



EDITOR'S
CHOICE

Impacts of climate change on national biodiversity population trends

B. Martay, M. J. Brewer, D. A. Elston, J. R. Bell, R. Harrington, T. M. Brereton, K. E. Barlow, M. S. Botham and J. W. Pearce-Higgins

B. Martay (blaise.martay@bto.org) and J. W. Pearce-Higgins, British Trust for Ornithology, The Nunnery, Thetford, UK. – M. J. Brewer and D. A. Elston, Biomathematics and Statistics Scotland, Aberdeen, UK. – J. R. Bell and R. Harrington, Rothamsted Research, Harpenden, Hertfordshire, UK. – T. M. Brereton, Butterfly Conservation, Wareham, UK. – K. E. Barlow, Bat Conservation Trust, London, UK. – M. S. Botham, Centre for Ecology and Hydrology, Wallingford, Oxfordshire, UK.

Climate change has had well-documented impacts on the distribution and phenology of species across many taxa, but impacts on species' abundance, which relates closely to extinction risk and ecosystem function, have not been assessed across taxa. In the most comprehensive multi-taxa comparison to date, we modelled variation in national population indices of 501 mammal, bird, aphid, butterfly and moth species as a function of annual variation in weather variables, which through time allowed us to identify a component of species' population growth that can be associated with post-1970s climate trends. We found evidence that these climate trends have significantly affected population trends of 15.8% of species, including eight with extreme ($>30\%$ decline per decade) negative trends consistent with detrimental impacts of climate change. The modelled effect of climate change could explain 48% of the significant across-species population decline in moths and 63% of the population increase in winged aphids. The other taxa did not have significant across-species population trends or consistent climate change responses. Population declines in species of conservation concern were linked to both climatic and non-climatic factors respectively accounting for 42 and 58% of the decline. Evident differential impacts of climate change between trophic levels may signal the potential for future ecosystem disruption. Climate change has therefore already driven large-scale population changes of some species, had significant impacts on the overall abundance of some key invertebrate groups and may already have altered biological communities and ecosystems in Great Britain.

Extinction rates have been far higher over the last 100 yr than over the 500 yr prior to industrialisation (Ceballos et al. 2015), driven by a range of anthropogenic pressures including habitat loss, climate change and competition from invasive species (Butchart et al. 2010). During the course of this century, climate change is projected to become an increasingly important pressure on many species (Thomas et al. 2004, Ballard et al. 2012). Whilst impacts of climate change on the distribution and phenology of many species are already well documented (Walther et al. 2002, Parmesan and Yohe 2003, Menzel et al. 2006, Thackeray et al. 2010, Chen et al. 2011), there have been fewer extensive, multi-species studies of the impacts of climate change upon population size (Gregory et al. 2009, Jiguet et al. 2010, Jørgensen et al. 2016). This is a critical gap, as it is primarily through impacts at the population level that climate change will inflate extinction risk and alter ecosystem function. There is an urgent need to quantify the extent to which climate change may already have altered biodiversity population trends across a range of taxa. In a bid to examine these issues, we have modelled the impact of post-1970s climate trends (which we subsequently

term climate change, although recognise that these trends will result from a combination of anthropogenic climate change, natural climatic fluctuations and annual variation in the weather) upon the abundance of 501 species across five vertebrate and invertebrate taxonomic groups in Great Britain (GB), and use these models to describe how climate change is likely to have contributed to long-term biodiversity trends in each group, individual species' population declines and changes to ecological communities.

Few previous studies have quantified the impacts of climate change on species with a method that allows a comparison between species of different taxa. Examples include a comparison of range shifts (Hickling et al. 2006) and phenological change (Thackeray et al. 2010) across British taxa. These highlighted differing impacts between trophic levels, which could signal potential future disruption of ecological networks and extreme ecosystem alterations (Tylianakis et al. 2008). However, those studies did not directly link climate change and abundance changes. Where this has been done, the methods used rarely allow between-taxa comparisons. The few which have been undertaken include two extensive

meta-analyses, one comparing predicted climate-driven changes with observed changes in communities, phenology and ranges across many taxa to compare geographic areas (Parmesan and Yohe 2003) and one examining species' population responses globally to temperature and precipitation (Pearce-Higgins et al. 2015). A further two studies include predicting extinction risk from climate envelope models (Thomas et al. 2004) and a trait-based framework for multi-taxa assessments of climate change vulnerability (Foden et al. 2013). A study undertaken across central Europe identified a stronger link between temperature niches and population trends in birds, butterflies and ground beetles than in bats, springtails and grassland plants (Bowler et al. 2015). This is the only previous standardised multi-taxa assessment of climate change impacts on population trends to our knowledge. In our study from GB, we similarly quantify the extent to which population trends can be attributed to climate change, and identify the potential role that recent climate change may have played in driving declines and increases in the abundance of individual species. Recognising the strong biodiversity trends that have occurred in GB (Oliver et al. 2015a, b, Burns et al. 2016), we consider the contribution of climate change in driving community-wide changes in abundance. This final step is vital to understand how species-specific responses scale up to community and ecosystem responses and to indicate where mitigation efforts could have the greatest impact.

There are a number of analytical challenges to comparing climate change impacts on abundance across multiple taxa, and particularly to disentangle the effects of potentially multiple climatic and other drivers upon population and community change (Eglington and Pearce-Higgins 2012, Jørgensen et al. 2016). For most species there is little ecological knowledge of what non-weather factors drive population change and in this void there is a risk of over-attributing population changes to weather. For example, populations may be impacted by multiple weather variables with non-linear effects because of complex biotic and abiotic interactions (Walther et al. 2002, Araújo and Luoto 2007) that would require extensive species-specific ecological knowledge to predict. Sufficient ecological knowledge is not available across most taxa to build such detailed species-specific models. Instead, the weather and ultimately climate change can be described by multiple inter-related and correlated variables. Developed in response to the problems of analysing multivariate data sets, ordination techniques can be used to identify and simplify the main trends hidden within a complex and correlated data set into a few variables (Peres-Neto et al. 2003). As a result, they have wide potential applicability for describing the impacts of climate change on species populations (Voigt et al. 2003).

Specifically, we use ordination techniques to summarise the main trends in temperature and precipitation that have occurred over 46 yr across GB, and general linear modelling to examine the component of species' national population change since the 1970s associated with these weather trends. Importantly, we identify the extent to which national-level climate change impacts differ between taxonomic groups and may signal significant ecosystem-level changes. We tested the following key hypotheses.

1) Trends in weather since the 1970s have had a detectable impact on the population abundance of many species.

2) The impact of climate change varies between taxonomic groups and within some taxa across-species population trends can be attributed to climate change. In particular, positive climate change impacts on butterflies (Warren et al. 2001) and resident bird species (Pearce-Higgins et al. 2015) are expected, whilst habitat degradation and loss is still generally considered to be the key driver of bird (Eglington and Pearce-Higgins 2012, Burns et al. 2016, Rushing et al. 2016) and moth (Fox 2014) trends.

3) The impact of climate change varies between species according to the following species traits: a) trophic level, (i.e. primary or secondary consumer) as faster rates of phenological and range change have been noted in primary consumers compared to secondary consumers (Thackeray et al. 2010, Devictor et al. 2012). Higher-level consumers are also more likely to be affected by climate change through biotic mechanisms than primary consumers (Ockendon et al. 2014). b) Conservation status, with species that are already rare or declining more likely to be affected detrimentally by climate change due to synergistic impacts of non-climate related threats and climate change (Heller and Zavaleta 2009, Green and Pearce-Higgins 2010, Davey et al. 2012). c) Pest status, as populations of pest species of economic importance may be more adaptable to climate change and therefore more likely to have benefitted from climate change (Cannon 1998).

Material and methods

We describe below several data processing steps leading to the formal analyses on which our findings are based. The relationship between these steps and the formal analyses are shown in a flow chart (Fig. 1).

Population indices

Robust long-term monitoring data on populations of aphids, butterflies, moths, birds and mammals were collated from existing schemes (Table 1), covering an initial total of 1396 species. Aphid and moth data were collected respectively from 12 and 13 sites across GB, with sites for both taxa in England and Scotland, and moth sites also in Wales; this low number of sites did not allow less common species to be monitored effectively. Species not recorded at least once in every surveyed year (625 moths and 270 aphids) were excluded from further analysis, leaving a total of 501 species across five taxa (Table 1). Although species included in this study were not a random sample of all species within taxonomic groups, they may be regarded as a relatively complete set of the most widespread species.

