

Appendix 4: Identifying the importance of different seasons in driving observed species' responses to climate change

Introduction

Climate change has had wide-ranging impacts on biodiversity; many species have undergone polewards range shifts, phenological changes and physiological changes (e.g. Walther *et al.* 2002; Parmesan & Yohe 2003; Menzel *et al.* 2006; Thackeray *et al.* 2010). These can lead to changes in population abundance and even extinctions through a range of physiological and biotic mechanisms (Cahill *et al.* 2013). For most species, disrupted interactions with other species; predators, prey, competitors and parasites; appear to be the most influential drivers of climate-related population change (Tylianakis *et al.* 2008, Van der Putten *et al.* 2010; Ockendon 2014). The complexity that comes with this makes species' vulnerability to climate change difficult to predict.

Despite this complexity, many studies of climatic impacts on biodiversity have focussed largely on relatively simple climatic metrics (McMahon *et al.*, 2011). For example, most studies of range shift described polewards shifts in distribution in response to mean temperature (Chen *et al.* 2011, Sunday *et al.* 2012), whilst studies of community change have also largely described changes relative to temperature (e.g. Devictor *et al.* 2008, 2012, Davey *et al.* 2012, 2013). Effects of precipitation have been much less studied (Bonebrake & Mastrandrea 2010), and may yield very different biodiversity responses to climate change (VanderWal *et al.* 2013). As a result of a focus on simple temperature metrics, it is likely that many studies of climate change impacts may therefore fail to fully attribute the observed responses to climate change. However, given the complexities of climate change, and the range of different ways that climate change may impact upon species' (e.g. Mustin *et al.* 2007), developing robust models that account for these potentially different impacts is extremely challenging.

In the case of single-species studies, existing ecological knowledge of species has often been the key to investigating the impact of climate change on species' abundance. Such information is used to select appropriate predictor variables (Knappe & Valpine 2011) and to disregard spurious relationships between weather variables and population abundance (e.g. Roy *et al.* 2001). However, this need for ecological knowledge restricts the range of species that can be studied, as well as climatic effects that can be investigated. Here we create models that go beyond simple summarised climate metrics and are applicable across a range of taxa, of which for some we have limited ecological knowledge. A key difficulty in identifying the timing of impacting weather events on population abundance is the correlation in weather throughout the year, which can make it difficult to determine the specific period of sensitivity that populations respond to (Sims *et al.* 2007). In order to produce robust models that can be applied to a wide-range of species, we use a recently developed modelling approach which attempts to resolve this issue. Firstly we assume that the impact of monthly weather variables on population abundance is correlated between adjacent months, with annual fluctuations in response. Secondly we assume that weather can affect population abundance for multiple years, and therefore the models allow the effects of weather to decay over time.

In addition to producing robust models linking species' abundance to weather, the temporal patterns of population responses to weather variables through the year can be used to identify potential mechanisms of climate change impacts. For example, a positive response to winter

temperatures implies that climate impacts are linked to winter mortality. Comparing the response of species with different overwintering strategies further indicates mechanisms; a physiologically-driven winter response would not be seen in birds that overwinter in the tropics. Indications of the impacts of phenological mismatch could also be inferred from the effect of overwintering strategy on response to spring weather; overwintering strategy may impact species' ability to show phenological flexibility to avoid phenological mismatch (Visser & Holleman 2001). Likewise mechanisms can be inferred if the impact of weather is linked to particular stages of life, such as insect emergence. Incorporating potential time-lags between weather events and population response into models allows species interactions to be identified, for example a species may decline due to weather-driven prey declines in the previous year (Pearce-Higgins *et al.* 2010). It is also an important detail in predicting future impacts of climate change as the impact of climate change is unlikely to be even across all season. For example, most global climate models predict that in northern Europe winter precipitation will increase while summer precipitation may decrease, and temperature is likely to rise more in the summer than in the winter (Gosling *et al.* 2011). Therefore, species vulnerability to future climate change may critically depend upon seasonal variation in their responses to temperature and precipitation.

In this study we use a robust modelling approach to identify the peak periods of response to monthly temperature and precipitation variables of over 500 UK species of bird, mammal, aphid, butterfly and moth. Time-series for these species start between 1966 and 1998 and continue to 2011, in which time both temperature and precipitation in the UK have increased (UK Meteorological Office, 2014). We examine the extent to which our models are applicable to species within taxa and identify each taxon's overall response to increasing temperature and precipitation. We identify times of year that weather has the greatest impact on each taxon, allowing for potential time-lags. Specifically we use the results to discuss potential mechanisms behind climate impacts on populations. To further examine mechanisms of climate change impacts we also determine whether overwintering strategies and the timing of Lepidoptera summer activity influences species' response to weather.

Methods

Data

We used data from national monitoring schemes for aphids, butterflies, moths, birds and mammals to create population indices for 501 widespread species. These represent all the species for which at least one record was available in every year (Table 1).

To ensure robustness of indices, we created English population indices for birds, butterflies and mammals, because these groups were surveyed across many sites (>1000) but with a large bias towards English sites. At a UK level this spatial bias could lead to biased indices of change (Freeman *et al.* 2007). However, maximising sample size was of greater importance for aphids and moths as these were surveyed in a small number of sites across Scotland, England and Wales (i.e. 12 and 13 different trap sites for aphids and moths). We therefore created UK population indices for aphid and moth species.

We calculated national population indices as the year effect found when population counts were modelled against site and year (as a categorical variable) on a log-linear scale with a GLM (ter Braak *et al.* 1994; Freeman & Newson 2008; Willis *et al.* 2009).

We modelled the resulting indices of population abundance against mean monthly temperature and precipitation. We used Met Office UKCP09 gridded datasets averaged across England for birds, mammals and butterflies and across all of the UK for aphids and moths (Perry & Hollis 2005). Additional methodological covariates including survey weather, type of bat detector and timing of survey were included in the models as recommended when calculating bat population indices (Bat Conservation Trust 2013) as these are factors, specific to the day of survey, known to strongly influence bat detection.

