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Climate Change Responses

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Did British breeding birds move north in the late 20th century?

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Abstract

Background: Contemporary climate change is the biggest experiment ever conducted by humans on a planetary scale, and its impact on the redistribution of life is potentially huge (e.g., Barnosky et al. Nature 471:51–57, 2011, Pereira et al. Science 330:1496–1501, 2010). An accurate diagnosis of the effects of climate change on the distributions of species requires, firstly, that methods used for detection of distributional changes are able to distinguish between directional and non-directional changes and, secondly, that they are able to tease apart distributional changes driven by natural population dynamics from changes driven by external forcing (climatic or non-climatic). We ask how appropriate are methods commonly used to detect directional shifts on species range changes.

Main: We compare a widely used range-shift detection method previously used to demonstrate that climate change caused British breeding bird distributions to move northwards with alternative approaches that more comprehensively examine directionality in range changes. We find that once range dynamics are examined across all geographical quadrants in Britain, and in contrast with previous reports, no clear directional patterns of range shift emerge for this period.

Conclusions: Some of the methods typically used for examining species range shifts are prone to false positive errors, whereby directional range shifts are detected when in fact they did not occur. Without entering the discussion of what is more important to avoid (false negative errors, whereby directional range shifts pass unnoticed by analysis, or false positive errors), we argue that methods exist to determine whether range changes are directional or non-directional (a prerequisite to discern the causes of range changes).

Background

Several studies have reported that range margins of many species moved poleward, probably in response to recent climate warming (e.g., [1–3]). In a highly influential study, Thomas and Lennon [4] reported that distributions of many British breeding birds moved north between 1968–1972 (T1) and 1988–1991 (T2) in what appeared to be a clear and predictable response to climate warming. We reanalyzed the data using methods designed to effectively distinguish directional and non-directional shifts in species range changes. We found that range expansions and contractions were non-directional in the ca. 20 years period examined by Thomas and Lennon (T&L). With some exceptions, expanding species expanded distributional limits across all geographical quadrants and contracting species contracted distributional limits across all quadrants. Late 20th Century patterns of range change among British breeding birds seem to be consistent with meta-population theory that predicts extinctions and colonization events to occur mainly in 'sink' habitats within the periphery of species ranges [5]; an observation that had already been made using the same data but different analyses [6, 7].

Climate limits the distributions of species, both directly by causing changes in the abiotic environment in which a species lives and, indirectly, by causing changes in biotic interactions and feedbacks between biotic interactions and abiotic processes (e.g., [8, 9]). The direct impact of climate change on species distributions is often investigated with phenomenological estimates of species-climate relationships. Usually, such relationships are inferred by matching present-day species distributions with climate variables (e.g., [10]). Yet, determining whether given climate change exceeds

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species climatic tolerances using analysis of species range data is difficult because there are many non-climatic factors constraining species distributional limits (e.g., [11, 12]). Species distributional dynamics across a given time period can be also examined by comparison with climate change patterns for the same period (e.g., [13–15]). The general principle is that if species distributional limits are moving in the same direction as climate change, then one might reasonably conclude that climate change is involved. Several studies have used the latter approach to detect latitudinal (e.g., [16]) and altitudinal (e.g., [17, 18]) shifts in species distributional limits.

However, detecting directional changes in species distributions requires that changes are compared across all geographical quadrants rather than just northern and southern range limits (see also [19]). In the northern hemisphere, the critical question is whether species distributions are, on average, moving northward—as expected if expansions were driven by climate warming—, or evenly across distributional margins—as expected if expansions were driven by population dynamics (e.g., [6, 7, 20]) or by multiple drivers acting in several directions and causing range changes to be complex and seemingly idiosyncratic (e.g., [21, 22]). Likewise, one should ask if local extinctions are, on average, occurring mainly at southern margins or whether they are ubiquitous across all margins of the species range.

Thomas and Lennon [4] measured distributional changes within the northern and the southern margins of species. Since distributional dynamics were expected to be different for southerly and northerly-distributed species, T&L grouped species based on their average geographical position within Britain. Consistent with the hypothesis that climate warming drove changes in the distributions of birds, they found that the northern margins of southerly-distributed species that increased ranges shifted northwards, while the northern margins of many southerly-distributed species that declined overall shifted southwards. In contrast, the southern margins of northerly-distributed species that increased ranges generally shifted southwards, whereas the southern margins of most of the northerly-distributed species that declined shifted northwards. In addition, they found that the northern margins of southerly-distributed species with no overall change in range size had a northward shift of 18.9 km, while no systematic distributional shift towards north or south was detected for northerly-distributed species. Gillings and colleagues [19] examined range dynamics more broadly and confirmed the general trend reported by T&L, while also detecting the existence of complex, multi-directional shifts that passed unnoticed in the original 1999 analysis.

