INSTAAR are also available from ftp://aftp.cmdl.noaa.gov/data/trace_gases. Data from Heidelberg University are available from http://www.iup.uni-heidelberg.de/institut/forschung/groups/kk/en/Data_html. Data measured by University of Washington and University of California, Irvine, were taken from http://cdiac.ornl.gov/ndps/quay.html and http://cdiac.ornl.gov/epubs/db/db1022/db1022.html, respectively. Yearly δ^{13} C values for individual stations and global annual averages are presented in tables S3 and S4. This research was supported by the Marsden Fund Council from New Zealand Government funding, administered by the Royal Society of New Zealand. Further support came from NIWA under Climate and Atmosphere Research Programme CAAC1504 (2014/15 SCI). The authors declare no competing interests. H.S. designed the data analysis; G.W.B., T.M.B., R.J.M., J.B.M., D.C.L., B.H.V., C.V., and S.E.M. performed δ^{13}C measurements; C.V., J.B.M., I.L., D.C.L., and J.W.C.W. designed sampling and analytical programmes and performed data quality control; E.J.D. provided $[CH_4]$ data; K.R.L. and H.S. designed the box model; S.E.M.F. and H.S. performed uncertainty analyses; and all authors contributed to the interpretation and the writing of the manuscript.

SUPPLEMENTARY MATERIALS

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References (*34–47*)

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CLIMATE CHANGE

Consistent response of bird populations to climate change on two continents

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Global climate change is a major threat to biodiversity. Large-scale analyses have generally focused on the impacts of climate change on the geographic ranges of species and on phenology, the timing of ecological phenomena. We used long-term monitoring of the abundance of breeding birds across Europe and the United States to produce, for both regions, composite population indices for two groups of species: those for which climate suitability has been either improving or declining since 1980. The ratio of these composite indices, the climate impact indicator (CII), reflects the divergent fates of species favored or disadvantaged by climate change. The trend in CII is positive and similar in the two regions. On both continents, interspecific and spatial variation in population abundance trends are well predicted by climate suitability trends.

Evidence that climate change is affecting biodiversity is accumulating (*1*). Most of this evidence reveals impacts on natural populations in the form of shifts in geographic ranges, changes in abundance, or changes in individual behavior or physiology (*2*, *3*). Meta-analyses have identified widespread changes, consistent with expectations, in both the distribution of populations and the timing of events in the annual cycles of organisms (*4*–*6*). A growing body of evidence also suggests that morphological changes are a common response to altered climates (*7*, *8*). However, despite some clear cases of climate-caused alterations of local population dynamics (*9*, *10*), multispecies, large-scale analyses of population responses to global climate change are rare (*11*, *12*).

One way to assess widespread population responses to anthropogenic drivers is to derive indicators from composite trends of species' abundance (*13*). Multispecies indicators are now widely used to aggregate biodiversity information in a way that is understood by policy-makers and members of the public, enabling evaluations of progress toward biodiversity targets (*14*, *15*). Less frequently, differences in composite trends for groups of species differentially affected by change are used to highlight the role of specific drivers of abundance. For example, large-scale aggregated trends in European species' abundance have been linked to expected future changes in climatic suitability within the region to produce composite trends for species that are expected either to gain or to lose climatically suitable range in the future (*16*). One shortcoming of that approach is that relating changes in a species' population at a subcontinental level to climate change ignores important information about variation in population trends in different areas within the subcontinent. A species showing climate-driven decline at the low-latitude range margin but climate-driven increase at its poleward range margin (*17*) might not show a clear overall trend in abundance across its range. Furthermore, accounting for spatial variation in species' population trends will reduce covariation between climate change and land-use change (*18*).

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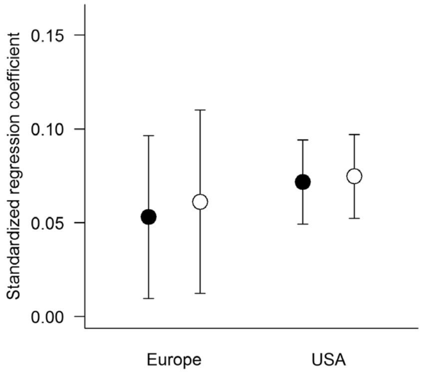
We developed an indicator to quantify the impacts of recent climate change on breeding range abundance in common birds, accounting for regional variation in both climate impacts and population trends. We applied this approach to two distinct subcontinents to evaluate, for the first time, how recent climate change has affected large numbers of species over extensive biogeographical regions. Developing our indicator involves six steps, including (1) selecting species abundance data for analysis; (2) fitting species' distribution models to species' occurrence data and concurrent long-term mean climate values for a single fixed time period, and applying those models to annual climate data to determine how climate suitability has changed for each species in each country or state in which it occurs; (3) checking that these climate suitability trends are informative predictors of abundance trends; (4) deriving composite multispecies abundance indices for each state or country, separately for species with positive climate suitability trends (hereafter, the CST+ group) and for those with negative climate suitability trends (the CST− group); (5) amalgamating country- or state-level information to produce subcontinental CST+ and CST− indices; and (6) contrasting the CST+ and CST− indices to produce a climate impact indicator (CII), which reflects the divergent fates of species favored and disadvantaged by climate change.

