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Martay, B., Dennis, E. B., Brereton, T. M., Bell, J. R., Crick, H. Q. P., Morecroft, M. D., Roy, D. B. and Pearce-Higgins, J. W. 2017. Impacts of climate change on national biodiversity population trends. *Ecography.* 40 (10), p. 1139–1151.

National-scale declines in Lepidoptera populations consistent with modelled impacts of climate change.

Running head: Climate change and Lepidoptera

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Keywords: Butterfly, Moth, UK, Population trend, ~~Precipitation, Temperature,~~ Traits, Weather

Abstract

Lepidoptera are sensitive to climate change, with documented impacts on their phenology, distribution and communities. However, there remains considerable uncertainty over which species are most vulnerable, and which have been most affected so far. To address this, we analyse 35-year UK or English population trends of 55 butterfly and 265 moth species to model the impacts of variation in temperature and precipitation upon population growth rates. We identify the weather variables and periods that species are most sensitive to, the long-term impacts of climate change, and the characteristics of species which show the greatest responses. Positive impacts of summer temperature on both butterflies and moths were partly offset by negative impacts of temperature in other seasons, particularly winter. Precipitation tended to have negative impacts on population growth rates, particularly for moths. Annual population fluctuations were strongly driven by inter-annual variation in weather conditions. Over 40% of a significant decline in mean moth abundance from the 1990s to 2000s was consistent with a weather-driven decline predicted by our models, which also explained up to 19% of the decadal variation in abundance between species. Species overwintering as larvae and multivoltine species were most sensitive to the effects of weather, whilst southerly-distributed species, species associated with woodland and unimproved grassland habitats, and pest species, showed the most positive long-term responses to climate change. Combined, these results show how climate change is already having significant impacts on the abundance of particular butterfly and moth species, with likely future consequences for ecosystem function and services.

1. Introduction

Climate change is an increasing threat to natural systems, the biodiversity they support and the ecosystem services they provide (Bellard et al., 2012; IPCC, 2014). There is an urgent need to document the impacts of climate change that have already happened in order to improve our ability to predict their future impacts on natural systems. There is growing evidence for distribution shifts and phenological change (Parmesan and Yohe, 2003; Chen et al., 2011), and of impacts on ecological communities and species' populations (Devictor et al., 2012; Oliver et al., 2017), leading to potential disruption in biotic interactions (Cahill et al., 2013; Ockendon et al., 2014). However, there remain significant gaps in our understanding of the climate change influence on population abundances of specific species over time, and the traits associated with vulnerability to such impacts. To narrow this gap in knowledge, we present a detailed analysis of the response of over 300 UK butterfly and moth species to climate change.

Due to their sensitivity to temperature and good data availability, UK butterflies and moths are a suitable model group to investigate climate change impacts. They are well monitored, with documented range expansions (Warren et al., 2001; Mason et al., 2015), phenological changes (Thackeray et al., 2010, 2016) and sensitivity to variation in the weather (Roy et al., 2001; WallisDeVries et al., 2011; Mair et al., 2012; McDermott Long et al., 2017). Recent work has also suggested that climate change, amongst other drivers, has caused long-term declines in moth populations (Fox, 2013; Martay et al., 2017), but has not identified how this impact varies between species. As well as containing many species of conservation concern (Fox et al., 2013, 2015) moths are also an important group from an economic and ecosystem service provision perspective, including a number of agricultural and horticultural pests (Ellis et al., 2015). They are a keystone group for community function, acting as pollinators for many flowering plants (Hahn and Brühl, 2016), and as important prey for other taxa, such as culturally significant bird and bat species (Krištín and Patočka, 1997).

There is increasing interest in the ecological traits associated with species' vulnerability to climate change, as a means of identifying future conservation priorities (e.g. Foden and Young, 2016). However, evidence to identify the species' characteristics impacted by climate change is generally lacking (Wheatley et al., 2017), or available only for a limited number of taxa (e.g. Pearson et al., 2014; Pacifici et al., 2017). In particular, there is little information to identify the traits of invertebrate species affected by climate change. As our sample of butterflies and moths include a wide range of species from habitat specialists to generalists, sedentary to mobile, southern to northern (at a national scale), this analysis provides an important opportunity to assess the traits associated with vulnerability to climate change impacts that may be relevant to other taxa.

In order to document climate change impacts on butterflies and moths, we examine the extent to which variation in population growth rates can be explained by temperature and precipitation, key variables which cover the majority of climate change impacts on terrestrial species (Pearce-Higgins et al., 2015b). First we model annual population changes from the mid-1970s to 2011 as a function of annual fluctuations in these weather variables, whilst also accounting for non-climatic trends in abundance through time. This analysis is best regarded as summarising impacts of annual variation in the weather upon the abundance of flying adults. Next we consider the extent to which these models can be used to explain long-term trends in abundance between decades, as this will show whether the impact of climate change increases over time (Eglington and Pearce-Higgins, 2012). Finally, we relate inter-specific differences in those responses to various ecological traits.

In doing so, we are able to test several key hypotheses for Lepidoptera, with more wide-ranging data than before:

1. That annual fluctuations in butterfly and moth populations are largely driven by weather (Roy et al., 2001).
2. That climate change impacts vary between seasons (Martay et al., 2016).
3. That extreme weather events will exert a disproportionate impact on populations compared to more typical weather fluctuations (Oliver et al., 2015).
4. That long-term population trends are largely driven by climate change, the impacts of which have increased through time (Martay et al., 2017).
5. That climate change impacts are more negative for habitat specialists, but positive for habitat generalists (Davey et al., 2012)
6. That climate change impacts are negative for northerly distributed species, but are positive for southern species (Devictor et al., 2012).
7. That climate change impacts vary with species' life-history (McDermott Long et al., 2017).

2. Materials and Methods

2.1. Butterfly and moth abundance indices

Butterfly data were derived from the UK Butterfly Monitoring Scheme (BMS), in which volunteer recorders count butterflies along fixed-transects each week (where possible) from April through to September, within set weather criteria (Pollard and Yates, 1993). The scheme has grown incrementally from its inception in 1976 to cover more than 1000 sites by 2011 (Botham et al., 2013). In early years of the scheme, recording was restricted almost entirely to England so we therefore restricted our analysis to data from England, the most evenly recorded country (Martay et al., 2016).

Moth data were derived from the Rothamsted network of light traps run by a mix of professionals and volunteers on a daily basis from 1975 (Woiwod and Gould, 2008). Here, analysis was restricted to the 13 sites from across the UK with a continuous data run to 2010, thus eliminating the need to account for spatial variation in coverage through time (Martay et al., 2016).

Commented [EBD1]: Is there a reason why butterflies were to 2011 and moths to 2010?
BM: Data beyond 2010 was not available for moths

Firstly, we generated annual abundance indices for each species at each site, accounting for missing weekly counts in the case of butterflies (Roy et al., 2001). Because we were interested in large-scale responses to climate, secondly, we collated these into annual multi-site indices of population change for each species ($n_{i,Y}$ in year Y for species i), using the freeware program TRIM, a widely used method to document national trends (e.g. Pannekoek and van Strien, 1998; Conrad et al., 2004). Species for which there were no records in any one year were excluded. Sufficient data were available for analysis of 55 butterfly species and 265 moth species.

2.2. Weather variables

We used UK Met Office 5km gridded datasets, averaged across England and the UK for butterflies and moths respectively (Perry and Hollis, 2005), to calculate average mean daily temperature and seasonally summed precipitation, separately for winter (Dec-Feb), spring (Mar-May), summer (Jun-Aug) and autumn (Sept-Nov). Given the potential for these variables to operate on populations through lagged effects (e.g. Pearce-Higgins et al., 2015a), we considered the 24 months preceding the season in which the last flight of a species was recorded; giving a total of 16 variables (2 variables calculated separately for each of the 8 seasons in the 2 years preceding the flight period). Thus for adults of species such as the Small Blue (*Cupido minimus*) which are active from May to August, we used data from summer in year_t to autumn in year_{t-2}. We refer to these variables describing annual variation in seasonal temperature and precipitation values as weather variables (V_W), but use climate to refer to decadal averages or change over longer time-periods. We tested whether there were trends in these mean seasonal weather variables throughout the study area (England for butterflies and UK for moths) between 1975 and 2010 using GLMs.

