Title: Consistent response of bird populations to climate change on two continents

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Abstract: 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. Here, we use long-term monitoring of the abundance of breeding birds across Europe and the USA 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.

One Sentence Summary: Common birds across Europe and the USA have been similarly affected by climate change over the last 30 years.

Main Text:

Evidence that climate change is impacting 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*), multi-species, 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*). Multi-species 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 towards 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 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 sub-continental level to climate change ignores important information about variation in population trends in different areas within the sub-continent. 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*).

Here, we develop 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 apply this approach to two distinct sub-continents to evaluate, for the first time, how recent climate change has impacted 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 within which it occurs; (3) checking that these climate suitability trends are informative predictors of abundance trends; (4) deriving composite multi-species 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 sub-continental 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.

For Europe, we assess indices of abundance for 145 species monitored by the Pan-European Common Birds Monitoring Scheme (*15*). For the USA, we use indices of abundance for 380 species monitored by the North American Breeding Bird Survey (BBS) (*19*). In both cases, we use 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 within Europe, or states within the USA. 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*). Importantly, 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 trend, 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 USA, 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 climate suitability trend was negligible. To produce sub-continental scale composite indices for CST+ and CST- groups, composite indices for each group were combined without weighting (Fig. 2A,B) (20).

The ratio of these indices (CST+:CST-), the Climate Impact Indicator (CII, standardized to 100 in 1980), will be >100 in any year if populations expected to have been positively impacted by climate change have increased more or declined less than those expected to have been negatively affected. We derive sub-continental CII values separately for Europe and the USA (combining country/state CIIs respectively) (20). Calculating CIIs for these geographically distinct sub-continents 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. As recent climate change is likely to have manifested itself in different ways across the two sub-continents, a common trend in the magnitude and direction of the CII would provide compelling evidence that recent climate change is impacting populations of many species across extensive areas of the world.

Overall trajectories of avian abundance in recent decades differ somewhat between the two sub-continents, 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 USA has been relatively stable over recent decades (22). This difference is reflected in the composite indices: whilst the CST+ group index has been largely static in Europe and the CST- group has declined, in the USA 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 sub-continental scale gives the sub-continental CIIs (Fig. 2C,D). The CII for Europe is based on fewer species, fewer geographic sub-divisions and a less consistent duration of monitoring across the region. This results in it being more variable than that for the USA. 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 c. 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, provides striking evidence that this phenomenon is not peculiar to a single sub-continent. Isolating the contribution of climate change on the two sub-continents from that of other potential drivers of avian population change should stimulate further research into the factors that underlie the strong differences between the USA and Europe in the trajectories of composite multispecies trends (both CST+ and CST-) (Fig. 2A,B). In both areas, the CII is more strongly positive than a previous index for Europe that linked multi-species trends in population size at a sub-continental 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 USA. For example, the 145 European species we consider comprise circa 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 impacting ecosystems and associated services. If similar abundance changes are occurring across common species in other taxa, ecosystems may be further impacted. 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 datasets are rare for large tropical and sub-tropical 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 towards achieving the UN Convention on Biological Diversity's Aichi biodiversity targets (*27*), as a metric of climate change impacts on terrestrial ecosystems. The new indicators we develop here 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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Supplementary materials

Materials and methods
Fig. S1
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References (*28-64*)

Fig. 1. Effect of climate suitability on bird population trends. Standardised regression coefficient of population trend at a country/state level on CST (with 90% confidence intervals) for European (left two points) and USA breeding birds (right two points). Coefficients are from model averaging of multiple regression models (which consider body mass, habitat and migratory behaviour) of population trend on CST (filled 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. Multi-species population indices for CST+ (━━━━━━) and CST- (━━━━━━) groups combined across all eligible countries of Europe (A) and states of the USA (B). Shaded polygons in each case indicate 90% confidence intervals (produced from 2,000 bootstrap replicates) (*20*). Annual values of the ratio of the CST+ index to the CST- index, the CII, are shown for Europe (C) and USA (D). In all four panels the index is arbitrarily set to 100 in 1980. Horizontal broken lines at index values of 100 show the expectation if there is no trend; in panels (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.

