

BICCO-Net II

Final report to the Biological Impacts of Climate Change Observation Network (BICCO-Net) Steering Group

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1. Executive Summary

- BICCO-Net Phase II presents the most comprehensive single assessment of climate change impacts on UK biodiversity to date.
- The results provide a valuable resource for the CCRA 2018, future LWEC report cards, the National Adaptation Programme and other policy-relevant initiatives linked to climate change impacts on biodiversity.
- The analysis has examined changes in all nationally monitored terrestrial animals using long-term schemes (aphids, moths, butterflies, birds, bats and other mammals). Analyses for birds, butterflies and mammals used widely distributed data from many sites (>1000) and are most likely to reflect national population trends. Although the aphid and moth data were from a limited number of sites with long-term monitoring, their geographical spread means they probably also track national population trends. Additional analyses of butterfly and moth population trends across 12 ECN sites complement these more national-scale analyses.
- Although no national-scale population monitoring exists for the freshwater environment, abundance trends of freshwater macroinvertebrate species were analysed separately from upland and lowland waters using population monitoring data from a non-random selection of geographically limited sites. Analyses of macroinvertebrate community change based on the occurrence of families, were possible for Wales and much of England, and provide an assessment closer to that of national-scale change, albeit at a much coarser taxonomic resolution.
- We used a combination of existing multivariate methods to describe overall patterns in population and climate changes, as well as new statistical methods developed during the project to account for *a priori* uncertainty in the time of year when different organisms respond to variation in temperature and precipitation and which were applied across both terrestrial and freshwater environments.
- The effects of these weather variables upon inter-annual variation in abundance (population growth) may be regarded as describing effects of weather. The extent to which long-term population trends can be accounted for by long-term variation in weather variables we regard as indicating the likely effects of climate change on species abundance. However, we recognise that formal attribution to climate change requires a consideration of the extent to which observed changes in these weather variables are due to anthropogenic forcing, rather than ‘natural’ fluctuations.
- Analyses of national-scale terrestrial biodiversity monitoring of 501 species trends suggests that long-term trends in the weather variables (climate change) had a significant impact on 64% of species, and were associated with strong increases (>30% per decade) in five species, and strong declines in nine moths. When aggregated within taxonomic groups, climate change has contributed significantly to overall national declines in moth populations and increases in aphid populations. There were no significant impacts of climate change on the overall abundance of birds, mammals and butterflies.

- Long-term trends in macroinvertebrate community composition in English and Welsh rivers have been caused by improving urban water quality rather than climate change. Such improvements have reduced the opportunity for adverse climate change effects to be detected, although shorter-term responses to discharge and temperature confirm that freshwater organisms remain sensitive to changes in these weather variables.
- Population-level fluctuations in freshwater macroinvertebrate populations were identified in both acidic upland environments, where weather variables accounted for some variation in 70% of populations at individual sites, and in more lowland contexts across Scotland and central England where the abundance of 65% of organisms was related to variation in weather variables.
- Across all species and populations examined in both terrestrial and freshwater environments, approximately 64% varied significantly with respect to changes in temperature and 62% with precipitation. These proportions were greatest for national-scale analysis of terrestrial population trends (84% and 74% respectively) compared to site-based analysis of individual populations, probably due to the greater stochasticity and uncertainty associated with the latter.
- Effects of temperature were largely positive for aphids, but negative for some freshwater macroinvertebrate groups including a number of caddisfly and stonefly families. Effects of precipitation were largely negative for aphids and moths, but more mixed for other groups.
- These gross patterns mask significant variation in species' responses to temperature and precipitation through the year. National-scale terrestrial analysis highlights that winter temperatures were positively correlated with bird abundance, but negatively with the abundance of butterflies and moths, particularly if also associated with wet winter weather. Warmer spring and summer temperatures may boost aphid, butterfly and moth populations, when they are most active, but there was some evidence for negative spring temperature effects on birds and mammals. Similar responses of butterflies and moths to temperature and precipitation were also apparent on ECN sites.
- In the freshwater environment, the majority of negative temperature effects on upland macroinvertebrates occurred during the summer (July – September), implicating hot summers as having negative effects on subsequent spring abundances. Warm summers were also found to decrease the prevalence of range-expanding macroinvertebrate families, which increased in response to warm spring weather during sampling.
- Summer rainfall negatively impacted the abundance of all terrestrial invertebrate groups, whilst butterflies and moths suffered additional negative impacts of winter and spring precipitation. Spring precipitation was also negatively related to bird and mammal populations. Effects of precipitation upon freshwater invertebrate populations were mixed, but increasing flow rates were associated with increasing prevalence of range-expanding taxa.
- Analyses of the response of populations to temperature across all taxa showed that the most widespread species respond most rapidly to warming. More detailed traits analysis suggests that the response of terrestrial species to temperature and precipitation varied

strongly with species' overwintering strategy. For example, butterflies and moths that overwinter as caterpillars were particularly vulnerable to warm, wet winters.

- Analyses of both upland and lowland freshwater macroinvertebrates suggest that species associated with cooler temperatures were most likely to be affected by warming. Thermal tolerance also affected lowland species sensitivity to precipitation. Additionally, lowland species of fast-flowing waters and predatory species were most negatively associated with warming, whilst the main driver of sensitivity to precipitation in lowland populations was pollution tolerance.
- National-scale bird and butterfly monitoring data provided sufficient samples to examine how population responses to temperature vary between sites. There was consistent evidence for both taxa that variation in climatic conditions had a greater impact upon population growth rates towards the cooler (range-edge) parts of the UK.
- There is considerable policy interest in the development of simple indicators of the impact of climate change upon species' populations. Three potential indicators that track changes in the abundance of different species with respect to the anticipated effect of climate change on those species were tested. The Gregory *et al.* indicator uses the results of bioclimate modelling to separate species likely to increase in response to climate change from those projected to decline, and tracks divergence in their population trends. The Community Temperature Index (CTI) is the mean breeding season temperature across a species' range averaged across species at a site. The BICCO-Net I index separates species into those whose annual fluctuations in population growth are positively associated with temperature from those which are negatively affected, and uses the divergent population trends of these two groups to track climate change.
- Computer simulations were developed to assess the potential sensitivity and specificity of these indicators to climate change. These demonstrated that the different indicator types can produce similar outputs that successfully track changes in temperature. However, all were potentially vulnerable to the effects of simulated non-climatic drivers of change, particularly if those drivers differentially impacted species with different sensitivities to temperature.
- Two indicative climate change indicator types were developed for the UK; CTI and BICCO-Net. The strongest indicator trend was for birds, which showed significant increases in both CTI and BICCO-Net indicators through time. CTI increases were greatest in western and upland Britain. Patterns for other taxa were less clear, potentially as a result of the effects of non-climatic environmental changes upon populations. A combination of all three indicator approaches may have the greatest potential to fully track climate change impacts upon populations, but will require careful interpretation in the light of potentially confounding non-climatic environmental change.
- Long-term trends in the overall abundance of aphids and moths may be related to climate change. Climate change has also differentially affected the abundance of different bird species, altering the composition of avian communities. In other taxa, potential climate change impacts upon long-term trends may be weak, or have been

masked by stronger effects of other, non-climatic changes. In particular, improving water quality may have reversed potential climate change impacts on macroinvertebrates in urban rivers, emphasising how reducing other stressors can offset climate change effects or help species adapt. However, there was good evidence that future warming is likely to continue to detrimentally affect upland freshwater species in fast-flowing waters.

- Although perhaps the most comprehensive single assessment of the impacts of climate change on UK biodiversity population trends that has been conducted to date, our results require careful interpretation. They are largely dependent upon regression and correlation, so that the attribution of observed long-term biodiversity trends to climate change should be made carefully, particularly as the observed trends in weather variables will partly result from anthropogenic forcing, and partly from natural fluctuations.
- We have attempted to minimise the risk of falsely attributing changes in species' populations to weather variables by including additional linear relationships between year and abundance to reduce the likelihood that long-term trends in unmeasured non-climatic drivers may result in spurious correlations between species' abundance and weather variables. Where possible, for the freshwater environment, we extended this approach by also including measurements of variables relating to changes in water quality. The importance of such non-climatic drivers was illustrated by our analysis of climate change indicators.
- The species covered by this project were a non-random selection of those for which extensive long-term monitoring data were available. For some groups, particularly the mammals, they spanned a relatively short time-series, which may have reduced our ability to identify significant relationships between abundance and weather variables. They will also have tended to be relatively common and widespread species. As rare or localised species may be more susceptible to climate change, particularly if associated with cooler northern or upland climates with fewer observers, then it is possible that our general results may underplay the potential impacts of climate change on UK biodiversity.
- The results from this project should input significantly to the 2018 Climate Change Risk Assessment and updates of the LWEC report cards. They will also provide important evidence for the National Adaptation Programme. There is considerable species-level information about the likely sensitivity of the species analysed to changes in temperature and precipitation which could be disseminated to a range of audiences if an appropriate route were found. This could be particularly informative for conservation organisations and to assist with adaptation planning.
- It is worth emphasising that continued extensive monitoring of UK biodiversity, whether through existing citizen science schemes such as the butterfly monitoring scheme or breeding bird survey, or professional surveys, such as conducted by Rothamsted Research or the Environment Agency, is essential to track biological responses to climate change. The collection of additional environmental data associated with such monitoring, such as occurs on ECN sites, or through the analyses of long-

term data about other drivers, will improve the ability to attribute observed changes to climate change, or other drivers. This will be increasingly important in the future, not just to track the impacts of climate change, but also the potential success of adaptation measures in response.

- A number of further evidence needs could be addressed through further analysis and interpretation of the results presented, and which are described at the end of the report.

2. Introduction

2.1. Scientific context

There is increasing evidence that climate change is impacting upon species and their natural populations. A number of reviews have already highlighted significant changes to the timing of biological events, particularly in response to warming (Parmesan & Yohe 2003, Root *et al.* 2003, Thackeray *et al.* 2010). Species' distributions have also shifted in response to climate change (Chen *et al.* 2011), particularly in a poleward direction at medium and high latitudes. Although there are species-specific studies that document significant impacts of climate change on species' populations (e.g. Frederiksen *et al.* 2006, Franco *et al.* 2006, Gregory *et al.* 2009, Pearce-Higgins *et al.* 2010, Johnston *et al.* 2013), there is perhaps greater evidence from studies of changes on the structure of species' assemblages that climate change has already had a detectable impact on populations and ecological communities (e.g. Devictor *et al.* 2008, 2012, Davey *et al.* 2012, 2013). Where these impacts have caused reductions in the abundance of species, they may have significant implications for conservationists, the delivery of ecosystem services, and for meeting legal obligations of biodiversity protection.

Future impacts of climate change are projected to be much more marked than those already detected (Thomas *et al.* 2004, Huntley *et al.* 2008, Araujo *et al.* 2011, Bellard *et al.* 2012, Warren *et al.* 2013). For the UK, the MONARCH project predicted many substantial changes in the distribution of selected BAP priority species in response to climate change (Walmsley *et al.* 2007). More recent Defra-funded studies have assessed the likely consequences of climate change on internationally important bird populations on UK Special Protection Areas (SPAs; Pearce-Higgins *et al.* 2011b, Johnston *et al.* 2013), on priority habitats (Carey *et al.* 2013) and on coastal habitats (Brooks *et al.* 2011). These generally suggest that an increasing proportion of vulnerable species or habitats in the UK will be threatened with increasing severity of climate change.

Significant proportions of species are projected to face local or global extinction under projected future scenarios of change, yet at present there is limited evidence of climate change having caused severe species' population declines and widespread ecosystem disruption (Cahill *et al.* 2013). For the UK, the terrestrial report card, which summarised the latest evidence of climate change impacts, reported with moderate to high confidence that warming has caused the northwards expansion of many species and has advanced spring phenology. The impact of these changes for populations was more mixed, with evidence for declines in some northern and upland communities, but increasing opportunities for population expansion for many others. These opportunities may be moderated by possible widespread negative impacts of increasing extreme events (Morecroft & Speakman 2013). This message that climate change may provide opportunities for some UK species, but have negative impacts on others, was also reflected in a recent project funded by Natural England which identified the risks and opportunities for species in England as a result of climate change (Pearce-Higgins *et al.* 2013). Whilst upland species and bryophytes were identified as being at particularly high risk from climate change, many other species may face new opportunities as climatic conditions improve for them.

Beyond the evidence for range shift and phenological change, many of these statements in the terrestrial report card, as well as many of the species' assessments of risks and opportunities for England, were associated with low confidence due to the uncertainties involved (Morecroft & Speakman 2013, Pearce-Higgins *et al.* 2013). As a result, there is an urgent need for robust collation and analysis of long-term biodiversity monitoring data to allow the impacts of climate change on species populations and communities to be fully documented. Such information may then be used to improve the evidence base used to underpin such assessments.

2.2. Policy context

The Climate Change Act of 2008 contained a commitment to a six-yearly appraisal of the risk that climate change poses to the UK (the Climate Change Risk Assessment; CCRA), the first iteration of which was published in 2012 (CCRA 2012). The Assessment required consideration of all sectors, including a biodiversity component, and highlighted that sensitive species are likely to come under increasing pressure from climate change, although a likely smaller number of species could benefit. However, the ability of the CCRA to provide a comprehensive assessment of biodiversity risks and impacts was limited by the availability of suitable data and completed studies which clearly identified impacts of climate change on biodiversity. With the next iteration of the CCRA due in 2018, there is a high policy-demand for updated and enhanced evidence of climate change impacts on biodiversity.

The recently published terrestrial biodiversity and freshwater report cards, funded by the UK Government and developed under the Living with Environmental Change (LWEC) partnership, were established with an aim to at least partially fill this evidence gap (Morecroft & Speakman 2013, Watts & Anderson 2013). For example, the terrestrial report card was the work of over 40 scientists from 20 different institutions, who authored a total of fifteen underpinning technical papers. These report cards were modelled on the previously established Marine Climate Change Impacts Partnership (MCCIP) reports, the latest version of which was published recently, and includes consideration of climate change impacts on marine and coastal biodiversity (MCCIP 2013).

The need for coordinated long-term monitoring of species populations and distributions, coupled with detailed analyses in order to identify and attribute climate change impacts, has long been recognised by the English Biodiversity Strategy and by the UK Biodiversity Partnership. Such analyses are an important component of climate change adaptation (Hopkins *et al.* 2007, Smithers *et al.* 2008), and specified in *Biodiversity 2020: A strategy for England's wildlife and ecosystem services*. These same pressures and needs increasingly apply to UK's devolved administrations, as covered by the SNH Strategy and Priorities 2012 to 2015, and the Wales Environment Strategy adopted in 2006.

There is a high policy demand for evidence of climate change impacts on biodiversity at both the UK and country level as a first step towards informing adaptation. The BICCO-Net project was set-up with the aim of centralising the collation of relevant biodiversity monitoring data in the UK in order to analyse those data to assess the effects of climate change on biodiversity. The first phase of BICCO-Net ran from 2009-2011, and focussed on

analyses of long-term trends in terrestrial biodiversity (Pearce-Higgins *et al.* 2011a), producing one scientific paper so far (Eglinton & Pearce-Higgins 2012). Some general results from the BICCO-Net project, which had not been completed at the time, fed into the CCRA for the Biodiversity and Ecosystem Services Sector. Many more of the BICCO-Net results input to the terrestrial report card, and it is anticipated that the developments of the current project will assist with future reporting of biodiversity impacts of climate change for the CCRA and other audiences. Such reporting is also likely to feed into the new National Adaptation Programme (NAP) to set out the Government's vision to deal with the priority risks and opportunities that climate change poses. This will include a natural environment theme, which must be underpinned with evidence of impacts of the sort reported through BICCO-Net.

Although, due to marketing restrictions, it has not been possible to promote the BICCO-Net I results through a searchable web-based resource as originally anticipated, BICCO-Net is providing an important tool for the collation and analysis of long-term biodiversity monitoring data, and has contributed significantly to the successful delivery of reporting of climate change impacts on biodiversity. As a result of these successes, Phase II was funded from 2012-2014, with the following objectives.

2.3. Aims

The aims of BICCO-Net II (bold) were subdivided into various tasks as follows, with a summary of task delivery given in Appendix 1:

1. Data update and extension.

1. Update and extend time-series used in Phase I to describe changes in terrestrial biodiversity.
2. Collate long-term time-series that describe changes in freshwater biodiversity

2. Co-ordination of statistical analyses.

3. Analyses of terrestrial population time-series.

1. To better identify climate change impacts, use multiple regression models to extend previous analyses of population trends at a national-scale.
2. Fine-scale analysis of population trends to distinguish climate change impacts from other drivers of change, and quantify interactions between different drivers. This will include:
 - i) Fine-scale analysis of national monitoring scheme data at the site level.
 - ii) Analyses of biodiversity measurements at the 12 terrestrial ECN sites accompanied by co-located meteorological, atmospheric deposition chemistry, soil temperature and soil chemistry data. Comparable analysis will be conducted on freshwater ECN data in Task 4.2.

4. Analysis of freshwater population time-series

1. Analysis of Upland Waters Monitoring Network (UWMN) lakes and streams, supplemented with longer-term data from the Llyn Brianne Stream Observatory.
2. Analysis of national-scale river macro-invertebrate monitoring data in the following ways:
 - i) Community level analysis across England and Wales.

- ii) Family and species-level analysis of distribution and abundance change.
- iii) ECN analysis of co-located species-level population and detailed environmental data, in common with terrestrial analysis of Task 3.2.

5. The development of climate change indicators

1. Short review in order to identify the most appropriate methodology to be developed and used through the BICCO-Net project and the production of national climate change indicators.
2. Production of example maps of spatial variation in the climate change indicator for birds.

6. Traits analysis

1. Report describing traits analysis of the sensitivity of populations to climate change, and comparing responses between terrestrial and freshwater systems to temperature

7. Knowledge transfer

1. Production of a knowledge transfer plan.
2. Dissemination of project information through appropriate web-pages to be identified in consultation with the project steering group.

This report presents a summary of the main findings and achievements of the project. A short methods section provides an overview of the scientific approaches used for the analysis, the key results from which are provided in the results section. The first part of this section summarises the key findings from the project, whilst the second part is divided into short letter-style reports on each of the analytical components of the project, each of which is designed to be a stand-alone summary of the work. More detailed outputs are provided in a series of accompanying appendices. The report concludes by setting the key messages in the wider scientific and policy context, and with suggestions for further work and potential next steps.

3. Methods

3.1. Summary of datasets

BICCO-Net I analysed data on the abundance of seven broad taxonomic groups across a combination of data from national monitoring schemes with extensive, large-scale coverage (mammals, birds, aphids, moths, butterflies) with additional data from Environmental Change Network (ECN) sites which may not be regarded as nationally representative. In BICCO-Net Phase II, the existing time-series were extended using data from extra years, and the scope of the data extended to the freshwater environment (Table 3.1). Due to their variable nature, different datasets were analysed separately, and using a number of complementary approaches. Thus, truly national monitoring schemes, with extensive coverage from widely distributed or stratified random sampling (mammals, birds, aphids, moths, butterflies, freshwater macroinvertebrates), were analysed to examine the impacts of climate change at a national level, although for freshwater macroinvertebrates, variation in the extent to which species-level abundance data are available means that only community-level analysis is possible at a national level. Species-level abundance data were only available for sites

covered by the upland waters monitoring network (UWMN) and a subset of sites in England surveyed by EA, and sites in Scotland surveyed by SEPA.

Table 3.1. Summary of population time-series analysed as part of BICCO-Net project.

Taxonomic group	No. sites	No. species	Survey years	Source
Mammals (BCT)	~1200	12	1998 – 2011	Bat Conservation Trust (BCT)
(BBS)	~3000	6	1995 – 2011	British Trust for Ornithology (BTO)
Birds (CBC/BBS) ¹	~3000	73	1966 – 2011	British Trust for Ornithology (BTO)
(WBS/WBBS) ²	~300	12	1980 – 2011	British Trust for Ornithology (BTO)
Butterflies (BMS)	1424	55	1976 – 2011	Butterfly Conservation (BC)
Moths (RR)	13	265	1975 – 2010	Rothamsted Research (RR)
Aphids (RR)	12	80	1970 – 2010	Rothamsted Research (RR)
Moths and butterflies (ECN)	12		1993 – 2011	ECN (CEH)
Macroinvertebrates - Family level (EA)	2339	78 families	1991 – 2011	Environment Agency (EA)
Species-level (EA/SEPA)				EA, SEPA
(UWMN)	22		1988-2011	UWMN (Ensis Ltd)
(Llyn Brianne)			1981-2011	Llyn Brianne Stream (Cardiff University)

¹The Breeding Bird Survey (BBS) covers 1994 onwards. Prior to that, Common Bird Census (CBC) data were used to produce national trends (see Freeman *et al.* 2007).

²The Waterways Breeding Bird Survey (WBBS) was used to provide data from 1998. Prior to that, the Waterways Bird Survey (WBS) was used to produce national trends.

Table 3.2. Summary of data requirements for the different tasks (listed in 2.3 Aims).

Taxonomic group	T3.1	T3.2i	T3.2ii	T4.1	T4.2i	T4.2ii	T4.2iii	T5.1	T5.2
Mammals (BCT)	X								
Mammals (BBS)	X								
Birds (BBS)	X	X							X
Birds (WBBS)	X								
Butterflies (BMS)	X	X							
Moths (RR)	X								
Aphids (RR)	X								
Moths and butterflies (EC)			X						
Macroinvertebrates – family (EA)					X				
Macroinvertebrates – species (EA/SEPA)						X			
Macroinvertebrates (UWMN)				X					
Macroinvertebrates (Llyn Brianne)				X					

¹Now included as part of the UWMN analysis, rather than considered separately.

Sample data from several monitoring schemes from a large number of locations were analysed to look at finer-grain spatial variation in trends in relation to spatially varied climatic measures (birds, butterflies, freshwater macroinvertebrates). The match between different datasets and the different project tasks is summarised in Table 3.2. It is worth noting that for some of these, the underpinning counts are necessarily of individuals at certain life-cycle stages or of certain forms. Thus, population estimates of butterflies and moths are based on numbers of flying adults, whilst for emergent aquatic macroinvertebrates, counts are of larvae. For multivoltine species, counts may represent the sum of multiple generations. This is most apparent in the counts for aphids which represent multiple generations of flying adults through the year. In addition, these may have a variable relationship with true population size

depending upon the proportion of winged vs unwinged individuals and the number of generations.

Weather was summarised using temperature and precipitation variables. For analyses of the terrestrial environment (T3.1, 3.2i), we used monthly averages in mean temperature and precipitation values, produced across a 5km grid (Met Office UKCP09 gridded datasets; Perry & Hollis 2005). For the national-scale analyses, these were used to generate national descriptions of climate change for England, England and Wales, Great Britain or the UK, as appropriate. For fine-scale analysis, individual sample locations were matched to the weather variables from the grid squares they were located in. For the analysis of ECN data (T3.2ii) and all freshwater analyses, temperature and discharge data were obtained from monthly sampling regimes located at or near invertebrate sampling locations. The patterns in these matched national-level trends in temperature and precipitation (e.g. Figure 3.1).

