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Geographical range margins of many taxonomic groups continue to shift polewards

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Many species are extending their leading-edge (cool) range margins polewards in response to recent climate change. In the present study, we investigated range margin changes at the northern (cool) range margins of 1573 southerly-distributed species from 21 animal groups in Great Britain over the past four decades of climate change, updating previous work. Depending on data availability, range margin changes were examined over two time intervals during the past four decades. For four groups (birds, butterflies, macromoths, and dragonflies and damselflies), there were sufficient data available to examine range margin changes over both time intervals. We found that most taxa shifted their northern range margins polewards and this finding was not greatly influenced by changes in recorder effort. The mean northwards range margin change in the first time interval was 23 km per decade ($N = 13$ taxonomic groups) and, in the second interval, was 18 km per decade ($N = 16$ taxonomic groups) during periods when the British climate warmed by 0.21 and 0.28 °C per decade, respectively. For the four taxa examined over both intervals, there was evidence for higher rate of range margin change in the more recent time interval in the two Lepidoptera groups. Our analyses confirm a continued range margin shift polewards in a wide range of taxonomic groups. © 2015 The Authors. Biological Journal of the Linnean Society published by John Wiley & Sons Ltd on behalf of Linnean Society of London, *Biological Journal of the Linnean Society*, 2015, 115, 586–597.

ADDITIONAL KEYWORDS: climate change – distributions – invasions – leading-edge – trailing-edge.

INTRODUCTION

In recent years, ecological responses to climate change have been observed in global fauna and flora as species have responded and adapted to new environmental conditions (Parmesan, 2006; IPCC, 2014). Species responses encompass genetic, physiological, phenological, and biogeographical changes, and these responses by species may have implications for ecosystem functioning and structure (Bellard *et al.*, 2012). One commonly observed response to climate change in a wide range of terrestrial and aquatic ecosystems is the polewards extension of species' distributions

(Parmesan & Yohe, 2003; Poloczanska *et al.*, 2013).

Climate influences the distribution of species, often acting as a limiting factor on the extent and location of species' range margins (Hill & Preston, 2015). Historical data have demonstrated how species' distributions have changed over time (Hill *et al.*, 2002), extending their ranges at leading-edge 'cool' margins when climates become more favourable for these species (Chen *et al.*, 2011). Some species have shifted their ranges at rates reflecting local rates of climate warming (Parmesan *et al.*, 1999; Chen *et al.*, 2011), whereas other species have lagged behind climate changes (Menéndez *et al.*, 2006; Devictor *et al.*, 2008; Valladares *et al.*, 2014). Considering the wide variety of habitats, pre-warming ranges, life histories,

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resource requirements, dispersal behaviours, and opportunities available to different taxonomic groups, the expectation has been for responses to climate change to vary between taxonomic groups (Angert *et al.*, 2011). Indeed, studies have reported large inter- and intraspecific variation in the responses of taxonomic groups to climate change (Thomas *et al.*, 2004; Hickling *et al.*, 2006; Rapacciuolo *et al.*, 2014). For example, butterflies have demonstrated idiosyncratic responses to climate change (Mair *et al.*, 2012), with interspecific variation partly explained by trends in abundance and habitat availability (Mair *et al.*, 2014). The availability of large data sets for a wide range of taxonomic groups in Great Britain provides an excellent opportunity to explore the responses of different taxonomic groups to recent climate change.

Many species reach their leading-edge 'cool' range margins in Great Britain, and hence might be expected to shift their range northwards under recent climate warming. There are some single-taxon studies that have examined range changes in Great Britain (Hill *et al.*, 2002; Hickling *et al.*, 2005), although not all taxonomic groups may respond in the same way to climate warming. Hickling *et al.* (2006) studied range margin changes in 16 taxa that reach a leading-edge range margin in Great Britain and, in the present study, we update and build upon this earlier study by analyzing 21 taxonomic groups, containing 1573 species monitored over four decades of climate warming. We also examine range margin changes over two time intervals, thereby investigating changes in response rates over time, as well as being able to compare range margin changes across more taxonomic groups than previously examined.

MATERIAL AND METHODS

SPECIES DATA SETS

We analyzed British data gathered mainly by volunteer naturalists through recording schemes overseen by the UK Biological Records Centre (<http://www.brc.ac.uk>), British Trust for Ornithology (<http://www.bto.org>), and Butterfly Conservation (<http://www.butterfly-conservation.org>). We categorized each observation (recorded presence) of individual species according to its location (Ordnance Survey 10 × 10 km grid square; 'hectad') and also the time period that it was recorded in (see below). Most observations were for a specific day, although some recording schemes collate observations into date ranges spanning several years. In the present study, we excluded observations with date ranges spanning more than 12 months. Species were grouped into taxonomic groups, determined primarily by the recording schemes that collated records for that group. A total

of 21 taxonomic groups had sufficient data for range margin changes to be calculated for at least one interval (the groups accepted or rejected for study are listed in the Supporting information, Table S1). Four taxonomic groups (birds, butterflies, macromoths, and dragonflies and damselflies) had sufficient data for range margin changes to be calculated for both intervals.

