

# Population trends of European common birds are predicted by characteristics of their climatic niche

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## Abstract

Temperate species are projected to experience the greatest temperature increases across a range of modelled climate change scenarios, and climate warming has been linked to geographical range and population changes of individual species at such latitudes. However, beyond the multiple modelling approaches, we lack empirical evidence of contemporary climate change impacts on populations in broad taxonomic groups and at continental scales. Identifying reliable predictors of species resilience or susceptibility to climate warming is of critical importance in assessing potential risks to species, ecosystems and ecosystem services. Here we analysed long-term trends of 110 common breeding birds across Europe (20 countries), to identify climate niche characteristics, adjusted to other environmental and life history traits, that predict large-scale population changes accounting for phylogenetic relatedness among species. Beyond the now well-documented decline of farmland specialists, we found that species with the lowest thermal maxima (as the mean spring and summer temperature of the hottest part of the breeding distribution in Europe) showed the sharpest declines between 1980 and 2005. Thermal maximum predicted the recent trends independently of other potential predictors. This study emphasizes the need to account for both land-use and climate changes to assess the fate of species. Moreover, we highlight that thermal maximum appears as a reliable and simple predictor of the long-term trends of such endothermic species facing climate change.

*Keywords:* breeding birds, climate niche, climate warming, global warming, long-term trends

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## Introduction

There is now general acceptance by the scientific community that anthropogenic release of greenhouse gases has led to changes in global climate (IPCC, 2001). Scientists have shown that many plants and animals have already been affected by the recent climate change (Parmesan & Yohe, 2003; Root *et al.*, 2005; Bradshaw & Holzapfel, 2007). Developing practical approaches to measure whether and how species are affected is vital in

predicting effects and potentially managing the responses of biodiversity. Europe has recently experienced a roughly linear increase in average temperature from the 1980s by over 0.9 °C (KNMI, 2007) and such temperature changes have affected species distributions and population dynamics (Julliard *et al.*, 2004; Huntley *et al.*, 2006; Lenoir *et al.*, 2008). Anthropogenic climatic change is expected to result in warmer global conditions by between 1.4 and 5.8 °C in 2100 (IPCC, 2001). Although global temperature increase is greater at higher northern latitudes (IPCC, 2007), in Europe it has been greatest in the south-west and least in Scandinavia, so that we would expect higher impacts of climate warming

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on species inhabiting the hottest parts of this geographical area.

A critical challenge for biodiversity conservation is to identify the characteristics of species that make them either resilient or susceptible to climate change so that we can improve assessments of impacts and risks, and thus develop appropriate mitigation strategies. It is difficult to achieve this ambitious goal because changes in population and distribution are taking place over large spatial (e.g. continental) and short temporal (few decades) scales, which are seldom captured simultaneously in current monitoring programmes (Yoccoz *et al.*, 2001). In addition, most approaches rely on modelling current and future distributions under climate change scenarios and lack empirical confirmation (Crick, 2004; Thomas *et al.*, 2004; Thuiller *et al.*, 2005; Araújo & Rahbek, 2006; Huntley *et al.*, 2008). Here we benefited from the development of breeding bird monitoring schemes across Europe, to tackle consistent key predictors of population changes over both large spatial and temporal scales. More precisely, we used data from the Pan-European Common Bird Monitoring Scheme (PECBMS; Gregory *et al.*, 2005, 2007, 2009) assessing long-term trends (1980–2005) of 110 common breeding bird species for 20 countries across the continent (Table S1).