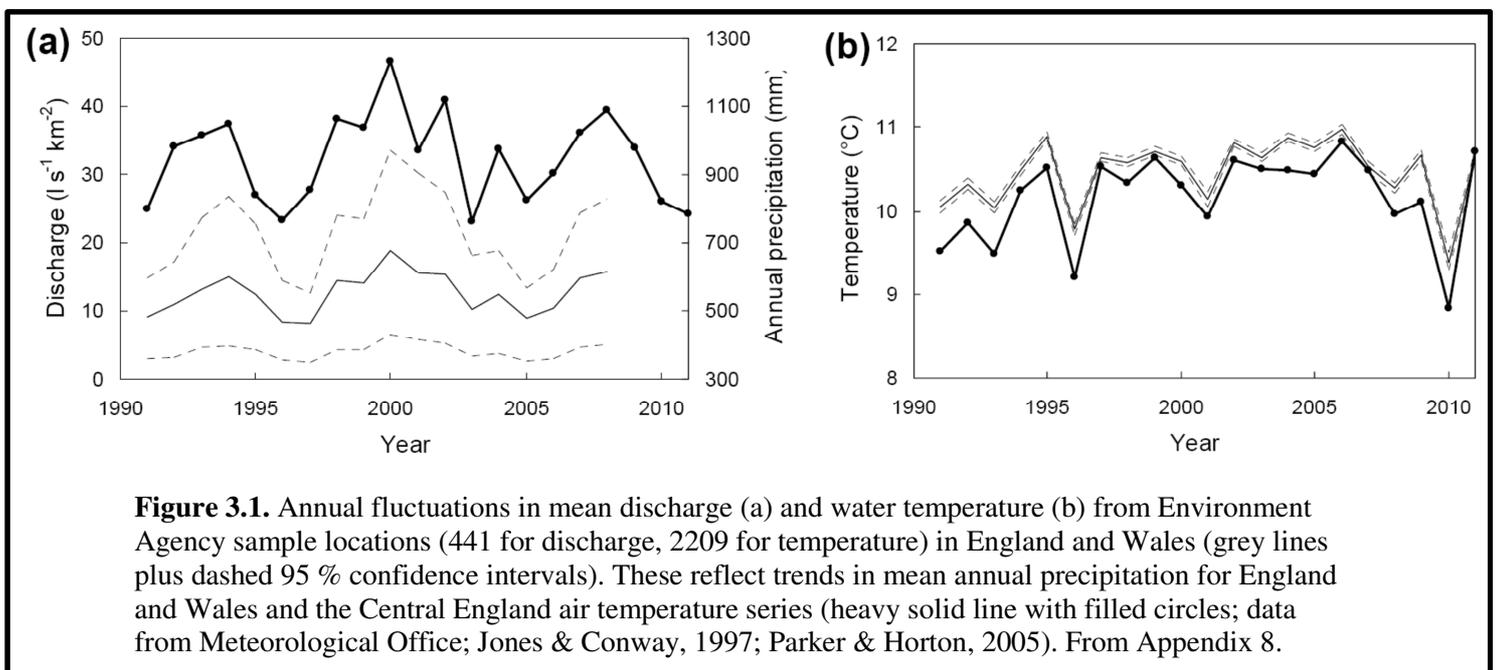


Figure 3.1. Annual fluctuations in mean discharge (a) and water temperature (b) from Environment Agency sample locations (441 for discharge, 2209 for temperature) in England and Wales (grey lines plus dashed 95 % confidence intervals). These reflect trends in mean annual precipitation for England and Wales and the Central England air temperature series (heavy solid line with filled circles; data from Meteorological Office; Jones & Conway, 1997; Parker & Horton, 2005). From Appendix 8.

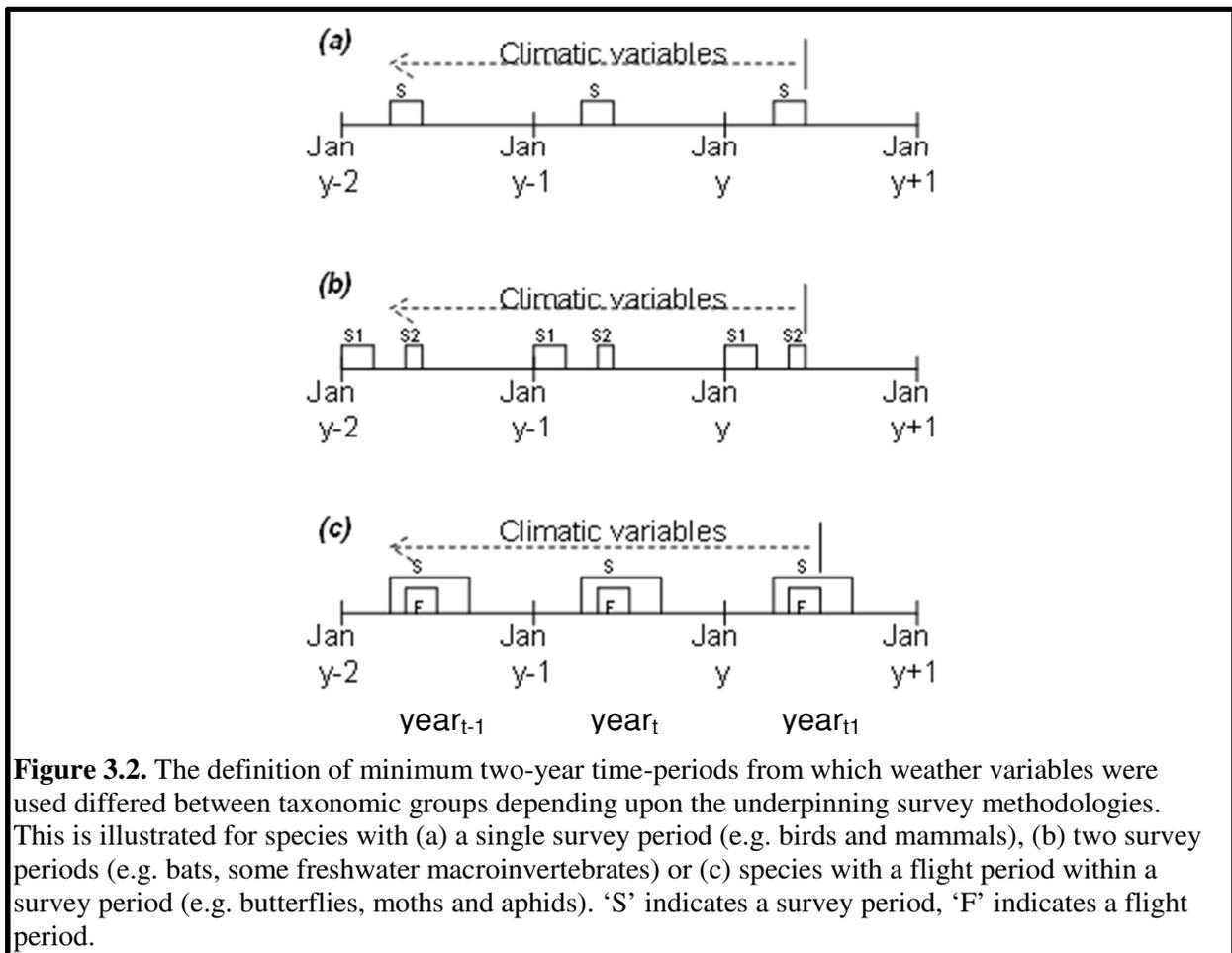
It is worth noting that we regard the effects of these variables upon inter-annual variation in abundance (population growth) as largely describing the effects of weather. The extent to which long-term population trends can be accounted for by long-term variation in weather variables provides an indication of the likely effect of climate change on species abundance. This is what we refer to climate change impacts in the report. However, this is not the same as formal attribution of observed population changes to anthropogenic climate change. Such attribution requires the consideration of the extent to which observed changes in these weather variables are due to climate change, rather than ‘natural’ fluctuations.

3.2. Analytical approach

The underpinning biological data used in this project are derived from long-term population monitoring schemes of terrestrial and freshwater biodiversity. For the purposes of analysis, these were summarised into annual estimates of relative abundance. Whilst this is relatively straightforward for individual sites, where required, national population trends were

produced using standard log-linear generalised linear models (GLM) in which site and year effects were fitted separately for each species; the year effects providing the estimates of national population change (ter Braak *et al.* 1994).

As the influence of weather upon abundance may vary with species, and potentially occur over a number of months or longer, it was important not to constrain assessments of the effect of weather variables to only those that are closely temporally matched to the timing of the biological data. Thus, for each analyses, we considered the potential effect of weather variables for a minimum of two years prior to the end of the sampling period of the species concerned (constrained by either survey protocols or the species' emergence or flight times) but for the longest time-series available (T3.1, 3.2ii) this period was extended up to ten years (Figure 3.2). This clearly results in a large number of potential predictor variables. For example, if one considers just one year of monthly weather data for both precipitation and temperature, this would lead to 24 potential predictor variables.



In order to avoid creating overly-complex models with large numbers of potential predictor variables that would be over-fitted relative to the sample size of the biological data, two main analytical approaches were used to summarise the weather variables for the purposes of analysis. The first, and more standard of the two, was to use an ordination approach, using Principal Components Analysis (PCA) to summarise the multiple monthly mean temperature and precipitation variables from two years prior to the survey into a small number of

combinations, termed the principal component axes. Annual population growth ($P_{Fy} = \log(n_y/n_{y-1})$) was then modelled against the top four PCA axes with strongest statistical support (PCA1:4) and previous population (n_{y-1}): $P_{Fy} = a + b_0 \ln(n_{y-1}) + b_1 \text{PCA1}_y + b_2 \text{PCA2}_y + b_3 \text{PCA3}_y + b_4 \text{PCA4}_y$. The parameters from this full model were used to predict the change in population that would have occurred under a stable average climate (i.e. $\text{PCA1:4} = 0$): $P_{Ny} = a + b_0 \ln(n_{y-1})$, using the modelled population in the previous year as n_{y-1} , enabling the model to be free-running from the second observation onward. Hence, the impact of climate change was estimated from the difference between the modelled trend based on the full model, and the trend based on a model with no climate change: $P_{Cy} = P_{Fy} - P_{Ny}$.

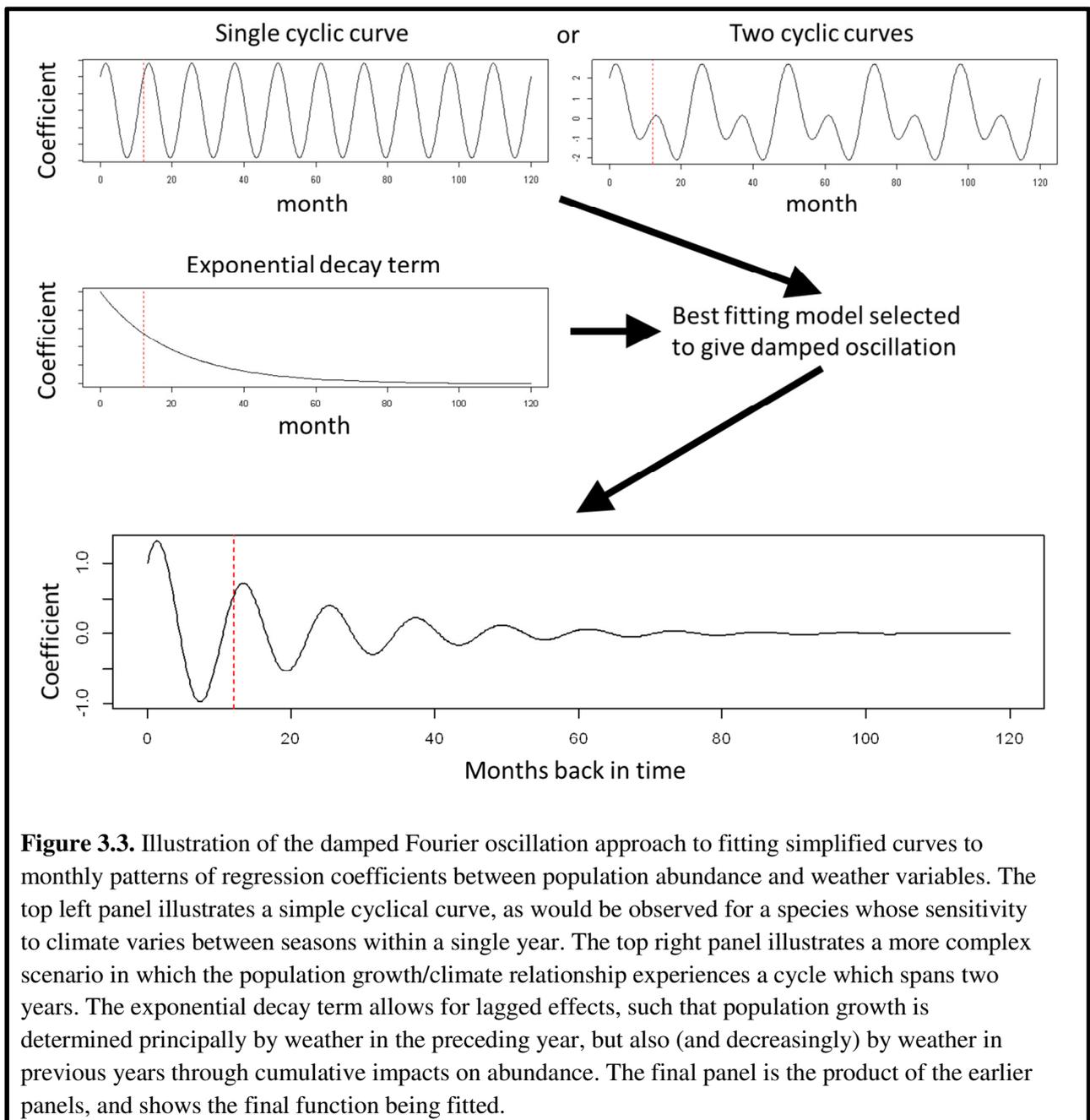


Figure 3.3. Illustration of the damped Fourier oscillation approach to fitting simplified curves to monthly patterns of regression coefficients between population abundance and weather variables. The top left panel illustrates a simple cyclical curve, as would be observed for a species whose sensitivity to climate varies between seasons within a single year. The top right panel illustrates a more complex scenario in which the population growth/climate relationship experiences a cycle which spans two years. The exponential decay term allows for lagged effects, such that population growth is determined principally by weather in the preceding year, but also (and decreasingly) by weather in previous years through cumulative impacts on abundance. The final panel is the product of the earlier panels, and shows the final function being fitted.

This approach was used in order to describe the effects of climate change upon population trends of a wide-range of terrestrial taxa (Appendix 3). Although an effective approach for dealing with multiple correlated predictor variables, the ordination may potentially reduce the impacts of some strong effects of weather variables in particular months by averaging those with other less-strong effects in a single axis. To better examine this, and particularly to identify the key periods in which species' populations respond to temperature and precipitation, an alternative approach was devised as part of the project.

This second approach was underpinned by a series of separate regressions between population abundance and monthly temperature and precipitation variables for each species. The relationships between the weather variables and abundance vary from month to month for each species, and it was necessary to obtain a procedure with relatively few parameters and which was also able to smooth out 'noise' in the monthly coefficients. This was achieved by allowing each monthly weather covariate to have its own regression coefficient, but constraining the series of coefficients to be defined by a parametric relationship which contained a seasonal component, to allow the effects of weather to vary at different times of year, and a persistence component, to model how long weather effects last with respect to abundance. The seasonal component was constrained to either a single sine wave over one year, or the superposition of two sine waves over either a single year, or two years, the latter allowing for differential lagged effects of weather variables to those apparent more immediately (e.g. Pearce-Higgins *et al.* 2010), as described mathematically in Box 3.1. The persistence component was modelled with an exponential decay term, and the seasonal and decay terms combined to produce the final model, which described potentially complex relationships between species abundance and weather variables with only a small number of underlying parameters, thus enabling this approach to be robustly fitted to time-series which are short relative to the number of the underpinning explanatory weather variables (Figure 3.3). Even then, due both to the number of parameters and the length of the data series, these models for temperature and precipitation cannot be fitted simultaneously, which means that potential correlations between the two variables cannot be accounted for.

Both ordination and damped Fourier oscillation approaches were applied to the national population trends analysis in Task 3.1, with outputs from the latter models used to synthesise the weather variables for individual sites in the fine-scale analysis (Task 3.2). Due to the complexities of fitting these models to shorter time-series with co-occurring non-weather data, either simplified forms of the Fourier models constrained to a single cyclic curve in a year were used (Task 4.1, 4.2ii, iii), or seasonal patterns are presented alongside equivalent outputs for the non-weather variables (Task 4.2i). Thus, although the broad approaches adopted were the same in each case (correlating abundance against monthly weather variables) we adapted these measures appropriately for each analysis depending upon their complexity and the need to account for other variables. These specifics are described in detail in each analytical appendix (Appendices 3 – 9), and also underpin the development of climate change indicators, described in Appendix 11.

Box 3.1. The forms of the damped Fourier oscillation models fitted.

The effect of weather on population abundance in a single year could depend on the weather covariate values for (we assume) up to the preceding 120 months. Schematically, this would give us a model which might look like this:

$$y_t = a + b_0x_0 + b_1x_1 + b_2x_2 + \dots + b_{119}x_{119} + e_t$$

for log-transformed abundances y_t , weather variables x_i (where i steps back in time through the 120 months), regression coefficients b_i , intercept a and error e_t . To avoid creating an overly-complex model with each of these 120 weather variables, the regression coefficients for these weather covariates (values of b_i) were simplified to one of the following four models. The first is a null model with no climatic effects but allowing for a linear trend over time with regression coefficient c , and the remainder incorporate weather variables in different ways. The population in the previous year (y_{t-1}) was also included in the models.

1. $y_t = a + by_{t-1} + ct + e_t$
2. $y_t = a + by_{t-1} + ct + \text{climatic effects from single cyclic wave over one year} + e_t$
3. $y_t = a + by_{t-1} + ct + \text{climatic effects from two cyclic waves over one year} + e_t$
4. $y_t = a + by_{t-1} + ct + \text{climatic effects from two cyclic waves over two years (to allow for differential lagged effects of weather in the previous year)} + e_t$.

4. Results

The results section is divided into subsections. The first (4.1) provides an overview of the main project results, summarising outputs across the different tasks completed in order to focus on the main messages. After this are a series of short reports (4.2 – 4.11) upon each task conducted as part of this project. This has been done so that each section can be read as a stand-alone document, whilst also contributing to the whole span of work presented in this report. Each short report is underpinned by a more detailed report presented in appendices 3-12 as draft papers, with the aim for eventual publication of most or all of these in the peer-reviewed scientific literature. Already, one such appendix (Appendix 8) that reports on Task 4.2i has been published in *Global Change Biology*.

4.1. An overview of key results

BICCO-Net II has examined the impacts of climate change on populations of both terrestrial and freshwater taxa using the results of all major national-scale long-term biodiversity monitoring schemes available. The importance of variation in weather variables in driving inter-annual fluctuations in population growth was examined, as well as the contribution that climate change has played in influencing long-term population trends. Taxa varied in their response to variation in temperature and precipitation-related variables (Table 4.1), with the greatest proportion of significant impacts detected for the national-scale analysis of terrestrial population trends. This probably reflects the greater stochasticity and uncertainty associated with the site-based analysis of individual populations used across the other studies. Effects of precipitation were also more apparent from terrestrial than freshwater time-series.

Overall immediate negative effects of temperature were apparent for Trichoptera (caddisflies) and Plecoptera (stoneflies), particularly in upland waters, whilst aphids tended to respond positively to warming. Effects were less consistent for other taxa (Sections 4.3, 4.6, 4.8, 4.11). For example, strong positive effects of spring and summer temperature apparent for butterflies and moths were countered by negative effects of winter temperature (Section 4.3, 4.5). Short-term variation in the prevalence of aquatic macro-invertebrate families was also related to temperature, where warm summers were found to decrease the occurrence of range-expanding families (Section 4.7).

The effects of precipitation were largely negative for aphids and moths, but more mixed for other groups. Indeed, summer rainfall had a negative impact on the abundance of all terrestrial invertebrates, which extended into the spring and winter for butterflies and moths (Section 4.3, 4.5). The abundance of birds and mammals was also negatively affected by spring precipitation (Section 4.3). Effects of precipitation upon freshwater invertebrate populations were mixed (Section 4.6, 4.8), but increasing flow rates were associated with increasing prevalence of range-expanding taxa (Section 4.7).

Table 4.1. Number of species (s) or populations (p) showing significant effects of temperature and precipitation as a function of the total number tested across the different analyses using the damped Fourier oscillations approach.

Analysis	Temperature	Precipitation	Total
Terrestrial national trends (T3.1)	421 (84%)	371 (74%)	501 s
Terrestrial ECN sites (T3.2i)	777 (65%)	838 (70%)	1196 p
Upland UWMN, ECN and Llyn Brianne sites (T 4.1)	268 (47%)	257 (45%)	566 p
Lowland EA/SEPA sites (T4.2ii)	70 (51%)	67 (49%)	137 s

The magnitude of the effects of these variables in driving inter-annual fluctuations varied between taxa. Of the terrestrial species covered, they were greatest in aphids, butterflies and moths, accounting 9-10% of annual variation in population growth rates alone, but a much smaller proportion of population change in birds (Section 4.2). In the freshwater environment, there was a tendency for population responses to temperature to be most marked in species associated with cool temperatures (Section 4.6). Across all species, there was not strong variation in temperature responses between freshwater and terrestrial environments, or between primary and secondary consumers (Section 4.11). However, there was evidence, particularly for moths, but also other species, that species' responses to temperature were greatest in the most widespread species, suggesting that other factors may limit the distribution and abundance of rarer species (Section 4.11).

The impact of climate change upon long-term trends was examined with respect to terrestrial species covered by national-scale monitoring data, and with respect to the prevalence of freshwater macro-invertebrate families across England and Wales. About 66% of the long-term decline in UK moth populations and 60 % of the long-term increase in aphid populations could be accounted for by the predicted population trends from models which describe the impact of climate change on population growth (Section 4.2). This was

the case, even though the models accounted for a relatively small (9-10%) proportion of annual variation in population growth. Nine moth species in particular appear to have undergone severe (>30% population declines per decade) consistent with equivalent predicted negative effects of climate change. Such climate change impacts on moths appeared a result of negative effects of precipitation and negative lagged effects of temperature. Conversely, there was little evidence of long-term impacts of climate change upon bat, terrestrial mammal, bird or butterfly populations (Section 4.2), or upon trends in the occurrence of freshwater macro-invertebrate families (Section 4.7). Instead, long-term trends in macro-invertebrate community structure, indicative of an expansion of upland and western taxa into the eastern lowlands, could be better explained by models based on improvements in water quality (Section 4.7).

Species sensitivity to weather variables varied between different times of the year. Variation in winter conditions was particularly important for Lepidoptera, with both moths and butterflies being strongly negatively affected by temperature and precipitation during winter and spring months; warm wet winters were associated with population declines in moths (Sections 4.3, 4.5). Such impacts were particularly notable in species that overwinter as caterpillars or pupae. Conversely, resident and short-distance migrant bird populations showed positive correlations between population growth and winter temperature; temperature effects were more negative in long-distance migrants. The abundance of all terrestrial invertebrate groups was positively correlated with spring and summer temperature during periods when they were active and sampled (Section 4.3). Conversely, upland aquatic macroinvertebrate groups, particularly Trichoptera and Plecoptera, were also sensitive to temperature, but showed generally negative impacts of summer and autumn temperatures upon abundance (Section 4.6), suggesting there may be differences in the sensitivity of freshwater and terrestrial invertebrate groups to temperature (Section 4.11).

Aside from gross population changes within taxonomic groups, there was significant evidence for variation in the response of species to climate change within groups. Declines in species of conservation concern relative to other species may be partly related to climate change, whilst primary consumers were more negatively impacted by climate change than secondary consumers (Section 4.2). In the freshwater environment, predatory species appeared more susceptible to warming than some feeding groups reliant upon detritus, which may therefore affect freshwater ecosystem structure and function. Species' sensitivity to climatic variation was also significantly related to thermal tolerance, preferences for water flow and tolerance to organic pollution, reinforcing the strong synergistic impacts of changes in temperature, precipitation and water quality upon this group (Section 4.6, 4.8). Thus, although climate change may not have had strong impacts upon macroinvertebrate populations and distributions so far (Section 4.7), there are good reasons to suspect that it will do so in the future (Sections 4.6-4.8). Across species, there was not strong variation in temperature responses between freshwater and terrestrial environments, or between primary and secondary consumers (Section 4.11). However, there was evidence, particularly for moths, but also other species, that species' response to temperature was greatest in

widespread species, suggesting that other factors may limit the distribution and abundance of rarer species (Section 4.11).