Main text

We reanalyzed the data [23, 24] using two different analytical approaches that more explicitly seek to distinguish directional shifts from non-directional ones (see Additional file 1), and then asked whether late 20th Century changes in distributional limits of British breeding birds were significantly different across geographical quadrants. We assumed that if distributional changes of birds were not significantly different among quadrants (a question not addressed in previous studies), warming of temperatures should not be immediately invoked as the key candidate driver of such changes (see Additional file 2: Figure S1).

Our analyses revealed that no clear directional shifts in the distributions of birds emerged when patterns were examined across the four geographic quadrants. In the first analysis, following T & L, we recorded the mean location of marginal cells (all cells at the edge of species ranges rather than 10 marginal cells, as done by T&L) for each species within the four geographical quadrants (Additional file 2: Figure S1B). Then, we examined if a relationship existed between changes in the mean position of the marginal cells and changes in the overall range sizes of species across Britain. Consistent with T&L, contracting species tended to shrink northward across the southern limit (Fig. 1a). However, they also contracted in every other direction and expanding species also expanded across all geographic quadrants. Range shifts were generally outwards—from the core to the periphery of the range—except for the western boundaries of northerly distributed species where no distinguishable patterns were detected (See also Additional file 3: Figure S2).

The northern limits of southerly distributed species that did not show an overall change in their range sizes (the interpretation of the $x = 0$ intercept in Fig. 1a) moved 22.35 km north on average, which is comparable with the 18.9 km northward shift reported by T&L (but $P = 0.545$). These species also shifted 5.96, 4.92 and 12.78 km inward, on average, along the southern, eastern and western margins of their ranges respectively (P <0.001, $P = 0.091$ and $P < 0.001$). The margins of northerly-distributed species followed similar patterns ($P < 0.001$) except along the western margins for which no meaningful range shift was detected ($P = 0.712$).

In the second analysis, we used a novel approach that counts the number of local expansion and contraction events in each geographical quadrant relative to the available land area (Additional file 2: Figure S1C). We found that the proportion of contracting and expanding marginal cells within each quadrant was not significantly different between quadrants for contracting and expanding species (Wilcoxon signed-rank test; $P > 0.05$) (Fig. 1b). An exception was recorded for southerly distributed species, whose patterns of range contraction were generally