2.3. Models of population growth

Population growth was described by $\Delta n_{\cancel{\Theta} i,Y} = \log(n_{\cancel{\Theta} i,Y} / n_{\cancel{\Theta} i,Y-1})$, where $n_{\cancel{\Theta} i,Y}$ is the observed annual national population index in year *Y* for species ~~*Θ*~~*i*. We modelled population growth as a function of weather variables $f(V_W)$ for each species as follows (Model 1).

$$\Delta n_{i,Y} = \alpha + b_0\, n_{i,Y-1} + b_1\, Y + f(V_W) \qquad \textit{Model 1}$$

Count in the previous year ($\cancel{n}_{\cancel{\Theta}} n_{i,Y-1}$) was included to account for potential density-dependence (Pearce-Higgins et al., 2015a), known to be important for some butterfly and moth species (Roy et al., 2001). Year was included to account for potential non-climatic drivers of long-term trends which could alter the population growth rate through time. Given the potential for non-linear relationships to occur between population growth and both weather variables (indicating disproportionate impacts of extreme weather events) and year, we also considered quadratic terms in cases where they were shown in preliminary analysis to have significant explanatory power when added to a model of population growth as a function of the related linear weather variable, year and count in the previous year. Quadratic terms were only included in combination with the associated linear term. Given the sample size of 35 years for both groups, population growth was modelled as a function of up to six variables (two of which were always count in the previous year and year), to reduce the risk of over-fitting.

All possible models were fitted using the lm function in R (R Core Team, 2015) and model selection was undertaken by Akaike information criterion corrected for small sample sizes (AICc; Anderson, 2007), using the dredge function from the MuMIn package (Barton, 2016) in R, selecting the best-fitting of the candidate models. We tested for multicollinearity between the variables in resulting models by examining whether the Pearson correlation coefficients r > 0.7, the threshold considered necessary to prevent reliable model estimation (Dormann et al., 2013). For only six of the 320 species was this threshold exceeded, and for each of these species the collinearity was between the year term and the count in the previous year. As very few species were affected, this should have a minimal impact on the results.

Model fit was assessed by r^2. Hierarchical partitioning (Chevan and Sutherland, 1991; Walsh and Mac Nally, 2013) was used to identify the proportion of the variance which could be attributed specifically to the weather variables (V_W). The product of r^2 and V_w gave the r^2 attributable to annual variation in the weather (sensitivity), used to test Hypothesis 1 (that annual fluctuations in butterfly and moth populations are largely driven by weather). We used t-tests to determine whether the r^2 or sensitivity differed between butterflies and moths after checking for normality.

To test Hypothesis 2 (that climate change impacts vary between seasons), we identified how many times each weather variable was included in the models (in each case indicating a significant relationship between the weather variable and the species' population growth) from the best-fitting model for each species, and whether these were positive or negative. The direction of quadratic relationships was determined by plotting their form over the range of the climatic data. We used Pearson's chi-squared test to test whether each of the 24 weather variables had notably positive or negative impacts across species (separating moths and butterflies), after applying a Bonferroni correction. The prevalence of significant quadratic relationships indicated the extent to which extreme events had a disproportionate impact on populations, as described by non-linear relationships between weather variables and population growth (Hypothesis 3).

2.4. Models of population trends

By predicting population growth using Model 1 and observed weather variables, we were able to test the extent to which observed long-term trends were consistent with the cumulative impact of modelled effects of annual variation in weather upon population growth. Thus, for each species in each year we predicted the weather-driven population growth ($\Delta n_{Vw\_i,Y}$) as a function of the observed relevant weather variables (Vw) using the best fitting models (described above). In these predictions we fixed the year terms to equal the first year in the time-series (Y_1), thus removing the impact of variation in non-climatic drivers of change. To predict this weather-related population growth between the first and second year only, observed population count in the first year was used but thereafter the predicted count in the previous year ($n_{Vw\_i,Y-1}$) was used to predict the population growth in the following year, ensuring that the model was ‘free-running’ (Model 2; see Eglington and Pearce-Higgins, 2012).

$$\Delta n_{Vw\_i,Y} = \alpha + b_0\, n_{Vw\_i,Y-1} + b_1\, Y_1 + f(V_W) \qquad \textit{Model 2}$$

In this prediction, annual growth rates ($\Delta n_{Vw\_i,Y}$) were therefore determined by the effects of density-dependence, weather and an underlying population growth rate (due to year being included in the model, representing linear non-weather related change). Long-term trends were quantified from the slope of the observed and weather-model predicted population estimates through time as a measure of overall change across the study period which we refer to as β_i and β_{Vw_i}, for species *i*. By modelling β_i as a function of β_{Vw_i}, taxa and the interaction between taxa and β_{Vw_i}, we tested whether the long-term population trends were consistent with expected effects of climate change (Hypothesis 4).

Based on observed population trends (β_i), species were classified by the extent to which their population trends were increasing (statistically significant ($P<0.05$) positive linear trend), decreasing (significant negative linear trend) or stable (non-significant linear trend). We then used the same criteria to determine the extent to which each species' population trend had been influenced by trends in the weather variables, based on the slope of the weather-model prediction through the time-series (β_{Vw_i}). We used tests of equal proportions to test whether within each taxon there are significant differences in the number of species with declining observed and weather-model predicted trends compared to increasing trends. The combination of observed trends and weather-model prediction trends was used to categorise species by the impact of weather trends upon their population (Table 2).

2.5. Traits analysis

Butterfly and moth traits were collated from a range of sources and databases (Dennis et al., 2005; Waring and Townsend, 2009; Dennis, 2010) to cover ecological and life-history parameters that may affect species' sensitivity to weather variables (Table 1). In order for the analyses to be comparable across both groups, which were modelled together, we used trait variables that were available for both butterflies and moths.

The influence of traits upon sensitivity (proportion of variance which could be attributed to weather variables) and the weather-model prediction trend (β_{Vw_i}) was tested to identify how variation in the importance of weather in driving population fluctuations and long-term trends varies between groups of species. Both responses were modelled as a function of the trait variables in Table 1. Given multiple habitat associations for many species, habitat category was separated into species that occur in woodland (D1), unimproved grassland (D2) and upland (D3) categories, the main associations of habitat specialists, and multiple associations were possible for each species. Linear mixed models were fitted in R (R Core Team, 2015) using the lme4 package (Bates and Maechler, 2010), with random factors for family, genus and taxa to account for phylogenetic correlation. Model selection was undertaken by AICc using the dredge function within the MuMIn package in R, allowing for up to five variables, in addition to the random factors. This analysis allowed us to test Hypotheses 5 – 7.

2.6. *Impacts of climate change*

Annual fluctuations in population growth for each species could be highly dependent on the weather, irrespective of the long-term impact of climatic trends. To better separate these fluctuations from the long-term impacts of changes in weather variables (climate change) upon overall butterfly and moth abundance, we examined the change in mean observed and weather-model predictions of population abundance between three decades for each species e.g. (Models 3 & 4).

$$\Delta n_{i,90s - 80s} = \log\left(\overline{n_{i,Y = 1990:1999}}/\overline{n_{i,Y = 1980:1989}}\right)$$

Model 3

$$\Delta n_{Vw\_i,90s - 80s} = \log\left(\overline{n_{Vw\_i,Y = 1990:1999}}/\overline{n_{Vw\_i,Y = 1980:1989}}\right)$$

Model 4

This focus on decadal means from 1981-2010 is complementary to our analyses of long-term trends, but avoided the results being overly influenced by extreme weather events at the start and end of the time-series; 1976 was characterised by summer drought, whilst the 2010/11 winter was extremely cold (Palmer et al., 2017).

