

Cross-realm assessment of climate change impacts on species' abundance trends

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Climate change, land-use change, pollution and exploitation are among the main drivers of species' population trends; however, their relative importance is much debated. We used a unique collection of over 1,000 local population time series in 22 communities across terrestrial, freshwater and marine realms within central Europe to compare the impacts of long-term temperature change and other environmental drivers from 1980 onwards. To disentangle different drivers, we related species' population trends to species- and driver-specific attributes, such as temperature and habitat preference or pollution tolerance. We found a consistent impact of temperature change on the local abundances of terrestrial species. Populations of warm-dwelling species increased more than those of cold-dwelling species. In contrast, impacts of temperature change on aquatic species' abundances were variable. Effects of temperature preference were more consistent in terrestrial communities than effects of habitat preference, suggesting that the impacts of temperature change have become widespread for recent changes in abundance within many terrestrial communities of central Europe.

Analyses of long-term trends in species' populations, such as the Living Planet Index, show global declines in abundances^{1,2}. Understanding the cause of changes in species' abundances is crucial to assess consequences for ecosystem functioning³, range shifts⁴ and extinction risk, and for making conservation decisions⁵. Much research has focused on the possible future impacts⁶ of climate change, but climate change has already affected species in multiple ways, with range shifts detected in diverse taxa^{7,8}. Species' abundances are potentially more sensitive to climate change than range boundaries—a binary presence/absence change in abundance^{9,10}. However, the effects of climate change that have

already occurred on species' abundances are much less recognized. Population abundances are affected by many environmental drivers, including habitat loss and degradation, along with pollution, invasive species and exploitation^{1,2,11}. Until now, the impact of climate change on population trends and how it compares with other large-scale drivers has not been assessed across major taxonomic groups and environmental realms.

Temporal changes in the abundances of organisms have been used to infer the impact of particular environmental drivers on communities. For instance, the effect of nitrogen pollution on a particular lichen species depends on its species-specific nitrogen tolerance.

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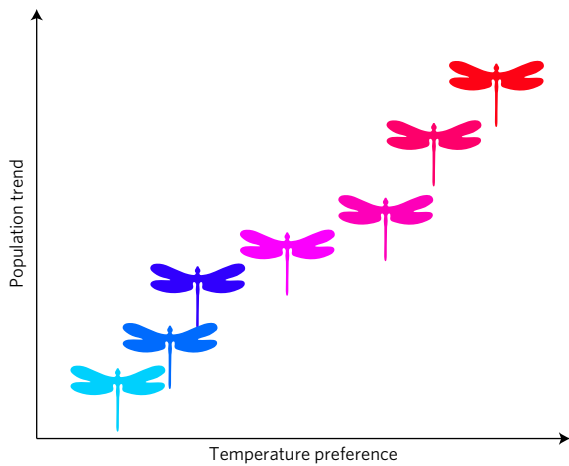


Figure 1 | Relationship between species' temperature preferences and population trends under climate change. Each dragonfly represents a species; temperature preference is reflected in the colour shading from warm (red) to cool (blue). If climate change is an important driver of long-term population trends, we predicted a positive relationship between species temperature preference and long-term population trend. This approach is a short-cut to understanding the effect of climate change (environmental change) on a community by assuming that species vary in their response according to their particular temperature preference (species attribute). This framework can be generalized to test the effects of other environmental change using the most relevant species attribute.

Consequently, declines in the abundance of nitrogen-sensitive lichens have been used as a bioindicator of pollution¹². Thus, given sufficiently detailed species-level knowledge, differential population trends of species according to their particular attributes (that is, specific characteristics of the species) can be used as a bioindicator of the impacts of environmental change. Such attribute-based approaches have a number of advantages. First, they integrate the effects of the components of environmental change that are most relevant to the organism, when environmental data often are either not available or complex to summarize. For example, declines of farmland birds have highlighted the negative impacts of agricultural intensification, mediated by various changes, including seasonal land-use practices, and fertilizer and pesticide usage^{13,14}. Second, observed species' responses integrate the effects of environmental change at the spatial and temporal scales that matter to the organism, for instance if effects act within particular time windows¹⁵ or spatial scales¹⁶.

We used a species attribute-based approach to test for signals of long-term temperature change on the abundances of species within terrestrial, freshwater and marine communities. In broad terms, we first aimed to detect population trends and then to attribute these trends to long-term temperature change¹⁷. If temperature change had affected abundances, we expected that some species had increased or that others had decreased. Changes in abundances can be driven by many factors, but long-term trends of abundance are most probably due to deterministic factors such as the persistent effects of a long-term change in the environment. Although such trends may correlate with temperature trends, they may also correlate with trends in other long-term drivers of biodiversity change. To attribute the population trends to temperature change, we related the variation in population trends within each community to species' temperature preferences. Because the impact of temperature change on a species can be predicted to depend on its temperature preference, more positive trends of warm-dwelling species over cold-dwelling species within each community imply a signal of climate change. Thus, we used the strength of the relationship between

species' temperature preferences and long-term population trends within each community as an indicator of climate change (Fig. 1).

We applied our approach to 22 long-term local or regional community datasets within central Europe, including abundance data for taxa from 40 classes (from algae to mammals). This represents, to our knowledge, the most taxonomically diverse analysis on population trends in Europe to date. Each dataset comprised 9–130 species for which population data were collected over a 12–34 year time span (1980 onwards) (Fig. 2a and Supplementary Tables 1 and 2). The datasets cover a broad range of habitats (forest, agricultural land, grassland, sand dunes, wetland, heathland, lakes, rivers, sea), but we cannot assume they are truly representative—long-term sampling is rarely done in highly disturbed environments. Our study profits from the inclusion of groups that are rarely studied in climate change assessments, such as soil invertebrates, which might show different responses from commonly studied mobile taxa, such as birds.