Table 1 Details of surveys used to produce yearly species indices

Taxonomic group	No. sites	No. species included	Survey years	Source
Mammals	~1200 for bats; ~3000 for others	16 (10 bats, 6 others)	Bats: 1998 - 2011 Other mammals: 1995 – 2011	http://www.bats.org.uk/pages http://www.bto.org/volunteer
Birds	~3000	85	Terrestrial birds 1966 - 2011; Wetland birds: 1980 – 2011	http://www.bto.org/volunteer http://www.bto.org/volunteer
Butterflies	1424	55	1976 - 2011	http://www.ukbms.org
Moths	13	265	1975 – 2010	http://www.rothamsted.ac.uk
Aphids	12	80	1970 – 2010	http://www.rothamsted.ac.uk

Modelling population against weather

Estimating the relationship between weather and species abundance is more complex than it might appear. The key challenge to be addressed is that the number of years for which data is available is small (always less than 50 in our case) considering the potential number of explanatory variables (monthly covariates for both mean temperature and rainfall, for as many years leading up to the index record as may be biologically relevant). Approaches that have been used to overcome this challenge generally involve using ecological understanding of a species to select a relatively small number of predictor variables (Roy *et al.* 2001 and more), or to summarise multiple weather variables into broad, general variables such as seasonal or annual means (Davey *et al.* 2012, Devictor *et al.* 2012). These methods either require good ecological knowledge of the species in question, often something which isn't available for many species, or are liable to overlook specific impacts, leading to under-estimation of climatic responses. Weather may also have multiple effects on a single population, which can be direct and immediate (e.g. direct mortality associated with extremes), cumulative (e.g. effects of prolonged cold or drought) or lagged (e.g. mediated through altered species interactions), which can be challenging to account for.

As a result, we have adopted an alternative approach to allow the weather data from a large number of past months (we use a ten-year period) to be included in the model for each response variable ($y = \log(\text{abundance})$), but to constrain the regression coefficients to lie on a curve defined by a small number of parameters. This makes this approach robustly estimable for a large-number of species

based on a moderate-length time-series. The general form of the relationship we use, written to allow a maximum of ten years of weather data to be included, has the following form

$$y_t = a + b_1x_1 + b_2x_2 + b_3x_3 + \dots + b_{120}x_{120} + ct + dy_{t-1} + e_t \quad (\text{Equation 1})$$

in which:

a is the intercept;

b_i is the regression coefficient for the i^{th} weather covariate (x), with $i=1$ denoting the most recent and $i=120$ denoting the end of the ten year period;

c is the regression coefficient of a year of survey covariate (t), included to account for linear trends in the time-series caused by non-climatic effects;

d is the regression coefficient of a covariate relating to the population in the previous year to account for density-dependence;

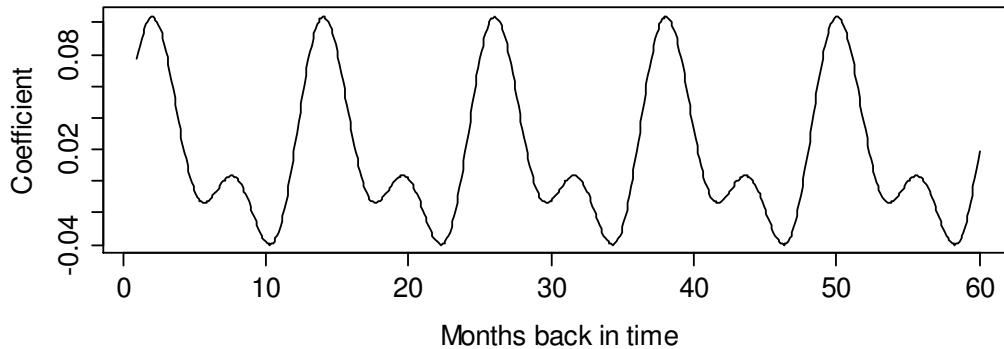
and e is an error term from a Normal distribution through which we allow for temporal correlation through a 1st order auto-regressive (AR1) process.

The form of the curve on which the series of regression coefficients, b_1 to b_{120} , were constrained to lie comprised a repeating, cyclic pattern combined with a decay towards zero. We used two versions of this model: in the first two cycles repeated themselves every year, allowing species responses to weather to change rapidly between seasons (Fig 1a); and in the second two cycles repeated themselves every two years, allowing for species to have a lagged response to weather. This allowed us to simplify the models to two parameters for each of the cyclic curves, and another parameter for the decay (Fig 1b). Mathematically, the above relationships in combination (Fig 1c) can be expressed as

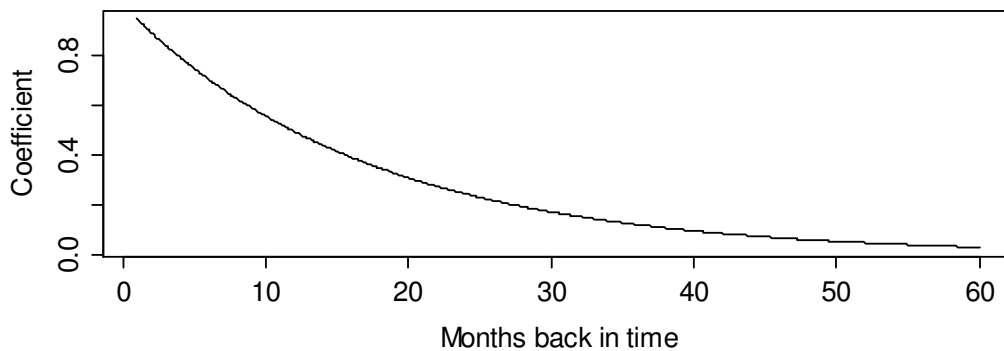
$$b_i = e^{-di} \cdot s(i),$$

where d is the decay parameter, constrained to be positive, for which large values indicate fast decay, and $s(i)$ is the cyclic term parameterised as a linear combination of sine and cosine terms of different periodicities. Note that both sine and cosine terms are required for each periodicity to allow the peak values to correspond to any month of the year.

(a) Two repeating cycles per year



(b) Exponential decay



(c) Combined, a damped seasonal pattern

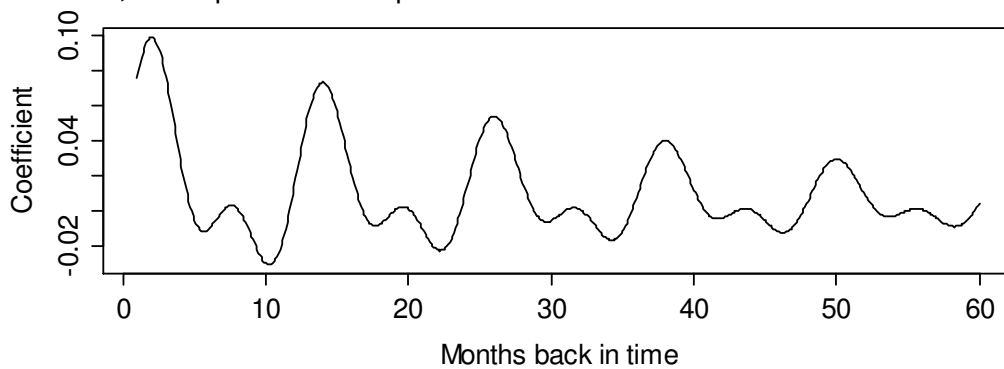


Figure 1 Plots showing how the pattern of coefficients for equation 1 is built up in stages. Firstly, a double yearly cycle (a) is obtained; then this is combined with an exponential decay (b); and a combination of (a) and (b), for example, produces a damped sine curve seasonal pattern (c).

