

### **Appendix 3: A cross-taxa appraisal of the impact of climate change on species' population size.**

#### **Abstract**

Climate change has had well-documented impacts on the distribution, phenology and physiology of species across most taxa. However, the direct impact of climate change on population abundance, and therefore extinction risk, has been harder to assess. As a consequence research has often focussed on a single species or taxon; here we carry out the most comprehensive multi-taxa comparison to date that shows that climate change is likely to have influenced population trends in 64% of species. We summarised the key axes of British weather variation over the last 50 years and then modelled population growth of over 500 animal species against these axes. National population indices of mammal, bird, aphid, butterfly and moth species were obtained from taxon-specific time series that began between 1966 and 1998 and continued to 2010 or 2011. Moths were particularly negatively impacted by climate change with 9% undergoing severe climate-driven declines in abundance (>3% decline per year). Conversely, the mean impact of climate change on aphid populations was positive. Population trends in mammals, birds and butterflies showed inconsistent or largely insubstantial responses to climate change. Severe population declines in species of conservation concern were a function of both weather (responsible for 0.6% annual decline) and other factors (responsible for 1.5% annual decline), while differential impacts of climate change between trophic levels (0.4% annual climate-driven decline in primary consumers compared to 0.1% in secondary consumers) signal the potential for future ecosystem disruptions as a result of climate change. Population increases in invasive non-native species were consistent with them being driven by climate change. Our results quantify the conservation implications of climate change that have occurred over recent decades, and highlight the potential for future change to increase the abundance of some invasive and aphid pest species, with likely economic consequences, but contribute to the extinction risk of others.

#### **Introduction**

Global biodiversity is under threat from a range of different drivers (Butchart *et al.*, 2010). During the course of this century, climate change is projected to have an increasingly detrimental impact on the long-term persistence of many species (Thomas *et al.*, 2004; Bellard *et al.*, 2012). Whilst impacts of climate change on the distribution, phenology and physiology of many species are already well documented (e.g. Walther *et al.*, 2002; Parmesan & Yohe, 2003; Menzel *et al.*, 2006; Thackeray *et al.*, 2010), ultimately it will be changes in the abundance of species which directly indicate extinction risk. Such processes are therefore fundamental to understanding the consequences of climate change for species, communities and ecosystems. However, many fewer examples of climate-related changes in population abundance have been documented, and have yet to be widely examined and generalised. With increasing recognition of the importance of species interactions in influencing species' responses to climate change (Tylianakis *et al.*, 2008; Van der Putten *et al.*, 2010; Cahill *et al.*, 2013), there is an urgent need to quantify the extent to which climate change may already be driving population trends, and how those responses may differ between taxa. If such differences exist, they may represent an early warning sign of potentially disruptive impacts of climate change on ecosystem functioning. It is not only important to understand these responses for the purposes of ecological science and biodiversity conservation, but also because they may have significant

implications for the delivery of ecosystem services, or impact on species of economic importance. In order to examine these issues, we carry out what we believe to be the most comprehensive multi-taxon comparison to date of the effect of climate change on species' population sizes.

There are a number of analytical challenges to examining the effect of climate change on abundance across multiple taxa because of complex biotic and abiotic interactions (Walther *et al.*, 2002; Araújo & Luoto, 2007); populations may therefore be impacted by multiple weather variables that would require extensive species-specific ecological knowledge to predict. Potential mechanisms of climate-driven changes in abundances include increased access to food in warmer winters (Robinson *et al.*, 2007), reduced food availability caused by phenological mismatch between predators and prey (Both *et al.*, 2006; Thackeray *et al.*, 2010), changes in predator or prey populations (Frederiksen *et al.*, 2006; Pearce-Higgins *et al.*, 2010) and increased competition between species as a result of differential shifts in distributions (Devictor *et al.*, 2012; Hof *et al.*, 2012). What few data exist suggest that disrupted interactions between species may be more important than direct physiological limitations (Cahill *et al.*, 2013, Ockendon *et al.*, 2014). As a result species will respond to a wide variety of climate variables with potential time lags between the weather events and population response.

The weather and, through time, climate change, can be described by multiple inter-related and correlated variables. Developed in response to the problems of analysing such multivariate datasets, ordination techniques can be used to identify and simplify the main trends hidden within a complex and correlated dataset into a few variables that describe much of the variation (Peres-Neto *et al.*, 2003). As a result, they have wide potential applicability for describing the impacts of climate change on species populations (e.g. Voigt *et al.*, 2003). Additionally, where there is substantial annual weather variation this method does not rely on spatial coverage across each species' climatic range, something that is required for many previous multi-species assessments of climate change impacts (Gregory *et al.*, 2009; Devictor *et al.*, 2012). This has enabled us to extend the assessment of climate change impacts to taxa such as moths and aphids.

This paper describes a standardized assessment of the effect of climate change on over 500 British species across five contrasting taxonomic groups (butterflies, moths, aphids, birds and mammals). We used ordination techniques to summarise the main patterns of weather variation that have occurred in Britain over forty six years, and general linear modelling to examine the component of species' national population growth due to climate change. Importantly, we identified the extent to which climate change impacts differed between taxonomic groups, and the extent to which variation between species may signal the potential for future ecological disruption in response to climate change. Specifically we tested the following key hypotheses.

1. Climate change has affected national population abundance of a large number of species in Britain.
2. The impact of climate change will vary between species according to the following species attributes:
  - a. Trophic level, signalling potential future disruption of ecological networks (Tylianakis *et al.*, 2008).
  - b. Conservation status, with specialist 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 & Zavaleta, 2009; Green & Pearce-Higgins, 2010; Davey *et al.*, 2012).

- c. Native status, as the expansion of non-native species may be facilitated by climate change (Dukes & Mooney, 1999).
- d. Pest status, as populations of pest species of economic importance may be more adaptable to climate change (Cannon, 1998).

## Materials and methods

### *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 1,396 species. Given the difficulties of modelling change from zero counts, 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).

The geographical and spatial distribution of survey locations varied between taxonomic groups, creating the need for bespoke models for each dataset 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. As spatial variation in population trends could result in biased indices of change at the British level (Freeman *et al.*, 2007), for these groups, population indices were produced only for England. The only exception to this was Scotch argus (*Erebia aethiops*) for which we produced a British index because of its rarity in England. Conversely, data for aphids and moths were from fewer but more widely dispersed sites across Wales, England and Scotland (12 and 13 trap sites respectively). In order to maximise our sample size, we used all of these data. In practice, the likely magnitude of geographical bias is small, as shown by the similarity of these results for birds and those derived by repeating the analysis using data from across Britain (SI Table 1 & 2). The timing of surveys also differed between taxa, necessitating taxon-specific weather variables as described below.

For each species under consideration, national (English or British) population indices ( $n_{0,y}$  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 & Newson, 2008; Willis *et al.*, 2009), taking the index value on the (natural) log scale of the first year as 0. Following existing protocols for bats (Barlow *et al.*, *in prep*), additional methodological covariates known to strongly influence their abundance (survey weather, type of bat detector, timing of survey) were included in these models. For clarity here and elsewhere, we do not include a subscript for species, although modelling of indices always takes 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, the two most extensively measured climatic

variables in the UK, and did not consider other aspects of climate, such as snow cover in our analyses. We used monthly averages in mean temperature and precipitation (Met Office UKCP09 gridded datasets; Perry & Hollis, 2005) from across England for birds, butterflies and mammals, and across Britain for aphids and moths. For aphid and moth species not recorded in Scotland, climate data were averaged across England and Wales only. We refer to temperature and precipitation on an annual or shorter time-scale as “weather” and the sustained changes in weather, i.e. weather over the entire time-series, as “climate”.

Due to the complexities of summarising multiple correlated climatic changes through time, we used Principal Components Analyses (PCA) to summarise annual variation in monthly mean temperatures and precipitation from 1967 to 2011. This and all other analyses were implemented using R software (R Version 2.15.2 ©2012). In order to allow for potential lagged impacts of these variables upon populations (e.g. 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) in response to mean monthly weather variables from windows spanning the 24 months up to the time of the survey in year Y.

Since the timing of surveys was species-specific, the most appropriate time-window for summarising weather variables was defined separately for each species. 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, the two-year time windows of climate 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. 1a). The timings of bat surveys were less consistent. Five species were surveyed during a single period (either spring field surveys or winter roost surveys), but population indices for five others were composite values derived from two surveys (Bat Conservation Trust, 2013). In each case, the termination of the last survey period was used to determine the final month of the time-window (Fig. 1b). Moths and 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 & Townsend, 2003) (Fig. 1c). The same approach of selecting species-specific flight periods was also used for butterflies, which were monitored between April and September, with the exception of late-flying butterflies active after September, in which case September was taken to be the final month of the time window from which weather data were used. The weather during adult Lepidoptera activity periods may spuriously appear to influence population abundance because of impacts on activity; the inclusion of two years of weather into the models is likely to minimise the impact of this on the results. However, we demonstrate that the inclusion of weather during Lepidoptera adult activity periods does not influence the outcomes by repeating analyses described below but with the Lepidoptera weather windows shifted backwards by two months to exclude adult activity periods (SI Table 1).

Weather variables were scaled to the mean standard deviation of temperature or precipitation variables as appropriate. For the purposes of further analysis, we focussed on the first four PCA axes of climate. Importantly, due to the differences in the time-windows applied, PCAs calculated for one particular species are not directly comparable to those calculated for all other species. Instead, they are used to provide the most appropriate predictor variables for each species in turn.