Specifically, we tested for whether the decadal changes in mean population estimates (e.g. $\Delta n_{i\cancel{O},90s - 80s}$) were significantly different from zero and whether they varied between taxa. We also tested whether the observed decadal population changes for each species (e.g. $\Delta n_{i\cancel{O},90s - 80s}$) correlated with weather-model predicted changes (e.g. $\Delta n_{Vw\_i\cancel{O},90s - 80s}$)

Commented [EBD2]: I'm not sure I understand this, unless it should be $n_{O,Y=1980:1989}$?

BM: Yes, that should be no,Y=1980:1989

and whether this varied between taxa. These analyses allowed us to test whether there were climate change impacts on long-term population trends and whether the climate change impacts increased over time (Hypothesis 4). This final analysis was undertaken in SAS 9.4 using PROC MIXED, applying a Kenward-Rogers correction for the degrees of freedom.

Unless specified, means are presented with standard errors throughout.

Table 1. Species traits used in the analysis.

Trait	**Definition**
A. UK latitudinal distribution	Simplified to four categories based on occurrence within 100km latitudinal band; 1 = southerly – occurring up to 300km north (the Wash), 2 = occurring up to 500km north (Cumbria / N. Yorkshire), 3 = occurring up to 600km north (Northumberland and southern Scotland), 4 = occurring to 1000km north or higher, virtually or totally throughout whole of UK.
B. type of main larval food plants	1 = deciduous trees, including low deciduous in hedgerows (Hawthorn etc), 2 = coniferous trees and shrubs, 3 = grasses, including sedges and rushes, 4 = dicots, including herbaceous and low woody shrubs such as heather etc. 5 = lichens, mosses, fungi and algae (majority are lichens), 6 = polyphagous (covering at least two of the above categories).
C. Broad categories of larval feeding specialisation	1 = monophagous (one species only or rarely other species), 2 = specialist (restricted to one family of food plant or lower taxa of plants apart from food resources rarely taken), 3 = intermediate generalist (restricted to one main larval food plant group), 4 = polyphagous (spanning at least two main larval food plant groups).
D. Broad habitat preferences	D1 = woodland, D2 = unimproved grassland (inc. downland), D3 = upland – each a binary term.
E. Wing span in mm	mean width of the span of the forewings (as surrogate for dispersal power, Sekar, 2011)
F. Overwintering	1 = egg, 2 = larva, 3 = pupa, 4 = adult, 5 = migrant

stage	
G. Voltinism	1 = always univoltine, 2 = variable between one to two (rarely three) generations, with multiple generations in the south and single generations further north, 3 = obligate multivoltine with two generations per year, 4 = obligate multivoltine, with three generations per year.
H. Flight period	1 = spring (March to May), 2 = summer (June to August), 3 = spring and summer (March to August), 4 = autumn (September to November), 5 = summer and autumn (June to November), 6 = spring, summer and autumn (March to November), 7 = autumn, winter and spring (September to May) and (rarely) all year round
I. Larval period	I1 = January to March, I2 = April to June, I3 = July to September, I4 = October to December – each a binary term such that larval periods can span multiple seasons.
J. Pest species	Binary term denoting if the species is regarded as an agricultural or horticultural pest.
K. Priority Species for Conservation	Binary term defining if a species is defined as ‘conservation priority species’ by formal Governmental processes prior to 2012 (Eaton el al., 2015)
L. Larval start month	Initial month for the larval stage.

Table 2. Categorisation of the impact of weather trends on species according to the cross-tabulation of observed population trends and weather prediction trends.

		Observed population trend		
		Decreasing	Stable	Increasing
Weather prediction trend	Decreasing	**Loser** Significant population decline matches weather prediction trend.	**Hindered** Population trend constrained by decreasing weather prediction trend.	**Hindered** Population trend constrained by decreasing weather prediction trend.
	Stable	**Unaffected** Stable weather prediction trend.	**Unaffected** Stable weather prediction trend.	**Unaffected** Stable weather prediction trend.
	Increasing	**Helped** Population trend ameliorated by increasing weather prediction trend.	**Helped** Population trend ameliorated by increasing weather prediction trend.	**Winner** Significant population increase matches weather prediction trend.

3. Results

3.1. Weather variables

Throughout the study area (England for butterflies and UK for moths) the mean seasonal temperatures increased significantly between 1975 and 2010 except for winter temperature (Supplementary material, Appendix A~~S1~~). Precipitation did not vary over time in any season except for an increase in summer rain across the UK (Supplementary material, Appendix ~~S1~~A). Mean annual temperatures increased between decades by 0.49 ± 0.10 °C/decade ($P < 0.001$) with the UK mean annual temperature in the 1980s, 1990s and 2000s respectively 8.4, 8.9 and 9.3 °C.

3.2. Models of population growth

The best-fitting models of population growth (Model 1) explained between 29.9% and 89.5% of the variation in observed populations (r^2) across both butterflies and moths (Supplementary material, Appendix B~~S2~~). There was a significant difference in the proportion of variation explained between butterflies (67.6%) and moths (63.8%; $t = 2.739$, $P = 0.007$). The proportion of this variation that could be attributed to weather variables (V_W) suggests annual variation in weather alone explained a mean of 28.8% of the variation in population growth across all species (ranging from 0% - 65.0% for individual species) (Hypothesis 1). This proportion did not differ significantly between butterflies and moths ($t = -0.588$, $P = 0.558$).

Eleven weather variables were found to affect population growth rates in significantly more species than the 1/20 expected by chance (Fig. 1) (Hypothesis 2). The most widespread impact of weather was a significant positive association between population growth rate and summer$_t$ temperature, found in 35% of butterflies and 44% of moth species. However, significant negative effects of temperature were apparent at other times of the year, with the growth rates of 29% of butterfly species negatively correlated with winter$_{t-1/t}$ temperature and population growth rates of 17%, 23% and 19% of moths species negatively correlated with summer$_{t-1}$, winter$_{t-1/t}$ and spring$_{t}$ temperature respectively. Moth population growth was significantly negatively associated with rainfall throughout the year, affecting 21% of species in autumn$_{t-1,}$ 16% in winter$_{t-1/t}$, 17% in spring$_{t}$ and 14% of species in summer$_{t}$, whilst population growth rates of 27% of butterfly species was negatively associated with autumn$_{t-1}$ rainfall.

Only 9% of significant relationships with weather variables were quadratic (Hypothesis 3). These relationships comprised more than 5% of the possible relationships in any season expected by chance for butterfly population responses to summer$_{t}$ temperature alone. In this instance only 4 species (*Hamearis luci*, *Pyronia tithonus*, *Thymelicus sylvestris*, *Lasiommata megara*) showed quadratic negative relationships indicative of extreme negative responses to summer$_{t}$ temperature.

