Bird population trends are linearly affected by climate change along species thermal ranges

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Beyond the effects of temperature increase on local population trends and on species distribution shifts, how populations of a given species are affected by climate change along a species range is still unclear. We tested whether and how species responses to climate change are related to the populations locations within the species thermal range. We compared the average 20 year growth rates of 62 terrestrial breeding birds in three European countries along the latitudinal gradient of the species ranges. After controlling for factors already reported to affect bird population trends (habitat specialization, migration distance and body mass), we found that populations breeding close to the species thermal maximum have lower growth rates than those in other parts of the thermal range, while those breeding close to the species thermal minimum have higher growth rates. These results were maintained even after having controlled for the effect of latitude *per se*. Therefore, the results cannot solely be explained by latitudinal clines linked to the geographical structure in local spring warming. Indeed, we found that populations are not just responding to changes in temperature at the hottest and coolest parts of the species range, but that they show a linear graded response across their European thermal range. We thus provide insights into how populations respond to climate changes. We suggest that projections of future species distributions, and also management options and conservation assessments, cannot be based on the assumption of a uniform response to climate change across a species range or at range edges only.

Keywords: biological traits; breeding bird monitoring; climate warming; climatic niche; population growth rate; thermal maximum

1. INTRODUCTION

Impact of climate warming on biodiversity has mainly been investigated using the change in local population dynamics (Sillett *et al.* 2000), phenology (Charmantier *et al.* 2008), distribution (Parmesan 2006; La Sorte & Thompson 2007), or projected changes in distributions (Thomas *et al.* 2004; Jetz *et al.* 2007). Species are not equally at risk when facing climate change: whether they are positively or negatively affected depends on many species-specific features. For instance, mismatch between a species phenology and its resources may threaten individual survival and reproductive success (Both *et al.* 2006; Sherry *et al.* 2007), and high-temperature dwelling species progressively replace other species (Devictor *et al.* 2008). Beyond the local effects of

temperature increase on population dynamics and community composition, climate change also induces large-scale modification of species distributions. In particular, shifts at the poleward limit of the distributional range or at the upper edge of the altitudinal range have been documented for many taxa (Parmesan & Yohe 2003; Hickling *et al.* 2006). But beyond changes at range limits, more subtle changes within the ranges of species are also likely and might have important ecological and evolutionary consequences. Looking at altitudinal distribution changes, Lenoir *et al.* (2008) found a significant upward shift in plant species optimum elevation during the twentieth century, but comparable studies focusing on population dynamics within species ranges have hardly been achieved. Therefore, how populations of a given species are affected by climate change along the species range is still unclear. Yet, the populations of a given species are not experiencing similar environmental conditions and are not similarly adapted to environmental changes within the species range

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(Holt 2003; Both & te Marvelde 2007; Angert 2009; Both *et al.* 2010). Consequently, following climate change, population dynamics of a given species could vary across the species range rather than being uniformly distributed.

The spatial distribution of a given species is limited by its population size and/or its range of tolerance for local environmental factors (e.g. climatic, topographic and biological; Brown & Lomolino 1998). Individuals should have a higher fitness in areas where the environmental variables are within the optimal ranges, with decreases towards niche limits where they experience higher physiological or ecological stress (Angert 2006). Beyond individual fitness, the trend in local populations is counterbalanced by source-sink dynamics (Pulliam 2000) across the entire ecological niche (Hutchinson 1957), so that in theory local population growth should roughly equal zero across the whole range, with larger variance near range limits (Brown *et al.* 1996). Obviously, climate change might first disrupt such equilibrium at range margins where populations are experiencing higher environmental stress. However, any population located within the species range could as well be negatively or positively affected by climate change (Both & te Marvelde 2007). One can thus predict that if climate warming is disrupting an existing equilibrium between population dynamics and climatic conditions, population dynamics should be more negatively affected when located near the hottest limit of a species distribution, and more positively affected when located near the coolest limit of a species distribution. Alternatively, the geographical variation in local population trends could ensue from variation in local spring warming, which may have ecological effects such as greater mistiming in areas with more warming. Climate warming has a strong latitudinal component across Europe (Both & te Marvelde 2007), and differential global climate change contributes to some species declines (Jones & Cresswell 2010). In that case, we expect population trends to be primarily structured latitudinally, independent of the position of the population within the species thermal range.