Fig. 3. Recent changes in climate in Europe and the USA. Changes in annual values of three measures of climate in the countries/states from which bird data were collected in Europe (A) and the USA (B): mean annual temperature (━━━━━━), mean temperature of the coldest month (━━━━━━) and growing degree days above 5°C (━━━━━━). Each variable is standardised to have zero mean and unit variance. Black lines show least squares regression fitted to the annual standardised 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 USA.
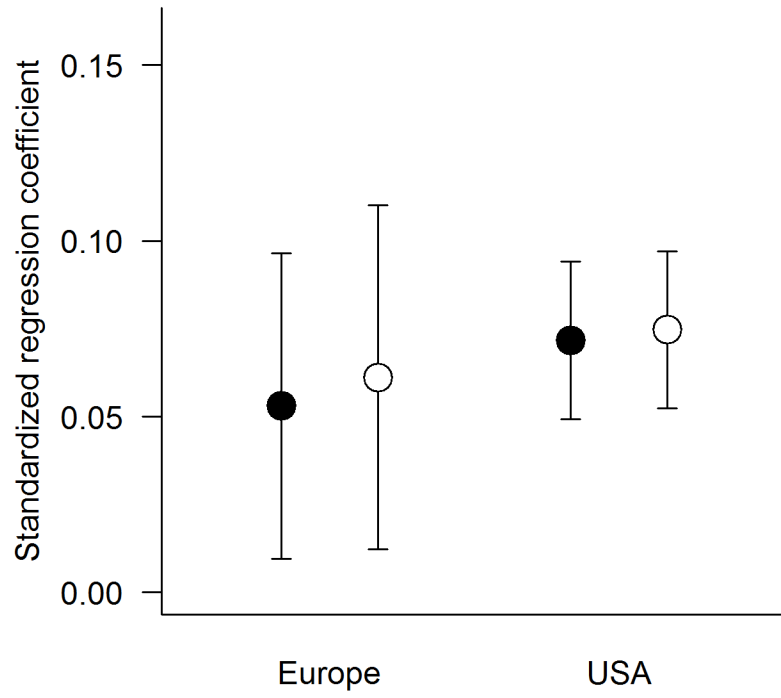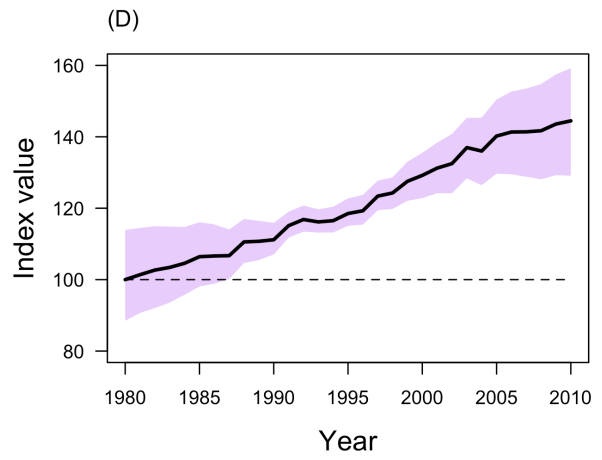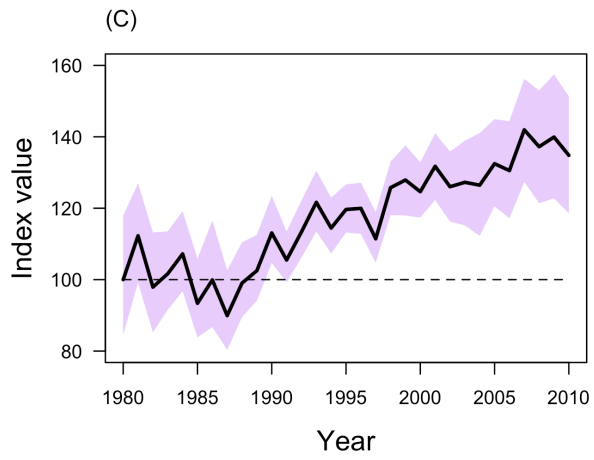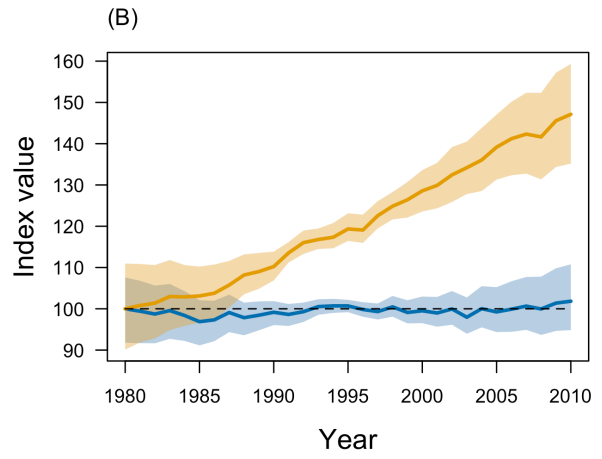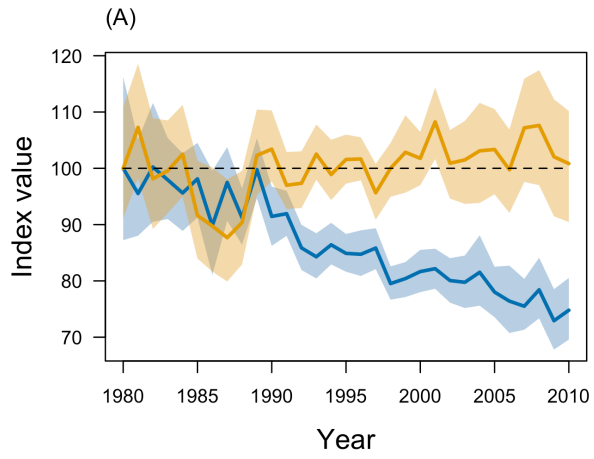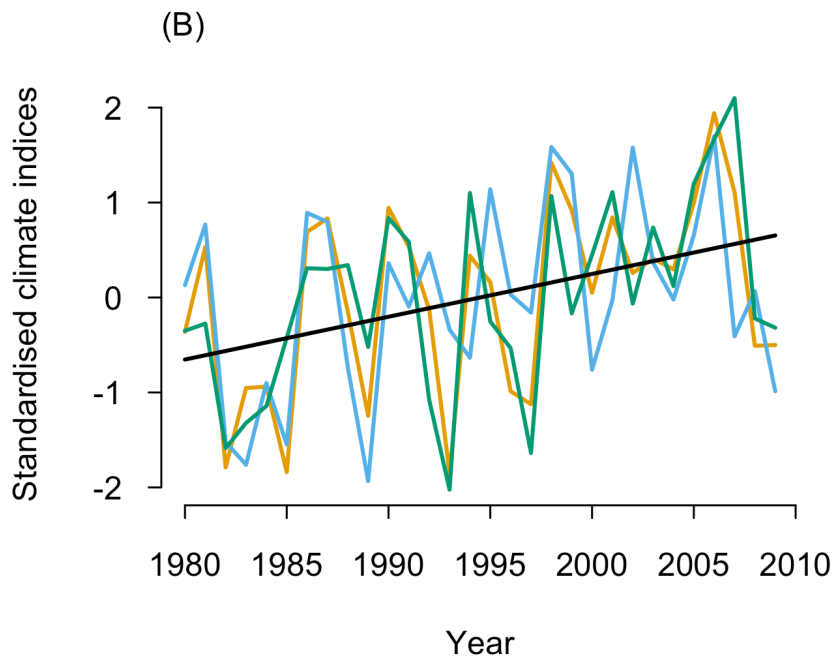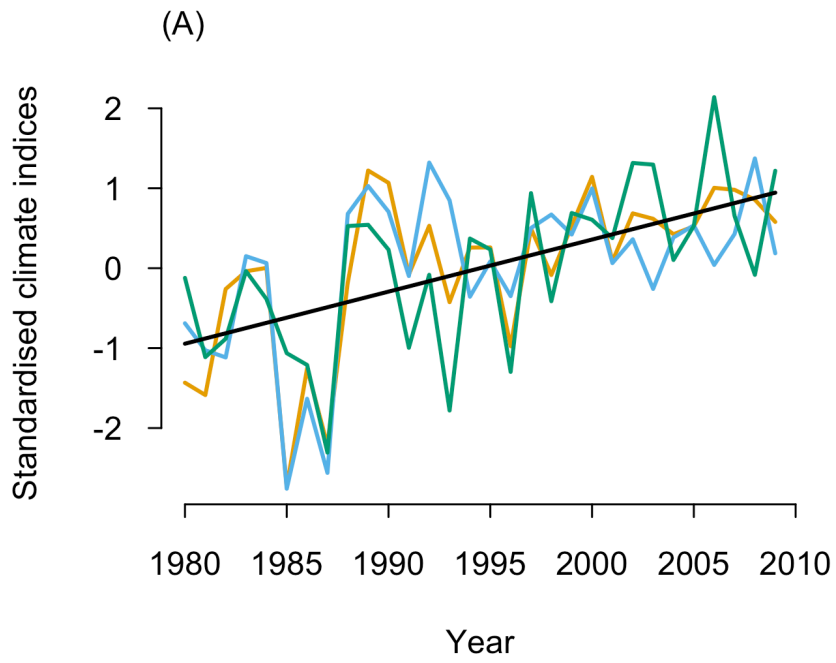
Fig. 1