Analysis at the site-level does show a degree of consistency in response across sites (Sections 4.4-4.6), supporting the value of the analysis of national population trends (Sections 4.2, 4.3, 4.7, 4.8). However, some variation in populations does exist at that site level, and provides much opportunity to further understand the processes by which climate change influences populations, and the potential for variation in management and site conditions to influence those responses. We show that populations towards the edge of a species' range margin tend to have greater sensitivity to temperature than elsewhere, which may be suggestive of local adaptation (Section 4.4). Some variation in population responses to temperature and precipitation was also apparent across both terrestrial and freshwater ECN sites. Although this could not be clearly related to specific variables for butterflies and moths (Section 4.5), for aquatic macroinvertebrates, there was evidence that populations at high altitude sites were more negatively affected by temperature (Section 4.6), results supported by wider analysis of macroinvertebrate populations (Section 4.8)

Population changes in response to climate change may be described by a number of potential biodiversity indicators of climate change impact. The Gregory *et al.* (2009) indicator was developed for common and widespread European breeding birds, and uses the results of bioclimate modelling to separate species likely to increase in response to climate change from those projected to decline before tracking the divergence in the population trends of the two groups. The Community Temperature Index (CTI) uses the distribution of each species to calculate mean breeding season temperature across a species' range. These values are then averaged for each species present at a location, weighted by abundance, to give the CTI. The BICCO-Net I index separates species into those whose annual fluctuations in population growth are positively associated with temperature from those which are negatively affected, and uses the divergent population trends of these two groups to indicate climate change impacts. Computer simulations suggest whilst simplified versions of each indicator appear to show similar ability to track the impacts of warming, they may all be vulnerable to potentially confounding non-climatic drivers of population change (Section 4.9). This is clear when examining observed indicator trends for a number of terrestrial taxa across the UK (Section 4.10), and also highlighted by long-term trends in aquatic macro-invertebrate communities (Section 4.7). Although observed climate change indicator trends for birds most closely matched the changes expected were they driven by warming, and indicator trends for aphids and moths were weakly consistent with expectation, butterfly indicator trends were contrary to the expectation from warming, because many southern (warm-associated) species have declined in recent years. The results of any climate change indicator, or combination of indicators, need to be interpreted carefully in the light of the potential impacts of other environmental changes upon the species of interest. Combined with the results from Section 4.2, this suggests that butterfly population trends do not show a strong climate-change signal over the years studied, but that moth, aphid and bird populations all show some evidence of responses to climate change, either between species (particularly birds), or across the group as a whole (aphids and moths).

4.2. A cross-taxa appraisal of the impact of climate change on species' population size (Task 3.1.)

Climate change appears to have significantly contributed to national declines in moth populations and to increases in aphid populations. Population trends of 64% of species showed some significant response to long-term changes in temperature and precipitation. Nine moth species were identified that appear to have shown strong declines in response to climate change.

Understanding the impacts of climate change upon species' populations is fundamental to attributing and predicting the consequences of climate change for species, communities and ecosystems. Here we used ordination methods to summarise the effects of climate change over the last 50 years upon national population trends of 500 mammal, bird, aphid, butterfly and moth species. We also tested the extent to which climatic impacts vary with respect to trophic level (climate change may disrupt ecological networks; Tylianakis *et al.* 2008, Ockendon *et al.* 2014), conservation status (already threatened species may be more sensitive to climatic impacts; Hodgson *et al.* 2009), native status (invasive non-native expansion may be promoted by climate change; Dukes & Mooney 1999) and pest status (pest species of economic importance may be more adaptable to climate change than other species; Cannon 1998).

Long-term data for birds, butterflies and mammals were from schemes that survey large numbers (>1000) of sites particularly concentrated in England, whilst data for aphids and moths were taken from fewer than 20 widely dispersed sites across Wales, England and Scotland. To describe the impacts of climate change on these two groups of taxa, we derived monthly averages in mean temperature and precipitation for England and Great Britain respectively from Met Office UKCP09 gridded datasets (Perry & Hollis 2005).

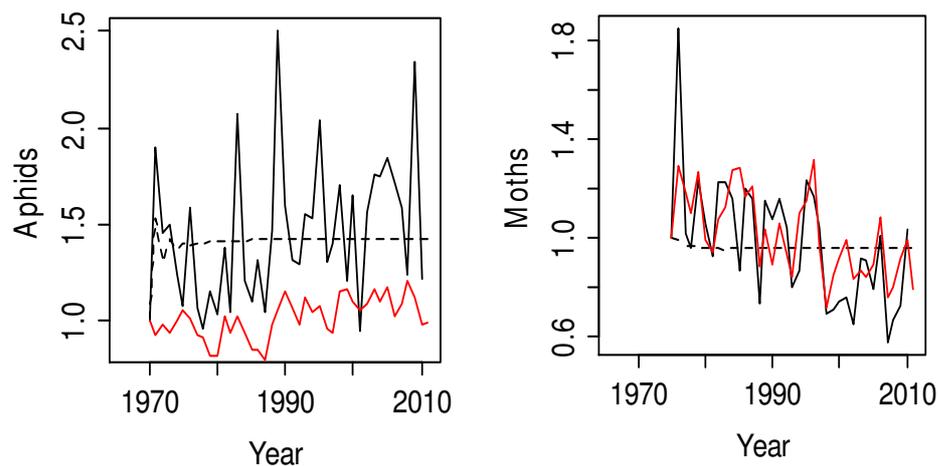
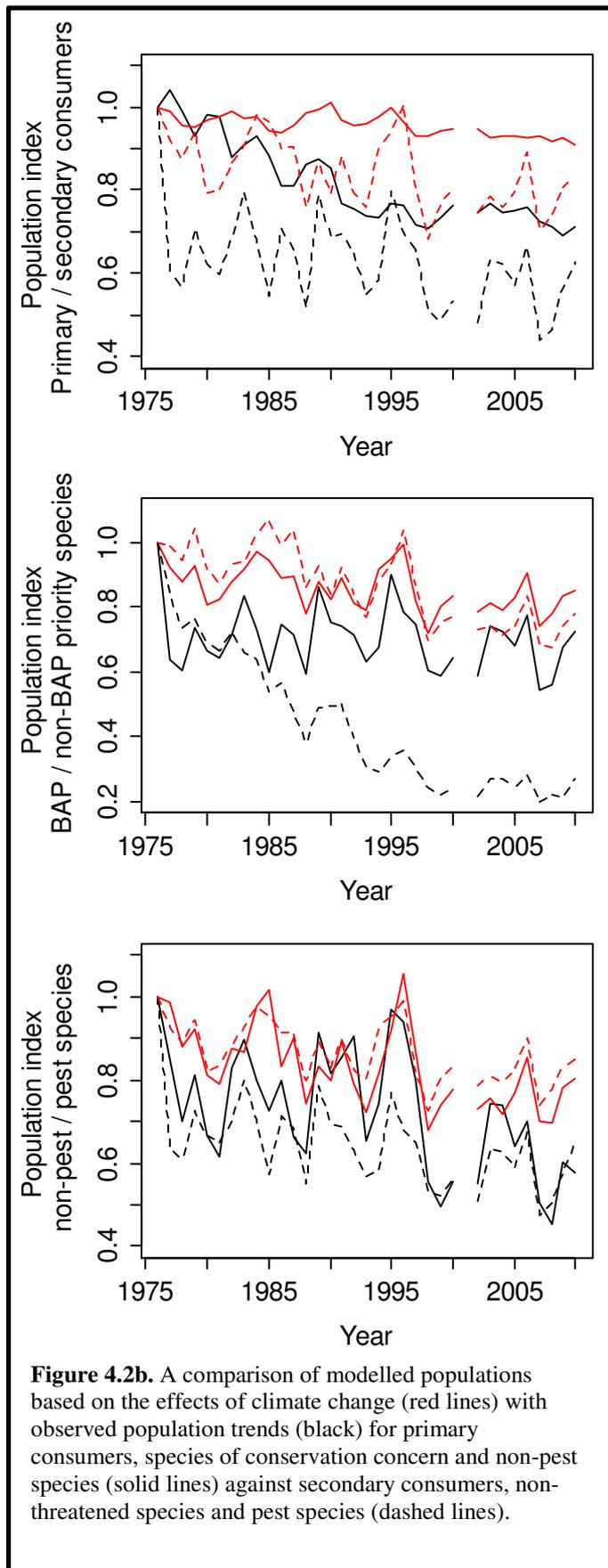


Figure 4.2a. Observed population indices (solid black lines) compared to estimates from free-running models assuming a stable climate (dashed black lines) and the climate-driven component of abundance (red lines) for aphids and moths.



Species population indices were calculated using standard log-linear generalised linear models (GLM) fitting site and year effects (ter Braak *et al.* 1994). Principal Components Analyses (PCA) were used to simplify variation in weather variables and into four components (PCA1-4). Annual population growth ($\log(n_y/n_{y-1})$) of each species was modelled against PCAs1-4, including population count in the previous year to account for density dependence (Freckleton *et al.* 2006). Models of population growth were used to predict population trends over the same period based either on only the effects of climate change, or just the linear population growth rate and density-dependence alone. The effects of trophic level, conservation status and pest status upon species' responses to climate change was tested, to identify the species most strongly affected by climate change.

Models varied considerably in their ability to explain annual variation in population growth from 9-10% in aphids, moths and butterflies, to 3% in birds. Despite these proportions, which reflect the high degree of stochasticity and strong density-dependence in some of the observed trends (Fig 4.2a), the models showed greater predictive power when used to describe the contribution of climate change to long-term population trends. Such modelled trends in response to changes in weather variables alone accounted for 66 % of population declines in moths and 60 % of population increases in aphids (Figure 4.2a). In particular, 9 moth species that have undergone

severe (>30% in 10 yrs) declines as a result of climate change were identified. Neither observed or modelled trends for other taxa showed significant long-term variation.

In addition to examining the impact of climate change upon gross changes in abundance of these taxonomic groups, impacts upon different components of ecological communities were also studied. Models suggested that climate change had a greater negative impact on species of conservation concern relative to other species, and has been more detrimental for primary consumers compared to secondary consumers, consistent with higher rates of phenological change (Thackeray *et al.*, 2010) and range shifts (Devictor *et al.*, 2012) in primary consumers. There was no evidence that climate change was driving increases in pest species (Figure 4.2b).

Our assessment of the impacts of climate change suggests that climatic changes in the UK from 1967 to 2011 have had a significant impact on the population trends of 64% of species. The most notable of these has been a general decline in moth populations, as previously documented, particularly across southern Britain (Conrad *et al.* 2002). Our models indicate empirically that $\frac{3}{4}$ of this decline may be due to climate change. Although declines in the garden tiger moth *Arctia caja* have been previously attributed to climate change (Conrad *et al.* 2003), a finding which our models support, this is the first time that the wider vulnerability of this group to climate change has been demonstrated, and appears linked to the frequency of warmer, wetter winters (Section 4.2). A significant proportion of the aphid population increases may also be linked to climate change, potentially through temperature-related reductions in generation time (Yamamura & Kiritani 1998). Gross changes in the abundance of other taxonomic groups appeared less impacted by climate change, matching previous analyses for farmland birds (Eglington & Pearce-Higgins 2012). Climate change may have contributed to declines in species of conservation concern. These are all signs that the anticipated impacts of climate change on ecosystem function and conservation interests may already be apparent.

These results are dependent upon the ability to disentangle the impacts of climate change from other factors. We have attempted to do so by using inter-annual variation in abundance to effectively relate population growth to weather variables, whilst accounting for temporal autocorrelation and including a constant of population growth to account for additional non-climatic trends. The risk of over-fitting is partly countered by the fact we have summarised climatic changes with four predictor variables. We may therefore be underestimating climate change impacts upon species which respond to very specific processes. Despite these limitations, our climate models produced results which, where available, were supported by other detailed studies, such as on the garden tiger moth (Conrad *et al.* 2002), butterflies (Roy *et al.* 2001) and passerines (Robinson *et al.* 2007).

4.3. Identifying the importance of different seasons in driving observed species' responses to climate change (Task 3.1.)

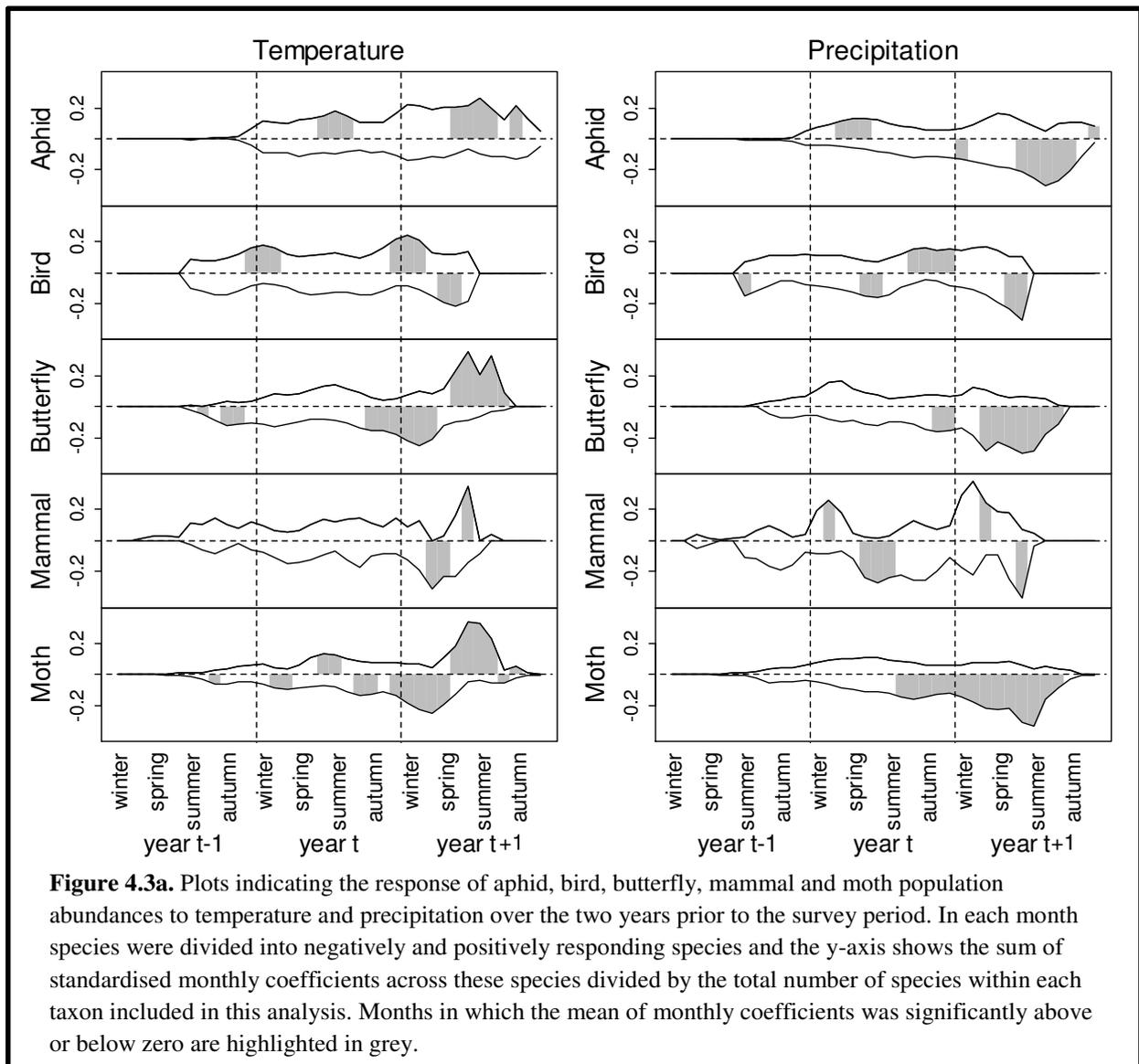
Warmer winter temperatures appear to enhance resident and short-distance migrant bird populations, but have negative effects on butterflies and moths, particularly if associated with wet weather. Warmer spring and summer temperatures may boost aphid, butterfly and moth populations. The sensitivity of species to weather variables at different periods differs with life-history, overwintering strategy and flight period.

Without good ecological knowledge, it is difficult to determine precisely which weather variables may be important for particular species. Here we use a novel statistical approach (damped Fourier oscillations; Section 3.2, Appendix 2), to identify peak periods of response to monthly temperature and precipitation variables of over 500 UK species of bird, mammal, aphid, butterfly and moth. Long-term data for birds, butterflies and mammals were from schemes that survey large numbers (>1000) of sites particularly concentrated in England, whilst data for aphids and moths were taken from fewer than 20 widely dispersed sites across Great Britain. To describe responses to weather variables in these two groups of taxa, we calculated species population indices using standard log-linear generalised linear models (GLM) fitting site and year effects (ter Braak et al. 1994). Separate regressions between population abundance and mean monthly temperature and precipitation variables were conducted for each species, and then smoothed using damped Fourier oscillations to produce simplified patterns that could be robustly fitted. In order to provide the greatest flexibility, we fitted data to a two-cyclic curve model over a single year and a two-cyclic curve model over two years and selected the best fitting model, thus allowing for up to two peaks and two troughs in species' population responses to weather variables to occur within a year or over two years, appropriate for incorporating lagged effects.

Overall, our models produced a significantly improved fit, relative to a null model of no effect of weather, for 94% of species. Temperature models generally provided a better fit than precipitation models. When averaged across species within each taxa, aphids showed significant positive responses to temperature, but negative responses to precipitation, whilst moth populations were significantly negatively associated with precipitation.

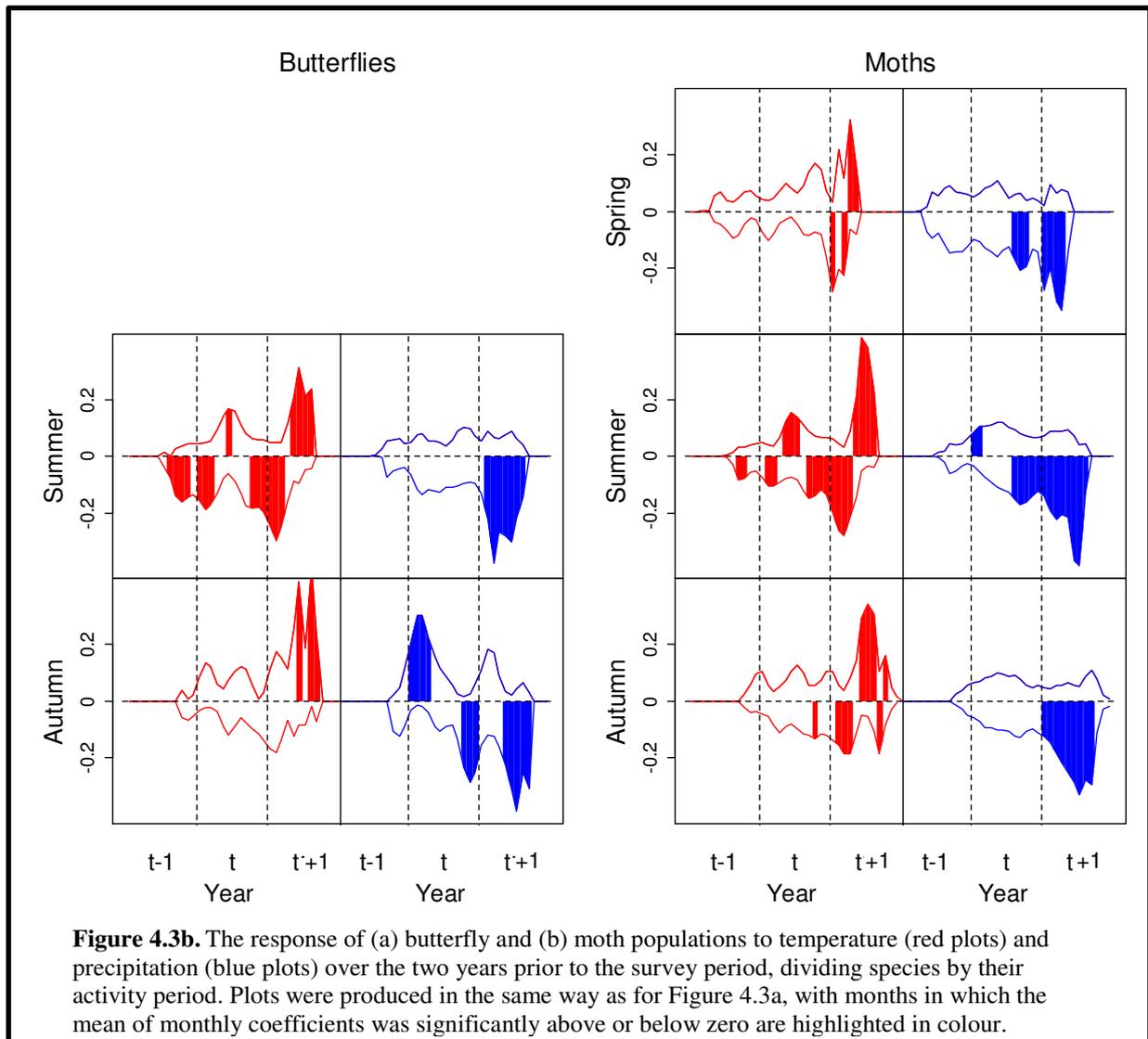
There was significant variation in the times of year that different taxa were sensitive to weather variables (Figure 4.3a), with sensitive periods defined as months with a greater negative or positive mean response than expected by chance. Aphids generally responded positively to temperature, particularly from May to October, with lagged positive effects of summer temperature in the previous year also. Positive effects of winter temperature were apparent for bird populations, whilst temperature during the second survey period (year_{t+1}) may have a negative impact on abundance. Butterflies and moths both showed similar temporal responses to each other, with strong positive impacts of temperature during spring and summer months, when they are recorded, but negative effects of temperature upon abundances during the preceding autumn and winter. Mammal populations appeared negatively affected by warm spring temperature (March and April), but positively by June temperature, when they are surveyed. Summer precipitation was negatively correlated with the abundance of all invertebrate groups, which extended back into the winter and spring for

moths and butterflies. Negative impacts of spring precipitation in both year_t and year_{t+1} also appeared to affect birds and mammals, although autumn precipitation (September to December) in year_t, was positively correlated with subsequent bird abundance.



These patterns differed strongly with respect to overwintering strategy. Thus, temperature effects were particularly negative for long-distance migrant birds, particularly in spring and autumn, which contrasted with positive effects of winter temperature upon resident and short-distance migrant populations. Effects of temperature and precipitation also differed significantly between hibernating bats and non-hibernating mammal species, the latter being more sensitive to precipitation in particular. Temperature responses were consistent across aphid species, but precipitation responses varied with life-cycle. Overwintering strategy had significant impacts upon the sensitivity of both moth and butterfly populations to temperature and precipitation. Butterflies overwintering as eggs showed the lowest sensitivity to summer and winter temperatures, as described above, but appeared negatively impacted by autumn

temperature in both year_{t-1} and year_t. Species' responses also differed with respect to flight period in equivalent ways (Figure 4.3b).



This study robustly identified the timing of populations' sensitivity to weather variables. Across all species, it was clear that changes in winter climate would have the greatest impact on species' populations, with warm winters favouring resident birds, but disadvantaging butterflies and moths, particularly if also wet. Spring and summer warming would also boost some invertebrate populations, particularly during the period that they are sampled. These results indicate the mechanisms that may underpin the putative population responses to climate change observed in 4.2. Thus population increases in aphids may be attributed to positive effects of temperature, likely to advance phenologies and reduce generation times, whilst population declines in moths appear particularly related to the vulnerability of overwintering caterpillars to warm, wet winter weather, which may cause increased risk of parasitism or pathogenic attack (Virtanen & Neuvonen 1999, Conrad *et al.* 2002).