Fig. 1. Effect of climate suitability on bird population trends. Standardized regression coefficient of population trend at a country/state level on CST (with 90% confidence intervals) for European breeding birds (left two points) and U.S. breeding birds (right two points). Coefficients are from model averaging of multiple regression models (which consider body mass, habitat, and migratory behavior) of population trend on CST (solid circles) or from univariate models of population trend on CST (open circles) (*20*). All models contained the random effects of country/state and species.



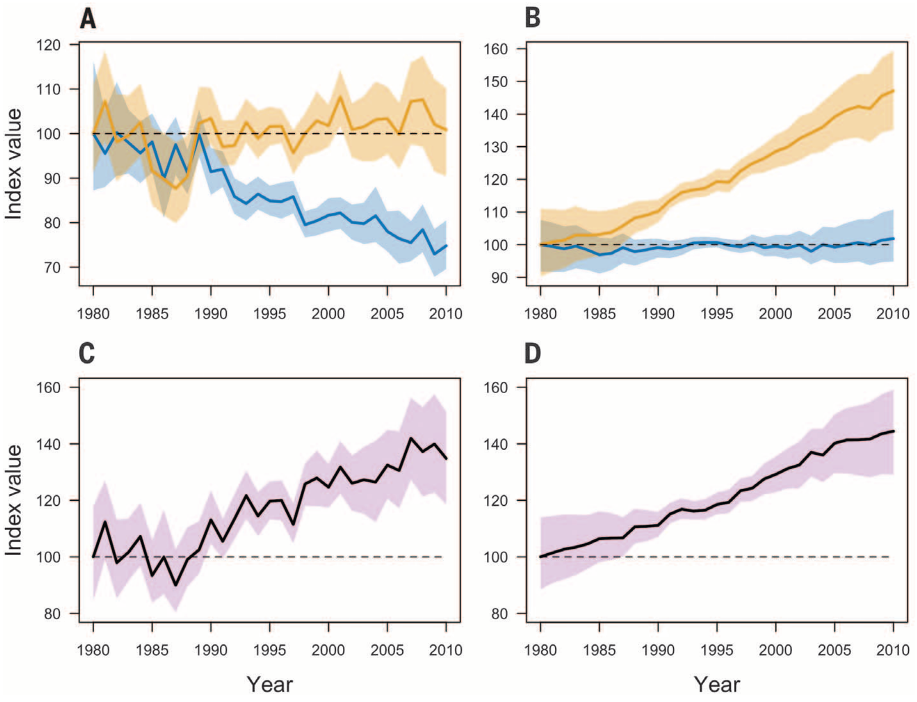


Fig. 2. Effect of climate on abundance trends of common birds. Multispecies population indices for CST+ (orange lines) and CST− (blue lines) groups combined across all eligible countries of Europe (**A**) and states of the United States (**B**). Shaded polygons in each case indicate 90% confidence intervals (produced from 2000 bootstrap replicates) (*20*). Annual values of the ratio of the CST+ index to the CST− index, the CII, are shown for Europe (**C**) and the United States (**D**). In all four panels, the index is arbitrarily set to 100 in 1980. Horizontal dashed lines at index values of 100 show the expectation if there is no trend; in (C) and (D), these indicate the expectation if climatic suitability played no role, and thus there was no difference in the composite trends for CST+ and CST− groups.

For Europe, we assessed indices of abundance for 145 species monitored by the Pan-European Common Birds Monitoring Scheme (*15*). For the United States, we used indices of abundance for 380 species monitored by the North American Breeding Bird Survey (BBS) (*19*). In both cases, we used data spanning the period from 1980 to 2010. To account for regional variation in climate impacts and species' trends, we used species' distribution models to identify the climate suitability trend for each species at the level of individual countries in Europe or states in the United States. The species' distribution models allow the calculation of probability of occurrence of the species under a particular combination of climatic conditions, represented by bioclimate variables (*20*), using species' distribution maps and concurrent long-term mean climate data. The climate suitability trend for a species represents the trend in its expected annual probability of occurrence, as derived from species' distribution models applied to annual climate data (*20*). These climate suitability trends are derived entirely independently of interannual changes in abundance within a focal species' range. We used linear mixed models to check that climate suitability trend was an informative explanatory variable for country- or state-level population trends, when potential confounding effects of life history and ecological covariates were allowed for (Fig. 1).