The model which describes this consists of two sine-wave cycles, one of period one year, and one of period six months. The net result is that the regression coefficients have a cyclic pattern with period one year, but with high flexibility as to the shape of the curve. The mathematical form for this is

$$y_t = a + b_1 \sin\left(\frac{2\pi}{12}\right) + b_2 \cos\left(\frac{2\pi}{12}\right) + b_3 \sin\left(\frac{2\pi}{6}\right) + b_4 \cos\left(\frac{2\pi}{6}\right) + ct + dy_{t-1} + e_t \quad (\text{Equation 2})$$

with parameters b_1 to b_4 of the sine and cosine terms augmented by the intercept a , which represents the median effect of temperature throughout a seasonal cycle. This parameter allows all the regression coefficients b_i within a cycle to be positive (or negative).

The alternative model consists of two sine-wave cycles, one of period of two year and one of period one year:

$$y_t = a + b_1 \sin\left(\frac{2\pi}{24}\right) + b_2 \cos\left(\frac{2\pi}{24}\right) + b_3 \sin\left(\frac{2\pi}{12}\right) + b_4 \cos\left(\frac{2\pi}{12}\right) + ct + dy_{t-1} + e_t \quad (\text{Equation 3})$$

The explanatory variables we examined were mean monthly temperature and precipitation from up to ten years prior to data collection. Thus this model gives us the ability to model and therefore identify rapidly changing or brief windows of response to these weather variables. More importantly, it avoids model of population and weather being determined solely by survey period weather events that affect activity and detection rate more than population abundance. However, we were constrained to modelling temperature and precipitation separately due to the complexities of ensuring adequate parameterisation of the models.

Summarising weather response and identifying peak response periods

For each species we created five models as described above, two with mean monthly temperature as the weather variable and two using monthly precipitation and a null model (with only previous population and year as explanatory variables). The pairs of temperature and precipitation models differed in that one allowed up to two fluctuations in response to weather each year (appropriate for species with rapid changes in response to weather), while the second allowed up to two fluctuations in response to weather every two years (appropriate for species with a time-lag in response to weather). For each species we examined whether their response to temperature and precipitation could be modelled under these assumptions using chi-sq tests to compare likelihood ratio of null models and weather models. We selected the most appropriate weather model for temperature and precipitation (distinguishing between two response cycles in one year or two response cycles in two years) by the likelihood ratio.

Firstly, we identified if populations could be better modelled by temperature or precipitation and whether relationships between temperature and precipitation were consistent within taxa. This was achieved by comparing the likelihood ratio (square-root transformed for normality) of temperature and precipitation models with a GLMM, with species as a random factor.

As we constrained the analysis to one or two-year cycles of repeated oscillations, we extracted monthly coefficients for the 24 months prior to the end of the species-specific weather windows. The mean of the monthly covariates characterised each species' overall response to temperature and precipitation. We used a GLM to determine whether the range of species' responses within each taxon was significantly above or below zero; species temperature or precipitation response.

We then identified times of year in which weather most influenced each taxon as follows. We standardised the monthly coefficients for each species within taxa by dividing monthly coefficients by the species' maximum (negative or positive) coefficient. To identify months in which the response across all species in a taxa was significantly more negative or positive than expected by chance, we

modelled the standardised coefficients against month as a factor. Species identity was included in the model as a random factor, weighted by the strength of evidence for their response to weather (log-likelihood of weather models). We then examined differences in response within taxa of species with differing overwintering strategies and for Lepidoptera, for species with different egg-laying seasons using the same method as above.

Where we discuss seasons we define seasons as 3-month periods: winter as December, January and February, spring as March, April and May, etc.

Results

Overall effects of temperature and precipitation

We found that 94.2 % of species could be modelled with respect to temperature or precipitation in the manner predicted by our models. This was based on the likelihood ratio tests (LRT) which examined the significance of species response to temperature and precipitation in each of the cyclic models (two cycles in two years or two cycles in two years), compared to the null models. Overall the fit of 64 % of species to both temperature and precipitation was better than for the null model, while population trends for 20 % and 10 % respectively was significantly accounted for by temperature or precipitation models only. Species' population trends fitted temperature models better than precipitation models (**Error! Reference source not found.**; square root of LRT for temperature models compared to precipitation models \pm standard error = 0.36 ± 0.05 , $P < 0.001$). For further analysis for each species we used the model coefficients from the best fitting of the two types of models (two responses cycles in one year or two response cycles in two years). We used the model coefficients to calculate species-specific monthly covariates, indicating species' response to temperature or precipitation in each month.

We characterised each species' response to temperature and precipitation from the mean of their monthly covariates, removing species with an insignificant response. Aphids responded positively to temperature (mean responses = 0.009 ± 0.001 , $t = 6.62$, $P < 0.001$) and negatively to precipitation (mean responses = -0.005 ± 0.002 , $t = -2.50$, $P = 0.013$). Moths had a negative response to precipitation (mean responses = -0.008 ± 0.001 , $t = -6.796$, $P < 0.001$) (Figure 2). Moths and aphids both had the most variable response to weather.

Seasonal variation in the effects of temperature and precipitation

Population responses to temperature and precipitation were non-randomly distributed through the year, and across years. Sensitive months were identified as months in which there was a greater positive or negative mean response to weather across species within taxa than expected by chance (Figure 3). Positive aphid population responses to temperature were strongest during year t_1 , when the abundance data were collected, particularly from May to August and in October; positive effects of temperature were weaker in September. There was also a lagged positive impact of summer temperature (June to August year t). There was a negative impact of precipitation upon abundance

in January t_1 and from June to October t_{-1} , but a lagged positive response to spring precipitation and a small but significantly positive response to December precipitation.

Positive effects of temperature upon bird populations were most apparent during the winter. Effects upon abundance in year t_1 were cumulative, with significant impacts from winter t/t_1 and winter t_{-1}/t . Conversely, populations were negatively impacted by temperature in April and May and precipitation in May and June in year t_1 , the period of the survey (Figure 3). Lagged negative impacts of May and June precipitation in year t and July precipitation in year t_{-1} were apparent. We also found a positive relationship between abundance and precipitation from September to December in year t .

Butterfly and moth populations responded similarly to both temperature and precipitation. Positive effects of temperature upon abundance were apparent from May t_1 to August t_1 (September t_1 in butterflies). Populations showed consistent negative effects of precipitation during this period also, indicating that the greatest numbers were recorded during warm, dry summers. However, strong negative effects of temperature upon abundance from October in year t (September t in moths) to March t_{-1} indicate harmful impacts of warm winter weather, particularly if also wet; negative effects of precipitation over this period were statistically significant across moth species to August t , or in November and December t in butterflies. Some effects of temperature were apparent in previous years.

