Sensitivity of UK Butterflies to local climatic extremes: Which life stages are most at risk?

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Abstract

1. There is growing recognition as to the importance of extreme climatic events (ECEs) in determining changes in species populations. In fact it's often the extent of climate variability that determines a population's ability to persist at a given site.
2. This study examined the impact of ECEs on the resident UK butterfly species (n=41) over a 37 year period. The study investigated the sensitivity of butterflies to four extremes (Drought, Extreme Precipitation, Extreme Heat, Extreme Cold), identified at the site level, across each species' life stages. Variations in the vulnerability of butterflies at the site level were also

compared based on 3 life history traits (voltinism, habitat requirement, and range).

3. This is the first study to examine the effects of ECEs at the site level across all life stages of a butterfly, identifying sensitive life stages and unravelling the role life history traits play in species sensitivity to ECEs.

4. Butterfly population changes were found to be primarily driven by temperature extremes. Extreme heat was detrimental during overwintering periods and beneficial during adult periods and extreme cold had opposite impacts on both of these life stages. Previously undocumented detrimental effects were identified for extreme precipitation during the pupal life stage for univoltine species. Generalists were found to have significantly more negative associations with ECEs than specialists.
5. With future projections of warmer, wetter winters and more severe weather events, UK butterflies could come under severe pressure given the findings of this study.

Key-words Butterfly population changes, climate change, life history traits, linear mixed effects model, sensitivity

Introduction

Climate change is causing direct and substantial changes to biodiversity and to entire ecosystems (Cramer *et al.* 2014); species have been altering their growth, phenology, and distribution (Root *et al.* 2003; Møller, Rubolini & Lehikoinen 2008; Chen *et al.* 2011). While species are changing their distribution in an attempt to track the climatic conditions optimal for their survival, i.e. their climatic niche, their ability to do so is often limited. Some species are lagging behind the high velocity of climate change (Loarie *et al.* 2009; Bertrand *et al.* 2011; Devictor *et al.* 2012) resulting in range contractions (Foden *et al.* 2007). Both widespread and range restricted species are projected to have range losses and/or increased extinction risks as a result of changes in mean climate (IPCC 2007; Warren 2011; Foden *et al.* 2013; Warren *et al.* 2013).

Most attribution of climate change impacts on biodiversity (Parmesan, Root & Willig 2000; Root *et al.* 2003; Chen *et al.* 2011; Doney *et al.* 2012), and the projection of future impacts (Pereira *et al.* 2010; Bellard *et al.* 2012; Pacifici *et al.* 2015), is based upon the observed or projected change in mean climate, however the impacts of climatic extremes, such as heatwaves, heavy rainfall, and droughts are much less frequently studies and the rate and magnitude of these events is likely to increase in the future (IPCC 2012; Jones *et al.* 2014).

Extreme climate events (ECEs) have been shown to directly affect species populations by influencing reproductive and mortality rates (Jiguet, Brotons & Devictor 2011). Changes in climate variability, as a result of climate change, leading to changes in the magnitude and frequency of ECEs may be more important for determining whether a species can persist in a given location, than are modest increases in average temperature (Parmesan *et al.* 2000; Bauerfeind & Fischer 2014).

Butterflies have been used to demonstrate ecological examples of species' responses to climate change (Parmesan *et al.* 1999; Warren *et al.* 2001; Wilson *et al.* 2005; Franco *et al.* 2006; Thomas, Franco & Hill 2006; Pöyry *et al.* 2009; Diamond *et al.* 2011) and due to their ectothermic characteristics are a good taxonomic group to look at effects of extreme climatic events. ECEs, such as drought and heavy precipitation events, have been shown to be detrimental to the survival of butterflies, causing local extinction events (McLaughlin *et al.* 2002; Oliver *et al.* 2015) which highlights the importance of incorporating these ECEs in ecological studies (Easterling *et al.* 2000; Jentsch & Beierkuhnlein 2008; Smith 2011; Fischer, Klockmann & Reim 2014). Warmer, wetter winters have been negatively associated with changes in population growth rates as has heavy rainfall (Pollard 1988; WallisDeVries, Baxter & Van Vliet 2011).

Univoltine and multivoltine species are under different selective pressures due to differing numbers and timings of life stages. Life stage can be incorporated into the analysis to allow identification of sensitive stages within a butterfly's lifecycle to particular extremes (WallisDeVries *et al.* 2011; Radchuk, Turlure & Schtickzelle 2013).

Impacts of ECEs can be examined at a large scale (Pollard 1988; Roy *et al.* 2001; WallisDeVries *et al.* 2011) or take into account site specific information to avoid hiding population losses in one area due to gains in another (Wilbanks & Kates 1999). By analysing the impacts of ECEs at site level these losses and gains can be unmasked, allowing for attributions to be identified that may not have been in a broader scale study (Pearce-Higgins 2011; Newson *et al.* 2014). Site specific differences may be a function of a species' local site adaption to regional climate variables (Ayres & Scriber 1994) and habitat availability and characteristics also affect species responses to ECEs. Oliver *et al.* (2015) showed that reducing habitat fragmentation was effective at countering negative drought effects on butterfly populations and reducing landscape-scale habitat fragmentation may influence a species ability to withstand weather-mediated population declines (Newson *et al.* 2014).

ECEs have been defined using specific arbitrary thresholds (WallisDeVries *et al.* 2011), such as extreme heat being anything above 30°C. This only identifies heat as an issue during the summer, excluding the possibility that heat may also play a role during other periods of the year and other stages of a species' life cycle.

This study takes a new approach to identifying species responses to extremes, accounting for both the life stage and site specific effects thus providing a more dynamic and biologically relevant approach in identifying climatic extremes for an organism. This study aims to assess the impacts of ECEs on UK species over the 37 year period from 1976- 2012. This study will (i) examine the influence of ECEs on butterfly population change over a 37 year period; (ii) determine which butterfly life stages are sensitive to which ECEs and (iii) determine whether butterfly population changes are more associated with extremes of temperature or precipitation?

