

Appendix 5: BICCO-Net II. Assessing the fine-scale impact of climate on bird and butterfly population dynamics

Abstract

Climate change is a key threat to biodiversity, driving changes in abundance, phenology and range patterns. Evidence suggests that species vary in their response to climate change, with some species benefitting from climate change, while others decline. Far less is understood about how different populations of the same species respond to climate. Here we examine if population responses to climate vary systemically with respect to local climatic conditions. Using long-term monitoring data of the butterfly and bird fauna in Britain, we found that populations in cooler climates tend to have a stronger association with inter-annual variation in weather conditions. This is consistent with the idea that populations near species' range margins experience a smaller proportion of available habitat in climatically suitable conditions, compared with populations in the core of a species climate range or niche space. On average we found butterflies had a stronger association with climate than birds, and attribute this to the greater dependence on external climatic conditions of ectotherms than endotherms. Our models may be used to predict population level impacts of climate change and therefore can inform which species and populations are most vulnerable to climate change.

Introduction

Anthropogenic climate change is as a major threat to biodiversity, with evidence showing that it has driven declines the abundance and distribution of species, and is responsible for shifts in species' ranges and phenological patterns (Parmesan *et al.*, 1999; Parmesan & Yohe, 2003; Thomas *et al.*, 2004; Thomas *et al.*, 2006; Wilson *et al.*, 2007; Willis *et al.*, 2008; Gregory *et al.*, 2009; Bellard *et al.*, 2012). With the continued rise in greenhouse gas emissions, the impact of climate change is likely to persist and intensify (IPCC, 2013). The impact of climate change on biodiversity can be direct, for example a previously suitable region may become climatically unsuitable due to a rise in temperature, or can be indirect, for example the climate driven loss of pollinators can inhibit plant reproduction (Thomas, 2010; Walther, 2010; Cahill *et al.*, 2013). In addition, some studies have suggested that climate change can exacerbate the negative impact of other aspects of environmental change, such as habitat loss and degradation (Travis, 2003; Hof *et al.*, 2011; Newbold *et al.*, 2012). Evidence suggests that species vary in their response to climate change, i.e. some species can benefit from climate change while others may decline (Hickling *et al.*, 2006; Angert *et al.*, 2011; Warren *et al.*, 2013). However, far fewer studies have examined how different populations of the same species respond to climate (but see Isaac *et al.*, 2011). In this study, we focus on the direct impact of climate on population dynamics, where we test if population responses to weather vary systemically with respect to local climatic conditions.

Variation in population abundance is an important measure for studies that examine species' response to environmental change. It is frequently used as the key response variable for research into biodiversity loss. In this study, we examine population dynamics of birds and butterflies in Britain. Birds and butterflies are ideal study groups for this study for two main reasons. Firstly, both taxonomic groups have shown population responses to climate change (Roy *et al.*, 2001; Hickling *et al.*, 2006; Gregory *et al.*, 2009; Pimm, 2009; Devictor *et al.*, 2012; Pateman *et al.*, 2012), with butterflies particularly reliant on temperature, due to their ectothermic life style (Warren *et al.*, 2001; Mattila *et al.*, 2011; Devictor *et al.*, 2012). Secondly, Britain has some of the best long-term

population datasets in the world, with projects such as the UKBMS and CBC recording butterfly and bird population numbers on set transects, using standardised survey methods, for over 40 years. This provides a valuable resource for examining the temporal and spatial impacts of environmental change on biodiversity.

Climate limits species distribution patterns, with the upper and lower thermal tolerance of a species forming the boundaries of its climate niche. Population abundance tends to be highest in the centre of a species climate niche, with declines towards the margins (Brown, 1995), and the dynamics of marginal populations have been shown to be more variable (Thomas *et al.*, 1994; Oliver *et al.*, 2009). One reason for increased fluctuations in marginal populations is that habitat specificity increases in these populations (Oliver *et al.*, 2009). Each habitat type will provide a set of microclimates that species will utilize in order to occupy a climatic condition that fits within their climatic niche. Marginal populations are likely to be occupying the warmest or coldest microhabitats in order to survive (Thomas *et al.*, 1999; Oliver *et al.*, 2009). In Britain, many species reach their leading cool margin, and therefore marginal population will be occupying the warmest microclimates. A drop in temperature will result in declines for the marginal populations, whereas core populations are buffered as they have a greater potential to persist by switching to a warmer microhabitat. Based on this, we predict that populations occurring at the limit of their climatic niche are likely to show a stronger response to climate variability than those in the centre of their niche. We predict that patterns for birds will be qualitatively similar but less pronounced.