Our analysis focussed on southerly-distributed species that reach a northern (leading-edge) range margin in Great Britain. The study area was the British mainland, including islands connected to the mainland according to the contiguous distribution of hectads (2566 hectads in total). Hence, near-shore islands were included, whereas off-shore islands were not. Montane species (defined as species with a mean elevation ≥ 200 m across their British range) were excluded from the analyses because latitudinal range changes by these species would be confounded by elevational shifts. We also excluded ubiquitous species (defined as those occurring in more than 90% of the study area), as well as species with a northern range margin in the first time period < 100 km from the north coast of mainland Great Britain, because these species would have little opportunity for polewards range shifts. Species were also excluded if they were listed in the Great Britain Non-native Species Information Portal (Roy *et al.*, 2014) because range changes by introduced species are likely to involve human-assisted dispersal and range filling unrelated to climate change. We also excluded observations where the identification of the species was uncertain (e.g. record listed as several possible species). Species listed with a sub-species trinomial were grouped to the species level (e.g. for the Dingy skipper butterfly, *Erynnis tages* subsp. *tages* was grouped with *Erynnis tages*).

TIME PERIODS OF ANALYSIS

With the exception of birds, data were collated into three time periods (1966–1975; 1986–1995; 2001–2010), defining the northern range margin of each species in a given period. Range margin changes were analyzed over two time intervals corresponding to range margin changes between the first and second periods (interval 1: 1966–1975 to 1986–1995) and between the second and third periods (interval 2: 1986–1995 to 2001–2010). We imposed gaps between time periods to provide opportunities over which range margin changes could occur. Bird data were analyzed over slightly different time periods and intervals (interval 1: 1968–1972 to 1988–1991; interval 2: 1988–1991 to 2008–2011) corresponding to bird atlas recording periods (Sharrock, 1976; Gibbons, Reid & Chapman, 1993; Balmer *et al.*, 2014). We

standardized the time periods as far as possible across the different taxonomic groups to ensure that all species were studied over similar periods, and hence experienced similar climatic changes. A preliminary analysis using the slightly different time periods analyzed by Hickling *et al.* (2006) produced results qualitatively similar to the standardized dates used in the present study.

CONTROLLING FOR VARIATION IN RECORDER EFFORT

The intensity of recorder effort in Great Britain has varied over time and space, as well as within and between taxonomic groups. Thus, for each time interval and taxonomic group, we controlled for variation in recording effort by selecting hectads with a minimum threshold of recording effort based on observed local species richness relative to the regional species richness pool. First, for each focal hectad, we identified the nearest 100 hectads (sufficient for the regional pool size of species to asymptote) where at least one species from that taxonomic group was recorded in both time periods (i.e. 1966–1975 and 1986–1995 for analyses of interval 1; 1986–1995 and 2001–2010 for analyses of interval 2; or equivalents for birds). Second, the species richness of these neighbouring hect-

ads was calculated from the total number of unique species recorded in both time periods. Focal hectads were included in analyses according to the level of recording effort they experienced, and hectads were termed ‘recorded’, ‘well-recorded’, and ‘heavily-recorded’. ‘Recorded’ hectads contained at least one species in both time periods; ‘well-recorded’ hectads contained at least 10% of the species richness of the surrounding hectads in both time periods; and ‘heavily-recorded’ hectads contained at least 25% of the species richness of the surrounding hectads in both time periods. This method for accounting for recorder effort was broadly similar to that used by Hickling *et al.* (2006), except that we used local species richness rather than the richness of all species in Great Britain when selecting hectads for inclusion. This new method is likely to be more sensitive in accounting for recorder effort because it takes better account of underlying spatial variation in species richness across Great Britain.

Our analyses of range margin changes were repeated for each of the three levels of control for recorder effort. For the four taxonomic groups (birds, butterflies, macromoths, and dragonflies and damselflies) studied over both time intervals, northern range margins were calculated in a second analysis