In birds, as in other taxa, there is compelling evidence for the impact of climate change (Crick, 2004; Møller *et al.*, 2004) on the distribution (Thomas & Lennon, 1999; Brommer, 2004; La Sorte & Thompson, 2007), migration phenology (Jonzén *et al.*, 2006; Møller *et al.*, 2008), breeding biology (Crick & Sparks, 1999) and population dynamics (Addo-Bediako *et al.*, 2000; Julliard *et al.*, 2004; Both *et al.*, 2006). Therefore, candidate traits that might be associated with climate-responsiveness in animals can be grouped into three broad types: (i) climate sensitivity, such as endo/ectothermy, thermal range and thermal limits (Warren *et al.*, 2001; Stillman, 2003); (ii) ecological tolerance, such as habitat or niche position/breadth and range size (Cardillo *et al.*, 2005; Jetz *et al.*, 2007); and (iii) life history traits, such as body size, fecundity, generation time, dispersal morphology/physiology and migration strategy (Cardillo *et al.*, 2005; Jiguet *et al.*, 2006; Brommer, 2008). Habitat specialists and long-distance Afro-Palaearctic migrant birds are also known to face larger declines in Europe (Julliard *et al.*, 2004; Gregory *et al.*, 2005; Sanderson *et al.*, 2006); large species are less resilient to land-use changes (Cardillo *et al.*, 2005). Here we defined key predictors corresponding to different ecological traits to investigate their associations with continent-wide long-term population trends of the species, with the aim to focus on traits of the climatic niche. After adjusting species long-term trends to habitat specialization, migration and demographic strategies, we looked for the best

candidate of species-specific climatic niche parameters that could predict long-term trends of species facing climate warming. In particular, we expect that if the problem encountered by bird species facing climate warming is overheating close to the hot edge of a geographic distribution, then the maximum temperature tolerated by a species would be a good predictor of population resilience to climate change. If population changes are mainly driven by the species thermal flexibility, then the thermal tolerance (or the range of tolerated temperatures) would be a better predictor (Jiguet *et al.*, 2006). Finally, if population changes are influenced by deviation from optimal climate conditions over the distribution range, the thermal average could capture more variance of long-term trends (Devictor *et al.*, 2008b). Note that these hypotheses are not mutually exclusive. Whether and how each of these species-specific climatic characteristics explains species long-term trends has yet to be explored.

## Materials and methods

### *European bird trends*

Long-term trends of European breeding birds came from PECBMS. The main project goal of this scheme is to use common birds as indicators of the general state of nature using scientific data on changes in breeding populations across Europe (Gregory *et al.*, 2005). The PECBMS is an association of experts and national organizations cooperating through the European Bird Census Council (EBCC) and BirdLife International, with technical assistance from Statistics Netherlands. Species trend information is derived from annually operated national breeding bird surveys spanning different periods from 20 European countries (Ireland, the United Kingdom, the Netherlands, Denmark, Sweden, Norway, Finland, Estonia, Latvia, Poland, Czech Republic, Hungary, Austria, Germany, Switzerland, Belgium, France, Spain, Portugal and Italy). National monitoring coordinators provide data to produce reliable European trends for 124 breeding species, available at <http://www.ebcc.info>. The trend used here is the average growth rate (log-scale) of the European population as the additive slope per species associated with its standard error over 1980–2005, as estimated by Gregory *et al.* (2005). National species' trends were obtained with Poisson regression allowing for missing counts in the time series and yielding unbiased annual indices of relative population size with standard errors (McCullagh & Nelder, 1989). Although national schemes differ in count methods in the field, these differences do not influence the supranational results because the national indices are converted into corresponding population

numbers before being combined (Gregory *et al.*, 2005). National indices and their associated standard errors and year–year covariances were combined in a hierarchical way to create a European index for each species in such a way as to estimate missing values in countries with incomplete time series (Gregory *et al.*, 2005). National indices were then converted into yearly national population sizes for all years using a weighting factor calculated as the national population size for a reference year (2000) divided by the estimated yearly scheme total for that year (calculated as the average 1999–2001 to reduce the effect of annual fluctuations). European population sizes in 2000 were calculated as the geometric mean of population minimum and maximum, estimated for the year 2000 and derived from BirdLife International (2004). Weighting allows for the fact that different countries hold different proportions of the species' European population. This resulted in the estimation of yearly totals at European level, which we converted into indices, with a start value set arbitrarily at 100 in 1980. Finally, we calculated an overall log-linear trend as a descriptive statistic of the changes in the log of these time-totals. The overall trend is the ordinary least-squares estimator of the slope parameter with its standard error (Pannekoek & Van Strien, 2001). For some species, long-term trends were calculated on a slightly shorter time period, starting at the time counts were available to estimate trends (later than 1980; see supporting information).

