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The distributions of a wide range of taxonomic groups are expanding polewards

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Abstract

Evidence is accumulating of shifts in species' distributions during recent climate warming. However, most of this information comes predominantly from studies of a relatively small selection of taxa (i.e., plants, birds and butterflies), which may not be representative of biodiversity as a whole. Using data from less well-studied groups, we show that a wide variety of vertebrate and invertebrate species have moved northwards and uphill in Britain over approximately 25 years, mirroring, and in some cases exceeding, the responses of better-known groups.

Keywords: climate change, distributions, range shifts

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Introduction

Global climates are warming (IPCC, 2001) and many species are responding to these changes by shifting their distributions to higher latitudes and/or altitudes (Walther *et al*., 2002; Parmesan & Yohe, 2003; Root *et al*., 2003). However, evidence for these range changes comes predominantly from studies of plants, birds and butterflies, for which historical data are available (Parmesan & Yohe, 2003; Root *et al*., 2003). It is not clear whether responses of these well-studied taxa are representative of biodiversity as a whole (Prendergast *et al*., 1993; Thomas *et al*., 2004) given that the prewarming distributions of different taxonomic groups may vary, and that species with different generation times, habitat associations, dispersal capacities or thermal physiologies might show very different responses to changing climate (Thomas *et al*., 2001; Warren *et al*., 2001; Hill *et al*., 2002; Kullman, 2002).

Britain has extensive fine-scale and long-term distribution data for a wide range of taxa and, thus, is probably the only region in the world where it is possible to assess whether comparable range margin shifts are taking place in many different groups. Here, we analyse distributional changes across a wide range of animal groups to investigate whether responses of less well-studied groups to recent climate warming are qualitatively similar to those for better-studied groups.

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Methods

Species selection

We analysed distribution data sets for 16 taxonomic groups that occur in terrestrial and/or freshwater environments in Great Britain, at a 10 km grid square resolution. The groups analysed were dragonflies and damselflies (Odonata), grasshoppers and allies (Orthoptera), lacewings (Neuroptera), butterflies (Rhopalocera), spiders (Araneae), herptiles (Amphibia and Squamata), freshwater fish (Teleostei), mammals (Mammalia), woodlice (Isopoda), ground beetles (Carabidae), harvestmen (Opiliones), millipedes (Diplopoda), longhorn beetles (Cerambycidae), soldier beetles and allies (Cantharoidea and Buprestoidea), aquatic bugs (Heteroptera) and birds (Aves).

For each group, species were only included in analyses if they were southern/low-elevation species; these species would be expected to increase their range sizes, move northwards, and/or shift to higher elevations if they were responding solely to temperature. Northern species were excluded from our analyses because of a lack of data; with the exception of birds, the taxa included in our study contain very few species which reach the southern (warm) boundary of their distributions in Britain and generally these species are poorly recorded, precluding the possibility of making among-taxon comparisons. Species were classified as southern if, according to UK or European distribution maps, they reached their northern range margin in Britain. For each group, species classifications were checked by an expert. Species were excluded from analyses if they were found only on the Channel Islands (close to the coast of northern France), were migratory, were clearly synanthropic, were introduced, if their taxonomy was still under debate, or if, after squares had been excluded by recorder effort and date, the species occupied fewer than twenty 10 km grid squares (i.e., less than approximately 1% of all 10 km grid squares) across the two time periods. Thus, we excluded species which may be expanding as a consequence of human activities (i.e., through recent introductions or because of their close associations with humans), as well as migrant species where records may not reflect the extent of their breeding distributions We excluded poorly recorded species because our method of identifying the northern margin would be likely to be unreliable for such species, and susceptible to sampling error.

Analysis of range changes

For each taxonomic group, two distinct time periods within the past 40 years (coincident with global (IPCC, 2001) and regional (CIP, 2005) warming) were selected. The time periods for each group were chosen so as to maximize the number of records available for analysis while still maintaining a substantial time interval between recording periods (Fig. 1). In most cases, each recording period was 11 years long, with a 14-year gap in between, corresponding with a 25-year period between the mid-points of the two recording periods.

In each time period, the location of the northern range margin of a species was defined as the mean latitude of the 10 most northerly occupied 10 km grid squares (on the Ordnance Survey National Grid of Great Britain). The shift of the range margin was calculated as the difference in these mean latitudes between the second and the first time period. Shift in altitude was calculated in a similar way to latitudinal shift. The mean altitude of the 10 highest elevation occupied 10 km grid squares was calculated in the two time periods. The altitudinal shift was calculated as the difference in the mean altitude between the second and the first time period. The 95% confidence limits of the mean values for each group were calculated, and used to determine if shifts were significantly different from zero.