Mammal populations switched from having a negative response to temperature in March and April to a positive response in June while they were negatively impacted by precipitation in June and had a negative lagged response to summer precipitation (Figure 3). They had a positive response to March precipitation and a lagged positive response to precipitation in February in year t .

Variation in the effects of temperature and precipitation in relation to life-cycle

Next we examined the response of species within taxa grouped by their overwintering strategy. The responses of resident bird species and short-distance migratory birds to temperature were very similar (Figure 4a). Winter temperatures positively impacted populations, and this impact carried over to the subsequent year, while spring temperatures (particularly May and June for residents and May for short distance migrants) negatively impacted populations. Their responses to precipitation were also similar. Resident birds were negatively impacted by April to June precipitation and positively impacted by October to December precipitation; short distance migrants were negatively impacted by May and June precipitation and positively impacted by September and October precipitation, an impact which carried over to the subsequent year. Very different temperature responses were seen in long distance migrants (comparison of temperature models with and without overwintering strategy: $\chi^2 = 253.2$, $P < 0.001$). They had negative responses and lagged responses to autumn temperature; in fact the lagged response was stronger than the immediate response. They also responded negatively to February and March temperature in years t and t_1 while they responded positively to June temperatures prior to their breeding season. Long distance migrants were negatively impacted by summer precipitation, with a significant response in June of their breeding and in the May and June in the year prior to the breeding season (Figure 4a;

comparison of precipitation models with and without overwintering strategy: chi-sq = 174.5, $P < 0.001$).

Mammal overwintering strategy divided species into hibernating bats and active non-winged mammals (Figure 4b) and these groups differed in their response to temperature (chi-sq = 80.5, $P = 0.007$) and precipitation (chi-sq = 97.1, $P < 0.001$). Non-winged mammals responded positively to June temperature and negatively to June precipitation, while population growth was enhanced by winter (January to March) precipitation, but negatively related to March temperature. Similar effects of precipitation were apparent in the previous year. Although bats appeared unaffected by variation in precipitation, spring temperature appeared to have a negative impact on bat population growth (Figure 4b). Bats also had a lagged positive response to temperature in September of year t_{-1} .

Aphid responses to temperature were all positive and there was no significant difference in the timing of responses determined by their overwintering strategy (Figure 5a, chi-sq = 95.0, $P = 0.173$), although the most consistent temperature effects through the year were apparent in holocyclic species. The effects of precipitation upon aphid population growth differed significantly between aphid groups (chi-sq = 217.0, $P < 0.001$). Positive precipitation responses in year t_1 were seen in September in anholocyclic species and December in facultative anholocyclic and holocyclic species, although there are towards the end of the survey period. Negative effects of April to June precipitation in year t_1 were seen facultative anholocyclic species in May and June, and in holocyclic species from July to October in year t_1 and from September to November in year t (Figure 5a).

Although butterfly and moth species show broadly similar responses to variation in temperature and precipitation through the year as outlined in Figure 3, the precise patterns differ significantly with overwintering strategy (butterfly temperature models: chi-sq = 268.4, $P < 0.001$; butterfly precipitation models: chi-sq = 128.1, $P < 0.001$; moth temperature models: chi-sq = 1311.8, $P < 0.001$; moth precipitation models chi-sq = 322.7, $P < 0.001$). Butterflies that overwintered as eggs differed most from the previously described pattern, showing the weakest response to summer temperature and were least affected by winter temperature. Instead they showed strong negative effects of temperature from September to November in both year t and year t_{-1} . These butterfly populations were negatively affected by June precipitation in year t and May to July precipitation in year t_{-1} . Butterflies overwintering as larva and pupa and moths irrespective of overwintering strategy fitted the general pattern of response well with largely positive responses to temperature during the summer in year t_1 (May of June to August) and negatively to winter temperature. Moths that overwintered as eggs or larva also had negative responses to autumn temperature. Precipitation in year t_1 generally had a negative impact on all groups of Lepidoptera, and extended back into the autumn of year t for moths that overwintered as larva and pupa (Figure 5b).

Similar patterns are apparent if species are grouped not by overwinter strategy, but by flight period (Figure 6; significance of activity period on butterfly temperature models: chi-sq = 219.3, $P < 0.001$; butterfly precipitation models: chi-sq = 153.0, $P < 0.001$; moth temperature models: chi-sq = 1266.2, $P < 0.001$; moth precipitation models: chi-sq = 287.3, $P < 0.001$). Sensitivity of butterflies and moths to temperature and precipitation during the summer was related to flight period, with autumn active flying species sensitive to conditions later. More complex variation was exhibited in the sensitivity of species to negative impacts of autumn and winter temperature, which was most apparent in summer flying butterflies and moths. Precipitation responses were largely negative in

year t_1 . Autumn active butterflies and summer active moths showed a lagged positive response to winter precipitation.

Discussion

This study robustly identified the timing of populations' sensitivity to weather throughout the year across multiple taxa, taking the correlation between weather in successive months into account. We modelled national-scale (UK or English depending upon the taxon) population abundance against mean monthly temperature and precipitation, assuming a decaying response to weather over a maximum of ten years, and two peaks and troughs in response each year or every two years. While this is unlikely to be the best possible weather model for all species, it provides a very flexible model that allowed us to identify variable responses to temperature and precipitation, both of which increased over the time-scale examined (UK meteorological Office, 2014), between months in a biologically realistic manner. As such, this modelling approach had proven ability to describe meaningful variation in species' abundance as a result of variation in weather variables in 94% of species. We found the model more applicable to species' response to temperature than to precipitation, particularly in birds; only 48% of bird populations could be modelled using the precipitation models. The key aim of this study was to identify times of sensitivity throughout the year of groups of species to give insight into likely mechanisms behind climate change impacts, and as a precursor to improving population projections. Most broadly, we examined the timing of sensitivity to temperature and precipitation within taxonomic groups, examining responses of aphids, butterflies, moths, birds and mammals. We also examined differences within taxa, between species with differing overwintering strategies and flight activity times.

Aphids responded positively to high temperatures throughout most of the year. Aphids have multiple asexual generations per year, and the number of generation increases with temperature allowing population to increase. Aphid species that were holocyclic (i.e. overwintering as eggs and reproducing sexually at least once annually) responded positively to temperature from May to August while anholocyclic species (i.e. having only asexual reproduction so overwintering as adult) were more benefitted by warm winters, probably due to the increased survival of cold-vulnerable adults (Strathdee *et al.* 1995). In warm springs holocyclic species have earlier migration times (Thomas *et al.* 1983) and are therefore likely to begin parthogenic reproduction earlier (Zhou *et al.* 1995) leading to population increases (Westgarth-Smith *et al.* 2007). Aphids were generally negatively impacted by summer and autumn rainfall, likely to be partly due to increased mortality and partly due to reduced activity during rain (Harrington *et al.*, 2007).