Fig. 2

Fig. 3

(A)

(B)

Supplementary Materials for

Consistent Response Of Bird Populations To Climate Change On Two Continents

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Materials and Methods
Fig. S1
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Materials and Methods

1. Deriving the Climate Impact Indicator (CII)

   Deriving the Climate Impact Indicator (CII) involves six steps, including: (1) selecting species abundance data for analysis; (2) determining climate suitability trends (CSTs) for the selected species at a country or state level; (3) checking that CST is an informative predictor of abundance trends; (4) deriving composite multi-species abundance indices for each state or country, separately for species with positive CSTs (the CST+ group) and for those with negative CSTs (the CST- group); (5) amalgamating country or state-level information to produce subcontinental CST+ and CST- composite abundance trends; and (6) contrasting the CST+ and CST- trends to produce a climate impact indicator (CII), which reflects the divergent fates of species favored and disadvantaged by climate change. We also (7) describe how we compute confidence intervals for all indices. We describe methods for each of these steps in turn.

1.1.   Selecting abundance data

   For Europe, we obtained population trend data from the Pan-European Common Bird Monitoring Scheme (http://www.ebcc.info/pecbm.html) for 145 species for which reliable European species' indices were available up to 2010 (Table S3). Indices of abundance were available for each species for 1-20 countries (where East and West Germany are included as 2 countries, owing to historical differences in bird monitoring) (Table S3). For North America, we focused on the 48 contiguous states of the USA, where monitoring is most widespread. Reliable survey-wide trends, estimated from the data held at https://www.pwrc.usgs.gov/bbs/RawData/ using hierarchical models (*22*), were available for 425 species monitored in the Breeding Bird Survey (BBS). We focused on terrestrial species and therefore excluded birds listed as seabirds by BirdLife International. We also excluded introduced species and one species (the northwestern crow, *Corvus caurinus*) with a very restricted range and highly variable dynamics in the focal area (see next paragraph). Analyses were based on the remaining 380 species (Table S4), each occurring in between one and 48 states (Table S3). Hereafter, we refer to lower level geographic areas (countries or states) simply as states.

   The existing compilations of annual abundance data that we used were based on surveys conducted annually using repeatable methods, generally point counts and line transects (*28*). Count data from individual surveys from a state were analysed using published methods to give a time series of annual population index values for each species and state (*22,29*). These time series data on abundance are totally independent from the spatial presence/absence data used in fitting species distribution models (see SOM 1.2.2.).

   All index values were coded as "NA" until the species' monitoring commenced in the state, and the index was set to 100 in the first year of monitoring. Index values of zero that occurred between non-zero values were changed to 0.1 to enable the calculation of log-changes (see further below). Terminal series of zero index values imply extirpation; in those cases, the first zero value was changed to 0.1 and subsequent zeros were changed to "NA" to prevent the calculation of changes among those years. The Europe and USA data sets were quality controlled using two a priori rules. First, state-

wide indices of abundance for any species were included only if that species had been monitored since at least 2000. Second, we excluded state-level indices of abundance for any species that displayed population fluctuations too large to be likely to be the result of population changes within that state. Such changes can occur in irruptive species, populations of which can change markedly from one year to the next within a state as a result of movement among states. Such population changes are likely to be strongly influenced by climate changes beyond the focal state. Large apparent fluctuations could also occur for species that are very rare or which have been poorly monitored. We saw examples of both the above situations when exploring the raw index data. We defined changes that were too large to reflect natural events, or that probably reflected irruptive events, as those where the population of a species in a state showed annual increases or reductions of a magnitude greater than a factor of 10 between two successive years. The result was that we analyzed 1,686 time series of abundance indices for species occurring within European countries and 6,760 time series of abundance indices for species occurring with states in the USA.

1.2. Deriving CSTs

Calculating CSTs requires appropriate climate data, species' occurrence data, species' distribution models (SDMs) to link the two and produce probabilities of occurrence, and slope estimation for the final CST. We describe these components in turn.

1.2.1 Climate data

Monthly mean values for cloud cover, precipitation and temperature from 1961 to 2010 were obtained from Worldclim (*30; http://www.worldclim.org/*) and CRUTS3.1 (*31*) Soil water capacity data were obtained from (*32*). For Europe, climate data were interpolated, using bilinear interpolation, onto a grid of c. 50 x 50 km Universal Transverse Mercator (UTM) squares adopted for the EBCC breeding birds atlas (*33*). For North America and North Africa (see 2.2, below), climate data were on a 0.5° grid. Bioclimate variables were derived from climate data following (*32*). Following (*16*), the bioclimate variables used in the SDMs were: annual temperature sum above 5°C (GDD5); mean temperature of the coldest month (MTCO); and an estimate of the annual ratio of actual to potential evapotranspiration (APET). These variables can serve to limit species' ranges either directly, or indirectly through effects on vegetation, prey, predators, competitors or diseases.

1.2.2 Species' occurrence data

To avoid truncating the climatic niche (*34*), SDMs for European birds used occurrence data from both Europe and North Africa (down to latitude 20° North), ensuring that the southern margin of the Palearctic Realm was fully encompassed. Occurrence (presence or absence) data for (taken from the EBCC atlas of European breeding birds; *33*) were on a 50km UTM grid, whilst those for North Africa, Turkey and Cyprus (gridded from polygons in *35*) were on a 0.5° grid. For North America, occurrence data (also gridded from polygons in *35*) spanned the whole continent (from latitude 10° North) on a 0.5° grid.

Sources of data for the distribution maps used to fit SDMs were derived from fieldwork done independently from, and generally earlier than, the point counts and transects from which population changes were measured (see SOM 1.1.). For example, the European distribution data are from an atlas project based mostly upon fieldwork done in the 1980s (*33*). Other distribution data for North Africa, Turkey, Cyprus and North America are from a global compilation of bird atlas information and distribution maps by BirdLife International (*35*). These surveys of distribution did not assess change and were not used in the estimation of population trends.

