, 2010).
30. Dunn, E. H. *et al.* Enhancing the scientific value of the Christmas Bird Count. *Auk* **122,** 338–346 (2005).
31. van Roomen, M. *et al. Waterbird and Site Monitoring along the Atlantic Coast of Africa: Strategy and Manual* (BirdLife International, Common Wadden Sea Secretariat and Wetlands International, 2014).
32. LeBaron, G. S. *The 115th Christmas Bird Count* (National Audubon Society, 2015).
33. van Roomen, M., van Winden, E & van Turnhout, C. *Analyzing Population Trends at the Flyway Level for Bird Populations Covered by the African Eurasian Waterbird Agreement: Details of a Methodology* (SOVON Dutch Centre for Field Ornithology, 2011).
34. Kaufmann, D., Kraay, A & Mastruzzi, M. *The Worldwide Governance Indicators: Methodology and Analytical Issues (September 2010)* https://ssrn.com/abstract=1682130 (2010).
35. Hsu, A. *et al. 2016 Environmental Performance Index* http://epi.yale.edu/reports/2016-report (2016).
36. BirdLife International. *The BirdLife Checklist of the Birds of the World: Version 7* http://www.birdlife.org/datazone/userfiles/file/Species/Taxonomy/BirdLife_Checklist_Version_70.zip (2014).
37. BirdLife International and NatureServe. *Bird Species Distribution Maps of the World* (BirdLife International and NatureServe, 2014).
38. Gill, F. & Donsker, D. (eds) *IOC World Bird List (v 5.1)* http://www.worldbirdnames.org/DOI-5/master_ioc_list_v5.1.xls (2015).
39. Amano, T., Okamura, H., Carrizo, S. F. & Sutherland, W. J. Hierarchical models for smoothed population indices: the importance of considering variations in trends of count data among sites. *Ecol. Indic.* **13,** 243–252 (2012).
40. Amano, T., Székely, T., Koyama, K., Amano, H. & Sutherland, W. J. A framework for monitoring the status of populations: an example from wader populations in the East Asian–Australasian flyway. *Biol. Conserv.* **143,** 2238–2247 (2010).
41. Link, W. A. & Sauer, J. R. Seasonal components of avian population change: joint analysis of two large-scale monitoring programs. *Ecology* **88,** 49–55 (2007).
42. Lunn, D. J., Thomas, A., Best, N. & Spiegelhalter, D. WinBUGS – a Bayesian modelling framework: concepts, structure, and extensibility. *Stat. Comput.* **10,** 325–337 (2000).
43. Sturtz, S., Ligges, U. & Gelman, A. R2WinBUGS: a package for running WinBUGS from R. *J. Stat. Softw.* **12,** 1–16 (2005).
44. R Core Team. *R: a Language and Environment for Statistical Computing* http://www.R-project.org/ (R Foundation for Statistical Computing, 2016).
45. Link, W. A., Sauer, J. R. & Niven, D. K. A hierarchical model for regional analysis of population change using Christmas Bird Count data, with application to the American Black Duck. *Condor* **108,** 13–24 (2006).
46. Gelman, A., Carlin, J., Stern, H. & Rubin, D. *Bayesian Data Analysis* 2nd edn (Chapman & Hall and CRC, 2003).
47. Pearce-Higgins, J. W. *et al.* Geographical variation in species' population responses to changes in temperature and precipitation. *Proc. R. Soc. Lond. Ser. B* **282,** 20151561 (2015).
48. Bare, M., Kauffman, C. & Miller, D. C. Assessing the impact of international conservation aid on deforestation in sub-Saharan Africa. *Environ. Res. Lett.* **10,** 125010 (2015).
49. Thomas, A., Best, N., Lunn, D., Arnold, R. & Spiegelhalter, D. *GeoBUGS User Manual* http://www.mrc-bsu.cam.ac.uk/software/bugs/ (2004).
50. van de Pol, M. & Wright, J. A simple method for distinguishing within- versus between-subject effects using mixed models. *Anim. Behav.* **77,** 753–758 (2009).
51. de Villemereuil, P., Wells, J. A., Edwards, R. D. & Blomberg, S. P. Bayesian models for comparative analysis integrating phylogenetic uncertainty. *BMC Evol. Biol.* **12,** 102 (2012).
52. Abadi, F. *et al.* Importance of accounting for phylogenetic dependence in multi-species mark–recapture studies. *Ecol. Modell.* **273,** 236–241 (2014).
53. Pagel, M. Inferring the historical patterns of biological evolution. *Nature* **401,** 877–884 (1999).
54. Freckleton, R. P., Harvey, P. H. & Pagel, M. Phylogenetic analysis and comparative data: a test and review of evidence. *Am. Nat.* **160,** 712–726 (2002).
55. Donoghue, M. J. & Ackerly, D. D. Phylogenetic uncertainties and sensitivity analyses in comparative biology. *Philos. Trans. R. Soc. Lond. B* **351,** 1241–1249 (1996).
56. Jetz, W., Thomas, G. H., Joy, J. B., Hartmann, K. & Mooers, A. O. The global diversity of birds in space and time. *Nature* **491,** 444–448 (2012).
57. Grossman, G. M. & Krueger, A. B. Economic growth and the environment. *Q. J. Econ.* **110,** 353–377 (1995).