Methods

Species data

We extracted species abundance estimates for Butterflies and Birds from the United Kingdom Butterfly Monitoring Scheme (UKBMS – <http://www.ukbms.org/>) and the Common Bird Census (CBC - <http://www.bto.org/about-birds/birdtrends/2011/methods/common-birds-census>), respectively. Each monitoring scheme used standardised survey methods, from which we extracted data at the species, site, year level. Data were extracted for a distinct time period for each taxonomic group, butterfly data were from 1976 to 2012, while bird data were from 1962 to 2002. Site with less than 10 years of data were excluded to ensure only well established sites were included in the analysis. As we are examining the impact of climate on population dynamics across temporal and spatial scales, we excluded species that were present in less than 10% of all sites in the analysis, thereby ensuring we had spatial variation in our climate data for each species.

Climate data

In this study, we examine the impact of temperature and precipitation, on population dynamics. We used gridded 5 x 5 km, monthly mean temperature and rainfall data taken from the Met Office UKCP09 datasets to determine the climate at each site (http://www.metoffice.gov.uk/climatechange/science/monitoring/ukcp09/download/monthly/gridded_monthly.html - Perry & Hollis 2005). We ensured that the time frame of the climate data closely matched that of the species abundance data, 1966 to 2011. The influence of climate on population dynamics can vary throughout a year, for example a wet spring can have a strong negative impact on many butterfly species (Warren, 1987). To account for this impact and any potential lagged influence of climate on populations, we used the results of the national-scale analysis based on Fourier oscillations to create year- and species-specific temperature and precipitation covariates.

The process of extracting and converting results from the national-scale analysis for use in the fine-scale study is fairly complex and is described in detail in Appendix II: Description of modelling methodology used in BICCO-Net II. To summarise, we extracted species' association with mean rainfall and temperature at the national scale for each year between 1966 and 2011. For each species- year combination, the weather associations were estimated as cumulative effect of each weather variable on population dynamics from year 0 to a 10 year lag period, from here on in we refer to these as the temperature (T_t) and rainfall indices (P_t). The two weather indices can be viewed simply as a measure of how suitable the annual weather condition is given the species response to weather taken from the national-scale analysis. In addition to the weather indices, for each site-year combination, we calculated the climate (both temperature and rainfall) anomaly as the difference in the mean annual climate of the site and the mean annual climate across all sites. The weather indices represent the annual variation in weather, while the climate anomalies are a measure of spatial variation in climate.

Analysis

Using the data at the site, year level, we ran generalised linear mixed effects models (GLMMs) separately for each species with log-link abundance as the response variable with Poisson error structure. We included the temperature and rainfall indices and both climate anomalies as predictors of fine-scale population dynamics. To examine if the relationship between the temperature index and population abundance varied based on local site conditions, we included the temperature index-temperature anomaly interaction term in the models. To account for density dependence we included the population index in the previous year ($t-1$) as a fixed effect in the GLMMs, such that our estimates for other parameter model the effect on population growth rates. Our model for each species is as follows:

$$Pois(y_{it}); \log(y_{it}) = a + bI + cy_{i(t-1)} + dT_t + eP_t + f(U_{it} - U_t) + g(Q_{it} - Q_t) + h(T_t(U_{it} - U_t)) + J_i + K_t$$

Y_{it} is the log-link abundance at site i in year t fitted using a Poisson GLMM. B is the estimated slope of a continuous effect for year l , c is the slope of the effect of the effect of abundance y at site i in the previous year $t-1$. d and e are the slopes of the effect of temperature T and rainfall P indices on population growth for year t , estimated from the national scale analysis. f and g are the slopes of the effect of the temperature ($U_{it} - U_t$) and rainfall ($Q_{it} - Q_t$) anomaly, U_{it} is the mean annual temperature at site i in year t , while Q_{it} is the mean annual rainfall in site i in year t . U_t and Q_t are the mean annual temperature and rainfall across all site in year t . h is the effect of the interaction term between T_t and ($U_{it} - U_t$). We also included a random effect for site J_i and year K_t to model variation in mean abundance, both of which were coded as categorical variables. Our null hypothesis is that $h = 0$.

To examine the importance of the fine scale drivers of abundance, we plotted histograms of the Z-scores for all parameters across all species. The key parameter of interest was h , the interaction term in our GLMMs. A significant negative h suggests species response to temperature is greater in cooler sites, matching our hypothesis. However, a significant positive interaction suggests species

show greater response to climate in warmer sites. In order to gain a better understanding of what drives the spatial variation in temperature association, we examined the fitted values for abundance plotted against the temperature index and temperature anomaly.

Results

We found widespread inter-species variability in explanatory variable significance (Table 1). Our decision to account for density dependence by including the previous year's abundance estimate proved to be important, as parameter c was significant in 97% of butterfly and 100% of bird models. For the vast majority of these models the relationship was positively correlated as expected.