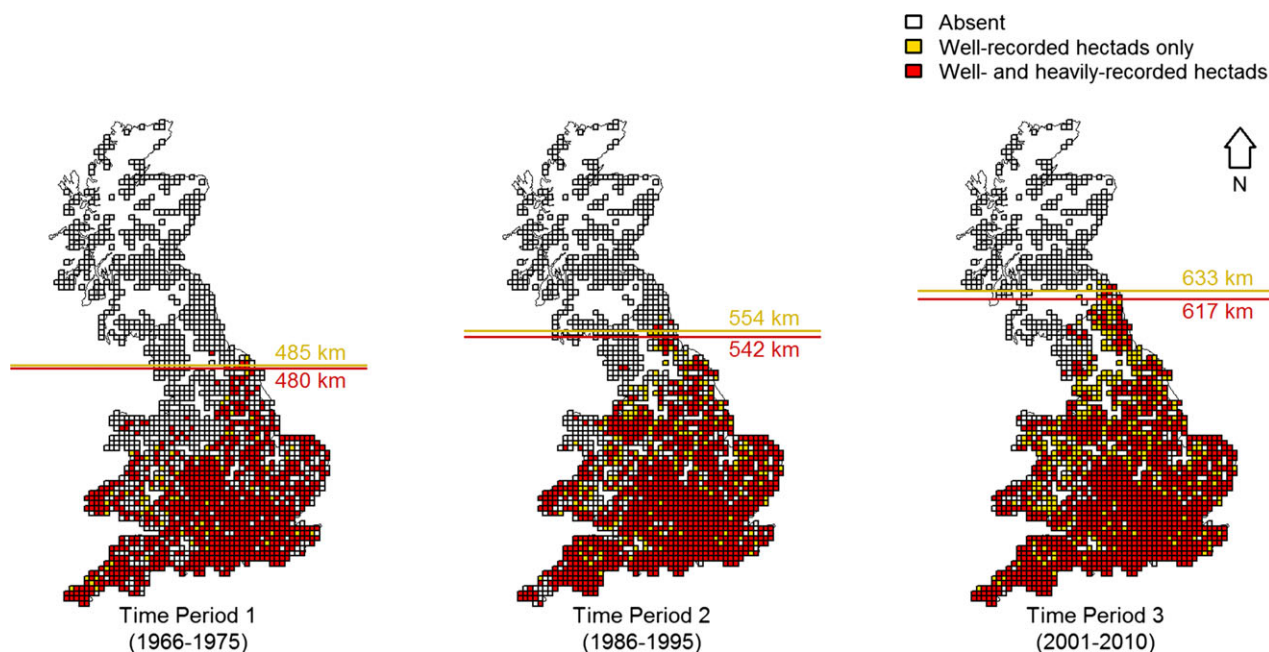


Figure 1. Locations of northern range margins calculated for different thresholds of recording effort control in each of three time periods of study (1966–1975, 1986–1995, and 2001–2010) for the small skipper butterfly (*Thymelicus sylvestris*). This exemplar species was selected because it has extended its range northwards in recent years. Maps show species presence in well-recorded and heavily-recorded hectads (10 × 10 km) and (apparent) absence (hollow squares) where butterflies were observed (but not the small skipper butterfly). Labelled lines indicate range margin locations from analyses of well- and heavily-recorded hectads in each time period.

that used a subset of well-recorded and heavily-recorded hectads from both intervals that were common to all three time periods (see below). Figure 1 shows how analyzing well-recorded or heavily-recorded hectads affected the calculation of the range margin location for an exemplar butterfly species, *Thymelicus sylvestris*. Compared with the other taxa studied, recorder effort variation is far less in birds than other taxonomic groups. For example, macromoths experienced a more than seven-fold increase in the number of observations over the study period (213 202 and 1 525 964 unique observations of species in GB hectads during time periods 1 and 3, respectively), such that hectads were more likely to have been intensively surveyed in the later time periods. By contrast, bird data are collated systematically for each atlas and so there is less change in the number of records of birds over time. Figure 2 shows the locations of well-recorded and heavily-recorded hectads for birds, butterflies, dragonflies and damselflies, and macromoths.

MINIMUM DATA REQUIREMENTS FOR TAXONOMIC GROUPS AND SPECIES

Each taxonomic group was selected for study if it occupied at least 20 well-recorded hectads during interval 1 or interval 2, and contained more than one species for which range margin changes could be calculated. Taxonomic groups without their own formal recording scheme (which apply various quality control measures; for example, to avoid misidentifications) were rejected. Those taxonomic groups that

had data from multiple sources (and hence no uniform quality control measures) were also rejected. Criteria for selecting taxonomic groups analyzed over both intervals were stricter, given the more statistically challenging task of trying to identify not only range margin changes, but also whether rates had changed over time. Thus, taxonomic groups needed at least 20 heavily-recorded hectads that were common to all three time periods to qualify for inclusion, and also had to contain five or more species for which a range margin could be calculated (see below) based on heavily-recorded hectads. These criteria resulted in four taxonomic groups being studied (birds, butterflies, macromoths, and dragonflies and damselflies).

For each time period, the range margin of each species was calculated for each level of recording effort control. We excluded species from a time period if they were observed in fewer than 20 hectads, for a given level of recording effort control, because estimates for the locations of range margins would be subject to high recording error. Once northern range margins were calculated (see methods below), species with fewer than 10 hectads within 100 km to the north and south of their range margin in the first time period were excluded. This excluded species whose estimates of potential range margin changes northwards or southwards would be confounded by poor recording effort.