1.2.3   Species distribution models

For each species, we determined the association between occurrence data and mean climate from 1961-1990 by fitting four types of SDM (following *36*). We chose methods that have performed well in comparisons of techniques (*37-42*) and that provide a contrast between parametric Generalized Linear Models (GLMs (*43*)); semiparametric Generalized Additive Models,(GAMs (*44, 45*)); and machine learning approaches including Generalized Boosted Models (GBMs (*46, 47*)) and Random Forests (RFs (*48, 49*)).

GLMs were fitted to binomial presence/absence data with each possible combination of up to four polynomial degrees (from linear to fourth order polynomial) for the three bioclimatic variables, resulting in 64 fitted models for each species. We used cross-validation to select among these models and to minimize spatial autocorrelation. Specifically, we used the 'blockTools' package in R (*50*) to divide the occupancy data into ten similarly-sized blocks, such that the blocks had similar mean values for the three bioclimate variables but each block spanned the full range of bioclimates. Blocks comprised spatially disaggregated sampling units which, themselves, consisted of global ecoregions (http://www.worldwildlife.org/science/data), or parts of ecoregions if the ecoregions were very large. Large ecoregions (greater than 250,000 km^2) were split into smaller sampling units by intersecting them with a 2.5° by 2.5° grid to create smaller subunits of a comparable size to smaller ecoregions. Areas separated geographically can comprise the same ecoregion; however, non-contiguous areas of the same ecoregion were considered separate sampling units. Models were fitted to data from nine blocks, excluding each block in turn. Each fitted model was used to predict probability of occupancy for each cell in the left-out block. When these probabilities of occupancy were reassembled for the entire area, the selected model (i.e., the best polynomial degree associated with each of the three bioclimate variables) was that which maximized AUC, the area under a receiver operating characteristic curve (*51*) (Table S5).

GAMs were fitted as thin-plate regression splines with the smoothness established using generalized cross-validation (*45*). Models were fitted to each species' data excluding one block at a time using the 'gam()' function from the 'mgcv' package in R (*52*). As with other modeling approaches, we determined overall model quality by amalgamating predicted probabilities of occupancy for all left-out blocks and reporting AUC (Table S5).

GBMs depend on parameters including the learning rate (lr), which controls the weight that is given to each component tree; the tree complexity (tc), which controls the number of nodes within each tree; and the number of trees (nt) kept in the final model. Building on the findings of Bagchi et al. (*36*) and also on our own preliminary

assessments, we found that results were robust to number of trees and to learning rate (as long as that was relatively low; (*47*); consequently, we used lr = 0.001 and nt = 5000 throughout. We summed error across omitted blocks (using the blocking and cross-validation approaches described for GLMs and GAMs) and chose the tree complexity (between 1 and 4) based on minimizing this criterion. Again, reported AUCs (Table S5) are determined based on the predicted probabilities of occupancy for the whole area, based on reassembling predictions for each left-out block.

Finally, RFs depend on the number of trees (nt) and the number of predictors used to build each tree (m) (*38*). The number of predictors, m, was allowed to vary between 1 and 3, and an RF with 1000 trees was fitted omitting each block in turn (*36*). The ability of the model to predict the species' occurrence in the omitted block was assessed using AUC. A further 500 trees were then added and the AUC for the omitted block computed again. If the larger model improved the AUC by more than 1% it was accepted. This was repeated iteratively until additional trees did not improve the AUC further. The value of m that maximized mean AUC for the excluded data across the 10 blocks, and the maximum nt used across the blocks, were used to fit final models for the species, excluding each block in turn. Reported AUCs (Table S5) were determined, again, based on the predicted probabilities of occupancy for the whole area, based on reassembling predictions for each left-out block.

Reported AUCs for both sub-continents and all modeling methods were high (Table S5). Mean AUC (± standard deviation) for all SDM types across species in Europe was 0.95 (± 0.03) (except random forests, mean = 0.96 ± 0.03). Similarly, for the USA, mean AUC was 0.97 (± 0.03) for all SDMs.

1.2.4   <u>Calculating the CST</u>

For a given species and geographic area (Europe or the USA), the ten models fitted using each SDM approach (i.e., the model fitted with each block omitted) were applied to annual bioclimate data from all focal states for each of the years 1980-2010. Predicted probabilities of occurrence were averaged across the ten models for each cell to give the probability of occurrence for that cell in that year from the given SDM method. Probability of occurrence for each cell was then averaged across the four SDM approaches to give an ensemble probability of occurrence for the given cell in the given year. For a given state and year, annual mean probability of occurrence was averaged across all cells in the state. For a given species in a given state, the CST was calculated as the slope of an ordinary least squares linear regression of logit annual mean ensemble probability of occurrence on year. CST was calculated from 1980 or the first year of monitoring (whichever was later) to 2010 or the year of extirpation (whichever was earlier).