### *Modelling population growth against weather variables*

We examined the impact of weather, encapsulated by the climatic PCA axes, on annual change in species' annual population indices, an evaluation of population growth. Thus, the observed relative population growth (hereafter simply population growth) of each species was calculated as  $\Delta n_{O,Y} = \log(n_{O,Y} / n_{O,Y-1})$ , where  $n_{O,Y}$  is the observed annual national population index in year Y of the species in question. Population growth was modelled as a function of the first four PCAs of the weather variables using General Least Squares (GLS) estimation approach. We modelled each species independently, the number of observations in each model being one 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). However, in nine cases positive correlations between the previous population index and population growth were found: in these cases the previous population was not included as the positive correlations were considered biologically implausible. To account further for the fact that potential responses in consecutive years may be more similar to each other than expected by chance we included a first order autoregressive correlation structure in the models. Thus the fitted values from the full model were calculated:

$$\Delta n_{F,Y} = \alpha + b_0 \ln(n_{O,Y-1}) + b_1 \text{PCA1}_Y + b_2 \text{PCA2}_Y + b_3 \text{PCA3}_Y + b_4 \text{PCA4}_Y$$

We tested the predictive ability of this modelling approach by estimating the models using available data from 1966 – 2000 and examining the size of residuals from predicted growth from 2002 – 2003 to 2009 – 2010 using observed previous population. The residuals were scaled to species' population growth variability by dividing the sum of residuals by the sum of squared growth anomaly. These were compared (using paired *t*-tests) with predictions made from (a) null models containing only  $n_{Y-1}$  and (b) simple climate models containing  $n_{Sy-1}$  and mean annual temperature (T):

$$(a) \Delta n_{\text{null},Y} = \alpha_{\text{null}} + b_{0\text{null}} \ln(n_{O,Y-1})$$

$$(b) \Delta n_{\text{simple},Y} = \alpha_{\text{simple}} + b_{0\text{simple}} \ln(n_{O,Y-1}) + b_{1\text{simple}} T$$

The parameter estimates from the full model ( $\Delta n_{F,Y}$ ) were the basis for all the estimates described below of population change under a stable and changing climate.

### *Using model coefficients to examine the impact of climate change on population abundance*

Following Eglington & Pearce-Higgins (2012), models of the effects of weather variables on population growth were used to predict annual population index. Modelled population growth in the first year was applied to the initial index value ( $n_{M,Y=1} = \Delta n_{F,Y=1} \cdot n_{O,Y=0}$ ), but thereafter applied to subsequent predictions of the index in the previous year ( $n_{M,Y} = \Delta n_{M,Y} \cdot n_{M,Y-1}$ ), rather than observed index. The effect of density dependence was also calculated from the predicted index in the previous year, rather than from the observed index.

Three separate modelled time series of annual population growth were produced for each species, using the parameter estimates from the species-specific models of population growth, weather and previous population. The first time-series ( $\Delta n_M$ ) was the predicted values from the full model and

included all parameter estimates from this model (the intercept  $\alpha$ ; the density dependence coefficient  $b_0$ ; and all coefficients associated with the four PCA axes  $b_1 - b_4$ ), differing from  $\Delta n_F$  in the use of  $n_{M,Y-1}$  to account for density dependence rather than  $n_{O,Y-1}$ . A second ( $\Delta n_N$ ) also used parameter estimates from the full model but excluded the parameter estimates associated with the four PCA axes (i.e. estimating population growth when all monthly temperature and precipitation values are at their mean, hence PCA values = 0) and indicated population growth in the absence of climate change, and a third ( $\Delta n_C$ ) described the contribution that could be attributed to climate change from the difference between the first and second time series. This estimation of  $\Delta n_C$  (instead of estimating  $\Delta n_C$  directly from the four weather coefficients) allowed us to identify the component of population growth driven by climate, taking density dependent growth into account.

$$\Delta n_{M,Y} = \alpha + b_0 \ln(n_{M,Y-1}) + b_1 \text{PCA1}_Y + b_2 \text{PCA2}_Y + b_3 \text{PCA3}_Y + b_4 \text{PCA4}_Y$$

$$\Delta n_{N,Y} = \alpha + b_0 \ln(n_{N,Y-1})$$

$$\Delta n_{C,Y} = \Delta n_{M,Y} - \Delta n_{N,Y}$$

We used the observed population growth and the latter two of these time-series of population growth ( $\Delta n_O$ ,  $\Delta n_C$  and  $\Delta n_N$ ) to calculate an annual population abundance index for each species ( $n_O$ ,  $n_C$  &  $n_N$  respectively). Thus for each species  $n_M$  is the population index predicted by our model,  $n_N$  is the population index predicted by our model under a stable climate and  $n_C$  is the climate-driven component of the population index.

### *Trends in observed and modelled population abundance*

In order to test our hypotheses outlined in the introduction we first used linear mixed models (LMMs) to examine whether observed and predicted population indices (log-transformed  $n_O$ ,  $n_C$  and  $n_N$ ) across all species within taxonomic groups changed significantly over time. We modelled each taxon separately and tested for significant changes in indices over time with species included as a random factor and a first order autoregressive correlation structure to account for the correlation between successive years within species.

We also examined the fit of the full models ( $\Delta n_F$ ) created with all available data using a standard calculation of adjusted  $r^2$  where  $n$  is the number of observation and  $p$  is the number of parameters in the model:

$$r^2 = 1 - \left( \frac{SS[\Delta n_F - \Delta n_O]}{SS_{total}} \right); \text{ adjusted } r^2 = 1 - (1 - r^2) \left( \frac{n - 1}{n - p - 1} \right)$$

We determined the proportion of the adjusted  $r^2$  value explained by the weather variables by multiplying the adjusted  $r^2$  by ratio between  $r^2$  recalculated with the intercept ( $\alpha$ ) and the density dependence term ( $b_0 \ln(n_{O,Y-1})$ ) subtracted from  $\Delta n_F$ ; and  $r^2$ :

$$\text{weather portion of adjusted } r^2 = \text{adjusted } r^2 \left( \frac{1 - \left( \frac{SS[\Delta n_F - \alpha - b_0 \ln(n_{O,Y-1}) - \Delta n_O]}{SS_{total}} \right)}{r^2} \right)$$

We repeated these analyses of variation in  $n_o$ ,  $n_c$  and  $n_N$  in relation to different ecological traits in order to test our key hypotheses. The four ecological factors we considered were 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; native compared to non-native invasive species to test whether climate change may be facilitating the expansion of non-native species; 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). It should be noted that there were only 11 non-native species numerous enough to be included in this analysis and that this category may be biased towards successfully expanding species. Species traits were collated from Carter (1984), Robinson (2005), (JNCC, 2007), van Emden & Harrington (2007), Chinery (2010), NNS (2011), RIS (2013), Natural England (2013), Fera (2013) and Harrop *et al.* (2013). Four different fixed effect models were fitted to each of  $\log(n_o)$ ,  $\log(n_c)$  and  $\log(n_N)$ , each with an intercept and a single two-level fixed effect for one of the three ecological grouping factors considered. Where before each taxonomic groups was modelled independently so no interaction between year and taxonomic groups was required, here we included an interaction between year and ecological factor so as to examine the difference in population trends between the factor levels. Taxonomic group, family, genera and species were included as nested random factors and again a first order autoregressive correlation structure was used. All dependent variables conformed to assumptions of normality and therefore models were conducted using a normal error distribution.

We also repeated the analysis of variation in model fit (log-transformed to normalise distribution) in relation to trophic level, conservation status, native and pest status, as outlined above. Given the non-random distribution of these species groups across taxa, these models were conducted within a linear mixed model (LMM) framework, with broad taxonomic group, family and genera as nested random effects.

### *Identifying climate-vulnerable species*

We used the observed and climate-driven population indices ( $n_o$  and  $n_c$ ) to separate species into those which have declined, been stable, or increased in abundance, and identified the species in which these changes could be attributed to climate change. We calculated the mean annual change in the population index as the regression coefficient of a linear model of population index against time. Non-stable trends showed a greater than 30% decline or increase in 10 years, this decline being equivalent to “vulnerable to extinction” under the IUCN red list criterion A2c (IUCN/SSC, 1999).

## **Results**

### *Variation in climate variables*

The sum of the first four PCA axes explained between 33.4% and 36.6% of variation in weather variables depending on taxonomic group. In all taxa, PCA1 varied significantly with time and described warming (the mean distance of monthly temperature along PCA1 was  $0.15 \pm 0.005$

compared to  $0.02 \pm 0.017$  for monthly precipitation; Fig. 2). The remaining PCA axes were not consistent between taxonomic groups and rarely showed long-term trends.

### *Impact of climate change on population trends of different taxa*

As there were multiple tests carried out for this section, we consider results where  $P > 0.01$  as insignificant. Our model framework had significant predictive ability across species: sums of squared residuals from our models were significantly smaller than those from null models (mean difference between residuals =  $-0.100 \pm 0.054$ ,  $t = -3.68$ ,  $P < 0.001$ ) and simple climate models: residuals =  $-0.153 \pm 0.051$ ,  $t = -6.05$ ,  $P < 0.001$ ). Overall species' populations declined over time (mean slope of  $n_o$  over time  $\pm$  standard error =  $-5.86 \times 10^{-3} \pm 7.01 \times 10^{-4}$ ,  $t = -8.37$ ,  $P < 0.001$ ), largely driven by climate change (mean slope of  $n_c$  over time =  $-3.39 \times 10^{-3} \pm 3.14 \times 10^{-3}$ ,  $t = -10.79$ ,  $P < 0.001$ ), while there was an inconsistent impact of non-climatic changes (mean slope of  $n_N$  over time =  $8.50 \times 10^{-4} \pm 8.99 \times 10^{-4}$ ,  $t = 0.95$ ,  $P = 0.344$ ) (Fig 3a).