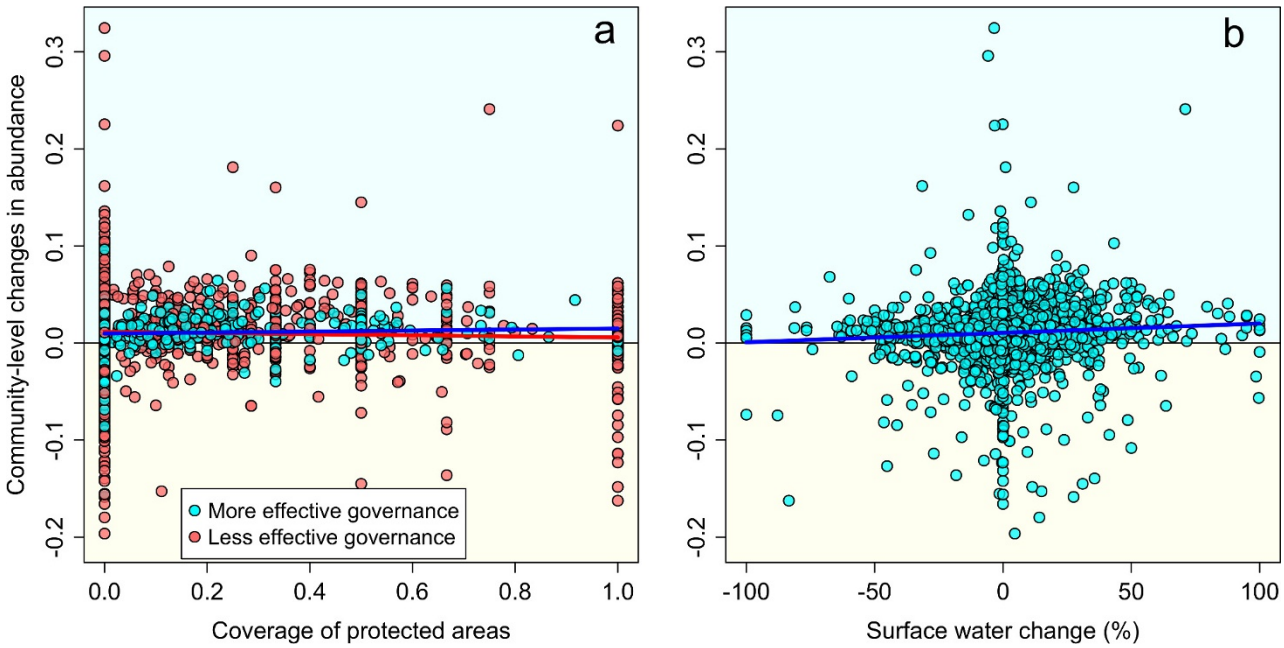
58. Cardillo, M. *et al.* Human population density and extinction risk in the world's carnivores. *PLoS Biol*. **2,** e197 (2004).
59. McKee, J., Chambers, E. & Guseman, J. Human population density and growth validated as extinction threats to mammal and bird species. *Hum. Ecol.* **41,** 773–778 (2013).
60. Center for International Earth Science Information Network - CIESIN - Columbia University, and Centro Internacional de Agricultura Tropical - CIAT. *Gridded Population of the World, Version 3 (GPWv3): Population Density Grid* http://sedac.ciesin.columbia.edu/data/set/gpw-v3-population-density (2005).
61. Green, R. E., Cornell, S. J., Scharlemann, J. P. W. & Balmford, A. Farming and the fate of wild nature. *Science* **307,** 550–555 (2005).
62. Friedl, M. A. *et al.* MODIS Collection 5 global land cover: algorithm refinements and characterization of new datasets. *Remote Sens. Environ.* **114,** 168–182 (2010).
63. Stephens, P. A. *et al.* Consistent response of bird populations to climate change on two continents. *Science* **352,** 84–87 (2016).
64. Harris, I., Jones, P. D., Osborn, T. J. & Lister, D. H. Updated high-resolution grids of monthly climatic observations – the CRU TS3.10 dataset. *Int. J. Climatol.* **34,** 623–642 (2014).
65. Kleijn, D., Cherkaoui, I., Goedhart, P. W., van der Hout, J. & Lammertsma, D. Waterbirds increase more rapidly in Ramsar-designated wetlands than in unprotected wetlands. *J. Appl. Ecol.* **51,** 289–298 (2014).
66. Pavón-Jordán, D. *et al.* Climate-driven changes in winter abundance of a migratory waterbird in relation to EU protected areas. *Divers. Distrib.* **21,** 571–582 (2015).
67. UNEP-WCMC and IUCN. *Protected Planet: The World Database on Protected Areas (WDPA)* www.protectedplanet.net (2015).
68. Mace, G. M. *et al.* Quantification of extinction risk: IUCN's system for classifying threatened species. *Conserv. Biol*. **22,** 1424–1442 (2008).
69. Sanderson, F. J., Donald, P. F., Pain, D. J., Burfield, I. J. & van Bommel, F. P. J. Long-term population declines in Afro-Palearctic migrant birds. *Biol. Conserv.* **131,** 93–105 (2006).
70. Robbins, C. S., Sauer, J. R., Greenberg, R. S. & Droege, S. Population declines in North American birds that migrate to the neotropics. *Proc. Natl Acad. Sci. USA* **86,** 7658–7662 (1989).
71. Pocock, M. J. O. Can traits predict species' vulnerability? A test with farmland passerines in two continents. *Proc. R. Soc. Lond. Ser. B* **278,** 1532–1538 (2011).
72. Owens, I. P. F. & Bennett, P. M. Ecological basis of extinction risk in birds: habitat loss versus human persecution and introduced predators. *Proc. Natl Acad. Sci. USA* **97,** 12144–12148 (2000).
73. Wilman, H. *et al.* EltonTraits 1.0: species-level foraging attributes of the world's birds and mammals. *Ecology* **95,** 2027 (2014).