Materials and Methods

The Datasets

The butterfly dataset – UKBMS

Site level butterfly population indices were obtained from The UK Butterfly Monitoring Scheme (UKBMS), a comprehensive dataset for UK Butterflies consisting of records from thousands of volunteers across the UK. This data covers a period from 1976 (38 monitored sites) to 2012 (878 monitored sites). In total over the 37 year period there have been 1,802 different recording sites. At monitored sites, weekly counts of adult butterflies were made over a 26 week period between the beginning of April and the end of September on fixed routes provided the weather conditions were favourable for butterfly activity (Pollard & Yates 1993). This procedure is repeated yearly allowing for comparisons between years at that particular site but also between sites. Full details of the sampling methodology can be found in (Pollard, Hall & Bibby 1986). Population indices are based upon all generations that fall within the recording period, the indices are not split by generation.

Species with fewer than 10 sites and/or less than 15 years of data were removed from the analysis as in (WallisDeVries *et al.* 2011) limiting the number of species included in the analyses to 41 of the 59 regularly occurring UK butterflies. A separate model was created for each species to account for different lifecycle timings, numbers of generations and overwintering strategies.

Information on life history traits (voltinism: univoltine / multivoltine, species range: Northern range limited / widespread species, habitat generalist / habitat specialist species) were collated using (Asher *et al.* 2001).

The weather observations dataset

Daily maximum, minimum temperature and precipitation data on a 0.25 degree regular lat/long grid were obtained from the E-OBS dataset for the UK between 1950 and 2012 (Haylock *et al.* 2008). Site specific daily data was extracted using the latitude and longitude of the survey sites from the UKBMS dataset. For more information on how the data is interpolated into its gridded format see (Haylock *et al.* 2008).

Identification of Extreme Weather Events and their biological relevance

Calendar dates were identified for all life stages of each butterfly (Ovum, Larvae, Pupae, Adult and Overwintering) according to their phenology (Eeles 2014). Overwintering period was set as a fixed period for all species (WallisDeVries *et al.* 2011), starting on the 1st of November and finishing on the 28th of February. The phenology of each species can vary from year to year in addition to the site to site variation (Van Strien *et al.* 2008; WallisDeVries *et al.* 2011). In this study we use fixed phenology dates for the butterflies to identify the start and end of each lifecycle for 37 years of data which the UKBMS covers.

Once the phenologies of each life stage for each species were identified, the climate data set was used to detect and extract any extreme climate events occurring during each life stage for each species at each site based on all 63 years covered by the climate data. Four types of ECEs were defined using site and species-specific thresholds, and the number of days exceeding that threshold was calculated (WallisDeVries *et al.* 2011), Table 1.Two standard deviations was chosen to set the extremes for temperature (Beaumont *et al.* 2011) and the 97.5 percentile to set extremes for precipitation as they were hypothesised to identify temperatures and precipitation beyond the climatic norm for species in each area. This was carried out at the site level over the 63 year period covered by the E-OBS dataset. All extremes were defined as the number of days exceeding the threshold criteria identified by the above methods for a given butterfly's life cycle stage.

The ECE definitions adopted give more flexibility, biological application and meaning in relation to time of the year and location of the extreme impacts than arbitrary thresholds. Each extreme is tailored specifically to each individual species. In addition to this it accounts for the historical climate a species has experienced at a given site for a given life stage. Arbitrary thresholds of temperature, such as 30°C used in previous studies, limit our capacity to understand how temperature may affect life stages that do not fall during the hottest periods of the year. This study uses site and species specific life stage climatic extremes enabling an understanding of how extremes occurring in different stages of the life cycle may impact on population change.

Statistical Analysis

Species-specific models

Species-specific linear mixed models were built which relate the annual adult butterfly abundance of a particular species to the ECEs previously identified for the different stages of that butterfly species' life cycle: ovum, larva, pupa, adult, (repeating in multivoltine species) and overwintering period. These models assess the impacts that identified extremes during each butterfly's life stages had on the butterfly's adult population across the UK. The dependent variable was chosen as the log of the indices of adult abundance from one year to the next and was used rather than just the indices for adult abundance in order to satisfy model assumptions of normality. The log transformation has been used as in similar studies (Roy *et al.* 2001; WallisDeVries *et al.* 2011) to account for the varying numbers of butterflies present at a site (Freeman 2009). Site was included as a random variable (Mair *et al.* 2014) to account for site specific adaptation between different populations of the same species due to issues such as habitat differences amongst sites. Counts of the number of ECEs identified for the different stages of that butterfly species' life cycle: ovum, larva, pupa, adult, and overwintering period were incorporated as fixed explanatory variables. Backwards stepwise selection using Akaike's Information Criterion (AIC) as recommended by (Thiele 2012) was used to remove variables that don't explain the variation in butterfly populations. Due to the possibility that several models may fit our data suitably well, the Pdredge function in the *MuMIn* package in R statistical software was used to dredge for all the possible model options using the variables selected for by the backwards stepwise selection. Any model with a Δ AIC of less that 4 was deemed similar to the best fit model and was incorporated in the model averaging which has been increasingly backed and applied in similar studies and is recommended for prediction and forecasting (Thiele 2012).

Combined univoltine and multivoltine models

Linear models were created by separating univoltine from multivoltine species and combining all species in each group to run a combined model for univoltine and multivoltine species. It displays the differences in response of the butterflies based on their voltinism. It also helps to understand the relative importance of variables found as being significant in the individual species models when looking at them from a univoltine and multivoltine perspective. The relative importance of each variable within the combined models was assessed using the package *relaimpo* (Grömping 2006) in R and defined as the percentage contribution of each predictor to the R^2 of the model. It allows us to give statistical support relevance to counts of variables gained from species-specific models.

Life history traits sensitivity to ECEs comparison: Welch t tests.

Welch t tests were used to make comparisons between species with different life history traits and their response to ECEs. Comparisons were based on the mean percentage of negative responses in relation to total number of possible variables from the individual species models when divided and grouped based on their life history traits.

Results

Which life stages are affected by which ECEs?