#### *Defining explanatory variables*

We used three species-specific measures of the climate niche (thermal maximum, range and average), two measures of the environmental niche (breeding range size and main habitat type) and two life history traits (age at first breeding, as a proxy for demographic traits and migration strategy). Some supplementary variables were considered in early stages of the analyses but were excluded from multivariate models because they were intercorrelated and redundant as potential predictors (these were body mass, annual fecundity, brood number and diet). Measures of climate niches were obtained using average spring and summer monthly temperature of atlas grid cells where a species is breeding in Europe (Hagemeijer & Blair, 1997): thermal maximum, defined as the mean for hottest 5% cells; thermal minimum, as the mean for the coldest 5% cells; thermal range, as the difference between thermal maximum and thermal minimum; and thermal average, as the mean for all breeding cells data (temperatures as mean monthly March to August temperature for the period 1950–2000; data from the Worldclim database, <http://www.worldclim.org>).

Note that using the 5% hottest/coolest grid cells from the atlas to estimate thermal maxima/minima, respectively, involves the same proportion of the total range for every species. A potential bias in this approach is that a species with a larger thermal range will usually occupy a larger total number of grid cells, such that the hottest 5% of cells for a 'thermal generalist' may include squares that are further away from the range edge than are the hottest 5% of cells for a 'thermal specialist'. If response to climate warming depends on distance from the range margin, the 5% rule could lead to statistical problems. An alternative is to use a constant number of grid cells for each species, such as the 50 hottest/coldest grid cells, which generate the same sample size for temperature data for every species. A consequence of this second approach is that a higher proportion of occupied cells is used for small-range than for large-range species. We therefore conducted a complementary analysis using this 50-cells rule and verified that the conclusions were robust to how we measured thermal maximum and minimum.

We used the EBCC Atlas of European Breeding Birds (Hagemeijer & Blair, 1997) to obtain breeding range size in Europe (measured as the total number of  $50 \times 50 \text{ km}^2$  grid cells with breeding, log-transformed) as well as the mean latitude where a species is breeding in Europe (as the average latitude of all atlas grid cells where a species is reported as breeding). From all European breeding species, we considered those breeding in at least 300 grid cells, so that cells used to estimate thermal maximum and minimum numbered at least 15. We therefore had available data for 110 species (listed in supporting information), which represent not all but a substantial sample of all European breeding species (about one quarter) but the vast majority of individual birds breeding in Europe (more than 95%; see e.g. Devictor *et al.*, 2008b). Current species ranges result from climatic constraints but also from nonclimatic human (habitat and other) effects. Impacts of such range reductions might bias our measures of the species climatic niche, although recent works on the same atlas data demonstrated that European distributions of breeding birds are determined by climate (Huntley *et al.*, 2008). Similarly, climate envelope models were efficient to retrodict recent changes in bird distribution (Green *et al.*, 2008).

Species characteristic for main habitat types have been classified using a procedure based on species classification within four main biogeographical regions: Atlantic, Boreal, Continental and Mediterranean. This produced a list of woodland and farmland specialists, and of species with other habitat preferences, from which eventual habitat specialization (for wetlands and human settlements) was deduced from

Jiguet *et al.* (2007). We defined main habitat type for each species, as farmland, woodland, wetland, urban for habitat specialists, with remaining species being habitat generalists, accordingly.