We allocated species at a country/state level to two groups: those expected from the species' distribution models to have been advantaged (climate suitability trend slope >0) or disadvantaged (climate suitability trend slope <0) by climate change during the study period (the CST+ and CST− groups). We derived composite population indices for both groups at the individual country or state level (see tables S1 and S2 for sample sizes in Europe and the United States, respectively). Individual species may occur in either group in different parts of their range. Within countries or states, composite population indices were derived by weighting abundance indices by the magnitude of species' climate suitability trends within CST+ and CST− groups (*20*). The result is that changes in populations of species that we expect (from species' distribution models) to be markedly affected by climate change would receive more weight in the composite index than would those of species for which the climate suitability trend was negligible. To produce subcontinental-scale composite indices for CST+ and CST− groups, composite indices for each group were combined without weighting (Fig. 2, A and B) (*20*).

The ratio of these indices (CST+:CST−), the CII (standardized to 100 in 1980), will be >100 in any year if populations expected to have been positively affected by climate change have increased more or declined less than those expected to have been negatively affected. We derived subcontinental CII values separately for Europe and the United

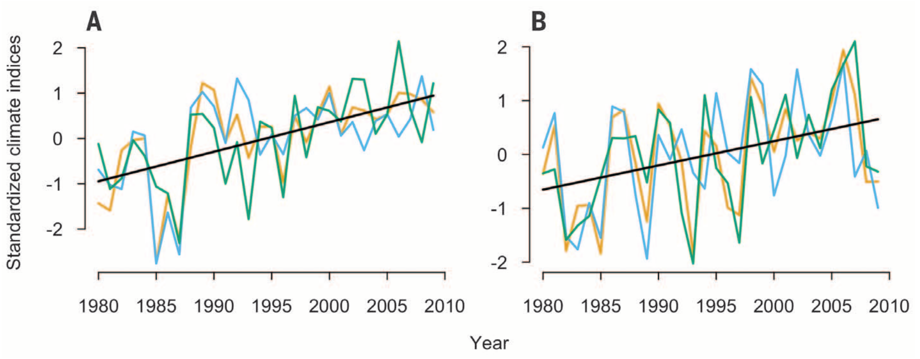


Fig. 3. Recent changes in climate in Europe and the United States. Changes in annual values of three measures of climate in the countries/states from which bird data were collected in Europe (**A**) and the United States (**B**): mean annual temperature (blue lines), mean temperature of the coldest month (orange lines), and growing degree days above 5°C (green lines). Each variable is standardized to have zero mean and unit variance. Black lines show a least-squares regression fitted to the annual standardized values for all three variables combined. Analysis of covariance provided no support for different slopes for the three climate variables or differences between Europe and the United States.

States (combining country and state CIIs, respectively) (*20*). Calculating CIIs for these geographically distinct subcontinents with very different breeding bird species assemblages allows us to examine the transferability of our approach. Plotting these CII values over time can demonstrate long-term trends in the response of species to climate. Because recent climate change is likely to have manifested itself in different ways across the two subcontinents, a common trend in the magnitude and direction of the CII would provide compelling evidence that recent climate change is affecting populations of many species across extensive areas of the world.

Overall trajectories of avian abundance in recent decades differ somewhat between the two subcontinents, suggesting rather different ecological backdrops. Specifically, the average trend of avian abundance in Europe has been largely negative since 1980 (*21*), whereas the average trend of avian abundance in the United States has been relatively stable over recent decades (*22*). This difference is reflected in the composite indices: Although the CST+ group index has been largely static in Europe and the CST– group has declined, in the United States these groups have shown a pronounced increase (CST+) or remained stable (CST–). Nevertheless, in both regions, the CST+ and CST– indices show a striking divergence, in the expected direction, with the composite population indices of species in the former group being markedly more positive than those in the latter group.

The ratio of the CST+ to CST– composite indices amalgamated to the subcontinental scale gives the subcontinental CIIs (Fig. 2, C and D). The CII for Europe is based on fewer species, fewer geographic subdivisions, and a less-consistent duration of monitoring across the region. This results in it being more variable than that for the United States. Nevertheless, trends in the two CIIs show some striking similarities. In particular, both clearly deviate from a value of 100 (indicating the divergence of the CST+ and CST– groups) by the mid- to late 1980s. Both then climb strongly to reach an index value of about 140 by 2010, highlighting the markedly stronger performance of species in the CST+ group. An analysis of standardized climate variables over the period shows no evidence for differences in the rate or scale of climate change in the two regions (Fig. 3) (*20*).