The percentage of species for which an extreme affected a certain life stage varied depending on voltinism. Thus results are presented for univoltine and multivoltine species separately. All quoted percentages in the results for species affected are based on significant effects in the individual species models.

Univoltine Species

The adult and overwintering life stages are the most sensitive for 29 univoltine species (Fig 1.). Extreme heat during the overwintering life stage and extreme cold during the adult life stage are the most frequently occurring negative extreme variables both causing population declines (affecting 45% and 35% of species respectively). Adult and overwintering life stages have opposing population responses to temperature extremes, extreme heat during the adult life stage is causes positive population change for 21% of species, while during overwintering it is associated with negative population change in 45% of species. Another extremely important variable to which univoltine species are vulnerable to is extreme precipitation during the pupal life stage affecting 28% of species. Drought appears to impact on the adult stage most negatively, 24% of the species, but appears to be beneficial during the ovum life stage also for 24% of species which is shown in the combined species model to be more importance for univoltine butterfly population change than its negative impacts, Table. 2. The combined model, including all univoltine species, identifies which of the variables from the species specific models to focus on when considering response of univoltine species. The first 5 variables account for 73.6% of the predictive power of the combined model (Table. 2). Extreme heat in the overwintering stage and precipitation in the pupal stage have strong negative effects on univoltine butterfly population trends. Extreme heat in the adult and pupal life stage drive positive population change in univoltine species. In summary, univoltine species seem particularly sensitive to temperature extremes at both ends of the scale (Heat or Cold) and it is the adult and overwintering phases that are vulnerable to these extremes. In addition to this, extreme precipitation during the pupal life stage is a detrimental driver of population change in a number of univoltine species.

Multivoltine Species

Extreme heat during overwintering and extreme precipitation during 1st and 2nd generation adult life stages are the most frequently occurring extreme variables causing population declines in multivoltine species (67%, 58% and 50% of all multivoltine species affected respectively, Figure 1). As in univoltine species, adult and overwintering life stages have opposite population responses to temperature extremes. Extreme heat during the adult life stage is associated with positive population change in 42% of species. Drought plays a much more important role in multivoltine species than univoltine species. Drought negatively affects 50% of species during their 2nd larval life stage but has a positive impact on 25% of the species during their 1st ovum life stage. In the model combining all multivoltine species, the 9 most important variables account for 73% of the predictive power of the combined multivoltine model (Table 3). The multivoltine model is clearly driven by extremes of temperature, five were extremes in heat and one a cold extreme. Unlike univoltine species however, multivoltine seem to be susceptible across all life stages with ovum, larvae, pupae, adult and overwintering all being represented in the nine most important variables in the combined model. Species' vulnerability to extremes appears to be most prominent in the 1st generation and is primarily driven by exposure to extreme heat with the exception of the negative impacts of precipitation during the adult stage. Multivoltine species have a significantly higher proportion of negative responses to ECEs across their life stages than univoltine species ($t_{(25)}$=-2.86, p=0.008), Table 4. The results suggest that multivoltine species are more sensitive to extremes than univoltine species.

Within univoltine species there is no significant difference in the number of negative responses when comparing specialist with generalist species ($t_{(20)}$=-1.6, *p*=0.122) Table 4.

There is no significant difference between widespread and northern range limited species nested in univoltine species, ($t_{(20)}$= 1.69, *p*=0.102) Table 4. However when nested in multivoltine species, widespread species show more responses to extremes across their life stage than northern range limited species ($t_{(8)}$=3.76, *p*=0.004) Table 4.

Discussion

UK butterfly populations are influenced by extreme climatic events. Extreme temperature events play a significant role in determining the population changes in species from year to year in both multivoltine and univoltine species. Previous studies found that cold weather during the adult phase negatively affect population change, while warm weather has positive associations to population (Calvert, Zuchowski & Brower 1983; Roy *et al.* 2001; Warren *et al.* 2001; WallisDeVries *et al.* 2011). The benefit of heat on butterfly populations is to be expected given their poikilothermic nature. This study examined the effects of extreme temperature and precipitation variables on all butterfly life stages, for both univoltine and multivoltine species. For UK butterflies the overwintering stage was found to be particularly sensitive to extremes. Butterfly populations are negatively affected by hotter temperatures while overwintering and benefit from colder winters. This concurs with previous studies such as (Radchuk *et al.* 2013; Oliver *et al.* 2015) who found in their laboratory experiments that the overwintering larval stage was extremely sensitive to increases in temperature. This study identified negative associations of high temperatures during the overwintering stage but did not find that this sensitivity was confined to species overwintering in their larval stage. Radchuk *et al.* (2013) argue that elevated temperatures during the overwintering period increase rates of mortality due to increased incidences of disease and fungi both of which are more abundant in milder winters (Harvell 2002). Whilst this may be the case, we hypothesise that in the case of butterflies overwintering as larvae or adults it may be due to extreme hot temperatures acting as a cue for butterflies or their larvae to come out from overwintering too early, decoupling from photoperiod cues, (Wiklund, Lindfors & Forsberg 1996) and subsequently killed off by temperatures returning to colder conditions or potentially the destruction of their food plant due to similar mechanisms (McLaughlin *et al.* 2002).

This study did not account for annual variation in butterfly phenology (Van Strien *et al.* 2008), the life stage periods were fixed based on the average of the last 37 years thus life stage exposure to extremes may have been less well quantified in years or sites with advanced or delayed phenology. Overall our approach is likely to be robust since it accounts site variability (by including the effects of climatic extremes at the site level), and includes a long-term data set (37 years) to quantify country wide species population responses to ECEs. These results should not be extrapolated beyond the UK due to issues such as local adaptation, it is prudent to expect potential differences in the responses of continental European populations of the same butterflies.