Notice that CST is based on the relationship between bioclimate and distribution, determined using SDMs conditioned on distribution data collated predominately from the second half of the 20th century, together with contemporaneous long-term mean climate data (see Sections 1.2.2 and 1.2.1). Applying these SDMs to annual bioclimate data from 1980-2010 allows us to determine the expected change in species-specific climate suitabilities in a way that is based only on changes in climate and is entirely independent of observed changes in species' abundances.

<u>1.3.</u>   <u>Relationship</u> <u>between</u> <u>CST</u> <u>and</u> <u>abundance</u> <u>trend</u>
    We explored the effect of CST on abundance trends using statistical models in which abundance trend was the response variable. For a given species and state, the abundance trend was calculated as the slope of the regression of the natural logarithm of abundance index on calendar year (n = 1686 for Europe; n = 6760 for USA) across the same time period used to develop the CST (1980–2010) (Table S6). A crude sense of geographic variability in the relationship between abundance trends and CST can be gained by examining that relationship at a state level, using simple linear regressions (Fig. S1).
    Simple regressions such as those underlying Fig. S1 are confounded by an array of species-specific attributes. For example, in addition to the effects of CST, abundance trends may be affected by factors such as breeding habitat, migratory status and life-history characteristics. We used linear mixed models (LMMs) to check whether CST was an important covariate of abundance trend when these other variables were taken into account. We used the natural logarithm of mean body mass in grams (Lmass) as a proxy for other life history traits (with which it is correlated). Body mass was estimated as the mean of reported male or female body mass in grams or, where this was not available, from unsexed birds, taken from reference (*53*) for Europe, or BirdLife International's World Bird Database (*54*) for the USA. All species on each continent were assigned to one of four habitat categories (HAB). For Europe, these were forest, farmland, inland wetland or other. Designations were taken from PECBMS species habitat classifications by country in each bio-geographical region (*55, 2012 version*), supplemented by the habitat classifications used by Gregory et al. (*16*) and expert opinion. For the USA, habitat preferences were obtained from BirdLife International (*56*) and were classified as forest and shrubland, grassland, wetland, or other. European birds were assigned a categorical migratory behavior variable (MIG) by allocating each species, by state, to one of the categories defined by Gregory *et al.* (*16*): *long-distance migrants* (LD) – all or most individuals make regular seasonal movements between the European breeding range and a non-breeding range that lies outside the countries contributing data to the PECBMS and outside the Palaearctic region (e.g. to sub-Saharan Africa); *short-distance migrants* (SD) – all or most individuals make regular migratory or dispersive movements within the Palaearctic region and the area covered by our population monitoring network; *residents* (R) – most individuals are non-migratory, though some individuals may make irregular long distance movements within the area covered by our population monitoring network. Where necessary, migratory behavior was clarified with detailed reference to the text and maps in reference (*53*), supplemented by available European migration Atlases (*57-60*). For the USA, we used four classifications of migration behavior: *long-distance migrants* (LD) – non-breeding range occurs predominately below 25°N (the southern tip of Florida); *short-distance migrants* (SD) – non-breeding range occurs predominately above 25°N; *residents* (R) – breeding and non-breeding ranges overlap by over 50%; and *mixed* (M) – insufficient information is available to determine where birds from that state migrate to outside the breeding season but the species is known to migrate to both short and long distance destinations. Where necessary, migratory behavior was clarified with detailed reference to the text and maps in Poole (*61*).

We fitted LMMs containing all possible combinations of HAB, MIG, Lmass, CST, and the 2- and 3-way interactions between HAB, MIG and LMASS. All models incorporated the crossed random effects of species and state, thus accounting for the non-independence of trends among states within species, and among species within state. These random effects were found to provide the best fit in terms of AIC_c (Akaike's Information Criterion corrected for small sample size (*62*)) when compared to models with alternative random effect structures. Models were run using the lmer function from the lme4 package in R (*52, 63*). Model selection followed the recommendations of Richards (*64*), whereby all models with $\Delta AIC_c < 6$ are retained, excluding those with higher AIC_c values than simpler, nested alternatives. Model log-likelihood, AIC_c and AIC_c weights were determined for each model (*62*) and were used to calculate weighted average multiple regression coefficients and unconditional standard errors of population trend on CST. We calculated 90% confidence intervals for each regression coefficient, as well as for the derived standardized regression coefficient (coefficients were standardized by multiplying the crude coefficient by the standard deviation of CST and dividing by the standard deviation of population trend) (Table S7).