The following two life history traits were obtained from the Handbook of the Birds of the Western Palearctic (Cramp *et al.*, 1977–1994): age at first breeding, as a proxy for generation time that is hardly available for short-lived passerines, so as a proxy for most demographic traits, and migratory strategy, as long-distance migrant opposed to sedentary or short-distance migrant, with no distinction between these two latter categories as for many European species northern populations are short-distance migrants while southern populations are sedentary (Cramp *et al.*, 1977–1994). Other traits were also initially considered: fecundity, brood number, body mass, nest location and diet. Within continuous predictors, demographic traits are correlated: age at first breeding is significantly correlated to brood number (Pearson's  $r = -0.191$ ), fecundity ( $r = -0.398$ ) and body mass ( $r = -0.583$ ), and therefore appears as a good proxy for most demographic traits. Other correlations between predictors, involving one categorical predictor, concerned: (1) diet and migration strategy ( $r = 0.530$ ), as almost all insectivorous species are trans-Saharan migrants; and (2) nest site and main habitat type ( $r = 0.402$ ), because farmland specialists nest mostly on the ground and woodland specialists nest mostly in bushes or trees. Therefore, in the main multivariate analyses, we considered only age at first breeding as a proxy for generation time and demographic traits, and kept main habitat type and migration strategy but dismissed nest location and diet because of collinearity. Body mass and diet were considered in univariate models because they correlate with the extent of recent polewards range shifts in northern birds (Brommer, 2008).

#### Testing explanatory variables

We tested the effects of predictors on species trends using Linear Models using the R statistical software. Each predictor was first tested alone (univariate ANOVA). We further performed a weighted linear model with a climate niche predictor, range size and main habitat type, and the two life history traits. In this model, thermal maximum was considered for climate niche measures, as it captured most variance (see 'Results') and as it is correlated with thermal range (Pearson correlation coefficient,  $r = 0.213$ ,  $P < 0.05$ ,  $N = 110$ ), thermal minimum ( $r = 0.392$ ,  $P < 0.05$ ) and thermal optimum ( $r = 0.836$ ,  $P < 0.001$ ). All linear models were performed as weighted or unweighted; in the former case, we weighted each estimate of annual growth rate by the inverse of its variance. The weighting process

allows accounting for the precision of trend estimates, as species with the smallest standard error of growth rate estimate will contribute more. On the opposite, unweighted models will avoid some species to overweight the analyses and drive the general pattern. To deal with possible collinearity between predictors and draw inferences about the likely causality of variables, we further performed a hierarchical partitioning analysis (Mac Nally, 2002) with the same five predictors, using the hier.part package of the R statistical software (note that weighting is not feasible in hierarchical partitioning). Hierarchical partitioning is specifically suitable to handle collinearity among variables, as it disentangles each variable-specific effect from its interactions with all other variables considered. From this analysis, probability of independent contribution of the predictors was assessed with z-scores obtained using 1000 repeated randomizations (with the rand.hp function and a  $R^2$  goodness-of-fit measure).

#### Phylogenetic relatedness and comparative analyses

Species are more or less related on a phylogenetic scale. Hence, some of the explanatory variables considered (especially life history traits) have relatively similar values for closely related species because these species have a common evolutionary history. On the other hand, because closely related species tend to compete between each other, their distribution and niche breadth (here as measures of their climate or environmental niches) show a greater difference than expected by chance (Wiens, 1989). When controlling for phylogenetic effects, the most important variable is the response variable and phylogenetic correction seems appropriate since a recent study found that long-term trends are phylogenetically correlated in British birds (Thomas, 2008). A correction for phylogenetic relatedness was therefore also performed using the generalized least-squares (GLS) phylogenetic comparative method, which tests the robustness of regression models to phylogenetic relatedness (Freckleton *et al.*, 2002; Martins *et al.*, 2002). We used the 'ape' package of the R software to compute the phylogenetic tree of the species and to run the GLSs with a model dependence linked to the phylogenetic tree assuming a Grafen correlation structure (as no branch lengths were available). We used the classification published by Sibley & Ahlquist (1990) adapted from the update by Møller (2006) (see supporting information).