For each species, we calculated its long-term population trend and its temperature preference using European distribution data and average temperature maps. For each community dataset, we built regression models that related population trends to species attributes affecting sensitivity to particular environmental drivers (see Table 1; temperature preference for temperature change, habitat preference for land-use change, pollution tolerance (for example, nitrogen tolerance) for pollution). The regression models also included attributes that might further modify species' responses (such as habitat breadth and dispersal ability, affecting the adaptive capacity of individuals, and life span or age at maturity, affecting population resilience)¹⁸ (Supplementary Fig. 1 shows an outline of the methods and Supplementary Table 3 shows the attributes tested for each dataset).

Regression statistics from each dataset were combined together by meta-analysis, allowing control of dataset-level effects such as number of species and sampling sites, start year, time span and temperature trend over the study period (Supplementary Table 4). From this combined analysis, we tested (1) whether the temperature preferences of species are generally positively associated with their population trends, as a signal of the impact of climate change in terrestrial, freshwater and marine realms, and (2) the relative strengths of these climate change signals compared with those of land-use change, pollution and exploitation.

Results

Average annual temperatures in the study areas had increased (mean \pm s.e.m., 0.33 ± 0.07 °C decade⁻¹; Supplementary Fig. 2 and Supplementary Table 5) and this trend did not significantly differ among realms. Local temperature trends for each dataset were not always significant over the time period of data collection, but they pointed towards positive trends when analysed since the 1980s (Supplementary Table 5). Overall, almost half of the species' populations showed a significant abundance trend (47%, 552/1,167; Supplementary Fig. 3). The percentage of populations with significant trends was 61% (132/216) in the marine realm, 48% (323/680) in the terrestrial realm and 35% (97/271) in the freshwater realm. Positive trends, that is, increases of abundance, were more common in the marine and terrestrial realm (62% and 60% of the significant trends, respectively), while negative trends were more frequent (60%) in the freshwater realm.

Averaging across all datasets, there was a significant relationship between species' temperature preferences and population trends (correlation coefficient (r) = 0.164, 95% confidence interval (CI) = 0.095, 0.234). Although the difference among realms was not statistically significant, only the effect in the terrestrial communities had a CI that did not overlap zero (Fig. 2b; r = 0.165, 95% CI = 0.046, 0.280; predicted at average start year, number of species and sampling sites). Thus, population trends were positively related with temperature preferences in terrestrial communities; that is, populations

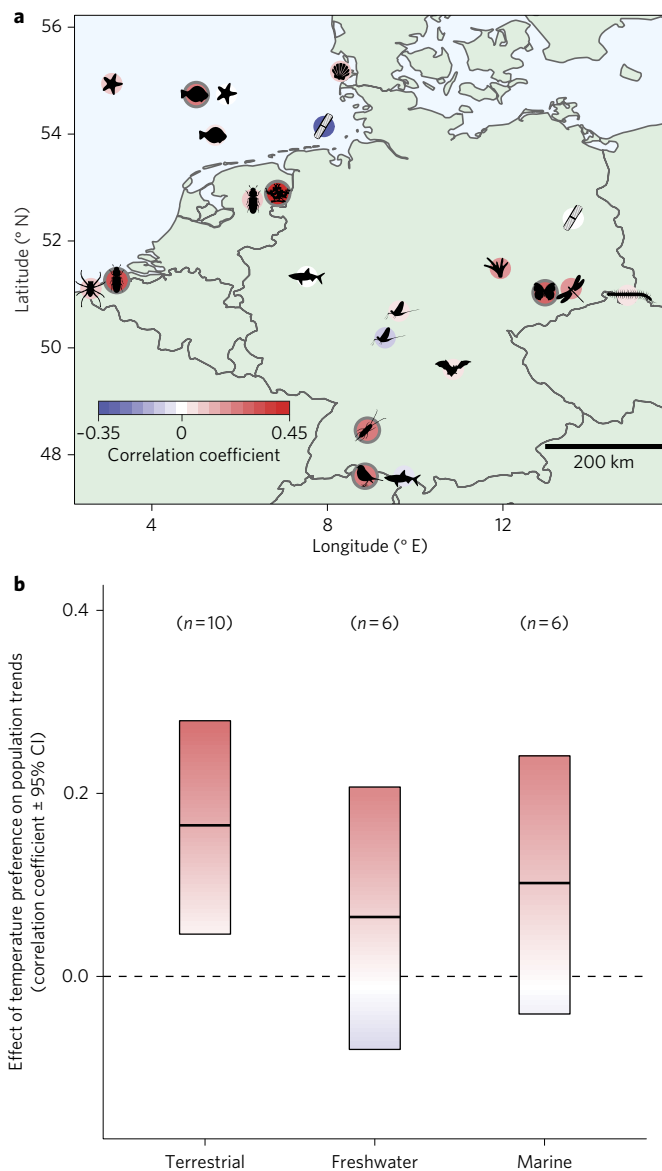


Figure 2 | Climate change impacts on local communities. **a**, The geographic location of each dataset (symbols explained in Supplementary Fig. 3) within central Europe; the colours behind the symbols represent the strength to which each community shifted towards warm (pink) or cold-dwelling species (blue) (that is, the correlation coefficient of the relationship between temperature preference and population trend). Significant effects are circled with a dark grey outline. **b**, The modelled average effect size (correlation coefficient \pm 95% CI) of temperature preference on population trends in each realm, predicted at average start year, log number of sampling sites and log number of species across all datasets.

of species with warmer temperature preferences increased more than those of species with colder temperature preferences. We found the strongest evidence of impacts for the bird, butterfly, ground beetle, springtail and lichen datasets (Supplementary Fig. 4). In contrast, average effects were not significant in the freshwater and marine communities, although we detected a signal in the marine fish dataset (Fig. 2).

