French birds lag behind climate warming

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Biodiversity responses to climate warming have been documented through the study of changes in distributions[1-3], abundances[4] or phenologies[1,5,6] of individual species or in more integrated measures such as species community richness[7] and composition[8]. However, whether these observed population and community changes are occurring fast enough to cope with new climatic conditions remain uncertain and hardly quantifiable[7,9]. Here, using spatial and temporal trends from the French breeding bird survey, we show that although bird assemblages are strongly responding to climate warming, this response is slower than expected for catching up with the current temperature increase. During the last two decades, French birds have only achieved 54% of the response required to follow temperature increase, and have accumulated, in 18 years, a 97 km delay in their northward shift. We thus developed a framework to measure both the observed and predicted response of species assemblage to climate change, an approach which is flexible enough to be applicable to any taxa with large-scale survey data[10], using either abundance or distribution data. For example, it can be further used to test if different delays are found across groups or if, for a given group, the delay depends on the land-use contexts.

Significant range shifts of many species are now documented[1,3] but a practical approach to assess whether these shifts are occurring fast enough to match new climatic conditions is still missing. For a given species, we first estimated the long term average temperature experienced by breeding individuals of that species over its European range (Species Temperature Index; STI). This measure is the simplest parameter of the species climate envelope, a concept used in most climate change investigations[11,12]. It can be easily calculated for many species using any spatial distribution data. Then, any local species assemblage can be characterized by the Community Temperature Index (CTI) calculated as the average of each individual's STI present in the assemblage. We used data from 1,514 sites from the French Breeding Bird Survey scheme to measure the temporal trend of the CTI between 1989 and 2006. We found that during this period, the CTI of French birds has increased steadily (+0.0060 ± 0.0007 s.e.m. per year; $F_{1,16}$=53.01, P<0.0001; Figure 1). This linear temporal trend, based on abundance data of the 105 most common terrestrial species (representing 99.5% of all individual birds recorded by the French Breeding Bird Survey), accounted for an amazingly high amount of the total between-year variation in CTI (R^2=93%). This estimate based on repeated counts over many sites, suggests that a highly consistent ongoing process is strongly affecting the breeding avifauna. Moreover, the same relationship was found before and after 2001, when a random stratified sampling scheme was launched (effect of change in the monitoring protocol on CTI trend: $F_{1,15}$=0.03, P=0.94). We are thus confident that the increase in CTI is representative of changes that occurred at a national scale.

The change in CTI is most likely the consequence of the rapid adjustment of the different bird populations to the increase in temperature during the period considered. Indeed, during 1989-2006, temperature in France was much warmer than it used to be[13]: mean temperature was on average 1.02 ± 0.15 °C higher (i.e., +0.056 ± 0.008 °C per year) than during the previous 18 years period (1973-1988). Moreover, species-specific climate niche measures were shown to predict both the short[14] and long term[15] responses of breeding bird species to climate warming in France. Here, the observed increase in CTI corresponds to 0.106 ± 0.020 unit of CTI per increase of one Celsius degree in temperature.

The CTI can also be easily related to the long term (1950-2000) average temperature in space. As temperature is a main determinant of species distribution, we expect this correlation to be strong[16]. In fact, as populations tend to inhabit climates similar to their optima, if temperature was the only determinant of species distribution, the slope of this relation should not differ from one. But current species distributions are shaped by multiple factors beyond temperature, including interactions with other species, habitat structure, genetic constraints, composition and dynamics[9,17]. Using the Breeding Bird Survey, we found that CTI was strongly positively correlated to spatial variation in temperature, but that the slope of the spatial adjustment was far from one (0.195 ±0.007, $F_{1,720}$=654, P<0.0001, Figure 2). This observed spatial relation provides an estimate of the actual adjustment of CTI with temperature, given all other factors. This spatial adjustment is also available using presence-absence data and can be calculated independently with very commonly used atlas datasets (supplementary information).

CTI variation in space reflects the strong effect of climate variation on the spatial distribution of bird populations among French regions which have existed for several thousand years. We thus assume that the spatial relation between CTI and temperature can be considered as a reference. If all bird populations were able to track climate change perfectly, one should expect the temporal trend of CTI to match the spatial relationship between CTI and long term average temperature. The temporal trend of CTI in the last 18 years is estimated as a fixed additive effect of time on CTI, and is considered to affect each local bird assemblage similarly over the 544,000 km^2 of France. Therefore, both statistically and biologically, there are no spurious links between the way the spatial and temporal relationships between CTI and temperature are estimated. Finally, as CTI variation in space and time are calculated with the same basic data (average STI), both trends are similarly affected by possible biases (e.g., variable species detectabilities; heterogeneous distribution of land mass in Europe) so that the relationships between CTI and temperature, calculated in space and time can be safely compared.