#### Results

In univariate analyses of variance, each niche predictor – but thermal minimum – as well as migrations strategy

**Table 1** Univariate analyses of variance of long-term population trends (1980–2005) of 110 bird species across Europe (20 countries)

Predictor	Linear effect		P-values		Phylogenetic comparative
	$r^2$	Slope $\pm$ SE	Weighted	Unweighted	
Thermal maximum	0.2135	0.0058 $\pm$ 0.0011	$\ll$ <b>0.001</b>	<b>0.047</b>	$\ll$ <b>0.001</b>
Thermal minimum	0.0052	–	0.452	0.083	0.137
Thermal range	0.0870	0.0038 $\pm$ 0.0012	<b>0.002</b>	0.597	<b>0.001</b>
Thermal average	0.1418	0.0093 $\pm$ 0.0022	$\ll$ <b>0.001</b>	<b>0.027</b>	$\ll$ <b>0.001</b>
Mean breeding latitude	0.1773	–0.0033 $\pm$ 0.0007	$\ll$ <b>0.001</b>	<b>0.029</b>	<b>0.632</b>
Breeding range size	0.0836	0.0202 $\pm$ 0.0065	<b>0.002</b>	0.393	<b>0.002</b>
Main habitat	0.1674	*	$<$ <b>0.001</b>	0.066	$<$ <b>0.001</b>
Migratory strategy	0.0806	–0.0104 $\pm$ 0.0032	<b>0.003</b>	0.659	$<$ <b>0.001</b> †
Age at first breeding	0.0004	–	0.827	0.096	0.351
Body mass	0.0017	–	0.673	0.219	0.746
Diet	0.0099	–	0.332	0.925	$<$ <b>0.001</b> †

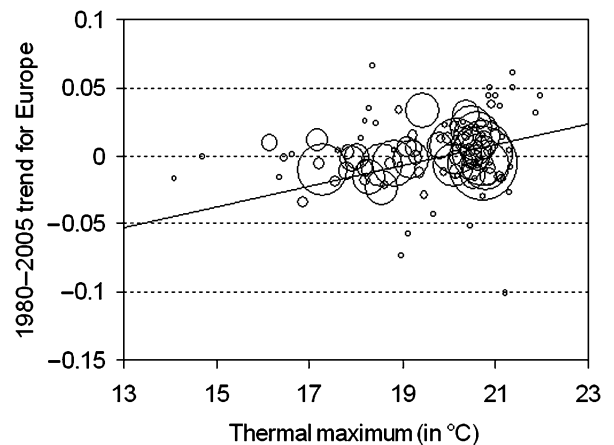
$r^2$ , slope parameter estimates (mean  $\pm$  SE) and  $P$ -value of  $F$ -tests are given (linear models,  $df = 1,108$  except for main habitat,  $df = 4,105$ ), first for weighted linear models, then  $P$ -values for unweighted models and for generalized least-squares (GLS) phylogenetic comparative model to test the robustness of the analysis to phylogenetic relatedness among species.

\*Significant difference between the control group (farmland species) and habitat generalists (slope  $\pm$  SE = 0.0178  $\pm$  0.0041,  $t = 4.29$ ,  $P \ll 0.001$ ); nonsignificant trends between control group and (i) woodland species (slope  $\pm$  SE = 0.0099  $\pm$  0.0053,  $t = 1.86$ ,  $P = 0.066$ ); (ii) urban species (slope  $\pm$  SE = 0.0120  $\pm$  0.0075,  $t = 1.61$ ,  $P = 0.111$ ).