Single generation vs multi-generation species

All life stages for univoltine species showed sensitivity to ECEs during the overwintering stage, with extreme cold events being beneficial and extreme heat detrimental on butterfly populations. One of the more prominent and consistent negative contributors to univoltine species' population change is precipitation events during the pupal and larval periods. This is an important finding as it hasn't been identified in previous studies but would be expected from heavy rainfall events (Pollard 1988). Indeed, Hill *et al.* (2003) have previously hypothesised the potential importance of precipitation having a detrimental impact on both the larval and pupal stage, which is clearly supported by our analysis of univoltine species. The impacts of drought are difficult to interpret in this study as species do not seem to respond as uniformly to this extreme as the other extremes. However, during the ovum life stage our combined species models have indicated it plays an important and significant role in determining increases in population size.

It would appear that univoltine species prefer warmer, drier climates outside of winter periods. Current predictions forecast that the UK will have a warmer climate with drier summers (Jenkins *et al.* 2009) which on the face of it would seem to benefit most univoltine species however this may not be the case as warmer, wetter winters could potentially be a driving force behind many population changes as in (Radchuk *et al.* 2013).

Temperature extremes are the primary driving factor when analysing the impact of ECEs on multivoltine butterfly populations. As in the univoltine species, hot weather during overwintering period is negative with extreme cold being beneficial. The adult stage is extremely sensitive to extremes in temperature but primarily the second generation stage, Table 3. This is probably due to the timing of the second generation for most multivoltine species, which have their flight period during summer. Temperature has been shown to be extremely important during these summer periods (Roy *et al.* 2001). Similar to the univoltine species, multivoltine appear to be positively impacted by drought conditions during the 1st generation ovum and adult stages. This apparent benefit of drought may indicate that the levels of drought identified in this study are not at a level that is detrimental to butterflies.

Our analysis shows that univoltine species are less sensitive to ECEs than multivoltine species. These results need to be interpreted with caution taking into account the small number of multivoltine (n=12) species included in the analysis. This may be a due to exposure to extremes during more life stages, more generations in a year may put more selection pressures on a species. (Radchuk *et al.* 2013) emphasise the importance of a resource based habitat approach and it is clear that more life stages would put more selection pressures on the species or potentially due to the fact that an extreme in one year can affect two consecutive generations when life stages overlap.

Generalists vs specialists

Generalist species have more significant negative associations with ECEs than specialist species. This suggest that ECEs may affect population change in generalist species, especially in populations on the edge of their climatic range (Hellmann *et al.* 2008), while population change of habitat specialists species is controlled by other factors (e.g. habitat loss and degradation) (Warren *et al.* 2001). We hypothesise that generalist species are more vulnerable as they are filling their climatic niche and hence many populations within the species range may be situated on the climatic range edge and be more vulnerable to increased climate variability outside of their comfort zone. In contrast specialist species are confined to particular host plants which may not ubiquitous across the specialist species' climatic niche, hence those specialist species are not filling their climatic niche and are effectively in or close to their core range and are not subjected to ECEs that are outside their ability to adapt and cope. It is also possible that specialist species are being buffered by their habitats where they have been able to persist (Oliver, Brereton & Roy 2013).

Widespread vs Northern range limited species

No significant difference in the number of negative associations between widespread and northern range limited species was found when nested within univoltine species. The opposite was found for multivoltine species with widespread species having significantly more negative associations when nested in multivoltine species. These results need to be interpreted with caution as mentioned previously. If validated this result may indicate that widespread species may be subjected to a much higher variation in climatic conditions than northern range limited species and as such may be subject to temperatures and precipitation levels that are detrimental.

Conclusion

This study has identified a hitherto unknown sensitivity of univoltine species to extreme precipitation during their pupal life stage. In addition, this study although using novel ECE definitions, found an agreement with previous studies, indicating that warm and even climatically extreme hot summers are beneficial to butterfly populations, while extremely wet cold summers are detrimental to their populations. The detrimental effect of extreme heat during overwintering has been evidenced previously but fewer studies have shown the sensitivity of the pupal stage to extreme precipitation events and warrants further attention. Interestingly the perceived sensitivity of butterflies to drought (Oliver *et al.* 2015) was not evidenced in our analysis but this could be due to limitations in our definition of drought.

Sensitivity to ECEs in butterflies was primarily dominated by temperature extremes which would support our hypothesis that butterfly population changes are more dependent on heat extremes as shown by both the combined species models and the proportion of species affected in the species specific models. This study has identified scope for future work. An interesting augmentation of this study would be to identify dramatic species decline events and examine the extent to which they are associated with ECEs. Finally, building on the work of (Oliver *et al.* 2015), further analysis is warranted on the ability of habitats to buffer extremes other than drought that have been identified as being detrimental by this study. Extreme wind could be factored into future studies also. Unfortunately, the appropriate data was not available through the weather sources used in this paper.

The novel identification of the sensitivity of the pupal life stage to extreme precipitation supports our decision to address the impacts of extremes at a finer scale than previous studies and has also shown the importance of looking at ECEs across all life stages given these relatively new findings.

This study has shown that butterflies could potentially benefit from increasing temperatures in the UK in the future but warmer and wetter winters and increases in severe weather events that have also been predicted (Defra 2009; Jenkins *et al.* 2009) could be detrimental to the survival of many of its butterfly species and further research is needed regarding the balance of importance that these variables could have and whether the benefits of warmer summers will be outweighed by the detrimental winter effects. Based on the results of this study, future conservation efforts hoping to mitigate against ECEs in the future should focus their efforts on the adult and overwintering life stages of UK butterflies.

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Data accessibility

Weather data (E-OBS dataset) available from http://www.ecad.eu/download/ensembles/download.php (Haylock *et al.* 2008).

The UKBMS (Butterfly) database is managed and maintained by the Biological Records Centre, based at the Centre for Ecology & Hydrology (CEH). Access to population indices available from the CEH Data catalogue http://doi.org/10.5285/378f0f77-1842-4789-ba15-6fbdf7d02299 (Botham *et al.* 2016).

References:

Asher, J., Warren, M., Fox, R., Harding, P., Jeffcoate, G. & Jeffcoate, S. (2001) *The Millenium Atlas of Butterflies in Britain and Ireland*. Oxford University Press, Oxford.