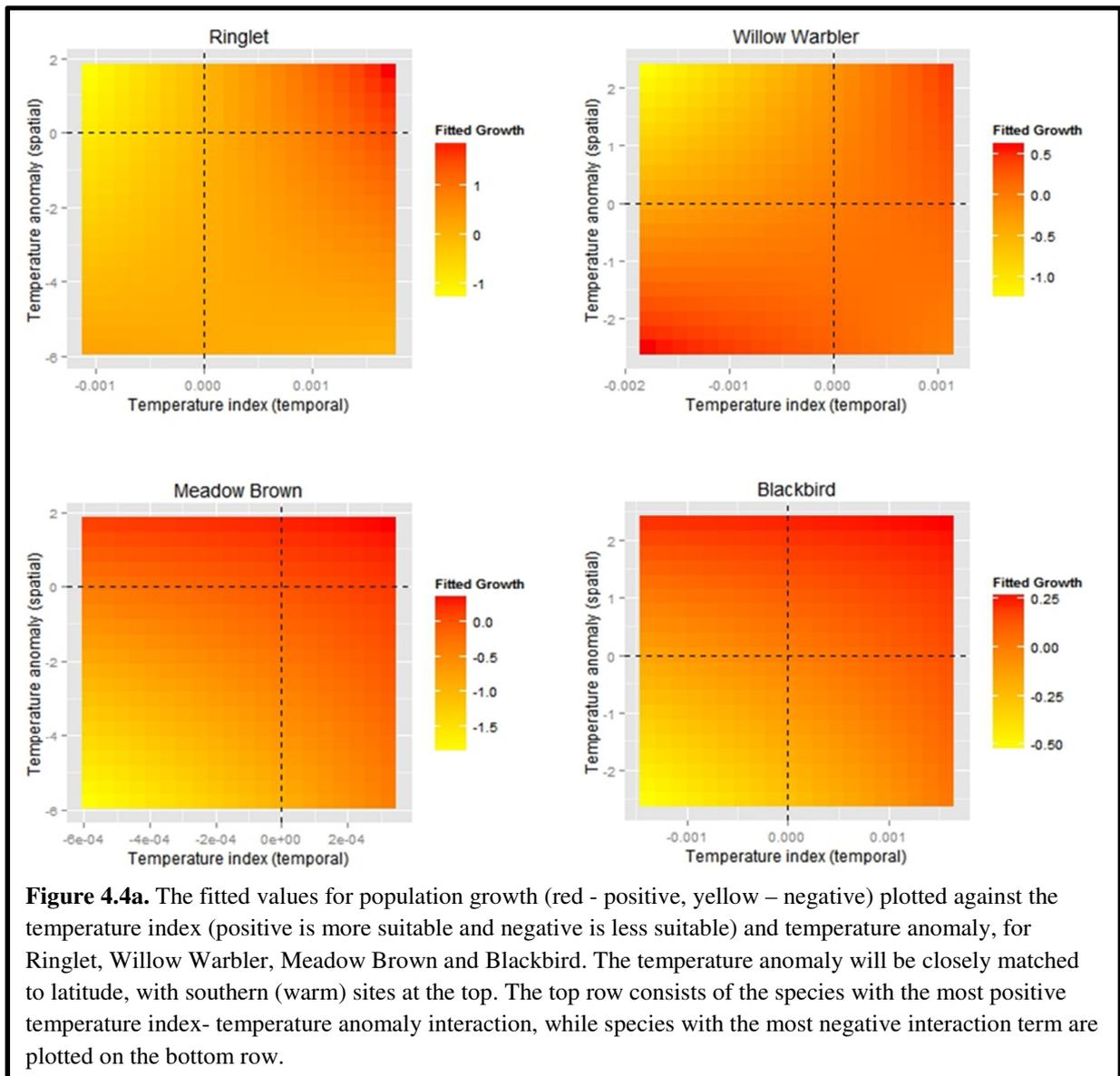
4.4. Evidence for local adaptation in fine-scale population responses to climate (Task 3.2i)

Fine-scale variation in population growth rates at individual recording sites was modelled as a function of annual variation in climatic suitability (assessed from the net effect of the national-scale analysis described in Section 4.3), local temperature anomaly, and the interaction between the two. Butterfly populations were more responsive to climatic suitability than birds, and showed greater spatial heterogeneity. Importantly, there was consistent evidence that climatic conditions had a greater impact upon population growth towards the cooler (range-edge) parts of the UK.

The majority of analyses presented in this report examined national-scale responses of populations to annual variation in weather variables, and assessed at that large scale, the impact that climate change had on population trends. The primary reason for this focus is that by doing so, much of the noise associated with stochastic population responses at the site level, and complications about fine-scale variation in climate, are averaged out when analysed at this large-scale, producing models which can demonstrate strong and meaningful climatic responses (e.g. Roy *et al.* 2001, Eglinton & Pearce-Higgins 2012). However, such analysis does simplify the fact that national-scale population trends are a composite of the combined birth and death rates of individuals exposed to a range of climatic conditions within an array of separate, but linked, populations. Species vary in their tolerance of thermal and precipitation variables, as described by their climatic niches, with individuals occurring towards the limit of their niche likely to show a stronger response to climate variability than those in the centre. There may also be spatial variation across a species' range in the effect of weather variables upon population growth rates due to local adaptation. To test this, we assessed the extent to which the national-scale relationships described in this report may directly translate into equivalent responses in specific local populations, focussing on birds and butterflies due to the large number of sites covered. As many species reach their cooler thermal margin in Britain, we predict population responses to temperature will be greater in cooler sites.

Long-term data for butterflies were taken from the butterfly monitoring scheme from 1976-2012, and for birds, from the common bird census (CBC; which at the site level has less stochasticity than the breeding bird survey counts) from 1976-2002. Sites with data from fewer than 10 years were excluded from the analysis. As the impact of climate on population dynamics can vary through the year, we used the results of the national-scale analysis based on Fourier oscillations to create year- and species-specific temperature and precipitation covariates (Section 4.3). This produced a value for each year describing annual temperature or precipitation suitability, given the species response at the national-scale analysis to those variables. Thus, we modelled annual abundance at each site as a function of count in the previous year, to account for potential density-dependence, climate effects from the national-scale analysis, and climatic anomalies at that site. The climate effects (the effect of temperature and rainfall indices on population growth) were estimated from the national scale analysis but applied to the weather data from that site. Note that a positive value indicates the combination of weather variables at the site should have produced a positive effect on population growth, not necessarily that that species is positively associated with temperature

or precipitation. The anomalies were the difference in the mean annual climate of the site and the mean annual climate across all sites. Finally, we included the interaction between the temperature index and the temperature anomaly to examine the extent to which population responses to climate vary with proximity to the limit of their climatic niche. 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. Significance was assessed comparing standardised regression coefficients with a Normal distribution (Z-score).



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), suggesting that on average, temperature has a greater impact on butterfly population dynamics. As scores tended to be positive, national-level models of abundance adequately describe equivalent population responses at the fine-scale. Butterflies had a higher average Z-score for the relationship between site temperature anomaly and abundance than birds (2.952 and 0.134, respectively), indicating that butterflies tended to show a more positive response to warmer temperatures. The temperature index- temperature anomaly interaction varied between species, and tended

to be negative in both groups, indicating that the influence of temperature on population dynamics was stronger in cooler than warmer sites. This effect was again stronger for butterflies (mean Z-score = -2.913) than birds (-0.315).

The fitted value plots of Figure 4.4a 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. For the latter two species, 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, whilst population growth in both species was largely positive in the south (positive spatial anomaly), irrespective of temperature. The ringlet also responded positively to warm sites in climatically suitable years. However, the ringlet was negatively associated with temperature from the national scale models, whereas the other three species were positively associated. As cooler years were more climatically suitable for the ringlet than warm years, the plot shows declines in ringlet populations were greatest in warm years on warm sites, supporting the results of previous studies showing that the ringlet is particularly vulnerable to drought events (Sutcliffe *et al.*, 1997; Oliver *et al.*, 2013). 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 found evidence of spatial variation in bird and butterfly population responses to temperature. Our hypothesis that temperature would have a stronger association with population dynamics in cooler (range-edge) sites was generally supported. This is likely to be because of the greater vulnerability of marginal populations to climatic fluctuations. 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. We also found stronger evidence of spatial variation in butterfly population responses to climate than bird population responses, as previously detected by Isaac *et al.* (2011), who modelled the relationship between butterfly abundance and climate on transects in Britain. This may be due to the ectothermic nature of butterflies and their faster generation time, which may make them more responsive to temperature than birds, and matches previous results on community change (Devictor *et al.* 2012). The greater spatial heterogeneity in butterfly population responses to temperature may also help explain why butterfly populations at the national scale show less impact of climate change upon their populations than other taxa (Section 4.2). The fine-scale modelling approach that we utilised 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 example of willow warbler was particularly informative in this regard.

4.5. Investigation of climate change effects on terrestrial invertebrate groups at the site-level using ECN data (Task 3.2ii).

Variation in butterfly and moth communities, and in the abundance of individual species, was analysed across 12 terrestrial ECN sites as a function of locally recorded temperature and precipitation variables. In common with the national results (Section 4.3), the abundance of both groups was generally negatively correlated with winter precipitation and temperature, effects which extended into the spring for moths. Both groups also tended to be more abundant during periods of warm summer temperature. Some differences were apparent between sites, which further work should investigate.

Populations of moths and butterflies have been monitored at the 12 terrestrial Environmental Change Network (ECN) sites since the early 1990s. While monitoring protocols network across the network are identical, the sites vary substantially with respect to habitats, land use and levels of atmospheric pollution and span a wide climatic range. Here, we assessed inter-annual variation and long-term change in butterfly and moth populations at individual sites to establish the degree of consistency of species-climate relationships between sites.

Butterfly monitoring complies with Butterfly Monitoring Scheme protocols, based on a walked transect methodology, while moths at ECN sites are monitored using light traps in accordance with UK Insect Survey protocols. Meteorological stations at each ECN site collect data according to Met Office-approved methodologies. In this analysis we focus on daily mean air temperature ($[\max + \min] / 2$) and monthly total precipitation data only, summarised at monthly and seasonal scales. The total annual abundance of each butterfly species recorded at each site in each year was divided by the total number of butterfly transects conducted in that year to account for between-year variation in sampling effort. ECN moth traps operate over most days of the year, and we therefore used the total annual catch of each moth species at each site to form the primary moth dataset. Species recorded in fewer than 8 years at individual sites were removed from the analysis in order to minimise the effect of rare species.

Firstly, we examined community-level inter-annual variation, using redundancy analysis (RDA) to summarise the largest component of annual variation in the abundance of different butterfly or moth species into a single variable (RDA Axis-1). Values of this single measure of community abundance were then related to seasonal temperature and precipitation values using linear regression. Secondly, we considered species-level relationships with weather variables, comparing a null model which contained only YEAR (a linear trend to account for potentially confounding, but unmodelled drivers), with TEMPERATURE or PRECIPITATION models that additionally contained the terms to describe the combined effects of temperature and precipitation respectively through the year, as described using damped Fourier oscillations (Section 3.2). Due to the limited length of the time-series (min 14 years), these were constrained to a single annual cyclic wave.

In contrast to RDA results for macroinvertebrate communities in freshwater ECN sites which show strong monotonic change (Murphy *et al.* 2014), there was no evidence for common linear trends across butterfly and moth communities. For most sites, interannual variation in

RDA Axis-1 was strongly correlated with the total number of individuals recorded. For both butterflies and moths, there was a greater degree of common inter-annual variation between sites than expected by chance (for butterflies, the strength of 21/66 pairwise correlations in RDA Axis-1 between sites were stronger than $r > 0.4$, whilst $r < -0.4$ between only 1 pair of sites. For moths, 23/45 correlations were stronger than $r > 0.4$ and none $r < -0.4$), indicative of large-scale variation in populations, which is certainly consistent with the hypothesis that they are influenced by large-scale climatic drivers. To test this, inter-annual variation in RDA Axis-1 were correlated with site-specific seasonal summaries of temperature and precipitation. Strong effects were again found more often than expected (Table 4.5a).

Table 4.5a. Pearson correlation coefficients for the relationships between butterfly (top) and moth (bottom) RDA Axis 1 sample scores, and site specific mean air temperature and total precipitation variables. Median coefficients across ECN sites are in the last column. Strong correlations ($r > 0.4$ or $r < -0.4$ are shaded red or blue respectively). Letter codes refer to individual ECN sites.

	DT	HB	AH	RS	NW	PT	WT	GS	SH	SN	MH1	MH2	median
winter T	-0.35	-0.27	-0.41	-0.29	-0.45	0.34	0.30	-0.37	-0.27	-0.53	-0.34	-0.40	-0.46
spring T	0.08	-0.04	-0.31	-0.08	-0.37	-0.15	-0.02	-0.28	-0.21	-0.38	-0.17	-0.25	-0.29
summer T	-0.22	0.48	0.59	0.34	0.41	0.14	0.45	-0.02	0.28	0.57	0.40	0.54	0.53
autumn T	0.22	0.49	0.48	0.09	0.35	-0.15	0.20	-0.05	0.30	0.39	0.20	0.35	0.45
Summer-1 T	-0.15	0.40	0.21	0.22	0.24	0.22	-0.12	0.27	0.44	0.47	0.63	0.38	0.48
winter P	-0.18	-0.24	-0.02	-0.02	0.18	-0.30	-0.30	-0.54	-0.44	-0.64	-0.32	-0.34	-0.43
spring P	-0.23	-0.23	-0.35	-0.60	-0.52	0.13	0.22	0.64	-0.05	0.12	-0.29	-0.08	-0.39
summer P	-0.10	-0.36	-0.42	-0.15	-0.31	0.22	-0.22	-0.09	-0.31	-0.65	-0.33	-0.10	-0.24
autumn P	0.07	0.17	-0.20	-0.45	-0.30	0.10	0.42	0.10	0.02	-0.24	-0.52	0.12	-0.03

	AH	DT	GS	HB	MH	NW	PT	RS	SH	WT	median
winter T	-0.24	-0.51	-0.56	-0.43	-0.56	-0.12	-0.14	-0.66	-0.73	-0.48	-0.63
spring T	-0.31	-0.23	-0.38	-0.38	-0.29	-0.17	-0.41	-0.37	-0.37	-0.26	-0.41
summer T	0.73	0.25	0.17	0.45	0.41	-0.25	0.24	0.28	0.18	0.27	0.45
autumn T	0.49	0.24	-0.05	0.28	0.09	-0.05	0.09	0.11	0.09	0.36	0.29
summer-1 T	0.41	0.45	-0.16	0.26	0.23	-0.38	-0.17	-0.11	0.02	0.40	0.14
winter P	-0.05	-0.28	0.48	-0.16	-0.05	0.45	0.27	-0.05	0.00	-0.23	-0.04
spring P	-0.36	-0.74	-0.38	0.02	-0.30	0.19	-0.03	-0.35	-0.40	-0.52	-0.59
summer P	-0.36	-0.23	-0.13	-0.52	-0.16	-0.06	-0.46	-0.48	-0.44	-0.22	-0.49
autumn P	-0.15	-0.53	0.16	0.39	-0.26	0.04	0.01	-0.12	-0.16	-0.23	-0.12

These results suggest common negative effects of winter temperature and precipitation, and positive effects of summer temperature upon moth and butterfly populations, supporting previous analyses (Section 4.3). In addition, moth populations also appear sensitive to warm, wet spring weather. Multivariate analysis based on these seasonal means highlights significant positive relationships with summer temperature and negative effects of winter temperature and precipitation upon the abundance of both groups. Additional positive effects of autumn temperature were apparent for butterflies, and negative effects of spring temperature and precipitation for moths. Hindcasting of long-term trends using these models suggest that climatic changes may have caused a slight increase in butterfly trends from 1970, but a decline in moth populations (Figure 4.5a)

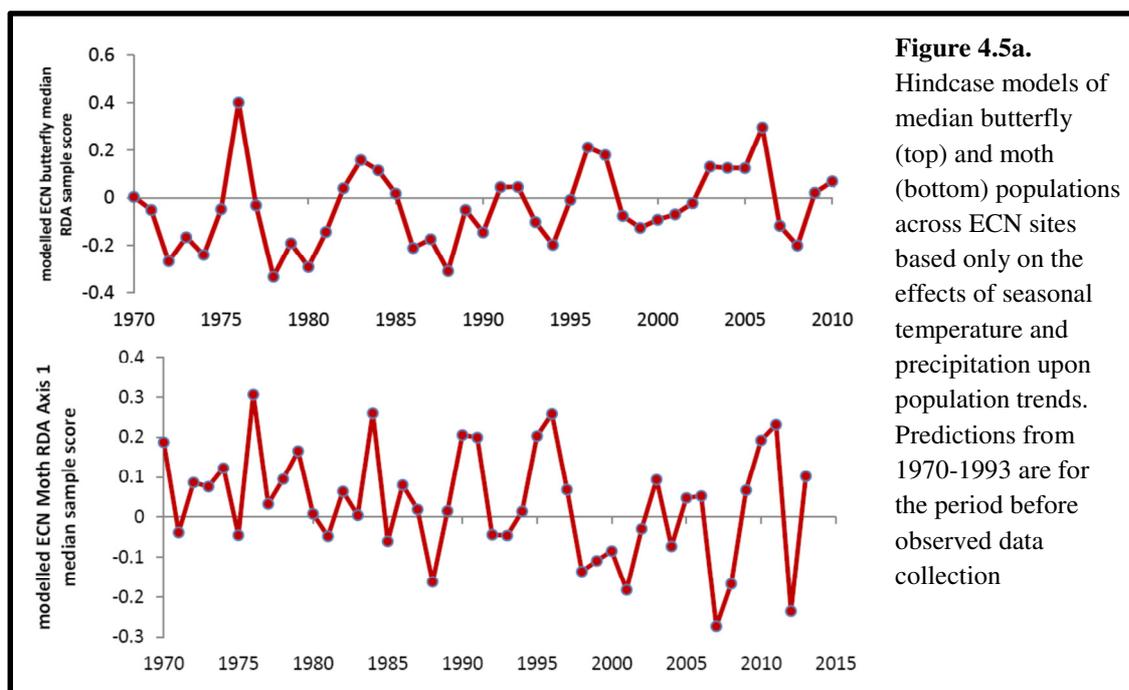


Figure 4.5a. Hindcase models of median butterfly (top) and moth (bottom) populations across ECN sites based only on the effects of seasonal temperature and precipitation upon population trends. Predictions from 1970-1993 are for the period before observed data collection

A total of 143 butterfly species-site combinations were analysed individually using the damped Fourier oscillation approach. Eighty-four showed significant effects of temperature, with a tendency towards positive summer temperature effects across species. Eighty-two combinations showed significant effects of precipitation, and tended towards negative effects during spring and summer. For moths, 692/1053 species-site combinations showed evidence for significant temperature effects. Most sites displayed a general tendency for species to show positive relationships with temperature in the late spring and summer, and negative relationships with temperature during winter and into early spring. A total of 756 species-site combinations showed significant effects of precipitation, and tended towards negative effects during the winter, with some evidence for positive impacts during the late spring and early summer. Although generally consistent between sites, there were differences in response between some sites, which require further investigation. Again, the responses from this analysis were broadly similar to the results of Table 4.5 (positive effects of summer and negative effects of winter temperature, negative effects of precipitation during the main flight periods).

To conclude, our analyses reveal strong similarities in inter-annual variation in community level metrics in butterfly and moth populations at ECN sites, both between sites and between the two groups. These similarities are likely to reflect the dominant influence of climate on the life cycles, survival and activity of these invertebrates. In both cases, variation in populations was linked to negative effects of warmer and wetter winters while summer temperatures showed a generally strong positive relationship, particularly for butterflies. In the case of moth populations there was also evidence for negative influences of spring and, in some cases summer, precipitation on assemblage structure. The results for some ECN sites deviated from this general pattern, potentially due to local climatic influences, or as a result of other specific site-factors such as altitude, soil-type or habitat.

4.6. Effects of climate change on macroinvertebrates of upland waters (Task 4.1.)

Annual fluctuations in upland macroinvertebrate populations were correlated with weather variables in 70% of cases. Effects of temperature tended to be negative, particularly in the summer and autumn, and were most notable in Plecoptera (stoneflies) and Trichoptera (caddisflies). There was a tendency that such effects were most marked at high altitude (>300m). The results from the models significantly correlated with Europe-wide assessments of temperature sensitivity, providing good independent validation of the approach used. Although important, precipitation effects were less consistent in their impact across taxa.

Due to their high sensitivity to organic pollution and acidity, aquatic macroinvertebrates are routinely used as bioindicators of water quality. Indeed, with recent improvements in water quality, significant changes in macroinvertebrate community composition have been observed (Vaughan & Ormerod 2012, 2014, Section 4.7), work primarily focussed on lowland habitats. With improving water quality, it is expected that changes in climate will become an increasingly important driver of their populations. Although recent work has identified community changes in upland streams in response to warming (Durance & Ormerod 2007), there have been few attempts to assess the wider sensitivity of upland populations to recent climatic variation, the aim of this work.

Upland macroinvertebrate time-series data from 1988 onwards were drawn from two sources, the UK Upland Waters Monitoring Network (UWMN), established to assess the impact of acid emission reductions on 11 acid sensitive lakes and 11 acid sensitive streams from across the UK uplands, and the Llyn Brianne catchment in Wales analysed by Durance & Ormerod (2007). In both cases, macroinvertebrates are sampled annually during spring using kick samples and where possible identified to species, although for some groups, genus- or family-level identification only was possible. Annual abundances in these groups were modelled as a function of mean monthly air temperature and total monthly precipitation for the 1 km grid square within which each site lies. In order to control for the possible influence of recovery from acidification on the populations, known to influence the occurrence and abundance of sensitive macroinvertebrate species (Montieth *et al.* 2005, Ormerod & Durance 2009), mean annual sulphate concentration, a surrogate for acid deposition, was also incorporated into the models.

We conducted separate analysis on populations at individual sites for which at least 15 years of data were available. For each site-taxon combination, four models were used to explain interannual variation in total abundance, containing the following terms; YEAR (a linear trend to account for potentially confounding, but unmodelled drivers), YEAR and SULPHATE (to account for additional effects of declining acidity), YEAR, SULPHATE and TEMPERATURE and finally YEAR, SULPHATE and PRECIPITATION (both describing effects of climatic variation). Temperature and precipitation variables were fitted using damped Fourier oscillations (Section 3.2), although due to the limited length of the time-series (min 15 years), were constrained to a single annual cyclic wave. We used the mean coefficients to summarise the direction and size of the climatic effect across the models.