The geographical and spatial distribution of survey locations varied between taxonomic groups, creating the need for bespoke processing of each data set to minimise the impact of potential geographical bias or inter-annual variation in the location of sites monitored upon our results. Data for birds, butterflies and mammals were based on large numbers (> 1000) of locations concentrated in England, particularly in the early years of monitoring. As there may

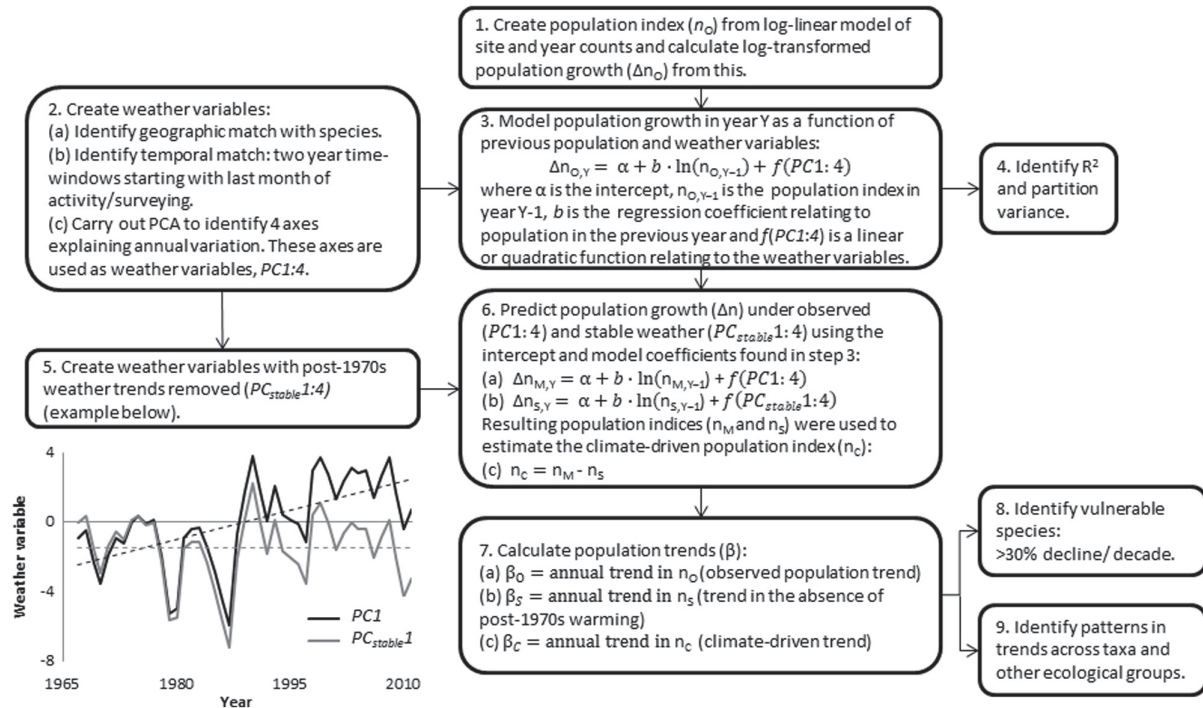


Figure 1. Flow chart of analytical steps, numbered in order of presentation, required to quantify species-specific climate change impacts and comparisons across taxa and ecological groups. Observed population growth (Δn_O) was modelled as a function of four weather variables ($PC1:4$) and this model was used to predict the modelled population (n_M), the population expected in the absence of post-1970s climate change (n_S), and the climate-driven population component (n_C).

be spatial variation in population trends (Freeman et al. 2007), population indices for these groups were produced only for England. The exception to this was the Scotch argus butterfly *Erebia aethiops* for which we produced a GB index because it mainly occurs in Scotland. Data for aphids and moths were collected from sites across England, Wales and Scotland, and therefore were regarded as representative of trends across GB.

For each species under consideration, national (GB or England) population indices ($n_{O,Y}$ in year Y) were calculated using standard log-linear generalised linear models (GLM) fitting site and year effects for each species (ter Braak et al. 1994, Freeman and Newson 2008, Willis et al. 2009), taking the index value on the (natural) log scale of the first year to be 0 (Fig. 1, step 1). We followed existing protocols for each national monitoring scheme, hence for bats additional methodological covariates known to strongly influence their abundance (survey weather, type of bat detector, timing of survey) were included in these models (Barlow et al. 2015). For clarity here and elsewhere, we

do not include a subscript for species in model equations, although modelling of the indices always took place at a species level.

Weather variables

We focussed on modelling inter-annual variation in species' national population abundance as a function of national temperature and precipitation measures, the two most extensively measured climatic variables. We used monthly averages in mean temperature and precipitation (Met Office UKCP09 gridded data sets; Perry and Hollis 2005) from across England for birds, butterflies and mammals, and across GB for aphids and moths. For aphid and moth species not recorded in Scotland and/or Wales, climate data were averaged across England or England and Wales as appropriate. We refer to temperature and precipitation on an annual or shorter time-scale as 'weather' and the sustained trend in weather over the entire time series, as 'climate'.

Table 1. Details of surveys used to produce yearly species indices.

| Taxonomic group | No. sites | No. species included | Survey years | Source |
|-----------------|---------------------------------------|------------------------|----------------------------------------------------------|-----------------------------------------------------------------------------|
| Mammals | ~ 1200 for bats; ~ 3000 for others | 16 (10 bats, 6 others) | Bats: 1998 (or 1997)–2011; other mammals: 1995–2011 | <www.bats.org.uk/pages/nbmp.html> <www.bto.org/volunteer-surveys/bbs> |
| Birds | ~ 3000 | 85 | Terrestrial birds 1966–2011; wetland birds: 1980–2011 | <www.bto.org/volunteer-surveys/bbs> <www.bto.org/volunteer-surveys/wbbs> |
| Aphids | 12 | 80 | 1970–2010 | <www.rothamsted.ac.uk/insect-survey/> |
| Butterflies | 1424 | 55 | 1976–2011 | <www.ukbms.org> |
| Moths | 13 | 265 | 1975–2010 | <www.rothamsted.ac.uk/insect-survey/> |

Due to the complexities of summarising multiple correlated climatic changes through time, we used principal components analyses (PCA) to describe annual variation in monthly mean temperatures and monthly total precipitation from 1967 to 2011. This allowed us create models applicable to all species across a wide range of taxa and enabled an objective comparison of climate change impacts between species. This and all other analyses were implemented using R software (R ver. 2.15.2). In order to allow for potential lagged impacts of these variables upon populations (Pearce-Higgins et al. 2010) and potential linkage in the weather between consecutive years, we examined annual index change (year $Y - 1$ to year Y , on a logarithmic scale) in response to mean monthly weather variables from time-windows spanning the 24 months up to the end of the survey period in year Y .

The most appropriate time-windows for summarising weather variables was defined separately for each taxon, based on the timing of surveys, or based on species-specific phenology for taxa monitored continuously throughout the year. For bird and mammal species we used the timing of the surveys to determine which months of weather data to use. Birds and mammals (excluding bats) were surveyed between April and June (inclusive). For these species, two-year time-windows of weather data corresponding to the population index in year Y ran from July in year $Y - 2$ to June in year Y , the latter being the end of the relevant survey period (Fig. 2a). The timings of bat surveys were less consistent. Five species were surveyed using one type of survey (either spring field surveys or winter roost surveys), but population indices for five others were composite values derived from two surveys (Bat Conservation Trust 2014). In each case, the

termination of the last survey period was used to determine the final month of the time-window (Fig. 2b). Moths and winged aphids were monitored continuously throughout the year, and we used species-specific flight periods to define the appropriate final month of the window for weather data (Waring and Townsend 2003) (Fig. 2c). The same approach of selecting species-specific flight periods was also used for butterflies, which were monitored between April and September.

All variables were centred on zero by dividing by their mean value. Temperature variables were then standardised by dividing by the mean standard deviation of all 24 monthly temperature variables, and precipitation variables were likewise scaled to the mean standard deviation of the monthly precipitation variables. We carried out a PCA analysis on these variables for each species, and the resulting PC axes were taken to be the weather variables used for further analysis. For the purposes of further analysis, we focussed on the first four principal components of climate ($PC1:4$). Importantly, due to the differences in the time-windows applied, PCs calculated for one particular species were not directly comparable to those calculated for all other species. Instead, they are used to provide appropriate predictor variables for each species in turn (Fig. 1, step 2). To identify whether the $PC1:4$ s represented trends in temperature and precipitation we examined for each species the mean adjusted R^2 values of models of $PC1:4$ as functions of temperature and precipitation (two-year means).

We also created four detrended weather variables ($PC_{stable}1:4$) for each species to encapsulate the same variation in weather found in $PC1:4$ but with the estimated post-1970s climate change signal removed. These variables were created from the residuals of $PC1:4$ as linear functions of time. Mean values of $PC_{stable}1:4$ were set to equal the means of $PC1:4$ between 1970 and 1979 to remove the post-1970s climate trends. $PC_{stable}1:4$ therefore do not include a long-term trend, but continue to capture annual fluctuations in these variables (Fig. 1, step 5).

Modelling population growth against weather variables

We examined the impact of weather, encapsulated by the weather PCs, on change in species' annual population indices. The change in observed relative population abundance (hereafter simply population growth) of each species was calculated as $\Delta n_{O,Y} = \ln(n_{O,Y}/n_{O,Y-1})$, where $n_{O,Y}$ is the observed annual national population index in year Y of the species in question. Firstly we tested the influence of density dependence on population growth by modelling population growth as a function of the population in the previous year. For 430 species, there was a significant negative relationship between growth and previous population, and a significant positive relationship for only one species. We therefore included a density dependence term, population in the previous year, in the following population models.