The strength and consistency of the CII across two very different assemblages (only six species are common to both), which appear to be experiencing very different overall population trends, provide evidence that this phenomenon is not peculiar to a single subcontinent. Isolating the contribution of climate change on the two subcontinents from that of other potential drivers of avian population change should stimulate further research into the factors that underlie the strong differences between the United States and Europe in the trajectories of composite multispecies trends (both CST+ and CST–) (Fig. 2, A and B). In both areas, the CII is more strongly positive than a previous index for Europe that linked multispecies trends in population size at a subcontinental level to the expected future effects of climate change (*16*). This emphasizes the value of using geographic variation of species' trends within the range and allowing a species to contribute to both the CST+ and CST– groups, according to differences in the suitability trend in different areas.

The widespread changes that we detect are based on the commonest bird species across a diversity of ecosystems in Europe and the United States. For example, the 145 European species we consider make up about 89% of the total number of individual terrestrial breeding birds in Europe (*23*). Common species dominate ecosystems, and even small changes in their abundance can lead to large changes in ecosystem structure, function, and service provision (*24*). Therefore, the changes that we have detected in common birds are already likely to be affecting ecosystems and associated services. If similar abundance changes are occurring across common species in other taxa, ecosystems may be further affected. Impacts arising from changes in bird abundances will become more pronounced if their populations continue to follow their current climate-influenced trajectories. Although our index is based on the abundance of common bird species, population trends of rare species have also been shown to be related to climatic changes (*25*). Our indicator could be applied wherever sufficient monitoring data exist. However, because long-term population monitoring data sets are rare for large tropical and subtropical regions and for the Southern Hemisphere (*26*), we cannot evaluate whether the changes we have observed apply globally. Population monitoring at low latitudes and in the Southern Hemisphere should be a future priority to identify climate-driven changes that might be occurring in these areas.

Ecological indicators, including some indicators of climate change impacts, are already being used to monitor the global state of ecosystems (*13*). Our precursor CII (*16*), based on future climate projections, has been adopted as an indicator to assess progress toward achieving the United Nations Convention on Biological Diversity's Aichi biodiversity targets (*27*), as a metric of climate change impacts on terrestrial ecosystems. The new indicators we have developed provide a first means of assessing impacts of contemporary climate on the abundance of populations, and we have shown their utility across two large areas of the world. Future updates of the CII should provide a valuable means to track the extent of impact of future climate change on species.

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CONFLICT BEHAVIOR

Social conflict resolution regulated by two dorsal habenular subregions in zebrafish

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When animals encounter conflict they initiate and escalate aggression to establish and maintain a social hierarchy. The neural mechanisms by which animals resolve fighting behaviors to determine such social hierarchies remain unknown. We identified two subregions of the dorsal habenula (dHb) in zebrafish that antagonistically regulate the outcome of conflict. The losing experience reduced neural transmission in the lateral subregion of dHb (dHbL)–dorsal/intermediate interpeduncular nucleus (d/iIPN) circuit. Silencing of the dHbL or medial subregion of dHb (dHbM) caused a stronger predisposition to lose or win a fight, respectively. These results demonstrate that the dHbL and dHbM comprise a dual control system for conflict resolution of social aggression.

Aggression is an evolutionarily conserved behavior critical for animal survival (*1*, *2*). When conflict is unavoidable, animals use aggression to establish a social hierarchy that determines how to share limited resources (*2*). Most animal conflicts aim at establishing a social hierarchy rather than causing lethal damage to opponents (*1*–*4*), which achieves the best cost-benefit for the group. However, the biological mechanisms governing the resolution of social conflict remain largely unknown. To address this question, we isolated adult male zebrafish for 24 hours and then put them together to fight in pairs (Fig. 1A) (*5*). Dyadic male zebrafish fights proceed in a stereotypic manner, starting with each animal exhibiting display behaviors, followed by circling and biting attacks, and ending when one fish shows fleeing behavior indicating surrender (Fig. 1B and movie S1) (*5*).