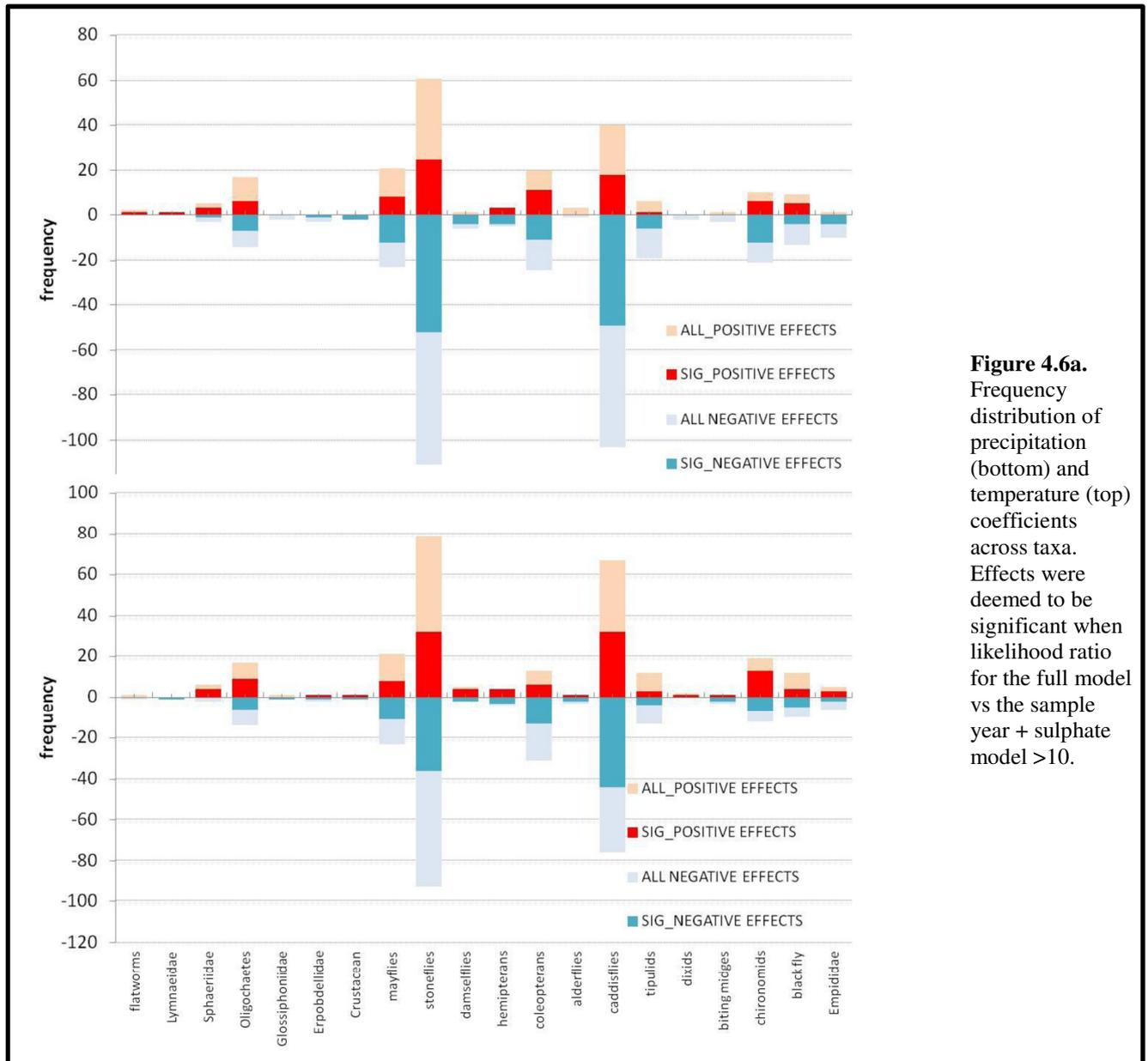
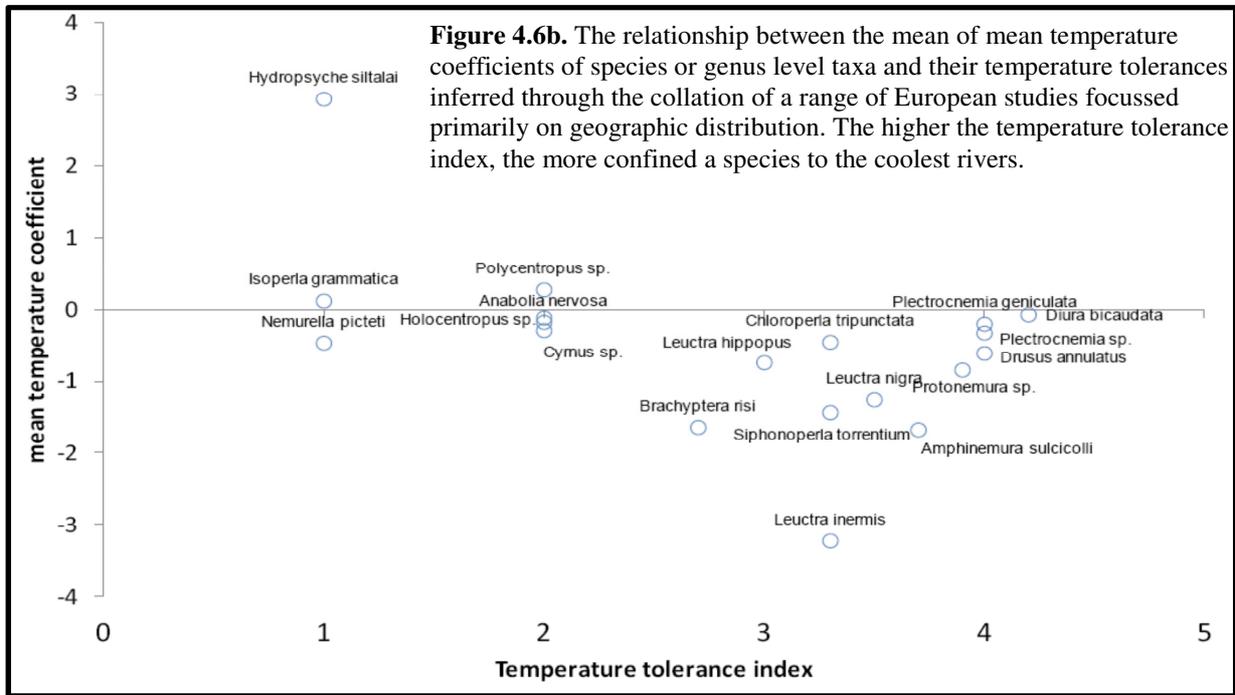


Figure 4.6a. Frequency distribution of precipitation (bottom) and temperature (top) coefficients across taxa. Effects were deemed to be significant when likelihood ratio for the full model vs the sample year + sulphate model >10.

Of the 566 site-taxon combinations, the YEAR and SULPHATE model explained significantly more variation than the NULL model in 23 cases. Stoneflies (30% of all site-taxon combinations) contributed 12 of these. The addition of TEMPERATURE or PRECIPITATION terms significantly improved model fit for 268 and 257 cases respectively. Climatic variation is therefore a key driver of annual variation in abundance across these invertebrate groups. Although the numbers of net positive and negative effects of precipitation were similar, negative temperature effects were more frequently observed than positive (Figure 4.6a).

Effects varied between different taxonomic groups. Two caddis families, the Limnephilidae and Polycentropidae, showed clear negative temperature coefficients, as did Chloroperlidae, Leuctridae, Chloroperlidae and Taniopterygidae stonefly families. The majority of negative effects, for example for *Plectrocnemia* spp. stoneflies, occurred during the summer (July – September), implicating hot summers as having a negative effect on spring abundances.

While Leuctridae and Nemouridae showed overall positive coefficients for precipitation, effects on Perlodidae were largely negative, although varied between sites. Temperature sensitivity, as assessed from our models, correlated with an assessment of species' temperature tolerances through the collation of a range of European studies (Figure 4.6b), emphasising the likely sensitivity of northern and upland taxa to warming.



The upland macroinvertebrate datasets examined in this analysis have been collated over a twenty year period (1988 – 2008) with relatively weak long-term climatic trends compared to interannual variability. The results highlight stronger effects of temperature than precipitation upon macroinvertebrate populations, particularly for some of the most commonly occurring taxa. This extends the conclusions of Durance & Ormerod (2007) from Llyn Brianne to a wider range of sites of varying acidification status. However, whilst Durance & Ormerod focussed on winter climate effects, the results here highlight the potential importance of hot summer conditions in driving population change.

Modelling was restricted to species that occurred at individual sites in at least all but five years, while our cross-site assessment was necessarily limited to the more widespread taxa. Different impacts of warming on more specialised species, less well represented in our dataset, cannot be ruled out at this stage and will require more detailed examination. Although attribution of specific climate-related effects is complicated by the fact that most meteorological variables tend to be correlated at various temporal and spatial scales, and by potentially confounding influences of other drivers (e.g. Section 4.7), by examining variation in both temperature and precipitation whilst also incorporating a measure of key water quality changes, these impacts should be minimised. That our results from a wide array of sites support those from the non-acid sensitive Llyn Brianne streams included within this dataset (Durance & Ormerod 2007), is encouraging in this regard.

4.7. Linking inter-decadal changes in British river ecosystems to hydrochemical and climatic dynamics (Task 4.2i).

Long-term trends in macroinvertebrate community structure, as measured by family-level occurrence, can be largely explained by improving water quality, rather than climate change. There is more evidence that shorter-term fluctuations in occurrence vary with discharge and temperature, suggesting that the macroinvertebrate groups covered are sensitive to climatic impacts. This study demonstrates how improvements in wider environmental conditions can buffer or reverse the direction of species' responses to climate change.

Previous studies have highlighted long-term changes to riverine macroinvertebrate community structure in recent decades (Vaughan & Ormerod 2012). These changes have occurred at a time of increasing water quality due to improved water treatment, and during a period of climatic change. Given the known sensitivity of these invertebrate species to both climatic and water quality metrics (Durance & Ormerod 2007), there is an urgent need to fully disentangle the relative importance of these processes in driving the observed changes.

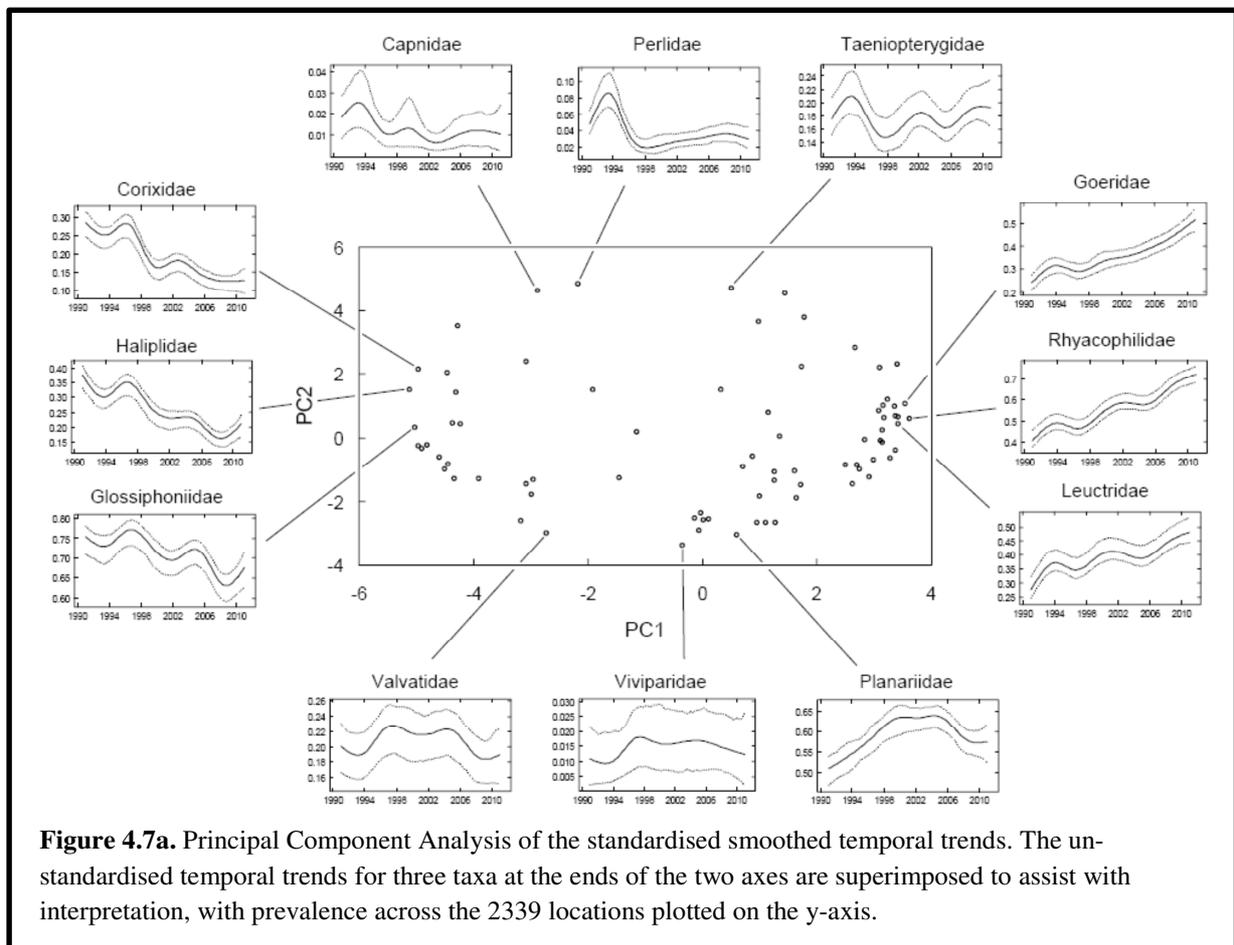


Figure 4.7a. Principal Component Analysis of the standardised smoothed temporal trends. The unstandardised temporal trends for three taxa at the ends of the two axes are superimposed to assist with interpretation, with prevalence across the 2339 locations plotted on the y-axis.

Trends in the prevalence of macroinvertebrate families over 21 years (1991–2011) were collated from routine monitoring by the Environment Agency in spring (March–May) and autumn (September–November). Temporal trends were described using Generalised Additive Models (GAMs) to produce smoothed curves with seven degrees of freedom. The form of these relationships were summarised for each of 78 taxa using Principal Components Analysis (PCA), which separated declining from increasing families (PC1) and families with

a peak in abundance during the middle of the study period from those with the opposite pattern (PC2, Figure 4.7a). To identify the factors associated with variation in these trends, these PC scores were analysed in relation to measures of pollution sensitivity, discharge and temperature preferences of each species, as well as a measure of family distribution described from sample locations in 1995 using Principal Coordinates Analysis (PCoA).

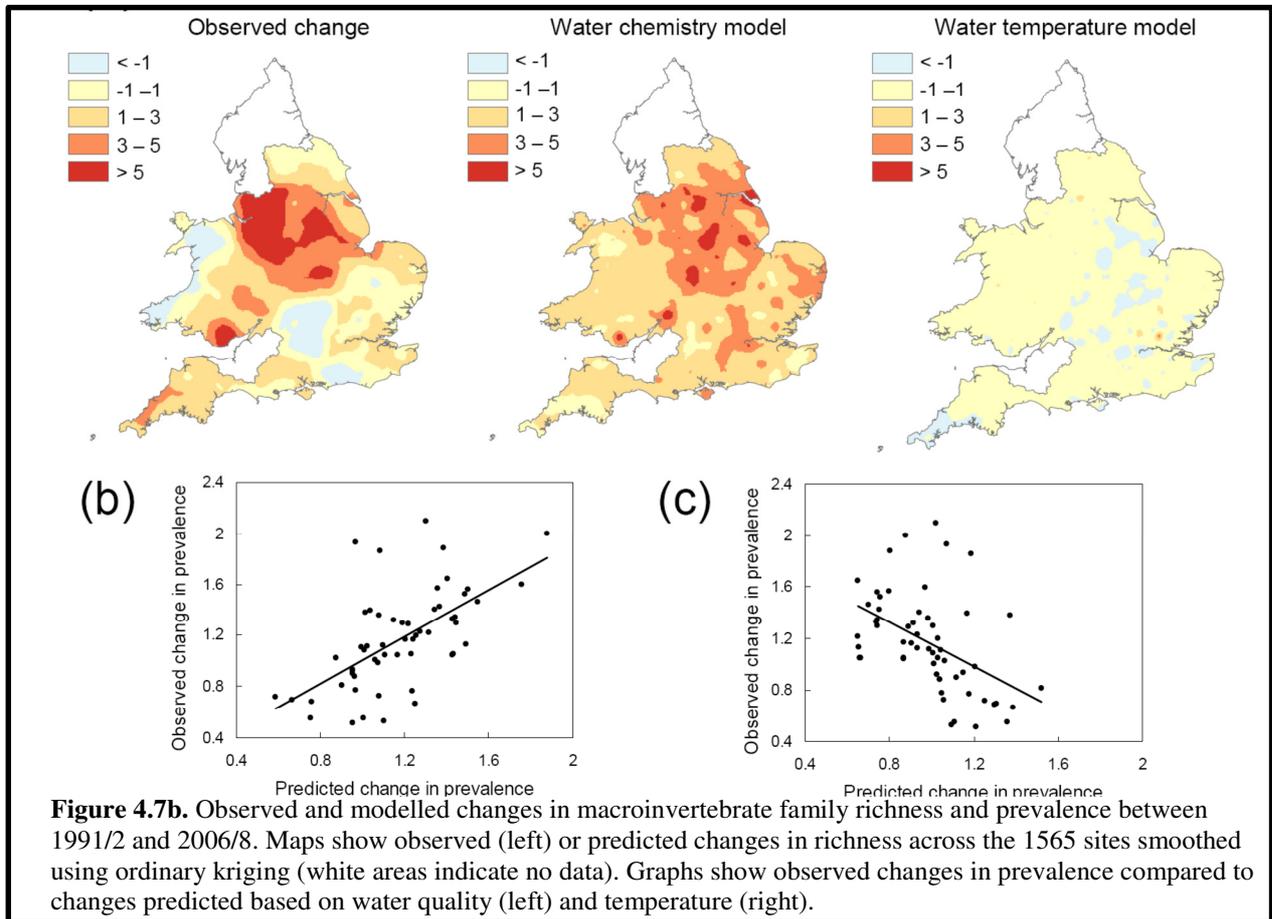


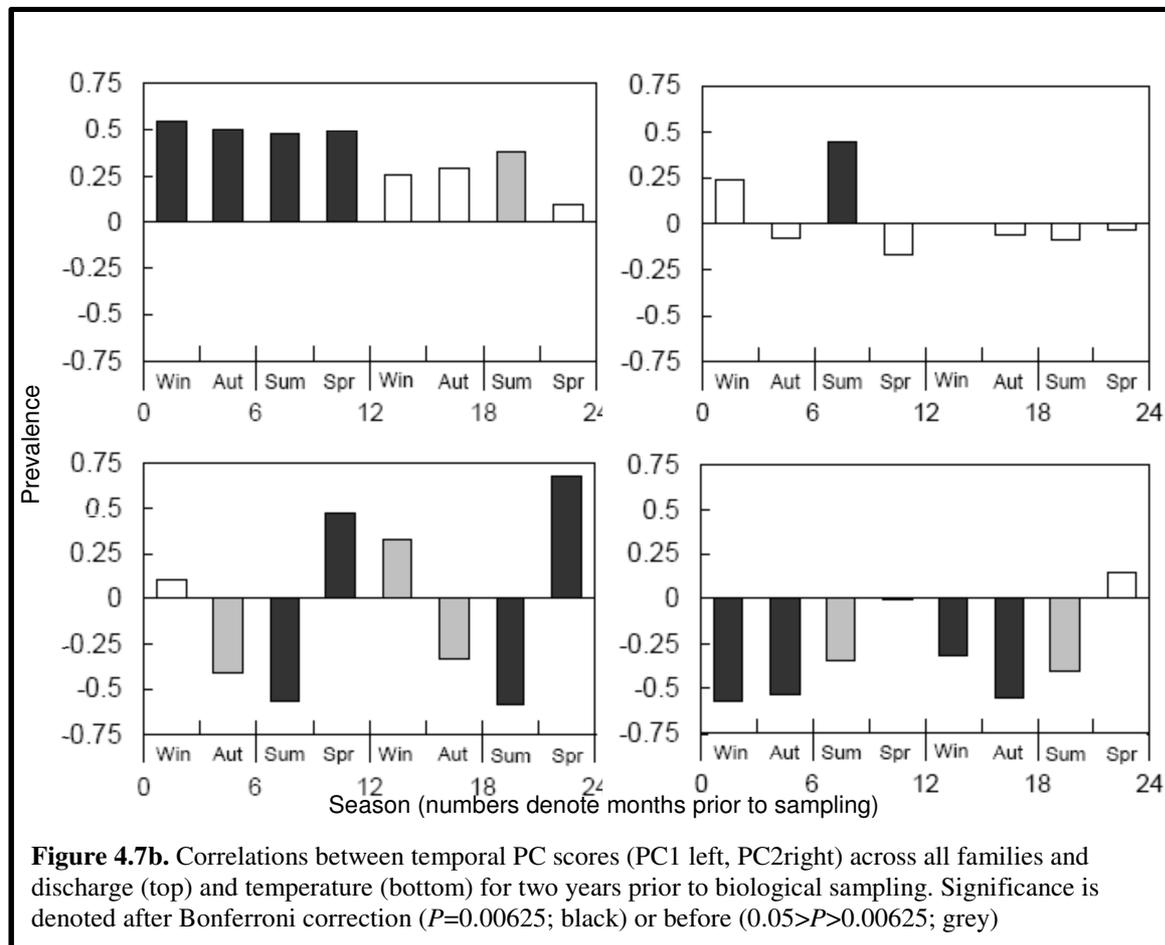
Figure 4.7b. Observed and modelled changes in macroinvertebrate family richness and prevalence between 1991/2 and 2006/8. Maps show observed (left) or predicted changes in richness across the 1565 sites smoothed using ordinary kriging (white areas indicate no data). Graphs show observed changes in prevalence compared to changes predicted based on water quality (left) and temperature (right).

Changes in macroinvertebrate distribution from 1991/2 to 2006/8 were modelled as a function of prevalence and the distribution PCoA. In order to attribute these changes to climate change or water quality, distribution models for 56 taxa were constructed from the 1991/2 data using GAM logistic regression. Occurrence was modelled as a function of water temperature, biochemical oxygen demand (BOD), and concentrations of ammonia, nitrate and phosphate, and the models used to predict future changes. Finally, inter-annual variation in prevalence was modelled as a function of correlation with the same environmental data over the preceding 12 months.

Water chemistry models accounted for just over a third of the variance in the observed changes in prevalence, contrasting with water temperature models, where predicted changes in prevalence were the opposite of those observed (Figure 4.7b). Water chemistry models successfully predicted a shift towards the lowlands by upland taxa, an eastward shift in the boundary of western taxa, some northward expansion of southern taxa (although this was not significantly different from zero) but no mean changes amongst lowland or eastern taxa. Water temperature models, by contrast, predicted that lowland taxa should have expanded further across the lowlands and eastern taxa expanded west, whilst upland taxa were

predicted to contract into the uplands and western taxa to retreat west (although the latter was not significantly different from zero).

Although water chemistry changes appeared responsible for the majority of long-term changes in prevalence, patterns of short-term variation were also correlated with temporal variation in discharge and water temperature. Strong correlations between PC1 (long-term population trend) and both discharge and temperature were indicative of expanding families (positive PCA1 score) benefitting from wet conditions, warm springs and cool summers in the preceding year. Families with positive PC2 score (a peak in prevalence in the mid-1990s and more recent increase post mid-2000s), were more likely to increase in prevalence following a wet summer and cooler year (Fig. 4.7c). The mechanisms underpinning such correlations are unclear, but in addition to reflecting direct effects, may also be related to effects of discharge upon pollution concentration, or interactions between water quality and climate.



Improvements in water quality have therefore been the main driver of recent trends in riverine macroinvertebrate community structure. However, in addition to these effects, short-term community responses to annual variation in discharge and temperature which are indicative of likely future sensitivities to climate change, although more work is required to examine the mechanisms underpinning these effects, which may be driven by changes in inter-specific interactions (e.g. Cahill *et al.* 2013, Section 4.8), or interactions between climate and water quality. Importantly, this study emphasises the value of improving wider environmental conditions as a means of buffering species' responses to climate change.

4.8. National-scale responses of river macroinvertebrate species to changes in temperature and precipitation (Task 4.2ii).