Population growth was modelled as a function of the first four principal components (PCs) of the weather variables using a linear model. We modelled each species independently, the number of observations in each model being one

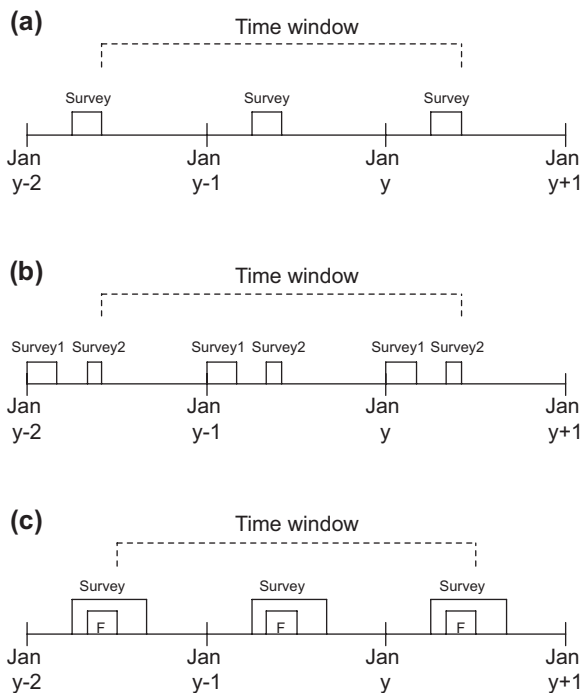


Figure 2. Illustration of how weather windows were selected for species with (a) a single survey period, (b) two survey periods or (c) species with a flight period within a survey period. 'F' indicates a flight period.

less than the length of the national index time series for that species. Population index (log transformed) for the previous year was included as an explanatory variable to account for potential density dependence in the rate of growth (Freckleton et al. 2006). The intercept allows for a constant population growth (thus a linear trend in population abundance) to be attributed to non-climatic factors which reduced the chance of over-attributing population trends to climate change. Thus population change was modelled for each species as:

$$\Delta n_{O,Y} = \alpha + b_0 \ln(n_{O,Y-1}) + b_1 PC1_Y + b_2 PC2_Y + b_3 PC3_Y + b_4 PC4_Y \quad (1)$$

It is likely that some relationships between population change and weather are not linear. To allow for that we also created a second model that replaced *PC3* and *PC4* with quadratic *PC1* and *PC2* variables:

$$\Delta n_{O,Y} = \alpha + b_0 \ln(n_{O,Y-1}) + b_1 PC1_Y + b_2 PC2_Y + b_3 (PC1_Y^2) + b_4 (PC2_Y^2) \quad (2)$$

This model retained the two weather variables that characterised the most annual variation in weather and avoided increasing the number of explanatory variables, which would have been inadvisable given the length of the time series. For each species we selected the model with the lowest AIC value (Fig. 1, step 3).

For six bird species with positive correlations between the previous population size and population growth, previous population was not included in the model as a positive correlation was considered biologically unlikely. Modelling population growth, rather than abundance, is likely to reduce temporal autocorrelation but we checked this by testing for autocorrelation structure in the residuals using Durbin–Watson tests. As there was significant autocorrelation for only 21 of the 501 species, we did not include an autoregressive correlation structure in the models. The R code for this analysis and the following analyses are in Supplementary material Appendix 1 with the necessary data in Appendix 1, Table A1–A5, available at <<https://figshare.com/s/aa407c2c0dd5c200dd40>>.

Impact of climate change on population abundance

We used variance partitioning to determine the contribution of weather variables and non-weather variables (year and previous population) to annual variation in each species' population growth and to identify the unexplained portion of variation (Graham and Edwards 2001). This method identifies the adjusted R^2 of the two groups of variables and variance explained by the combination of the two groups. We present the proportion of variance that can be explained by weather variables, both separately and in combination with other variables (Fig. 1, step 4).

Following Eglington and Pearce-Higgins (2012), models of the effects of weather variables on population growth were used to predict annual population index values starting from the first observed index value. For each species we obtained predictions of population abundance over the years in which

the species was monitored, where predictions were calculated from the species-specific population change model under observed weather conditions (*PC1:4*). In the first year in which the species was monitored we set the population index value to equal 1, the arbitrarily defined first population index value, but thereafter model predictions were used to estimate the population in the previous year (n_{Y-1}) in order to predict population change, rather than using observed data. The model was therefore 'free-running' from year 1, driven by changes in weather variables through time. We then repeated these model predictions but replaced the observed weather variables with the detrended weather variables (*PC_{stable}1:4*), in which the post-1970s climate trends were removed, to predict population trends in the absence of linear climate change. Thus for each species we created a time series of predicted population indices under observed weather conditions (n_M) and under detrended weather conditions (n_S):

$$\Delta n_{M,Y} = \alpha + b \times \ln(n_{M,Y-1}) + f(PC1_Y : PC4_Y) \quad (3)$$

$$\Delta n_{S,Y} = \alpha + b \times \ln(n_{S,Y-1}) + f(PC_{stable}1_Y : PC_{stable}4_Y) \quad (4)$$

The difference between these time series ($n_C = n_M - n_S$) indicated the portion of population change that we could attribute to climate change (Fig. 1, step 6).

Identifying climate-vulnerable species

In order to test our first hypothesis, that climate change has affected the abundance of many British species, we used linear models (LMs) to examine whether observed and predicted species' populations indices from observed or detrended weather variables (log-transformed n_O , n_C and n_S respectively) changed significantly over time. For each species each of these three population indices were regressed independently against calendar year and the resulting slope taken to represent the average annual observed or modelled population change. We refer to these slopes as β_O , β_C , and β_S (e.g. $\ln(n_{O,Y}) = \beta_O \times Y$) respectively, and use these slopes to describe the likely impact that climate change will have had on the abundance of different groups through time (Fig. 1, step 7). Thus, if $\beta_C = \beta_O$ we assume that climate change, as described by the post-1970 trends in temperature and precipitation, has entirely driven the observed trends, whereas if $\beta_S = \beta_O$ population trends are assumed to be unrelated to climate change. To identify whether a significant change in population abundance was likely to be due to climate change for each species, we calculated confidence intervals for $\beta_C = \beta_M - \beta_S \pm SE \times t_{df}(0.975)$ where the degrees of freedom, df , are taken from the regression models fitted to the relative abundance growth rates and the standard error, SE , is calculated in a manner that allows uncertainty in the coefficients of the regression model for growth rate (see Supplementary material Appendix 1, 'Calculation of standard errors of differences' for details). It is worth noting that by climate change, we are specifically referring to linear trends in the climate variables. This reduces the likelihood of inflating the apparent importance of climate change due to the impacts of extreme values towards the start and end of each time series, although means that we are not considering

the potential role of climate change in inflating the degree of stochasticity in the weather variables through time.

We used the slope coefficients of observed population indices (β_O) to separate species into those which have declined, remained stable, or increased in abundance according to whether the slope coefficient was less than -0.035 , between -0.035 and 0.035 or greater than 0.035 . These thresholds were chosen because a slope coefficient of less than -0.035 is equivalent to the 30% decadal decline required for a species to be considered 'vulnerable to extinction' under the IUCN red list criterion A2c (IUCN/SSC 1999). Thus, we identified species in which climate change was the major driver of population change, where β_C was at least ± 0.035 (Fig. 1, step 8).

Impact of climate change across species

To test our second hypothesis that climate change impacts will vary between taxa, we used LMs to determine whether the mean annual population change (β_O , β_C , and β_S) within taxonomic groups (the explanatory factor) differed significantly from zero. This two-step modelling approach was used to account for variation in the number of years species were monitored for. In this analysis the species represent a largely complete set of relatively widespread equitable species. The results for the species are therefore not a sample from the average response across a wider spread of species within the taxa. As all species meeting the distribution criteria are present, including random factors to account for phylogenetic correlation was not necessary here, so each species was treated equally (Fig. 1, step 9).

Our third hypothesis stated that the impact of climate change would vary according to three ecological traits: primary and secondary or higher consumers to test for differences with trophic level; species of conservation concern identified from the Biodiversity Action Plan (BAP) list (JNCC 2007) compared to other species to test for differences with conservation status; and pests compared to non-pest species, to test whether climate change may promote increases in the abundance of agricultural or silvicultural pests (Table 2; Fig. 1, step 9). Species traits were collated from Carter (1984), Robinson (2005), JNCC (2007), van Emden and Harrington (2007), Chinery (2010), Fera (2013), Harrop et al. (2013), Natural England (2013) and RIS (2013). Herbivorous species were classified as primary consumers and all other species, including omnivorous species, were classified as secondary consumers. Insect species were classified as pest species if they cause widespread damage in the UK to livestock, agriculture, horticulture or wildlife. Bird and mammal species were classified as pests

Table 2. Number of species within species-groupings.

| Taxa | Total species | Primary consumers | Species of conservation concern | Pest species |
|-----------|---------------|-------------------|---------------------------------|--------------|
| Mammal | 16 | 5 | 6 | 1 |
| Birds | 85 | 9 | 23 | 7 |
| Aphids | 80 | 80 | 0 | 22 |
| Butterfly | 55 | 55 | 22 | 3 |
| Moth | 265 | 265 | 31 | 32 |

if they can legally be killed without application to preserve public health or safety (Natural England 2013). To test this hypothesis we examined whether the mean annual change in observed and predicted species' populations indices (β_O , β_C , and β_S) differed significantly between ecological groups using linear mixed models (LMMs) with a single two-level explanatory factor (trophic level, conservation status or pest status). In this analysis we used the species for which we had data to generalise across the specified ecological groups as best we could, accepting our species complement was non-random. We therefore included taxonomic group, family and genera as nested random factors to account for phylogenetic correlation.