Ayres, M.P. & Scriber, J.M. (1994) Local adaptation to regional climates in Papilio canadensis (Lepidoptera: Papilionidae). *Ecological Monographs*, **64**, 465–482.

Bauerfeind, S.S. & Fischer, K. (2014) Simulating climate change: Temperature extremes but not means diminish performance in a widespread butterfly. *Population Ecology*, **56**, 239–250.

Beaumont, L.J., Pitman, A., Perkins, S., Zimmermann, N.E. & Yoccoz, N.G. (2011) Impacts of climate change on the world 's most exceptional ecoregions. *Proceedings of the National Academy of Sciences of the United States of America*, **108**, 2306–2311.

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.

Bertrand, R., Lenoir, J., Piedallu, C., Riofrio-Dillon, G., de Ruffray, P., Vidal, C., Pierrat, J.-C.J.-C., Gegout, J.-C., Riofrío-Dillon, G. & Gégout, J.-C. (2011) Changes in plant community composition lag behind climate warming in lowland forests. *Nature*, **479**, 517–20.

Botham, M., Roy, D.B., Brereton, T. & Middlebrook, I. (2016) United Kingdom Butterfly Monitoring Scheme: site indices data 2015.

Calvert, W., Zuchowski, W. & Brower, L. (1983) The Effect of Rain, Snow and Freezing Temperatures on Overwintering Monarch Butterflies in Mexico. *Biotropica*, **15**, 42–47.

Chen, I., Hill, J.K., Ohlemüller, R., Roy, D.B. & Thomas, C.D. (2011) Rapid range shifts of species of climate warming. *Science*, **333**, 1024–1026.

Cramer, W., Yohe, G.W., Auffhammer, M., Huggel, C., Molau, U., da Silva Dias, M. a. F., Solow, a., Stone, D. a. & Tibig, L. (2014) Detection and Attribution of Observed Impacts. In: Climate Change 2014: Impacts, Adaptation and Vulnerability. Part A: Global and Sectoral Aspects. Contribution of Working Group II to the Fifth Assessment Report of the Intergovermental Panel on Climate Ch. *Climate Change 2014: Impacts, Adaptation and Vulnerability. Contribution of Working Group II to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change*, p. Cambridge University Press, Cambridge, UK and New York, NY, USA.

Defra. (2009) Adapting to climate change UK Climate Projections. *Uk Climate Projections*, 52.

Devictor, V., van Swaay, C., Brereton, T., Brotons, L., Chamberlain, D., Heliölä, J., Herrando, S., Julliard, R., Kuussaari, M., Lindström, Å., Reif, J., Roy, D.B., Schweiger, O., Settele, J., Stefanescu, C., van Strein, A., van Turnhout, C., Vermouzek, Z., WallisDeVries, M.F., Wynhoff, I. & Jiguet, F. (2012) Differences in the climatic debts of birds and butterflies at a continental scale. *Nature climate change*, **2**, 121–124.

Diamond, S., Frame, A., Martin, R. & Buckley, L. (2011) Species' traits predict phenological responses to climate change in butterflies. *Ecology*, **92**, 1005–1012.

Diaz, H.F. & Murnane, R.J. (2008) *Climate Extremes and Society* (eds HF Diaz and RJ Murnane). Cambridge University Press.

Doney, S.C., Ruckelshaus, M., Duffy, J.E., Barry, J.P., Chan, F., English, C.A., Galindo, H.M., Grebmeier, J.M., Hollowed, A.B., Knowlton, N., Polovina, J., Rabalais, N.N., Sydeman, W.J. & Talley, L.D. (2012) Climate change impacts on marine ecosystems. *Ann Rev Mar Sci*, **4**, 11–37.

Easterling, D.R., Meehl, G.A., Parmesan, C., Changnon, S.A., Karl, T.R. & Mearns, L.O. (2000) Climate Extremes: Observations, Modeling, and Impacts. *Science*, **289**, 2068–2074.

Eeles, P. (2014) UK Butterflies - Phenologies. URL http://www.ukbutterflies.co.uk/species_phenologies.php [accessed 4 February 2015]

Fischer, K., Klockmann, M. & Reim, E. (2014) Strong negative effects of simulated heat waves in a tropical butterfly. *The Journal of experimental biology*, **217**, 2892–8.

Foden, W.B., Butchart, S.H.M., Stuart, S.N., Vié, J.-C., Akçakaya, H.R., Angulo, A., Devantier, L.M., Gutsche, A., Turak, E., Cao, L., Donner, S.D., Katariya, V., Bernard, R., Holland, R. a, Hughes, A.F., O'Hanlon, S.E., Garnett, S.T., Sekercioğlu, C.H. & Mace, G.M. (2013) Identifying the World's Most Climate Change Vulnerable Species: A Systematic Trait-Based Assessment of all Birds, Amphibians and Corals. *PloS one*, **8**, e65427.

Foden, W., Midgley, G.F., Hughes, G., Bond, W.J., Thuiller, W., Hoffman, M.T., Kaleme, P., Underhill, L.G., Rebelo, A. & Hannah, L. (2007) A changing climate is eroding the geographical range of the Namib Desert tree Aloe through population declines and dispersal lags. *Diversity and Distributions*, **13**, 645–653.

Franco, A.M.A., Hill, J.K., Kitschke, C., Collingham, Y.C., Roy, D.B., Fox, R., Huntley, B. & Thomas, C.D. (2006) Impacts of climate warming and habitat loss on extinctions at species' low-latitude range boundaries. *Global Change Biology*, **12**, 1545–1553.

Freeman, S. (2009) Towards a method for the estimation and use of averaged multi-species trends , as indicators of patterns of change in butterfly populations. *Centre for Ecology and Hydrology*.

Grömping, U. (2006) Relative Importance for Linear Regression in R : The Package relaimpo. *Journal of Statistical Software*, **17**.

Harvell, C.D. (2002) Climate Warming and Disease Risks for Terrestrial and Marine Biota. *Science*, **296**, 2158–2162.