The mean Z-score of the relationship between fine-scale abundance and the temperature index was higher in butterflies (3.146) than in birds (1.774, figure 1), suggesting that on average temperature has a greater impact on butterfly population dynamics than on bird dynamics. The species with the most extreme Z-scores taken from the relationship abundance and the weather indices are listed in Table 2.

Butterflies had a higher average Z-score for the relationship between site temperature anomaly and abundance than birds (2.952 and 0.134, respectively). A positive relationship between temperature anomaly and abundance reflects an increase in population size in warmer sites, therefore butterflies tended to show a more positive response to warmer temperatures than birds. On average, butterflies had a negative relationship with rainfall anomaly, while the mean was marginally negative for birds.

As with all other parameters in this study, the temperature index- temperature anomaly interaction (h) varied between species. A significant interaction suggests that the relationship between temperature index and fine-scale abundance varies along the site temperature anomaly gradient. A significant negative interaction effect translates to the influence of temperature on population dynamics being stronger in cooler sites than warmer sites. Both birds and butterflies tended to have negative interaction Z-scores, however the mean Z-score for butterflies was substantially more negative (butterfly mean = -2.913, bird mean = -0.315). The fitted value plots of figure 3 highlight the spatial and temporal variation in climate association for two butterfly and two bird species. The Ringlet & Willow Warbler both had significantly positive temperature index- temperature anomaly interaction, while for Meadow Brown and Blackbird the interaction was significantly negative. In Figure 3c & d, the vertical gradient in colour is greater in cooler sites than warmer sites, a trend that reflects the increased influence of climate on population dynamics in cooler sites. The contrasting pattern and trend can be seen in Figure 3a & b.

The variation in fine-scale abundance explained by the models varied between species (Figure 4). R^2 values for butterflies varied from 0.01 to 0.2, with a mean of 0.07, while for birds it varied between 0.01 and 0.30, with mean of 0.09. On average we found that butterflies had a greater proportion of significant parameters than birds (Table 1). This is likely due to the increased ability to detect significant relationships with a larger sample size, in this case the number of sites included in the species model tended to be higher in the butterfly models (Figure 5).

Discussion

In this study, we found evidence of spatial variation in bird and butterfly population responses to temperature. We find support for our hypothesis as temperature tended to have a stronger association with population dynamics in cooler sites. We believe this relationship is due to the greater vulnerability of marginal populations to climatic fluctuations. Microclimates can vary between habitats, for example a north facing open grassland may have a warmer microclimate than dense woodland. Populations at the cooler limit of their climatic niche are likely to be occupying the habitats with the warmest microclimate in order to survive (Thomas *et al.*, 1999; Oliver *et al.*, 2009; Isaac *et al.*, 2010). A drop in temperature will therefore result in a population decline in these marginal populations, while populations that occur within the core of the climatic niche will be less vulnerable to climatic fluctuations as they can persist by shifting into a warmer microclimate. There are similarities between this result and the work of Oliver *et al.*, (2010), who found that habitat heterogeneity was associated with more stable population dynamics. In our case, there are fewer microclimate opportunities in marginal populations and therefore less stable population dynamics with a greater dependence on climatic conditions. An interesting area for future study would be to directly test if population responses to climate vary with respect to habitat heterogeneity of the local landscape. Based on the results in this study and the research of Oliver *et al.* (2010), we hypothesise that climate association would be greater in sites with more homogenous local landscape compositions. We also predict that including an estimate of local landscape conditions would improve the r^2 of the species models, which currently have a mean of 0.07 and 0.09 for butterflies and birds, respectively.

On average we found stronger evidence of spatial variation in butterfly population responses to climate than bird population responses. This is likely due to the ectothermic nature of butterflies, meaning as a group they are more susceptible to climatic pressures than the endothermic birds. When examining climatic debts and distributional shifts in European butterflies and birds, Devictor *et al.*, (2012) found that butterflies tended to show a greater dependence and response to climate change than birds. They attributed this to the difference between an ectothermic and endothermic life style, but also suggested that the shorter generation time of butterflies allowed them a faster evolutionary response to climate change. We found further evidence of the greater association of butterfly populations with climate than birds, in the species' relationships with the two weather indices and also with site temperature anomaly (Figure 1). For both, the temperature index and the site temperature anomaly, butterfly Z-scores tended to be more positive than birds, suggesting that climate is having a greater effect on butterfly population dynamics than birds. Again, this is likely due to the difference in the reliance on external temperature conditions between ectotherms and endotherms. In our analysis, sample size (number of sites included in the model) for butterfly species tended to be larger than birds, this can enable greater power to detect a stronger significant relationship in the butterfly models, and therefore could have driven the increased evidence of spatial variation in butterfly population responses to climate. However, we feel this is unlikely as due to the wealth of evidence that suggests ectotherms should respond more strongly to climatic pressures than endotherms (Thomas *et al.*, 2004; Hickling *et al.*, 2006; Devictor *et al.*, 2012).