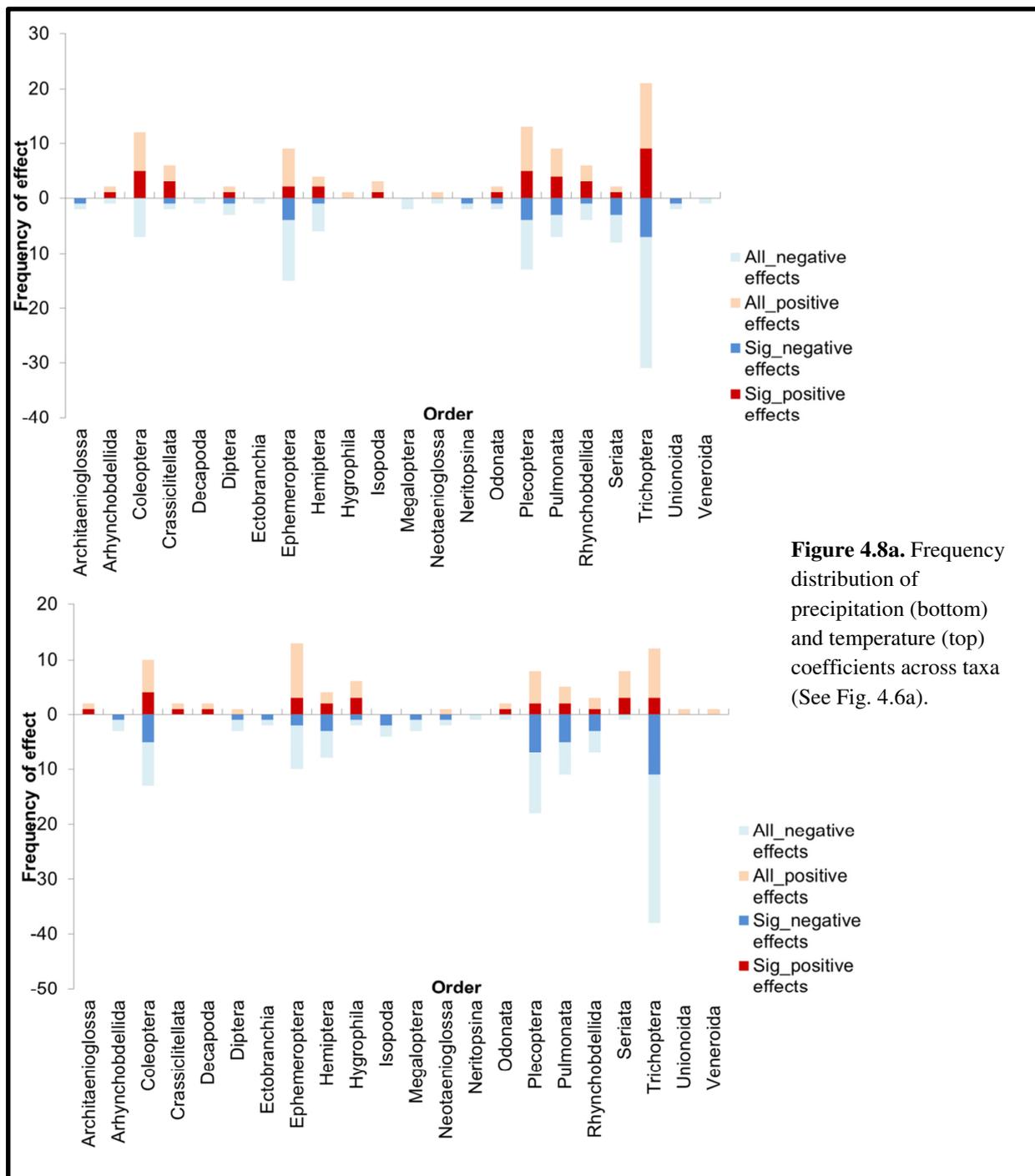
Long-term trends in the abundance of 137 macroinvertebrate species were modelled as a function of temperature and precipitation. Species' sensitivity to weather variables did not vary consistently with taxa, but did vary with respect to ecological traits, such as feeding group, tolerance to temperature, water flow and pollution.

There is no single monitoring scheme for macro-invertebrate populations across the UK. Analyses of UWMN (Section 4.6, Task 4.1) have examined the sensitivity of upland invertebrate populations to temperature and precipitation in the context of declining acidity. Large-scale patterns in the occurrence of macroinvertebrate families across England and Wales have been described and related to climatic and water quality trends (Section 4.7, Task 4.2i). Here, using a subset of locations covered in Task 4.2i for which abundance data are available, we examine changes in the abundance of invertebrate species in lowland waters, as a complement to the upland-focussed analysis of Task 4.1.

Long-term data on species-level macroinvertebrate population abundances were supplied from two independent sources: the Environment Agency (EA) in England and the Scottish Environment Protection Agency (SEPA) in Scotland. The data are based on regular samples using a standardised three-minute kick sampling methods (Moss *et al.* 1999). As taxa are typically identified to family-level, analysis was restricted to 1,588 sites from Scotland and central / eastern England where species-level data were available. Excluding species recorded for fewer than 15 years and on fewer than 20 sites, sufficient data were available for analysis for 137 species. These data were used to produce an index of overall abundance across sites, by modelling abundance as a function of year and site. Mean monthly air temperature and precipitation data for the 1km² grid of square each sample were calculated from CHES (Climate, Ecological and Hydrological research Support System) database. These were converted into bespoke weather variables for each species by including data from only sites where each species was present.

The following models were used to assess the importance of temperature and precipitation in driving annual variation in species' abundance. Firstly, a null model described annual abundance as a linear function of year only, in order to control for potential improvements in water quality through time (Section 4.7). Secondly, models additionally including either temperature or precipitation effects were also tested, where temperature and precipitation variables were fitted using damped Fourier oscillations (Section 3.2). As in Section 4.6 for the upland macroinvertebrates, due to the limited length of the time-series (min 15 years), data were again constrained to a single annual cyclic wave, with a three-year decay. The importance of temperature or precipitation variables in describing population abundance was examined using likelihood ratio-tests of the fit of each of the climate models compared to the null model. In order to synthesise and explain the patterns observed, species-specific responses to temperature and precipitation were modelled as a function of a number of ecological traits using boosted regression trees designed to model such nonparametric trait data.

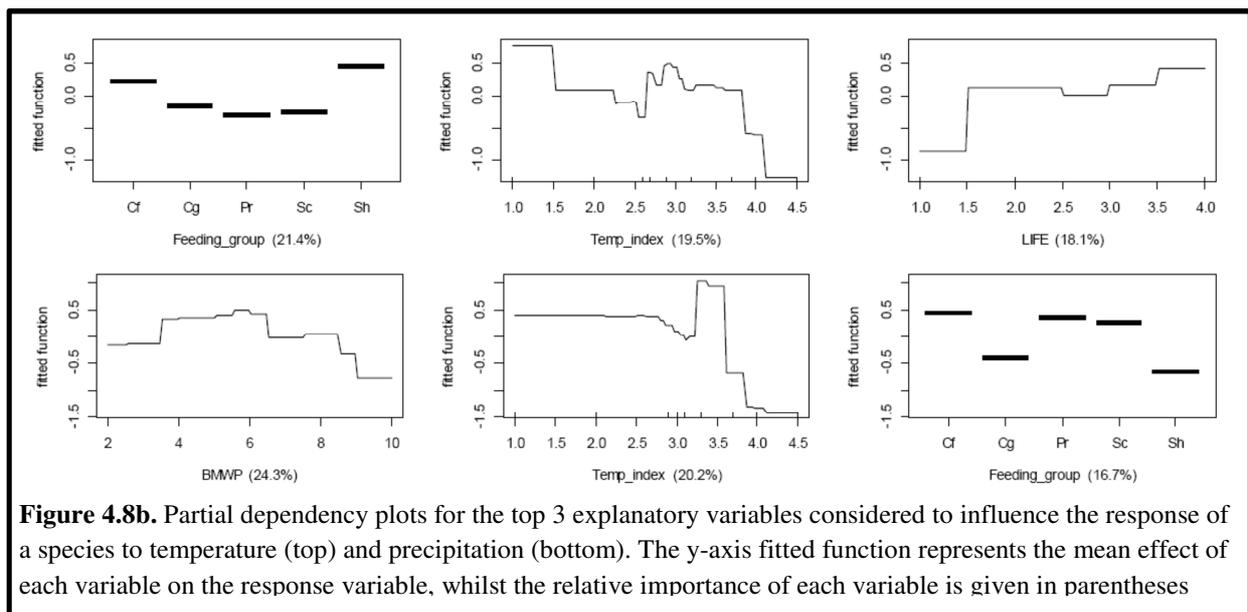
Out of 137 species, climate models for 70 and 67 species showed a statistically significant better explanation of abundances for precipitation and temperature, respectively, of which 46 species showed significant association with both. There was considerable variation in the importance of different variables within taxonomic groups, but relatively few patterns between them (Fig 4.8a).



Species' responses to temperature and precipitation varied significantly with ecological traits. The most important driver of sensitivity to temperature was species feeding group, followed by a measure of temperature tolerance and species' flow preferences (LIFE). Sensitivity to precipitation was strongly related to species' tolerance to organic pollution, as measured by

the BWMP score, followed again by thermal tolerance and feeding group. Species that belong in the ‘shredder’ and ‘collector-filter’ feeding groups showed the most positive population responses to temperature, whilst ‘shredders’ and ‘collector-gatherers’ showed the most negative responses to precipitation. Shredders were therefore particularly tolerant of drought conditions. Species sensitive to high temperatures (cold stenotherm) were most likely to show negative population responses to both temperature and precipitation, whilst species with intermediate pollution tolerance were most likely to show positive associations between abundance and precipitation. Finally, species associated with rapid-flows (low LIFE score) showed the most negative associations between temperature and abundance (Figure 4.8b).

Our results indicate that the majority of freshwater macroinvertebrate species studied have the potential to be sensitive to variation in temperature and precipitation, and as a result, may be affected by long-term climatic trends. Responses varied strongly within higher taxonomic groupings, but could be explained by environmental preferences and functional traits. Of these, feeding group, temperature sensitivity, water-flow sensitivity and pollution sensitivity were the most important traits considered. Strong interactions between pollution tolerance, water flow and temperature, all of which affect species’ oxygen requirements, show again the importance of considering both climatic and water quality changes when explaining freshwater biodiversity trends through time.



The importance of feeding group highlights how species’ tolerance to temperature and precipitation may be affected by trophic level, matching the results of other studies (e.g. Ockendon *et al.* 2014). In particular, predatory species tended to have a more negative relationship between abundance and temperature than some other feeding groups. This may be because predators tend to have relatively larger body sizes (Woodward *et al.*, 2010b) and hence greater thermo-regulatory demands and food requirements than other groups. In contrast, the two functional feeding groups that show increases in abundance with rising temperatures are further down the food chain, exploiting the less limited basal resources such as organic detritus, whose availability may be related to microbial activity which will be proportional to temperature (Graça, 2001, Artigas *et al.*, 2009, Boyero *et al.*, 2011).

4.9. The development of climate change indicators for the UK (Task 5.1).

Computer simulations were used to assess the likely sensitivity and specificity of three different approaches to biodiversity indicators of climate change impacts on populations and ecological communities. All indicators produced outputs that were correlated with each other, and with annual variation in temperature. They are therefore all sensitive to climate change. However, they were all potentially vulnerable to impacts of confounding non-climatic trends. Any climate change indicator needs to be interpreted carefully in the light of potential impacts of other environmental changes upon the species of interest.

There is considerable policy interest in the potential to develop indicators of the potential impacts of climate change on biodiversity, and in using changes in biodiversity state to monitor the ecological impacts of climate change. Although a range of impacts of climate change on species have been documented, including phenological change and range change (Parmesan & Yohe 2003, Root et al. 2003, Thackeray et al. 2010, Chen et al. 2011), there is less-consistent reporting of impacts on populations, but yet it is impacts of climate change on populations which will be of greatest interest to those concerned about ecosystem function and biodiversity conservation. Two potential indicators of biodiversity impacts on populations and communities have already been developed and adopted, whilst a third was developed through the BICCO-Net I project, and is also tested.

The indicator of Gregory *et al.* (2009) was developed for common and widespread European breeding birds, and uses the results of bioclimate modelling to separate species likely to increase in response to climate change from those projected to decline before tracking the divergence in the population trends of the two groups. The Community Temperature Index (CTI) of Devictor *et al.* (2008, 2012) uses spatial distribution data for each species to calculate mean breeding season temperature across a species' range; the species temperature index (STI) value. These are then averaged for each species present at a location, weighted by abundance, to give the community temperature index (CTI). Thirdly, the BICCO-Net index separates species into those in which population growth is positively correlated with temperature from those with a negative association, and uses the divergent population trends of these two groups to indicate climate change impacts (Pearce-Higgins *et al.* 2012).

Both Gregory and Devictor (CTI) indicators are already used to track community changes. However the underpinning bioclimate models of the former have been subject to criticism (Beale *et al.* 2008), whilst the STI values underpinning the CTI score may be confounded with habitat, leading to spurious trends as a function of non-climatic drivers (Clavero *et al.* 2011, Barnagaud *et al.* 2012, Kampichler *et al.* 2012). As a result, we developed a simulation to test the sensitivity and specificity of these measures to climate change. Simulations were undertaken for the UK and based on observed increases in mean temperature from 1980-2011. Each simulation modelled the distribution and abundance of one of 20 dummy species with randomly selected demographic and ecological characteristics, and crucially, a random relationship between population growth and temperature that determined distribution and population trend (Figure 4.9a). With a constant temperature scenario as a control, each indicator exhibited a mean trend of zero (stability). When indicator trends were simulated under a climate change scenario, the outputs from all indicator types were closely correlated

with each other ($r > 0.76$ in all cases) and with temperature ($r > 0.49$ in all cases), and exhibited a significant positive trend. Upon the introduction of random stochasticity to the population trends, and particularly when random non-climatic population trends were also included, trends in climate change indicator values were associated with much greater uncertainty, and were less likely to be significantly correlated with temperature (Table 4.9a).

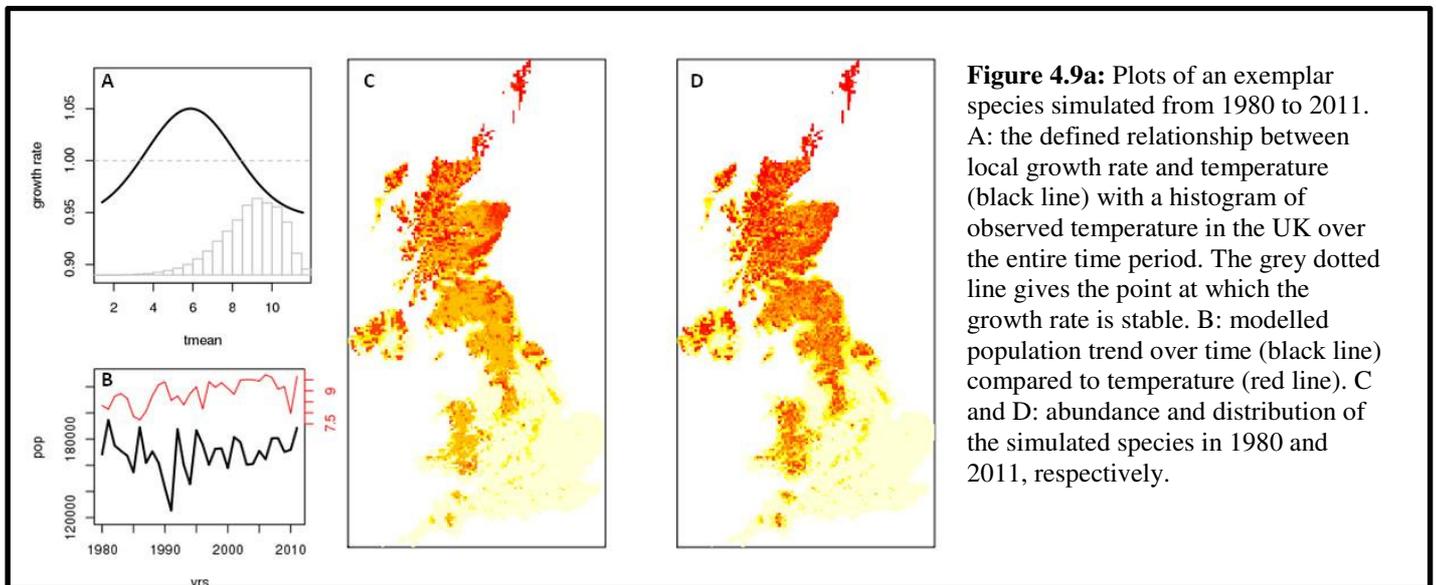


Figure 4.9a: Plots of an exemplar species simulated from 1980 to 2011. A: the defined relationship between local growth rate and temperature (black line) with a histogram of observed temperature in the UK over the entire time period. The grey dotted line gives the point at which the growth rate is stable. B: modelled population trend over time (black line) compared to temperature (red line). C and D: abundance and distribution of the simulated species in 1980 and 2011, respectively.

Table 4.9a. Summary of the key results of the indicator simulations for four scenarios (no climate change, climate change, climate change + stochasticity and climate change + stochasticity + non-climatic population trends). The top value gives the percentage of 20 simulations significantly correlated with temperature, whilst the bottom value is the mean (90% confidence intervals) indicator trend (standardised for comparability across indicators so the value with climate change = 1 and the absence of a trend = 0).

	BICCO-Net	CTI-type	Gregory-type
Constant temperature	15%	0 %	0%
	0.0 (-0.6 - 1.0)	0.1 (-0.9 - 1.5)	0.0 (-1.0 - 1.1)
Climate change	95%	100%	85%
	1.0 (0.1 - 2.3)	1.0 (0.4 - 1.8)	1.0 (0.3 - 3.3)
+ stochasticity	90%	75%	75%
	0.9 (-0.2 - 2.3)	1.0 (-0.5 - 2.0)	1.1 (-0.4 - 2.8)
+ trends	75%	65%	45%
	2.6 (-4.4 - 7.0)	3.24 (-9.9 - 17.9)	-0.5 (-6.3 - 4.9)

Although based upon a relatively limited number of simulations, none of the indicators differed strongly in their performance. The BICCO-Net indicator showed the greatest sensitivity to climate change, with the greatest proportion of simulations in the context of climate change (bottom three rows) being significantly correlated with temperature (85%), compared to 80% for the CTI-type indicator and 68% for the Gregory-type indicator. However, the BICCO-Net indicator was least specific, being most likely to exhibit spurious correlations with temperature. When assessed using Defra’s scoring system for indicators, each method was similarly scored, as the differences outlined by these simulations are relatively small compared to the criteria for rating indicators from poor to good (Table 4.9b).

It is therefore necessary to also consider other practical and ecological considerations when making recommendations concerning these indicators.

Table 4.9b. Assessment of each of the three main indicator types, based on Defra’s scoring system for indicators. Each indicator is scored on a scale from 1 (poor) to 3 (good) for each criterion.

	BICCO-Net	CTI-type	Gregory-type
Data Issues			
Transparency and auditability	3	3	3
Verification	2	2	2
Frequency of updates	3	3	3
Security	3	3	3
Spatial coverage	2, 3 ¹	2, 3 ¹	2, 3 ¹
Temporal coverage	3	3	3
Capacity for disaggregation	2, 3 ¹	2, 3 ¹	2, 3 ¹
Methodology			
Transparency and soundness	2	3	3
Precision	2	2	2
Indicator characteristics			
Policy relevance	3	3	3
Biodiversity relevance	3	3	3
Cause-effect relationship	3	3	3
Human induced vs natural changes	1	1	1
Communication	1	2	2

¹Depending upon the monitoring scheme underpinning the indicator.

Based on spatial data, both CTI and Gregory-type indicators are likely to better reflect the full range of mechanisms by which temperature or climate change will impact upon species, but require extensive spatial data; indicator performance was reduced when based on distribution data from only the UK. Where such data are available, the CTI-type indicator may appropriately track community changes in response to temperature, although the extent to which it is differentially sensitive to seasonally variable responses, or may be adapted to measure the impacts of other elements of climate change, such as precipitation, is unclear. For species for which bioclimatic models have been produced, the Gregory-type indicator may track a greater range of responses to climate change than the STI, although the results of ongoing work outside of this consortium to develop this metric should also be appraised. In the absence of occurrence data, the BICCO-Net indicator may also track the impacts of climate change, but may fail to detect incremental long-term responses to climate change.

We suggest that where extensive spatial distribution are available across a species’ distribution, CTI is the best supported method to assess community changes in response to temperature, whilst the Gregory indicator may provide a more generic measure of population responses to climate change. In the absence of spatial information about species’ distributions, the BICCO-Net indicator may also give useful outputs. A combination of all three approaches may have the greatest potential to fully track climate change impacts upon populations, although all measures appear vulnerable to potentially confounding non-climatic trends that may drive non-random population changes. The results of any putative climate change indicator will therefore need careful interpretation (Section 4.10).

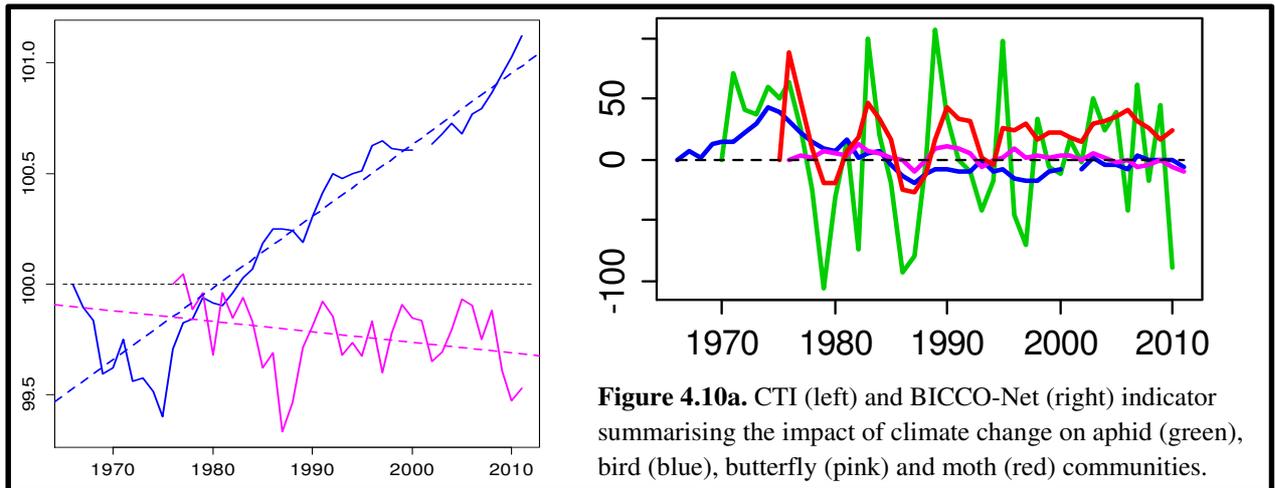
4.10. Production of climate change indicators for the UK, including example spatial maps for birds (Task 5.2).

Using long-term population monitoring data analysed as part of the BICCO-Net project, illustrative CTI and BICCO-Net indicators are calculated for the UK for up to four terrestrial taxa (butterflies, moths, aphids and birds) from the late 1960s or 1970s onwards. Indicator trends were largely positive for birds (broadly matching expectation) but negative for butterflies (opposite to expectation). Due to the lack of distribution data it was only possible to generate BICCO-Net indicators for aphids and moths, which were non-significantly positive in trend. Spatial variation in CTI was mapped for the first time for birds, and showed the expected latitudinal and altitudinal gradients as well as highlighting the Highlands and west coast of Scotland as where the greatest changes had occurred.