Results

Variation in weather variables

The first four PCA axes explained between 33.4 and 36.6% of variation in the weather variables depending on species. Across species, the scores for *PC1* varied significantly over years and largely described warming: temperature (two-year means) explained an average of 80.5% of variation in *PC1* scores (adjusted R^2 from model of *PC1* as a linear function of temperature) while precipitation explained only 4.9%. The loadings for *PC2*, *PC3* and *PC4* were not consistent between species and rarely showed long-term trends in the corresponding scores.

Impact of climate change on population growth

For 341 species (68.1%), the linear model (model *a*) had a lower AIC than the quadratic model (model *b*) and therefore more effectively described variation in population change than the quadratic model. The models explained a mean of $38.0 \pm 18.5\%$ (SD) of variance in population growth, of which $11.5 \pm 11.4\%$ was accounted for by the weather variables alone or $9.8 \pm 14.4\%$ including both weather only and combined effects of weather and non-weather effects (there were negative combined effect of weather and non-weather effects, indicating a negligible combined effect).

Across all species, there was no overall trend in abundance (β_O , with taxa, family and genera as grouping factors $= -2.38 \times 10^{-3} \pm 4.01 \times 10^{-3}$ (SE here and elsewhere unless specified), $t = -0.59$, $p = 0.554$), no consistent change in abundance predicted under a stable climate ($\beta_S = -1.73 \times 10^{-3} \pm 1.99 \times 10^{-3}$, $t = -0.87$, $p = 0.388$) and no consistent effect of climate change ($\beta_C = -4.72 \times 10^{-4} \pm 1.85 \times 10^{-3}$, $t = -0.26$, $p = 0.799$) (values of β_O , β_C , β_S , variance explained and variance accounted for by weather variables for all species can be found in the Supplementary material Appendix 1, Table A1).

Although there was no overall consistent direction of population change across species, there was evidence that 296 species (59.1%) showed long-term trends that differed significantly from zero. The models indicated that climate change influenced population trends of 104 species (20.8%), as identified by those in which β_C differs significantly from zero. In both cases, 5% of species may show a false significant

trend using $\alpha = 0.05$. By subtracting possible false positives (5% of 501 = 25.05 species) from species with positive trends, we can be confident that observed and climate trends were significant for at least 111 species (54.1%) and 79 species (15.8%) species respectively.

Identifying climate-vulnerable species

Annual rates of population decline were greater than 3.5% (equivalent to 30% decadal decline) in 80 species (15.97%) and 28 (5.59%) showed equivalent rates of increase. For all species with extreme population trends attributed to climate change we show species-specific population indices, n_O , and climate-components of population indices, n_C , in Supplementary material the Appendix 2, Fig. A1. Of the 80 species with extreme declines (13 birds, three aphids and 64 moths), there was evidence that climate change may have been a major driver for eight species ($\beta_C < -3.5\%$); two birds (*Carduelis cabaret*, *Gallinago gallinago*; Supplementary material Appendix 2, Fig. A1a, b) and six moths (*Brachylomia viminalis*, *Erannis defoliaria*, *Jodis lactearia*, *Melanchnra pisi*, *Operophtera fagata*, *Perizoma didymata*; Supplementary material Appendix 2, Fig. A1c, h). Of the 28 species with extreme population increases (one mammal, three birds, ten aphids and 14 moths) climate change may have been a major driver ($\beta_C > 3.5\%$) for two birds, *Anser anser* and *Branta canadensis*, one moth, *Cosmia affinis*, and the mammal, *Muntiacus reevesi* (Supplementary material Appendix 2, Fig. A1i, l).

Models suggested that climate change may have exerted significant negative pressure on populations of a further two mammal species with stable populations (*Capreolus capreolus*, *Rhinolophus hipposideros*; Supplementary material Appendix 2, Fig. A1m, n) and had a large positive impact on population growth rates of one mammal with a stable population (*Oryctolagus cuniculus*; Supplementary material Appendix 2, Fig. A1o), suggesting that other processes were countering population responses to climate change.

Impact of climate change across species: taxonomic groups

The impacts of climate change varied across the five taxonomic groups. An average population decline of 1.4% annually was

seen in moths (Table 3, β_O , $t = -7.45$, $p < 0.001$; Fig. 3f). The modelled impact of climate change predicted a negative trend equal to 48% of the observed decline that could be attributed to climate change (β_C , $t = -7.79$, $p < 0.001$), whilst the linear trend, density dependence and detrended weather variables combined, accounted for an additional 27.3% of the negative trend (β_S , $t = -4.59$, $p < 0.001$; Fig. 3f). A mean of 12.4% of annual variance in moth population growth rates could be attributed to weather variables; overall the full models explained a mean of 40.7% of annual variance in population change (Table 3).

Conversely, winged aphids increased on average by 0.70% annually (β_O , $t = 2.78$, $p = 0.006$; Fig. 3d) of which 62.7% could be accounted for by climate change (β_C , $t = 3.15$, $p = 0.002$). There was no evidence that detrended weather variables, density dependence and linear population trends combined had a consistent impact on aphid trends (β_S , $t = 0.80$, $p = 0.425$), although our models explained a mean of 49.3% of annual variation in winged aphid population growth of which 5.6% was attributable to the weather variables (Table 3).

Mammal populations did not change consistently over time (β_O , $t = 1.36$, $p = 0.175$; Fig. 3b) or in response to climate change (β_C , $t = 0.17$, $p = 0.867$; Fig. 3b). However, in the absence of post-1970 climate change their populations were predicted to increase (β_S , $t = 2.45$, $p = 0.015$). Weather variables explained a mean of 15.0% of annual variation in population growth rates (higher than all other taxa) out of a total of 39.9% of variation explained (Table 3). We repeated the analysis for bats and other mammals separately, and found that climate change may have had a positive impact on other mammals ($1.13 \times 10^{-2} \pm 5.71 \times 10^{-3}$, $t = 1.98$, $p = 0.048$) and bat populations were predicted to have undergone significant increases in the absence of post-1970s climatic trends ($1.42 \times 10^{-2} \pm 4.29 \times 10^{-3}$, $t = 3.32$, $p < 0.001$).

Across-species bird population trends were inconsistent or largely stable, as were their responses to climate and other factors (Table 3, Fig. 3c). The models accounted for a mean of 17.0% of variance in population change; less than half the variance explained for any other taxa. A mean of 5.1% of annual variation in avian population growth rates could be explained by weather variables, lower than other taxa (Table 3). Butterflies also showed no consistent population trend across species and there was no evidence for overall population changes caused by climate change or other factors

Table 3. Within taxonomic groups the mean annual % change in three population indices \pm standard error are presented. The three population indices are observed (n_O), climate driven (n_C) and non-climate driven (n_S). P-values relate to significance of difference of trends (regression slopes of n_O , n_C and n_S modelled against time) from zero as indicated by linear models of regression slopes against taxa. The % variance explained by the models and % variance explained purely by weather variables are also presented for each taxonomic group. See methods for model details.

| Taxon | % annual observed population growth (n_O) | % annual fitted population growth in response to climate change (n_C) | % annual fitted population growth under stable climate (n_S) | % variance by all variables | % variance by weather variables |
|-------------|---------------------------------------------------|---------------------------------------------------------------------------|------------------------------------------------------------------|-----------------------------|---------------------------------|
| Mammals | $1.04 \times 10^{-2} \pm 7.67 \times 10^{-3}$ | $5.86 \times 10^{-4} \pm 3.51 \times 10^{-3}$ | $8.34 \times 10^{-3} \pm 3.40 \times 10^{-3*}$ | 39.9 | 15.0 |
| Birds | $-4.82 \times 10^{-3} \pm 3.33 \times 10^{-3}$ | $5.33 \times 10^{-4} \pm 1.52 \times 10^{-3}$ | $-2.68 \times 10^{-3} \pm 1.48 \times 10^{-3*}$ | 17.0 | 5.1 |
| Aphids | $6.97 \times 10^{-3} \pm 3.43 \times 10^{-3*}$ | $4.37 \times 10^{-3} \pm 1.57 \times 10^{-3**}$ | $1.22 \times 10^{-3} \pm 1.52 \times 10^{-3}$ | 49.3 | 5.6 |
| Butterflies | $2.52 \times 10^{-4} \pm 4.14 \times 10^{-3}$ | $6.43 \times 10^{-4} \pm 1.89 \times 10^{-3}$ | $-3.25 \times 10^{-4} \pm 1.83 \times 10^{-3}$ | 40.5 | 8.7 |
| Moths | $-1.40 \times 10^{-2} \pm 1.89 \times 10^{-3***}$ | $-6.72 \times 10^{-3} \pm 8.63 \times 10^{-4***}$ | $-3.82 \times 10^{-3} \pm 8.36 \times 10^{-4***}$ | 40.7 | 12.4 |

p-values are: * < 0.1 , ** < 0.05 , *** < 0.001 .