Haylock, M.R., Hofstra, N., Klein Tank, a. M.G., Klok, E.J., Jones, P.D. & New, M. (2008) A European daily high-resolution gridded data set of surface temperature and precipitation for 1950-2006. *Journal of Geophysical Research Atmospheres*, **113**, D20119.

Hellmann, J.J., Pelini, S.L., Prior, K.M. & Dzurisin, J.D.K. (2008) The response of two butterfly species to climatic variation at the edge of their range and the implications for poleward range shifts. *Oecologia*, **157**, 583–592.

Hill, J.K., Hamer, K.C., Dawood, M.M., Tangah, J. & Chey, V.K. (2003) Rainfall but not selective logging affect changes in abundance of a tropical forest butterfly in Sabah, Borneo. *Journal of Tropical Ecology*, **19**, 35–42.

IPCC. (2007) *Climate Change 2007: Impacts, Adaptation and Vulnerability. Contribution of Working Group II to the Fourth Assessment Report of the Intergovernmental Panel on Climate Change* (eds ML Parry, OF Canziani, JP Palutikof, CE Hanson, and PJ van der Linden). Cambridge University Press, Cambridge.

IPCC. (2012) *2012: Managing the Risks of Extreme Events and Disasters to Advance Climate Change Adaptation. A Special Report of Working Groups I and II of the Intergovernmental Panel on Climate Change [Field, C.B., V. Barros, T.F. Stocker, D. Qin, D.J. Dokken, K.L. Eb* (eds CB Field, V Barros, TF Stocker, and Q Dahe). Cambridge University Press, Cambridge, UK and New York, NY, USA.

Jenkins, G.J., Murphy, J.M., Sexton, D.M.H., Lowe, J. a., Jones, P. & Kilsby, C.G. (2009) *UK Climate Projections: Briefing Report*. Exeter, UK.

Jentsch, A. & Beierkuhnlein, C. (2008) Research frontiers in climate change: Effects of extreme meteorological events on ecosystems. *Comptes Rendus - Geoscience*, **340**, 621–628.

Jiguet, F., Brotons, L. & Devictor, V. (2011) Community responses to extreme climatic conditions. *Current Zoology*, **57**, 406–413.

Jones, M.R., Blenkinsop, S., Fowler, H.J. & Kilsby, C.G. (2014) Objective classification of extreme rainfall regions for the UK and updated estimates of trends in regional extreme rainfall. *International Journal of Climatology*, **34**, 751–765.

Loarie, S.R., Duffy, P.B., Hamilton, H., Asner, G.P., Field, C.B. & Ackerly, D.D. (2009) The velocity of climate change. *Nature*, **462**, 1052–1055.

Mair, L., Hill, J.K., Fox, R., Botham, M., Brereton, T. & Thomas, C.D. (2014) Abundance changes and habitat availability drive species' responses to climate change. *Nature Climate Change*, **4**, 127–131.

McLaughlin, J.F., Hellmann, J.J., Boggs, C.L. & Ehrlich, P.R. (2002) Climate change hastens population extinctions. *Proceedings of the National Academy of Sciences of the United States of America*, **99**, 6070–6074.

Møller, A.P., Rubolini, D. & Lehikoinen, E. (2008) Populations of migratory bird species that did not show a phenological response to climate change are declining. *Proceedings of the National Academy of Sciences of the United States of America*, **105**, 16195–16200.

Newson, S.E., Oliver, T.H., Gillings, S., Crick, H.Q.P., Morecroft, M.D., Duffield, S.J., Macgregor, N. a. & Pearce-Higgins, J.W. (2014) Can site and landscape-scale environmental attributes buffer bird populations against weather events? *Ecography*, **37**, 872–882.

Oliver, T.H., Brereton, T. & Roy, D.B. (2013) Population resilience to an extreme drought is influenced by habitat area and fragmentation in the local landscape. *Ecography*, **36**, 579–586.

Oliver, T.H., Marshall, H.H., Morecroft, M.D., Brereton, T., Prudhomme, C. & Huntingford, C. (2015) Interacting effects of climate change and habitat fragmentation on drought-sensitive butterflies. *Nature Climate Change*, **5**, 1–6.

Pacifici, M., Foden, W.B., Visconti, P., Watson, J.E.M., Butchart, S.H.M., Kovacs, K.M., Scheffers, B.R., Hole, D.G., Martin, T.G., Akçakaya, H.R., Corlett, R.T., Huntley, B., Bickford, D., Carr, J. a., Hoffmann, A. a., Midgley, G.F., P., P.-K., Pearson, R.G., Williams, S.E., Willis, S.G., Young, B. & Rondinini, C. (2015) Assessing species vulnerability to climate change. *Nature Climate Change*, **5**, 215–225.

Parmesan, C., Root, T.L. & Willig, M.R. (2000) Impacts of Extreme Weather and Climate on Terrestrial Biota*. *Bulletin of the American Meteorological Society*, **81**, 443.

Parmesan, C., Ryrholm, N., Stefanescu, C., Hill, J.K., Thomas, C.D., Descimon, H., Huntley, B., Kaila, L., Kullberg, J., Tammaru, T., Tennent, W.J., Thomas, J. a & Warren, M. (1999) Poleward shifts in geographical ranges of butterfly species associated with regional warming. *Nature*, **399**, 579–583.

Pearce-Higgins, J.W. (2011) Modelling conservation management options for a southern range-margin population of Golden Plover Pluvialis apricaria vulnerable to climate change. *Ibis*, **153**, 345–356.

Pereira, H.M., Leadley, P.W., Proença, V., Alkemade, R., Scharlemann, J.P.W., Fernandez-Manjarrés, J.F., Araújo, M.B., Balvanera, P., Biggs, R., Cheung, W.W.L., Chini, L., Cooper, H.D., Gilman, E.L., Guénette, S., Hurtt, G.C., Huntington, H.P., Mace, G.M., Oberdorff, T., Revenga, C., Rodrigues, P., Scholes, R.J., Sumaila, U.R. & Walpole, M. (2010) Scenarios for global biodiversity in the 21st century. *Science*, **330**, 1496–1501.