Such differences among realms might partly exist because some of the time series from the freshwater and marine communities were shorter, having begun more recently, reflecting the lesser extent of aquatic long-term monitoring. However, average realm effects were robust and independent of dataset characteristics (start year, number

of species and sampling sites) as well as of different data weightings or subsampling (Supplementary Figs 5 and 6). Pooling together the freshwater and marine data to achieve similar numbers of datasets (terrestrial, $n = 10$; aquatic, $n = 12$) still gave an average insignificant effect across the aquatic communities, but it did tend to be positive (aquatic effect size: 0.08, 95% CI = $-0.01, 0.18$; predicted at average start year, number of species and sampling sites).

To examine whether the relationship between temperature preference and population trend was mostly driven by increases of warm-dwelling species or decreases of cold-dwelling species, we tested whether species in the upper and lower temperature preference quartiles had positive and negative trends, respectively. Increases of warm-dwelling species were found for birds, butterflies, springtails and lichens as well as marine fish, while decreases of cold-dwelling species were only seen in birds and ground beetles (Supplementary Fig. 7). On average across terrestrial species, warm-dwelling species had increased (difference of trends from zero, z -score (z) = 2.26, $P = 0.02$), while aquatic warm-dwelling species had not ($z = -0.27, P = 0.78$).

Although habitat preferences were significant for some taxa, such as farmland birds (Supplementary Fig. 8), the average effect across all ten terrestrial communities did not reach statistical significance ($z = 1.54, P = 0.12$; Fig. 3). There was an effect of pollution tolerance in lichen communities ($z = 4.21, P < 0.01$), with increases of nitrophilous species¹⁹, but not in the plant community; this was not tested for the other eight datasets because of a lack of information on nitrogen/nutrient preferences. In contrast, in freshwater communities, species preferring low-nutrient environments had more positive population trends ($z = -2.37, P = 0.02$; Fig. 3). Effects of exploitation were detected for marine fish ($z = -3.99, P < 0.01$), but not for freshwater fish ($z = -1.19, P = 0.24$). Commercially exploited marine fish had less positive population trends than non-commercial fish (Fig. 3).

Discussion

We tested for climate change signals on population trends across the broadest range of taxa in Europe to date. The long-term increases and decreases of species' abundances provided evidence for a long-term driver affecting these communities. Based on the relationship between species' temperature preferences and population trends, we interpret our results as showing an average effect of temperature change in the terrestrial communities and more variable effects in the aquatic communities.

Although other routes through which climate change might affect communities, such as biotic interactions, are increasingly debated²⁰, our findings suggest that direct effects of warming are widely important in the terrestrial realm. Habitat loss, fragmentation and degradation are among the leading causes of biodiversity loss in the past century. However, land conversion to cropland peaked in the 1950s²¹. Although past land-use change is still of great importance for spatial patterns of species' abundances, it may be less so for recent temporal changes of abundance within the remaining local communities of central Europe. Our terrestrial datasets may be biased towards areas where land-use change has been low, but recent effects of land-use change might be now limited to specific localities, where change is still occurring, and to particular taxa, such as farmland birds²² and grassland butterflies²³, being affected by such change. Indeed, recent changes in the human footprint, based on human population size, land use and infrastructure, suggest an improvement (using data between 1993 and 2009) in many parts of Europe²⁴. In contrast, communities in most localities are experiencing some temperature change, suggesting that the impacts of climate change are now more geographically widespread than those of land-use change.

For aquatic communities, the higher heat capacity of water may buffer aquatic systems from rapid temperature changes. However,

Table 1 | Hypotheses regarding which species attributes modify the response of species to different environmental drivers.

Environmental driver	Modifying species attribute	Hypothesis if driver is important for long-term population trends
Long-term temperature change	Temperature preference	More positive trends of warm-dwelling species over cold-dwelling species (Fig. 1).
Land-use change	Habitat use or breadth	More positive trends of species whose habitats have expanded or matured (for example, forest), have been less affected by human activities (for example, not farmland) or are habitat generalists.
Pollution	Nitrogen/pollution tolerance	More positive trends of species with a preference for or tolerance of nutrient-rich conditions.
Over-exploitation	Exploited or not	More positive trends of unexploited species over exploited species.

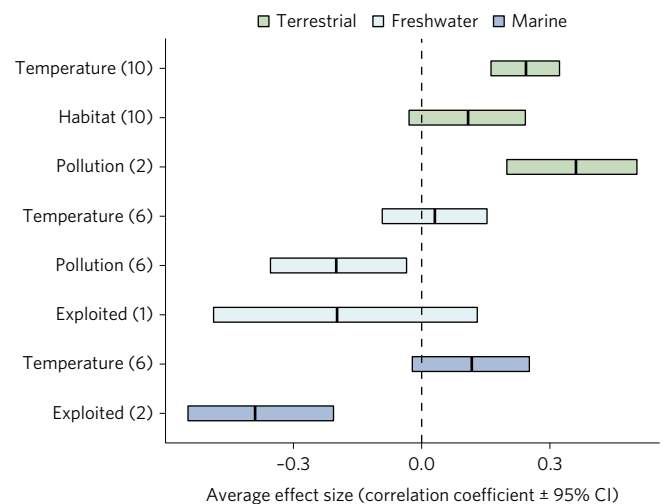
this would not prevent long-term changes and, like others²⁵, we did find a climate change signal in marine fish. Patterns from local freshwater fish and benthic invertebrate communities in France^{26,27} have also suggested community shifts towards warm-dwelling or thermally tolerant species, which we did not observe in our freshwater datasets. Impacts on aquatic groups might be locally variable, depending on the landscape context. Other long-term environmental drivers, especially changes in external nutrient load, may have overridden any effects of temperature change on long-term population trends in the communities in our analysis. This driver was suggested by the effect of pollution-related attributes on the population trends of freshwater species and is consistent with recent declines in nutrient loads of lakes and rivers in Europe²⁸ (an outcome of improved wastewater treatment). As information on pollution-related attributes was missing for many freshwater species, this community shift should be re-assessed as additional data become available. Exposure to weaker temperature change in the marine and freshwater communities would also explain the less consistent climate change signal in these communities. Although this interpretation was not supported by annual time series of average daily temperatures from the sites, this summary variable might not capture the temperature change relevant for aquatic organisms. Our analysis also does not exclude climate change impacts in aquatic systems being mediated by alternative routes, for instance, by changes in river discharge²⁷ and patterns of thermal stratification²⁹.