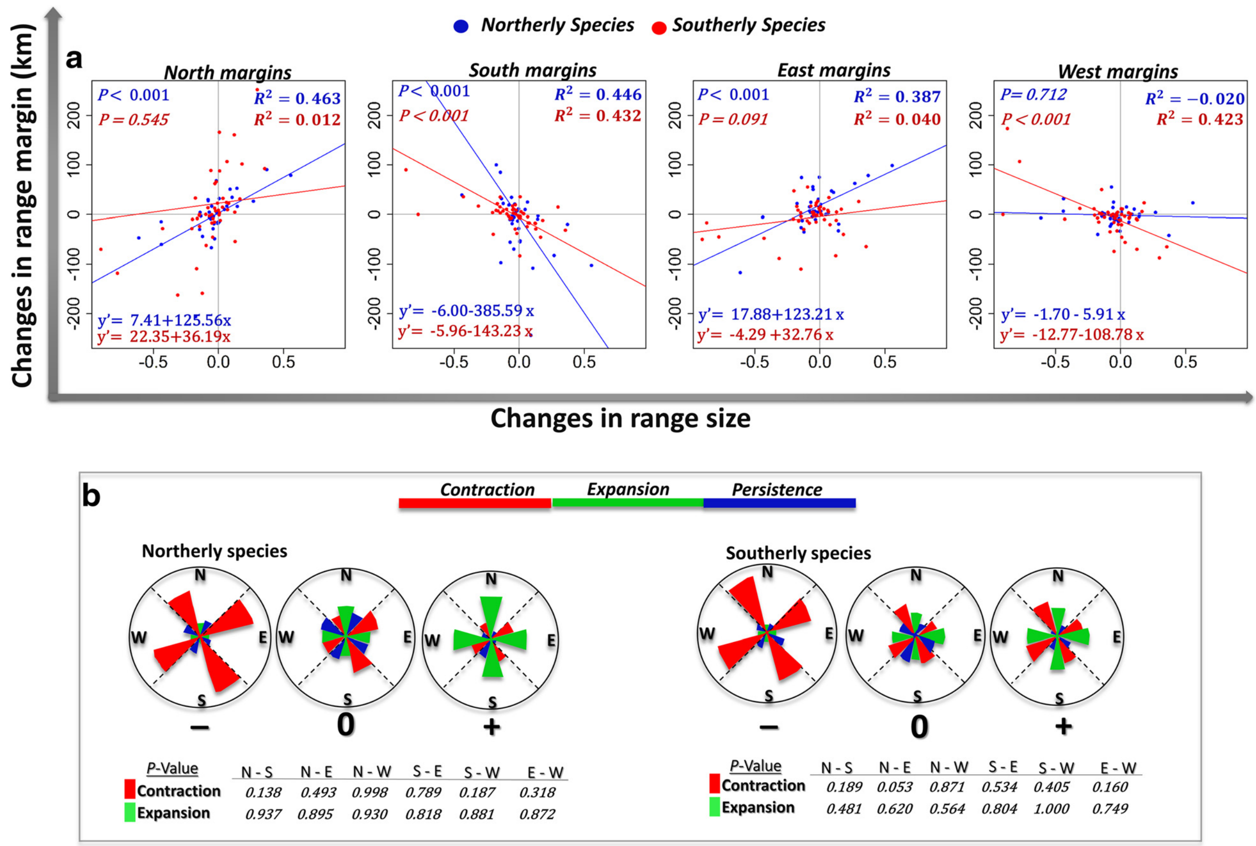

Fig. 1 Distributional shifts among British breeding bird species between 1968–72 vs. 1988–91. Changes in species range sizes were calculated as $\log_{10}$ transformation of the ratio of the number of occupied cells in T2 to the number of occupied cells in T1. **a** Plots the overall change in distributional margins (defined as the mean distance of all marginal cells recorded in the second period of the comparison minus all marginal cells in the first period). Positive values on the x-axis indicate range expansions (outward shifts), while negative values indicate range contractions (inward shifts). Regression statistics were obtained after regressing changes in range size against changes in mean position of marginal cells. X = 0 regression intercepts in **a** indicate mean distributional shifts (km) for species with no overall change in the number of grid cells occupied. **b** plots changes in occupancy (contractions and expansions) among marginal cells for contracting species (–), species with stable ranges (0), and expanding species (+). The size of the bars is proportional to the mean proportion of the marginal cells over all species in the group (see Additional file 2: Figure S1 for details)

greater in the northern quadrant compared to the eastern one ($P = 0.021$). Overal, given these multiple significant tests across the four geographical quadrants we can argue that shifts were not significant at the level 0.05.

Several analysis and meta-analysis have reported pole-ward and elevation-ward shifts in distributional limits of species without contrasting them with distributional changes across their full range. Whether range shifts provide evidence that climate change is acting on them depends on the congruence of the range shifts patterns with climate change patterns [19]. If range dynamics for expanding species are measured at only a single range edge, then, the likelihood is great that an expansion will be detected and erroneous conclusions could be made. But if range shifts, or pulses of range expansion and contraction, are ubiquitous across the range, then natural population dynamics, or non-linear interactions between climate and non-climatic vectors, such as biological invasions (e.g., [25]), land use (e.g., [26]), and/or disease (e.g., [27]), might be reasonably invoked as alternative driving forces of change.

Conclusions

There is a consensus that attribution of climate change effects to species range shifts should, ideally, be based on multiple lines of evidence (e.g., [28]). We agree. However, whenever inferences of climate change effects on range dynamics are based on statistical analysis of species range change data, it is crucial that tests are able to adequately distinguish directional and non-directional shifts (see also [29]). Such comparisons between observed species distributional patterns and expected distributional patterns under absence of process are the underlying principle of null models [30], and are becoming standard practice in different sub-fields of ecology (e.g., [31, 32]), biogeography (e.g., [33, 34]), conservation and global change biology (e.g., [35, 36]). Failure to undertake such comparisons in studies examining species range changes can lead to inflation of false positive errors by equivocally concluding for the existence of directional range shifts when they are no different from the null expectation.

Raising the bar of evidence in studies attributing climate change effects on species range changes is important to reduce errors of interpretation that could lead to erroneous management decisions. For example, if particular change in land-use practices causes a given species to contract its range, attributing the effect to climate change might lead to inappropriate management actions and inefficient allocation of funds to conservation in the short term. In the long term, failing to adhere to high standards could have the consequence of decreasing of confidence in climate change attribution studies as well as models, which would bring about the risk of neglecting important climate change impacts in management decisions.

Additional files

Additional file 1: Supplementary Information – Describing the data, the analytical procedure, including the R code used for the analysis, and some complementary results. (DOCX 65 kb)

Additional file 2: Figure S1. General analytical framework. (TIFF 3789 kb)

Additional file 3: Figure S2. Analogous to Fig. 1 but without exclusion of species with > 2000 records in Britain. Exclusion of ubiquitous species did not change the overall trends detected in Fig. 1, despite changes in p and R2 values. (TIFF 76585 kb)

Abbreviations
T&L, Thomas & Lennon

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ST, BN, and MBA designed the analysis. ST led the analysis with important contributions from BN. MBA wrote the article with contributions from all authors. All authors read and approved the final manuscript.

Competing interests
The authors declare that they have no competing interests.

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