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Abundance changes and habitat availability drive species' responses to climate change

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There is little consensus as to why there is so much variation in the rates at which different species' geographic ranges expand in response to climate warming[1,2]. Here, we show for British butterfly species that the relative importance of species' abundance trends and habitat availability vary over time. Species with high habitat availability expanded more rapidly from the 1970s to mid-1990s, when abundances were generally stable, whereas habitat availability effects were confined to the subset of species with stable abundances from the mid-1990s to 2009, when abundance trends were generally declining. This suggests that stable (or positive) abundance trends are a prerequisite for range expansion. Given that species' abundance trends vary over time[3] for non-climatic as well as climatic reasons, assessment of abundance trends will help improve predictions of species' responses to climate change, and help understand the likely success of different conservation strategies for facilitating their expansions.

Identifying species' traits associated with rapid range expansions in response to climate change provides insight into the conservation strategies most likely to be successful[4].

However, such understanding may be difficult to attain, given that the ability of species' traits, such as reproductive rate, to explain responses to climate change is frequently low[2]. Previous studies suggest that the expansion of species' distributions across landscapes will depend on species' dispersal abilities[1,5,6], the availability of habitat[7], and population abundance trends, which determine the supply of migrants to colonise new locations[8]. Species' population and distribution trends will also be affected by interactions between traits and the environment, thus predictions of range expansions may be limited if habitat availability and population trends are not considered simultaneously. Furthermore, abundance trends vary over time[3], associated with variability in climate warming[9] and habitat quality and quantity[10], so it might be expected that the relative importance of predictors of distribution changes also vary over time.

Here, we consider the roles of abundance trends, habitat availability and dispersal capacity in the range changes of 25 British butterfly species during two periods. Distribution changes were measured between blocks of time (1970-82 to 1995-99 and then 1995-99 to 2005-09) to ensure sufficient data to record distribution changes in a robust manner (1970-82, 1995-99 and 2005-09 represent periods with intensive recording; > 1,220,000 distribution records and > 262,000 abundance transect records). Butterflies are an ideal group for this analysis. Not only are there more long-term species-specific datasets than any other poikilothermic animal group worldwide, but most between-species variation in expansion rates exists within taxonomic groups rather than between groups[9] and so our conclusions are likely to be relevant to other taxa. Average annual temperature increased at a rate of 0.03 °C yr^{-1} in the first study period (1970-82 to 1995-99), and 0.01 °C yr^{-1} in the second (1995-99 to 2005-09). We expected the lower rate of temperature increase in the second period to have relatively little effect on rates of distribution change due to climate distribution lags[11,12], and indeed species showed idiosyncratic responses to climate warming; some expanded their ranges in both periods, some in only one period, and some retracted in both periods[13] (Table S1).

We studied 25 southerly-distributed butterfly species which have the potential to extend their distributions under climate change (migrants, northern and ubiquitous species were excluded, further exclusions were due to insufficient data). We quantified changes in distribution area using the Butterflies for the New Millennium (BNM) dataset[14] as the percentage change in the number of 10 km grid squares occupied per year, to account for the different lengths of study periods and different initial species' range sizes. Changes in abundance were calculated using the UK Butterfly Monitoring Scheme (UKBMS) transect dataset[15] by regressing abundance indices from continuously occupied transect sites (sites at which a species was present every year during the study period) against year[16], to give percentage change in abundance per year for each species. We used a rank mobility score[17] to represent species dispersal ability (derived from expert opinion). Habitat availability was calculated by combining remote-sensed land cover[18,19] estimates with expert assessments of species' habitat associations[14] (see SI). We only considered the availability of habitat in the 10 km grid squares which the species colonised during each period, thus focussing measures on those areas where species' distributions were changing. It was not possible to quantify landscape change over time because annual habitat data are not available and the categorisation of land cover data in the two study periods has changed[18]. We employed an information-theoretic approach to identify the best models for explaining distribution changes. For each study period separately, we constructed general linear models to assess distribution changes against all three variables (abundance trends, habitat availability, dispersal ability) including their interactions, and AICc values and Akaike weights were used to determine the best fitting models. When ΔAICc < 2, models are considered to be of equal strength[20] so model averaging was used. (Incorporation of phylogenetic correlations did not improve the fit of models so we do not present phylogenetic analyses; see SI).