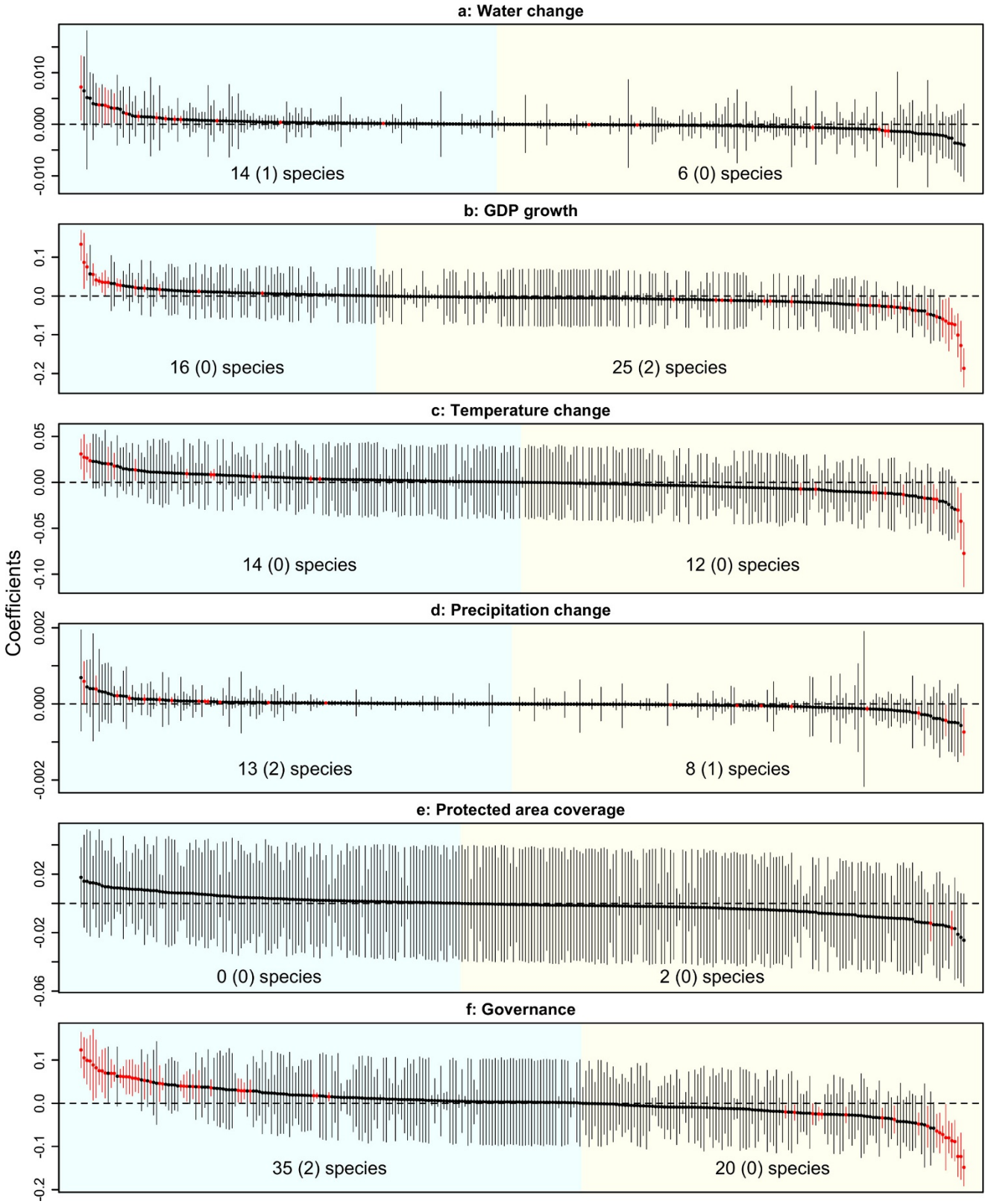
Extended Data Figure 1 | Distribution of the 25,769 survey sites used in the analyses. Sites from the International Waterbird Census are shown in yellow (African–Eurasian Waterbird Census), pink (Asian Waterbird Census) and green (Neotropical Waterbird Census). Christmas Bird Count shown in cyan.