†When correcting for phylogenetic relatedness in a GLS, the larger declines of long-distance migrants was maintained (slope  $\pm$  SE = –0.0439  $\pm$  0.0115,  $F_{1,108} = 14.6$ ), while insectivorous birds were revealed as facing larger declines too, although migratory strategy and diet are correlated (Pearson's  $r = 0.530$ ).

Bold  $P$ -values are significant at 0.05.

(with long-distance migrants facing larger declines) was significantly associated with population trends (Table 1). The significant effects of thermal maximum, thermal average and mean breeding latitude were maintained in nonweighted models. Thermal maximum taken as a separate key predictor captured the largest part of the variance in population changes ( $>21\%$ ;  $F_{1,108} = 29.3$ ,  $P < 0.001$ ; Fig. 1), and this result was robust to the account of phylogenetic relatedness among species (Table 1;  $F_{1,108} = 31.2$ ,  $P < 0.001$ ). When controlling for environmental niche measures and life history traits, thermal maximum still predicted population changes ( $F_{1,101} = 19.3$ ,  $P < 0.001$ ; Table 2). The significant effect of thermal maximum was robust to the way we estimated this niche measure (model with estimates obtained with a 50-cells, rather than a 5% rule: thermal maximum with a partial  $r^2$  of 0.11 and  $P < 0.001$ ) and to the account of phylogenetic relatedness among species (Table 2;  $F_{1,101} = 7.5$ ,  $P = 0.007$ ). Finally, hierarchical partitioning confirmed that thermal maximum predicted population changes ( $z$ -score = 3.13,  $P < 0.001$ ) independently of the other considered predictors, i.e. environmental niche measures and life history traits (Table 2). Overall, we estimated a yearly decrease of 0.47–0.69% (when considered as a lone predictor; Table 1) or 0.52–0.82% (when adjusted to environmental niche measures and life history traits; Table 2) in annual population growth



**Fig. 1** Relationship between long-term trend and thermal maximum of 110 breeding bird species in Europe. The trend is the additive annual growth rate over 1980–2005 in 20 countries across Europe. Thermal maximum was obtained as the mean of local spring and summer average monthly temperatures for the hottest 5% breeding grid cells in Europe. Each circle represents one species, the size of the circle is proportional to the precision of the slope coefficient estimating a species trend: the larger the circle, the better the quality of annual growth rate estimate. The plain line is the regression line of the direct weighted effect.

rate per 1 °C decrease in the upper limit of a climate niche. In models with adjusted effects of predictors presented in Table 2, we also found a significant effect

**Table 2** Long-term trends (1980–2005) of 110 bird species across Europe (20 countries) predicted by thermal maximum, two environmental niche measures and two life history traits: results of a weighted linear model, a hierarchical partitioning of variance and a generalized least-squares (GLS) phylogenetic comparative model

Predictor	Linear model		Hierarchical partitioning		Phylogenetic comparative model
	Partial $r^2$	$P$	z-score	$P$	$P$
Thermal maximum	0.1179	<0.001*	3.13	<0.001	<b>0.007</b>
Breeding range size	0.0092	0.224	0.30	0.382	0.154
Main habitat	0.1468	<0.001†	1.99	<b>0.023</b>	<b>0.025</b>
Migratory strategy	0.0145	0.126	−0.08	–	0.166
Age at first breeding	<0.001	0.971	1.46	0.072	0.071

In the linear model and the GLS, effects of predictors were tested adjusted to each others. Partial  $r^2$  and  $P$ -value of  $F$ -tests are given for the linear model ( $df = 1, 101$  except for main habitat,  $df = 4, 101$ ). 38.3% of total variance was captured. Results of the hierarchical partitioning analysis include  $z$ -scores (obtained using 500 repeated randomizations) and the associated probability. Note that negative joint effects are possible for variables that act as suppressors of other variables (here migration strategy, brood number and diet). Last column presents  $P$ -values of a GLS testing the robustness to phylogenetic relatedness among species.