Our cross-dataset assessment suggests that effects of temperature change may differ between terrestrial and aquatic communities. Temperature preference was the most consistent predictor of recent population trends in the terrestrial realm, indicating that temperature change is important for different kinds of organisms in different localities. Similar in philosophy, the Community Temperature Index has also been used to show increases in the proportion of warm-dwelling species over cold-dwelling ones, especially for birds and butterflies^{10,30}, as an indicator of climate change impacts. However, by using a multiple regression approach, our approach simultaneously accounted for the effects of other species attributes (see Supplementary Table 3) on population abundance before interpreting the effect of species temperature preference. This approach provides more confidence that any estimated effects are due to temperature change rather than some other driver³¹.

The simplicity of our approach meant it was practical enough to be applied across a broad range of species. However, there are many challenges to cross-taxa analysis. As much as possible, we have corrected for effects of variation in dataset attributes on our findings, but continued sampling, especially in freshwater and marine communities, which have been less sampled, is essential. Inferring species temperature preferences from coarse distribution is complicated by differences between species' fundamental and realized niches³² and microclimatic variation³³. In particular, estimating the thermal tolerances of freshwater organisms is hindered by the lack of large-scale freshwater water temperature maps. Including physiological measurements of species' thermal tolerances would strengthen the conclusions that could be made from our approach,

but such data are limited to few species. Unfortunately, the data available (on populations, distributions and species attributes) for different taxa still varies in quality; it is most probably of the highest quality for birds. Although trait databases are now being developed for organisms such as beetles³⁴ and soil organisms³⁵, there is still less, and more variable quality, information available for invertebrates. Because we were able to estimate temperature preference of organisms on a finer scale than habitat preference, this might have increased our ability to detect temperature effects over habitat effects. However, even coarsening the temperature preference data (comparing species in the upper tertile versus those in the lower tertile of temperature preferences; Supplementary Fig. 9) still suggested that warm-dwelling species had more positive population trends than cold-dwelling species in the terrestrial communities. Finally, it is important to emphasize that we focused on the effects of temperature change on recent population trends. An absence of an effect on population trends does not rule out species responding to climate change in some other way, such as phenology³⁶.

Although vital to inform assessments of the Convention on Biological Diversity targets and for conservation decision-making, long-term datasets on population abundances remain scarce. Clearly, land-use change was the predominant factor affecting terrestrial communities during the twentieth century. Our conclusions

**Figure 3 | Impacts of environmental drivers on population trends.**

Crossbars are average effect sizes (correlation coefficient \pm 95% CI) of species attributes related to temperature preference, habitat preference (mediating response to land-use change), pollution tolerance and exploitation, as predictors of population trends in terrestrial (green), freshwater (light blue) and marine (dark blue) communities. Number of datasets used are shown in brackets (for pollution, only lichens and plants were included in the terrestrial datasets; for exploitation, only fish were included in the aquatic datasets).

are restricted to changes in local communities over the past two or three decades and concern which drivers have been more widespread. Land-use change has the potential to strongly affect local communities, but its impacts are spatially variable. Our results suggest that many communities have been less exposed to and less affected by land-use change over this time period than previously. In contrast, climate change is a widespread driver and thus has the potential to affect populations over a large scale. We find stronger evidence that climate change has affected the recent abundance changes within many central European terrestrial communities, compared with aquatic communities, particularly leading to increases of species with warm temperature preferences.

Methods

Population data. We compiled long-term datasets with at least four census years since 1980 (average number of census years = 19) within a geographical extent of central Europe and the southern part of the North Sea—the majority of the data were from standardized scientific surveys, but in a few cases they were sourced from citizen science or government agency monitoring programmes (see Supplementary Table 1).

Rationale of approach. Supplementary Fig. 1 shows an outline of the methods. We analysed each dataset in a way that was as similar as possible, to determine the signals of long-term temperature change and other environmental drivers that could be detected. It was not possible to analyse the individual datasets in exactly the same way throughout because some datasets had additional issues; for example, variation in sampling effort or within-year sampling. In addition, we wanted to ensure that our patterns were not driven by a few common species. The most important steps of our analysis were fitting a population trend for each species in each dataset (Supplementary Fig. 1, step c), estimating the effect of species attributes on population trends within each community using regression (Supplementary Fig. 1, step d) and bringing the individual dataset regression results together by meta-analysis (Supplementary Fig. 1, step f). We took this stepwise approach so that we could (1) modify the fitting of population trends to account for details of each dataset (for example, addition of sampling effort offset term or month of sampling fixed effect, when appropriate) and (2) examine patterns at the species level and test the effect of weighting species data points by the confidence of the trends, so that we could ensure that patterns were not driven by a few common species within each dataset.

Prior subsetting. Before analysis, we restricted the data to 1980 onwards and species seen in at least 25% of census years (Supplementary Table 2). The analysis was also repeated using a higher threshold for species occurrence, which yielded similar results (Supplementary Figs 6 and 10).