The fine-scale modelling approach that we utilise in this study enabled us to detect that species response to climate varied systemically with local climatic conditions, a result that would be missed using a broader national-scale analysis. The widespread variation in population response to climate across species is likely due to inter-species variation in a selection of attributes that can influence species' vulnerability to climate change, such as habitat specialism, thermal tolerance, dispersal ability (Mattila *et al.*, 2011; Devictor *et al.*, 2012). High levels of inter-species variation was also detected by Isaac *et al.*, (2011), who modelled the relationship between butterfly abundance and climate on transects in Britain. The variation in species' response to climate can be clearly seen in the examples in Figure 4. Using these figures, we see that meadow brown (Figure 4c) and blackbird (Figure 4d) populations respond positively to warmer sites in climatically suitable (warm, for these species) years, but that declines are most pronounced in cold sites in climatically unsuitable years. As with the meadow brown and blackbird populations, the ringlet (Figure 4a) responds positively to warm sites in climatically suitable years. However, the ringlet has a negative association with temperature from the national scale models, whereas the other two species were positively associated. As cooler years are more climatically suitable for the ringlet than warm years, the plot in figure 4a shows declines in ringlet populations were greatest in warm years on warm sites. Studies have shown that the ringlet is particularly vulnerable to drought events (Sutcliffe *et al.*, 1997; Oliver *et al.*, 2013), we believe our result (in particular figure 4a) provide further evidence of this vulnerability. The results for willow warbler indicate that climatic suitability had opposite effects on population trends in the warm south and the cool north. In climatically suitable years (positive temperature index), population growth was positive in the south, but it was most positive in the north during unsuitable years (negative temperature index). This is indicative of a potential northwards shift in distribution as climatic suitability deteriorates (Morrison *et al.* 2010).

To conclude, we find species' response to climate can vary systematically with respect to local site conditions. We found that butterflies tend to show a stronger response to climate than birds, and attribute this to the differences between ecto- and endotherms. Our models may be used to predict population level impacts of climate change and therefore can inform which species and populations are most vulnerable to climate change. Finally, to help mitigate the negative impacts of climate change, we recommend conservation efforts should be focussed on increasing the habitat heterogeneity with the landscape of Britain. The greater availability of habitat types the more microclimates within which individuals can shift between in order to persist during climate fluctuations (Thomas *et al.*, 1999; Oliver *et al.*, 2010).

References

- Angert, A.L., Crozier, L.G., Rissler, L.J., Gilman, S.E., Tewksbury, J.J. & Chunco, A.J. (2011) Do species' traits predict recent shifts at expanding range edges? *Ecology letters*, **14**, 677–89.
- Bellard, C., Bertelsmeier, C., Leadley, P., Thuiller, W. & Courchamp, F. (2012) Impacts of climate change on the future of biodiversity. *Ecology Letters*, no–no.
- Brown, J.H. (1995) *Macroecology*, The University of Chicago Press, Chicago.

- Cahill, A.E., Aiello-Lammens, M.E., Fisher-Reid, M.C., Hua, X., Karanewsky, C.J., Ryu, H.Y., Sbeglia, G.C., Spagnolo, F., Waldron, J.B., Warsi, O. & Wiens, J.J. (2013) How does climate change cause extinction? *Proceedings. Biological sciences / The Royal Society*, **280**, 20121890.
- 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 Strien, A., Van Turnhout, C., Vermouzek, Z., WallisDeVries, M., Wynhoff, I. & Jiguet, F. (2012) Differences in the climatic debts of birds and butterflies at a continental scale. *Nature Climate Change*, **2**, 121–124.
- Gregory, R.D., Willis, S.G., Jiguet, F., Vorísek, P., Klvanová, A., van Strien, A., Huntley, B., Collingham, Y.C., Couvet, D. & Green, R.E. (2009) An indicator of the impact of climatic change on European bird populations. *PloS one*, **4**, e4678.
- Hickling, R., Roy, D.B., Hill, J.K., Fox, R. & Thomas, C.D. (2006) The distributions of a wide range of taxonomic groups are expanding polewards. *Global Change Biology*, **12**, 450–455.
- Hickling, R., Roy, D.B., Hill, J.K., Fox, R. & Thomas, C.D. (2006) The distributions of a wide range of taxonomic groups are expanding polewards. *Global Change Biology*, **12**, 450–455.
- Hof, C., Araújo, M.B., Jetz, W. & Rahbek, C. (2011) Additive threats from pathogens, climate and land-use change for global amphibian diversity. *Nature*, **480**, 516–9.
- IPCC (2013) *Climate Change 2013: the Physical Science Basis. Contributions of Working Group I to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change*, Cambridge, UK.
- Isaac, N.J.B., Girardello, M., Brereton, T.M. & Roy, D.B. (2011) Butterfly abundance in a warming climate: patterns in space and time are not congruent. *Journal of Insect Conservation*, **15**, 233–240.
- Mattila, N., Kaitala, V., Komonen, A., Päivinen, J. & Kotiaho, J.S. (2011) Ecological correlates of distribution change and range shift in butterflies. *Insect Conservation and Diversity*, **4**, 239–246.
- Morrison, C.A., Robinson, R.A., Clark, J.A. & Gill, J.A. (2010) Spatial and temporal variability in population trends in a long-distance migratory bird. *Diversity & Distributions*, **16**, 620–627.
- Newbold, T., Scharlemann, J.P.W., Butchart, S.H.M., Sekercioglu, C.H., Alkemade, R., Booth, H. & Purves, D.W. (2012) Ecological traits affect the response of tropical forest bird species to land-use intensity. *Proceedings of the Royal Society B: Biological Sciences*, **280**, 20122131–20122131.
- Oliver, T., Hill, J.K., Thomas, C.D., Brereton, T. & Roy, D.B. (2009) Changes in habitat specificity of species at their climatic range boundaries. *Ecology letters*, **12**, 1091–102.
- Oliver, T., Roy, D.B., Hill, J.K., Brereton, T. & Thomas, C.D. (2010) Heterogeneous landscapes promote population stability. *Ecology letters*.