Among simple species-specific traits likely to influence species responses to climate change, the thermal maximum of the species climatic niche, defined as the maximal average spring–summer temperature a species can tolerate when breeding across its range, has been identified as a key predictor of recent population trends in European breeding birds facing climate warming (Gregory *et al.* 2009). Indeed, species with a high value of thermal maximum have a better fate across Europe, probably because they benefit from potential extended newly suitable areas owing to increasing temperatures across Europe, or because they can better cope with local climate warming and spring advancement (Jiguet *et al.* 2010). However, this global pattern is silent on whether all populations of a given species have similar responses to climate change. In other words, an average trend for a given species at a European level can mask high heterogeneity in the populations responses of that species within Europe (see Both *et al.* 2006). To investigate this issue one should test whether population responses to climate warming within the core-range of species thermal distribution differ from those occurring near species thermal range edges (Jamera *et al.* 2009; Jones & Cresswell 2010).

Here, we focused on recent population long-term trends (1989–2008, i.e. 20 years) of 62 terrestrial breeding bird species monitored in three European countries, France, The Netherlands and Sweden. Measuring species trends within these three countries reflects, for each species, population dynamics measured in very different thermal conditions where they breed within their European range along a latitudinal gradient. We then tested whether the trends of local populations of a given species are dependent on their distance from their thermal maximum. As France and Sweden are clearly large countries, we divided them in three latitudinal belts. As we focused on species-specific differences in population dynamics according to their location within the species range, we controlled analyses for differences in life-history traits already identified as influencing trends of vertebrates and/or varying across a species range in birds: habitat specialization (Jiguet *et al.* 2010), migration distance (Jones & Cresswell 2010), and body mass (Cardillo *et al.* 2005; Brommer 2008). While estimating the thermal location of a population within the species European breeding range, we also had to account for variations in breeding timing (phenology) along the latitudinal gradient considered and for different migration strategy. This variation can be responsible for a differential response of breeding populations to uneven climate change (Deutsch *et al.* 2009; Jones & Cresswell 2010).

2. MATERIAL AND METHODS

(a) *Bird population trends*

Bird number data came from national breeding bird survey schemes implemented in the three countries. In brief, these schemes allow the monitoring of breeding populations of common birds with standardized methodology using point counts or territory mapping (Julliard *et al.* 2003; Lindström *et al.* 2009; Van Turnhout *et al.* 2010). The sampling design, survey methods and studied species are detailed in the electronic supplementary materials, S1–S4. We used data from France, The Netherlands and Sweden altogether to test the effect of population locations within species range. In order to refine the study of trends near range limits and to have trends of populations at a similar spatial scale between country subsamples, we subdivided France and Sweden into three latitudinal belts of equal width, and estimated population trends for each species in each belt when data were available (see electronic supplementary material S1 and S2). For each species, raw data were the maximum number of individuals (point counts) or territories (territory mapping) counted yearly at a site. Our study period was 1989–2008, which is the longest available period of joint data. Log-linear models, developed for each latitudinal belt, with an additive effect of the site and a continuous effect of year, provided the average growth rate of populations of each species in each latitudinal belt over the 20 years. According to variability in sample size and sampling errors, each trend was not estimated with similar confidence. Therefore, for each species and for each latitudinal belt, the standard error associated with the estimated trend was further used for weighting in other statistical models. In other words, precedence was given to those trends with lower associated standard error. Note that the trend estimates obtained from this analysis are directly comparable between countries despite some differences in field survey

methodologies (see Gregory *et al.* (2005) for a rationale). We considered all species ($n = 62$) for which long-term trends in at least three latitudinal belts (one in each country, The Netherlands being considered here as a latitudinal belt on its own) and ecological traits (see below) were available for each country; this resulted in a dataset with a total sample of 406 growth rate estimates (171 for France, 61 for The Netherlands, 174 for Sweden).