A mean decline of 1.2% annually were seen in moths (Table 3,  $n_o$ ,  $t = -10.19$ ,  $P < 0.001$ ; Fig. 3f) for which about 75% of the decline was driven by climate change ( $n_c$ ,  $t = -17.86$ ,  $P < 0.001$ ) rather than other factors ( $n_N$ ,  $t = -1.03$ ,  $P = 0.302$ ; Fig. 3f). Moths were also the taxa with the most variation explained by weather: a median of 6.3% of the annual variation in population growth of moths was explained by their response to weather (adjusted model fit from weather variables only, Table 3).

Conversely, aphid populations increased by 0.69% annually ( $n_o$ ,  $t = 4.43$ ,  $P < 0.001$ ; Fig. 3d) of which 60% of aphid increases could be accounted for by climate change ( $n_c$ ,  $t = 5.40$ ,  $P < 0.001$ ) and 30% by other factors ( $n_N$ ,  $t = 4.13$ ,  $P < 0.001$ ). Although aphids showed an increasing trend over time, they also showed large non-weather driven annual fluctuations, hence only 0.5% of annual variation could be attributable to weather (adjusted model fit from weather variables only, Table 3). When the impact of density dependent growth was included in the assessment of model fit (adjusted  $r^2$ ), 44.1% of annual variation in growth could be explained, more than for any other taxa (Table 3).

Mammal populations increased by 1.0% annually ( $n_o$ ,  $t = 4.11$ ,  $P < 0.001$ ; Fig. 3b), largely due to non-climatic factors ( $n_N$ ,  $t = 2.78$ ,  $P = 0.006$ ; Fig. 3b). Their response to climate was inconsistent ( $n_c$ ,  $t = 0.58$ ,  $P = 0.563$ ) and weather had no influence on the annual population fluctuations of most species (adjusted model fit from weather variables only, Table 3). Trends and response to climate change were less consistent or largely stable for birds and butterflies (Table 3, Fig. 3e). However, while weather accounted for 2% of annual variation in bird population growth, it accounted a relatively high proportion of variation for butterflies (4.6%).

Although the median impact of weather on annual population fluctuations was relatively low, the impact of weather variables was meaningfully high ( $> 10\%$ ) for many species across all taxa. The proportion of species for which weather variables explained more than 10% of annual population fluctuation differed between taxa (chi-sq = 21.54,  $P < 0.001$ ), with 18.75% of mammals, 21.18% of birds, 16.25% of aphids, 32.73% of butterflies and 39.25% of moths.

### *Variation in the impact of climate change between different species groups*



Population trends of secondary consumers were not significantly different from those of primary consumers (Table 4,  $n_o$ ,  $t = -1.54$ ,  $P = 0.124$ ; Fig. 4a), However, climate change was more detrimental to primary consumers than secondary consumers ( $n_c$ ,  $t = 3.79$ ,  $P < 0.001$ ; Table 4, Fig. 4). 4.5% of annual fluctuations in population growth in primary consumers could be attributed to weather variables while only 1.6% could for secondary consumers (Table 4,  $t = 0.84$ ,  $P = 0.403$ ). Density dependence and linear non-weather driven growth accounted respectively for a further 29.2% and 9.9% of inter-annual fluctuations in growth for primary and secondary consumers.

Species of conservation concern declined by 3.25% annually over the period considered compared to the 0.07% annual decline of other species ( $n_o$ ,  $t = -18.60$ ,  $P < 0.001$ ; Fig. 4b). Roughly 45% of the decline in these species appears related to factors other than climate ( $n_N$ ,  $t = -7.09$ ,  $P < 0.001$ ), while climate change appears to contribute to under 20% of these species' declines ( $n_c$ ,  $t = -4.54$ ,  $P < 0.001$ , Table 4, Fig. 4). The models of weather, density dependence and linear change could not explain variation in inter-annual variation in growth for species of conservation concern as well as for other species (16.8% and 29.8% respectively,  $t = 4.05$ ,  $P < 0.001$ ) yet a similar portion was explained by weather (3.8% and 4.0% respectively,  $t = 1.35$ ,  $P = 0.180$ ).

Non-native species showed population increases of 1.5% per year that contrasted with declines seen in native species (Table 4,  $n_o$ ,  $t = 4.56$ ,  $P < 0.001$ ; Fig. 4c). 40% of this increase was driven by a positive effect of climate change on non-native population trends ( $n_c$ ,  $t = 5.56$ ,  $P < 0.001$ ), while the average impact of non-climatic factors was high but not consistently higher than for native species ( $n_N$ ,  $t = 1.85$ ,  $P = 0.065$ ; Fig. 4). Despite the effect of climate change on non-native species the weather variables had little power to explain inter-annual variation in non-native species' population growth. However, this was not significantly lower than the percentage explained by weather variables in native species (-0.2% and 4.1% respectively,  $t = -1.95$ ,  $P = 0.052$ ), reflecting the small sample of non-native species. There was also no significant difference in the percentage of inter-annual variation in growth between non-native and native species explained by all variables (29.8% and 16.8% respectively,  $t = 0.06$ ,  $P = 0.953$ ).

There was no statistical evidence for a difference in the mean population trend of pest species relative to other species ( $n_o$ ,  $t = -0.338$ ,  $P = 0.734$ ; Fig. 4d), or in their response to climate change ( $n_c$ ,  $t = -0.43$ ,  $P = 0.665$ ) or other factors (Table 4;  $n_N$ ,  $t = 0.20$ ,  $P = 0.843$ ). Similar percentages of interannual fluctuations were explained by weather variables for pest species and others (3.6% and 7.0% respectively;  $t = 0.59$ ,  $P = 0.553$ ) and by all variables (28.4% and 41.7% respectively,  $t = 1.48$ ,  $P = 0.140$ ).

### *Identifying climate-vulnerable species*

A total of 63.5% of species showed evidence for changes in climatic suitability through time, as measured by a significant trend in  $n_c$ . This did not differ significantly between taxa: significant changes in climatic suitability were seen in 62.5% of mammals, 75.3% of birds, 57.5% of aphids, 60.0% of butterflies and 62.3% of moths ( $\text{chi-sq} = 6.81$ ,  $P = 0.146$ ). In 32.3% of species observed rates of population change were greater than the 30% change in ten years threshold; 16.8% with population growth and 15.6% with population decline. A total of eight species (one mammal population consisting of two difficult to distinguish bat species, one bird, three aphids and two

moths) showed evidence for large increases that could be attributed to climate change, whilst large declines in 18 moth species matched the expectation from the climate models ( $n_c$ ) (Table 5).

## Discussion

In this study we have carried out what is currently the most wide-ranging assessment of climate change impacts on British terrestrial animals. We divide population trends into the climate-driven component and the component that would have been seen under a stable climate. These assessments are clearly influenced by our definition of a stable climate; here we defined it as the mean monthly weather from 1966 to 2011. Our models suggest that long-term population trends of 63.5% of species from a wide range of taxa were significantly influenced by climate change, driven largely by rising temperatures. Our results indicated both high-level population changes across individual taxa, reflecting policy concerns associated with large-scale biodiversity declines within the UK and globally (Butchart *et al.*, 2010; Burns *et al.*, 2013); and species-level population changes in response to climate change which could cause significant changes in species composition within taxa, and potentially drive some species towards extinction. Our results provide clear evidence that climate change is differentially impacting taxa and species within taxa, altering community composition (Davey *et al.*, 2011; Devictor *et al.*, 2012). Further research into the impact of these community changes on ecosystem function and vulnerability is of high importance (Bellard *et al.*, 2012). However, the impacts of climate change, although significant and important, should not be overstated. Other drivers of change appear to have also been important (compare  $n_c$  with  $n_N$ ) and of the 78 species undergoing large population declines (>30% population decline in 10 years), for only 18 were projected climate change impacts of a similar magnitude (Table 5).

We modelled population growth against four variables summarising weather variation. This broad summarization meant that for many of the 501 species weather variables had little power to explain inter-annual population fluctuations. However, they accounted for more than 10% of variation in population growth for 31% of species. This varied between 16%, 19% and 21% in aphids, mammals and birds to 33% and 39% in butterflies and moths. These small impacts on annual population fluctuations lead to significant long-term trends: we found climate-driven population declines in moths and increases in aphids. Eglinton & Pearce-Higgins (2012) similarly found that land-use models accounting for similar portions of variation in population growth closely described observed population trends of farmland birds through time.

Declining moth populations are of significant conservation concern, particularly in southern Britain (Conrad *et al.*, 2006). Our results attribute approximately 75% of their annual 1.2% annual decline to climate change (Table 3, Fig. 3f). They appear more impacted by climate than any other taxa, particularly as their annual population fluctuations were also better modelled by weather than other taxa (6.3% of variation explained by weather variables). Although climate change has been previously proposed as causing declines in one UK moth species, particularly in the south of England (Conrad *et al.*, 2002, 2006), this is the first time that the vulnerability of this group to climate change has been demonstrated more broadly. A number of potential mechanisms for this have been proposed, and include decreases in survival and egg production, increased rates of larval parasitism and increased asynchrony between moth hatching and bud burst of host plants (Virtanen & Neuvonen, 1999; Visser & Holleman, 2001). However, more research is required for a wide range of species to investigate this fully.