3.3. Models of population trends

There was no overall relationship between observed trends (β_i) and weather-model predicted trends (β_{Vw_i}) ($F_{1,317} = 0.31$, $P = 0.58$), or any difference in this relationship between butterflies and moths ($F_{1,316} = 0.06$, $P = 0.80$), although moths exhibited more negative population trends than butterflies ($F_{1,317} = 9.64$, $P = 0.0021$). Cross-species trends across all species were not therefore strongly related to weather-model predicted trends across 35 years. Likewise, there were more moths with significantly declining population trends than increasing ($\chi = 40.1$, $P < 0.001$) but no difference in the proportion of moth species with increasing and declining weather-model predicted trends ($\chi = 0.59$, $P = 0.44$) and no difference in the proportions of butterflies with increasing and declining observed ($\chi = 1.10$, $P = 0.29$) or weather-predicted trends ($\chi = 0.66$, $P = 0.42$). Six species of butterfly and 36 species of moth were classified as losers, with a further 10 and 48 respectively classified as hindered (Table 4). These numbers compare with 5 and 9 species respectively classified as winners and 17 and 61 species respectively, classified as helped. The final classification of each species is given in the supplementary material, Appendix ~~S2~~B. Although long-term trends across all species were not consistently linked to climate change, for a sizeable subset of species, trends were consistent with the modelled expectation of climate change (Hypothesis 4). For observed, modelled and weather-model predicted abundances for all species see the supplementary material, Appendix ~~S3~~C.

3.4. Traits analysis

The best-fitting model for describing the sensitivity of species' populations to weather by traits showed significant effects of upland habitat association, overwintering strategy and voltinism (Table 3), although combined, these variables only accounted for 9% of the variation between species. Sensitivity was lowest in species occupying upland habitats compared to other habitats. Sensitivity in species overwintering as larvae was greater than in species overwintering as pupae and higher in non-migratory species compared to migratory species (Hypothesis 7). Finally, univoltine species showed the lowest sensitivity to weather variables, particularly compared to species with variable voltinism that were most sensitive.

Between-species variation in weather-model prediction trends (β_{Vw_i}) varied strongly with UK latitudinal distribution (Hypothesis 6), habitat (Hypothesis 5) and pest status, accounting for 10% of the variance between species (Table 3). The effect of weather on long-term trends was most positive in the most southerly-distributed species, and most negative in northerly-distributed or widespread species. Species associated with woodland and unimproved grassland habitats showed more positive weather trends than those from other habitats. The modelled effect of weather upon trends was also significantly more positive for pest species than other species.

3.5. Impacts of climate change

Given strong inter-annual fluctuations in butterfly and moth populations which may have influenced the slope of the long-term trends, we regard the impacts of climate change as better assessed from changes in decadal averages (Fig. 2a & b). Between the 1980s and 1990s the mean observed and weather predicted decadal moth abundances remained stable ($\Delta n_{\text{moths},90s\text{-}80s} = -0.056 \pm 0.031$, P = 0.074; $\Delta n_{\text{Vw\_moths},90s\text{-}80s} = 0.037 \pm 0.024$, P = 0.13) while observed and decadal butterfly abundances increased by about 4% ($\Delta n_{\cancel{O}\text{butterflies},90s\text{-}80s} = 0.037 \pm 0.012$, P = 0.003) of which about 76% was consistent with the expectation from the weather-model predicted increase ($\Delta n_{\text{Vw\_butterflies},90s\text{-}80s} = 0.028 \pm 0.011$, P = 0.019). Between the 1990s and the 2000s moth populations declined by 28% ($\Delta n_{\text{moths},00s\text{-}90s} = -0.280 \pm 0.032$, P < 0.001), of which about 38% was consistent with the weather-model predicted expectations ($\Delta n_{\text{Vw\_moths},00s\text{-}90s} = -0.108 \pm 0.022$, P < 0.001), indicating the contribution that climate change may have made to the decline (Hypothesis 4). Between the 1990s and 2000s butterfly populations were largely stable ($\Delta n_{\text{butterflies},00s\text{-}90s} = -0.026 \pm 0.014$, P = 0.065; $\Delta n_{\text{Vw\_butterflies},00s\text{-}90s} = -0.010 \pm 0.009$, P = 0.306) (Fig. 2c).

Commented [EBD3]: Are these averages across species? I'm confused as I think the O in $\Delta n_{O,90s\text{-}80s}$ etc is an index for species but this is for multiple species? Similarly with the other comparisons

BM: hopefully clearer now. I've changed the "o" to "i" as I was getting confused about whether the O was for species or observed.

There was a significant correlation between observed and weather-predicted species-specific differences in abundance between the 1980s and 1990s (respectively $\Delta n_{i,90s\text{-}80s}$ and $\Delta n_{\text{Vw\_}i,90s\text{-}80s}$) ($F_{1,318} = 8.61$, $P < 0.0001$, $r^2 = 0.19$; Fig. 3a), that did not differ significantly between butterflies and moths (taxa * weather-trend interaction, $F_{1,319} = 0.01$, $P = 0.93$; taxa, $F_{1,318} = 0.15$, $P = 0.13$). Between the 1990s and 2000s there was also no difference in the correlation between observed ($\Delta n_{i,00s\text{-}90s}$) and weather-predicted differences in abundance ($\Delta n_{\text{Vw\_}i,00s\text{-}90s}$) between taxa (taxa * weather-trend interaction, $F_{1,318} < 0.01$, $P = 0.98$), although butterfly population trends were more positive than moths (taxa, $F_{1,318} = 9.24$, $P = 0.0026$) and there was again a strong correlation between observed and weather-predicted trends ($F_{1,318} = 33.06$, $P < 0.0001$, $r^2 = 0.13$; Fig. 3b).

Table 3. The results of the traits analysis, presenting the final models for Sensitivity and Weather trend, where the traits were selected by AICc.

Variable	**Parameter estimate**	**SE**
Sensitivity r^2=0.089		
Intercept	28.019	1.493
D3 (upland)	-2.746	1.356
F2 (larvae)	2.898	1.823
F3 (pupae)	-1.504	1.909
F4 (adult)	-1.923	4.336
F5 (migrant)	-20.889	6.803
G2 (variable voltinism)	5.519	1.721
G3 (obligate multivoltine 2 generations)	2.454	2.292
G4 (obligate multivoltine 3 generations)	7.391	7.950
Weather trend r^2=0.101		
Intercept	0.005	0.006
A UK latitude 2	-0.010	0.006
A UK latitude 3	-0.017	0.007
A UK latitude 4	-0.019	0.006
D1 (woodland)	0.007	0.004
D2 (unimproved grassland)	0.008	0.003
J Pest species	0.009	0.004

Table 4. Butterfly and moth population trends and modelled trends from the weather-related model to indicate the long-term impact of climate change. See methods and Table 2 for criteria used to categorise species' responses.

Climate response	**Weather-related trend**	**Observed trend**	**Butterflies**	**Moths**
Winner	Increase	Increase	5	9
Helped	Increase	Stable	11	30
		Decline	6	31
Unaffected	Stable	Increase	4	16
		Stable	9	49
		Decline	4	46
Hindered	Decline	Increase	2	10
		Stable	8	38
Loser	Decline	Decline	6	36