(b) Bird traits

We first adjusted species trends to variations in life-history traits and habitat specialization across countries before investigating potential links with climatic niche characteristics. Traits were assigned nationally and obtained from Jiguet *et al.* (2007) for France, Van Turnhout *et al.* (2010) for The Netherlands and BWPI (2006) for Sweden (Cramp *et al.* 1977–1994). We considered the following life-history traits that have been shown to relate to species fate when facing global change. (i) Log-transformed body mass was considered as a proxy for demographic traits (Julliard *et al.* 2003; Cardillo *et al.* 2005). (ii) Long-distance migrants are facing large population declines, so we considered the log-transformed distance between the breeding grounds and the wintering grounds of national populations as a predictor (obtained from ringing recoveries for all the three countries, as detailed in Jiguet *et al.* 2007). (iii) Habitat specialization was defined on a country-basis, as a continuous measure of the variance in relative density among the main habitat classes recorded by the breeding bird survey schemes (18 classes; see the electronic supplementary material). This specialization index (Devictor *et al.* 2007) was further standardized so that for each country, the mean (m) equals zero and the standard deviation (sd) equals 1: each value (v) of a country (c) was transformed as $(v_c - m_c)/sd_c$. In doing so, habitat specialization indices had the same mean and dispersion in the three countries and embodied a similar range of variations in habitat specialization across the three countries, despite differences in the number of habitats present.

(c) Thermal metrics of bird populations

We estimated the thermal distance between the thermal maximum of a species and the thermal average of the considered breeding populations. Note that in estimating the thermal location of a population within the species European breeding range, we directly accounted for variations in breeding phenology between long-distance migrants (breeding later) and residents or short-distance migrants. Furthermore, breeding phenology varies also among populations of each species according to their geographical location, here mainly latitude. To consider all these among and within species variations in thermal breeding conditions, we used a species-specific time-window to estimate the population thermal maximum and thermal range, depending on the breeding time. To do so, we adapted the estimation of the thermal metrics from Jiguet *et al.* (2007) by considering time-windows varying according to the migration strategy of a species and to the northern/southern location of a breeding population. More precisely, the thermal maximum was defined as the average temperature of the hottest 5 per cent of grid cells where the species are breeding (Jiguet *et al.* 2007), using a specific time-window for each species: March–August for resident or short-distant migrants and April–August for long-distance migrants. The considered grid cells were those from the European Bird Census Council

(EBCC) Breeding Birds atlas (Hagemeijer & Blair 1997). The population thermal average was defined as the average temperature of all grid cells of the EBCC atlas where a species is breeding in a latitudinal belt within a country (Jiguet *et al.* 2007). The thermal average of a given population was also adjusted to its specific time-window: March–August for resident and short-distance migrants in France and The Netherlands, April–August for the same species in Sweden and for long-distance migrants in France and The Netherlands, and May–August for the long-distance migrants in Sweden.

Finally, since the distance of a breeding population to the species thermal maximum is dependent on the extent of the species total thermal range, we divided this thermal distance by the species thermal range, and considered 1 minus this value (see formula below) to reflect a standardized measure of the relative position of the population within the species thermal range. Indeed, as species thermal ranges varied from 8.1 to 16.3°C for the studied species, being at e.g. 8°C from the thermal maximum could correspond to a thermal coordinate of 0 (the coolest limit) or to approximately 0.5 (half way between the thermal minimum and maximum). The thermal range was estimated as the difference between the thermal maximum and the thermal minimum (coldest 5% of atlas grid cells). In doing so, the distance varied between 0 and 1, and could be considered as the coordinate of the breeding populations along this (0–1) range, independent from the species-specific range extent. Values close to 0 represent populations near the species thermal minimum; values closer to 1 are populations near the species thermal maximum. This metric, hereafter called the thermal coordinate, was therefore given by $d = 1 - [$(species thermal maximum − population thermal average)/(species thermal maximum − species thermal minimum)$]$.