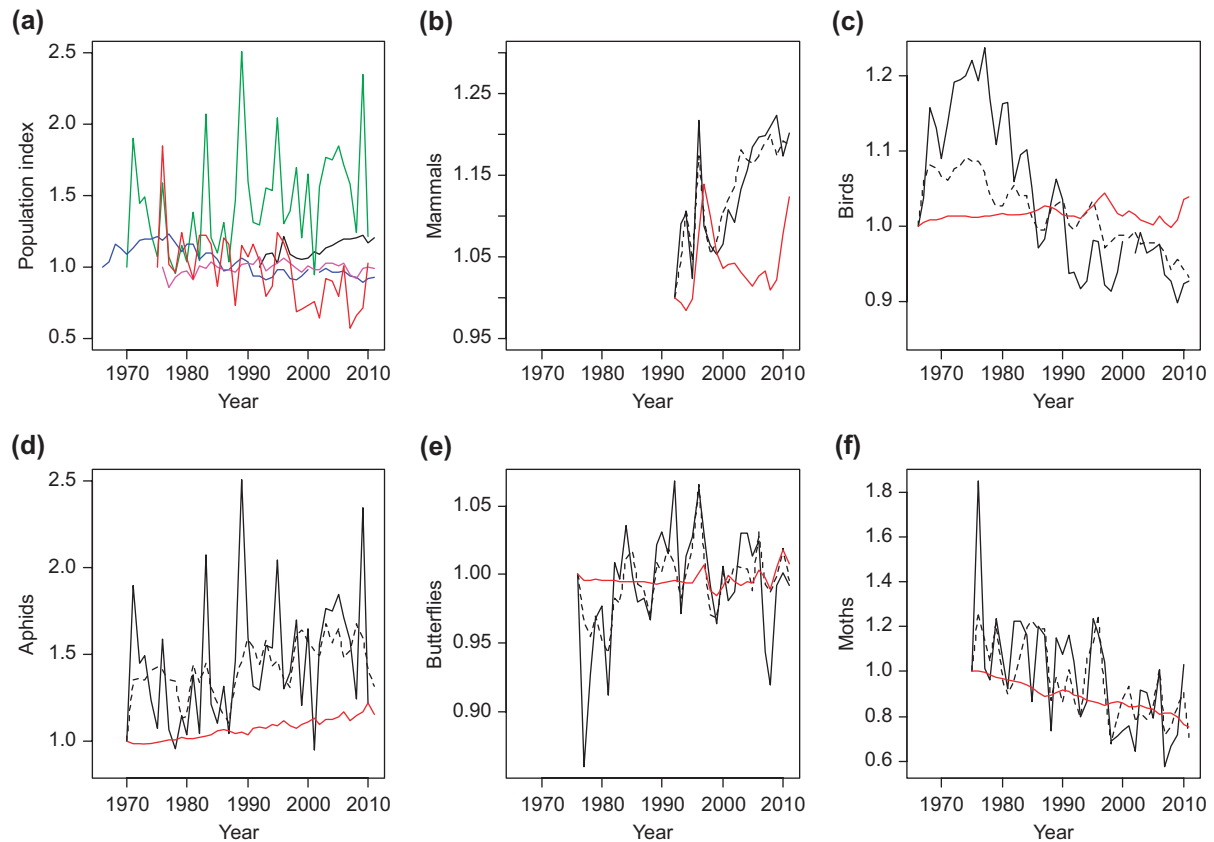


Figure 3. (a) Geometric means of observed population indices (n_O) of mammals (black), birds (blue), aphids (green), butterflies (magenta) and moths (red). (b) Mammal, (c) bird, (d) aphid, (e) butterfly and (f) moth geometric means of observed population indices (n_O ; solid black lines), abundance estimated from free-running models assuming observed weather (n_M ; dashed black lines) and the climate change-driven component of abundance (n_C ; red lines) within each of the taxonomic groups. Note the varying scales on y-axes between taxa. Error bars are not included because of large variation in species' population trends. It is worth noting that the peaks in butterfly and moth abundances in 1976 may reflect the positive effects of an extreme hot summer.

(Table 3, Fig. 3e). The models could explain annual variation in butterfly population growth rates relatively effectively, with a mean of 40.5% of variance explained by the models of which 8.7% was accounted for by weather variables.

Impact of climate change across species: ecological groups

On average population trends of primary consumers were largely stable, whilst those of secondary consumers tended towards decline (β_O , $t = -1.92$, $p = 0.056$; Table 4, Fig. 4a). Secondary consumers were significantly more negatively affected by climate change than primary consumers (β_C : $t = 3.81$, $p < 0.001$; Table 4), although the magnitude of divergence was relatively small, accounting for $< 10\%$ difference in multi-species population trends over 35-yr (Fig. 4a). Species of conservation concern declined on average by 2.6% annually over the period considered compared to the 0.7% mean annual increase of other species (β_O , $t = 8.94$, $p < 0.001$; Fig. 4b). This decline could be attributed to both linear climate change and non-climatic factors (β_C , $t = 4.76$, $p < 0.001$; β_S , $t = 6.55$, $p < 0.001$; Table 4). Pest species population trends did not differ significantly from those of non-pest species (β_O , $t = -1.78$, $p = 0.076$; Fig. 4c), with

similar predicted responses to climate change (β_C , $t = -0.94$, $p = 0.350$) and other factors (β_S , $t = -1.02$, $p = 0.311$; Table 4). There was no significant difference in the contribution of weather variables to population growth rates between groups (Table 4), although the models explained a lower proportion of variance in growth rates for species of conservation concern than for other non-BAP species (difference = -0.066 ± 0.020 , $t = -3.35$, $p = 0.001$).

Discussion

Across a wide range of taxa, we found evidence that climate change since the 1970s has influenced the long term population trends of 15.8% of species. In this large-scale analysis of 501 species we also found that declines in eight of 80 species vulnerable to extinction ($> 30\%$ population decline per decade), were consistent with attribution to linear changes in climate, largely rising temperatures. Thus climate change may already be significantly adding to the threat of extinction for some species in Great Britain. More broadly, our models indicate that climate change may account for much of the documented large-scale decline across moth species (Conrad et al. 2006) and the increase in the abundance of winged aphids (Bell et al. 2015) across Great Britain. There

Table 4. Species were split three ecological groups: trophic level (primary or secondary consumer), conservation concern (species of conservation concern or not) and pest status (pest or not). Within each of these ecological groupings the mean annual % change in three population indices are presented. The three population indices are observed (n_O), climate driven (n_C) and non-climate driven (n_S). P-values relate to significance of difference of trends (regression slopes of n_O , n_C and n_S modelled against time) between groups as indicated by linear mixed models of regression slopes against ecological group. The % variance explained by the models and % variance explained purely by weather variables are also presented for each ecological group.

| Group | % annual observed population growth (n_O) | % annual fitted population growth in response to climate change (n_C) | % annual fitted population growth under stable mean climate (n_S) | % variance by all variables | % variance by weather variables |
|---------------------------------|------------------------------------------------|---------------------------------------------------------------------------|-----------------------------------------------------------------------|-----------------------------|---------------------------------|
| Primary consumers | $4.18 \times 10^{-3} \pm 6.39 \times 10^{-3}$ | $5.10 \times 10^{-3} \pm 4.17 \times 10^{-3}$ | $-4.35 \times 10^{-4} \pm 2.69 \times 10^{-3}$ | 42.0 | 10.5 |
| Secondary consumers | $-1.16 \times 10^{-2} \pm 8.04 \times 10^{-3}$ | $-1.06 \times 10^{-2} \pm 4.88 \times 10^{-3}$ | $-3.05 \times 10^{-3} \pm 2.38 \times 10^{-3}$ | 19.3 | 6.1 |
| Species of conservation concern | $-2.57 \times 10^{-2} \pm 5.81 \times 10^{-3}$ | $-6.60 \times 10^{-3} \pm 2.46 \times 10^{-3}$ | $-9.17 \times 10^{-3} \pm 2.27 \times 10^{-3}$ | 28.9 | 10.9 |
| Other species | $6.73 \times 10^{-3} \pm 5.20 \times 10^{-3}$ | $1.75 \times 10^{-3} \pm 2.13 \times 10^{-3}$ | $1.22 \times 10^{-3} \pm 1.99 \times 10^{-3}$ | 39.8** | 9.6 |
| Non-pest species | $-1.88 \times 10^{-3} \pm 3.83 \times 10^{-3}$ | $-2.90 \times 10^{-4} \pm 1.81 \times 10^{-3}$ | $-1.41 \times 10^{-3} \pm 2.08 \times 10^{-3}$ | 37.1 | 9.7 |
| Pest species | $-9.36 \times 10^{-3} \pm 5.27 \times 10^{-3}$ | $-2.09 \times 10^{-3} \pm 2.46 \times 10^{-3}$ | $-3.21 \times 10^{-3} \pm 2.59 \times 10^{-3}$ | 44.3 | 10.6 |

p-values are: * < 0.1, ** < 0.05, *** < 0.001.