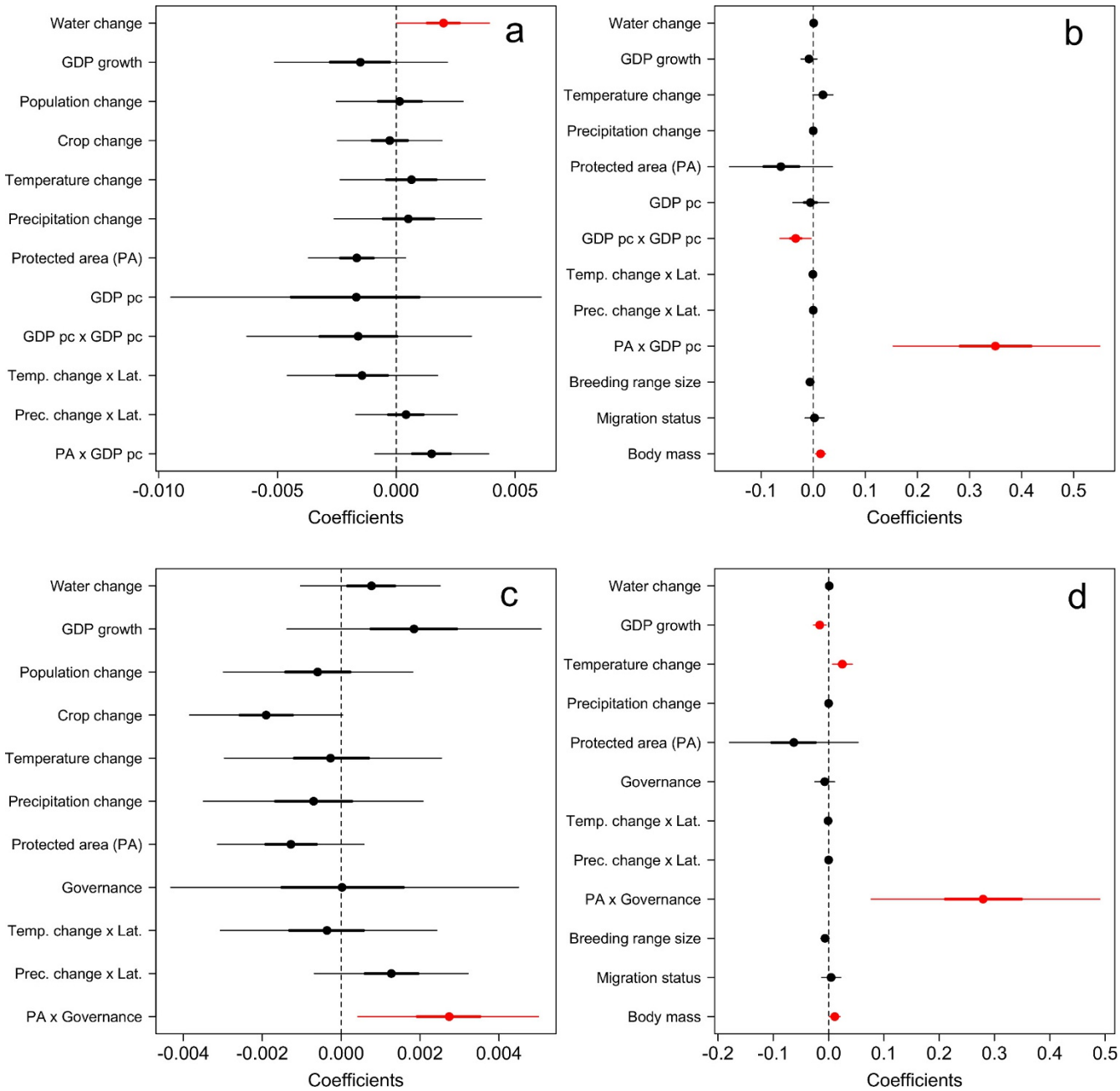
Extended Data Figure 2 | Global distribution of mean annual changes in abundance. a, **b**, Mean annual changes in abundance for 373 migratory (**a**) and 88 non-migratory (**b**) waterbird species (that is, community-level changes). The migratory status of each species was assigned using the BirdLife Data Zone (see Methods).



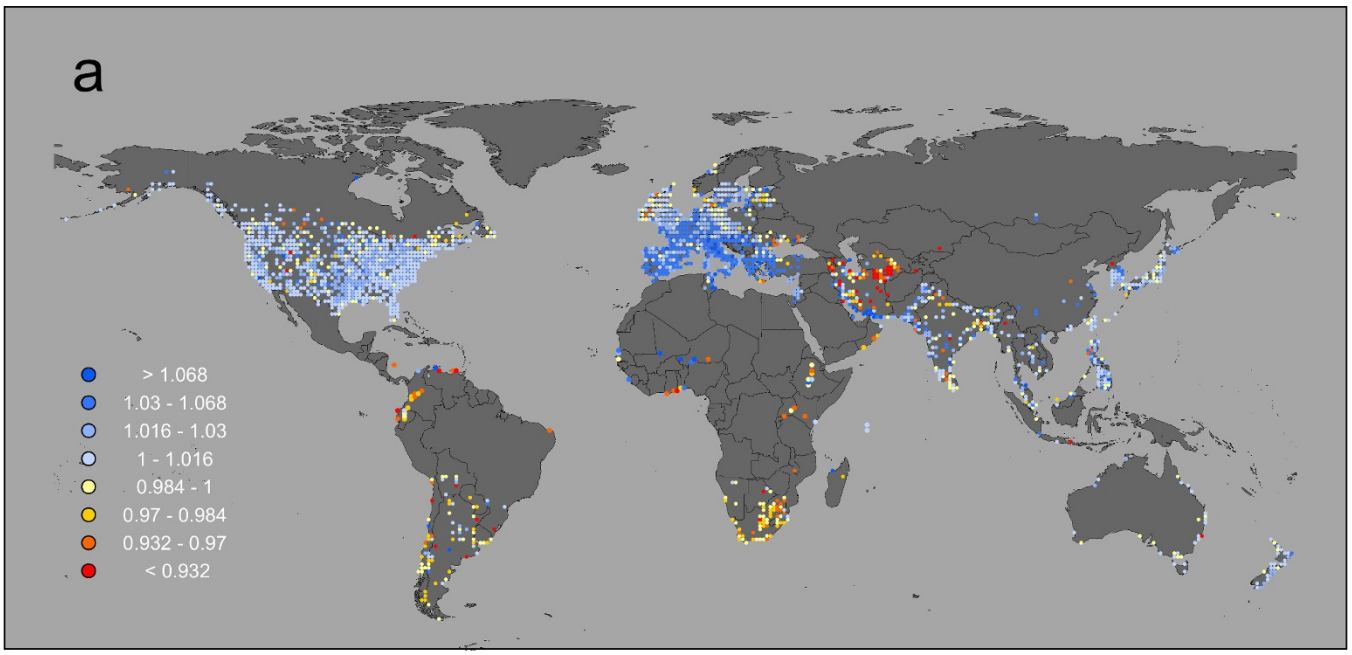
Extended Data Figure 3 | Relationships between community-level changes in abundance and protected areas or surface water. **a**, Relationship between community-level changes in abundance and the proportion of sites covered by protected areas. **b**, Relationship between community-level changes in abundance and surface water change. Regression lines are based on the estimated coefficients in Fig. 3a; values and regression lines for grid cells in areas with more (in blue) and less (in red) effective governance in **a**. $n = 2{,}079$ grid cells.