(d) Statistical analyses

We analysed the variations in 20 year average growth rates for the 62 species with linear mixed-effect models (assuming a normal distribution of the errors) using the R statistical framework and the lme4 package (http://lme4.r-forge.r-project.org/). We first ran simple analyses of growth rate variations across Europe using single covariates, before running more complicated models that attempt to control for these covariates. In the complete models, we first controlled for effects of three predictors (considered as fixed effects) known to correlate with trends of bird population at a European scale and known to vary within species between the studied countries: body mass (log-transformed), migration distance (log-transformed) and habitat specialization index. We also further considered the average latitude of each belt as a fixed-effect covariate. These variables were accounted for to further test the linear effect (i) of the thermal distance of the population to the species thermal maximum, or (ii) of the thermal coordinate of the population within the species standardized thermal range. Thus, we focused on the results concerning the effects of each of these two thermal estimates, adjusted to the other traits, in two separate mixed models. We also examined potentially important interaction terms in these mixed-effects models: interactions of the thermal metric with migration distance and with habitat specialization, as migration distance affects bird trends (Jones & Cresswell 2010) and as habitat specialists might be impacted differently by climate change owing to their sensitivity to land-use changes.

Table 1. Results of the linear mixed-effect models, with random effects of country, species and taxonomic family nested in order. (The two models differ in the considered estimate of the thermal niche predictor: (*a*) distance of the population from the species thermal maximum ($r^2 = 0.084$); (*b*) coordinate of the population along the thermal range of the species (ranging from 0 to 1, i.e. from thermal minimum to thermal maximum; $r^2 = 0.069$). d.f. = 396.)

predictor	estimate $\pm$	*t*-test	*p*
(*a*) body mass	0.0025 ± 0.0027	0.92	0.358
migration distance	-0.0001 ± 0.0012	-0.07	0.944
habitat specialization index	-0.0039 ± 0.0028	-1.41	0.159
distance to the thermal maximum	0.0048 ± 0.0014	3.56	<0.001
migration distance * distance to the thermal maximum	0.0002 ± 0.0004	0.50	0.620
habitat specialization * distance to the thermal maximum	0.0017 ± 0.0009	1.88	0.061
(*b*) body mass	0.0019 ± 0.0026	0.71	0.476
migration distance	0.0002 ± 0.0012	0.18	0.860
habitat specialization index	-0.0050 ± 0.0027	-1.85	0.065
population coordinate along thermal range	-0.0891 ± 0.0198	-4.49	<0.001
migration distance * population coordinate	-0.0030 ± 0.0057	-0.52	0.601
habitat specialization * population coordinate	-0.0353 ± 0.0128	-2.76	0.006

To further test for the potential nonlinear response of growth rates to the thermal niche measures, we conducted generalized additive mixed-effects models with the mgcv package under R with a smooth function for the thermal metrics to test the robustness of the linearity assumption. We computed graphic outputs of the response of population growth rate to the thermal metrics using these gamms.

In all models, we analysed data from the three countries which had different land-use histories (but also differences in size, biotic and abiotic characteristics); country was therefore considered as a random effect. Similarly, species identity was considered a random effect to account for differences in global population dynamics between species. We also included a random effect of the taxonomic family nested within the taxonomic order (following the phylogeny published in Jiguet *et al.* 2010) to account for phylogenetic dependency between the species. To verify that the identified patterns were not driven by particular subsets of the data, we repeated these analyses: (i) within the two large countries in which population growth rates were estimated in three latitudinal belts of similar width (electronic supplementary material, S1 and S2); (ii) by using only 50 per cent of the populations, deleting the 25 per cent of data with the lowest and the largest thermal metrics values (to verify that the patterns are not only driven by edge populations at the edges of distribution ranges); and (iii) by using only one belt per country (to eliminate the possibility of artefactual results ensuing from pseudoreplication).