Population trends. We calculated the population trend of each species as its average annual population growth. In the standard analysis, these trends were estimated using a generalized linear model with Poisson errors including year (a continuous variable) and site (a factor) as predictor variables, as well as an autoregressive term to account for residual autocorrelation of counts as a function of time between censuses and an additional observation-level error term to account for any overdispersion, which was fitted by Bayesian inference using R-INLA (<http://www.r-inla.org/>)³⁷. Because we were interested in the species long-term trend, we only considered the linear trend over time. An ‘effort’ offset term was included in the model when appropriate. A significant population trend was identified when the trend estimate was significantly different from zero (except in one case (birds), when it was inferred from consistent direction of change between each decadal census). See Supplementary Table 1 for deviations to this standard analysis.

Species temperature preference. We approximated each species temperature preference using distribution data (see Supplementary Table 3 for the distribution data sources used for each taxonomic group). As much as possible we aimed to get range maps (that is, polygons); when this was not possible, we used point occurrence records from the Global Biodiversity Information Facility (GBIF), the Ocean Biographic Information System (OBIS) or country checklist data. Our aim with the calculation of temperature preference was to create a variable that reflected the rank and relative differences of species towards warmer and cooler temperatures, and not necessarily species’ optimal performance temperatures. Thus, using restricted and coarse distribution data should be sufficient for this purpose. Using temperature data maps delineated to Europe, we extracted the grid temperatures from locations intersecting with the distribution of each species. We restricted calculation to a European temperature map because, for most species, the best distribution data available were restricted primarily to Europe. For terrestrial and freshwater datasets, we used temperature maps from the E-Obs gridded dataset³⁸ of average temperature between 1961 and

1990, projected onto a 25 km equal area grid. Although ideally we would have used water temperature for the freshwater datasets, such European-wide freshwater temperature data are not readily available and air temperature data are commonly used. In addition, air and water temperature are highly correlated³⁹. For the marine datasets, we used sea surface (for plankton) and bottom surface (for benthic invertebrates and fish) temperature maps from Aquamaps on a 50 km equal area grid (according to availability: 1982–1999 for sea surface temperature; 1990–1999 for bottom surface temperature)⁴⁰. For dragonflies, data were already available⁴¹ on a 50 km grid, so we used this resolution for them. For butterflies, temperature preference data were extracted from a database. Because we only wished to assess the mean temperature over each species range, the coarse grid size of 25–50 km was adequate, given that the maps are based on a European extent and the distribution data are coarse. For the bird dataset, which included migratory species, we calculated temperature preference as the breeding temperature preference using average temperature data for April, May and June and the range maps restricted to breeding and/or resident areas.

Temperature preference was summarized for all species as the mean temperature across the range (mean of all occupied cells, weighted by grid cell coverage for range maps and removing duplicate records within the same cell for point occurrence data). We did further consider a more complex approach, fitting unimodal species response curves to identify species optimum temperatures. This led to temperature values that were correlated with the mean temperatures across species’ ranges; however, since it also led to extreme estimates in a few cases (Supplementary Fig. 11), we decided to continue with our original simpler approach that made fewer assumptions about the shape of species responses.

We also calculated species’ temperature ranges as the difference between the maximum and minimum temperature preference (mean of the five occupied grid cells with the warmest and coolest average temperature, respectively). Range size was estimated as the number of climatic grid cells intersecting with each species’ distribution (because this was usually correlated with temperature range, we focused on temperature range instead, except for marine organisms, where we considered it as a proxy of habitat breadth). Because of the limited freely available occurrence data for freshwater plankton, temperature preference was approximated using the seasonal, rather than spatial pattern of species occurrences, within the population dataset, using a similar approach, with daily water temperature data.

Additional species attributes. Additional species attributes (for example, on habitat preference, dispersal ability and age at maturity) were obtained from the literature or databases in most cases (see Supplementary Table 3 for resources). For attribute data that had been fuzzy coded (for example, species given affinities to different levels associated with the attribute), we produced one attribute value by taking a weighted average of the affinities to different classes of the attribute when the underlying attribute was continuous (for example, size) or instead used cluster analysis to allocate each species to a single group. Habitat preferences for springtails and myriapods were inferred from the occurrence records that included information on habitat for each occurrence. Habitat breadth was calculated as the coefficient of variation of species affinities to different habitat categories⁴². In some cases, expert assessment was used to compile species attribute data (these are annotated in Supplementary Table 3). When species attribute data were ordinal, but represented a continuous variable, data were treated as continuous if there were at least five categories and graphical exploration suggested a linear relationship was reasonable. The few species that were not listed in the main attribute database were excluded from the analysis. Remaining missing attribute data were imputed using a random forest model, including all the variables of the subsequent regression models and the first eigenvector of the decomposed phylogenetic/taxonomic tree as predictors⁴³. The amount of missing data was generally less than 10% in most cases. However, for freshwater benthic invertebrates, only genus-level data were available for many attributes and even then up to 25% of data were missing for some attributes. The variable with the most missing data was pollution-related attributes (water-quality flexibility was only available for 50% of fish in one dataset).

Local temperature data at the study sites. Mean monthly temperature data were extracted for the study areas of all datasets. We used high-resolution data (in contrast to the large-scale coarse temperature data used for the species temperature preference calculation, see ‘Additional species attributes’) to retrieve temperature data at the very specific sites of population data sampling. Air temperatures for the terrestrial datasets were sourced from national weather service agencies (Deutsche Wetterdienst for Germany, www.dwd.de; Royal Meteorological Institute of Belgium for Belgium, www.meteo.be; and the European Climate Assessment and Dataset, <http://www.ecad.eu>, and local weather stations, <http://www.weerstation-eelde.nl>, for the Netherlands). For all but one of the marine realm datasets, water temperature data were sourced from the International Council for the Exploration of the Sea (ICES); for the remaining dataset, temperature data had been collected locally by the population dataset owner. Missing data were imputed using a generalized additive model. For the freshwater datasets, we used air temperature data when water temperature had not been collected (for the freshwater river fish and benthic invertebrates). These data were used to calculate annual averages of

daily mean temperatures. We smoothed the time series as a three-point lagged moving average and fitted a generalized least-square model to estimate the trend.