Over half of the 0.7% annual aphid population increase could be attributed to climate change despite linear non-weather terms and density dependence accounting for all but 1% of the model fit (Table 3, Fig. 3d). This is because the climate models fail to account for strong inter-annual fluctuations in abundance (Fig. 3d) but do contribute significantly to the long-term trend. One possible mechanism underpinning these changes is rising temperatures allowing more generations per year (Yamamura & Kiritani, 1998). Newman (2005) and Harrington *et al.* (2007) found that climate change had a far greater impact on aphid abundance and phenology than other variables such as fertilization and land-use. However, as with moths, there is little literature on the response of individual aphid populations to climate change and most literature thus far has focussed only on advancing phenology (Zhou *et al.*, 1995; Harrington *et al.*, 2007). There could be large-scale economic consequences due to potential future aphid population increases as aphids are significant crop pests and vectors of crop diseases (van Emden & Harrington, 2007).

Bird populations did not change consistently between species and there was little evidence that climate change or linearly changing non-climate factors had a consistent (Table 3). Previous work has demonstrated significant bird community changes driven by recent warming in the UK (Davey *et al.* 2012, Johnston *et al.* 2013) and across Europe (Gregory *et al.*, 2009, Devictor *et al.*, 2012), with increases in southern, warm-associated species relative to northern species (Jiguet *et al.*, 2010). Many migrant bird species have declined in the south of Britain but remained stable further north (Morrison *et al.*, 2013) while winter warming benefits resident species (Robinson *et al.*, 2007) potentially creating conflicting climate change impacts. Land-use change has been the main driver of changes in farmland bird populations during this period (Eglington & Pearce-Higgins, 2012), which is reflected in the strong decline in the bird population index from the mid-1970s to mid-1990s (Fig. 3c), but may not be well represented by a variable that changes linearly over time. Some caution is therefore required when using these results to attribute population changes to non-climate factors as any land-use changes that do not change linearly through time could be underestimated.

We also found mammal populations to be increasing. Our mammal data cover a range of readily detectable British mammals (Wright *et al.*, 2014) and bats (Bat Conservation Trust, 2013), including increasing deer (Newson *et al.*, 2012) and bat (Barlow *et al.*, *in prep*) species. We found little evidence of climate change impacts and instead the increases in mammal species appeared related to other factors. The lack of climate impact could reflect the shorter time period covered by available population indices (Table 3, Fig. 3). Rebelo *et al.* (2010) found that the projected impact of climate change on bats was largely insubstantial on a 20-30 year time-scale, but considerable if a longer time-scale was considered. Using bat population indices created from multiple survey types may also lower the chance of picking up climate impacts (Barlow *et al.*, *in prep*).

Butterflies did not show strongly consistent population trends or modelled trends in response to climate change (Table 3, Fig. 3), despite 60% showing significant climate-driven trends. Annual butterfly population fluctuations were almost as closely linked to weather as moth populations but unlike moths, climate change did not lead to a consistent response among butterfly species (Isaac *et al.*, 2011). No butterfly species were predicted to have had extreme population declines or increases due to climate change, despite previous research attributing both localised population extinctions (Franco *et al.*, 2006), increases (Roy *et al.*, 2001) and community change (Devictor *et al.*, 2012) to climate change (Table 5). Although climate change has differentially affected individual butterfly species, impacts have not yet had a consistent impact upon overall butterfly abundance and further

research is required into why climate has had a much more consistently detrimental impact on moths compared to butterflies.

In this paper, we have also examined the community changes across taxa which are most likely to be of policy-interest from an ecosystem function, ecosystem service or conservation perspective, and the extent to which they may be related to climate change. Firstly, we considered the potential for consistent differential effects of climate change between trophic levels (Tylianakis *et al.*, 2008). We found climate change was associated with more negative population impacts upon primary consumers than secondary consumers (Table 4, Fig. 4). Previous studies have highlighted slower rates of phenological change (Thackeray *et al.*, 2010) and range change (Devictor *et al.*, 2012) in secondary consumers; our study further emphasises the potential for climate change to disrupt species' interactions across trophic levels. Species of conservation concern exhibited the expected decline in abundance through time, which probably largely reflects the classification of species as being of conservation concern during the early years of the time-series analysed here. However, we found that a component of these population declines was consistent with an expected deterioration in climate suitability as modelled by annual variation in population growth as a function of temperature and precipitation. This highlights the possibility that some of the decline in species of conservation concern may have been exacerbated by recent climate change, and suggests a potential synergistic impact of non-climate related threats and climate change (Heller & Zavaleta, 2009; Hodgson *et al.*, 2009; Green & Pearce-Higgins, 2010).

It has been suggested that climate change may facilitate increases in the abundance of non-native over native species because of their greater adaptability (Dukes & Mooney, 1999; Davidson *et al.*, 2011), and similarly promote increases in pest species of economic importance (Cock *et al.*, 2013). We found that climatic conditions were more likely to have benefitted non-natives, particularly *Muntiacus reevesi*, *Oryctolagus cuniculus* and *Branta canadensis*, over native species. However, given our limited data of only 11 non-native species (Table 1), which will be biased towards successful non-natives by data availability, this effect may not be causal, and further research is required to assess the importance of climate change in driving population increases in non-native species. Population trends in pest species (i.e. species with a high economic impact) differed with respect to native status and taxon: for example, both of the pest species showing large climate-driven population increases were non-natives (*Oryctolagus cuniculus* and *Branta canadensis*) whilst all four pest species showing large climate-driven declines were moths. Thus, climate change may further promote range expansion in non-native pest species, but have little consistent impact on trends of native species (Cannon, 1998).

Our results are dependent upon our ability to disentangle the impacts of climate change from other factors. Although there is considerable debate about the potential to attribute ecological changes to climate change (Parmesan *et al.*, 2011, 2013), we have attempted to do so by using inter-annual variation in abundance to effectively relate population growth to weather variables. Given that other ecological changes are likely to have also affected population growth (e.g. Eglington & Pearce-Higgins, 2012), and may also be correlated with climatic change, it was important to reduce the risk of Type I error in our models of population growth by accounting for temporal autocorrelation and including a constant of population growth to account for additional non-climatic trends. The potential risk of over-fitting is likely to have been offset by the use of multivariate techniques to simplify the climatic changes into four predictor variables. This may have produced Type II errors,

under-estimating climate change impacts in the case of species which respond to very specific climatic changes, for example changes in temperature or precipitation during a very narrow window of sensitivity. This may partly account for the relatively limited explanatory power of our models when modelling population growth (Table 3), although this is also likely to be a function of strong inter-annual fluctuations being apparent in many taxa, for example due to strong density-dependent processes accounted for by the full models which had much greater ability to describe annual population growth. Despite these limitations, our climate models produced results which, where available, were supported by other detailed studies. Thus the position of the garden tiger moth *Arctia caja* on the PCA axes were indicator of negative effects of December to March temperature, and January precipitation, supporting previous studies suggesting this species has declined in response to warm wet winter and spring weather (Conrad *et al.*, 2002). Anticipated positive effects of climate change upon both *Melanargia galathea* and *Polyommatus icarus* (Roy *et al.*, 2001) are supported by positive modelled trends from the climate models. Four passerines sensitive to severe winter weather (*Troglodytes troglodytes*, *Erithacus rubecula*, *Prunella modularis* and *Turdus philomelos*; Robinson *et al.*, 2007), showed strong positive responses to winter temperature, and a higher proportion of variation explained by weather variables ( $r^2 = 0.13 - 0.40$ ) than the mean across all bird species (Table 3).

To conclude, we provide the most comprehensive quantitative assessment of the impacts of climate change upon cross-taxa biodiversity trends to date. Climate change is likely to have detrimentally affected many moth species but benefited most aphid species. 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 UK moth species. While climate change had significant impacts on many mammal, bird and butterfly species, there was variation within these taxa as to whether climate change was beneficial or detrimental. Our results also provide empirical support for the impacts of climate change being most detrimental for species of conservation concern and were consistent with the hypothesis that they may benefit invasive non-native species (Dukes & Mooney, 1999; Heller & Zavaleta, 2009). Our results also signal potential disruption of ecological networks as climate-driven declines in primary consumers become more apparent. However, our results also suggested that much of observed biodiversity changes do not appear to have been caused by climate change, and therefore other factors such as land-use and management changes may have driven these changes (e.g. Eglinton & Pearce-Higgins, 2012; Vaughan & Ormerod, 2014). Climate change has already had a detectable impact on UK terrestrial biodiversity. More in-depth modelling of the relationship between abundance indices and weather would be beneficial to elucidate mechanisms, indicate factors that could mitigate climate change impacts and enhance vulnerability predictions. Continued large-scale monitoring schemes such as those analysed here are essential to track potential future changes in response to what are projected to be much greater climatic changes.