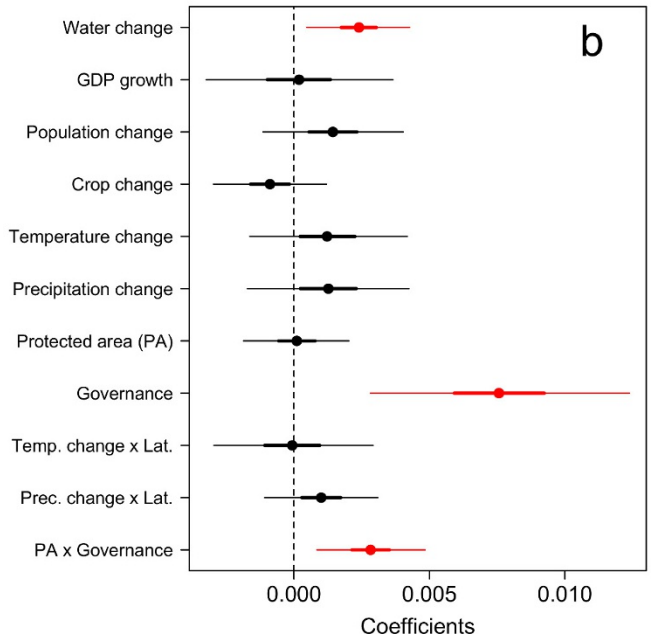


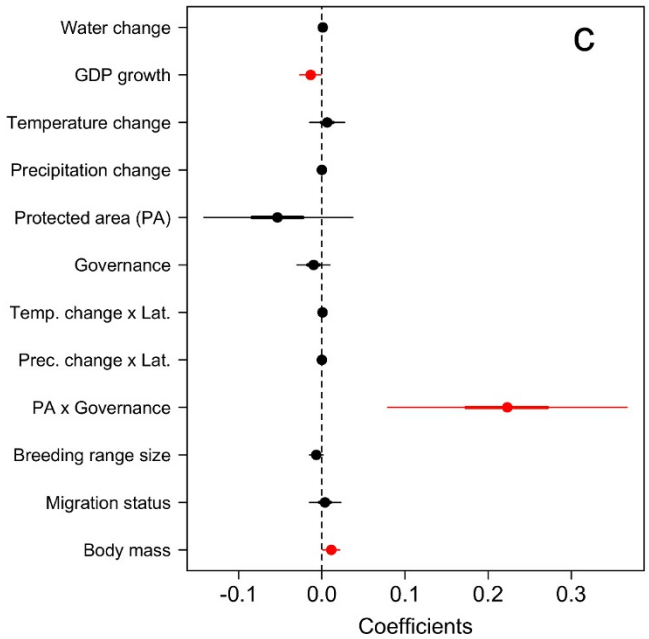
Extended Data Figure 4 | Effects of six hypothesized predictors on population-level changes in abundance. a–f, Medians and 95% credible intervals of the estimated coefficients for 293 species are shown in order of decreasing positive effect size from the left (those with 95% credible intervals not overlapping 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. See Extended Data Table 1 for more detail regarding predictors.