To take account of changes in recorder effort over time, all calculations were first made for a subset of 10 km grid squares for which at least one species of a given taxonomic group was recorded present in both time periods (subsequently termed 'recorded' squares). Analyses were repeated by selecting only those grid squares with higher levels of recording, defined as grid squares with at least 10% (subsequently termed 'well-recorded' squares) and 25% ('heavily recorded' squares)

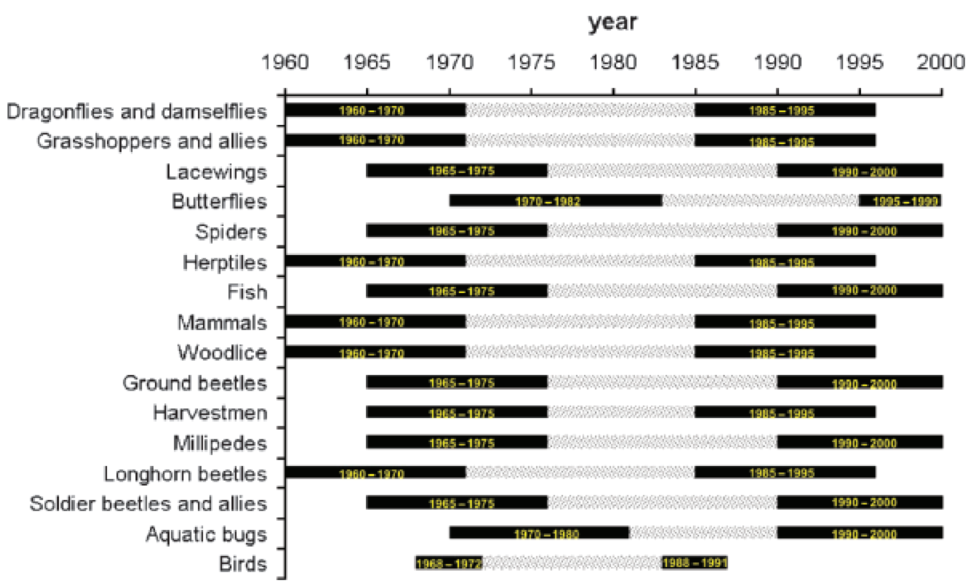

Fig. 1 Time periods chosen for analysis (solid black) for each taxonomic group, and time gap in between (speckled black). The exact years (inclusive) within which records were analysed are shown in yellow.

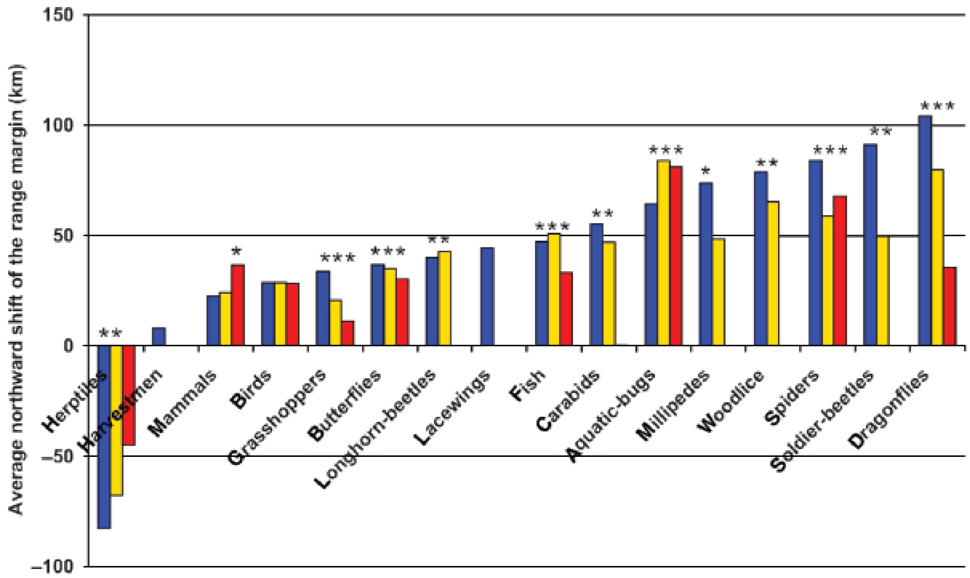

Fig. 2 Latitudinal shifts in northern range margins for 16 taxonomic groups during recent climate warming. Results are given for three levels of subsampling of data (recorded, blue; well-recorded, yellow; heavily recorded, red). Only species occupying more than twenty 10 km grid squares across the two time periods are included in analyses; for several of the species-poor groups, these criteria excluded all species from the analysis of 'heavily recorded' squares.

of species for a particular taxonomic group recorded present in both time periods.