In the earlier period, nine species expanded their distribution area (mean change = 0.8% yr^{-1} ±0.1 s.e.m.) and 16 species retracted (mean change = -2% yr^{-1} ±0.2 s.e.m.). The abundance trends of species were generally stable in permanently occupied sites (mean abundance change = -0.5% yr^{-1} ±1.75 s.e.m.). The best fitting models included habitat availability and dispersal ability, but not abundance (Table 1a). Habitat availability was the most important explanatory variable ($R^2 = 0.35$, Table S4a); range expansions were greatest for species with high habitat availability (Fig. 1a). Dispersal ability was much less important, and in models where it was included it showed a negative relationship. This unexpected relationship suggests that once habitat availability was accounted for, less dispersive species did not fare any worse than more dispersive species.

In the later study period, 11 species extended their ranges (mean change = 1.4% yr^{-1} ±0.3 s.e.m.) and 14 species retracted (mean change = -0.8% yr^{-1} ±0.1 s.e.m.), during a period when overall abundance trends were negative (mean change = -6.99% yr^{-1} ±3.04 s.e.m.). In contrast to the first period, the best fitting model included only abundance (Table 1a; Fig 1b). Distribution change showed a positive association with abundance change ($R^2 = 0.15$, Table S4b); species which retracted their ranges showed larger declines in abundance (mean abundance change = -11.47% yr^{-1} ±4.23 s.e.m), whereas species with expanding ranges showed considerably smaller declines or had stable abundances (mean change = -2.39% yr^{-1} ±2.92 s.e.m). Thus there was little consistency in the responses of species over the two study periods[13], and the importance of habitat availability as a determinant of range expansion also varied over time, associated with abundance trends. We found little evidence that dispersal was important, which supports other studies indicating that species' traits are poor predictors of distribution changes[2], and our results suggest that the importance of species' traits may be context-specific.

Previous research has found a strong relationship between abundance changes and distribution changes[5,16] and we show that abundance trends are important for determining whether or not species expand their range. The absence of abundance as an important predictor of distribution changes in the best fitting models in the first study period may be because we analysed abundance trends only at continuously occupied sites. When data for transect sites colonised during the first period were also included in estimates of species' abundance trends, abundance was positively related to change in distribution area, suggesting that increased overall abundance was a consequence rather than a cause of expansion (Table 1b). This implies that species with generally stable abundances in long-established populations exhibit density-dependent, positive population growth at newly-colonised sites[21]. In contrast, species with steeply-declining abundances in long-established sites would be unlikely to produce many migrants and may show negative population growth at newly-colonised sites, and hence fail to establish and expand their ranges[22].

We further tested these determinants of distribution changes by examining factors associated with colonisation in the subset of species that expanded their ranges in the second study period (N = 11 species; see Fig. 2 and SI). We found that habitat availability was the most important explanatory variable of median colonisation distance ($R^2 = 0.55$, Table S6), and that dispersal ability and abundance trends were not important (Table 1c; Fig 3). Thus for the subset of species in the second period with stable abundances and expanding ranges, species with greater habitat availability colonised over longer distances, in agreement with our findings in the first period and supporting the notion that species' traits (e.g., dispersal ability), other than those that affect habitat availability, may be poor predictors of distribution change[2]. For declining species the null model was best, as was expected because colonisation is not usually an important feature of declining distributions.

Our results suggest that positive or stable abundance trends are a prerequisite for species range expansion[23], enabling species to establish populations in new sites. Once these conditions are met, habitat availability, which arises from the interaction between a species' niche-related traits and the environment, becomes a limiting factor. During the first study period, when abundance trends generally were not limiting, habitat availability was the most important determinant of range expansion (10 km grid resolution data). During the second period, when declining abundance trends limited expansion, habitat availability had no predictive power, but was the most important explanatory variable for the subset of species with expanding distributions and stable abundance trends (for colonisation distances estimated at 1 km grid resolution).

We conclude that drivers of range expansion in response to climate warming vary over time and that species' abundance patterns are crucial to interpreting these responses. It is unclear why the abundances of many butterfly species have declined in Britain, but the abundances of many other taxa are also declining[24]. Current evidence suggests that many species fail to expand because of lack of suitable habitat[7], and so habitat connectivity should be improved[25]. Our results strongly support this conclusion for the subset of species with stable abundances whose ranges are already expanding, and management such as habitat restoration may increase their rates of expansion[26]. However this type of habitat management is likely to prove ineffective for species with declining abundances. We conclude that conservation management to stabilise and increase abundance trends within the core of species' ranges is required (e.g. improving habitat quality), and that habitat creation to increase the number of species extending their range margins polewards will only be effective once species' abundance trends are stable or increasing.

Methods Summary

Change in species' distribution area was the percentage change in the number of 10 km x 10 km grid squares occupied. Sub-sampling was carried out on the dataset to account for the temporal increase in recording effort using established methods to give similar number of records and spatial coverage over time[27] (see SI).