CALCULATING NORTHERN RANGE MARGIN CHANGES

The locations of northern range margins were calculated in each of the three time periods. For each spe-

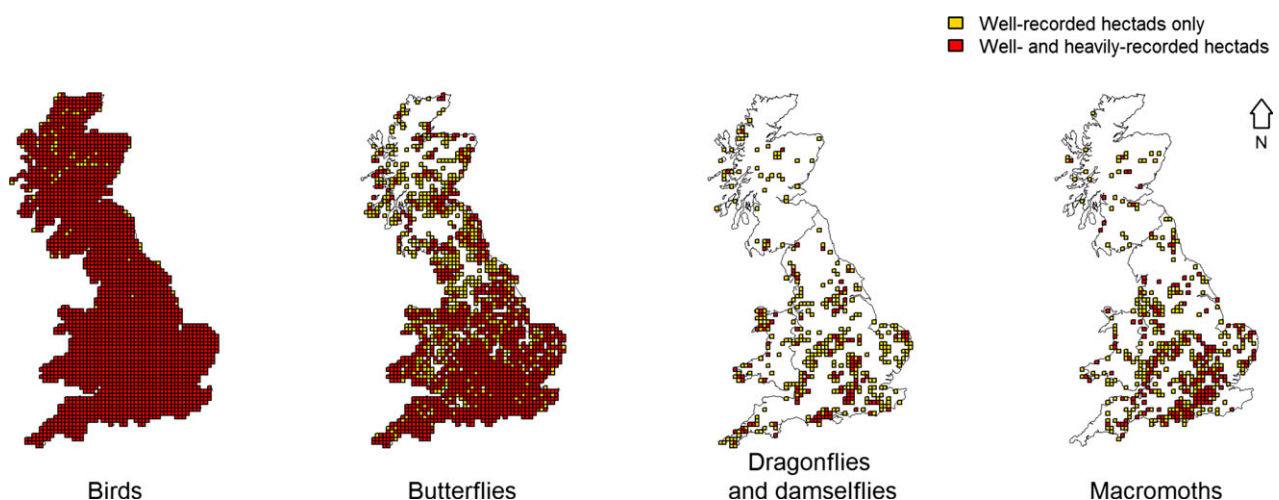


Figure 2. Distribution of well-recorded and heavily-recorded hectads across both time intervals for the four taxonomic groups analyzed in Fig. 4. Sample sizes for well-recorded hectads are 2561, 1729, 477, and 414 for birds, butterflies, macromoths, and dragonflies and damselflies, respectively. Sample sizes for heavily-recorded hectads are 2500, 1218, 205, and 119 for the respective groups.

cies that was included, the location of its northern range margin was computed as the mean northing (in km north, from the Ordnance Survey GB grid) of the species' 10 most northerly occupied hectads in that time period. For each taxonomic group and time interval, the mean rate of change (and 95% confidence intervals) in northern range margin was then calculated as the distance moved in km per decade (based on the number of years between the mid-points of each time period), with positive rate values indicating northward shifts, and negative values indicating southward shifts. These analyses were carried out for each of the three levels of recording effort. We used analysis of variance (ANOVA) and one-sample *t*-tests to examine differences in rates of range margin change among the taxonomic groups in each time interval, and whether rates of range margin change were significantly different from zero.

We examined whether rates of range margin change differed between time intervals 1 and 2 in the four selected taxonomic groups (birds, butterflies, macromoths, and dragonflies and damselflies). We generated linear mixed models using lme4 package in R (Bates *et al.*, 2014) with rate of range margin change (km per decade) as the response variable, time interval and taxonomic group as explanatory variables, and species identity as a random effect. We fitted models with all possible combinations of explanatory variables and their interaction term and examined the goodness of fit of each model using Akaike information criterion (AIC) values, and models where ΔAIC was < 2 were assumed to be equally good at explaining the data (Burnham & Anderson, 2002). Additionally, rates of range margin change in the two time intervals in each taxon were compared using paired *t*-tests and one-sample *t* tests were used to examine whether rates of range margin change in each interval were significantly different from zero. All statistical analyses were performed in R, version 3.0.2 (R Core Team, 2013).

TEMPERATURE VARIATION ACROSS THE STUDY PERIOD

Mean seasonal temperature data from the Hadley Centre Central England Temperature (HadCET) series were downloaded from the UK Met Office (<http://www.metoffice.gov.uk/hadobs>). Over the study period (1966–2010), annual mean temperature was computed from the mean value of each of the four seasons (i.e. annual temperature was measured from December through to the subsequent November). Descriptive analyses were undertaken to describe changes in temperature over the years included in interval 1 (1966–1995) and interval 2 (1986–2010), as well as between these two intervals. We used regres-

sion analysis to examine changes in mean seasonal and annual temperatures within each time interval, as well as analysis of covariance to determine whether there was a difference in the rate of temperature change between the two time intervals.

RESULTS

NORTHERN RANGE MARGIN CHANGES

We focus primarily on describing the results for well-recorded hectads because we consider this level of control for recorder effort to be the best compromise between robustness of data analysis and retaining large numbers of species and taxonomic groups in our analyses, although we also report full statistical results for the other two levels of recording effort control in the Supporting information (Tables S2 and S3). The locations of the northern range margins of all species during each time period are provided in the Supporting information, (Table S4, interval 1; Table S5, interval 2). Generally, most taxonomic groups shifted northwards for all levels of recording effort for which they could be analyzed (Fig. 3). The mean overall rate of range margin change, calculated from each taxonomic groups' mean rate of range margin change, was 23.2 km per decade (SE = 5.8; $N = 13$ taxa) in time interval 1 and 18.0 km per decade in interval 2 (SE = 4.0; $N = 16$ taxa).