Regression of species attributes on population trends. For each dataset, multiple regression models were built to predict species' population trends using species attributes as predictors (that is, explanatory variables). We checked whether predictor variables were correlated before model fitting and also examined variance inflation factors of the fitted models to check for multicollinearity. We combined as many attributes as possible but always allowed for at least five species per model parameter. Because analysis was more often limited by the number of species than the number of attributes, we first identified the attributes that would probably be most important based on simple regressions and only included the most important (that is, lowest *P* value) in the maximum multiple regression model. From this model, we excluded variables that were not significant in a stepwise manner. Coefficients of interest (temperature, habitat and pollution/nutrient preference/tolerance) that were not retained after model simplification were tested separately by adding them to the final simplified regression model. Rather than making a binary distinction between a significant or non-significant population trend, we used data from all species but weighted them by the precision (that is, inverse variance) of their trend estimate in the regression. This means that data points (that is, species) with a small standard error (that is, with more confidence, whether in a negative, stable or positive trend) had a greater weight in the model. Because highly fluctuating species (with low precision of the trend estimate) are more likely to be rare species, we additionally tested the results at two different thresholds of species inclusion, as well as with and without these weights (see Supplementary Figs 6 and 10). In addition, we used robust regression for our analysis to down-weight any influential species with high leverage⁴⁴.

As a sensitivity analysis of the accuracy of our temperature preference estimation, we also condensed our continuous temperature preference variable into a three-level factor (cold, average and warm temperature preference) and reran the analysis (see Supplementary Fig. 9). The conclusions were unaffected by this sensitivity analysis. Because our estimates of the temperature preferences of freshwater organisms were based on air temperature data, we also used stream zonation preferences as a measure of species' temperature preferences⁴⁵; the results did not change (Supplementary Table 3). Analysis of species population trends fitted at the site-level within each dataset did not reveal any further habitat effects (see Supplementary Fig. 12).

Phylogeny. As species within each dataset do not necessarily provide independent data points due to shared ancestry, we tested whether phylogeny or taxonomy explained any variation in the residuals of our models and accounted for this in the few cases it did (see Supplementary Methods). Phylogenies with branch lengths were obtained for the birds⁴⁶ (using Beast⁴⁷ to produce a maximum credibility clade tree from the tree distribution), bats⁴⁸ and plants⁴⁹. For the butterflies, we used an undated phylogeny from a molecular phylogenetic maximum likelihood analysis of the genes cytochrome *c* oxidase I and elongation factor 1 alpha (*M. Wiemers and O. Schweiger*, unpublished observations). For the rest, we obtained the species taxonomic classification (mostly from the catalogue of life, except for the springtails and phytoplankton⁵¹) and used the taxonomy to create a tree, setting branch lengths to one for each taxonomic rank. To check whether there was a phylogenetic signal in the residuals of the multiple regression models of population trends, we used Abouheif's C_{mean} test⁵² using the R package *adephylo*⁵³. In most cases, there was no evidence that phylogeny or taxonomy explained any residual variation in the final simplified multiple regression models. In cases when it did (marine fish, springtails, beetles and bats), we specified a *corPagel* correlation structure using the R package *ape*⁵⁴ and reran the analysis as a generalized least-squares model.

Effect size calculation. The *t*-statistics of the model coefficients from the regression for each dataset were converted into correlation coefficients⁵⁵, which we used as a comparable effect size across all taxa and different species attributes. For categorical variables with multiple levels, we used the *t*-statistic of whichever pair-wise comparison was the largest. The *t*-statistics, and associated degrees of freedom (df), were converted into *r*, the correlation coefficient, using the following formulas⁵⁵.

For continuous variables, we calculated *r* as:

$$r = \frac{t}{\sqrt{t^2 + \text{df}}}$$

For categorical data, we initially used the *t*-statistic to calculate Cohen's *d* as:

$$d = \frac{t(n_1 + n_2)}{\sqrt{n_1 n_2} \sqrt{\text{df}}}$$

where n_1 and n_2 are the numbers of species in each group being compared. In cases when the categorical variable had multiple levels, we used the pair-wise contrast with the largest difference. For categorical variables that did not have any natural direction of effect (for example, habitat preference for birds, coded as forest, urban, farmland and wetland), the direction of effect was assigned according

to predictions relating to the associated environmental driver (for example, farmland birds were predicted to have the lowest trends, due to agricultural intensification). For comparability with other effect sizes, Cohen's *d* was subsequently converted to *r* as:

$$r = \frac{d}{\sqrt{d^2 + \frac{(n_1 + n_2)^2}{n_1 n_2}}}$$

For meta-analysis, *r* was *z*-transformed and its standard error (s.e._{Zr}) calculated as:

$$Zr = 0.5 \ln \left[\frac{(1+r)}{(1-r)} \right]$$

$$\text{s.e.}_{Zr} = \frac{1}{\sqrt{n-3}}$$

Meta-analysis. Effect sizes (*z*-transformed correlation coefficients) from each dataset were combined using a random-effects meta-analysis⁵⁶ and the resulting pooled estimate and confidence intervals were back-transformed from *Zr* to *r* for presentation. Statistical significance was assessed by whether the 95% confidence intervals of the effect sizes overlapped zero. Because there was some variation in the datasets, variables such as the start year of data collection, sampling sites and species number were centred and tested in the meta-analysis (Supplementary Table 4). The corrected effects of average temperature preference effects for each realm were produced by predicting the coefficients for each realm at the average value of all dataset-level variables across all datasets. Because there was overlap (taxonomic/spatial) among some of the datasets, we tested whether additional random terms that reflected dataset grouping could explain any variation; since they did not, they were removed. We also tested whether species in the upper and lower quantiles of temperature preference had average population trends that differed from zero using the *t*-statistic of the intercept term from a robust regression of the trends for each quartile and dataset. We then averaged the trends for each quartile and realm using a random-effects meta-analysis (sample sizes for each quartile and dataset are found in Supplementary Fig. 7). All analyses were conducted with R v3.0.2⁵⁷.