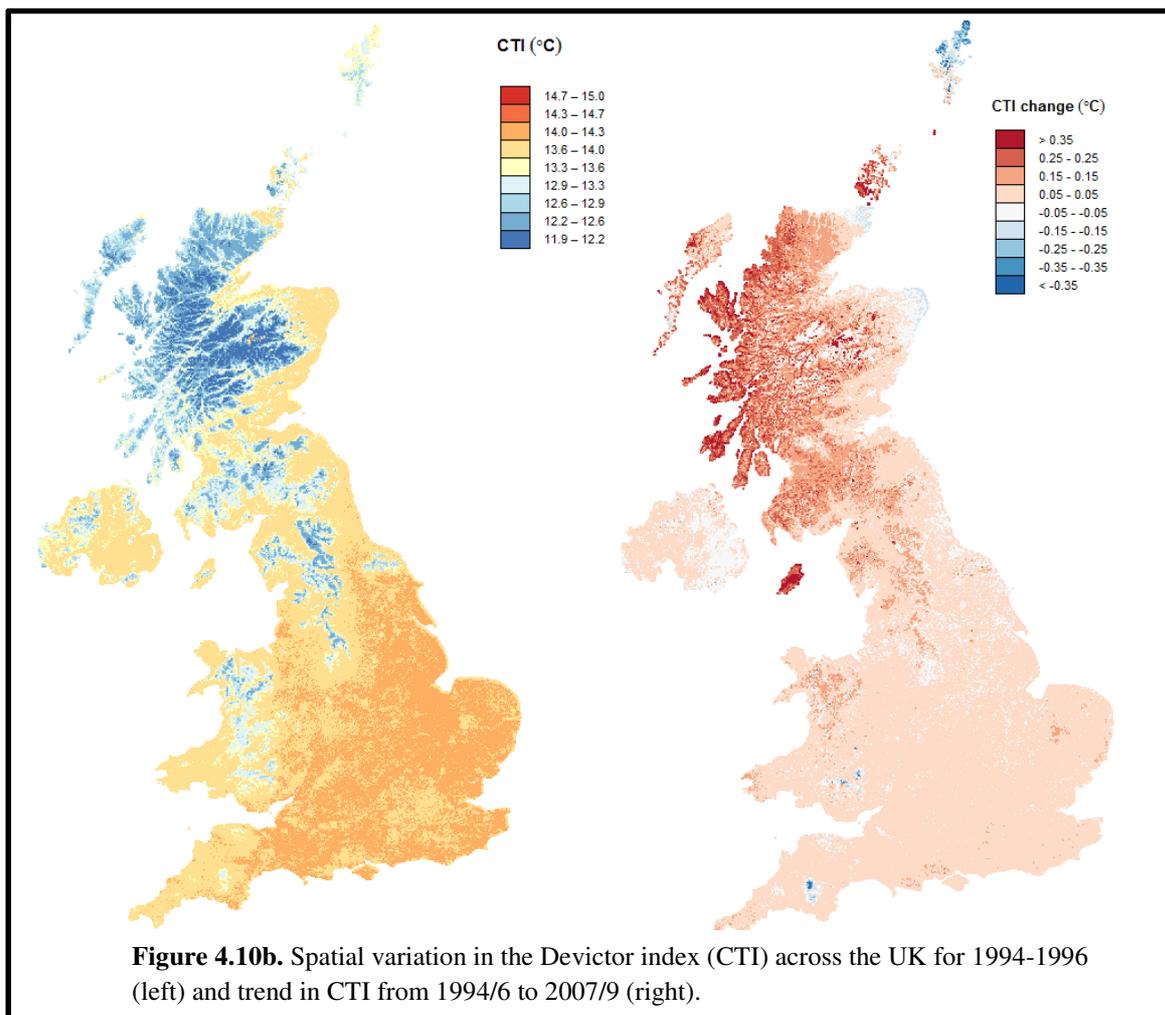
A number of climate change indicators have been proposed and developed based on impacts on European or UK biodiversity. The Gregory *et al.* (2009) indicator tracks divergent population trajectories in European bird species projected to increase in response to climate change from those projected to decline. The Community Temperature Index (CTI) of Devictor *et al.* (2008, 2012) tracks the relative composition of bird and butterfly communities as assessed by species' spatial association with temperature. The BICCO-Net indicator separates species by their direction of association between population growth and temperature, and separately tracks the population trends of these two groups (Pearce-Higgins *et al.* 2011). There is considerable interest in the production of climate change indicators for the UK as a means of tracking the ecological impacts of climate change on species' populations, and as described in Section 4.9, each indicator has some ability to track biodiversity responses to climate change. Whilst ongoing work is extending the Gregory indicator for individual European countries, including the UK, here we focus on the production of CTI and BICCO-Net indicators for the UK.

We calculated the Devictor index (CTI) for English birds and butterflies, the taxa for which species temperature indices are already established, and the geographical area over which these trends to the 1970s were regarded as robust (Section 3.1). The BICCO-Net index was calculated for birds, aphids, butterflies and moths; the four taxa with longest time-series, using the relationships between population growth and temperature from the best-fitting damped Fourier oscillations model for each species to separate species into two groups.

There was a strong positive trend in CTI for birds from the mid-1970s ($P < 0.0001$), whilst the butterfly trend over this period was weakly negative ($P = 0.068$). Both trends were continued over the last 20 years, but more weakly for butterflies ($P = 0.15$). Over their entire time-series, the bird and butterfly BICCO-Net indices show long-term negative trends ($P < 0.0001$, $P = 0.004$ respectively), which continue for butterflies from 1991-2011, but was positive for birds over this shorted timescale ($P = 0.009$). Index values for moths and aphids show strong inter-annual fluctuations, but no significant long-term trend (Figure 4.10a).



Spatial variation in CTI for birds followed the expected pattern, with warm-associated species dominating communities in the south and in the lowlands. There were strong spatial gradients in CTI trend through time (Figure 4.10b), which were strongly positive across the Highlands and west coast of Scotland, but limited across lowland England.



The CTI pattern observed for birds replicated the previously published positive trends for the UK from 1990 onwards from Devictor *et al.* (2012). This is consistent with a strong warming

trend apparent from the mid-1980s (Gregory *et al.* 2009, Thackeray *et al.* 2010), although does not explain the positive bird CTI trend in the 1970s. The lack of positive butterfly CTI trend contrasts with Devictor *et al.* (2012) but is matched by Oliver *et al.* (unpubl), and may additionally reflect the impacts of recent cold winters upon butterflies. It is possible that non-climatic drivers, such as changes in agricultural management (e.g. Eglington & Pearce-Higgins 2012) may also have influenced these trends (cf. Clavero *et al.* 2011, Kampichler *et al.* 2012). Temporal trends in the BICCO-Net indicator were variable, with evidence for a warming signal in recent years only strongly apparent in birds, but weakly indicated for moths and aphids.

When mapped, the greatest proportion of cold-associated bird species were found in northern and upland habitats as expected (e.g. Devictor *et al.* 2008). The strongest CTI increases through time were in western upland areas. Here, increasing numbers of warm-associated species may have colonised upland habitats previously occupied by cold-adapted specialists; these are the areas where increases in species diversity have been most marked (Davey *et al.* 2012).

Based upon warming trends, we would have expected largely stable indicator trends to the mid-1980s, but then biodiversity indicators to increase in response to warming from the mid-1980s onwards. This pattern was only really apparent in birds. This could be regarded as increasing evidence that bird populations and communities are showing long-term responses to climate change in the UK, although it is clear from Section 4.2 and elsewhere (Clavero *et al.* 2011, Kampichler *et al.* 2012, Eglington & Pearce-Higgins 2012), that other factors have also driven some of the observed population changes. For other taxa, there was less strong evidence for a consistent and measurable impact of climate change summarised by a single indicator. Although aphid and moth populations in general show significant long-term trends consistent with significant impacts of climate change (Section 4.2), the extent to which species-specific population trends diverge in accordance with the expectation from climate change, as measured by these indicators, was weaker than expected, and potentially may have been masked by strong interannual population fluctuations, potentially due to the combined effects of density-dependence and weather. The lack of strong indicator trends in butterflies is counter to the conclusion of Devictor *et al.* (2012), but may reflect the impact of recent cold weather combined with the importance of non-climatic factors in influencing population trends of southerly distributed species.

This section highlights the challenges associated with the production of climate change biodiversity indicators. Whilst some appear to ‘work well’ and produce the expected result (Gregory *et al.* 2009, Devictor *et al.* 2008, 2012, Pearce-Higgins *et al.* 2011), in other circumstances, they may not (e.g. Kampichler *et al.* 2012). This variation in the performance of climate change indicators is difficult to predict. It is unclear whether a trend contrary to the expectation from climate change means that the species being tracked are not responding to climate change, or that any response to climate change is being countered by other, stronger, environmental changes. At present, our results suggest that climate change is having a detectable impact on bird communities, weaker impact on aphid and moth populations, and little impact on butterfly populations.

4.11. Overall synthesis of patterns (Task 6.1)

Models suggest that 1°C warming in a single year would have a positive effect on aphid, moth and butterfly populations. The response of species varied with occurrence and thermal association, suggesting that widely occurring species may respond most rapidly to warming. Being based only on a single year of warming, this assessment indicates the likely immediate short-term response of populations to warming, but excludes potential negative lagged effects of temperature upon populations, as well as potential impacts of precipitation, important for butterflies and moths in particular.

The BICCO-Net project has examined species sensitivity to variation in precipitation and temperature across a wide range of both terrestrial and freshwater taxa. Although analyses of individual datasets and species-groups have been used to identify the traits associated with variation in population responses to these variables, here we collate all of the main national-scale, species-level results across both freshwater and terrestrial habitats to examine whether there is strong variation in responses across all taxa, which can be related to a number of key traits. Previous analyses have shown that the impacts of climate change upon phenologies differ between terrestrial, freshwater and marine environments, and between trophic levels (Thackeray *et al.* 2010), whilst there is further strong evidence of differential impacts of climate change upon terrestrial and marine environments and species (Poloczanska *et al.* 2013).

In this study, we examined a range of key traits that were expected to influence a species response to climate warming. We focussed on temperature because precipitation does not have equivalent effects upon freshwater and terrestrial habitats (Section 4.1), and used the results of the damped Fourier oscillation models for butterflies, moths, mammals, birds and aphids from Section 4.3, and for freshwater invertebrates from Section 4.8 to summarise species' responses. In order to produce a standard metric which is comparable across groups, the outputs from these models were used to estimate the likely population increase associated with a 1°C rise in temperature during each month of the final year of the population time series, compared to the predicted value in that final year based on observed temperature and precipitation values. Note, however, that this limits the applicability of our results to a true climate change scenario when precipitation would also change, and the warming would be sustained.

We compared variation in population responses to temperature between different taxonomic groups (largely based upon different sources of population monitoring data), and then consider how those vary with respect to four key ecological traits; occurrence, temperature index, trophic level and habitat. Occurrence was the proportion of survey sites that a species occupied during the survey period. The temperature index was estimated from gridded 5 x 5 km, monthly mean temperature data taken from the Met Office UKCP09 datasets (http://www.metoffice.gov.uk/climatechange/science/monitoring/ukcp09/download/monthly/gridded_monthly.html; Perry & Hollis 2005), averaged from 1970 and 2010 across the sites occupied by each species. This index was therefore very similar in principle, to the STI of Section 4.9, but based only on data from the UK. To ensure that values of the temperature index were comparable across the taxonomic groups and not biased by the spatial variation in

site locations, we subtracted the respective mean climate variable across all sites surveyed for the taxonomic group from the species mean climate score. As few tertiary consumers were included in the data, trophic level was restricted to a comparison of primary and secondary consumers. The habitat term differentiated obligate freshwater species from those which are wholly or partially terrestrial.

There was widespread variation in species predicted response to a one degree rise in temperature (Fig. 4.11a). Aphids, moths and butterflies showed positive mean temperature sensitivity scores that were significantly different from zero, suggesting that an individual species from these groups (particularly aphids and moths) would likely increase in abundance were there to be a 1°C rise in temperature across all months in a single year.

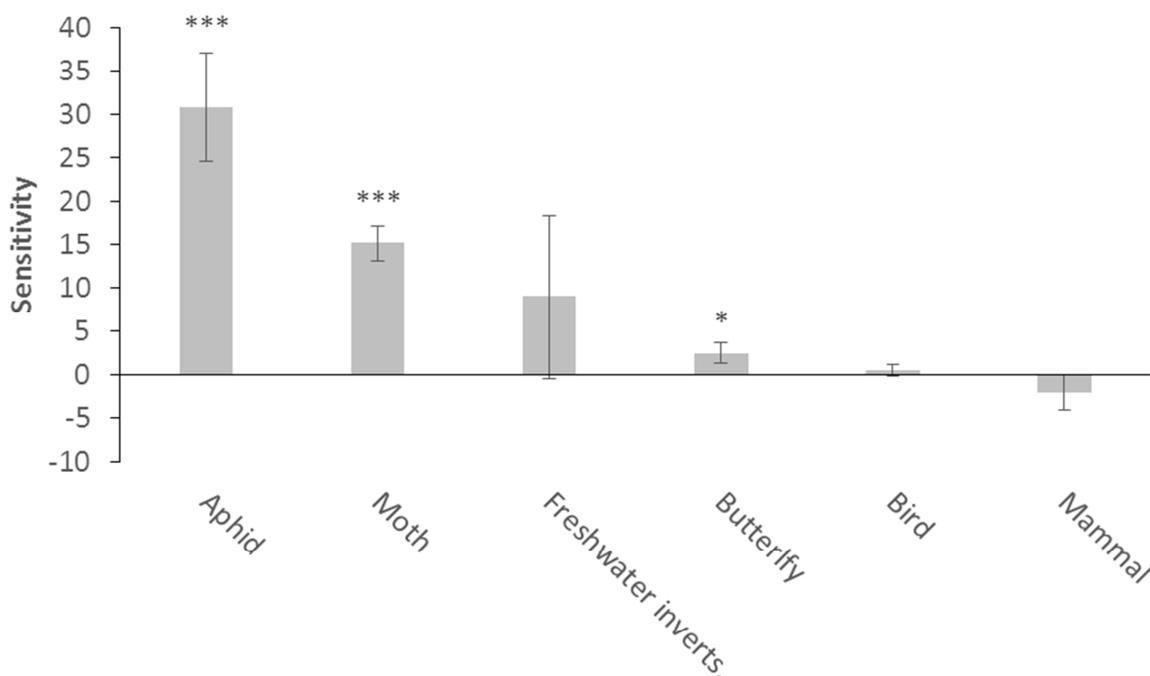
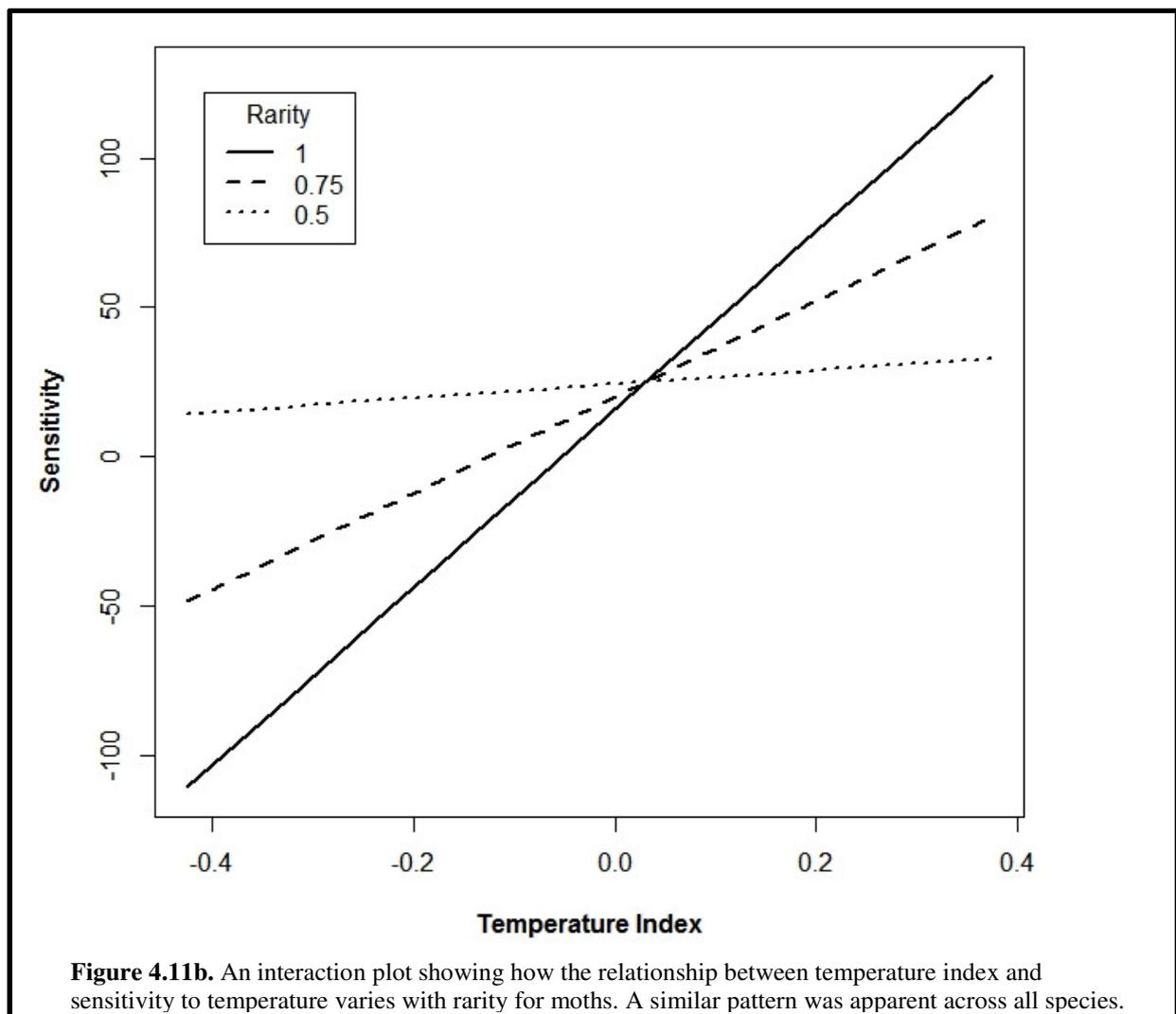


Figure 4.11a. The mean temperature sensitivity for each group included in the analysis, based upon mean population responses to a 1°C warming. The standard error of the mean are plotted with asterisks added to highlight those mean estimates that are significantly different from zero (* = $p < 0.05$, ** = $p < 0.01$, *** = $p < 0.001$).

There was a positive effect of occurrence upon the sensitivity of butterfly populations to warming ($P = 0.03$), indicating that the most widespread species were those which tended to show more positive effects of temperature. For moths, the interaction between rarity and temperature index was significant ($P < 0.001$), indicating that the most widespread moths were those whose population response to warming was most sensitive to their thermal association, as described by the temperature index. Conversely, rarer species showed little relationship between the temperature index and population sensitivity to temperature (Fig. 4.11b). Together, this emphasises that widespread generalists may be those whose occurrence and abundance is more likely to be influenced by temperature. Given the number of moths in the sample, similar results were apparent across all species. There was no significant difference in species' population sensitivity to temperature between terrestrial and freshwater habitats, or between primary and secondary consumers.

Our results emphasise the potential sensitivity to temperature of terrestrial insects, and particularly suggest that warming may increase the abundance of aphid, moth and butterfly populations, at least in the short term. The results for aphid strongly support the conclusions of Sections 4.2 and 4.3 as a result of the strong association between aphid populations and temperature. The results for moths and butterflies also partly support the conclusions of these sections. The median response of moths to temperature across all species was positive (Appendix 4), largely due to stronger positive effects of summer temperature upon abundance than negative impacts of winter and spring temperature, although that of butterflies was not. However, as Section 4.2 has shown, this does not mean that moth populations have benefited from recent climate change, partly due to the strong negative impacts of winter and spring precipitation upon moth populations, and also partly because the analysis presented here constrains the temperature effects to only the final year of the time-series, rather than additionally including the negative impact of temperature in year t (Section 4.3).



Finally, the inference from the analysis of traits associated with species' sensitivity is that it is the most widespread generalist species whose populations are most likely to increase in response to warming, and to show equivalent relationships between occurrence and abundance, as recently examined for butterflies (Mair *et al.* 2014).

5. Discussion

5.1. *Scientific achievements*

In phase II of the BICCO-Net project, we have completed much new analysis to look at the impacts of climate change upon a range of UK taxa. This has included analysis of all terrestrial animal taxa subject to national-scale long-term population monitoring schemes (aphids, moths, butterflies, birds, bats and other mammals), and analyses of long-term datasets describing trends in the occurrence or abundance of freshwater macroinvertebrate taxa from upland and lowland sources. This project therefore presents what may be regarded as the most comprehensive single assessment of the impacts of climate change on UK biodiversity population trends that has been conducted to date. To achieve this, we have utilised new statistical methods that account for uncertainty in the time of year at which different groups will respond to variation in temperature and precipitation variables. In particular, the damped Fourier oscillation approach enables flexible patterns in population responses to weather variables to be fitted in a manner that reduces the risk of over-fitting, which given the length of some of the time-series analysed (min 14 years), is essential (Section 3.2). However, due both to the number of parameters and the length of the data series, models for temperature and precipitation cannot be fitted simultaneously using this approach. This means that potential correlations between the two variables, which could lead to spurious correlations and patterns, cannot be accounted for. For this reason, complementary analysis using standard multivariate ordination techniques are used to describe broad patterns in population changes of terrestrial taxa (Section 4.1), site-based analysis of moths and butterflies on ECN sites (Section 4.5) and in the occurrence of freshwater macroinvertebrate families (Section 4.7), in order to assess the overall strength of climate change impacts on these groups through time in a way that combines the effects of temperature and precipitation in a single analysis.

Among our key results are potential large-scale impacts of climate change on the abundance of some key taxonomic groups, as inferred from the effects of long-term changes in weather variables. Our models suggest that climate change may have resulted in increases in aphid abundance since 1975, but caused general declines in moth populations. In particular, nine moth species were identified for which particularly strong declines were consistent with modelled climate change impacts (Section 4.2). Data from ECN sites support these results for moths, but suggest that warming could have had a slight positive impact on butterfly populations (Section 4.5). In the freshwater environment, gross changes in family-level prevalence data across England and Wales were unrelated to climate change, but instead showed direct response to improving water quality, particularly in urban environments, that resulted in the expansion of previously upland taxa into lowland areas (Section 4.7). Interestingly, this was the opposite response to that expected in response to warming, but can be explained by the strong inter-relatedness of population responses to temperature, water flow and pollution (see also Section 4.8). Thus across all the taxonomic groups and monitoring data considered, significant long-term impacts of climate change on abundance or occurrence were largely restricted to aphids and moths (Table 5.1), whilst long-term abundance trends in other groups, particularly birds (Eglington & Pearce-Higgins 2012) and

macroinvertebrates (Vaughan & Ormerod 2014, Section 4.6) appear to have been largely driven by other processes.

However, this coarse overview masks more subtle impacts of climate change within taxonomic groups, and particularly, the apparent sensitivity of populations of many species to annual variation in temperature and precipitation. Most groups show some degree of consistency in temperature responses. Bird population changes tended to be positively correlated with winter temperature. There is good evidence that warmer winter weather improves the overwinter survival of many bird species in the UK (e.g. Greenwood & Baillie 1991, Robinson *et al.* 2007), and has at least been partly responsible for some population increases in recent years. Positive effects of temperature were also apparent for aphids, moths and butterflies during spring and summer months of the second survey (year_{t1}). For aphids, this is likely to be a consequence of temperature-related reductions in generation time and earlier commencement of parthenogenesis (Zhou *et al.* 1995, Yamamura & Kiritani 1998), whilst for Lepidoptera, may reflect a combination of enhanced activity and improved survival of winged adults.

Table 5.1. Summary of the key findings of BICCO-Net II.

Taxonomic group	Climate change impact on overall long-term trends	Climate change impact on species trends within taxa affecting communities	Effects of increasing temperature on population growth	Effects of increasing precipitation on population growth
Mammals	Non-significant		Negative (Spr) Positive (Sum)	Mixed
Birds	Non-significant	Yes	Positive (Win)	Positive (Aut) Negative (Spr)
Butterflies	Non-significant	No	Negative (Win) Positive (Sum)	Negative
Moths	Negative	No	Negative (Win) Positive (Sum)	Negative
Aphids	Positive	No	Positive(Sum)	Negative (Sum)
Freshwater				
Family level (EA)	Non-significant			
Species-level (EA/SEPA)			Mixed	Mixed
Species-level (UWMN)			Negative	Mixed

However, strongly negative relationships between winter temperature and precipitation upon population growth were apparent for moths and butterflies. These results were not just identified by the national-scale analysis (Section 4.2), but also the site-level analysis across ECN sites (Section 4.5), emphasising the robust nature of this finding. It therefore appears that warm wet winter weather, is generally harmful for Lepidoptera, and particularly affects species that overwinter as larvae or pupae. Declines in the numbers of garden tiger moth which overwinters as a young larva, have previously been attributed to warm wet winter and spring weather, potentially by making them vulnerable to fungal attack (Conrad *et al.* 2002). Our results suggest that this may also be the case with other Lepidoptera. A total of 16 moth species were modelled to show strong response to climate change, of which 9 have

undergone severe population declines consistent with model predictions (Appendix 3). Despite the similar weather relationships being identified for butterflies, unlike the moths, UK butterfly population trends appear largely stable across species, and the trend towards warmer, wetter winters has not significantly impacted upon their populations, potentially due to weaker effects of precipitation upon their populations than moths, or more positive effects of summer temperature. This supports the fact that apart from a small number of upland species with a northern distribution, most UK butterflies are anticipated to increase in range in response to climate change (Thomas *et al.* 2011). Interestingly, there is little evidence of such trends across recent years, with no general tendency for warm-associated southern butterflies to have increased in abundance relative to cold-associated northern or generalist species (Section 4.10).