Seven of the 13 groups in interval 1 and six of the 16 groups in interval 2 significantly extended their range margins northwards in the analysis of well-recorded hectads (Fig. 3; see also the Supporting information, Table S3). Qualitatively similar results were obtained for the other levels of recording effort control (Fig. 3); nine of the 13 groups analyzed in interval 1 demonstrated significant northwards range margin changes for at least one level of recording effort, and eight out of 16 taxa showed significant northwards shifts for one or more levels of recording effort control in interval 2 (Fig. 3; see also Supporting information, Table S3). Despite most taxa shifting their range margins northwards in both time intervals, macromoths showed a significant southwards range margin change in interval 1 (but only for well-recorded hectads) and three other taxa demonstrated southwards retractions in interval 2, although the significance of the change depended on levels of control for recorder effort (Fig. 3; see also Supporting information, Tables S2 and S3). For taxonomic groups that occurred in both time periods (Fig. 3B,D), their rates of range margin change are not directly comparable between the two intervals because different sets of hectads and species were used to calculate rate of range margin change in each interval.

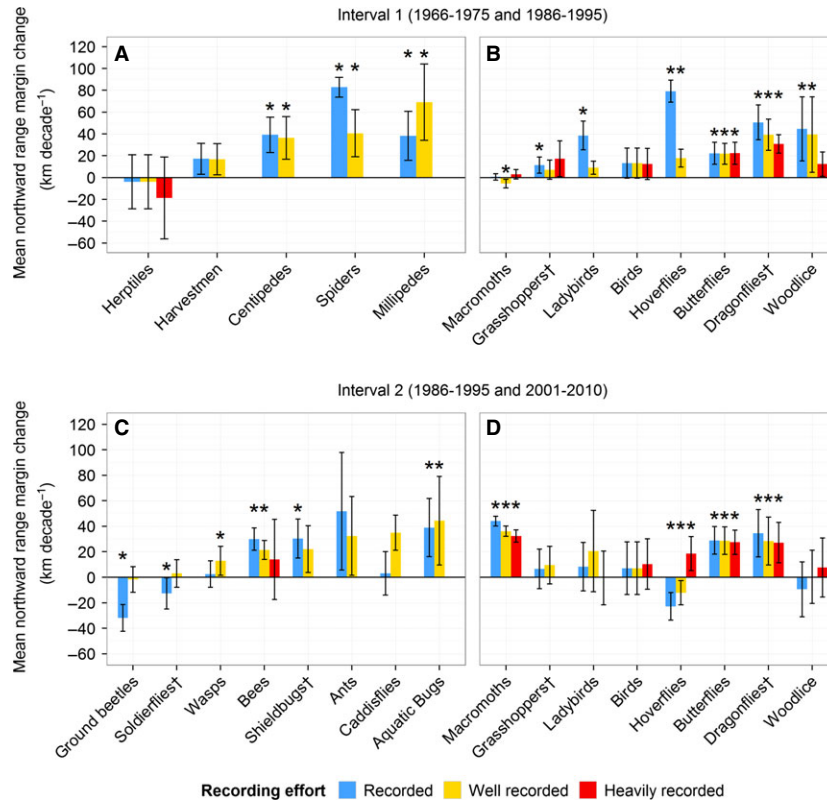


Figure 3. Mean rates of northern range margin changes of species in 21 taxonomic groups over interval 1 (upper) and interval 2 (lower) for each level of recording effort control. A, C, range margin changes for taxonomic groups studied over one time interval only (13 taxa). B, D, taxa studied in both intervals (8 taxa). Error bars represent 95% confidence intervals of the mean. Asterisks above bars indicate range changes that were significantly different from zero (one-sample *t*-test). A–C, bars are ordered along the *x*-axis by magnitude of range margin changes according to analyses of well-recorded hectads. D, ordered according to the order in B. The number of species per taxonomic group varied among groups, recording effort control levels and intervals (see Supporting information, Table S3). Heavily-recorded bars are absent for some taxa because this level of analysis was not possible. For taxonomic groups studied in both intervals, there were different species compositions in each interval and different sets of recorded, well-recorded, and heavily-recorded grid squares. Thus, differences in rates of range change between time intervals may be a result of differences in the species included and locations recorded and so any comparisons should be made with caution. Taxonomic group names accompanied by a dagger symbol indicate that the group contains allied species (see Supporting information, Table S1).

Taxonomic groups differed in their rates of range margin change, and this was evident in both time intervals (ANOVA, interval 1, $F_{12,511} = 7.66$, $P < 0.001$; interval 2, $F_{15,868} = 9.64$, $P < 0.001$) and this finding was insensitive to the level of control for recorder effort (see Supporting information, Table S2).