Data availability. As much as possible, references that include data owner contacts for each population dataset are given in Supplementary Table 1. Further information and data on species' local population trends are available from the corresponding author.

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References

- Butchart, S. H. M. *et al.* Global biodiversity: indicators of recent declines. *Science* **328**, 1164–1168 (2010).
- Living Planet Report 2016: Risk and Resilience in a New Era* (WWF International, 2016).
- Winfree, R., Fox, J. W., Williams, N. M., Reilly, J. R. & Cariveau, D. P. Abundance of common species, not species richness, drives delivery of a real-world ecosystem service. *Ecol. Lett.* **18**, 626–635 (2015).
- Mair, L. *et al.* Abundance changes and habitat availability drive species' responses to climate change. *Nat. Clim. Change* **4**, 127–131 (2014).
- Johnston, A. *et al.* Observed and predicted effects of climate change on species abundance in protected areas. *Nat. Clim. Change* **3**, 1055–1061 (2013).
- Urban, M. C. Accelerating extinction risk from climate change. *Science* **348**, 571–573 (2015).
- Chen, I. C., Hill, J. K., Ohlemuller, R., Roy, D. B. & Thomas, C. D. Rapid range shifts of species associated with high levels of climate warming. *Science* **333**, 1024–1026 (2011).
- Gillings, S., Balmer, D. E. & Fuller, R. J. Directionality of recent bird distribution shifts and climate change in Great Britain. *Glob. Change Biol.* **21**, 2155–2168 (2015).
- Virkkala, R. & Lehikoinen, A. Patterns of climate-induced density shifts of species: poleward shifts faster in northern boreal birds than in southern birds. *Glob. Change Biol.* **20**, 2995–3003 (2014).
- Devictor, V. *et al.* Differences in the climatic debts of birds and butterflies at a continental scale. *Nat. Clim. Change* **2**, 121–124 (2012).
- Sala, O. E. *et al.* Biodiversity—global biodiversity scenarios for the year 2100. *Science* **287**, 1770–1774 (2000).
- Conti, M. E. & Cecchetti, G. Biological monitoring: lichens as bioindicators of air pollution assessment—a review. *Environ. Pollut.* **114**, 471–492 (2001).
- Donald, P. F., Green, R. E. & Heath, M. F. Agricultural intensification and the collapse of Europe's farmland bird populations. *Proc. R. Soc. Lond. B* **268**, 25–29 (2001).