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## References

- Araújo MB, Luoto M (2007) The importance of biotic interactions for modelling species distributions under climate change. *Global Ecology and Biogeography*, **16**, 743–753.
- Barlow K, Briggs P, Haysom K, *et al.* (*in prep*) Citizen science reveals trends in bat populations: the National Bat Monitoring Programme in Great Britain
- Bat Conservation Trust (2013) *The National Bat Monitoring Programme. Annual Report 2012*. Bat Conservation Trust, London. ([www.bats.org.uk](http://www.bats.org.uk))
- Bellard C, Bertelsmeier C, Leadley P, Thuiller W, Courchamp F (2012) Impacts of climate change on the future of biodiversity. *Ecology Letters*, **15**, 365–377.
- Both C, Bouwhuis S, Lessells CM, Visser ME (2006) Climate change and population declines in a long-distance migratory bird. *Nature*, **441**, 81–83.
- Burns F, Eaton MA, Gregory RD, Al Fulaij N, August T, Biggs J, ... & Wynde R (2013) State of nature.
- Butchart SHM, Walpole M, Collen B *et al.* (2010) Global Biodiversity: Indicators of Recent Declines. *Science*, **328**, 1164–1168.
- Cahill AE, Aiello-Lammens ME, Fisher-Reid MC *et al.* (2013) How does climate change cause extinction? *Proceedings of the Royal Society B: Biological Sciences*, **280**.
- Cannon, RJC (1998) The implications of predicted climate change for insect pests in the UK, with emphasis on non-indigenous species. *Global Change Biology*, **4**, 785–796.
- Carter DJ (1984) *Pest Lepidoptera of Europe: with special reference to the British Isles*. Kluwer Academic Publishers, Lancaster, England.
- Chinery M (2010) *Garden pests of Britain and Europe*. A & C Black, London.
- Cock MJ, Biesmeijer JC, Cannon RJ *et al.* (2013) The implications of climate change for positive contributions of invertebrates to world agriculture. *CAB Reviews*, **8**, 48.
- Conrad KR, Woidwod IP, Perry JN (2002) Long-term decline in abundance and distribution of the garden tiger moth (*Actia caja*) in Great Britain. *Biological Conservation*, **106**, 329–337.
- Conrad KF, Warren MS, Fox R, Parsons MS, Woiwod IP (2006) Rapid declines of common, widespread British moths provide evidence of an insect biodiversity crisis. *Biological Conservation*, **132**, 279–291.
- Davey CM, Chamberlain DE, Newson SE, Noble DG, Johnston A (2012) Rise of the generalists: evidence for climate driven homogenization in avian communities. *Global Ecology and Biogeography*, **21**, 568–578.
- Davidson AM, Jennions M, Nicotra AB (2011) Do invasive species show higher phenotypic plasticity than native species and, if so, is it adaptive? A meta-analysis. *Ecology Letters*, **14**, 419–431.
- Devictor V, van Swaay C, Brereton T *et al.* (2012) Differences in the climatic debts of birds and butterflies at a continental scale. *Nature Climate Change*, **2**, 121–124.

Dukes JS, Mooney HA (1999) Does global change increase the success of biological invaders? *Trends in Ecology & Evolution*, **14**, 135–139.

Eglington SM, Pearce-Higgins JW (2012) Disentangling the Relative Importance of Changes in Climate and Land-Use Intensity in Driving Recent Bird Population Trends. *PLoS ONE*, **7**, e30407.  
doi:10.1371/journal.pone.0030407

Fera (Food and Environment Research Agency) (2013) Plant pest and disease factsheets [online] Available at: <http://www.fera.defra.gov.uk/plants/publications/plantPestDiseaseFactsheets.cfm> [Accessed 18 July 2013].

Franco AMA, Hill JK, Kitschke C, *et al.* (2006) Impacts of climate warming and habitat loss on extinctions at species' low-latitude range boundaries. *Global Change Biology*, **12**, 1545–1553.

Freckleton RP, Watkinson AR, Green RE, Sutherland WJ (2006) Census error and the detection of density dependence. *Journal of Animal Ecology*, **75**, 837–851.

Freeman SN, Newson SE (2008) On a log-linear approach to detecting ecological interactions in monitored populations. *Ibis*, **150**, 250–258.

Freeman SN, Noble DG, Newson SE, Baillie SR (2007) Modelling population changes using data from different surveys: the Common Birds Census and the Breeding Bird Survey. *Bird Study*, **54**, 61–72.

Green RE, Pearce-Higgins J (2010) Species management in the face of a changing climate. *Species Management: Challenges and Solutions for the 21st Century* (eds Baxter JM, Galbraith CA), pp517–536, Scottish Natural Heritage, TSO Scotland, Edinburgh.

Gregory R, Willis S, Jiguet F, Voríšek P, Klvanová A, van Strien A *et al.* (2009) An indicator of the impact of climatic change on European bird populations. *PLoS One*, **4**, e4678.

Harrington R, Clark SJ, Welham SJ *et al.* & European Union Examine Consortium (2007) Environmental change and the phenology of European aphids. *Global Change Biology*, **13**, 1550–1564.

Harrington R, Taylor LR (1990) Migration for survival: fine scale population redistribution in an aphid, *Myzus persicae*. *Journal of Animal Ecology*, **59**, 1177–1193.

Harrop AHJ, Collinson JM, Dudley SP, Kehoe C, The British Ornithologists' Union Records Committee (BOURC) (2013) The British List: A Checklist of Birds of Britain (8th edition). *Ibis*, **155**, 635–676.

Heller NE, Zavaleta ES (2009) Biodiversity management in the face of climate change: a review of 22 years of recommendations. *Biological conservation*, **142**, 14–32.

Hodgson JA, Thomas CD, Wintle BA, Moilanen A (2009) Climate change, connectivity and conservation decision making: back to basics. *Journal of Applied Ecology*, **46**, 964–969.

Hof AR, Jansson R, Nilsson C (2012) How biotic interactions may alter future predictions of species distributions: future threats to the persistence of the arctic fox in Fennoscandia. *Diversity and Distributions*, **18**, 554–562.

Isaac NJB, Girardello M, Brereton TM, Roy DB (2011) Butterfly abundance in a warming climate: patterns in space and time are not congruent. *Journal of Insect Conservation*, **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, Gregory RD, Devictor V, Green RE, Voříšek P, van Strien A, Couvet D (2010) Population trends of European common birds are predicted by characteristics of their climatic niche. *Global Change Biology*, **16**, 497–505.

JNCC (Joint Nature Conservation Committee) (2007) UK BAP priority Species [online]. Available at: <http://jncc.defra.gov.uk/page-5717> [Accessed 18 July 2013].

Menzel A *et al.* (2006) European phenological response to climate change matches the warming pattern. *Global Change Biology*, **12**, 1969–1976.

Morrison CA, Robinson RA, Clark JA, Risely K, Gill JA (2013). Recent population declines in Afro-Palaeartic migratory birds: the influence of breeding and non-breeding seasons. *Diversity and Distributions*, **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 JA (2005) Climate change and the fate of cereal aphids in Southern Britain. *Global Change Biology*, **11**, 940–944.

Newson SE, Johnston A, Renwick AR, Baillie SR, Fuller RJ (2012) Modelling large-scale relationships between changes in woodland deer and bird populations. *Journal of Applied Ecology*, **49**, 278-286.

NNSS (GB Non-native species secretarial) (2013) GB Non-native Species Information Portal [online]. Available at: <https://secure.fera.defra.gov.uk/nonnativespecies/factsheet/index.cfm> [Accessed 18 July 2013]

Ockendon N, Baker DJ, Carr JA *et al.* (2014) Mechanisms underpinning climatic impacts on natural populations: altered species interactions are more important than direct effects. *Global Change Biology*, n/a–n/a. doi:10.1111/gcb.12559.

Parmesan C, Burrows MT, Duarte CM, Poloczanska ES, Richardson AJ, Schoeman DS, Singer MC (2013) Beyond climate change attribution in conservation and ecological research. *Ecology Letters*, **16**, 58–71.

Parmesan C, Duarte C, Poloczanska E, Richardson AJ, Singer MC (2011) Overstretching attribution. *Nature Climate Change*, **1**, 2–4.

Parmesan C, Yohe GA (2003) Globally coherent fingerprint of climate change impacts across natural systems. *Nature*, **421**, 37–42.

Pearce-Higgins JW, Dennis P, Whittingham MJ, Yalden DW (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 Biology*, **16**, 12–23.



- Peres-Neto PR, Jackson DA, Somers KM (2003) Giving meaningful interpretation to ordination axes: Assessing loading significance in principal component analysis. *Ecology*, **84**, 2347-2363.
- Perry M, Hollis D (2005) The generation of monthly gridded datasets for a range of climatic variables over the UK. *International Journal of Climatology*, **25**, 1041–1054.
- R Core Team (2012) R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. ISBN 3-900051-07-0, URL <http://www.R-project.org/>.
- Rebello H, Tarroso P, Jones G (2010) Predicted impact of climate change on European bats in relation to their biogeographic patterns. *Global Change Biology*, **16**, 561–576.
- RIS (Rothamstead Insect Survey) (2013) Aphid Bulletin Archive 2013 Number 1: 22 April – 28 April [online]. Available at: <http://www.rothamsted.ac.uk/insect-survey/STAphidBulletinArchive-Year=2013.html> [Accessed 18 July 2013].
- Robinson RA (2005) BirdFacts: species profiles of birds occurring in Britain and Ireland. *BTO Research Report*, **407**.
- Robinson RA, Baillie SR, Crick HQP (2007) Weather-dependent survival: implications of climate change for passerine population processes. *Ibis*, **149**, 357–364.
- Roy DB, Rothery P, Moss D, Pollard E, Thomas JA (2001) Butterfly numbers and weather: predicting historical trends in abundance and the future effects of climate change. *Journal of Animal Ecology*, **70**, 201– 217.
- Ter Braak CJF, van Strien AJ, Meijer R, Verstrael TJ (1994) Analysis of monitoring data with many missing values: which method? In: *Distribution, monitoring and ecological aspects* (eds Hagemeyer EJM, Verstrael TJ), PP. 663-673. Proceedings of the 12th International Conference of IBCC and EOAC, Noordwijkerhout, The Netherlands.
- Thackeray SJ, Sparks TH, Frederiksen M *et al.* (2010) Trophic level imbalances in rates of phenological change for marine, freshwater and terrestrial environments. *Global Change Biology*, **16**, 3304-3313.
- Thomas CD, Cameron A, Green RE *et al.* (2004) Extinction risk from climate change. *Nature*, **427**, 145–148,
- Tylianakis JM, Didham RK, Bascompte J, Wardle DA (2008) Global change and species interactions in terrestrial ecosystems. *Ecology Letters*, **11**, 1351–1363.
- Van Emden HF, Harrington R (2007) *Aphids as crop pests*. CABI.
- Van der Putten WH, Macel M, Visser ME (2010) Predicting species distribution and abundance responses to climate change: why it is essential to include biotic interactions across trophic levels. *Philosophical Transactions of the Royal Society B: Biological Sciences*, **365**, 2025–2034.
- Vaughan IP, Ormerod SJ (2014) Linking interdecadal changes in British river ecosystems to water quality and climate dynamics. *Global Change Biology*, n/a–n/a.