1.4.   Composite abundance indices at the state level
     From the set of species analyzed, all bird species in a state were divided into two groups on the basis of their CST. Hereafter, these are referred to as CST+ species, for which climate suitability showed an increasing trend throughout the period of monitoring, and CST- species, for which climate suitability showed a declining trend. Within each state, we determined the composite abundance indices for both the CST+ and CST- groups, weighted for the expected impact of climate (e.g., species with a highly negative CST had a stronger impact on the composite index of the CST- group than did species with only a slightly negative CST). Composite indices for a given group (CST+ or CST-) were determined as follows.
     Following Gregory et al. (*16*), we converted the abundance index series for the *i*th species, of length *k*, into *k*-1 values of $X_{i,j} = \log(N_{i,j+1} / N_{i,j})$, where $N_{i,j}$ is the population index value for the year *j* and $N_{i,j+1}$ is the population index in the following year. We calculated a weight, $w_{i,j}$, for the *i*th species in the *j*th year as

$$w_{i,j} = \frac{|CST_i|}{\sum_{S=1}^{v} |CST_S|} \tag{1}$$

where *v* is the number of species for which there is an eligible value of $X_{i,j}$ in the *j*th year, any species for which no value could be calculated being excluded in that year. We then calculated the sum of $w_{i,j}X_{i,j}$ across species for the *j*th year. This represents the weighted log of the proportional change in the index between year *j* and year *j*+1 for this group of birds. The last such value relates to the change in abundance from 2010 to 2010. Setting the initial value of the index to 100 in 1980, we then used the proportional changes to calculate successive values of an overall index of abundance for all the years in the series. This yielded, at the state level, composite indices of abundance for the CST+ and CST- groups, for 1980 to 2010 (respectively, $A_{plus,z}$ and $A_{minus,z}$ for state *z*).

1.5.   Amalgamating state-level composite abundance indices to give subcontinental CST+ and CST- indices

To create CST+ and CST- composite indices of abundance at the subcontinental scale, we combined state-level indices by repeating the process outlined in step 4. Specifically, $A_{sign,z}$, where $sign \in \{plus, minus\}$ and z is the state's identity, is a series of abundance indices of length k. As in step 4, we converted this to k-1 values of $X_{sign,z,j} = \log(A_{sign,z,j+1} / A_{sign,z,j})$, where $A_{sign,z,j}$ is the composite abundance index value for the group $sign$, the state z and the year j, and $A_{sign,z,j+1}$ is the composite abundance index in the following year. It is possible to conjecture a variety of differences between states which might suggest that data from one state should be given more weight than that from another state. However, to retain simplicity and avoid further assumptions, all states were given equal weight in the subcontinental index. We then calculated the average of $X_{sign,z,j}$ across all states for which there is an eligible value of $A_{sign,z,j}$ in the jth year. As before, we set the initial value of the index to 100 in 1980 and used the proportional changes to calculate successive values of an overall index of abundance for all the years in the series. This yielded, at the subcontinental level, composite indices of abundance for the CST+ and CST- groups, for 1980 to 2010. Hereafter, these are termed $A_{sign,c}$, where $sign \in \{plus, minus\}$ and $c \in \{Europe, USA\}$.

1.6   Using CST+ and CST- indices to produce the Climate Impact Indicator
    As discussed by Gregory et al. (*16*), the composite abundance indices for the CST+ and CST- species do not in themselves provide an indicator of the impact of climatic change upon bird population trends. If there was no effect of climatic change and if both groups are similarly susceptible to other environmental changes, such as agricultural intensification or habitat loss, then they might show similar rates of change. However, we would expect that the group of species for which climatic suitability has been increasing (CST+) would show a more positive trajectory than that group for which suitability has been declining (CST-). Hence, the impact of climatic changes (both positive and negative) on bird populations can then be summarized in a single indicator, which we term the Climatic Impact Indicator (CII). This is calculated in a given year as the ratio of the index for CST+ species to that for CST- species, standardized to take the value 100 in the first year.

1.7.   Computing confidence intervals
    We determined 90% confidence intervals for subcontinental-level CST+ and CST-indices, and for the subcontinental CII. The process was the same, regardless of the nature of the index, so here we detail the generalized method for creating confidence intervals from any time series, M, where M is a vector of index values, M_j, for year j, where j falls in the range 1 to k.
    In all cases, bootstrap replicates of M, denoted M^{*b} for the bth replicate, were derived by resampling with replacement from the original set of species in the subcontinent ($n = 145$ for Europe and $n = 380$ for USA). To create M^{*b} for any replicate, we performed all analyses, as above, but using the set of species in that bootstrapped sample. To obtain confidence intervals, we took the logarithm of the index in a given year and expressed it as a deviation from the mean of that bootstrap replicate's logged index across all years. This yielded a vector, R^{*b}, of annual indices centered around zero, where the value in year j is given by:

$$R_j^{*b} = \log(M_j^{*b}) - \frac{\sum_{y=1}^{k} \log(M_y^{*b})}{k} \qquad (2)$$

We then calculated R_1, the difference between the logged index value in the first year of the (non-bootstrapped) index series and the mean of all logged values in that (non-bootstrapped) series:

$$R_1 = \log(M_1) - \frac{\sum_{y=1}^{k} \log(M_y)}{k} \qquad (3)$$

For year j and bootstrap b, the deviation from the expected anomaly (relative to the non-bootstrapped data set) was calculated as:

$$\Delta_j^{*b} = R_j^{*b} - R_1 \qquad (4)$$

We repeated this bootstrap sampling and estimation procedure 2,000 times. The 90% confidence limits for the index in year j were taken to be defined by the central 1,800 of the ranked bootstrap set of Δ_j^{*b} estimates for that year. The bounds of the confidence interval were then back-transformed.