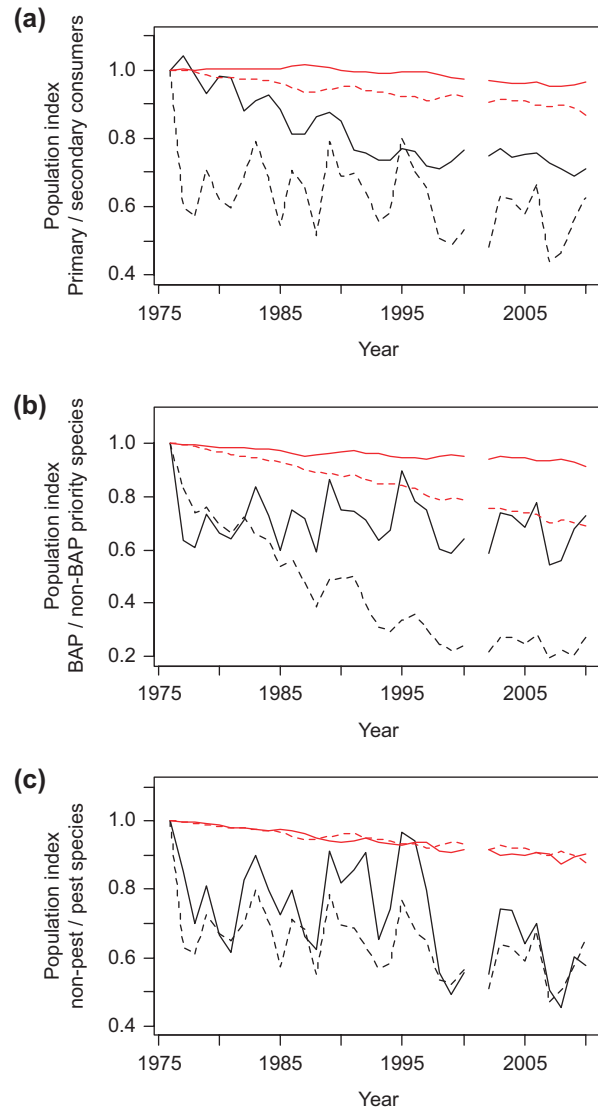


Figure 4. Geometric means of observed population indices (n_O ; black lines, solid and dashed) and climate-driven abundance (n_C ; red lines, solid and dashed). Solid lines show indices of (a) secondary consumers, (b) species of no conservation concern, (c) pest species. Dashed lines show indices of (a) primary consumers, (b) species of conservation concern, (c) non-pest species. Only species monitored from 1975–2010 (excluding 2001 because of foot-and-mouth disease) were included in graphs to make values comparable within groups. Error bars are not included because of large variation in species' population trends.

has been considerable research into climate change impacts on species distribution, phenology and physiology across large spatial scales (Walther et al. 2002, Parmesan and Yohe 2003, Menzel et al. 2006, Thackeray et al. 2010) but many fewer studies address the climate change impacts on species abundance, and abundance monitoring schemes for different taxa over similar geographical areas are rare. This study provides one of the most widespread assessments of climate change impacts on species abundance, in a consistent manner across taxa, so far conducted. This information is important for predicting local or global extinction risks, and assessing impacts on ecological communities.

Importantly, climate change is likely to have driven significant changes in the overall abundance of some key groups. We identified moths as particularly vulnerable to climate change and declining moth populations are of significant conservation concern (Conrad et al. 2006, Fox et al. 2013). Approximately half of the 1.4% annual decline in moth populations was attributable to linear trends in climate (Table 3, Fig. 3f) but suggest that the remainder may have occurred in the absence of post-1970 climatic trends, for example due to land-use change (Fox 2014). Climate change has previously been linked to declines in one UK moth species, *Arctia caja* (Conrad et al. 2002), a finding supported by our results (Supplementary material Appendix 2, Fig. A1p). This response may be common across many moth species, potentially caused by decreases in survival and egg production, increased rates of larval parasitism or increased asynchrony between moth hatching and bud burst of host plants (Virtanen and Neuvonen 1999, Visser and Holleman 2001). Conversely, butterflies did not show consistent population trends or consistent responses to climate trends (Table 3, Fig. 3e) and no butterfly species were predicted to have had extreme population declines or increases due to climate change. Previous research has attributed localised population extinctions (Franco et al. 2006), increases (Roy et al. 2001) and community change (Devictor et al. 2012) to climate change but found spatial and temporal inconsistency in these patterns (Isaac et al. 2011). For many butterfly species, population abundance correlates with summer temperatures (Roy et al. 2001) while extreme weather events such as droughts (Oliver et al. 2015a, b) and warm winters can also cause declines (Dennis and Sparks 2007). Further research is required into why population declines and likely climate change impacts are much greater in moths than butterflies.

Almost two-thirds of the 0.7% annual aphid population increase was consistent with a potential positive impact of climate trends, while there was no evidence that aphid populations would have increased significantly in the absence of post-1970s climate change (Table 3, Fig. 3d). A likely mechanism underpinning these changes is rising temperatures allowing more generations per year (Yamamura and Kiritani 1998, Bell et al. 2015). Previous studies have also identified climate change as the major driver of population and phenological change, compared to other variables such as fertilisation (Newman 2005) and land-use (Harrington et al. 2007). However, it should be noted that the climate-related trend was small compared to the amplitude of annual fluctuations in aphid populations (Bell et al. 2015). Importantly, an increase in the annual total of winged aphids may not mean more pest problems because it is the timing of those aphids relative to the crop that is key; aphids generally have a greater impact in spring than in autumn, although there are exceptions depending on crop (van Emden and Harrington 2007).

Our mammal data cover a range of readily detectable bats and other mammals (Bat Conservation Trust 2014, Wright et al. 2014), including increasing deer (Newson et al. 2012) and bat (Barlow et al. 2015) species. We found little evidence of consistent population growth or climate change impacts, despite weather explaining more of the variance in population growth than for any other taxa. There was some

inconclusive evidence that climate change had a negative impact on some bat species that was inconsistent with current understanding of UK bat species' sensitivity to climate change. As the mammal data covered relatively short time periods (13–16 yr) we cannot rule out type I and type II errors.

Bird populations also did not change consistently across species and there was little evidence that climate change had a consistent effect on overall abundance (Table 3). Instead we found that rapid population declines in some species (in particular *Carduelis cabaret* and *Gallinago gallinago*; Supplementary material Appendix 2, Fig. A1a, b) and rapid increases in others (*Anser anser* and *Branta canadensis*; Supplementary material Appendix 2, Fig. A1i, j) were consistent with a potential climate change attribution. Identifying climate change as the likely driver of *Carduelis cabaret* declines is a useful result as habitat loss has been previously identified as a contributing factor but unlikely to be the major driver (Burgess et al. 2015). Our models predicted positive impacts of climate change on four passerines known to be sensitive to severe winter weather (*Erithacus rubecula*, *Prunella modularis*, *Troglodytes troglodytes* and *Turdus philomelos*; Robinson et al. 2007; Supplementary material Appendix 2, Fig. A1q, t), providing support for their validity. Furthermore, a similar modelling exercise for farmland birds in which non-climatic factors were explicitly modelled, identified a similarly weak effect of climate change in driving large-scale bird population declines (Eglington and Pearce-Higgins 2012). Although climate change is likely to have driven variation in population trends between species, leading to changes in the composition of communities (Gregory et al. 2009, Jiguet et al. 2010, Davey et al. 2012, Johnston et al. 2013, Morrison et al. 2013, Pearce-Higgins et al. 2015), overall our models suggest that large-scale changes in bird populations, such as the decline in farmland birds from the mid-1970s to mid-1990s, are largely unrelated to climate change (Eglington and Pearce-Higgins 2012).

We also examined the climate change impacts across taxa on species groups which are most likely to be of policy-interest from an ecosystem function, ecosystem service or conservation perspective. Firstly, we considered the potential for consistent differential effects of climate change between trophic levels (Tylianakis et al. 2008) and found that climate change may have had a consistently more negative impact on secondary consumers than on primary consumers (Table 4, Fig. 4). Previous studies have highlighted faster rates of phenological change (Thackeray et al. 2010) and range change (Devictor et al. 2012) in primary consumers; our study further emphasises the potential for climate change to disrupt species' interactions across trophic levels, for example through cascading effects on species at different trophic levels (Ockendon et al. 2014), although the magnitude of effect was relatively small. As species within a taxonomic group are generally also of the same trophic level, examining species from a wider range of taxa would be beneficial to confirm the generality of this finding. As expected, species of conservation concern showed significantly more negative population trends than other species, which our models suggested is consistent with differential population responses to temperature and precipitation. Most UK BAP species were designated between 1995 and 1999, based largely on

population trends over the previous 25 yr. A warming signal in the UK was apparent by the mid-1990s but it does not include the major warming period seen in the 2000s so it is likely that BAP species designations were based on declines driven mainly by habitat loss. This highlights the possibility that some of the decline in species of conservation concern may have been exacerbated by recent climate change, and could support the hypothesis that non-climate related threats make species more vulnerable to climate change (Heller and Zavaleta 2009, Hodgson et al. 2009, Green and Pearce-Higgins 2010). We found no evidence that climatic conditions were more likely to have benefitted pest species, contrary to suggestions by Cock et al. (2013).