Bird populations of species which overwintered in the UK or Europe increased in warm winters, likely to be associated with lower energy demands and higher food availability (Robinson *et al.* 2007). A decline in a number of resident birds after cold winters has been noted previously (Robinson *et al.* 2007). Long-distance migrants instead declined with autumn and winter temperatures, with the lagged effect having a greater impact than the most recent autumn. This high lagged impact is likely to be mediated through interactions with other species, although more work is required to identify specifically how these impacts may occur. An example of lagged impacts mediated through species interactions is that high temperatures in August have been shown to decrease in Tipulidae abundance, leading to a lagged negative impact on upland breeding waders (Pearce-Higgins *et al.*,

2010). Most bird populations declined due to breeding season precipitation, probably due to lower nestling survival with heavy rainfall (Anctil *et al.* 2013). Residents, short-distance migrants and long-distance migrants also declined with, respectively, high April to June, May to June, and June temperatures. This could be driven by phenological mismatch: high temperatures in spring advance the timing of caterpillar emergence creating a mismatch between the timing of peak caterpillar abundance and peak energy requirements for breeding birds (Visser *et al.* 2006). Further research is required to determine whether phenological mismatch is common and has a demonstrable impact on across a range of bird species.

Mammal overwintering strategies were entirely determined by whether the species was a bat (hibernatory) or not (overwintering as an active adult). Non-bat mammal populations had a positive relationship with temperature and a negative relationship with precipitation in June, very likely to be due to increased mortality of juveniles in cold wet weather. Conversely these mammals declined after a warm dry March, and a dry winter. There is much evidence of phenological asynchrony in early springs between herbivorous mammal reproduction and peak plant nutritional value (Campbell *et al.* 2013, Douhard *et al.* 2013, Gaillard *et al.* 2013). High spring precipitation has been linked to higher mammal survival through increased vegetation growth (Portier *et al.* 1998). Almost all of these mammals responded positively to winter temperature (although this was not significant) and would be expected due to greater winter food availability in warm winters (Bell & Webb 1991, Schmidt *et al.* 2004). One of the only two significant responses of bats to weather was a negative relationship with March and April temperature, similar to the negative responses to spring temperatures seen in birds and could also be due to phenological mismatch between peak energy demands and peak insect abundance. Bats also had a lagged positive response to September temperature in year t_{-1} .

The overall impact of rising temperatures on moths and butterflies was highly variable. However, the timing of responses to temperature was similar between butterflies and moths. Populations generally increased with warm temperatures in late spring and summer (Roy *et al.*, 2001), probably partly due to increased activity during survey periods (Cormont *et al.*, 2011), while declined with warm temperatures in winter and early spring. The response of butterflies that overwintered as eggs differed most from this general pattern; instead they responded negatively to autumn temperatures. Rising winter temperatures also had no impact on butterflies that were active in autumn. Our results counter the common assumption that winter mortality is a limiting factor for butterflies (Crozier 2003). Instead, warm winters increase the abundance of natural enemies and larval parasites (Virtanen & Neuvonen 1999) plausibly causing Lepidoptera declines. This mechanism would explain climate-driven declines in species that were not near the northern edge of their range (e.g. *Arctia caja* Conrad *et al.*, 2002; Fox *et al.*, 2014). Our results suggest that butterfly eggs may be less susceptible to parasitical attacks than overwintering larvae or pupae. An alternate mechanism to explain the negative impacts of rising winter temperature is phenological mismatch, as reported in the winter moth *Operophtera brumata*, whose phenology has advanced more than the bud burst of its hostplant *Quercus rubur* (Visser & Holleman, 2001; van Asch *et al.*, 2013).

Lepidoptera, particularly moths, also generally had a negative response to precipitation especially during and prior to activity times. This may be partly due to the detrimental impact of precipitation on activity during survey periods but this relationship started earlier in the year than surveying begins so we can be confident that this is not the only mechanism driving this relationship. Some

Lepidoptera species had a lagged positive response to winter precipitation, particularly butterflies active in autumn and moths active in summer. Breed *et al.* (2013) suggested that northern American butterflies that overwintered as eggs may be declining because of a high vulnerability to desiccation. However, it is likely that the benefits of winter precipitation are mediated through interactions with other species as the impact is most evident over a year after the precipitation event. The mechanisms behind this relationship are not known and further research would be beneficial, particularly in light of the clear detrimental impact of climate change on moth populations.

This modelling approach provides a valuable tool for identifying the timing of population response to weather events, allowing intercorrelated weather variables to be examined within a single model. A drawback of this method is that precipitation and temperature were modelled separately: these models could be adapted to include both types of variable in a single model. However, this would add an extra four explanatory variables and longer time series would be required for these models. This approach also carries the risk of missing detailed responses to weather. For example summer drought is known to be detrimental for many insects and hence some insectivorous bird species (Pearce-Higgins *et al.* 2010), something that we found little evidence of. However, we have identified the key peaks in responses to climate. Most of our identified peaks have been previously noted but often in species-specific contexts and their relative importance previously unknown. Here we have examined the impact of overwintering strategies on the timing of response to weather but this method would allow the examination of many more traits and could be extended to test for weather-mediated population interactions, for instance between predator and prey species or competing species. Our results also provide a strong basis for projecting changes in species' status. These sorts of prediction are likely to be much more robust than predictions based solely on species distribution models (e.g. Thomas *et al.*, 2004; Gregory *et al.*, 2009) because our results can be integrated into stochastic climate projections that account for seasonal and annual climatic variability rather than simply mean temperatures. Importantly our results have emphasised the impact of high precipitation and winter temperatures in moth declines and the impact of increasing temperatures in aphid increases. Further research to explicitly make species-specific population projections from UK climate projections should be of high priority to identify vulnerable species.

