Natural England Commissioned Report NECR112

Testing the effectiveness of climate change adaptation principles for biodiversity conservation

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Foreword

Natural England commission a range of reports from external contractors to provide evidence and advice to assist us in delivering our duties. The views in this report are those of the authors and do not necessarily represent those of Natural England.

Background

Climate Change is a threat to the conservation of ecosystems, the biodiversity they support and the benefits they provide to people. In response to the threat that climate change poses, various sets of principles have been identified to guide adaptation for conservation.

Within the UK conservation community, the most widely quoted sets of adaptation principles are those produced for the UK Biodiversity Partnership and the England Biodiversity Strategy. The principles are based on good ecological theory, but there has been very little practical testing or assessment of which approaches work best in particular, real - life circumstances. Without stronger empirical evidence of this sort it is difficult to translate high level principles into practical initiatives on the ground and to prioritise scarce resources.

We established this project to start the process of testing and evaluating these high level adaptation principles. The UK is fortunate to have a number of long term monitoring datasets which allow changes in populations to be identified and relationships to a range of habitat and landscape variables identified. Two of the best datasets are for birds and butterflies with wide geographical coverage, long time series and annual data. The long time series allow us to test the sensitivity of species to year-to-year variations in the weather, long-term climatic trends and one-off climatic extremes.

On the basis of ecological theory encapsulated in the adaptation principles we would expect any sensitivity to be moderated - and thus resilience increased – by a range of environmental variables such as increasing size of habitat patches, site and landscape heterogeneity and connectivity of habitat patches.

This work is part of a process of developing the evidence base to ensure that ecological networks are developed in ways that promote their resilience to climate change and thereby ensure their long-term value.

Ecological networks and the relationship between protected sites and the wider landscape are important issues for conservation and land management and are a priority in England at the present time, particularly in the establishment of Nature Improvement Areas (NIA).

The results will also help inform the targeting and development of current and future agri-environment schemes.

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Further information
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Natural England’s summary and perspective on the project

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Introduction

Climate Change is a threat to the conservation of ecosystems, the biodiversity they support and the benefits they provide to people. This much has been widely recognised and the evidence continues to grow, with impacts such as changes in species distributions and community composition starting to emerge (DEFRA, 2012; Natural England 2012). The questions is how to respond to this threat, how to take advantage of any opportunities that climate change presents for conservation; in other words how, to adapt to climate change?

Adaptation is defined by the Intergovernmental Panel on Climate Change as *adjustment in natural or human systems in response to actual or expected climatic stimuli or their effects, which moderates harm or exploits beneficial opportunities.* (IPCC 4th Assessment report Working Group 2 Glossary www.ipcc.ch/pdf/glossary/ar4-wg2.pdf. Over the last decade, various sets of principles have been identified to guide climate change adaptation for conservation. Heller and Zaveleta (2009) reviewed 113 scientific papers which made recommendations of this sort, and the number has continued to grow since then. Conservation agencies, NGOs and government departments have also been active in developing adaptation strategies in many countries (Mawdsley *et al.*, 2009) including the UK and England specifically (Mitchell *et al.*, 2007).

Within the UK conservation community, the most widely quoted sets of adaptation principles are those produced for the UK Biodiversity Partnership (Hopkins *et al.*, 2007; Table 1) and the England Biodiversity Strategy (EBS) (Smithers *et al.*, 2008; Table 2). The UKBP principles focus on guidance for conservation practice; the EBS incorporate these into a wider context. At the present time in England there is a considerable emphasis on developing coherent and resilient ecological networks, following the recommendations of the Making Space for Nature Review (Lawton *et al.*, 2010). These recommendations, which have been picked up in the white paper ‘The Natural Choice’ (HM Government 2011) and the new England Biodiversity Strategy ‘Biodiversity 2020’ (DEFRA 2011), focus on the concept that protected sites need to be ‘bigger, better, more and joined’. This message is consistent with recent thinking on climate change adaptation and presents a good opportunity to accelerate progress towards climate change adaptation.

The various sets of adaptation principles are based on sound ecological theory, but there has been little practical testing or assessment of which approaches work best in particular, real - life circumstances. Without stronger empirical evidence of this sort it is difficult to translate high level principles into practical initiatives on the ground and to prioritise scarce resources. We established this project to start the process of testing and evaluating climate change adaptation principles.

The UK is fortunate to have a number of long term monitoring datasets which allow changes in populations to be identified and relationships to a range of habitat and landscape variables identified. Two of the best datasets are for birds and butterflies with wide geographical coverage, long time series and annual data. The long time series allow us to test the responsiveness of species to year-to-year variations in the weather, long-term climatic trends and one-off climatic extremes, all elements of sensitivity to climate change. On the basis of ecological theory encapsulated in the adaptation principles we would expect this sensitivity to be moderated - and thus resilience increased - by increasing size of habitat patches, site and landscape heterogeneity and connectivity of habitat patches. Spatial data from a variety of sources, including the Land Cover Map 2000, Habitat Inventory datasets and a grid based national hydrological model are available to test these hypotheses.

We contracted a consortium of the Centre for Ecology and Hydrology (CEH), British Trust for Ornithology (BTO) and AEA Ltd. to investigate relationships of population resilience and community composition with spatial and climate variables, working closely with specialists in Natural England. The following chapters in this report provide a full account of the analyses and their results.

Headline results

Perhaps the most striking result in this study was that the community composition of birds and butterfly species has been changing over recent decades consistent with impacts of a changing climate. Both groups show a shift towards species typical of warmer climates, but there is a contrast between birds and butterflies in the underlying cause. In birds there has been a significant decrease in the abundance of birds adapted to cool climates, whilst for butterflies, the change has been an increase in warm adapted species. These findings add to the weight of evidence that climate change is having important ecological impacts and illustrates how the impacts can be both positive and negative.