- 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.
- 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.
- Parmesan, C. & Yohe, G. (2003) A globally coherent fingerprint of climate change impacts across natural systems. *Nature*, **421**, 37–42.
- Pateman, R.M., Hill, J.K., Roy, D.B., Fox, R. & Thomas, C.D. (2012) Temperature-dependent alterations in host use drive rapid range expansion in a butterfly. *Science (New York, N.Y.)*, **336**, 1028–30.
- Perry, M. & Hollis, D. (2005) The generation of monthly gridded datasets for a range of climatic variables over the UK. *International Journal of Climatology*, **25**, 1041–1054.
- Pimm, S.L. (2009) Climate disruption and biodiversity. *Current biology : CB*, **19**, R595–601.
- Sutcliffe, O.L., Thomas, C.D., Yates, T.J. & Greatorex-Davies, J.N. (1997) Correlated extinctions, colonizations and population fluctuations in a highly connected ringlet butterfly metapopulation. *Oecologia*, **109**, 235–241.
- Thomas, C.D. (2010) Climate, climate change and range boundaries. *Diversity and Distributions*, **16**, 488–495.
- Thomas, C.D., Cameron, A., Green, R.E., Bakkenes, M., Beaumont, L.J., Collingham, Y.C., Erasmus, B.F.N., de Siqueira, M.F., Grainger, A., Hannah, L., Hughes, L., Huntley, B., van Jaarsveld, A.S., Midgley, G.F., Miles, L., Ortega-Huerta, M.A., Peterson, A.T., Phillips, O.L. & Williams, S.E. (2004) Extinction risk from climate change. *Nature*, **427**, 145–148.
- Thomas, C.D., Franco, A.M. a & Hill, J.K. (2006) Range retractions and extinction in the face of climate warming. *Trends in ecology & evolution*, **21**, 415–6.
- Thomas, J.A., Moss, D. & Pollard, E. (1994) Increased fluctuations of butterfly populations towards the northern edges of species' ranges. *Ecography*, **17**, 215–220.
- Thomas, J.A., Rose, R.J., Clarke, R.T., Thomas, C.D. & Webb, N.R. (1999) Intraspecific variation in habitat availability among ectothermic animals near their climatic limits and their centres of range. *Functional Ecology*, **13**, 55–64.
- Thomas, J.A., Telfer, M.G., Roy, D.B., Preston, C.D., Greenwood, J.J.D., Asher, J., Fox, R., Clarke, R.T. & Lawton, J.H. (2004) Comparative losses of British butterflies, birds, and plants and the global extinction crisis. *Science (New York, N.Y.)*, **303**, 1879–81.