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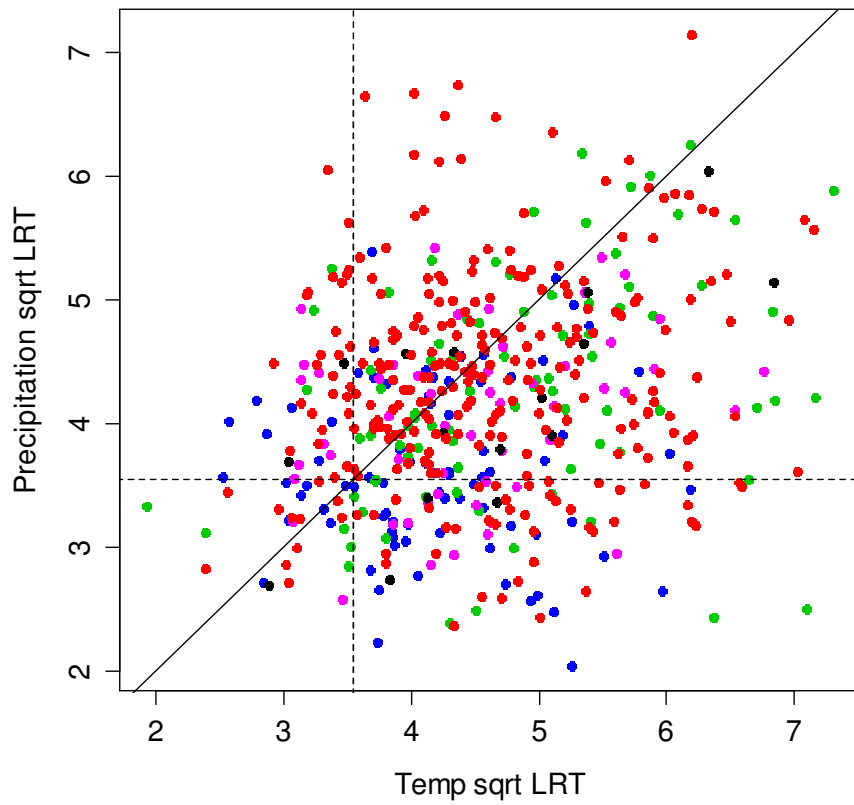


Figure 1. Likelihood ratio tests for species' responses to mean monthly temperature and precipitation. An LRT score of above 3.55^2 indicates that the weather model was significantly better than the null model. A line showing a 1:1 relationship has been added and taxonomic group is indicated by the point colour: mammals (black), birds (blue), aphids (green), butterflies (magenta) and moths (red).

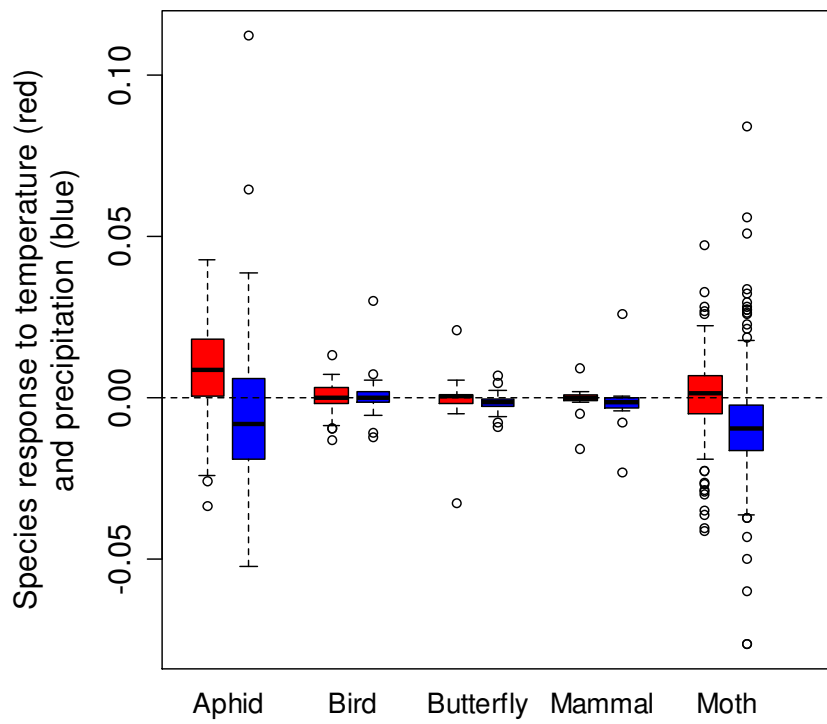


Figure 2 Species' responses to temperature (red) and precipitation (blue) showing median, quartiles and outliers..