3. RESULTS

The results of the univariate mixed-effects models (using single predictors) revealed significant effects of distance to the thermal maximum ($t = 3.75$, $p = 2 \times 10^{-4}$), of the thermal coordinate ($t = -4.50$, $p < 0.0001$), and to a lesser degree of latitude (d.f. = 402, $t = 2.32$, $p = 0.021$), on population growth rate. The fixed effects of the two complete linear mixed-effect models (i.e. testing effects of thermal distance to the thermal maximum or the thermal coordinate of the population, controlled for phylogenetic relatedness) are presented in table 1. In the first model, the average population growth rate increases significantly with distance from the species

thermal maximum ($p = 4 \times 10^{-4}$). In the second model, the average population growth rate decreases significantly as the population coordinate increases along the thermal range of the species ($p = 9 \times 10^{-6}$). These effects were detected beyond other effects probably to affect population growth rates such as the decline of habitat specialists (table 1), while we did not find any tendency for either larger species or short-distance migrant species to have better fate (table 1). We also did not find significant interactions between the thermal metrics and migration distance or habitat specialization. The detected effects were maintained after controlling for latitude (distance to the thermal maximum, $t = 3.15$, $p = 0.002$; thermal coordinate, $t = 4.42$, $p = 1 \times 10^{-5}$). The interaction of habitat specialization with distance to the thermal maximum was no more significant (positive effect, $p = 6 \times 10^{-2}$), while it was significant with population thermal coordinate (negative effect, $p = 6 \times 10^{-3}$).