\*For thermal maximum, slope  $\pm$  SE =  $0.0067 \pm 0.0015$ ; this effect was maintained if not weighting the data ( $F_{1,101} = 2.74$ ,  $P = 0.007$ ).

†Significant differences between farmland (as the control group) and (i) woodland species, slope  $\pm$  SE =  $0.0156 \pm 0.0048$ ,  $t = 3.23$ ,  $P = 0.002$ ; (ii) 'other habitats' species (including habitat generalists), slope  $\pm$  SE =  $0.0165 \pm 0.0036$ ,  $t = 4.51$ ,  $P \ll 0.001$ . No significant difference between control group (farmland birds) and wetland species ( $t = 0.59$ ,  $P = 0.557$ ) and urban species ( $t = 0.81$ ,  $P = 0.419$ ).

Bold  $P$ -values are significant at 0.05.

of main habitat type on growth rate, with woodland birds and habitat generalists showing higher average growth rates than farmland, wetland and urban birds.

## Discussion

We found that long-term trends of common European birds were highly correlated to several species-specific traits, among which climatic characteristics had strong explanatory power, independent of other traits. Our results allowed us to highlight more particular findings, the first one being some support for the large-scale decline of long-distance migrants (Table 1), already pinpointed for European breeding birds (Sanderson *et al.*, 2006). However, this effect (although robust to the account of phylogenetic relatedness among species) was not maintained when adjusted to other predictors. We presume that this negative trend reflects the difficulty for long-distance migrants to reach their breeding grounds at the appropriate time when facing climate warming (Both *et al.*, 2006). Advanced food peak leads to birds failing to breed at the time of maximal food supply (Visser *et al.*, 2006), and such climate-induced mistiming can lead to population decline (Møller *et al.*, 2008). An alternative explanation of this result is that increasing winter temperatures favour resident species and have negative impacts on migratory species through diffuse competition. Generation time, as a proxy for demographic rates, might influence the resilience of species to changing environment, especially in

short-lived species (Saether & Bakke, 2000), but we failed to find an effect of age at first breeding on long-term trends of European breeding birds: the shorter-lived bird species were indeed not more sensitive or resilient to global change than other species.

Habitat-specialized species are declining at a much higher rate than habitat generalists (Warren *et al.*, 2001; Jiguet *et al.*, 2007), which we assume are more tolerant to environmental conditions and change. That habitat specialists are declining is a sign that habitat quality is globally decreasing through fragmentation and land-use changes (Devictor *et al.*, 2008a) and this may lead to functional biotic homogenization (Olden *et al.*, 2004). In particular farmland birds are known to face large population declines across Europe (Gregory *et al.*, 2005). Yet, the causes of habitat deterioration may be different for different habitats, specialization itself, rather than living in a particular habitat, and may affect global biodiversity (Jiguet *et al.*, 2007). In our analyses, habitat type for farmland birds is therefore likely to partly capture effects of agriculture intensification, so that our results clearly quantify adjusted effects of habitat and climate changes on the collapse of farmland breeding birds (Donald *et al.*, 2001). Large distribution ranges should provide a buffer against global change (Jetz *et al.*, 2007). Concerning European common breeding birds we found that range size as a lone predictor was positively correlated with long-term trends, although range size was not identified as a significant predictor when considered adjusted to thermal

maximum and life history traits (especially in the hierarchical partitioning of variance), probably because it is positively correlated with thermal maximum (Pearson's  $r = 0.278$ ). This emphasizes the need to consider simultaneously land use and climate sensitivity of species when seeking an explanation of their long-term trends, as we did here.