Altogether, we found that the linear increase in CTI with time is only 54.3 ± 10.4 % of the expected adjustment given by the spatial relationship between CTI and long-term average temperature. We also reanalysed our data using presence-absence data instead of counts to calculate CTI. Because such measure is less powerful to quantify change in community composition, the estimated slope relating CTI to temperature in time and in space were substantially lower than the one found with abundance data (supplementary information). However, the estimated delay was hardly affected (53.2 ± 10.1%). Hence, our method to estimate the delay in bird response is robust to the precision of the basic data. A very wide spectrum of database is thus prone to be analysed following the same approach.

As average temperature is approximately decreasing spatially by 0.45°C (±0.0007) per 100 km from south to north in France, the current increase in temperature corresponds to temperature conditions moving northward by 12.4 (±2.7) km each year. Hence, the change in CTI corresponds to bird populations shifting their distribution by only 6.7 (±1.46) km per year. Birds are thus accumulating year after year 5.7 (±1.46) additional kilometres in their delay. Eventually, after the 18 years considered, French birds are lagging 97.7 (±25) km behind climate warming.

Methods Summary

French Breeding Bird Survey.

A breeding bird survey (BBS) was started in France in 1989 based on volunteer skilled ornithologists counting birds following a standardized protocol at the same site for several years. In each site, a given observer monitored 10 point-counts separated by at least 200m. All visible individuals and singers were counted on these permanent point-counts during a fixed period of 5 min. To be validated, the count must be repeated on approximately the same date of the year (±7 days within April to mid-June), the same time of the day (±15 min within 1-4 h after sunrise), and in the same order, by the same observer. A new sampling design was launched in spring 2001, for which surveyed sites were not freely-chosen but selected randomly, ensuring that sampled habitats were representative: each observer provided a locality, and a 2x2 km plot to be prospected was randomly selected within a 10km-radius (i.e. among 80 possible plots). In each site, the observer also monitored 10 point counts following the standardized protocol already mentioned. Such random selection ensures the survey of varied habitats (including intensive farmlands, forests, suburbs and cities).

Spatial and Temporal trends of CTI.

For a given species, STI is obtained from the combination of data from the EBCC Atlas of European Breeding Birds[18] and the spatial distribution of the average temperature (for the period 1950-2000, from Worldclim database http://www.worldclim.org) of the bird breeding season (from March to August). The year-to-year temporal variations of CTI was then calculated using generalized linear mixed model (GLMM) and the CTI calculated on each sites (*n*=1,514) monitored by the BBS during 1989-2006. In these models, year was considered as a fixed factor and the site as a random effect.

The spatial correlation between the CTI and temperature was calculated using all Breeding Bird Survey plots monitored in 2005, the year with the maximum number of surveyed sites (*n*=878). We excluded sites located in mountains (*n*=156) as it would have induced unwanted disparity between temperature of the site (biased toward localized very low temperatures) and species recorded in survey plots not necessarily located in altitude. The temperature at each remaining site (*n*=722) was calculated as the long term (1950-2000) mean temperature of the breeding season using temperature data from the Worldclim database.

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Supplementary Information is linked to the online version of the paper at www.nature.com/nature.

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Fig. 1 Temporal trend of the Community Specialization Index (CTI). The CTI is the average of each species temperature index (STI) of a given species assemblage. It was calculated for each year and on each point count monitored by the French Breeding Bird Survey scheme during 1989-2006 for the 105 commonest species. STI for a species is the long term average temperature experienced by breeding individuals of that species over its European range. Dashed lines represent standard error around the mean (s.e.m). The year 2001 is fixed as a reference so that there is no standard error for that year

Fig. 2 Spatial correlation between the Community Specialization Index (CTI) and temperature. Each point represents a breeding bird survey plot, monitored in 2005. For each site (*n*=722), the CTI was calculated as the average of the CTI calculated in the 10 point counts of that site. In a given point count, the CTI is the average of each STI of all individuals detected in that point count. The temperature was calculated as the long term mean temperature (1950-2000) of the breeding season (from March to August) using temperature data from the Worldclim database (http://www.worldclim.org)

Figure 1

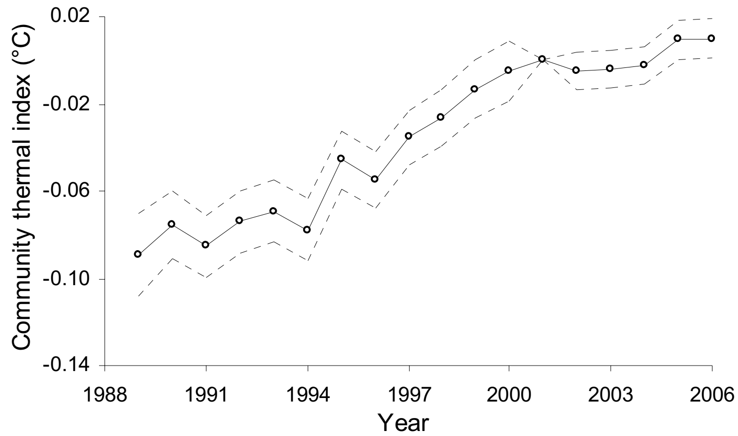

Figure 2