As with most correlative studies, these conclusions are dependent upon our ability to disentangle the impacts of climate change from other factors, which we have not measured. Although there is considerable debate about the potential to attribute ecological changes to climate change (Parmesan 2011, Parmesan et al. 2013), we have attempted to do so by using inter-annual variation in abundance to relate population growth to weather variables. The potential risk of over-fitting when modelling the impact of multiple climatic variables was reduced through the use of multivariate techniques to simplify the climatic changes into four predictor variables. This is likely to have produced conservative estimates of climate change impacts because the method does not account for extreme weather events which are likely to have a disproportionate impact on species (Easterling et al. 2000), and will not identify climate impacts where species respond to weather during a very narrow seasonal window of sensitivity.

We attempted to carry out an unbiased cross-taxa comparison of climate change impacts. However, differences between the methods used to monitor taxonomic groups could impact the results. For example, aphids and moths were monitored at only 12 and 13 sites respectively, compared to over 1000 sites for other taxa. National population indices for these taxa could therefore be influenced by site-specific events, making national-scale conclusions less reliable. To enable cross-taxa comparisons without biases towards ecologically well-known species and taxa, we did not include non-climatic factors in our models. However, by including a density-dependent growth factor and an intercept, non-stable population trends resulting from non-climatic factors were taken into account. The degree to which the omission of other drivers is likely to have affected our conclusions is dependent on the extent to which these non-climatic factors correlate with trends in the weather variables measured. In most cases, where we have been able to compare our conclusions for particular well-studied species, our results correspond to the results of that other research. Evidence presented by correlative studies such as this can never be as robust as evidence from experimental studies. However, complex species interactions underpin most climate change impacts on populations (Ockendon et al. 2014) making temporal correlative studies one of the best available tools. Results from these should be supported by evidence of, and lead to further research on, mechanisms that drive population trends.

To conclude, we provide the most comprehensive quantitative assessment of the impacts of climate change upon cross-taxa national biodiversity trends to date, using a

method that allows impacts to be compared between taxa. This has shown that climate change has already had a detectable impact on British terrestrial biodiversity, causing declines in the abundance of many moth species but increases in winged aphids. The magnitude of such impacts was sufficient to increase vulnerability to extinction, based on IUCN red-list criteria, for a small, but notable, proportion of species, including two bird and six moth species, whilst large population increases in four species, including two that are non-native (*Branta canadensis*, *Muntingia reevesi*) were consistent with large positive climate change impacts. We also provide empirical support for the impacts of climate change being most detrimental for species of conservation concern and add to the evidence that climate change may disrupt ecological communities through differential impacts on different trophic levels. However, for many species, population trends could not be attributed to climate change, and other factors such as land-use and management changes may have driven these changes (Eglington and Pearce-Higgins 2012, Vaughan and Ormerod 2014). The ability to compare climate change impacts between species and taxa is vital to inform conservation resource allocation decisions, and the modelling approach used, particularly with the inclusion of non-linear relationships between weather and populations, would enable some prediction of future climate change impacts (Dornelas et al. 2013). Continued large-scale monitoring schemes such as those analysed here are essential to validate our models and to track future population changes in response to projected climatic changes.

Acknowledgements – We would like to dedicate this paper to our co-author Kate Barlow who sadly died 23 November 2015 and will be missed. This work was funded jointly by Defra, Natural Resources Wales (NRW), Natural England (NE), Scottish Natural Heritage (SNH) and the Joint Nature Conservation Committee (JNCC) (WC1037). We would like to thank members of the project Steering Group for input and advice on the methodology and comments to an earlier draft of the manuscript. The Rothamsted Insect Survey is a BBSRC-supported National Capability. The National Bat Monitoring Programme (NBMP) is run by the Bat Conservation Trust, in partnership with the Joint Nature Conservation Committee, and supported and steered by Natural England, Natural Resources Wales, Northern Ireland Environment Agency and Scottish Natural Heritage. The NBMP is indebted to all volunteers who contribute data to the programme. We are very grateful to all the volunteers who participate in the BBS and the UKBMS. The BBS is a partnership between the BTO, Joint Nature Conservation Committee (on behalf of Countryside Council of Wales, Natural England, Council for Nature Conservation and Countryside and Scottish Natural Heritage) and Royal Society for Protection of Birds. The UKBMS is operated by the Centre for Ecology and Hydrology, Butterfly Conservation and funded by a consortium of government agencies. We would also like to thank Katherine Boughey at BCT for her input to the manuscript.

References

- Araújo, M. B. and Luoto, M. 2007. The importance of biotic interactions for modelling species distributions under climate change. – *Global Ecol. Biogeogr.* 16: 743–753.
- Barlow, K. E. et al. 2015. Citizen science reveals trends in bat populations: the National Bat Monitoring Programme in Great Britain. – *Biol. Conserv.* 182: 14–26.

- Bat Conservation Trust 2014. The National Bat Monitoring Programme. Annual report 2013. – Bat Conservation Trust, London, <www.bats.org.uk>.
- Bell, J. R. et al. 2015. Long-term phenological trends, species accumulation rates, aphid traits and climate: five decades of change in migrating aphids. – *J. Anim. Ecol.* 84: 21–34.
- Bellard, C. et al. 2012. Impacts of climate change on the future of biodiversity. – *Ecol. Lett.* 15: 365–377.
- Bowler, D. E. et al. 2015. A cross-taxon analysis of the impact of climate change on abundance trends in central Europe. – *Biol. Conserv.* 187: 41–51.
- Burgess, M. D. et al. 2015. The impact of changing habitat availability on population trends of woodland birds associated with early successional plantation woodland. – *Bird Study* 62: 39–55.
- Burns, F. et al. 2016. Agricultural management and climatic change are the major drivers of biodiversity change in the UK. – *PLoS One* 11: e0151595.
- Butchart, S. H. M. et al. 2010. Global biodiversity: indicators of recent declines. – *Science* 328: 1164–1168.
- Cannon, R. J. C. 1998. The implications of predicted climate change for insect pests in the UK, with emphasis on non-indigenous species. – *Global Change Biol.* 4: 785–796.
- Carter, D. J. 1984. *Pest Lepidoptera of Europe: with special reference to the British Isles.* – Kluwer Academic Publishers.
- Ceballos, G. et al. 2015. Accelerated modern human-induced species losses: entering the sixth mass extinction. – *Sci. Adv.* 1: e1400253.
- Chen, I. C. et al. 2011. Rapid range shifts of species associated with high levels of climate warming. – *Science* 333: 1024–1026.
- Chinery, M. 2010. *Garden pests of Britain and Europe.* – A and C Black.
- Cock, M. J. et al. 2013. The implications of climate change for positive contributions of invertebrates to world agriculture. – *CAB Rev.* 8: 1–48.
- Conrad, K. F. et al. 2002. Long-term decline in abundance and distribution of the garden tiger moth (*Arctia caja*) in Great Britain. – *Biol. Conserv.* 106: 329–337.
- Conrad, K. F. et al. 2006. Rapid declines of common, widespread British moths provide evidence of an insect biodiversity crisis. – *Biol. Conserv.* 132: 279–291.
- Davey, C. M. et al. 2012. Rise of the generalists: evidence for climate driven homogenisation in avian communities. – *Global Ecol. Biogeogr.* 21: 568–578.
- Dennis, R. L. and Sparks, T. H. 2007. Climate signals are reflected in an 89 year series of British Lepidoptera records. – *Eur. J. Entomol.* 104: 763.
- Devictor, V. et al. 2012. Differences in the climatic debts of birds and butterflies at a continental scale. – *Nat. Clim. Change* 2: 121–124.
- Dornelas, M. et al. 2013. Quantifying temporal change in biodiversity: challenges and opportunities. – *Proc. R. Soc. B* 280: 20121931.
- Easterling, D. R. et al. 2000. Climate extremes: observations, modelling, and impacts. – *Science* 289: 2068–2074.
- Eglinton, S. M. and Pearce-Higgins, J. W. 2012. Disentangling the relative importance of changes in climate and land-use intensity in driving recent bird population trends. – *PLoS One* 7: e30407.
- Fera 2013. Plant pest and disease factsheets [online]. – Food and Environment Research Agency, <www.fera.defra.gov.uk/plants/publications/plantPestDiseaseFactsheets.cfm> accessed 18 July 2013.
- Foden, W. B. et al. 2013. Identifying the world's most climate change vulnerable species: a systematic trait-based assessment of all birds, amphibians and corals. – *PLoS One* 8: e65427.
- Fox, R. 2014. Long-term changes to the frequency of occurrence of British moths are consistent with opposing and synergistic effects of climate and land-use changes. – *J. Appl. Ecol.* 51: 949–957.
- Fox, R. et al. 2013. The state of Britain's larger moths 2013. – Butterfly Conservation and Rothamsted Research, Wareham, Dorset, UK.
- Franco, A. M. A. et al. 2006. Impacts of climate warming and habitat loss on extinctions at species' low-latitude range boundaries. – *Global Change Biol.* 12: 1545–1553.
- Freckleton, R. P. et al. 2006. Census error and the detection of density dependence. – *J. Anim. Ecol.* 75: 837–851.
- Freeman, S. N. and Newson, S. E. 2008. On a log-linear approach to detecting ecological interactions in monitored populations. – *Ibis* 150: 250–258.
- Freeman, S. N. et al. 2007. Modelling population changes using data from different surveys: the Common Birds Census and the Breeding Bird Survey. – *Bird Study* 54: 61–72.
- Graham, M. H. and Edwards, M. S. 2001. Statistical significance versus fit: estimating the importance of individual factors in ecological analysis of variance. – *Oikos* 93: 505–513.
- Green, R. E. and Pearce-Higgins, J. W. 2010. Species management in the face of a changing climate. Species management: challenges and solutions for the 21st century. – In: Baxter, J. M. and Galbraith, C. A. (eds), *Scottish Natural Heritage. TSO Scotland, Edinburgh*, pp. 517–536.
- Gregory, R. et al. 2009. An indicator of the impact of climatic change on European bird populations. – *PLoS One* 4: e4678.
- Harrington, R. et al. 2007. Environmental change and the phenology of European aphids. – *Global Change Biol.* 13: 1550–1564.
- Harrop, A. H. J. et al. 2013. The British list: a checklist of birds of Britain, 8th ed. – *Ibis* 155: 635–676.
- Heller, N. E. and Zavaleta, E. S. 2009. Biodiversity management in the face of climate change: a review of 22 years of recommendations. – *Biol. Conserv.* 142: 14–32.
- Hickling, R. et al. 2006. The distributions of a wide range of taxonomic groups are expanding polewards. – *Global Change Biol.* 12: 450–455.
- Hodgson, J. A. et al. 2009. Climate change, connectivity and conservation decision making: back to basics. – *J. Appl. Ecol.* 46: 964–969.
- Isaac, N. J. B. et al. 2011. Butterfly abundance in a warming climate: patterns in space and time are not congruent. – *J. Insect Conserv.* 15: 233–240.
- IUCN/SSC Criteria Review Working Group 1999. IUCN Red List criteria review provisional report: draft of the proposed changes and recommendations. – *Species* 31–32: 43–57.
- Jiguet, F. et al. 2010. Population trends of European common birds are predicted by characteristics of their climatic niche. – *Global Change Biol.* 16: 497–505.
- JNCC 2007. UK BAP priority Species [online]. – Joint Nature Conservation Committee, <<http://jncc.defra.gov.uk/page-5717>> accessed 18 July 2013.
- Johnston, A. et al. 2013. Observed and predicted effects of climate change on species abundance in protected areas. – *Nat. Clim. Change* 3: 1055–1061.
- Jørgensen, P. S. et al. 2016. Continent-scale global change attribution in European birds-combining annual and decadal time scales. – *Global Change Biol.* 22: 530–543.
- Menzel, A. et al. 2006. European phenological response to climate change matches the warming pattern. – *Global Change Biol.* 12: 1969–1976.
- Morrison, C. A. et al. 2013. Recent population declines in Afro-Palaearctic migratory birds: the influence of breeding and non-breeding seasons. – *Divers. Distrib.* 19: 1051–1058.
- Natural England 2013. LICENCE (general) to kill or take certain wild birds to prevent serious damage or disease. – WML – GL04, Wildlife and Countryside Act 1981.