- Virtanen T, Neuvonen S (1999) Performance of moth larvae on birch in relation to altitude, climate, host quality and parasitoids. *Oecologia*, **120**, 92–101.
- Visser ME, Holleman LJM (2001) Warmer springs disrupt the synchrony of oak and winter moth phenology. *Proc. R. Soc. Lond. B*, **268**, 289-294.
- Voigt W, Perner J, Davis AJ *et al.* (2003) Trophic levels are differentially sensitive to climate. *Ecology*, **84**, 2444–2453.
- Walther G-R, Post E, Convey P *et al.* (2002) Ecological responses to recent climate change. *Nature*, **416**, 389–395.
- Waring P, Townsend MC (2003) *Field Guide to the Moths of Great Britain and Ireland*. British Wildlife Publishing, UK.
- Warren MS, Hill JK, Thomas JA *et al.* (2001) Rapid responses of British butterflies to opposing forces of climate and habitat change. *Nature*, **414**, 65–69.
- Willis SG, Doswald N, Freeman SN, Roy DB, Girardello M, Bell J, Newson SE, Chamberlain DE (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 (BICCONet) Steering Group
- Wright LJ, Newson SE, Noble DG (2014) The value of a random sampling design for annual monitoring of national populations of larger British terrestrial mammals. *European Journal of Wildlife Research*, **60**, 213-221.
- Yamamura K, Kiritani K (1998) A simple method to estimate the potential increase in the number of generations under global warming in temperate zones. *Applied Entomology and Zoology*, **33**, 289–298.
- Zhou X, Harrington R, Woiwos IP, Perry JN, Bale JS, Clark SJ (1995) Effects of temperature on aphid phenology. *Global Change Biology*, **1**, 303–313.

**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	<a href="http://www.bats.org.uk/pages/nbmp.html">http://www.bats.org.uk/pages/nbmp.html</a> <a href="http://www.bto.org/volunteer-surveys/bbs">http://www.bto.org/volunteer-surveys/bbs</a>
Birds	~3000	85	Terrestrial birds 1966 - 2011; Wetland birds: 1980 – 2011	<a href="http://www.bto.org/volunteer-surveys/bbs">http://www.bto.org/volunteer-surveys/bbs</a> <a href="http://www.bto.org/volunteer-surveys/wbbs">http://www.bto.org/volunteer-surveys/wbbs</a>
Butterflies	1424	55	1976 - 2011	<a href="http://www.ukbms.org">http://www.ukbms.org</a>
Moths	13	265	1975 – 2010	<a href="http://www.rothamsted.ac.uk/insect-survey/">http://www.rothamsted.ac.uk/insect-survey/</a>
Aphids	12	80	1970 – 2010	<a href="http://www.rothamsted.ac.uk/insect-survey/">http://www.rothamsted.ac.uk/insect-survey/</a>

**Table 2** Number of species within species-groupings

Taxa	Total species	Primary Consumers	Species of concern	Non-native	Pest species
Mammal	16	5	6	3	1
Birds	85	9	23	6	6
Aphids	80	80	0	1	22
Butterfly	55	59	22	1	3
Moth	265	265	31	0	32

**Table 3** Annual change in observed ( $n_o$ ), climate driven ( $n_c$ ) and non-climate driven ( $n_N$ ) abundance indices  $\pm$  standard error of fixed effects, model fit (median  $r^2$ ) and model fit from weather variables of taxonomic groups. P-values relate to significance of difference of trends from zero.

Taxon	Mean change in observed population abundance ( $n_o$ )	Mean change in modelled abundance in response to climate change ( $n_c$ )	Mean change in modelled abundance under stable mean climate ( $n_N$ )	Model fit (median adjusted $r^2$ )	Model fit from weather variables only
Mammals	$1.02 \times 10^{-3} \pm 2.48 \times 10^{-3} ***$	$2.54 \times 10^{-3} \pm 4.38 \times 10^{-3}$	$7.74 \times 10^{-3} \pm 2.78 \times 10^{-3} **$	0.242	-0.056
Birds	$-2.16 \times 10^{-3} \pm 2.39 \times 10^{-3}$	$-6.87 \times 10^{-4} \pm 6.00 \times 10^{-4}$	$-7.22 \times 10^{-4} \pm 7.52 \times 10^{-4}$	0.103	0.020
Aphids	$6.91 \times 10^{-3} \pm 1.56 \times 10^{-3} ***$	$4.29 \times 10^{-3} \pm 7.94 \times 10^{-4} ***$	$2.09 \times 10^{-3} \pm 5.06 \times 10^{-4} ***$	0.441	0.005
Butterflies	$1.84 \times 10^{-4} \pm 4.47 \times 10^{-4}$	$1.28 \times 10^{-5} \pm 2.23 \times 10^{-4}$	$7.79 \times 10^{-6} \pm 7.71 \times 10^{-4}$	0.288	0.046
Moths	$-1.18 \times 10^{-2} \pm 1.16 \times 10^{-3} ***$	$-8.95 \times 10^{-3} \pm 5.01 \times 10^{-3} ***$	$-1.18 \times 10^{-3} \pm 1.14 \times 10^{-3}$	0.326	0.063

P-values are:  $^{\circ}$  < 0.1, \* < 0.05, \*\* < 0.01, \*\*\* < 0.001.

**Table 4** Annual change in abundance in observed, climate driven and non-climate driven abundance indices  $\pm$  standard error of fixed effects, model fit (median  $r^2$ ) and model fit from weather variables of groups. P-values relate to significance of difference between groups. Each species was assigned one value in each pair of groups.

Group	Mean change in observed population abundance ( $n_o$ )	Mean change in modelled abundance in response to climate change ( $n_c$ )	Mean change in modelled abundance under stable climate ( $n_N$ )	Model fit (median $r^2$ )	Model fit from weather variables only
Primary consumers	$-5.43 \times 10^{-3} \pm 8.12 \times 10^{-4}$	<b><math>-4.15 \times 10^{-3} \pm 3.82 \times 10^{-4}</math></b>	$1.41 \times 10^{-3} \pm 1.08 \times 10^{-3}$	0.337	0.045
Secondary consumers	$-3.78 \times 10^{-3} \pm 2.24 \times 10^{-3}$	<b><math>-1.06 \times 10^{-3} \pm 5.97 \times 10^{-4}</math> ***</b>	$-1.52 \times 10^{-4} \pm 6.82 \times 10^{-4}$	0.115	0.016
Species of conservation concern	<b><math>-3.25 \times 10^{-2} \pm 1.87 \times 10^{-3}</math></b>	<b><math>-6.30 \times 10^{-3} \pm 8.31 \times 10^{-4}</math></b>	<b><math>-1.45 \times 10^{-2} \pm 1.56 \times 10^{-3}</math></b>	0.111	0.038
Other species	<b><math>-6.72 \times 10^{-4} \pm 7.18 \times 10^{-4}</math> ***</b>	<b><math>-2.86 \times 10^{-4} \pm 3.45 \times 10^{-4}</math> ***</b>	<b><math>3.61 \times 10^{-3} \pm 1.01 \times 10^{-3}</math> ***</b>	0.325	0.040
Native	<b><math>-6.35 \times 10^{-3} \pm 7.12 \times 10^{-4}</math></b>	<b><math>-3.67 \times 10^{-3} \pm 3.18 \times 10^{-4}</math></b>	$6.01 \times 10^{-4} \pm 8.99 \times 10^{-4}$	0.298	0.041
non-native	<b><math>1.51 \times 10^{-2} \pm 2.45 \times 10^{-3}</math> ***</b>	<b><math>5.76 \times 10^{-3} \pm 1.58 \times 10^{-3}</math> ***</b>	$8.41 \times 10^{-3} \pm 1.26 \times 10^{-3}$	0.168	-0.002
Non-pest species	$-5.69 \times 10^{-3} \pm 7.65 \times 10^{-4}$	$-3.34 \times 10^{-3} \pm 3.30 \times 10^{-4}$	$7.88 \times 10^{-4} \pm 9.50 \times 10^{-4}$	0.284	0.036
pest species	$-6.72 \times 10^{-3} \pm 1.76 \times 10^{-3}$	$-4.10 \times 10^{-3} \pm 9.81 \times 10^{-4}$	$1.19 \times 10^{-3} \pm 2.68 \times 10^{-3}$	0.417	0.070

P-values are:  $^{\circ}$  < 0.1, \* < 0.05, \*\* < 0.01, \*\*\* < 0.001.