Results

Out of a total of 329 species analysed across 16 taxa, 275 species shifted northwards at their range margin, 52 species shifted southwards, and two species' range margins did not move, with an average northwards shift across all species of 31–60 km (depending on level of subsampling of data). Comparable findings were obtained with respect to elevation shifts: 227 species shifted to higher altitude and 102 species shifted to lower altitude, resulting in a mean increase of 25 m overall. Twelve of the 16 taxonomic groups showed significant ($P < 0.05$) northwards shifts (Fig. 2) and shifts to higher elevation (Table 1). Only three species of amphibians and reptiles shifted significantly southwards and to lower elevation. For most groups, taking account of recording effort decreased the number of species available for analysis, but had little qualitative impact on our findings (Table 1; Fig. 2). Species from well-studied groups (butterflies, mammals and birds) on average moved north by 30–32 km, whereas previously less well-studied groups moved north by 32–66 km (depending on level of subsampling of data).

Discussion

Our results show that most taxonomic groups have shown significant distributional shifts northwards and to higher elevation during a period of climate warming. For taxonomic groups which have been studied previously, our results show comparable northward shifts with those already documented (Parmesan *et al*., 1999; Thomas & Lennon, 1999; Warren *et al*., 2001) although the rates of range extension have been somewhat faster than reported in Parmesan & Yohe's (2003) broader analysis. We found northwards shifts of 12.5–19 km decade^{-1} (mean of 10 and 16 taxonomic groups) and 13.7–24.8 km decade^{-1} (mean of 137 and 329 species) for heavily recorded and recorded squares, respectively. It has been suggested that groups with extensive recording could reflect changes in other taxonomic groups (Thomas *et al*., 2004) but empirical support for this contention has been scarce. Our analysis suggests that the rates of range shifting are not significantly different for birds and butterflies compared with other taxa (given the current data), even though some of the less well-studied taxa give the appearance of showing an even stronger response to climate change (Fig. 2). Our results for altitudinal shifts are also comparable with previous studies (Kullman, 2002; Konvicka *et al*., 2003; Penuelas & Boada, 2003; Wilson *et al*., 2005; Table 1) and show that most groups have shifted to higher elevation. We found uphill shifts of 4.7–10.7 m decade^{-1} (mean of 10 and 16 taxonomic groups) and 2.8–10.1 m decade^{-1} (mean of 137 and 329 species) for heavily recorded and recorded squares, respectively. Increased recorder effort over time may have led to some over-estimation of range changes in analyses of the full data sets ('re-

Table 1 Data show the number of species available for analysis, the mean northward shift at the range margin (km), the mean altitudinal shift (m) and the time period of analysis (years), for 16 taxonomic groups included in our analyses

	Recorded squares			Well-recorded squares			Heavily-recorded squares			
Taxonomic group	Number of species	Mean northward shift at the range margin, km (SE)	Mean altitudinal shift, m (SE)	Number of species	Mean northward shift at the range margin, km (SE)	Mean altitudinal shift, m (SE)	Number of species	Mean north-ward shift at the range margin, km (SE)	Mean altitudinal shift, m (SE)	Time period (years)
Dragonflies and damselflies	20	104 (17.0)*	61.9 (13.08)*	19	80 (11.3)*	31.1 (8.47)*	19	36 (8.9)*	16.8 (6.17)*	25
Grasshoppers and allies	22	34 (8.0)*	30.5 (7.48)*	22	21 (6.3)*	18.8 (5.30)*	19	11 (4.3)*	6.1 (4.25)	25
Lacewings	6	44 (27.9)*	7.4 (13.46)	1	–	–	0	–	–	25
Butterflies	29	37 (9.7)*	11.1 (6.75)	29	35 (9.6)*	7.4 (5.71)	29	30 (9.0)*	−1.2 (6.06)	21
Spiders	85	84 (8.0)*	24.3 (4.97)*	54	59 (7.2)*	15.5 (4.92)*	15	68 (10.5)*	−0.9 (7.54)	25
Herptiles	3	−83 (29.8)*	−33.0 (27.14)	3	−68 (28.5)*	−22.8 (10.76)*	3	−45 (44.0)	−22.9 (5.93)*	25
Fish	15	47 (15.4)*	32.7 (12.71)*	15	51 (15.7)*	22.0 (11.12)*	15	33 (9.3)*	9.0 (8.68)	25
Mammals	9	22 (38.4)	31.0 (27.70)	8	24 (33.0)	41.0 (29.11)	5	37 (13.7)*	103.9 (22.65)*	25
Woodlice	8	79 (18.4)*	55.3 (12.02)*	7	65 (12.1)*	37.9 (11.52)*	2	–	–	25
Ground beetles	59	55 (8.4)*	12.7 (6.31)*	28	47 (12.4)*	7.3 (8.04)	6	0 (28.6)	0.2 (28.55)	25
Harvestmen	4	8 (29.9)	35.8 (11.22)*	2	–	–	0	–	–	20
Millipedes	6	74 (17.0)*	24.0 (10.21)*	3	48 (26.8)	−5.7 (12.76)	1	–	–	25
Longhorn beetles	11	40 (10.4)*	39.3 (9.24)*	8	43 (7.3)*	26.1 (6.37)*	0	–	–	25
Soldier beetles and allies	16	91 (13.3)*	62.1 (9.89)*	5	50 (22.1)*	41.3 (18.37)*	0	–	–	25
Aquatic bugs	14	64 (19.7)*	19.2(8.49)*	8	84 (24.4)*	25.6 (9.35)*	4	81 (13.2)*	8.4 (7.76)	20
Birds	22	29 (20.0)	−2.1 (13.14)	22	29 (20.0)	−2.1 (13.14)	22	28 (20.0)	−2.1 (13.14)	19.5