Mean annual temperature generally increased in Great Britain during the study period (on average by 0.21 °C per decade during interval 1 and 0.28 °C per decade during interval 2), with mean spring (March to May) temperature increasing significantly during interval 1 and mean autumn (September to November) temperatures increasing significantly in interval 2 (see Supporting information, Table S6).

CHANGES IN RATES OF RANGE MARGIN CHANGE OVER TIME

We examined whether rates of range margin change were similar in the two time intervals for four taxonomic groups (birds, butterflies, macromoths, and dragonflies and damselflies) with sufficient data to analyze the same hectads across all three time periods. The estimates of rates of range margin change from this subset of hectads generated estimates similar to those from the larger set of hectads used to calculate rates of change separately for intervals 1 and 2 (see Supporting information, Fig. S1). All four taxonomic groups shifted northwards in both intervals (Fig. 4), and macromoths and butterflies showed significantly faster rates of range margin

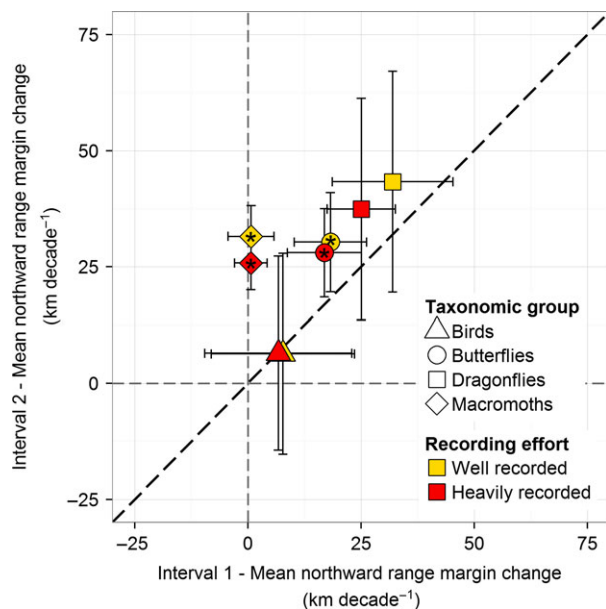


Figure 4. Comparison of rates of northern range margin change for four taxonomic groups across two time intervals (for time interval dates, see text). Taxonomic groups: birds (31 species), butterflies (35 species), dragonflies and damselflies (seven species), and macromoths (127 species). These estimates of rate of range margin change differ slightly from those in Fig. 3 because only those hectads that were well-recorded in all three time periods were included. Asterisks indicate groups where range margin changes differed over time (two-tailed paired t -test, $P \leq 0.05$; see Supporting information, Table S7). 'Dragonflies' represents all Odonata, including damselflies.

change in interval 2 compared to interval 1 (see Supporting information, Table S7; macromoths paired t -test, $t_{126} = -7.51$, $P = <0.001$; butterflies $t_{34} = -2.26$, $P = 0.03$). The locations of the northern range margins of all species during all three time periods are provided in the Supporting information (Table S8).

The most parsimonious statistical model of rate of range margin change for these four groups included the interaction term between taxonomic group and interval (Table 1). The interaction occurred primarily because macromoths showed little range margin change in interval 1 but significant northwards shifts in interval 2, and butterflies almost doubled their rates of polewards range margin change between intervals 1 and 2 (interval 1 = 18.3 km per decade; interval 2 = 30.3 km per decade), whereas rates of range margin change of birds and dragonflies and damselflies did not significantly differ over time (see Supporting information, Table S7). This conclusion was not dependent on the inclusion of any single taxonomic group, and serial omission of each taxonomic group (and of all Lepidoptera, i.e. excluding both butterflies and macromoths) con-

tently found that a mixed model with the interaction term between taxon and interval had the lowest AIC value (i.e. represented the best model; see Supporting information, Table S9). This apparently faster rate of range margin change in Lepidoptera in interval 2 was evident despite the fact that the rate of temperature warming was similar between interval 1 (1966–1995) and interval 2 (1986–2010; see Supporting information, Table S10) for most measures of temperature. However, mean autumn temperature increased significantly between interval 1 and 2 (see Supporting information, Table S10).

DISCUSSION

We analyzed rates of range margin change in 1573 southerly-distributed species from 21 animal groups in two time intervals. Overall, most of the taxonomic groups in the present study shifted their range margins northwards in both time intervals (23.2 km per decade in interval 1; 18.0 km per decade in interval 2), supporting the findings of Hickling *et al.* (2006). Rates of range margin change varied between taxonomic groups and, for some groups, over time. For the four groups with sufficient data to undertake robust analyses of whether these rates have changed over time, there was evidence that rates of range margin change have been faster more recently for macromoths and butterflies. These findings were relatively insensitive to control for recorder effort, although increasingly strict control for recorder effort reduced the number of hectads that could be analyzed.