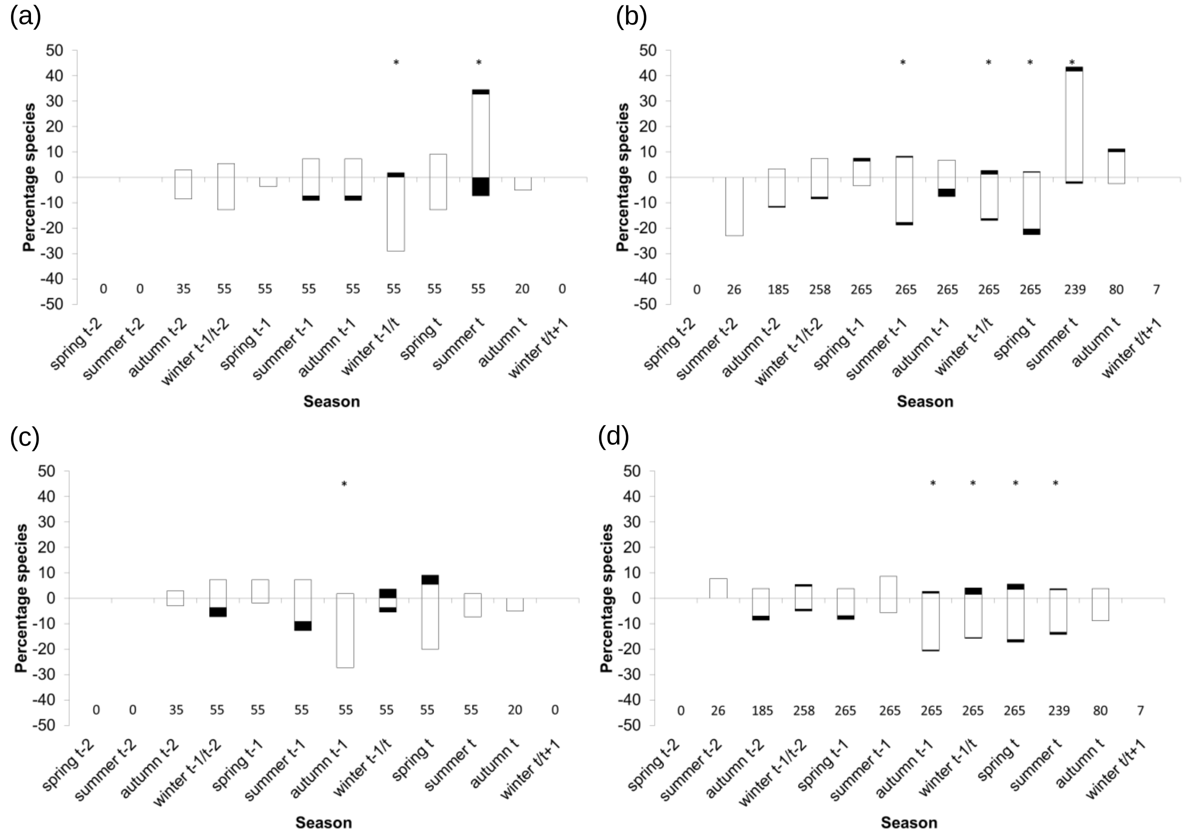
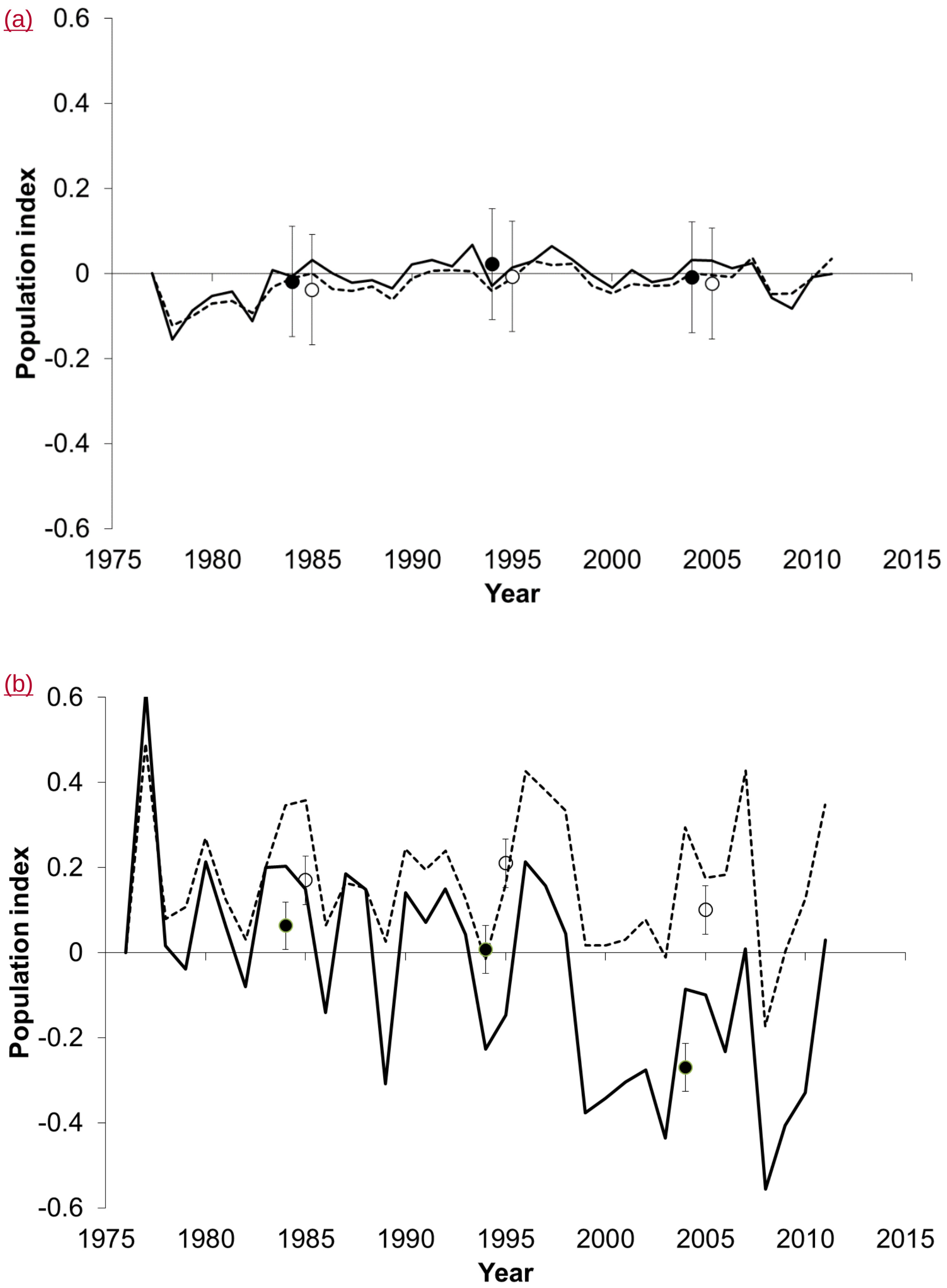


Fig. 1. Percentage of butterfly (left) and moth (right) species whose population growth rates correlate with seasonal temperature (top) and rainfall (bottom) variables, from the year in which the population was monitored (year$_t$) to two years prior to monitoring (year$_{t-2}$). The percentage of significant positive (above the line) or negative (below the line) relationships is shown by the open bars. The percentage of significant quadratic relationships with increasingly positive (above the line) or negative (below the line) relationships is shown by the black bars. Asterisks identify significant ($P < 0.001$) differences in the frequency of positive or negative relationships. The numbers under the bars indicate the number of species for which each variable was tested for; only species active and monitored in winter would have winter$_{t/t+1}$ (i.e. the winter in which their activity was monitored) included as a potential variable in their population models.


(a)
0.6
0.4
0.2
0
-0.2
-0.4
-0.6
Population index
1975
1980
1985
1990
1995
2000
2005
2010
2015
Year
(b)
0.6
0.4
0.2
0
-0.2
-0.4
-0.6
Population index
1975
1980
1985
1990
1995
2000
2005
2010
2015
Year