#### *Climate niche measures*

We found that all three measures of climate niche were related to long-term trends. Hence, southern species have a better fate than northern species across Europe, and the problem encountered by bird species facing climate warming could be either overheating close to the hot edge of a geographic distribution, departure from the species thermal tolerance or deviation from the species thermal optimum. However, thermal maximum captured a larger proportion of variance in long-term trends (regardless of how large is the rest of the thermal distribution), and had a significant effect when adjusted to the other two climate niche predictors that were robust to weighting, to the account of phylogenetic relatedness and to the way in which we estimated climatic niche measures. Species with a high thermal maximum, as deduced by the mean temperature for the hottest parts of a distribution, had a greater capacity than low thermal maximum species to show population growth rates that were resilient to climate change.

Within the niche theory framework (Brown & Lomolino, 1998), the Shelford's law of tolerance states that the distribution of a species will be limited by its range of tolerance for local environmental factors (e.g. climatic, topographic and biological). A species is most abundant in areas where the environmental variables are within the optimum range for that species. The species is rare in areas where it experiences physiological stress because the environmental variables depart from this optimum range. The species does not occur at all in areas beyond its upper and lower limits of tolerance. Interestingly, we can apply these concepts to climatic niches (instead of ecological niches) in using the potential effects of temperature increase on each species according to their thermal average (a proxy for the optimum range centre), thermal range (niche breadth) or thermal maximum (niche upper limit). As we found that thermal maximum was the best predictor of long-term trends, we suggest that population trends decrease more strongly close to niche limits, and that the problem faced by bird populations in Europe may be overheating close to the hot edge of a distribution. The lower the thermal maximum, the closer the European population of a species is to this hot edge and the risk of overheating as global temperature increases.

This overheating experienced by European birds could affect demographic parameters directly (e.g. impact on the physiological tolerance of juvenile and/or mature birds) or indirectly through mechanisms affecting various interactions with other species that impact upon the focal species and affect its ability to breed (higher asynchrony with or depletion of some temperature-dependent food resources, prevalence of a parasite, etc.). We hypothesize that decreases in fitness are larger at the upper niche limit than close to its centre, so that there is a visible effect on population trends. Having a small niche breadth could constitute a further risk factor, because niche limits are closer to the niche centre for such species, although we did not find such an effect in our study (thermal maximum  $\times$  thermal range interaction was not significant if added to the model presented in Table 2:  $F_{1,100} = 2.74$ ,  $P = 0.101$ ).

#### **Conclusion**

Our aim was not to demonstrate the causal mechanisms driving long-term species trends but rather to identify useful and powerful predictors of such trends, especially concerning the response of species to climate warming. The presented results are interesting for their simplicity. Bird species with the highest thermal maxima, as measured by the average spring and summer temperature in the hottest locations where they breed in Europe, show no significant trend in population changes, whereas species with the lowest thermal maxima are declining in the long term. Therefore, thermal maximum appears as a reliable predictor of the response of these endothermic vertebrates to climate warming, which is also in accord with the expectations of distribution/climate envelope models: species with cool-limited climate envelopes (e.g. distributed at highest latitudes or altitudes) face higher extinction risk from climate change (Jetz *et al.*, 2007). We suggest that thermal maximum is likely to provide a simple estimator and therefore a critical measure of the potential risk species faces in the context of climate change. As common species provide the largest part of ecosystem services (Schwartz *et al.*, 2000; Gaston & Fuller, 2008), so that identifying species-specific traits predicting their response to climate change is crucial in assessing the potential risks ecosystems are facing with the combined impacts of land-use and climate changes (Sekercioğlu *et al.*, 2004).

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### Supporting Information

Additional Supporting Information may be found in the online version of this article:

**Figure S1.** Phylogenetic tree of the 110 species used in the comparative analyses. We made the assumption that all branches in the phylogeny were of equal length. The tree was plotted using the software Mesquite (Maddison, W.P. & D.R. Maddison. 2006. Mesquite: A modular system for evolutionary analysis. Version 1.12. <http://mesquiteproject.org>).

**Table S1.** The 110 common breeding bird species we studied and their long-term trend, thermal maximum, main habitat type, number of breeding atlas grid cells.

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