Pollard, E. (1988) Temperature, rainfall and butterfly numbers. *Journal of Applied Ecology*, **25**, 819–828.

Pollard, E., Hall, M.. & Bibby, T.. (1986) *Monitoring the Abundance of Butterflies 1976-1985*.

Pollard, E. & Yates, T. (1993) *Monitoring Butterflies for Ecology and Conservation*.

Pöyry, J., Luoto, M., Heikkinen, R.K., Kuussaari, M. & Saarinen, K. (2009) Species traits explain recent range shifts of Finnish butterflies. *Global Change Biology*, **15**, 732–743.

Radchuk, V., Turlure, C. & Schtickzelle, N. (2013) Each life stage matters: The importance of assessing the response to climate change over the complete life cycle in butterflies. *Journal of Animal Ecology*, **82**, 275–285.

Renwick, A.R., Massimino, D., Newson, S.E., Chamberlain, D.E., Pearce-Higgins, J.W. & Johnston, A. (2012) Modelling changes in species' abundance in response to projected climate change. *Diversity and Distributions*, **18**, 121–132.

Root, T.L., Price, J.T., Hall, K.R., Schneider, S.H., Rosenzweig, C. & Pounds, J.A. (2003) Fingerprints of global warming on wild animals and plants. *Nature*, **421**, 57–60.

Roy, D.B., Rothery, P., Moss, D., Pollard, E. & Thomas, J.A. (2001) Butterfly numbers and weather: Predicting historical trends in abundance and the future effects of climate change. *Journal of Animal Ecology*, **70**, 201–217.

Smith, M.D. (2011) An ecological perspective on extreme climatic events: A synthetic definition and framework to guide future research. *Journal of Ecology*, **99**, 656–663.

Van Strien, A.J., Plantenga, W.F., Soldaat, L.L., Van Swaay, C.A.M. & WallisDeVries, M.F. (2008) Bias in phenology assessments based on first appearance data of butterflies. *Oecologia*, **156**, 227–235.

Thiele, J. (2012) Potential of GLMM in modelling invasive spread. *CAB Reviews: Perspectives in Agriculture, Veterinary Science, Nutrition and Natural Resources*, **7**, 1–10.

Thomas, C.D., Franco, A.M. a & Hill, J.K. (2006) Range retractions and extinction in the face of climate warming. *Trends in Ecology and Evolution*, **21**, 415–416.

WallisDeVries, M.F., Baxter, W. & van Vliet, A.J.H. (2011) Beyond climate envelopes: Effects of weather on regional population trends in butterflies. *Oecologia*, **167**, 559–571.

Warren, R. (2011) The role of interactions in a world implementing adaptation and mitigation solutions to climate change. *Philosophical transactions. Series A, Mathematical, physical, and engineering sciences*, **369**, 217–241.

Warren, M., Hill, J.K., Thomas, J.A., Asher, J., Fox, R., Huntley, B., Roy, D.B., Telfer, M.G., Jeffcoate, S., Harding, P., Jeffcoate, G., Willis, S.G., Greatorex-Davies, J.N.N., Moss, D. & Thomas, C.D. (2001) Rapid responses of British butterflies to opposing forces of climate and habitat change. *Nature*, **414**, 65–69.

Warren, R., VanDerWal, J., Price, J., Welbergen, J. a., Atkinson, I., Ramirez-Villegas, J., Osborn, T.J., Jarvis, A., Shoo, L.P., Williams, S.E. & Lowe, J. (2013) Quantifying the benefit of early climate change mitigation in avoiding biodiversity loss. *Nature Climate Change*, **3**, 1–5.

Wiklund, C., Lindfors, V. & Forsberg, J. (1996) Early male emergence and reproductive phenology of the adult overwintering butterfly Gonepteryx rhamni in Sweden. *Oikos*, **75**, 227–240.

Wilbanks, T.J. & Kates, R.W. (1999) Global change in local places: How scale matters. *Climatic Change*, **43**, 601–628.

Wilson, R.J., Gutiérrez, D., Gutiérrez, J., Martínez, D., Agudo, R. & Monserrat, V.J. (2005) Changes to the elevational limits and extent of species ranges associated with climate change. *Ecology Letters*, **8**, 1138–1146.

Tables

Table 1 Extreme Climatic Events (ECEs) included in this study and their definitions (Diaz & Murnane 2008; Beaumont *et al.* 2011)

Extreme	Definition
Extreme Heat	Number of days above 2 standard deviations above the mean daily maximum temperature for the life cycle period of the species in question at a particular site
Extreme Cold	As for extreme heat but 2 standard deviations below the mean of the minimum daily temperature
Drought	15 days with a combined total of less than 0.02 mm of rain with each day on top of this being counted as an extra day of drought
Extreme Precipitation	Number of days above the 97.5 percentile for rainfall during the life cycle period in question for a particular species at that particular site. 2 standard deviations were not used in this case due to the shape of precipitation data (non-normal).

Table 2 Significant variables obtained from the combined univoltine species linear model. Bonferroni corrections applied and variables ordered by relative importance in the model using the *relaimpo* package. Variables bolded show a negative relationship with univoltine populations.