CONTROLLING FOR VARIATION IN RECORDER EFFORT

Variation in levels of recorder effort across spatial and temporal scales can present problems to ecologists aiming to quantify range shifts (Tingley & Beissinger, 2009; Isaac *et al.*, 2014). Our results showed that most of the taxa studied have shifted their range margins northwards for all levels of recording effort under consideration. However, there were some taxonomic groups where the shift in the northern range margin was qualitatively different according to the level of control for recorder effort. For example, northern range margins of hoverflies apparently retracted southwards in interval 2 if recorded and well-recorded hectads were analyzed, although they extended northwards according to analysis of heavily-recorded hectads (Fig. 3D). As the control for recorder effort became stricter, the number of hectads included was reduced, and so the number of species included was also reduced. Hence, 137 and 131 species of hoverfly were included in analyses of 'recorded' and 'well-recorded' hectads,

Table 1. Linear mixed effects models for rate of northern range margin change (response variable in km per decade) in well-recorded hectads, between two time intervals (spanning 1966–2010), for the four most heavily-recorded taxonomic groups ($N = 200$ species in total)

Model	Fixed effects	Δ AIC	Fixed effects (breakdown)	Coefficient	Standard error	t
1	1	87.71	Intercept	16.9	1.9	8.695
2	Group	66.43	Intercept (birds)	7	5	1.413
			Group (butterflies)	17.3	6.8	2.525
			Group (dragonflies and damselflies)	30.6	11.6	2.642
			Group (macromoths)	9.1	5.6	1.642
3	Interval	48.9	Intercept (interval 1)	−15.9	5.6	1.642
			Interval (2)	21.9	3.5	6.311
4	Interval + Group	27.62	Intercept (interval 1, Birds)	−25.8	7.2	−3.581
			Interval (2)	21.9	3.5	6.311
			Group (butterflies)	17.3	6.8	2.525
			Group (dragonflies and damselflies)	30.6	11.6	2.642
			Group (macromoths)	9.1	5.6	1.642
5	Interval + Group + Interval:Group	0	Intercept (interval 1, birds)	9.2	13.8	0.665
			Interval (2)	−1.4	8.6	−0.166
			Group (Butterflies)	−3	18.9	−0.157
			Group (Dragonflies and damselflies)	11.5	32.1	0.358
			Group (Macromoths)	−39.3	15.4	−2.553
			Interval: Group (Butterflies)	13.5	11.8	1.146
			Interval: Group (Dragonflies and damselflies)	12.8	20	0.639
			Interval: Group (Macromoths)	32.3	9.6	3.373

respectively, whereas only 21 species were included for heavily-recorded hectads. If recorded and well-recorded hectads were assessed for just these 21 species, the recorded range margin shift (9 km per decade southwards) was smaller than when all available species were analyzed, and the well-recorded range margin shift changed to a northwards direction (8 km per decade northwards). Thus, our reported range margin changes are a function of both the hectads included in the analyses, as well as the identity of species included. Using the most thoroughly surveyed (heavily-recorded) subset of data, the observed trend was for 13 out of 14 measured changes (taxon by interval combinations) to show a northwards margin shift (Fig. 3) and the overall data showed significant northwards trends across all taxa in both periods for all three levels of recording effort control (see Supporting information, Table S2). Thus, our qualitative findings appear robust to variation in recorder effort (at least for the three control methods assessed), although the quantified rate of change depends on the level of control for recorder effort.

Our approach to filtering data for analysis represents an assessment of the sensitivity of our conclusions to variation in recording effort, rather than a true measure of ‘control’ for recording effort, given

that the true recorder effort is unknown. We adopted the same general approach as Hill (2012) and assumed that any species that might potentially be recorded in a particular location (hectad) would be drawn from the pool of species found in the surrounding region (which we defined as the nearest 100 hectads with any records for the taxon). The distribution of species richness in Great Britain does not change greatly from one hectad to the next (Fox *et al.*, 2011; Balmer *et al.*, 2014) and so the percentage of the regional species pool recorded as present in a hectad represents a first approximation for the relative level of recording effort. However, the percentage of species actually recorded in a hectad depends on the actual number of species present (which itself depends on local environmental conditions), as well as on the level of recording that has taken place. Hence, we adopted an approach whereby we used thresholds (> 0%, 10%, 25% of the regional species pool) rather than a continuous metric of species recorded.