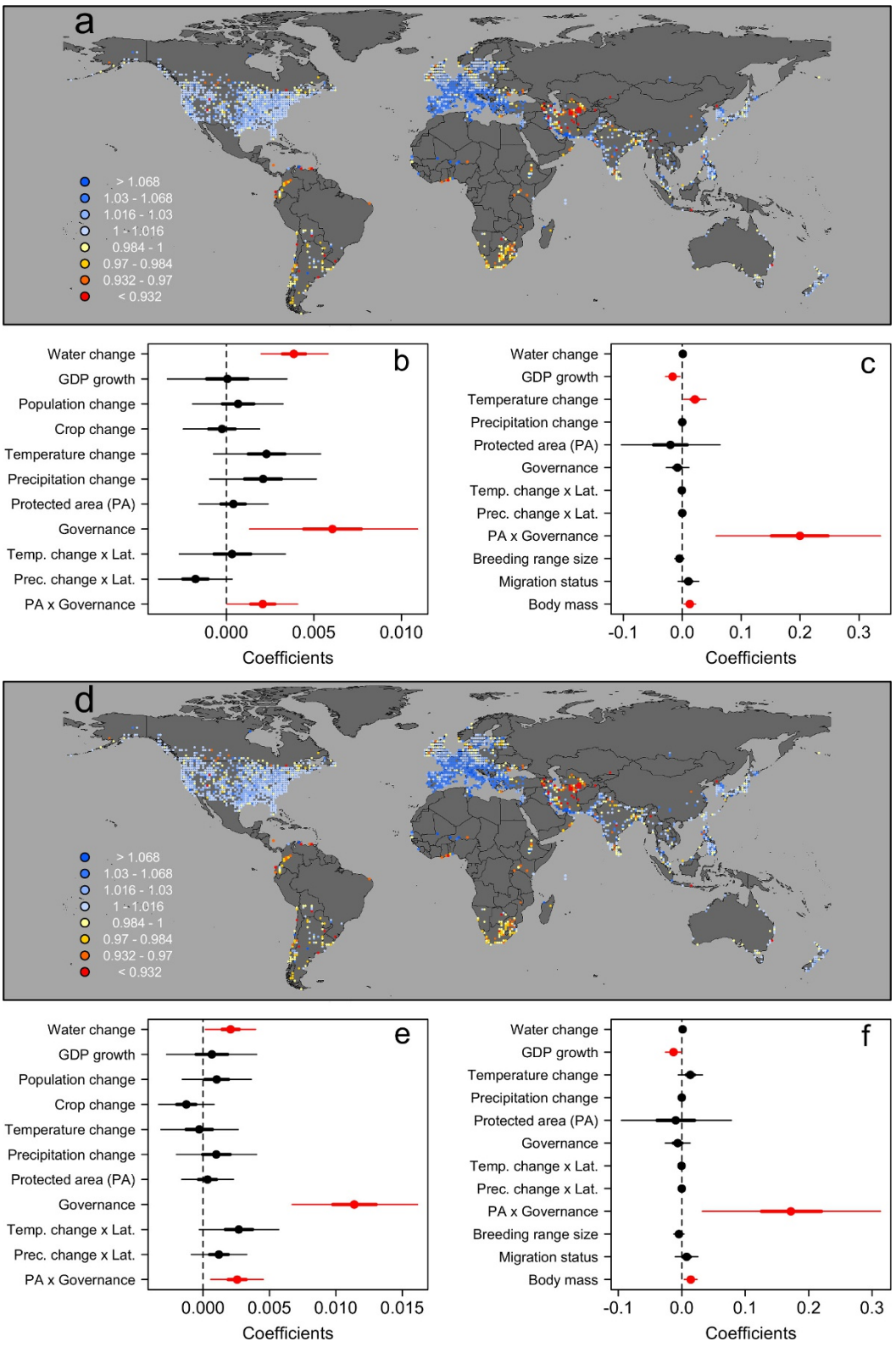
Extended Data Figure 5 | Sensitivity of results to the correlation between governance and GDP per capita and designation years of protected areas. a, **b**, Estimated coefficients in the multivariate analysis of community-level ($n = 2{,}079$ grid cells) (**a**) and species-level (on the basis of 293 species; see Supplementary Data 2 for the number of grid cells for each species) (**b**) changes in abundance, in which governance was replaced with linear and quadratic terms of GDP per capita. **c**, **d**, Estimated coefficients in the multivariate analysis of community-level ($n = 2{,}079$ grid cells) (**c**) and species-level (on the basis of 293 species; see Supplementary Data 2 for the number of grid cells in each species) (**d**) changes in abundance, in which only protected areas known to have been designated before 1990 (the first survey year in our dataset) were used (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.