To test for possible nonlinear responses, we further ran generalized additive mixed-effect models. In the model including the distance to thermal maximum as a smooth term, the estimated optimal dimension of the smooth term—allowing the best fit—equalled 1, matching a linear effect (figure 1*a*), while it was close to 1 for the model concerning the thermal population coordinate (figure 1*b*). Note that when this dimension was fixed to four, to force a nonlinear response, we obtained a response that closely matched the one expected from our initial hypotheses (figure 1*c*): higher increases in growth rate close to the cool edge, higher decreases close to the hot edge. However, the linear model better fitted the data, so there is no statistical reason to consider that the linearity of the response is not supported. To further verify that the linear response is not only driven by the response of populations at the range edges, we repeated the analysis using only 50 per cent of the populations, by deleting the 25 per cent of data with the lowest and the largest thermal metrics values. We then compared the slope estimates obtained with those obtained with the complete dataset: the negative linear response of growth rate to the thermal coordinate was maintained with similar
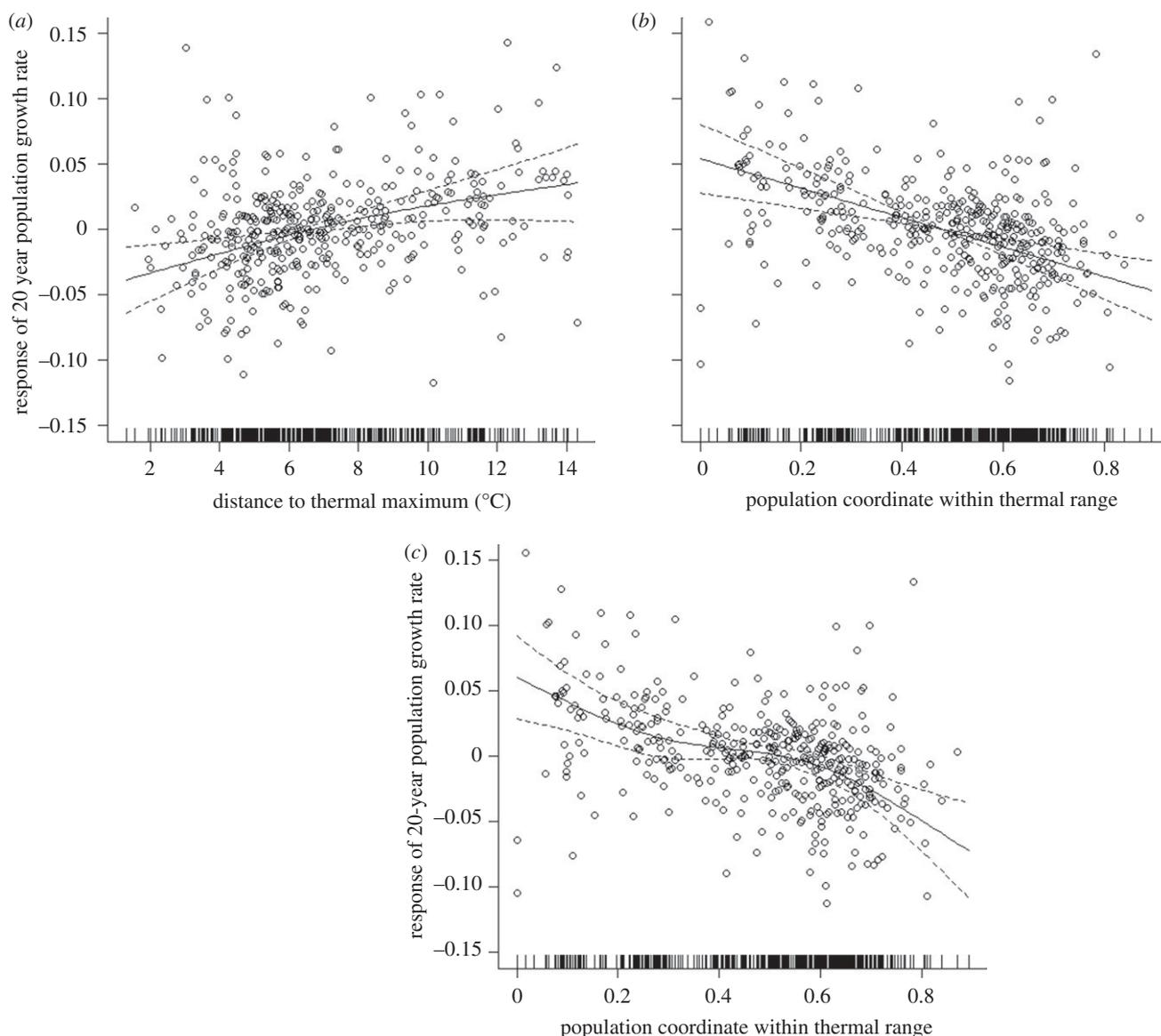
Figure 1. Response of population growth rate to (*a*) the distance of the population from the species thermal maximum (°C), and to (*b*) the population coordinate within the thermal range of the species, as obtained with generalized additive models with optimal degree of freedom; (*c*) shows the smooth response of population growth rate in a generalized additive mixed-effect model with a dimension of the smooth term fixed to four. Regression lines are presented ± 1 standard error (dashed lines). The bar plot along the *x*-axis illustrates the distribution of the data used in the analysis, further represented by open circles on the graphs.

amplitude ($t = -2.09$, d.f. $= 195$, $p = 0.038$; slope estimate -0.084 ± 0.040, compared with -0.089 ± 0.020 for the complete dataset). The same was true for the positive response to the distance to thermal maximum ($t = 2.57$, $p = 0.011$; slope estimate 0.007 ± 0.003, compared with 0.005 ± 0.001 for the complete dataset).

To consider the possibility of artefactual results owing to pseudoreplication (as we have three population replicates in two of the three countries, which might show quite similar responses), we repeated the analysis by retaining the middle latitudinal belt of France and Sweden, and obtained similar results (distance to the thermal maximum, $t = 2.21$, d.f. $= 177$, $p = 0.028$; thermal coordinate, $t = -2.54$, $p = 0.012$). Finally, when performing the same models within countries (France and Sweden), we obtained very similar results which are presented in the electronic supplementary material, S1 and S2.

4. DISCUSSION

We analysed long-term population growth rates of 62 bird species from three countries along a latitudinal gradient in Europe (France, The Netherlands and Sweden), thereby studying populations located near the hottest, central and coldest parts of the species European distributions. Overall, we found that the average annual growth rate of a given population over the last 20 years was positively predicted by its distance to the species thermal maximum. This result shows that while populations breeding close to the species thermal maximum (i.e. southern populations) are declining, those breeding far from this maximum (i.e. northern populations) rather benefit from local climate warming, which is in accordance with results found for wintering waterbirds (Maclean *et al.* 2008).