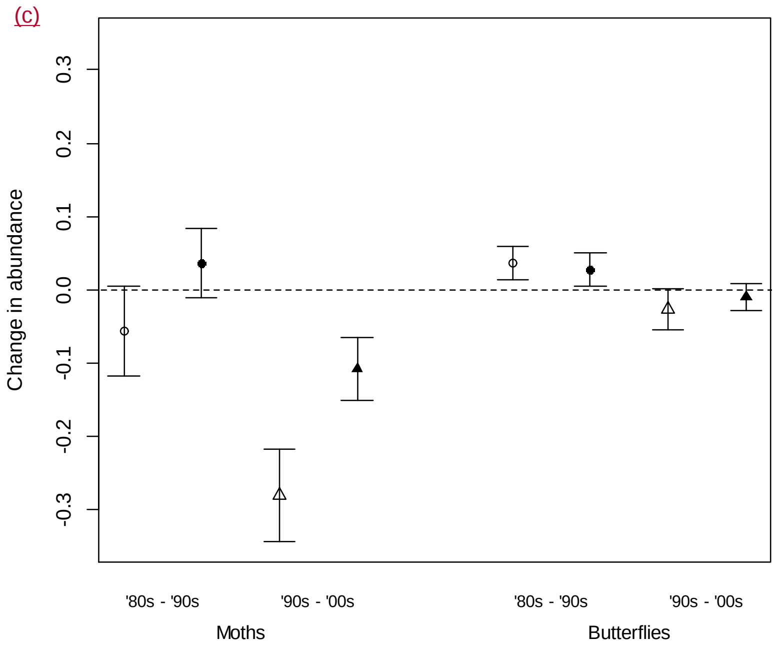
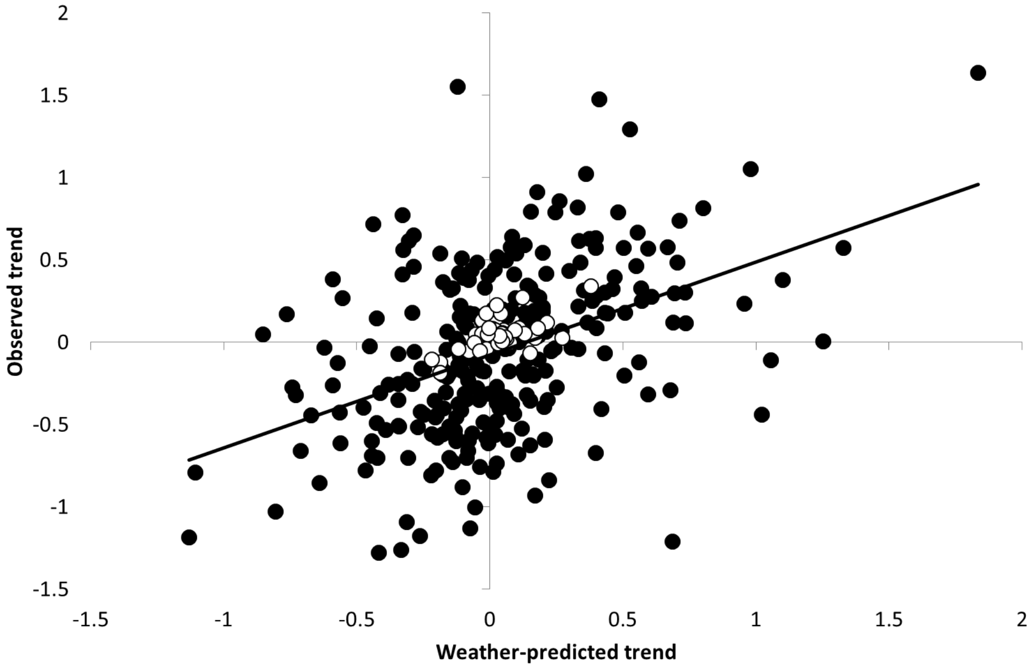
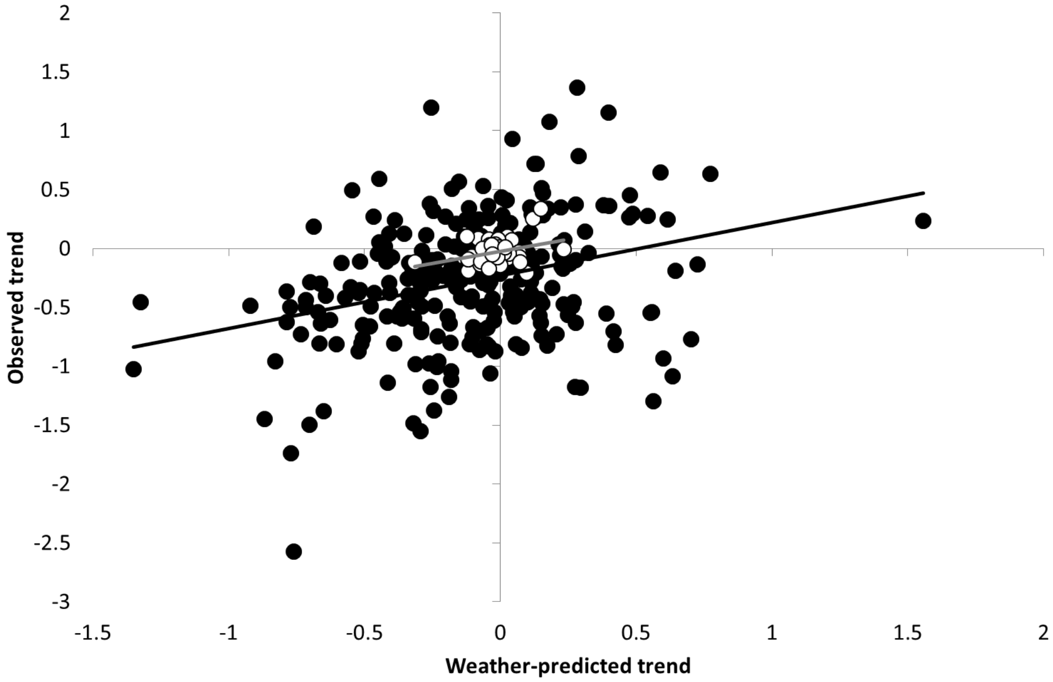


Fig. 2. (a & b) Multi-species mean observed (solid) and weather-predicted (dotted) population ~~trends~~ indices for buterflies (a) and moths (b). Decadal means (±s.e.) based on observed populations (filled) and weather- predictions (open) are shown for the 1980s, 1990s and 2000s. (c) Change in mean decadal abundance of moths (left side) and butterflies (right side) from the 1980s to the 1990s (circles) and from the 1990s to the 2000s (triangles). Observed abundance changes are shown with open symbols (left of pairs) and weather-predicted changes are shown with closed symbols (right of pairs).

Commented [EBD4]: Aren't these indices rather than trends? Also do we say in the methods how we combine the indices to get multi-species indices?

BM: You're right – it should be indices. We have removed the methods section on how we calculate the multispecies indices as we don't actually use them for anything except in this fig, and just for visualisation here. The methods for the decadal averages are included though.


Observed trend
2
1.5
1
0.5
0
-0.5
-1
-1.5
-1.5
-1
-0.5
0
0.5
1
1.5
2
Weather-predicted trend


Observed trend
2
1.5
1
0.5
0
-0.5
-1
-1.5
-2
-2.5
-3
-1.5
-1
-0.5
0
0.5
1
1.5
2
Weather-predicted trend