A rank mobility score[17] based on expert opinion was used to represent species' dispersal ability. Habitat availability was quantified separately for the two study periods as the proportion of each species' breeding habitat in the landscape using LCM2000[19] and LCM2007[18] 25m resolution raster datasets respectively. Landcover categories relevant to species breeding habitat were identified using expert opinion[14], and weighted based on the frequency with which species distribution records were associated with that landcover type (see SI). Change in abundance from the UKBMS transect dataset was calculated for continuously-occupied transect sites, but subsequent analyses also included recently-colonised sites (see main text). To estimate change in abundance for each species, $\log_{10}$ abundance index was regressed against year[16], with transect site as a random variable.

For each species during the second study period, we quantified colonisation distances from the BNM dataset (1 km grid resolution). The distances and frequencies of newly colonised sites (new 1 km grid square records in 2005-09) from the nearest occupied sites (existing 1 km records in 1995-99; Fig. 2 and Fig. S1) were computed. We included only colonisations at species' distribution edges (10 km squares which were unoccupied in 1995-99 but colonised by 2005-09; N = 12234 colonisations). Inverse power functions were fitted to the colonisation-distance distributions for each species, and the median distances from the fitted curves were used in analyses (Table S5).

Annual temperature data from the Central England Temperature series were downloaded from the UK Met Office (http://www.metoffice.gov.uk) to compute temperature change.

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

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Author contributions

JKH and CDT conceived and supervised the study and edited the manuscript. RF, MB and TB provided data and edited the manuscript. LM analysed the data and wrote the manuscript.

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Figure legends

Figure 1. Change in species distribution area in relation to habitat availability, dispersal ability and change in abundance (at continuously-occupied transect sites). Distribution change is plotted against standardized variables: $\log_{10}$ habitat availability index, rank order dispersal ability and change in abundance (% yr^{-1}) for **a** the first study period (1970-82 to 1995-99) and **b** the second study period (1995-99 to 2005-09). Solid line is the fitted relationship for the most important explanatory variable (Table 1). The size of points reflects weighting in analyses involving abundance change (weight = 1/S.E. abundance), which improved the model fit for the second period, but not the first.

Figure 2. The distribution and colonisation distances of *Polygonnia c-album*. **a** The change in distribution of the butterfly from 1995-99 to 2005-09 (10 km resolution). Blue squares = occupied in 1995-99, green squares = colonised in 2005-09. **b** A selection of the distribution data at 1km resolution, showing presence in 1995-99 (blue squares) and new records in 2005-09 (green squares). The distances from new locations at the species distribution edge (defined as 10km squares which were unoccupied in 1995-99 but colonised in 2005-09) to the nearest existing records (red arrow) were found, and used to compute **c** colonisation distance distributions.

Figure 3. Colonisation distance for distribution-expanding species in relation to habitat availability, dispersal ability and change in abundance. Median colonisation distance (km) is plotted against standardized **a** $\log_{10}$ habitat availability index, **b** rank order dispersal ability and **c** change in abundance (% yr^{-1}, at continuously-occupied transect sites) for the second study period (1995-99 to 2005-09). Solid line is the fitted relationship for the most important explanatory variable (Table 1).

Tables

Table 1. Average model parameter estimates, standard errors and relative importance of variables.

Model variables	Estimate	Unconditional S.E.	Relative importance*
a Change in distribution (abundance from continuously-occupied sites)			
1970-82 to 1995-99			
Habitat availability	1.835	0.584	1
Dispersal ability	-0.659	0.715	0.28
1995-99 to 2005-09			
Change in abundance	1.427	0.631	1
b Change in distribution (abundance from all sites)			
1970-82 to 1995-99			
Change in abundance	1.996	0.531	1
Habitat availability	2.059	0.626	1
Abundance x habitat	1.670	0.803	0.61
Dispersal ability	-0.873	0.531	0.68
Abundance x dispersal	1.858	1.017	0.21
1995-99 to 2005-09			
Change in abundance	1.258	0.442	1
c Median colonisation distance			
1995-99 to 2005-09			
Habitat availability	3.802	1.045	1

a response variable is change in distribution area (using species' abundances from only continuously-occupied transect sites)

b response variable is change in distribution area (using species' abundances from all sites including those that were colonised during the study period)

c response variable is median colonisation distances

* Relative importance of variables of 1 indicates that the variable was present in all top models, or was the only variable when model averaging was not necessary because the difference in AICc between the first and second highest ranking models was > 2 (Tables S4 and S6).