- Travis, J.M.J. (2003) Climate change and habitat destruction: a deadly anthropogenic cocktail. *Proceedings of the Royal Society B - Biological Sciences*, **270**, 467–73.
- Walther, G.-R. (2010) Community and ecosystem responses to recent climate change. *Philosophical transactions of the Royal Society of London. Series B, Biological sciences*, **365**, 2019–24.
- 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., Moss, D. & Thomas, C.D. (2001) Rapid responses of British butterflies to opposing forces of climate and habitat change. *Nature*, **414**, 65–69.
- Warren, M.S. (1987) The ecology and conservation of the heath fritillary butterfly, *Melitica athalia*. III. Population dynamics and the effect of habitat management. *Journal of Applied Ecology*, **24**.
- 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**, 678–682.
- Willis, C.G., Ruhfel, B., Primack, R.B., Miller-Rushing, A.J. & Davis, C.C. (2008) Phylogenetic patterns of species loss in Thoreau’s woods are driven by climate change. *Proceedings of the National Academy of Sciences of the United States of America*, **105**, 17029–33.
- Wilson, R.J., Gutiérrez, D., Gutiérrez, J. & Monserrat, V.J. (2007) An elevational shift in butterfly species richness and composition accompanying recent climate change. *Global Change Biology*, **13**, 1873–1887.

Table 1 The proportion of species within each taxonomic group which had a significant relationship with each parameter.

Parameter	Equation name	Butterfly	Bird
Year	I	0.64	0.50
Abundance estimate of year-1	$Y_{i(t-1)}$	0.97	1.00
Temperature	T_{it}	0.74	0.36
Rainfall	P_{it}	0.67	0.23
Temperature Anomaly	$U_{it} - U_t$	0.90	0.27
Rainfall anomaly	$Q_{it} - Q_t$	0.82	0.12
Interaction term (temp : temp anomaly)	$T_{it}(U_{it} - U_t)$	0.79	0.20

Table 2 A list of species with the most positive and most negative Z-scores for the relationship between abundance and each of the fixed effects.

A) Butterfly

Explanatory parameter	Positive	Negative
Predicted effect of temperature	Brimstone, White Admiral, Gatekeeper	White-letter Hairstreak, Peacock
Predicted effect of rainfall	Small Heath, Speckled Wood, Small Copper	Pearl-bordered Fritillary, Adonis Blue, Purple Hairstreak
Temp-temp anomaly interaction	Peacock, Ringlet, Chalk-hill Blue	Speckled Wood, Red Admiral, Meadow Brown

B) Bird

Explanatory parameter	Positive	Negative
Predicted effect of temperature	Wren, Whitethroat, Willow Warbler	Swallow, Oystercatcher, Woodcock
Predicted effect of rainfall	Turtle Dove, Sedge Warbler, Blackbird	Greenfinch, Tufted Duck, Lapwing
Temp-temp anomaly interaction	Willow Warbler, House Sparrow, Treecreeper	Wren, Linnet, Blackbird

Figure 1 A histogram for each fixed effect showing the spread of the Z-scores for the relationship between abundance and the fixed effect in question. The dashed line represents the mean Z-score for the taxonomic group, red = butterflies, blue = birds.