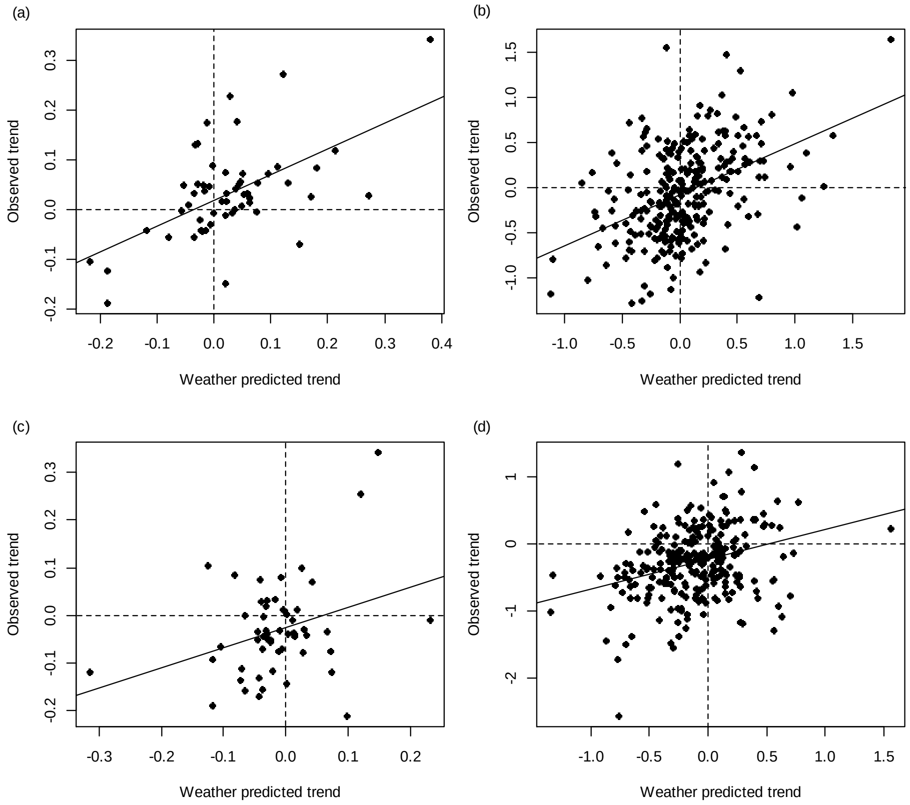


Fig. 3. Correlations between observed and weather-predicted changes in mean abundance from the 1980s to 1990s (~~top~~a & b) and 1990s to 2000s (~~bottom~~c & d) for butterflies (a & c) ~~open circles and grey line)~~ and moths (~~filled circles and black line~~b & d).

Commented [EBD5]: Is there a grey line in the top plot? If so I can't see it! Would it be better to have 4 subplots to separate butterflies and moths?

4. Discussion

The weather had a strong impact on the national abundance of butterflies and moths, accounting for over a quarter of the annual variation in abundance, and over 50% in 15 species (13 moths and 2 butterflies). Using information about the weather over the preceding two years, we can therefore model population growth rates of many species with a reasonably high degree of confidence, providing support for hypothesis 1.

Despite this, the evidence in support of hypothesis 4, that long-term population trends are driven largely by climate change, was more equivocal. From the 1980s to the 1990s there was no consistent effect of weather on overall UK moth populations while butterfly populations marginally benefitted from weather changes. However, between the 1990s and the 2000s, climate change (as measured by the contribution of weather to population growth rates and abundances between decades) contributed to a significant decline in overall moth abundance. Over the length of the time-series, climate change had a significant negative effect on 32% of moth species and 29% of butterflies. A greater proportion of butterflies were classified as climate change winners or helped (40%), but there were fewer moths (26%) in this category. Despite a lack of correlation between observed and weather-predicted trends across the entire time-series, there was a significant correlation between weather-predicted and observed mean abundances between both the 1980s and 1990s, and 1990s and 2000s. Given the weather-predicted trends are based upon free-running models, these findings suggest that across a 35-year timescale, error can propagate to reduce their predictive power, particularly given the stochastic nature of butterfly and moth populations which can make long-term trends sensitive to rapid changes in abundance. However, the significant relationships between observed and predicted changes in abundances between decades, and the modelled impact on moth population growth rates and abundances, particularly in the 2000s, indicate that climate change has probably reduced the abundance of many moth population during this period, and therefore contributed to the previously observed decline in moth populations (Conrad et al., 2004, 2006).

Research comparing climate and habitat change impacts on UK butterflies between 1977 and 2007 concluded that habitat factors were the main driver of change (Oliver et al., 2012). Our results are consistent with this finding. Moth declines have previously been attributed to both habitat changes in the agriculturally intensive lowlands (Fox et al., 2014) and climate change (Martay et al., 2017), which again, our results support. We estimate that about 40% of the moth decline from the 1990s to 2000s could be attributed to climate change as modelled by weather-related population trends, and 60% is therefore potentially due to other factors. Although moth populations are being driven by multiple factors, climate change appears to be a significant driver of change, particularly given their sensitivity to annual changes in the weather. The fact that the magnitude of impact increased in the most recent decade is consistent with the hypothesis of increasing impacts of climate change through time (hypothesis 4).

Although 40% of butterflies were predicted to have benefitted from climate change, fewer than 10% of species were clear winners with increasing populations matching weather-modelled trends. Of 18 butterfly species which have shown poleward range expansions over the sampling period attributable to climate warming (Fox et al., 2006), we identified only two of these as ‘winners’ with substantial population level increases (*Aphantopus hyperantus* and *Erebia aethiops*). There is a close link between the rate of population change and range expansion in butterflies, with evidence of declining abundance trends from the mid-1990s to 2009 limiting further range expansion (Mair et al., 2014). The weaker relationship between weather-predicted trends and observed trends from the 1990s to 2000s, compared to the 1980s to 1990s, suggests that many of the population increases and range expansions of the 1980s and 1990s could have been mediated by climate change, but that since then, other processes have become more important and limited continued increase and expansion. The ability of many butterflies to expand their distribution in response to warming is also limited by habitat availability (Warren et al., 2001; Oliver et al., 2012; Mair et al., 2014).

Sensitivity to weather was greatest in species which overwintered as larvae and were multi-voltine, but was lowest in migratory and upland species. Unsurprisingly, migratory species had low sensitivity to weather, as we did not include weather variables from their wintering grounds and migratory routes in the models. Low sensitivity to weather in upland species was surprising given previously identified vulnerabilities of some mountain butterflies to climate change (Franco et al., 2006), but could reflect a high availability of temperature ranges over small distances due to altitudinal gradients and microhabitats on mountainous ground. Alternatively, it may be a function of the greater uncertainty associated with the estimated population indices in such species, due to low monitoring coverage in uplands.

The sensitivity of species overwintering as larvae indicates that the negative impacts of winter warming are likely to be most important for these species, through the mechanisms of fungal or pathogenic attack, increased energy loss or mismatch, as described below. Multi-voltine species were more sensitive to weather than univoltine species but did not have increased weather-modelled population trends, suggesting that increasing generations per year will benefit some species, but drive declines in others. Increasing temperature can drive declines in multi-voltine species due to a disruption in synchrony with plant host species (Altermatt, 2010).

Weather-modelled population trends were most positive for southerly distributed species, providing support for hypothesis 6, and suggesting that climate change is likely to have played a part in facilitating the long-term northwards expansion of many butterfly and moth species (Warren et al., 2001; Mason et al., 2015). This is also consistent with previous analyses of butterfly trends across the UK and Europe indicating that species associated with warmer temperatures have increased in abundance relative to cold-associated species (Devictor et al., 2012; Oliver et al., 2017). In an analysis of UK moth communities across a gradient of long-term monitoring sites, northern and upland species declined in warmer years more than southerly-distributed species (Martay et al., 2016). Weather-modelled trends were more positive for species associated with woodland and unimproved grassland habitats. This supports previous work suggesting that semi-natural habitats may increase resilience to climate change (Oliver et al., 2015, 2017), although runs counter to the previous finding for birds (Davey et al., 2012), that impacts of climate change are more negative for habitat specialists compared to generalists (hypothesis 5). The predicted impacts of weather trends were also more positive for pest species than other species, indicating that climate change may play a role in driving population increases of agricultural and horticultural pests, which may be more adaptable to climate change (Cannon, 1998). Alternatively, many such species are also migratory, and therefore in warm years, UK populations may be boosted by immigration from continental Europe. There was therefore evidence across measures of both sensitivity and weather-modelled population trends that climate change impacts will vary with species' life-history traits (hypothesis 7), although actually the strength of such effects may be fairly limited.