- Newman, J. A. 2005. Climate change and the fate of cereal aphids in southern Britain. – *Global Change Biol.* 11: 940–944.
- Newson, S. E. et al. 2012. Modelling large-scale relationships between changes in woodland deer and bird populations. – *J. Appl. Ecol.* 49: 278–286.
- Ockendon, N. et al. 2014. Mechanisms underpinning climatic impacts on natural populations: altered species interactions are more important than direct effects. – *Global Change Biol.* 20: 2221–2229.
- Oliver, T. H. et al. 2015a. Declining resilience of ecosystem functions under biodiversity loss. – *Nat. Commun.* 6.
- Oliver, T. H. et al. 2015b. Interacting effects of climate change and habitat fragmentation on drought-sensitive butterflies. – *Nat. Clim. Change* 5: 941–945.
- Parmesan, C. 2011. Overstretching attribution. – *Nat. Clim. Change* 1: 2–4.
- Parmesan, C. and Yohe, G. A. 2003. Globally coherent fingerprint of climate change impacts across natural systems. – *Nature* 421: 37–42.
- Parmesan, C. et al. 2013. Beyond climate change attribution in conservation and ecological research. – *Ecol. Lett.* 16: 58–71.
- Pearce-Higgins, J. W. et al. 2010. Impacts of climate on prey abundance account for fluctuations in a population of a northern wader at the southern edge of its range. – *Global Change Biol.* 16: 12–23.
- Pearce-Higgins, J. W. et al. 2015. Drivers of climate change impacts on bird communities. – *J. Anim. Ecol.* 84: 943–954.
- Peres-Neto, P. R. et al. 2003. Giving meaningful interpretation to ordination axes: assessing loading significance in principal component analysis. – *Ecology* 84: 2347–2363.
- Perry, M. and Hollis, D. 2005. The generation of monthly gridded datasets for a range of climatic variables over the UK. – *Int. J. Climatol.* 25: 1041–1054.
- RIS 2013. Aphid bulletin archive 2013 number 1: 22 April–28 April [online]. – Rothamstead Insect Survey, <www.rothamsted.ac.uk/insect-survey/STAphidBulletinArchive-Year=2013.html> accessed 18 July 2013.
- Robinson, R. A. 2005. BirdFacts: species profiles of birds occurring in Britain and Ireland. – BTO Research Report, 407.
- Robinson, R. A. et al. 2007. Weather-dependent survival: implications of climate change for passerine population processes. – *Ibis* 149: 357–364.
- Roy, D. B. et al. 2001. Butterfly numbers and weather: predicting historical trends in abundance and the future effects of climate change. – *J. Anim. Ecol.* 70: 201–217.
- Rushing, C. S. et al. 2016. Quantifying drivers of population dynamics for a migratory bird throughout the annual cycle. – *Proc. R. Soc. B* 283: 20152846.
- ter Braak, C. J. F. et al. 1994. Analysis of monitoring data with many missing values: which method? – In: Hagemeyer, E. J. M. and Verstrael, T. J. (eds), *Distribution, monitoring and ecological aspects*. Proceedings of the 12th International Conference of IBCC and EOAC, Noordwijkerhout, the Netherlands, pp. 663–673.
- Thackeray, S. J. et al. 2010. Trophic level imbalances in rates of phenological change for marine, freshwater and terrestrial environments. – *Global Change Biol.* 16: 3304–3313.
- Thomas, C. D. et al. 2004. Extinction risk from climate change. – *Nature* 427: 145–148.
- Tylianakis, J. M. et al. 2008. Global change and species interactions in terrestrial ecosystems. – *Ecol. Lett.* 11: 1351–1363.
- van Emden, H. F. and Harrington, R. (eds) 2007. *Aphids as crop pests*. – CAB International.
- Vaughan, I. P. and Ormerod, S. J. 2014. Linking interdecadal changes in British river ecosystems to water quality and climate dynamics. – *Global Change Biol.* 20: 2725–2740.
- Virtanen, T. and Neuvonen, S. 1999. Performance of moth larvae on birch in relation to altitude, climate, host quality and parasitoids. – *Oecologia* 120: 92–101.
- Visser, M. E. and Holleman, L. J. M. 2001. Warmer springs disrupt the synchrony of oak and winter moth phenology. – *Proc. R. Soc. B* 268: 289–294.
- Voigt, W. et al. 2003. Trophic levels are differentially sensitive to climate. – *Ecology* 84: 2444–2453.
- Walther, G.-R. et al. 2002. Ecological responses to recent climate change. – *Nature* 416: 389–395.
- Waring, P. and Townsend, M. C. 2003. *Field guide to the moths of Great Britain and Ireland*. – British Wildlife Publishing.
- Warren, M. S. et al. 2001. Rapid responses of British butterflies to opposing forces of climate and habitat change. – *Nature* 414: 65–69.
- Willis, S. G. et al. 2009. A review of analytical techniques for assessing the impacts of climate change on wildlife populations. – Report to the Biological Impacts of Climate Change Observation Network (BICCO-Net) Steering Group
- Wright, L. J. et al. 2014. The value of a random sampling design for annual monitoring of national populations of larger British terrestrial mammals. – *Eur. J. Wildl. Res.* 60: 213–221.
- Yamamura, K. and Kiritani, K. 1998. A simple method to estimate the potential increase in the number of generations under global warming in temperate zones. – *Appl. Entomol. Zool.* 33: 289–298.

Supplementary material (Appendix ECOG-02411 at <www.ecography.org/appendix/ecog-02411>). Appendix 1–2.