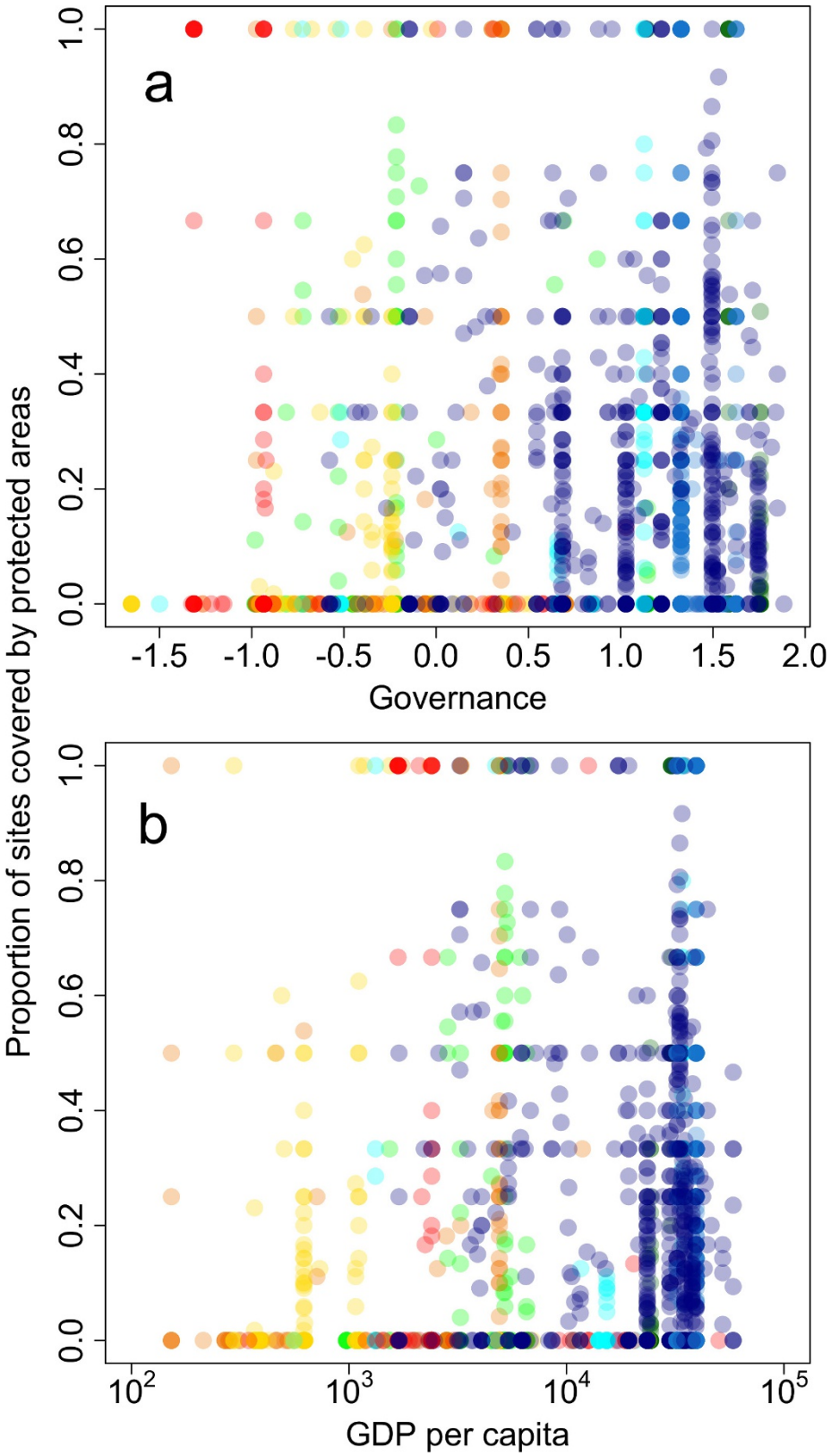




Extended Data Figure 6 | Sensitivity of the results to the inclusion of seabird species. a, Global distribution of mean annual changes in abundance across 447 waterbird species, excluding the 14 seabird species, between 1990 and 2013. **b**, **c**, Estimated coefficients in the multivariate analysis of community-level ($n = 2{,}079$ grid cells) (**b**) and species-level (on the basis of 447 species; see Supplementary Data 2 for the number of grid cells in each species) (**c**) changes in abundance, in which the 14 seabird species 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 Figure 7 | Sensitivity of the results to the choice of 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 that contained neither landscape-scale wetland areas nor local-scale surface water occurrences within 1km of all the survey sites included. **b**, **c**, Estimated coefficients in the multivariate analysis of community-level ($n = 2{,}038$ grid cells) (**b**) and species-level (on the basis of 293 species) (**c**) changes in abundance, in which 41 CBC grid cells that contained 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 in which the proportion of urban areas was over 0.3. **e**, **f**, Estimated coefficients in the multivariate analysis of community-level ($n = 2{,}071$ grid cells) (**e**) and species-level (on the basis of 293 species) (**f**) changes in abundance, in which 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 Figure 8 | Relationships between the proportion of sites covered by protected areas and governance or GDP per capita. **a**, **b**, The relationship between governance (**a**) or GDP per capita (**b**) and the proportion of sites covered by protected areas. Colours indicate regions: blue, North America; green, South America; navy, Europe; orange, Africa; red, western and central Asia; yellow, south and southeast Asia; cyan, east Asia and Russia; and dark green, Oceania.

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[57].	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[58] and rapid human population growth[59].	Mean changes in human population density between 1990 and 2000	Population Density Grid v3[60]
	Agricultural expansion	Farming is the biggest source of threats to bird species[61].	Changes in crop area (croplands and cropland/natural vegetation mosaics) between 2001 and 2010	Collection 5 MODIS Global Land Cover Type product[62]
	Climate change	Climate change is a strong predictor of bird abundance changes[63].	Changes in mean Dec-Feb temperature between 1985-1990 and 2005-2010	CRU TS3.10 Dataset[64]
			Changes in mean Dec-Feb precipitation between 1985-1990 and 2005-2010	CRU TS3.10 Dataset[64]
Conservation efforts and effectiveness	Protected areas	Waterbird abundance increased more rapidly in protected than in unprotected wetlands[65,66].	Proportion of sites covered by protected areas	World Database on Protected Areas[67]
	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[68].	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[69,70].	Migrant or non-migrant	Birdlife Data Zone§
	Body size	Body size is a strong predictor of bird abundance changes[71] but its association with bird extinction risk can be both positive and negative, depending on threats to the species[72]	Body mass (g)	EltonTraits 1.0[73]

*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 ($n = 2{,}079$ grid cells)

	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

Gross domestic product (GDP) per capita is given as $\log_{10}$-transformed values. Strong correlations ($|r| > 0.7$) are shown in bold.

nature research

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☐ Initial submission ☐ Revised version ☒ Final submission

Life Sciences Reporting Summary

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For further information on the points included in this form, see Reporting Life Sciences Research. For further information on Nature Research policies, including our data availability policy, see Authors & Referees and the Editorial Policy Checklist.