2.   Comparison of trends in temperature-related climate variables

To evaluate changes from 1980 to 2010 in MTEMP, MTCO and GDD5 in the states contributing data on bird populations, we fitted an ordinary least squares two-factor anova model (STATE x YEAR) to the data on each dependent variable, excluding years for a particular state when it was not contributing bird data to our analyses. The main effect of YEAR from these models was taken to represent changes over time in the climatic variable. The year effects were standardized to have zero mean and unit variance. These standardized variables are plotted against year in Figure 3.

We performed an ordinary least squares analysis of covariance to check whether the regression slope of standardized climate variables on year differed among the three variables. We used a variance-ratio (F) test to compare a regression model with a single slope and single intercept for the relationship of all three standardized climate variables to year with a model in which the slopes and intercepts were fitted separately for the three variables. Because the variables were all standardized to have the same mean (zero) there is no reason to fit a model with a common slope but variable-specific intercepts. There was no indication of any difference among the three variables in slopes and intercepts for Europe ($F_{4,84} = 0.114$, $P = 0.977$) or the USA ($F_{4,84} = 0.096$, $P = 0.983$).

We performed similar analysis of covariance F tests to check whether the regression slope of each standardized climate variable on year differed between Europe and the USA. There was no indication of any difference between Europe and the USA for mean temperature ($F_{2,56} = 0.505$, $P = 0.606$), MTCO ($F_{2,56} = 0.249$, $P = 0.780$) or GDD5 ($F_{2,56} = 0.170$, $P = 0.844$).
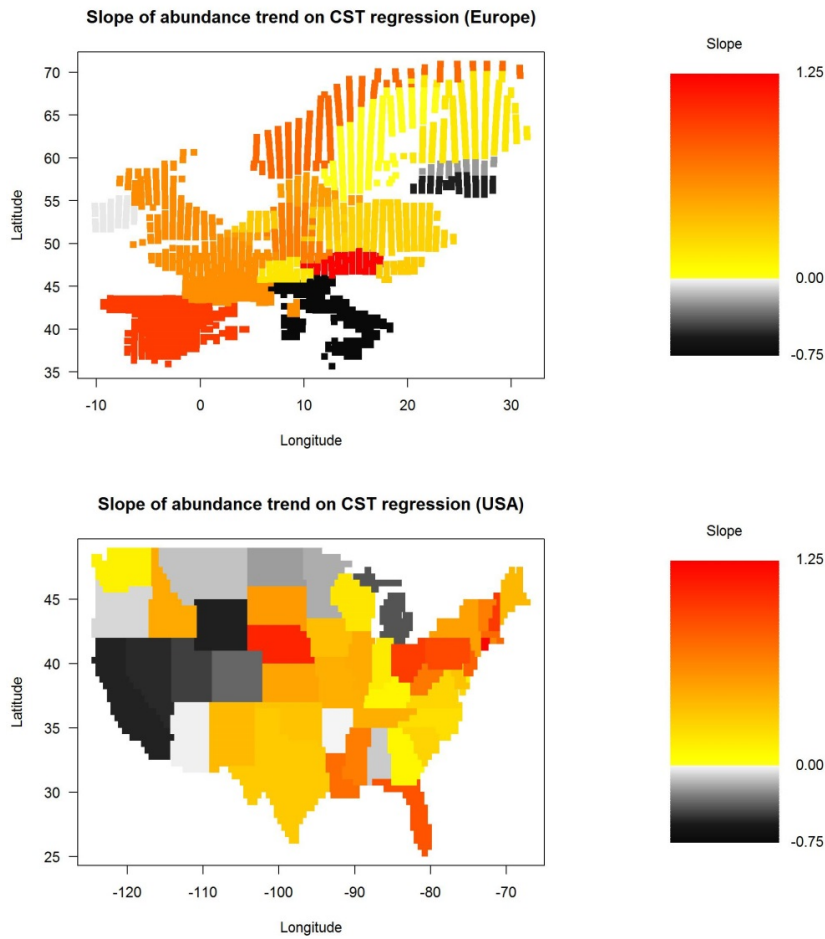
Fig. S1.

Slopes from regressing the abundance trends of all species occurring in a state on the modelled state-level CSTs of those same species. Note that relatively few state-specific relationships are statistically significant, emphasising the difficulty of analysing this relationship at a very fine geographic scale, and the importance of controlling for confounds (see further below). Importantly, no negative slopes for individual states were significant.

Supplementary tables will be available online (via the *Science* site) following publication.