Recorder effort has changed over time and the number of records of species in Great Britain has increased rapidly. However, if increased recording effort through time is primarily responsible for generating the erroneous impression of range margin changes, we would expect the recorded rate of range

margin changes of common species to be less rapid than the rate of range margin changes of all species taken together because rare species are more likely to go unnoticed during lower intensity surveys (Bates *et al.*, 2015). Indeed, we found few differences when we repeated our analyses to include only common species (defined as the top 50% of species ranked by number of presences in heavily recorded hectads). Analyzing only common species, the estimated rate of range margin change was decreased for common birds (despite little or no increase in recording effort), largely unaffected for macromoths (which showed the greatest increase in recording effort), and increased for butterflies (see Supporting information, Fig. S2). If sampling effort has an important influence, we would also expect higher levels of recording effort to generate markedly reduced estimates of range margin change, which we did not observe. Poor recorder effort may be an issue in interval 1, although analysis of well-recorded and heavily-recorded hectads in interval 2 produced higher estimates of northwards range margin change than data from recorded hectads, suggesting that northwards range margin changes are not primarily artefacts of recorder effort changes, at least after 1986–95. Examination of the rate of range margin changes of individual species (Fig. 1) and differences in the distribution changes of northern and southern species also indicate that the polewards range margin shifts in the present study are real (Warren *et al.*, 2001; Hickling *et al.*, 2005; Fox *et al.*, 2013, 2014; Cham *et al.*, 2014).

VARIATION OVER TIME AND BETWEEN TAXONOMIC GROUPS

Our results suggest that some taxa differed in their rates of range margin change over time, and that Lepidoptera apparently spread northwards more rapidly in the more recent time period, when autumn temperatures significantly increased. The more recent faster rate of range margin change in Lepidoptera does not obviously align with any major morphological, habitat-use or other features of this group, and trait-based analyses have rarely explained very much of the variation in rates of range shift among species within taxonomic groups (Angert *et al.*, 2011). Species may vary in their sensitivity to different aspects of climate, and responses of species may also reflect the amount of warming, as well as habitat availability (Hill *et al.*, 2001), which may contribute to these differences among taxa. We only compared four taxonomic groups, two of which were Lepidoptera, comprising too few groups from which to draw any firm conclusions. In addition, the considerable variation that is exhibited between species within individual taxonomic groups (Chen *et al.*,

2011) and over time (Mair *et al.*, 2012) suggests that there may be no simple explanation for variation among taxa in their responses to climate change.

Climate change is driving many species to extend their ranges northwards (Chen *et al.*, 2011) and most of the taxonomic groups investigated in the present study supported that finding. However, we found variation in rates of range margin change amongst the animal taxa studied. Taxa may vary in their response to temperature at different time of the year, as well as to different aspects of climate (Araújo, Thuiller & Pearson, 2006; Jiguet, Brotons & Devictor, 2011; Schweiger *et al.*, 2012). Taxa may also vary in the extent to which they occupy their climatic niche (Sunday, Bates & Dulvy, 2012) and hence nonclimatic constraints could account for differences in the rate of range margin changes that we observe between groups. For example, Fox *et al.* (2013) suggested that the range extension of footman moths in Great Britain could be related to an increased availability of larval hosts (algae and lichens), which in turn could benefit from changes in air quality and nutrient availability, as well as climate change (Morecroft *et al.*, 2009; Pescott *et al.*, 2015a). In addition, evolutionary changes in dispersal ability and ecological changes in habitat associations may contribute to variation in rates of range change (Thomas *et al.*, 2001; Hill, Griffiths & Thomas, 2011; Pateman *et al.*, 2012). However, although resource and habitat availability are important for individual species, it is not clear whether they and many other range-determining factors (e.g. natural enemies, competing species) are important causes of the differences that we observed between broader taxonomic groups.

CONCLUSIONS

The present study provides further support for most of the taxonomic groups studied having shifted their leading-edge margins northwards. We also have evidence that rates of range margin change vary over time and between taxonomic groups, just as they vary between species within each taxonomic group. Hence, conservation planning and habitat management strategies should be aware that rates of species' range changes in response to environmental change are highly variable. Our analyses have benefitted from the extensive data sets that exist for a large number of taxa in Great Britain, recording changes in distributions over the past four decades. Such recording schemes are vital for understanding biodiversity changes in human-dominated landscapes. Establishing robust monitoring systems that build on those that already exist will increase our capacity to detect, understand, and manage these changes (Prescott *et al.*, 2015b).

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SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article at the publisher's web-site:

Figure S1. Comparison of mean rates of range margin change calculated for four taxonomic groups when the hectads selected for analysis are common to two time periods in a single interval or the subset of hectads common to intervals 1 and 2.

Figure S2. Comparison of mean rates of range margin change for common species in three taxonomic groups across two intervals (as in Fig. 4).

Table S1. List of taxonomic groups considered for analysis.

Table S2. Overall mean rate of range margin changes (and SEs) across taxonomic groups.

Table S3. Summary table and statistics corresponding to Figure 3.

Table S4. Summary of northern range margins for all species included in Figure 3 in interval 1.

Table S5. Summary of northern range margins for all species included in Figure 3 in interval 2.

Table S6. Seasonal and annual temperature trends across the study period (1966-2010).

Table S7. Summary table relating to Figure 4 (taxonomic groups studied over both intervals).

Table S8. Northern range margins of all species included in Figure 4.

Table S9. Results of linear mixed effects models for the rate of range margin change between two intervals spanning 1966-2010.

Table S10. ANCOVAs of seasonal and annual temperatures in each interval.