Univoltine Species							
Variable			Estimate	Std. Error	t value	p-value	Relative Importance
Extr. Heat	**during**	**Overwintering**	**-0.064**	**0.004**	**-17.681**	**<0.0001**	**19.93%**
Extr. Heat	during	Adult stage	0.052	0.005	11.068	<0.0001	17.54%
Extr. Heat	during	Pupal stage	0.040	0.005	8.309	<0.0001	14.24%
Extr. Precipitation	**during**	**Pupal stage**	**-0.051**	**0.004**	**-12.915**	**<0.0001**	**12.74%**
Drought	during	Ovum stage	0.044	0.004	11.365	<0.0001	9.14%
Extr. Cold	**during**	**Adult stage**	**-0.040**	**0.004**	**-10.593**	**<0.0001**	**4.93%**
Extr. Precipitation	**during**	**Larval stage**	**-0.026**	**0.004**	**-6.476**	**<0.0001**	**3.99%**
Drought	during	Pupal stage	0.031	0.004	7.259	<0.0001	3.96%
Extr. Cold	during	Overwintering	0.030	0.004	8.104	<0.0001	3.96%
Extr. Heat	**during**	**Ovum stage**	**-0.023**	**0.005**	**-4.560**	**<0.0001**	**2.79%**
Extr. Precipitation	**during**	**Adult stage**	**-0.009**	**0.004**	**-2.399**	**0.0165**	**2.01%**
Extr. Precipitation	**during**	**Ovum stage**	**-0.019**	**0.004**	**-5.031**	**<0.0001**	**1.98%**
Extr. Heat	**during**	**Larval stage**	**-0.017**	**0.005**	**-3.308**	**0.0009**	**1.38%**
Drought	**during**	**Adult stage**	**-0.011**	**0.004**	**-2.663**	**0.0077**	**0.74%**
Extr. Precipitation	**during**	**Overwintering**	**-0.015**	**0.004**	**-3.954**	**0.0001**	**0.69%**

Table 3 Significant variables obtained from the combined multivoltine species linear model. Bonferroni corrections applied and variables ordered by relative importance in the model using the *relaimpo* package. Variables bolded show a negative relationship with univoltine populations.

Multivoltine Species							
Variable			Estimate	Std. Error	t value	Pr(>|t|)	Relative Importance
Extr. Heat	during 2nd generation	Adult stage	0.105	0.006	17.921	<0.001	14.81%
Drought	during 1st generation	Adult stage	0.076	0.006	13.599	<0.001	8.45%
Extr. Cold	during 2nd generation	Larval stage	0.083	0.005	15.740	<0.001	8.31%
Extr. Heat	**during**	**Overwintering**	**-0.100**	**0.007**	**-14.427**	**<0.001**	**8.22%**
Extr. Heat	during 2nd generation	Ovum stage	0.064	0.006	11.262	<0.001	7.82%
Drought	during 1st generation	Ovum stage	0.086	0.005	16.283	<0.001	7.12%
Extr. Heat	**during 1st generation**	**Pupal stage**	**-0.066**	**0.006**	**-10.533**	**<0.001**	**6.59%**
Extr. Heat	**during 1st generation**	**Ovum stage**	**-0.034**	**0.006**	**-5.253**	**<0.001**	**6.33%**
Extr. Precipitation	**during 1st generation**	**Adult stage**	**-0.050**	**0.006**	**-8.701**	**<0.001**	**5.48%**
Extr. Cold	during	Overwintering	0.080	0.006	13.284	<0.001	4.25%
Extr. Precipitation	**during 2nd generation**	**Ovum stage**	**-0.018**	**0.006**	**-2.849**	**0.004**	**2.98%**
Extr. Precipitation	**during 2nd generation**	**Larval stage**	**-0.027**	**0.007**	**-3.813**	**0.000**	**2.88%**
Extr. Cold	**during 2nd generation**	**Ovum stage**	**-0.042**	**0.005**	**-7.846**	**<0.001**	**2.28%**
Drought	**during 2nd generation**	**Larval stage**	**-0.053**	**0.007**	**-7.992**	**<0.001**	**1.80%**
Drought	during 2nd generation	Ovum stage	0.016	0.006	2.400	0.016	1.69%
Drought	**during**	**Overwintering**	**-0.031**	**0.005**	**-5.700**	**<0.001**	**1.61%**
Extr. Cold	**during 1st generation**	**Pupal stage**	**-0.052**	**0.005**	**-9.946**	**<0.001**	**1.44%**
Extr. Heat	**during 1st generation**	**Adult stage**	**-0.021**	**0.006**	**-3.468**	**0.001**	**1.38%**
Extr. Precipitation	**during 1st generation**	**Pupal stage**	**-0.036**	**0.006**	**-6.144**	**<0.001**	**1.37%**
Extr. Precipitation	**during 1st generation**	**Larval stage**	**-0.032**	**0.005**	**-6.089**	**<0.001**	**1.37%**
Extr. Cold	**during 2nd generation**	**Adult stage**	**-0.023**	**0.005**	**-4.526**	**<0.001**	**1.29%**
Extr. Cold	**during 1st generation**	**Adult stage**	**-0.031**	**0.005**	**-5.788**	**<0.001**	**0.62%**
Extr. Precipitation	during 2nd generation	Pupal stage	0.027	0.006	4.280	<0.001	0.61%
Drought	**during 2nd generation**	**Adult stage**	**-0.027**	**0.006**	**-4.370**	**<0.001**	**0.51%**
Extr. Precipitation	during	Overwintering	0.012	0.006	2.183	0.029	0.32%
Drought	during 2nd generation	Pupal stage	0.014	0.007	2.106	0.035	0.25%

Table 4 Welch T tests results *comparing the mean percentage of negative responses in relation to total number of possible variables from the individual species models when divided based on their life history traits.*

Life history Group (Traits being tested tested)	t Statistic	Degrees of freedom	Means (% vs %)	*p-value*
Voltinism (Univoltine versus Multivoltine)	-2.86	25.66	(13.62 vs 22.22)	0.008
Requirement (Specialist versus Generalist)	-3.00	35.99	(10.95 vs 19.81)	0.004
Within Univoltine Species (Widespread versus Northern Range limited)	1.69	25.57	(17.5, 11.25)	0.102
Within Multivoltine Species (Widespread versus Northern Range limited)	3.76	8.77	(26.98 vs 15.56)	0.005

Figure Legends

Figure 1 Percentage of species, from the species specific models, for each life stage which there was a significant ($p<0.05$) positive or negative relationship with an Extreme Climatic Event (ECE) related to temperature or precipitation. Univoltine (A and B) and multivoltine (C and D) species are shown separately. Impact of temperature extremes (A and C) and precipitation extremes (B and D) on univoltine and multivoltine species are also shown separately. Columns above the 0 line in the y axis indicate the % of species positively impacted by ECEs while below indicates the % of species positively impacted by ECEs.

669 # Figures

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