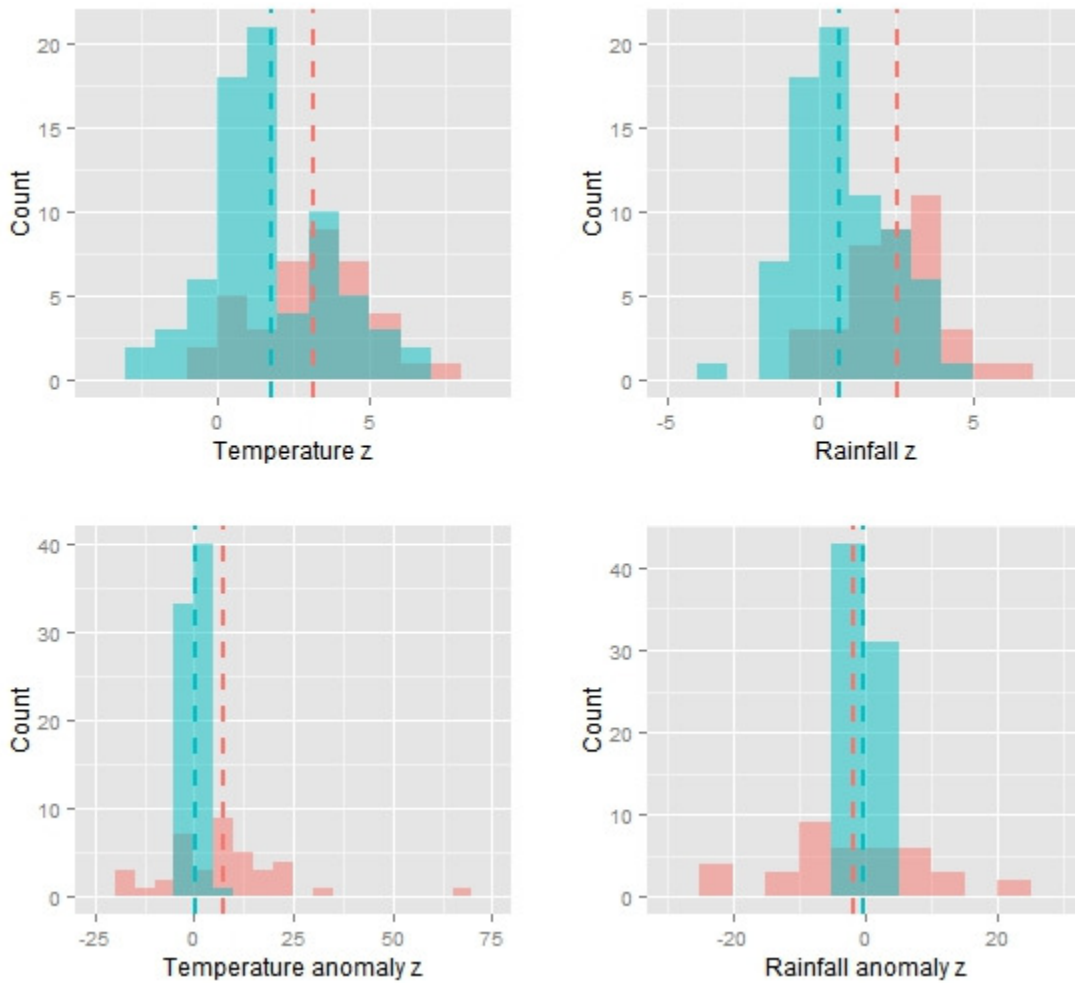


Figure 2 A histogram showing the spread of the Z-scores for the interaction effect of the site temperature anomaly on the relationship between predicted temperature impact and abundance. The dashed line represents the mean Z-score for the taxonomic group.

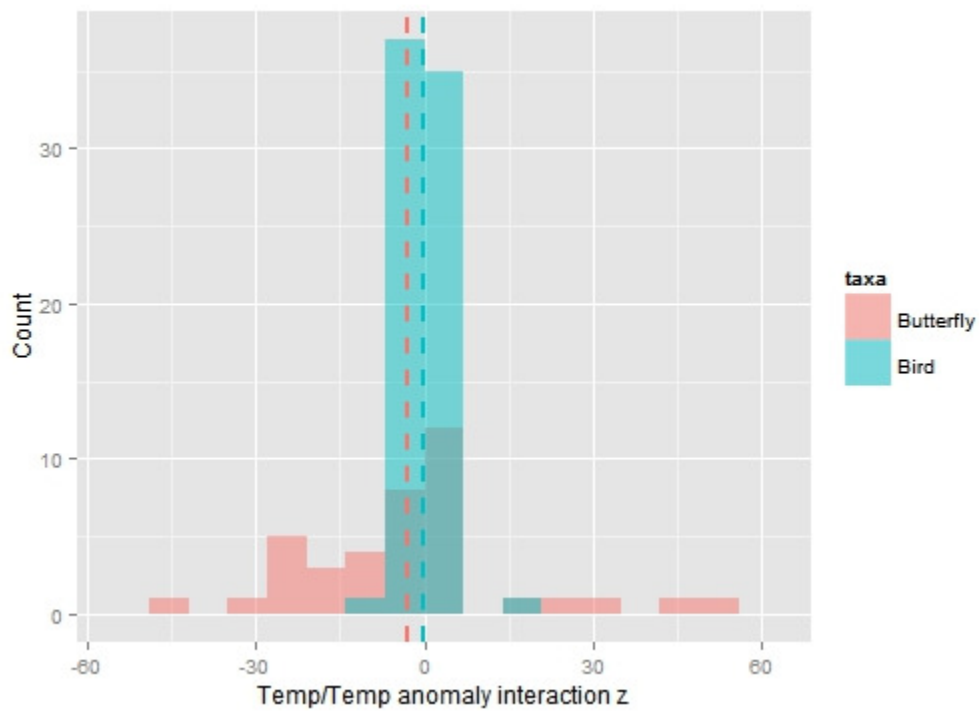


Figure 3

The fitted values for abundance plotted against the temperature index and temperature anomaly, for a) Ringlet b) Willow Warbler, c) Meadow Brown and d) Blackbird. The top row (Ringlet & Willow Warbler) consists of the species with the most positive temperature index- temperature anomaly interaction, while species with the most negative interaction term are plotted on the bottom row (Meadow Brown and Blackbird). Fitted values were plotted as continuous surface running from the minimum to maximum values of the temperature index and temperature anomaly for each species. For these plots, each explanatory variable was centred on 0 prior to running fine-scale model. Fitted values were extracted using the *predict* function in *R*, with all non-temperature model input parameters fixed at 0.

a)

b)