**Table 5** Number of declining, stable and increasing species within taxa from observed trends ( $n_o$ ) and climate-driven trends ( $n_c$ ) based on a 30% change in 10 years. Species with extreme climate-driven population declines or increases are stated.

	observed ( $n_o$ ) \ climate ( $n_c$ )	declining	stable	increasing
<b>mammals</b>	declining	0	0	0
	stable	0	11	2 <i>(Oryctolagus cuniculus, Myotis mystacinus / brandtii)</i>
	increasing	0	2	1 <i>(Muntiacus reevesi)</i>
<b>birds</b>	declining	0	5	0
	stable	1 <i>(Gallinago gallinago)</i>	60	0
	increasing	0	18	1 <i>(Branta canadensis)</i>
<b>aphids</b>	declining	0	14	0
	stable	0	42	0
	increasing	0	21	3 <i>(Forda formicaria, Acyrthosiphon malvae, Capitophorus elaeagni)</i>
<b>butterflies</b>	declining	0	0	0
	stable	0	54	0
	increasing	0	1	0
<b>moths</b>	declining	18*	41	0
	stable	6**	162	1

	increasing	0	35	( <i>Cosmia affinis</i> ) 2 ( <i>Gymnoscelis rufifasciata</i> , <i>Eilema griseola</i> )
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\* Moth species with extreme climate-driven declines and observed declines: *Agrotis exclamationis*, *Allophyes oxyacanthae*, *Apeira syringaria*, *Apocheima pilosaria*, *Arctia caja*, *Brachylomia viminalis*, *Caradrina morpheus*, *Cerastis rubricosa*, *Diarsia mendica*, *Erannis defoliaria*, *Eupithecia succenturiata*, *Hylaea fasciaria*, *Lomographa bimaculata*, *Operophtera fagata*, *Perizoma didymata*, *Petrophora chlorosata*, *Polyploca ridens*, *Trichiura crataegi*.

\*\* Moth species with extreme climate-driven declines but observed stable populations: *Cidaria fulvata*, *Eulithis populata*, *Habrosyne pyritoides*, *Hoplodrina blanda*, *Laspeyria flexula*, *Melanchnra pisi*.



**Figure 1** 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.

**Figure 2** Annual variation in PCA scores along PCA1 (black points), centred by the central point of the two-year weather window that the point represents. Points represent PCA1 estimates for combinations of time-window and geographical area from which the climate data are estimated, as used for different species (Fig. 1). The two-year moving average temperature anomaly for the UK is also shown (red line), again centred by the central point of the two-year weather window. In all cases PCA axis 1 increased significantly over time (slopes of all linear models between 0.238 and 0.344, P values all < 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 - f) Geometric means of observed population indices ( $n_o$ ; solid black lines), abundance estimated from free-running models assuming a stable mean climate ( $n_N$ ; dashed black lines) and the climate-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.

**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) invasive species and (d) pest species. Dashed lines show indices of (a) primary consumers, (b) species of conservation concern, (c) native species and (d) 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.

Figure 1.

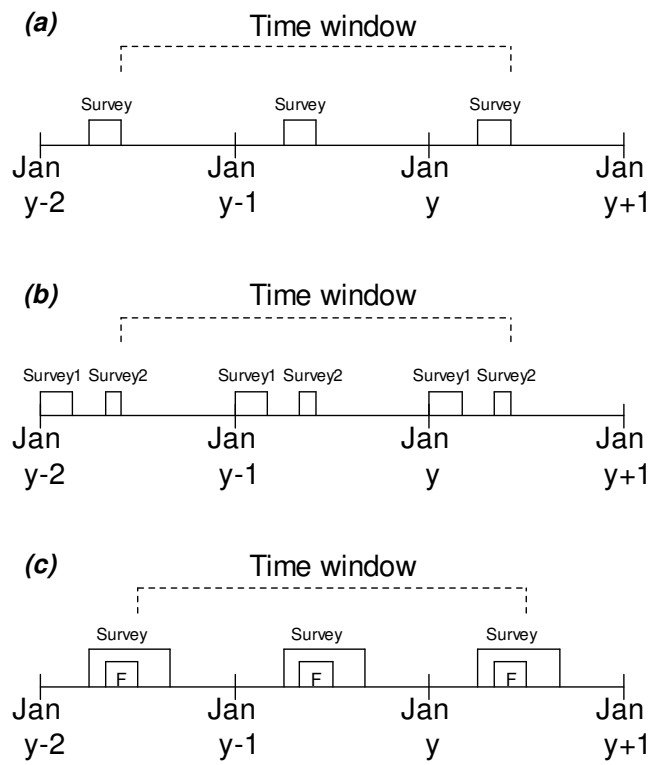


Figure 2.

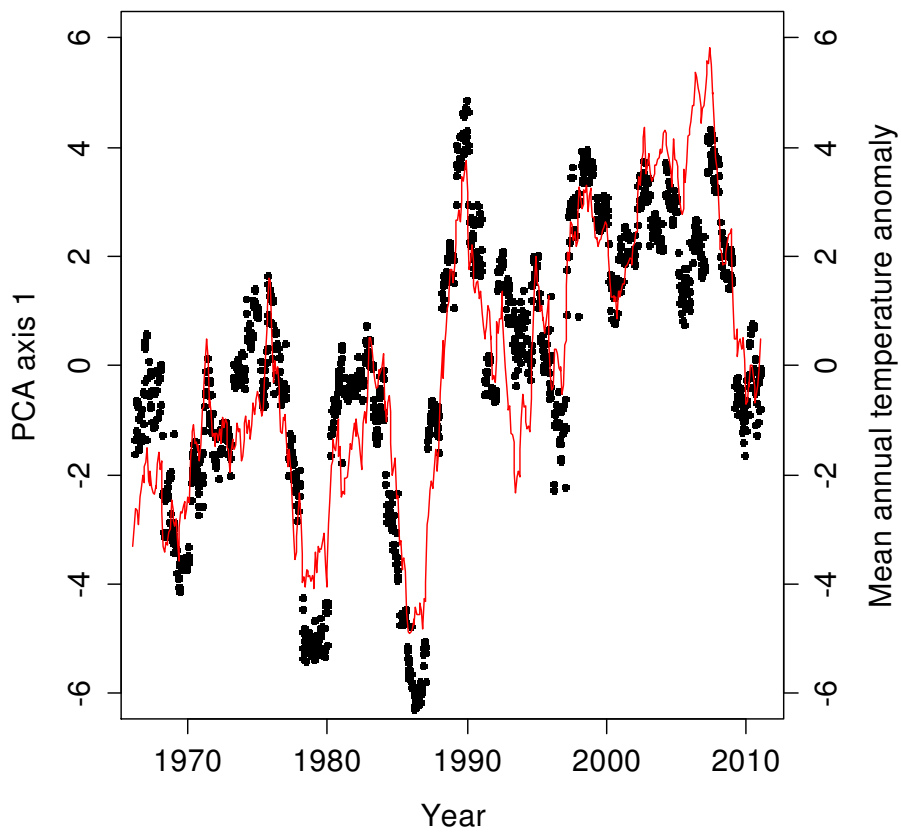


Figure 3.