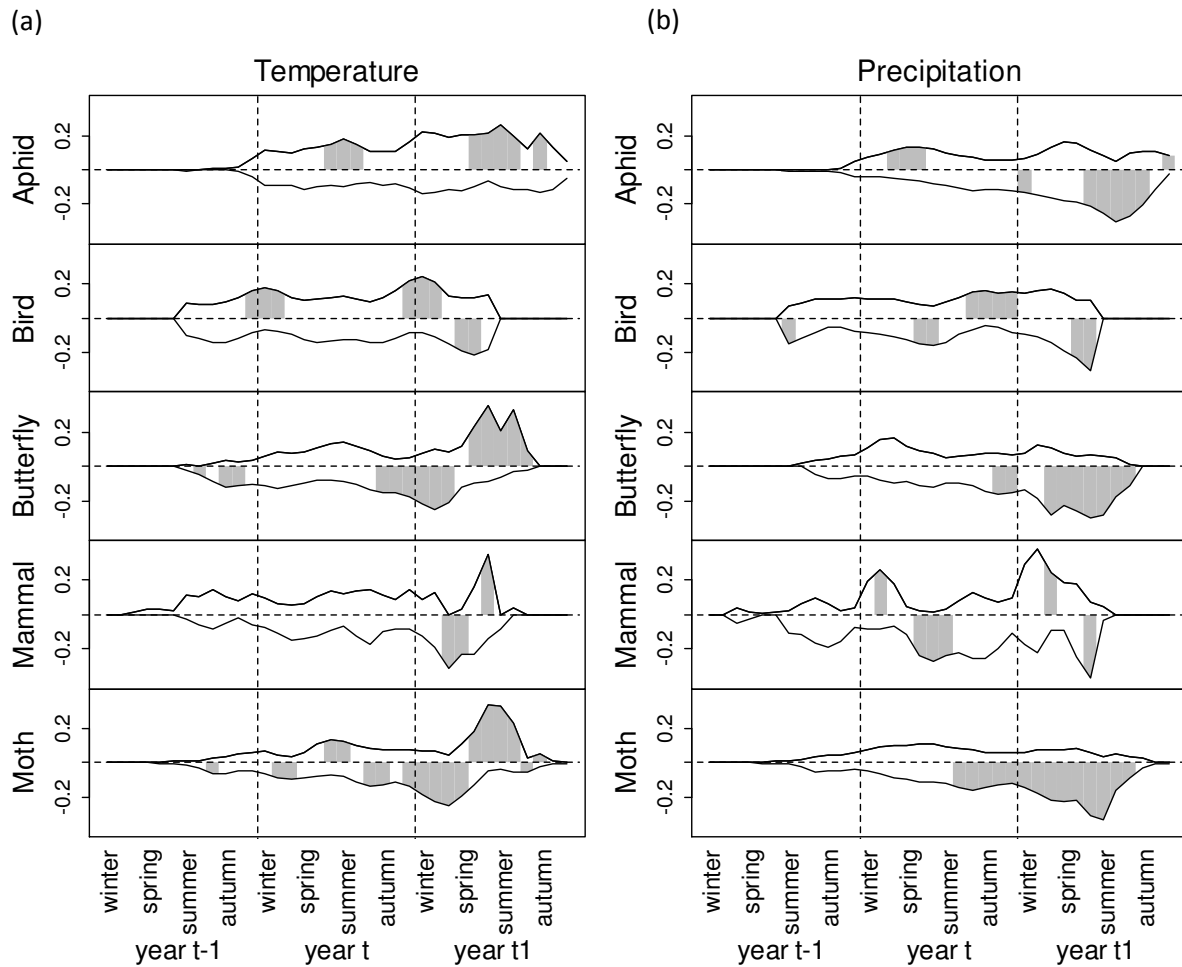


Figure 3. Plots indicating the response of aphid, bird, butterfly, mammal and moth population abundances to (a) temperature and (b) precipitation over the two years prior to the survey period. In each month species were divided into negatively and positively responding species and the y-axis shows the sum of standardised monthly coefficients across these species divided by the total number of species within each taxon included in this analysis. The division of species into negatively and positively responding species illustrates the diversity of responses to weather within each taxon. Months in which the mean of monthly coefficients was significantly above or below zero are highlighted in grey.

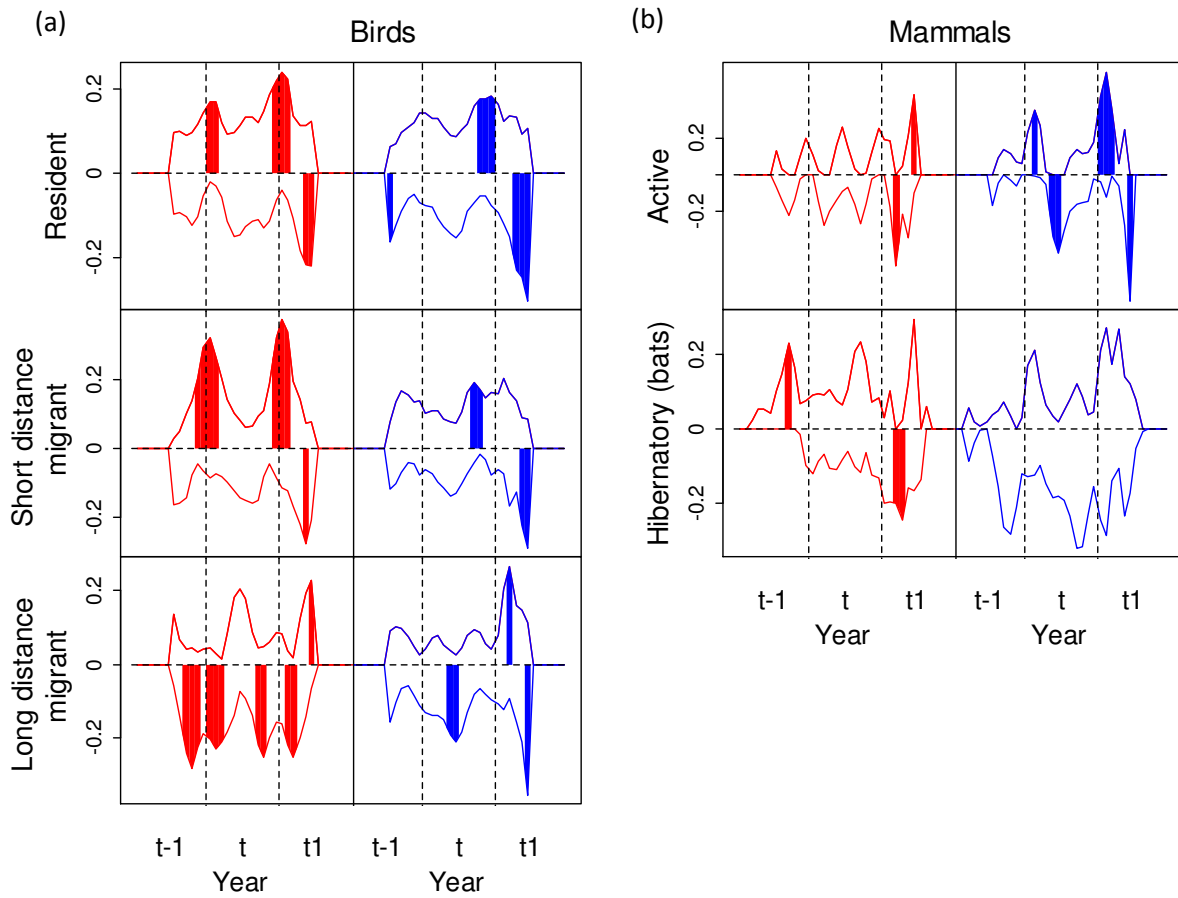


Figure 4 Plots indicating the response of (a) bird and (b) mammal population abundances to temperature (red plots) and precipitation (blue plots) over the two years prior to the survey period, dividing species by their overwintering strategy. In each month species were divided into negatively and positively responding species and the y-axis shows the sum of standardised monthly coefficients across these species divided by the total number of species in each group. In mammals all bat species were hibernatory while all other mammals were active throughout winter. Months in which the mean of monthly coefficients was significantly above or below zero are highlighted in red (for temperature responses) and blue (for precipitation responses).