14. Burns, F. *et al.* Agricultural management and climatic change are the major drivers of biodiversity change in the UK. *PLoS ONE* **11**, e0151595 (2016).
15. Adrian, R., Gerten, D., Huber, V., Wagner, C. & Schmidt, S. R. Windows of change: temporal scale of analysis is decisive to detect ecosystem responses to climate change. *Mar. Biol.* **159**, 2533–2542 (2012).
16. Guisan, A. & Thuiller, W. Predicting species distribution: offering more than simple habitat models. *Ecol. Lett.* **8**, 993–1009 (2005); erratum **10**, 435–435 (2007).
17. Parmesan, C. *et al.* Beyond climate change attribution in conservation and ecological research. *Ecol. Lett.* **16**, 58–71 (2013).
18. Williams, S. E., Shoo, L. P., Isaac, J. L., Hoffmann, A. A. & Langham, G. Towards an integrated framework for assessing the vulnerability of species to climate change. *PLoS Biol.* **6**, 2621–2626 (2008).
19. van Herk, C. M., Aptroot, A. & van Dobben, H. F. Long-term monitoring in the Netherlands suggests that lichens respond to global warming. *Lichenologist* **34**, 141–154 (2002).
20. Cahill, A. E. *et al.* How does climate change cause extinction? *Proc. R. Soc. B* **280**, 20121890 (2013).
21. Seppelt, R., Manceur, A. M., Liu, J. G., Fenichel, E. P. & Klotz, S. Synchronized peak-rate years of global resources use. *Ecol. Soc.* **19**, 50 (2014).
22. Eglington, S. M. & Pearce-Higgins, J. W. Disentangling the relative importance of changes in climate and land-use intensity in driving recent bird population trends. *PLoS ONE* **7**, e30407 (2012).
23. van Swaay, C., Warren, M. & Lois, G. Biotope use and trends of European butterflies. *J. Insect Conserv.* **10**, 189–209 (2006).
24. Venter, O. *et al.* Sixteen years of change in the global terrestrial human footprint and implications for biodiversity conservation. *Nat. Commun.* **7**, 12558 (2016).
25. Simpson, S. D. *et al.* Continental shelf-wide response of a fish assemblage to rapid warming of the sea. *Curr. Biol.* **21**, 1565–1570 (2011).
26. Daufresne, M. & Boet, P. Climate change impacts on structure and diversity of fish communities in rivers. *Glob. Change Biol.* **13**, 2467–2478 (2007).
27. Flourey, M., Usseglio-Polatera, P., Ferreol, M., Delattre, C. & Souchon, Y. Global climate change in large European rivers: long-term effects on macroinvertebrate communities and potential local confounding factors. *Glob. Change Biol.* **19**, 1085–1099 (2013).
28. Jeppesen, E. *et al.* Impacts of climate warming on the long-term dynamics of key fish species in 24 European lakes. *Hydrobiologia* **694**, 1–39 (2012).
29. Wagner, C. & Adrian, R. Consequences of changes in thermal regime for plankton diversity and trait composition in a polymictic lake: a matter of temporal scale. *Freshwat. Biol.* **56**, 1949–1961 (2011).
30. Devictor, V., Julliard, R., Couvet, D. & Jiguet, F. Birds are tracking climate warming, but not fast enough. *Proc. R. Soc. B* **275**, 2743–2748 (2008).
31. Clavero, M., Villero, D. & Brotons, L. Climate change or land use dynamics: do we know what climate change indicators indicate? *PLoS ONE* **6**, e18581 (2011).
32. Guisan, A. & Thuiller, W. Predicting species distribution: offering more than simple habitat models. *Ecol. Lett.* **8**, 993–1009 (2005).
33. Storie, C. *et al.* Stepping inside the niche: microclimate data are critical for accurate assessment of species' vulnerability to climate change. *Biol. Lett.* **10**, 20140576 (2014).
34. Homburg, K., Homburg, N., Schaefer, F., Schuldt, A. & Assmann, T. Carabids.org—A dynamic online database of ground beetle species traits (Coleoptera, Carabidae). *Insect Conserv. Div.* **7**, 195–205 (2014).
35. Burkhardt, U. *et al.* The Edaphobase project of GBIF-Germany—a new online soil-zoological data warehouse. *Appl. Soil Ecol.* **83**, 3–12 (2014).
36. Poloczanska, E. S. *et al.* Global imprint of climate change on marine life. *Nat. Clim. Change* **3**, 919–925 (2013).
37. Rue, H., Martino, S. & Chopin, N. Approximate Bayesian inference for latent Gaussian models by using integrated nested Laplace approximations. *J. R. Stat. Soc. B* **71**, 319–392 (2009).
38. Haylock, M. R. *et al.* A European daily high-resolution gridded data set of surface temperature and precipitation for 1950–2006. *J. Geophys. Res.* **113**, D20119 (2008).
39. Caissie, D. The thermal regime of rivers: a review. *Freshwat. Biol.* **51**, 1389–1406 (2006).
40. Kaschner, K. *et al.* *AquaMaps Environmental Dataset: Half-Degree Cells Authority File (HCAF) v. 07/2010* (AquaMaps, accessed 25 July 2013); www.aquamaps.org/data
41. Grewe, Y., Hof, C., Dehling, D. M., Brandl, R. & Brandle, M. Recent range shifts of European dragonflies provide support for an inverse relationship between habitat predictability and dispersal. *Glob. Ecol. Biogeogr.* **22**, 403–409 (2013).
42. Devictor, V., Julliard, R. & Jiguet, F. Distribution of specialist and generalist species along spatial gradients of habitat disturbance and fragmentation. *Oikos* **117**, 507–514 (2008).
43. Penone, C. *et al.* Imputation of missing data in life-history trait datasets: which approach performs the best? *Methods Ecol. Evol.* **5**, 961–970 (2014).
44. Koller, M. & Stahel, W. A. Sharpening Wald-type inference in robust regression for small samples. *Comput. Stat. Data Anal.* **55**, 2504–2515 (2011).
45. Domsich, S. *et al.* Modelling distribution in European stream macroinvertebrates under future climates. *Glob. Change Biol.* **19**, 752–762 (2013).
46. 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).
47. Drummond, A. J., Suchard, M. A., Xie, D. & Rambaut, A. Bayesian phylogenetics with BEAUti and the BEAST 1.7. *Mol. Biol. Evol.* **29**, 1969–1973 (2012).
48. Fritz, S. A., Bininda-Emonds, O. R. P. & Purvis, A. Geographical variation in predictors of mammalian extinction risk: big is bad, but only in the tropics. *Ecol. Lett.* **12**, 538–549 (2009).
49. Durka, W. & Michalski, S. G. Daphne: a dated phylogeny of a large European flora for phylogenetically informed ecological analyses. *Ecology* **93**, 2297–2297 (2012).
50. Dunger, W. & Burkhardt, U. *Synopses on Palearctic Collembola* (Museum Natural History, Görlitz, 2012).
51. Guiry, M. D. & Guiry, G. M. *AlgaeBase* (National University of Ireland, 2017); <http://www.algaebase.org>
52. Münkemüller, T. *et al.* How to measure and test phylogenetic signal. *Methods Ecol. Evol.* **3**, 743–756 (2012).
53. Jombart, T., Balloux, F. & Dray, S. Adephylo: new tools for investigating the phylogenetic signal in biological traits. *Bioinformatics* **26**, 1907–1909 (2010).
54. Paradis, E., Claude, J. & Strimmer, K. APE: analyses of phylogenetics and evolution in R language. *Bioinformatics* **20**, 289–290 (2004).
55. Nakagawa, S. & Cuthill, I. C. Effect size, confidence interval and statistical significance: a practical guide for biologists. *Biol. Rev.* **82**, 591–605 (2007).
56. Koricheva, J., Gurevitch, J. & Mengersen, K. *Handbook of Meta-analysis in Ecology and Evolution* (Princeton Univ. Press, 2013).
57. R: *A Language and Environment for Statistical Computing* (R Foundation for Statistical Computing, 2013).

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Author contributions

D.E.B. performed the analysis and wrote the outline of the paper with K.B.G. The study and analysis was perceived and designed by D.E.B., C.H., P.H., I.Kr., O.S. and K.B.G. All remaining authors contributed data towards the analysis. All authors helped draft the manuscript.

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Competing interests

The authors declare no competing financial interests.