Experimental design

1. Sample size

Describe how sample size was determined.

The sample size in this study was not pre-determined but essentially driven by the availability of data.

For the first part of our analyses ("Model for quantifying abundance changes" in the method section), we used as many available count records as possible, which determined the sample size in each population. We only used populations with 21 or more count records and this has resulted in 461 species being analysed in this study. We believe that having 21 or more records is sufficient to estimate the rate of change for the maximum of 23 years (between 1990 and 2013). The 461 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 driver analysis at the community level, sample size was 2,079, which was the total number of grid cells with at least one estimate of population-level change in any species. These grid cells are well scattered across the globe (as shown in Fig 2a, also see Supplementary Discussion) and we also believe that this sample size is large enough to test eleven explanatory variables.

For the driver analysis at species and population levels, we used only 293 species with change estimates available at ten or more grid cells. We believe that 293 species are sufficient to test the effect of 12 species-level predictors. The number of population-level predictors (six) may seem to be relatively large compared to the number of grid cells in some species, but coefficients for the population-level predictors were estimated as the random effect each governed by hyper-parameters; this structure is known to facilitate better parameterisation even with a relatively small amount of information.

We have also performed three types of sensitivity analyses, where (i) 14 seabird species in Alcidae, Procellariidae and Sulidae, (ii) 41 Christmas Bird Count (CBC) grid cells with neither landscape-scale wetlands nor local-scale surface water occurrences, and (iii) eight CBC grid cells with the proportion of urban areas over 0.3 were excluded respectively from the full dataset described above.

2. Data exclusions

Describe any data exclusions.

From the count data provided by data-providers, we only used data at survey sites with coordinate information. We then excluded populations with 20 or fewer records from the following analyses.

For the trend analysis, we excluded grid cells with, on average, three or fewer non-zero records per site in each population. After the trend analysis, we removed grid cells where parameter estimates did not converge even with the increased iterations (5,000,000) although the number of removed cells was very small (see the methods).

For the driver analysis at species and population levels, we excluded species with change estimates available at nine or fewer grid cells.

3. Replication

Describe whether the experimental findings were reliably reproduced.

Our study is not based on experiments and we thus did not replicate the analyses.

4. Randomization

Describe how samples/organisms/participants were allocated into experimental groups.

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 driver analyses, we used as many covariates as possible to account for effects of such potential biases in the data. We also used CAR models to account for spatial autocorrelation; this also reduces the effect of such spatial biases in data.

5. Blinding

Describe whether the investigators were blinded to group allocation during data collection and/or analysis.

Blinding is not relevant to our study as we did not use any experiments.

Note: all studies involving animals and/or human research participants must disclose whether blinding and randomization were used.

6. Statistical parameters

For all figures and tables that use statistical methods, confirm that the following items are present in relevant figure legends (or in the Methods section if additional space is needed).

n/a	Confirmed
☐	☒ The exact sample size (*n*) for each experimental group/condition, given as a discrete number and unit of measurement (animals, litters, cultures, etc.)
☐	☒ A description of how samples were collected, noting whether measurements were taken from distinct samples or whether the same sample was measured repeatedly
☒	☐ A statement indicating how many times each experiment was replicated
☐	☒ The statistical test(s) used and whether they are one- or two-sided (note: only common tests should be described solely by name; more complex techniques should be described in the Methods section)
☐	☒ A description of any assumptions or corrections, such as an adjustment for multiple comparisons
☐	☒ The test results (e.g. *P* values) given as exact values whenever possible and with confidence intervals noted
☐	☒ A clear description of statistics including central tendency (e.g. median, mean) and variation (e.g. standard deviation, interquartile range)
☐	☒ Clearly defined error bars

See the web collection on statistics for biologists for further resources and guidance.

Software

Policy information about availability of computer code

7. Software

Describe the software used to analyze the data in this study.

R 3.3.2 and WinBUGS 1.4.3

For manuscripts utilizing custom algorithms or software that are central to the paper but not yet described in the published literature, software must be made available to editors and reviewers upon request. We strongly encourage code deposition in a community repository (e.g. GitHub). *Nature Methods* guidance for providing algorithms and software for publication provides further information on this topic.

Materials and reagents

Policy information about availability of materials

8. Materials availability

Indicate whether there are restrictions on availability of unique materials or if these materials are only available for distribution by a for-profit company.

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.

9. Antibodies

Describe the antibodies used and how they were validated for use in the system under study (i.e. assay and species).

We did not use any antibodies.

10. Eukaryotic cell lines

a. State the source of each eukaryotic cell line used. — Not applicable

b. Describe the method of cell line authentication used. — Not applicable

c. Report whether the cell lines were tested for mycoplasma contamination. — Not applicable

d. If any of the cell lines used are listed in the database of commonly misidentified cell lines maintained by ICLAC, provide a scientific rationale for their use. — Not applicable

Animals and human research participants

Policy information about studies involving animals; when reporting animal research, follow the ARRIVE guidelines

11. Description of research animals

Provide details on animals and/or animal-derived materials used in the study. — We used observation data on 461 waterbird species (detail shown in Supplementary Data S2). Sex and age were not recorded in the surveys.

Policy information about studies involving human research participants

12. Description of human research participants

Describe the covariate-relevant population characteristics of the human research participants. — We did not use any human research participants.