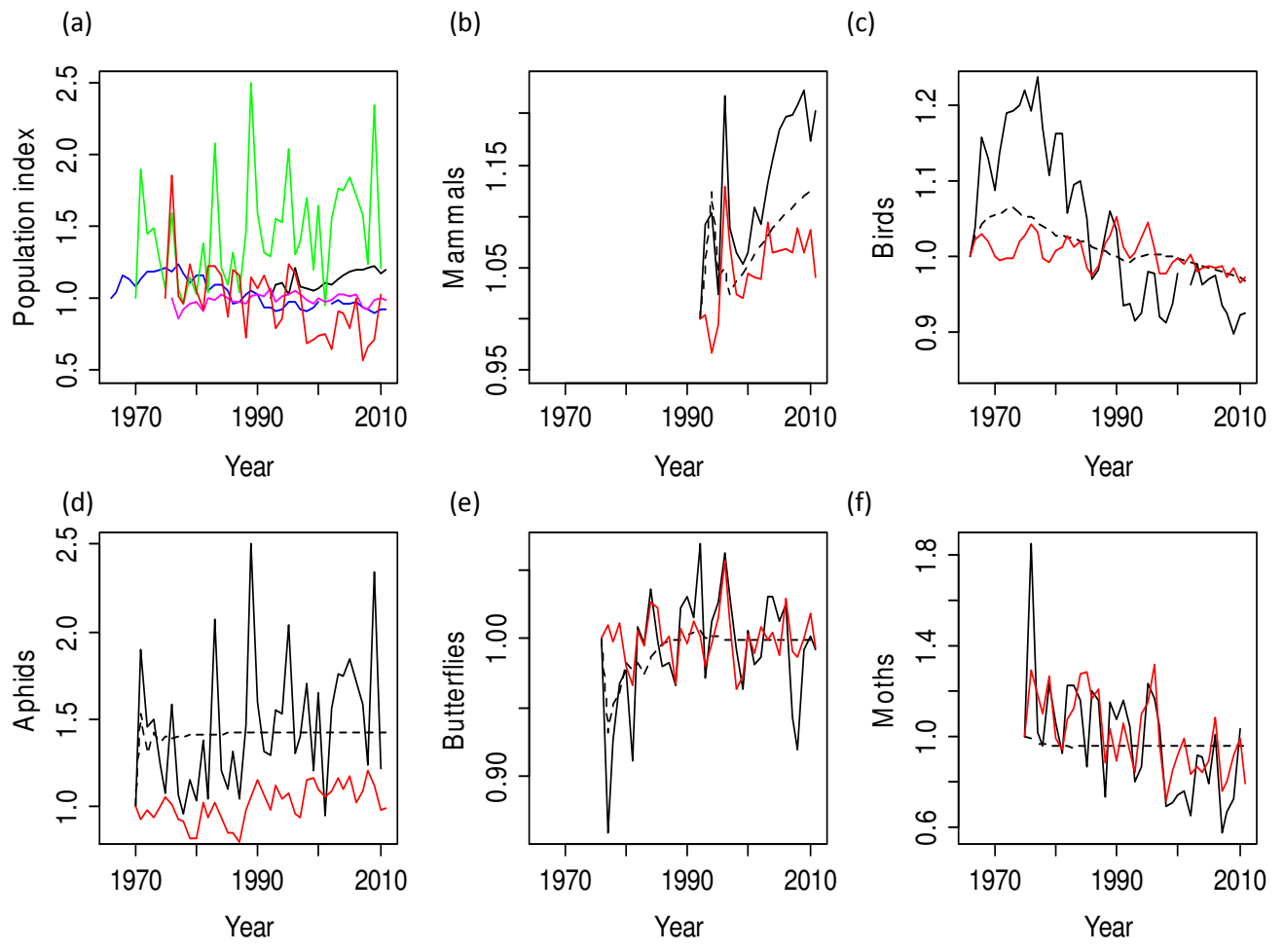
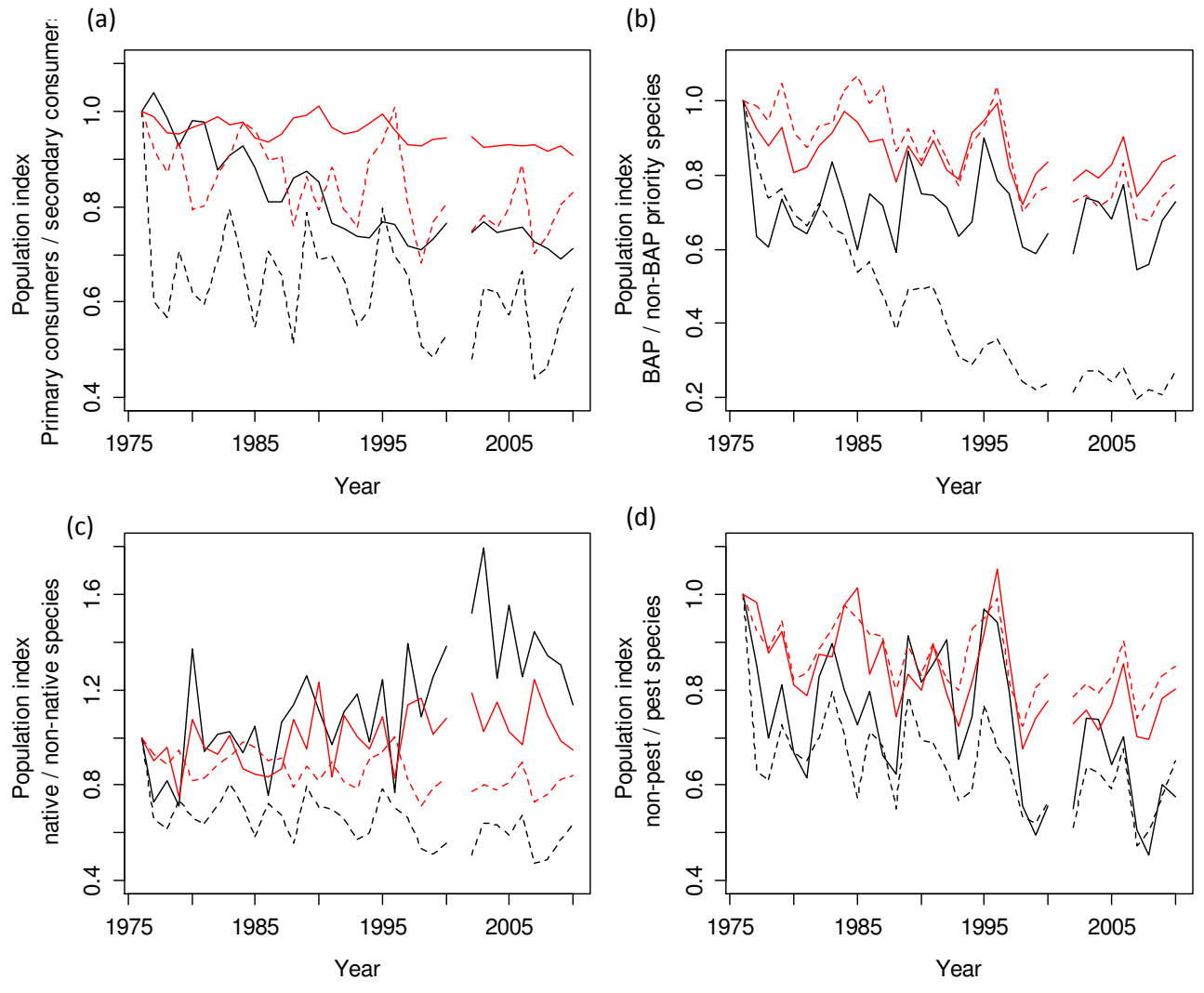


Figure 4.



## Supporting Information

**SI Table 1** Annual change in observed ( $n_o$ ), climate driven ( $n_c$ ) and non-climate driven ( $n_N$ ) abundance indices  $\pm$  standard error of fixed effects, model fit (median  $r^2$ ) and model fit from weather variables (as in Table 3) of birds using bird data from all of the UK, and butterflies and moths using shifted weather windows to exclude adult activity periods. P-values relate to significance of difference of trends from zero.

Taxon	Mean change in observed population abundance ( $n_o$ )	Mean change in modelled abundance in response to climate change ( $n_c$ )	Mean change in modelled abundance under stable climate ( $n_N$ )	Model fit (median $r^2$ )	Model fit from weather variables only
Birds	$-2.75 \times 10^{-3} \pm 2.25 \times 10^{-3}$	$-2.19 \times 10^{-4} \pm 7.86 \times 10^{-4}$	$-1.47 \times 10^{-3} \pm 6.71 \times 10^{-4} *$	0.101	0.015
Butterflies	$1.84 \times 10^{-4} \pm 4.47 \times 10^{-4}$	$1.81 \times 10^{-4} \pm 2.29 \times 10^{-4}$	$-5.28 \times 10^{-5} \pm 7.78 \times 10^{-4}$	0.264	0.031
Moths	$-1.18 \times 10^{-2} \pm 1.16 \times 10^{-3} ***$	$-9.92 \times 10^{-3} \pm 4.87 \times 10^{-3} ***$	$-1.17 \times 10^{-3} \pm 1.16 \times 10^{-3}$	0.313	0.042

P-values are:  $^{\circ}$  < 0.1, \* < 0.05, \*\* < 0.01, \*\*\* < 0.001.

**SI Table 2** Annual change in abundance in observed, climate driven and non-climate driven abundance indices  $\pm$  standard error of fixed effects, model fit (median  $r^2$ ) and model fit from weather variables of groups, using bird data from all of the UK. P-values relate to significance of difference between groups. Each species was assigned one value in each pair of groups.

Group	Mean change in observed population abundance ( $n_o$ )	Mean change in modelled abundance in response to climate change ( $n_c$ )	Mean change in modelled abundance under stable climate ( $n_N$ )	Model fit (median $r^2$ )	Model fit from weather variables only
Primary consumers	$-5.45 \times 10^{-3} \pm 8.11 \times 10^{-4}$	$-4.16 \times 10^{-3} \pm 3.81 \times 10^{-4}$	$1.38 \times 10^{-3} \pm 1.08 \times 10^{-3}$	0.339	0.044
Secondary consumers	$-4.00 \times 10^{-3} \pm 2.13 \times 10^{-3}$	$-3.36 \times 10^{-4} \pm 5.39 \times 10^{-4} **$	$-2.21 \times 10^{-3} \pm 6.11 \times 10^{-4}$	0.101	0.019

Species of conservation concern	$-3.16 \times 10^{-2} \pm 1.77 \times 10^{-3}$	$-5.24 \times 10^{-3} \pm 1.67 \times 10^{-4}$	$-1.49 \times 10^{-2} \pm 1.54 \times 10^{-3}$	0.114	0.045
Other species	$-7.25 \times 10^{-4} \pm 7.17 \times 10^{-4} ***$	$-2.83 \times 10^{-3} \pm 3.44 \times 10^{-4} ***$	$3.50 \times 10^{-3} \pm 1.01 \times 10^{-3} ***$	0.323	0.039
Native	$-6.18 \times 10^{-3} \pm 7.04 \times 10^{-4}$	$-3.43 \times 10^{-3} \pm 3.16 \times 10^{-4}$	$4.79 \times 10^{-4} \pm 8.97 \times 10^{-4}$	0.293	0.042
non-native	$1.37 \times 10^{-2} \pm 2.45 \times 10^{-3} ***$	$5.28 \times 10^{-3} \pm 1.67 \times 10^{-3} ***$	$7.50 \times 10^{-3} \pm 1.22 \times 10^{-3} \cdot$	0.245	-0.009
Non-pest species	$-5.525 \times 10^{-3} \pm 7.56 \times 10^{-4}$	$-3.09 \times 10^{-3} \pm 3.29 \times 10^{-4}$	$6.41 \times 10^{-4} \pm 9.48 \times 10^{-4}$	0.281	0.039
pest species	$-6.85 \times 10^{-3} \pm 1.75 \times 10^{-3}$	$-4.12 \times 10^{-3} \pm 9.80 \times 10^{-4}$	$1.03 \times 10^{-3} \pm 2.68 \times 10^{-3}$	0.417	0.052

P-values are:  $\cdot < 0.1$ , \* < 0.05, \*\* < 0.01, \*\*\* < 0.001.