To investigate the neural circuits underlying the regulation of social conflict, we focused on the dorsal habenula–interpeduncular nucleus (dHb-IPN) pathway. We previously demonstrated that the lateral subregion of the zebrafish dHb (dHbL) sends axons to the dorsal IPN (dIPN) and the intermediate IPN (iIPN) (Fig. 1C), and efferent axons from the d/iIPN pass through the dorsal raphe to reach the dorsal tegmental area (DTA) (*6*, *7*) containing a putative region corresponding to the mammalian periaqueductal gray (PAG) (Fig. 2A). Because the PAG regulates fight, flight, and freezing behaviors (*8*), we wondered if the dHbL-d/iIPN pathway signals information critical for fight and flight behaviors during aggressive conflicts. We performed calcium imaging of acute brain slices to visualize neural activity after electrical stimulation of the Hb (Fig. 2A and fig. S1). In both naïve and winner fish, we found an intense activity spot in the dIPN and scattered spots in the DTA region (Fig. 2, B and C, and movies S2 and S3), reflecting activation of the dHbL-d/iIPN-DTA pathway. In contrast, in loser fish we observed intense activity mainly in the ventral IPN (vIPN) and the median raphe (MR) (Fig. 2D and movie S4). In the dIPN, the peak of fluorescence intensity in winners was similar to that in naïve fish but was significantly reduced in losers (Fig. 2E). In the vIPN, we found a higher fluorescence intensity in loser fish than in winner and naïve fish, although it did not reach statistical significance (Fig. 2E).

To further investigate neural activity of the dHbL-d/iIPN and dHbM-i/vIPN circuits in winner and loser states, we performed in vivo electrophysiological recordings of local field potential (LFP) in the IPN (Fig. 2F). In the dIPN, the LFP amplitude evoked by electrical stimulation in the left Hb was similar between winners and naïve fish but was significantly reduced in losers (Fig. 2, G and H). In contrast, naïve fish, winners, and losers showed similar LFP levels in the vIPN (Fig. 2, G and H) (*9*). Reduction in the transmission of the dHbL-d/iIPN circuit thus reflects a loser state, consistent with our calcium imaging data. The peak time latency and half decay time were similar among all conditions (fig. S2). Moreover, tract tracing results showed that the dIPN neurons coursed dorsally and caudally to extend to the DTA (Fig. 2I), whereas the vIPN neurons projected to the MR (Fig. 2J), which is consistent with our previous data (*6*) and supports our calcium imaging results.

To investigate how the dHbL-d/iIPN and dHbM-i/vIPN pathways participate in fighting behaviors, we perturbed these neural circuits in adult zebrafish. To silence the dHbL-d/iIPN pathway, we used a double transgenic line *Tg*(*narp:GALVP16*);*Tg*[*UAS:tetanus neurotoxin* (*TeNT*)] in which neurotransmission from the dHbL to the d/iIPN is selectively inhibited (*6*). We confirmed that TeNT is specifically expressed in the dHbL, by checking its expression in the *Tg*(*narp:GALVP16*);*Tg*(*UAS:TeNT*);*Tg*(*brn3a-hsp70:GFP*) zebrafish (Fig. 3A), and effectively blocks neurotransmission (fig. S3). To inhibit the dHbM-i/vIPN pathway, we first generated a transgenic line *Tg*(*gpr151:GALVP16*);*Tg*(*UAS:GFP-TeNT*) and then confirmed the gpr151:GALVP16-induced green fluorescent protein (GFP) expression in the dHb (Fig. 3B-1). Next, we crossed the *Tg*(*brn3a-hsp70:GFP-Cre*) with a glutamatergic neuron-specific line, *Tg*(*vglut2a:loxP-DsRed-loxP-GFP*) (*10*), in which glutamatergic neurons in the dHbM and ventral Hb (vHb) express GFP (Fig. 3B-2). Finally, we generated a triple transgenic line *Tg*(*gpr151:GAL4VP16*);*Tg*(*brn3a-hsp70:GFP-Cre*);*Tg*(*UAS:loxP-DsRed-loxP-GFP-TeNT*) in which GFP-TeNT was induced intersectionally only in the dHbM, and their axons could be observed in the vIPN (Fig. 3B-3 and fig. S4). These two Tg lines showed normal growth at developmental and adult stages, and the Hb-IPN circuit and structures throughout the whole brain were not affected (fig. S4) (*6*).

Next, we let the dHbL- and the dHbM-silenced fish fight against their wild-type (WT) siblings.

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Consistent response of bird populations to climate change on two continents

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Editor's Summary

Birds populations allied in abundance

Changes in climate can cause populations of species to decline, to increase, or to remain steady. Stephens *et al.* looked across species of common birds in Europe and the United States. Despite many differences between the two regions, expectations about how a species might respond to climate change did predict actual responses. Species predicted to benefit from increasing temperatures, or their associated effects, tended to increase, whereas those predicted to be negatively affected declined. Thus, even across widely varying ecological conditions and communities, climate change can be expected to alter population sizes.

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