Results are presented for three levels of subsampling of data, analysing 'recorded', 'well-recorded' or 'heavily recorded' grid squares (see text for details). Asterisks indicate significant range shifts ($P < 0.05$).

corded' squares), but qualitatively similar results were obtained with more stringent criteria for inclusion of data, which suggests that our general conclusions are robust.

Our results for latitudinal shifts appear stronger than those for elevation shifts, where most of the significant shifts uphill were restricted to analyses of the full data set (i.e., not taking account of recording effort). This may be due to several reasons. First, the elevation range of Britain is not great, and so there are relatively few high elevation areas for southerly species to colonize near their range boundaries. Second, higher elevation locations tend to be less well recorded than lowland sites and, thus, these areas will disproportionately be excluded from analyses which take account of recorder effort. In addition, high and low elevation sites often occur in close geographic proximity to one another, such that individuals or populations moving to higher elevations within 10 km grid cells would not be detected in our relatively course-resolution analyses. This is likely to lead to underestimates of the true elevation shift. Our estimates of latitudinal shifts should be far more reliable: latitudinal shifts of 30–60 km clearly represent the establishment of large numbers of new northern populations over a succession of generations. Few of the species considered are likely to colonize more than a few kilometres per generation. Thus, the latitudinal shifts reveal substantial changes to species' breeding ranges.

Despite the wide range of taxonomic groups considered, our results show no clear taxonomic, ecological or physiological pattern in terms of the response of groups to climate warming. A wide range of responses were found among species within almost all taxonomic groupings, which suggests that within-taxon variation in ecological traits such as habitat requirements and dispersal capacity (Warren *et al*., 2001), and longevity and body size (Perry *et al*., 2005) may preclude broader taxonomic generalizations. This suggests that further within-taxon comparisons are necessary for revealing the importance of different ecological traits and the potential mechanisms responsible for range shifts. All distribution changes are taking place not only in the context of climate warming but also in the context of land use and other environmental changes. This is best exemplified by the three amphibian/reptile species that were included in the analysis. Each of them is at the north–western edge of its distribution in Britain and should, in principle, have benefited from the warming that has been experienced in recent decades. Nonetheless, their distributions have collapsed southwards, each species surviving in remnant populations restricted to only a small fraction of their former distribution. This trend has been documented in other species which lack the dispersal ability to persist in fragmented habitats (Hill *et al*., 1999b; Honnay *et al*., 2002). Most previous studies of range shifts focused on species which are particularly limited by climate, or are highly mobile (Hughes, 2000) and excluded species whose distributions were likely to have been greatly affected by habitat changes (Parmesan *et al*., 1999). In our analyses, species were excluded only if recording effort was poor. Thus, the fact that species' distributions are also responding to other factors makes it all the more impressive that it is possible to identify a significant average northwards shift in the distributions of almost all taxonomic groups for which a sample size of more than 10 species could be analysed.

Conclusion

Species from a wide range of taxonomic groups are moving north and to higher elevations, during a period of regional (CIP, 2005) climate warming. For some less well-known groups, these responses may even be greater than those already observed for more widely studied groups.

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