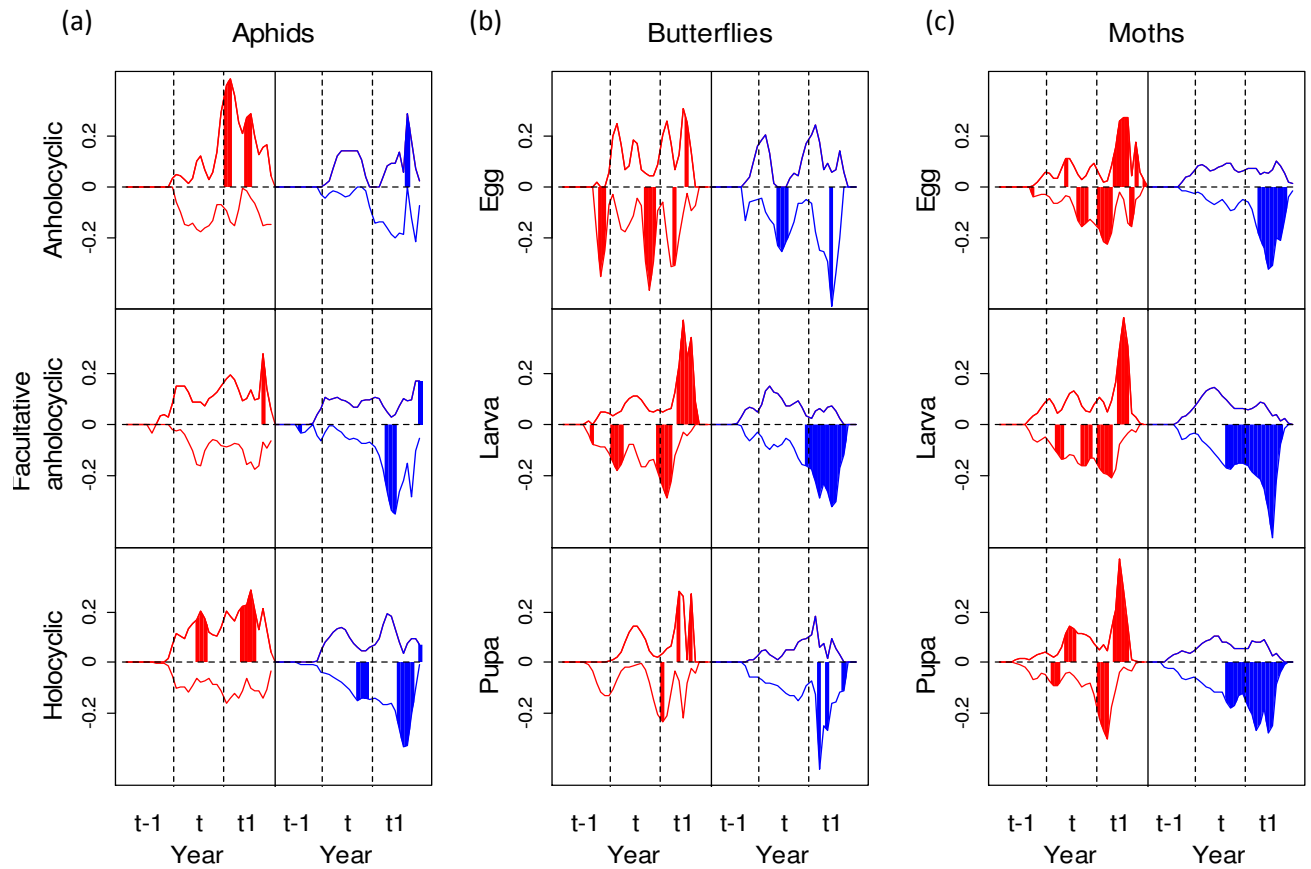


Figure 5 Plots indicating the response of (a) aphid, (b) butterfly and (c) moth population abundances to temperature (red plots) and precipitation (blue plots) over the two years prior to the survey period, dividing species by their overwintering strategy. In each month species were divided into negatively and positively responding species and the y-axis shows the sum of standardised monthly coefficients across these species divided by the total number of species in each group. Months in which the mean of monthly coefficients was significantly above or below zero are highlighted in red (for temperature responses) and blue (for precipitation responses).

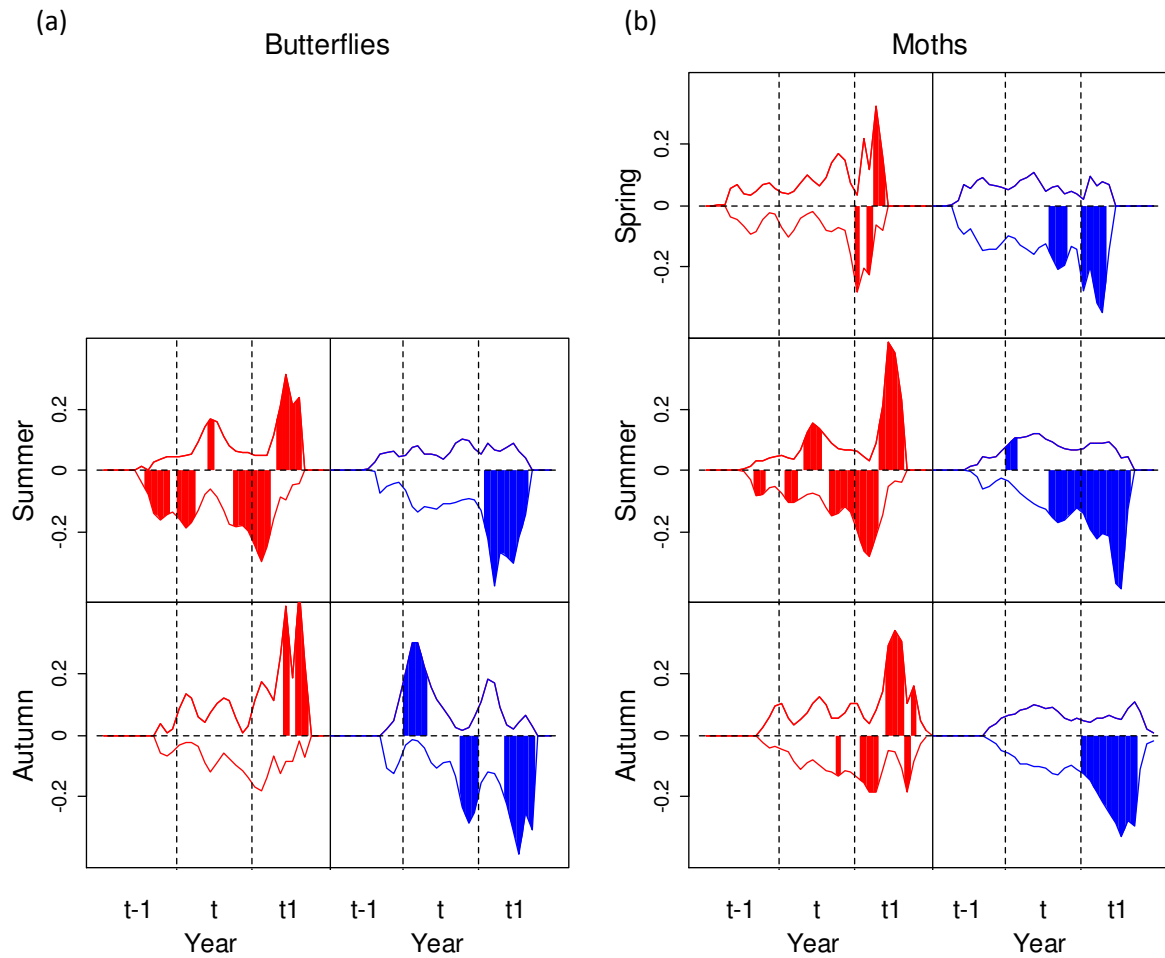


Figure 6 Plots indicating the response of (a) butterfly and (b) moth population abundances to temperature (red plots) and precipitation (blue plots) over the two years prior to the survey period, dividing species by their activity period. In each month species were divided into negatively and positively responding species and the y-axis shows the sum of standardised monthly coefficients across these species divided by the total number of species in each group. Months in which the mean of monthly coefficients was significantly above or below zero are highlighted in red (for temperature responses) and blue (for precipitation responses).