But more interestingly, beyond population dynamics near range limits, we revealed that population dynamics were not randomly distributed within species range,
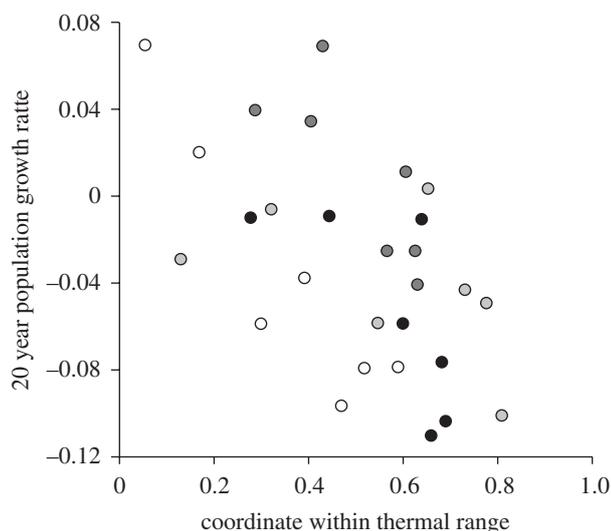
Figure 2. Response of the growth rate to the population coordinate within the thermal range in four species, the Whinchat (*Saxicola rubetra*; black circles), the Lesser Whitethroat (*Sylvia curruca*; dark grey circles), the Linnet (*Carduelis cannabina*; white circles) and the Bullfinch (*Pyrrhula pyrrhula*; light grey circles). These species illustrate extreme examples for species, which growth rates are directly affected by population coordinate within the thermal range, even not first considering potential variations in other drivers of population changes.

suggesting that European breeding birds are influenced by climate warming and are experiencing demographic disequilibrium along their whole thermal range. At first sight, demographic disequilibriums induced by climate warming should translate as decreases in populations located close to the hottest distribution limit of the species (Jiguet *et al.* 2007), and increases close to the coolest distribution limit, where climatic conditions become more suitable for the species. In this case, populations should have a constant growth rate across the thermal niche except, where the species thermal maximum or minimum is reached. Instead, we found that the population growth rate of a given species is continuously and positively related to its distance to the thermal maximum. We also tested, independent of the extent of the species range, whether the location of the population along the species range was a good predictor of species trends. We found a negative effect of the location of a population within the thermal range (standardized between 0 and 1), which supports our previous findings but which is based on a thermal niche predictor standardized across the whole thermal range of the same bird species. Thus, the disequilibrium is rather led by a linear increase when departing from the thermal maximum, witnessing that growth rates are destabilized by temperature increases. For the 62 species considered, the global pattern is a gradual and linear increase in long-term population growth rate along the thermal range when moving towards a species coolest range limit. Overall, we showed that populations are not just responding to changes in temperature at the hottest and coolest parts of a species range, but have a graded response across the complete thermal range of the study populations. It is also possible that populations may show stronger effects near to the edges of thermal ranges compared with the

core and smaller effect towards the centre. We indeed confirmed that the linear responses were not driven by the response of edge populations by repeating the analyses using only 50 per cent of the populations, those located in the core thermal range. The fit of simple smooth terms in nonlinear models further support the detected linearity of the response (figure 1*a*,*b*). To further illustrate the observed response for the set of 62 species, we present the results obtained for four species (including two long-distance migrants) in figure 2, plotting the average population growth rate against the population thermal coordinate.

One alternative explanation could be that the geographical variation in population trends could be owing to variation in local spring warming, which may have ecological effects such as greater mistiming in areas with more warming (Jones & Cresswell 2010). There is some evidence that the rate of increase in local spring temperature differs mainly latitudinally (Both & te Marvelde 2007), which is reflected in differential responses in breeding date of some species (Both *et al.* 2004), especially according to their migration strategy (Saino *et al.* 2009). Accordingly, the patterns identified here could have been explained just by the latitude of the different survey areas, rather than by the location within the thermal range. This was however not the case, because the effects of the thermal metrics remained significant after having controlled for latitude, which has a clear link to migration distance and to body mass.