The response of species to temperature and precipitation varied widely between seasons, strongly supporting hypothesis 2. Effects of temperature were consistently positive during the summer$_t$ for both butterflies and moths, but were negative during the winter$_t$ and for moths, during the spring$_t$ and previous summer$_{t-1}$ as well. Thus, although warm conditions during the summer boosted adult activity and survival, it appears that warming at other times of the year can have a detrimental impact on populations. The positive effects of summer warming on butterflies are well known (Roy et al., 2001; Warren et al., 2001; McDermott Long et al., 2017), but the negative effects of warm winter weather have only recently been documented for butterflies (Dennis et al., 2016; McDermott Long et al., 2017), and are further supported by our analysis. That such conditions may also affect moths, along with more negative impacts of temperature at other times of the year, is a novel finding, but is consistent with the recent finding that overall moth abundance may be sensitive to variation in temperature during summer, winter and spring months (Martay et al., 2016), and previous analyses on *Actia caja* populations in the UK (Conrad et al., 2002).

Several potential mechanisms have been suggested to underpin this negative impact of warm winters and springs. It may be mediated through increased fungal attack of overwintering life-stages (Radchuk et al., 2013), increasing metabolic rates over winter, draining energy reserves, and leading to poorer quality adults (Mercader and Scriber, 2008), or earlier emergence, leading to subsequent mismatch with environmental conditions (Wiklund et al., 1996). Negative lagged temperature effects in summer$_{t-1}$ may be related to drought conditions which can affect host plant growth and therefore reproductive success, and have previously been highlighted as being of concern for some butterfly species (Oliver et al., 2013, 2015). Although we did not find a consistent negative impact of summer $_{t-1}$ temperature across butterflies, it is noteworthy that the one species, *Aphantopus hyperantus*, showing a negative quadratic relationship with summer$_{t-1}$ temperature, and therefore most vulnerable to extreme summer temperatures has previously been identified as highly drought sensitive (Oliver et al., 2013). Fifty moth species showed negative relationships between summer $_{t-1}$ temperature and population growth rates, suggesting that they may be even more constrained by hot summer conditions than butterflies. Thus, despite the fact that greater numbers of species tend to exhibit positive relationships between summer$_{t}$ temperature than negative relationships with summer$_{t-1}$ temperature, some species are clearly sensitive to negative lagged effects of high summer temperatures and may therefore be particularly vulnerable to climate warming

(Supplementary material, Appendix C~~S2~~). Negative lagged effects of summer heat have also been identified for various bird species (Pearce-Higgins et al., 2010; Pearce-Higgins et al., 2015a), suggesting more broadly that the ecological impacts of extreme summer heat may be immediately apparent, but manifest only in subsequent years. Conversely, periods of high precipitation from autumn$_{t-1}$ to summer$_t$ were detrimental to many moth species. Whilst immediate negative impacts of summer$_t$ rainfall are probably related to impacts on activity and adult survival, rainfall at other times of the year, particularly in autumn and winter, may promote fungal attack overwinter (Radchuk et al., 2013).

Relatively few non-linear relationships were identified. Quadratic relationships with weather variables would be expected if extreme weather events had a disproportionate impact on populations. Whilst as just discussed, there are clearly some species which are sensitive to extreme conditions, such as summer drought (see also Oliver et al., 2013, 2015), our results suggests that it is not the response to those extreme events which have so far driven recent population trends (see also Palmer et al., 2017). Thus, hypothesis 3 is rejected, although given that extreme events are rare within a 35-year time-series, they may still be important in the future.

Although we believe that this study is a significant advance in documenting the species-specific climate change impacts on UK Lepidoptera, and estimating the totality of that impact across species, it does have a number of limitations. Firstly, we examined the response of national population trends to nationally-averaged climate data, which may hide climate-change or habitat impacts if a species is increasing in some areas and declining in others. This may also decrease our ability to identify the impact of extreme weather events, especially if they are local events (Oliver et al., 2013). However, our results are broadly consistent with those of McDermott Long et al. (2017), who also identified few responses to extreme events in butterfly populations using local data. Indeed, given the potential for local adaptation in populations to climate (Roy et al., 2015), our national-scale approach may be more appropriate for documenting large-scale climate change impacts. A second drawback is that non-climate factors were characterised by the model intercept, year and a quadratic year term, rather than being modelled directly. Whilst this means that we cannot identify important non-climatic factors, we were able to at least partially account for such effects; the model intercept allowed a constant non-weather model prediction trend to be identified and two terms relating to year allowed a cubic relationship between population abundance and non-climate factors (i.e. a quadratic relationship between population change and non-climate factors). Thus habitat factors that changed over time would be included in the model provided that the fluctuations occurred over a long-term basis, although any influential non-climatic factors that fluctuated annually would not be modelled well using this approach. It is also worth noting that a stable population growth rate contributed to the weather only prediction, which may not always be biologically accurate in some circumstances. Conversely, some variation due to long-term climate change may also have been soaked up by the year terms, wrongly attributing some long-term impacts of climate change to non-weather factors. Despite these limitations, our results generally mirrored previous research into climate change impacts where equivalent studies were available, and the good descriptive power of our models at the national-level is encouraging.

To conclude, we have documented that moth and butterfly populations fluctuate strongly in relation to inter-annual variation in weather conditions. These conditions have deteriorated during the 2000s for many moths, leading to a 24% decline in average moth populations, 43% of which is consistent with an impact of climate change. This closely matches the estimated 48% contribution of climate change to the decline in moths in the UK from the 1970s to 2011 derived independently by Martay et al. (2017) using an ordination approach. This adds to the evidence that climate change has exerted a significant downward pressure on moth populations, although clearly other factors have also contributed significantly to their decline. There was strong interspecific variation in the impacts of climate change with species in both groups having apparently increased in response to climate change, and others having declined. A significant proportion of this inter-specific variation can be attributed to the modelled impact of weather variables through time. Although our trait-based models were only able to account for a limited amount of variation between species, species overwintering as larvae, and multivoltine species, appeared most sensitive to the effects of weather. Southerly-distributed species were those most likely to have benefited from climate change, along with woodland, unimproved grassland and pest species. Climate change is therefore already having a major impact on the abundance of some butterfly and moth species, with potential implications for their conservation. More broadly, it is also leading to a general decline in national moth populations, as previously documented for a single species by Conrad et al. (2002), and by Martay et al. (2017). Given the importance of these species as pollinators, as keystone species within ecosystems and food webs, and in some cases, as agricultural and horticultural pests, these declines have wide implications for ecosystem health and functioning, for natural capital and if they lead to impacts on food production, for human health and wellbeing (Fox et al., 2010). Given projected trends for warmer, wetter winters in the UK due to future climate change (Jenkins et al., 2009), these trends are likely to be exacerbated in the future.

Acknowledgements

This work was funded by Natural England, Butterfly Conservation (BC) and the British Trust for Ornithology (BTO). The UKBMS is run by BC, the Centre for Ecology and Hydrology (CEH) and the BTO, in partnership with the Joint Nature Conservation Committee (JNCC), and supported and steered by Forestry Commission (FC), Natural England (NE), Natural Resources Wales (NRW), Northern Ireland Environment Agency (NIEA), and Scottish

Natural Heritage (SNH). Light-trap data were provided by the Rothamsted Insect Survey, a BBSRC-supported National Capability. Rothamsted Research is a national institute of bioscience strategically.

Supplementary data

Appendix A. Excel spreadsheet of seasonal trends in UK and English temperature and precipitation between 1976 and 2010.

Appendix B. Excel spreadsheet of species, model coefficients, trends and classification as presented in Table 4.

Appendix C. Excel spreadsheet of data on observed, full predicted and weather-model predicted indices, enabling species-specific plots to be produced.

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~~**Appendix S1. Excel spreadsheet of seasonal trends in UK and English temperature and precipitation between 1976 and 2010.**~~

~~**Appendix S2. Excel spreadsheet of species, model coefficients, trends and classification as presented in Table 4.**~~

~~**Appendix S3. Excel spreadsheet of data on observed, full predicted and weather-model predicted trends, enabling species-specific plots to be produced.**~~