A tendency towards negative impacts of temperature upon upland waters macroinvertebrates also highlights their potential vulnerability to future warming (Section 4.6), although given the strong signal of improving water quality due to reduced acidification, there is little evidence that warming has significantly limited their populations so far (see also Section 4.7). However, our analysis does suggest that in common with other taxonomic groups in the uplands (Franco *et al.* 2006, Pearce-Higgins 2010), future warming may have a negative impact upon their populations. Indeed, the results of a recent climate change risk assessment for species in England identified upland species as amongst those at greatest risk from climate change (Pearce-Higgins *et al.* 2013). Unlike butterflies and moths, these negative effects of warming did not appear to occur in response to warmer, wetter winter weather, but in response to increasing summer temperatures (Section 4.6). There is increasing evidence that summer drought or heat wave conditions can have negative impacts on upland invertebrates (e.g. Pearce-Higgins *et al.* 2010, Pearce-Higgins 2010), which our analysis suggests may also affect aquatic species. The impact of weather variables upon variation in lowland aquatic macroinvertebrate populations again showed a tendency towards greater sensitivity to temperature than precipitation (Section 4.8). Negative impacts of temperature were most apparent in predatory species, cold temperature specialists (stenotherms), and species associated with fast-flowing waters, supporting the results of the analysis of upland waters, that cold-associated species of fast-flowing waters are most sensitive to warming.

Aside from gross changes in the abundance of different taxonomic groups, there is also some evidence that more subtle community changes have occurred in response to climate change. There is mounting evidence that bird communities in the UK, and across Europe, have changed in response to recent warming. Increasing temperatures have increased species richness and community diversity, but reduced the proportion of that community comprised of habitat specialists (Davey *et al.* 2012). Since the late 1980s, populations of southerly distributed species associated with warmer temperatures have tended to increase in abundance more than cold-adapted northern species (Devictor *et al.* 2008, 2012, Jiguet *et al.* 2010). We have repeated the Devictor analysis CTI for England, the area over which the underpinning data are most likely to be representative. This showed a significant long-term positive trend in the avian community temperature index (CTI) from the mid-1970s, although it is possible that some of this increase may not be directly related to warming as it starts

before the main warming period from the mid-1980s. We were unable to reproduce the positive butterfly CTI trends of Devictor over the same period, which instead indicated a non-significant decline in CTI. This contrast may be due to methodological differences (see Oliver *et al.* unpubl), the effects of recent cold weather post 2008, and our focus on English, rather than UK trends, but suggests that more work is required to fully understand how well the CTI index tracks climate change (Section 4.10). Certainly in recent years, butterfly populations appear to have largely stabilised (Mair *et al.* 2014), rather than showing the expected increase in response to warming. In addition to CTI, we also used the associations between temperature and population growth rate modelled through this project to separate those species positively associated with temperature from those with a negative association to produce what we call the BICCO-Net index. This resulted in a significant positive indicator trend for birds from 1990 onwards, non-significant positive trends for aphids and moths, but a significant declining index trend for butterflies (Section 4.10). Combined, it appears that bird community changes from both CTI and BICCO-Net indices largely follow that expected in response to climate change, although butterfly index trends do not. Based on the BICCO-Net indicator, there are strong annual fluctuations in both moth and aphid values, although both tend towards positive values from 1990-2011.

To conclude, long-term population increases in aphids and declines in moths may be partly attributed to climate change, although this is also dependent upon the extent to which the temperature and precipitation trends on which this analysis is based are directly attributable to anthropogenic climate change, as opposed to natural fluctuations. Within each species' group, species-level variation in such population trends was not strongly accounted for our models due to a weak climate change indicator signal for both groups. Although gross changes in bird and mammal populations do not appear related to climate change, relative variation in the performance of different bird species can be accounted for by species' responses to warming, particularly since 1990. We can find little evidence that long-term butterfly community and population trends are strongly related to warming, and may be better explained by other factors. In the freshwater environment, although population fluctuations of both upland and lowland taxa can be strongly related to temperature and precipitation, and cold-associated upland species of fast-flowing waters appear most sensitive to warming, there is little evidence that long-term population trends and changes in community composition have so far been driven by climate change. Any climate change impacts have been masked or reversed by large-scale improvements in water quality, emphasising the potential for sympathetic environmental management to help species adapt to anthropogenic climate change. The interpretation of our analysis, and the long-term trends presented, is therefore dependent upon a good understanding of changes in non-climatic drivers of populations of the species of interest that may also have occurred. The potential interaction between climate change and other factors is indicated by the finding that the most widespread species, whose distributions is largely unlimited by habitat-availability, were those showing the greatest response to warming (Section 4.11).

These issues make it difficult to produce a simple, single indicator of climate change impacts on species' populations. Although all of the potential approaches appear to be appropriately

sensitive to temperature impacts, they are all potentially vulnerable to non-random effects of non-climatic drivers of population trends that may cause spurious indicator changes. It is difficult to judge the extent to which this represents meaningful changes in an indicator (i.e. if climate change fails to produce a strong indicator trend because of greater non-climatic impacts that could be argued to correctly indicate an appropriate lack of response), or erroneous changes which are misleading (i.e. variation in species' populations between habitats which are non-randomly distributed and more likely to impact species associated with a particular climate could result in an indicator trend in the absence of climate change). Whilst there are examples of both in the literature (see Appendix 11), we recommend that multiple climate change indicators would be most likely to be robust to this issue, but should always be interpreted in the light of likely non-climatic drivers that could be affecting the observed trends.

5.2. Limitations

Although this is perhaps the most comprehensive single assessment of the impacts of climate change on UK biodiversity population trends that has been conducted to date, our results require careful interpretation. It is worth emphasising that our results are largely dependent upon regression and correlation; significant results do not automatically mean causation. In particular, the attribution of the observed long-term biodiversity trends to climate change should be made carefully. As just emphasised, many other environmental pressures have changed in recent years, and which may also be correlated with climatic trends.

We have attempted to minimise the risk of Type I error, of falsely attributing changes in species' populations to weather variables, in a number of ways. Firstly, for most analyses of long-term trends (Sections 4.2, 4.3, 4.6, 4.8), we have additionally included linear relationships between year and species abundance. Although such linear trends are unlikely to accurately reflect changes in non-climatic drivers, they do reduce the likelihood that long-term trends in unmeasured non-climatic drivers may result in spurious correlations between species' abundance and weather variables. Secondly, where possible, for the freshwater environment, we extended this approach by also including variables relating to changes in water quality. Thus, in the analysis of changes in the abundance of species in upland waters, we included a measure of changing acidity, known to also impact populations (Section 4.6), whilst community-level changes in macro-invertebrate occurrence were accounted for by changes in water quality (Section 4.7). Unfortunately, it was not possible to secure the water chemistry data to repeat this approach for the analysis of macroinvertebrate abundance in Section 4.8.

The potential importance of non-climatic drivers in influencing population trends, and resulting in false biological signals of climate change, was illustrated by the simulations of climate change indicators (Section 4.9). This means that any summary metric of biological responses to climate change must be interpreted carefully in the light of other potential non-climatic drivers of change, and where those are strong, particular care must be taken when attempting to document the impacts of climate change on species populations or communities. It is possible that the mixed trends in biodiversity indicators for the UK (Section 4.10), which showed the expected trends for birds, but not for butterflies, may reflect

the importance of non-climatic factors limiting the abundance of warm-associated, southern butterfly species.

Aside from these analytical considerations, the wider generality of our results to other species and taxa should be considered. Firstly, it is worth emphasising that the species covered by this project were those for which extensive long-term monitoring data were available. For some groups, particularly the mammals, they spanned a relatively short time-series, extending <20 years, which may have reduced our ability to identify significant relationships between abundance and weather variables, particularly for such long-lived species. Secondly, this means that our analysis is based upon a non-random selection of species. Those not covered will tend to be rare or threatened species. As such species may be more susceptible to climate change (Section 4.2), particularly if associated with cooler or northern upland areas (Section 4.6, 4.6), where observers tend to be fewer, then it is possible that our general results may underplay the potential impacts of climate change on UK biodiversity.

Finally, when examining spatial variation in population responses to weather variables, there was some evidence that population responses vary with space (Section 4.4). This means that it is important to consider the representativeness of the biological data upon which the trends analysed in relation to weather variables are based. Although we were able to ensure that the terrestrial biodiversity data were reasonably representative of the geographical areas they covered, and indeed, the results of the national-scale analysis and fine-scale analysis based on ECN data for moths and butterflies produced similar results, the data from the freshwater environment cannot properly be regarded as such, and therefore the results for this environment may be less likely to fully represent the national picture – although in practice, the contributing datasets were pretty extensive and widespread. Having developed these fine-scale analytical methods, however, there is considerable potential to investigate the drivers of such variation more fully.

5.3. Policy relevance

Understanding and detecting the likely impacts of climate change on UK biodiversity is an important component of climate change adaptation (Hopkins *et al.* 2007, Smithers *et al.* 2008). A number of new initiatives exist to report on such impacts. Firstly, there is a legislative requirement for reporting on a six-year cycle as part of the UK's Climate Change Risk Assessment (CCRA 2012). Reporting in 2012 was too early for significant input from BICCO-Net I, but there is significant potential for the results presented here to input to that process. Secondly, the publication of the new LWEC climate change report cards provide an opportunity for a more regular summary of the latest scientific evidence regarding the impact of climate change on UK biodiversity (Morecroft & Speakman 2013). One of the underpinning papers for that report was heavily based on outputs from BICCO-Net I (Pearce-Higgins 2013). Again, the result presented here, from BICCO-Net II, should form a key evidence source for future iterations of that report card. There is currently considerable interest in the potential to develop biological indicators of climate change impacts (e.g. Gregory *et al.* 2009, Devictor *et al.* 2012). Our assessment of these and attempts to develop novel indicators from the BICCO-Net analysis have highlighted some of the challenges in

interpreting these scores, and their potential vulnerability to non-climatic factors. It is striking that only a proportion of the indicators developed as part of this project seem to produce the expected trends. This could be because non-climatic factors have driven the observed changes (e.g. Clavero *et al.* 2011, Barnagaud *et al.* 2012, Kampichler *et al.* 2012), or because the indices adopted are not sufficiently sensitive to climatic impacts.

In order to maximise their impact, it is important that elements of this project are independently published in peer-reviewed scientific journals. One paper from BICCO-Net I was published (Eglinton & Pearce-Higgins 2012), whilst a second has been accepted for publication (Pearce-Higgins *et al.* in press). Already from BICCO-Net II, one manuscript has been published (Appendix 8; Vaughan & Ormerod 2014), whilst a further manuscript is well-advanced towards submission (Appendix 3). It is anticipated that over the course of the next one to two years, a significant proportion of the underpinning appendices will be submitted for publication to strengthen the scientific value of the work, and to provide greater confidence for scientists and policy makers on its validity.

Whilst there is much potential to feed these results into such policy-relevant summary documents, both phases of the BICCO-Net project have produced an array of detailed species-specific information about the relative sensitivity of different taxa to temperature and precipitation. This more detailed information will not be presentable in scientific or policy-focussed summary documents, but is none-the-less useful. It can provide important information for other policy-relevant climate-change products. Such information could be made widely available through the internet, as shown for birds by the BTO's BirdTrends website which provides an annual summary of the population status of common breeding birds in the wider UK countryside (Baillie *et al.* 2012), or BirdFacts, which summarises species-level traits for birds (Robinson 2005), and is not just useful for conservation and more species-specific purposes, but also a valuable tool to feedback information to the volunteers responsible for collecting the data. However, this has not been possible during the course of the project, as originally envisaged, due to the need for marketing exemption, and restrictions associated with the development of the Government website, which limited opportunities for specific projects such as this to develop and report findings through their own project websites.

There is increasing interest in using evidence to inform adaptation. For example, the new National Adaptation Programme (NAP) will set out the Government's vision to deal with the priority risks and opportunities that climate change poses, and will include a natural environment theme. The results presented here should be an important source of evidence for that programme by identifying the groups and species which appear to be responding most strongly to climate change impacts. Further, our results also may be used to provide some evidence for adaptation principles, particular for the freshwater environment. It is particularly striking that both in lowland and upland contexts, although population fluctuations of macroinvertebrates were related to temperature and precipitation, long-term trends in the abundance and occurrence of these groups are largely a result of improving water quality trends (Vaughan & Ormerod 2012, Section 4.5, 4.6). Thus, reducing the effect of other pressures has counteracted the negative impacts of climate change.

By necessity, most of the analysis in this report has focussed on fully analysing large-scale population trends. However, these are comprised of the sum of multiple local population changes with varying trends. There is much potential to analyse population data at this finer-scale in order to investigate the extent to which variation in habitat quality and extent may buffer or exacerbate climatic impacts upon populations, which we have investigated in Appendix 5. Recent analysis has started to do this for woodland birds (Newson *et al.* 2014) and butterflies (Oliver *et al.* 2013), but should be extended to other habitats and taxa. For example, it would be possible to examine the extent to which variation in land cover, the extent of semi-natural habitat and topography affect the strength and direction of individual population responses to weather variables, and should be a high priority for further work in this area, particularly as a test for a number of adaptation measures proposed in the literature (Hopkins *et al.* 2007, Smithers *et al.* 2008, Heller & Zavaletta 2009).

Finally, it is important to state that the continued monitoring of population, species and community responses to climate change is required to input to initiatives such as the CCRA, and also to inform adaptation. It is therefore essential that the schemes which have contributed to our analysis are at least maintained in the long-term, in order to continue to track change. Additional monitoring schemes should be developed and supported to cover other important taxa. Where possible, existing schemes should also be extended, as only with relatively detailed spatial coverage can the results be downscaled from national (UK or English) assessments to more regional resolutions increasingly required by devolved assemblies and by policy-makers. For example, detailed spatial variation in responses to climate change can only be produced from monitoring schemes comprised 1000s of samples, such as aquatic macroinvertebrate sampling by EA or SEPA (e.g. Section 4.7) or the BTO breeding bird survey (e.g. Section 4.10). Increasing the number of samples of schemes will not only produce increased precision of estimates of the impacts of climate change, but also provide greater opportunity to examine variation in population responses at individual sites to variation in the characteristics of those sites, for example to inform climate change adaptation responses (e.g. Newson *et al.* 2014).

5.4. Future research

The majority of analyses undertaken through BICCO-Net have involved modelling fluctuations in species populations as a function of variation in weather variables, and then using those models to underpin assessments of species' sensitivity to climate change, in order to identify the impact that climate change has had on populations and communities through time. As such, we have identified strong patterns at the national level of species' responses to temperature and precipitation. However, our ability to fully disentangle these effects from other drivers is limited by a lack of information about those other drivers. Where such data exists, then analyses have been extremely informative (e.g. Eglinton & Pearce-Higgins 2012, Vaughan & Ormerod 2014). As a result, there should be potential to further extend the current models in particular habitats to better incorporate temporal changes in environmental conditions through time where such data exist. As demonstrated by the analysis of freshwater community change (Section 4.7), this will be particularly informative for identifying the potential for reducing the severity of other threats as a means of climate change adaptation

for vulnerable species. Therefore a number of potential future research areas to examine further ways of improving the evidence for the link between climate change and population change, or of understanding the mechanisms behind some of the observed changes, can be suggested as follows.

Extending the analyses of the effects of non-climatic drivers of change to other habitats and taxa. This would provide a wider comparison of climate vs other environmental change in driving recent population changes that would assist with the production of climate change indicators and further inform adaptation. Following the approaches sent out in this report, this could be achieved for woodland birds, farmland and woodland Lepidoptera, and aquatic macroinvertebrates, using large-scale statistics for changes in woodland and agricultural management, and changes in water quality, as additional predictors of population change. Not only would this improve the reporting of climate change impacts, but also identify potential opportunities for adaptation by reducing the strength of non-climatic drivers of change. The results of this analysis would therefore indicate the habitats where climate change adaptation should focus, whilst additional analyses of interactions between management and climate may be used to quantify potential adaptation options. For example, models linking farmland bird population growth to weather and land-use intensity (e.g. Pearce-Higgins & Eglinton 2012) may be used to explore the potential consequences of different scenarios of climate change and land-use intensity on future population trends to inform future policy. Given the uncertainties associated with the strength of non-climatic factors impacting upon community-level summaries of climate change impacts, and the reporting of climate change indicators, this would aid the further development and interpretation of such indicators.

Collating linkages between different biological responses to climate change from phenological to population and distribution change, and presenting that information to users at a species level, which would improve knowledge transfer from this project and set the results in a wider context of the impacts of climate change on each species. There is considerable potential to integrate ongoing research led by CEH, but involving a number of the BICCO-Net consortium, examining the impacts of climate change upon species' phenological responses (http://www.ceh.ac.uk/sci_programmes/shifting-seasons-uk.html), with research on population impacts. Not only may changes in phenology cause changes in populations, but both phenological and demographic responses may be driven by related mechanisms (Pearce-Higgins & Green 2014). Similarly, given increasing evidence for changing species' distributions in response to warming (e.g. Hickling *et al.* 2006), there is considerable potential to also link large-scale population changes documented by BICCO-Net with large-scale changes in distribution. This will help link the large-scale results of BICCO-Net with policy around adaptation and the importance of protected areas to facilitate species distribution shifts (e.g. Thomas *et al.* 2012). There is significant demand in the user community for a single location of information to synthesise the range of climate change impacts upon species and taxa, and that could also be linked to the results of other work, such as the Natural England funded species' risk assessment (Pearce-Higgins *et al.* 2013), and therefore potential to synthesise and report on species phenological, distributional and

population responses to climate change, and consider its future vulnerability to future change, in a single location.

Extending the population models on the impacts of climate change produced by this project, to disentangle the contribution of anthropogenic climate change from climatic fluctuations, enabling proper statements about attribution to be made. It would be possible to use climate models to generate long-term scenarios of climate change that account for only natural forcings, and both natural and anthropogenic forcings. These two scenarios could then be used to model long-term biodiversity population changes from the models developed in this project, in order to appropriately partition the role of the anthropogenic element of climate change in driving observed population and community changes. Such work was particularly called for in the IPCC AR4 report, and would be a significant advancement for future iterations of the CCRA.

Understanding impacts of extreme events upon species' populations. Recent years have been characterised by a number of severe weather events such as heavy snow, drought and flooding. The frequency of extreme events is likely to increase as a result of climate change, and may result in significant changes to populations and communities (e.g. Morecroft et al. 2002, Jiguet et al. 2006). However, by their very nature, the impacts of such events are difficult to study, and so far, BICCO-Net has largely focussed on analyses of linear responses of species to temperature and precipitation. Extensive, long-term monitoring data, such as that collated as part of the BICCO-Net consortium, provide a resource to do that through the development of statistical approaches that test for nonlinearities in population responses, and identify the potential for thresholds in population responses to occur. For example, this could include consideration of combined impacts of precipitation and temperature to cause drought conditions, or to increase overwinter mortality in Lepidoptera. As such responses are identified, future climate change projections can be examined to assess the potential for extreme events to become more common in response to climate change.

Further developments and production of climate change indicators. For species with distributional information, the community temperature index (CTI) shows potential for tracking long-term community changes in response to warming. However, this metric is based upon spring and summer temperature associations, and does not consider relationships with temperature in other seasons, or with other weather variables, such as precipitation. There is a need to consider further developments and refinements of this approach to develop a family of climate change indices that describe different spatial associations of species to climate, in order to track changes through time, such as various temperature and precipitation indices. Further work is also required to assess whether it is appropriate to use distribution data from the UK to calculate such indices for taxa where European distribution data do not readily exist. More widely, a range of alternative community metrics are available, and have not yet been considered in a climate change context, which would also be included in this work.

Development of fine-scale analyses of terrestrial and freshwater taxa to inform adaptation, for example by analysing site-specific variation in population responses to weather

variables as a function of different environmental variables. Beyond the detection of climate change impacts upon populations, there is increasing policy interest in the potential for adaptation to increase the resilience of species, communities and habitats to climate change. Best practice is reviewed in recent evidence published by Natural England (<http://publications.naturalengland.org.uk/publication/5629923804839936>), whilst the National Adaptation Programme (https://www.gov.uk/government/uploads/system/uploads/attachment_data/file/209866/pb13942-nap-20130701.pdf) sets out actions to make the country resilient to climate change, including the natural environment. There is considerable potential to take advantage of the analytical developments during BICCO-Net to further extend analysis of variation in population responses to weather variables at the fine-scale, to inform adaptation policy (see Newson *et al.* 2014).

The analytical framework developed in Section 4.4 can be used to assess how species' responses to climate vary with a number of features of the site or landscape they are in. Thus interactions between population response and landcover and landscape context could be used to identify whether populations in particular habitats are more or less sensitive to climatic variation. For example, it may be hypothesised that populations in less-preferred habitats show greatest sensitivity to climatic variation. Additionally, it would be possible to test the extent to which more connected landscapes result in reduced population responses to climatic sensitivity, as a test of some of the Lawton principles (Lawton *et al.* 2010). Alternatively, it would be possible to examine the extent to which protected areas help buffer population responses to climate change. Whilst Natural England has funded some work in this area, there is considerable potential to extend this further, and to examine similar questions in the freshwater environment.

Undertake future projections of population responses to climate change using the BICCO-Net models to inform species' risk assessments. The models developed through BICCO-Net may be extended into the future to explore the potential impacts of climate change upon populations and communities through time. Although not currently part of the BICCO-Net project, such future projections, particularly of abundance, may usefully inform climate change vulnerability assessments, and assess the potential for particular species to become more or less common through time (e.g. Pearce-Higgins *et al.* 2013). If further work on the potential for adaptive management to increase species' resilience to climate change is considered, then it would be possible to compare the relative potential for such adaptive intervention to buffer populations against future impacts of climate change, and therefore to quantify the relationship between the amount of climate change and the size of the adaptation challenge, at least for some components of UK biodiversity.

Further development of the models relating weather variables to species abundance indices. The regression models developed in this project for relating national species indices to weather variables represent a considerable advance on previous work. The underlying principles of the models are that abundance indices may be influenced by long sequences of monthly weather data and that the regression coefficients for successive months should be related to one another. Although the parameterisation we used was sufficient for meeting the

goals of the project, alternative parameterisations are possible and the performance of these should be explored.

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7. References

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8. List of appendices supplied with the report

Appendix 1: Summary of delivery of project objectives and milestones.

Appendix 2: Description of modelling methodology used in BICCO-Net II.

Appendix 3: A cross-taxa appraisal of the impact of climate change on species' population size (M3.1).

Appendix 4: Identifying the importance of different seasons in driving observed species' responses to climate change (M3.1).

Appendix 5: Assessing the fine-scale impact of climate on bird and butterfly population dynamics (M3.2).

Appendix 6: Fine-scale assessment of climate sensitivity of invertebrate populations at Environmental Change Network sites (M3.3).

Appendix 7: Evidence for systematic effects of antecedent temperature and precipitation on the inter-annual variability of macroinvertebrate taxa in upland streams and lakes (M4.1).

Appendix 8: Linking inter-decadal changes in British river ecosystems to hydrochemical and climatic dynamics (M4.2).

Appendix 9: : National-scale responses of river macroinvertebrates species to changes in temperature and precipitation (M4.3)

Appendix 10: An assessment of climate change indicators (M5.1)

Appendix 11: Production of climate change indicators for the UK (M5.1, M5.2)

Appendix 12: A comparative trait-based analysis of temperature sensitivity across a variety of taxonomic groups (M 6.1).

Appendix 13: Policy-focussed summary (M 7.7)