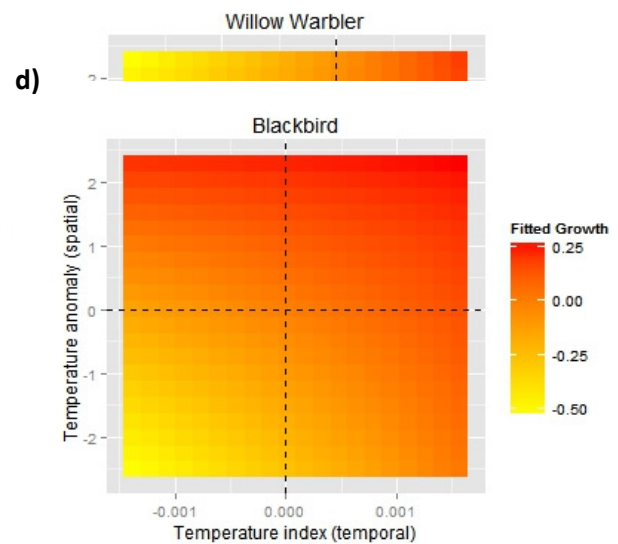
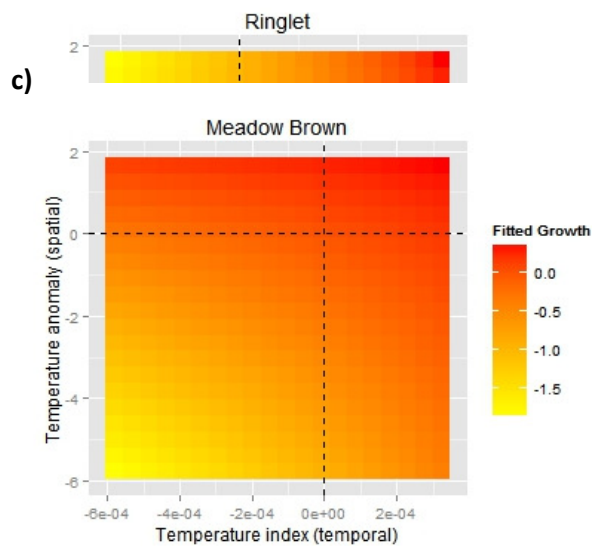


Figure 4 The spread of the r^2 values for the butterfly and bird fine-scale models. The dashed lines represent the mean r^2 for each taxonomic group.

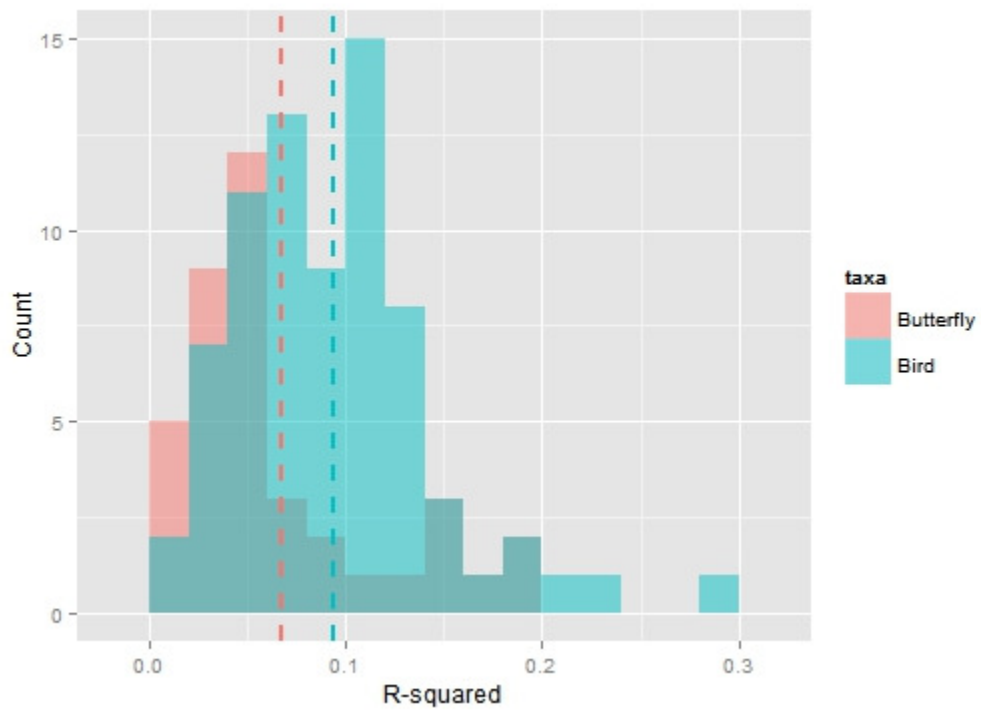


Figure 5 A histogram of the spread of the number of sites included in each species model. The dashed lines represent the mean number of site included in a model for each taxonomic group.