Obviously, many intrinsic and human-induced factors are also influencing long-term population trends. For instance, in this study, disentangling specific impacts of climate warming beyond these factors meant, we first had to account for other traits known to affect breeding bird trends across Europe. We used body mass as a proxy for demographic traits (Julliard *et al.* 2003), because this trait is known to vary between populations of the same species breeding in the three considered countries, with individuals from northern populations displaying larger body size than southern populations, according to Bergmann's rule (Schreider 1950). Moreover, long-distance migrants are known to suffer major population declines across Europe (Sanderson *et al.* 2006) increasing with the migration distance (Jones & Cresswell 2010), while Scandinavian populations are known to display longer migration distances than southern European populations of similar species. We therefore considered a continuous measure reporting the migration strategy of national breeding populations, as the average distance between country-specific breeding and wintering grounds. We failed to highlight that long-distance migrants were more prone to decline, probably because the studied set of species was restricted, excluding some Afro-Palaearctic migrants—that do not occur in all the three studied countries. Also, recent declines in long-distance migrants are most severe in seasonal habitats in Western Europe (Both *et al.* 2010), whereas here a broader array of habitats and countries is studied. Finally, habitat specialization affects population fates within the global biotic homogenization process, in which habitat specialists are more negatively affected by disturbance than generalists (McKinney & Lockwood 1999). We therefore adjusted the studied trends to a country-specific continuous metric reflecting variation between species specialization, which happened also to

explain to some extent bird population trends in our study (see Jiguet *et al.* 2010 for a study at a European scale). Interestingly, interactions within the linear models revealed that the observed responses along the thermal range were amplified for habitat specialists, which are therefore more sensitive to climate change. Finally, we had to account for potential phylogenetic dependency between species, as closely related species might display similar trends (Thomas 2008). We included all these potentially confounding variables in the statistical analyses in an attempt to control for these alternative effects, although we cannot be certain that all relevant ecological traits were considered. Yet, as we found that distance to the thermal maximum had a major effect after controlling for these variables, and as long-term trends of European birds were shown to be currently deeply affected by global changes (Gregory *et al.* 2009; Jiguet *et al.* 2010), we suggest that our results mirror a large-scale disequilibrium of population dynamics in response to temperature increase.

Potential limits to our findings might come from the part of the thermal range we have captured while studying French, Dutch and Swedish breeding populations. Indeed, we probably did not reach the final thermal niche limits of most species (figure 1*b*). The identified linear response might come from this limitation to the thermal range of the species. If considering further populations breeding in more extreme cold climates, we could have detected a final decrease in species growth rate at sites located at the coldest thermal niche limit, although not necessarily. An alternative might be that following climate warming, this cold limit is no more effective and that population presence is just limited by local colonization processes and species dispersal ability, while their growth rates are at best. Further multi-species and multi-country analyses could refine these findings and reveal eventual similar disequilibrium induced by climate changes in other taxa.

Beyond the interest of describing how populations are affected by climate change within a species range (Deutsch *et al.* 2009), our results should be useful to link the niche theory and modelling with spatially explicit demographic models to determine how variations in life-history traits, disturbance regime and distribution patterns will influence the viability of populations under stable and changing climate scenarios (Keith *et al.* 2008). There is an increasing need to clarify the relationship between the ecological niche theory and species distribution models and metrics (Guisan & Thuiller 2005; Elith *et al.* 2006). In this context, an important step forward is to understand variations in population dynamics across the temperature range of a species when it faces climate warming. Our results suggest that considering that all populations of a given species share a constant response to climate change across the species range is highly hazardous. We therefore suggest that management, to enhance resilience or adaptation, for example, cannot be based on the assumption of a uniform response to climate change across a species range.

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