Turning to relationships between species and site and landscape characteristics, there are more significant relationships than you would expect by chance indicating the potential for land use and management decisions to influence climate change resilience. This is encouraging in that it shows the potential for adaptation by manipulating land use and management to reduce the adverse impacts of climate change. The results are however complex and in some cases the signals are mixed. This is not unexpected given the number of potential relationships between driving and response variables and the wide range of species, habitats and landscapes encompassed by the analysis. Further analysis will be necessary to get a better understanding, including a detailed assessment of differences between different species as most of the analyses here deal with species groupings. Nevertheless, the present study has delivered some potentially important results.

The clearest result was that species typical of relatively cool climates have declined less where there is a large area of semi-natural habitat. This was true of both butterflies and birds and indicates that maintaining a sufficient area of habitat is a necessary starting point for climate change adaptation. It emphasises the ongoing importance of protecting and creating semi-natural habitat – the mainstay of conservation over many decades: climate change makes this more, not less important.

The abundance and interannual variability of populations of butterflies and birds was influenced by the area of particular habitats. Some of these results are not surprising, for example bird density is higher, and interannual variability lower, in areas with high woodland cover and the opposite where arable land predominates. Others are more interesting. The observed beneficial effects of arable land on butterfly populations for example presumably reflects the importance of hedgerows and other field margin habitats and is a reminder of the importance of the agricultural environment for some aspects of biodiversity. Areas with a relatively high proportion of urban land cover had relatively low interannual variability in populations of both groups, implying greater resilience to climatic fluctuations. We do not know the reason for this, although we may speculate on factors which may be important such as the supplementary feeding of garden birds and watering of gardens in dry summers or it could simply be that more climate sensitive species have already been lost from these places. The role of urban and suburban habitats needs to be looked at more closely in the context of climate change adaptation.

Habitat and landscape heterogeneity is an issue which is of considerable current interest for climate change adaptation of conservation. Heterogeneity has a number of aspects. Variation in topography provides a greater variety of microclimates (e.g. north facing slopes are cooler than south facing slopes) and increases the chances of suitable conditions being maintained at a small scale, despite climate change. Heterogeneity in vegetation structures similar provides a diversity of microclimates and potential niches. Different habitats can have a similar effect, for example woodland edge may provide shade to grassland species and also increases the chances of alternative food sources. Different soils and catchment characteristics will create a diversity of soil moisture conditions which may buffer species from the effects of drier summers and wetter winters, which are expected from climate change projections for the UK. The results show some evidence of the beneficial effects of heterogeneity: a diversity of habitats at both site and landscape scale was associated with greater stability of butterfly populations. There was however little evidence of heterogeneity effects on bird populations and few topographical effects on butterflies, contrary to some earlier research. Much may depend on individual species' habitat requirements and more detailed study may reveal clearer signals.

The role of ecological networks and particularly connectivity between sites, is a high priority issue at the moment. Greater connectivity of habitat patches should allow mobile species to redistribute to cooler places during warm conditions. It should also allow the functioning of metapopulations in which populations in adjoining patches can interchange individuals. This project did find significant effects of habitat configuration on population density and stability, although results were mixed and highly contingent on the configuration metric tested. Greater connectivity might be expected to aid recovery from an extreme event such as a drought. However, this project did not find consistent relationships across species for the sensitivity or recovery of populations from drought events. More detailed investigation may well reveal strong relationships between some species populations and some aspects of connectivity of habitats. It is does however sound a cautionary note about making generalisations about the benefits of connectivity.

Application and next steps

This work is part of a process of developing the evidence base to make sure that ecological networks are developed in ways that promote their resilience to climate change and thereby ensure their long-term value.

Ecological networks and the relationship between protected sites and the wider landscape are important issues for conservation and land management and are a priority in England at the present time with the establishment of Nature Improvement Areas (NIA). Climate change is also high on the agenda with a National Adaptation Programme (NAP) being developed for publication in 2013. Another important dimension to this is the support for agrienvironment schemes provided by the Rural Development Programme for England under the Common Agriculture Policy, of which climate change adaptation is an objective. In recent years, the largest source of funding for environmental management and habitat creation over much of England has been the Environmental Stewardship Schemes. Under the Higher Level Scheme in particular there is considerable scope to target resources to the places and options which are likely to deliver most benefit and we are working to factor climate change adaptation into the decision making process of farmers and land management advisors.

The finding that species typical of cooler climates have survived better in areas where semi-natural habitat predominates, reinforces the ongoing importance of protected areas and support for maintaining extensive land management systems. One of the basic tenets of climate change adaptation has been to reduce other pressures on species and this supports that principle.

Another implication of this finding is that the creation of semi-natural habitat will be beneficial to maintaining biodiversity in future climates – assuming the habitat produced is of the necessary quality. But where is it best to target habitat creation? Should existing areas of semi-natural habitat be expanded (larger patches) or should new patches be created to increase the heterogeneity of the landscape or connectivity between patches be maximised? This study provides evidence that these decisions do matter, but does not provide easy generalisations. Local knowledge, expertise and a clear understanding of the objectives for habitat creation in a particular place will be essential to making the best decision. Further research is, however, important to develop a better understanding to guide decision making.

There are a number of immediate priorities for follow-up research on these datasets. In particular species- specific analyses will help to identify more clearly which factors matter most to which species and to allow contrasts between different functional types. This will in turn allow more habitat-specific understanding. We expect that this will allow a better understanding of the relative merits of patch size, heterogeneity and connectivity in different contexts. There are also good opportunities to use a similar approach to investigate whether agri-environment scheme options have increased aspects of population resilience. Another area which requires more work is the role that condition of sites plays in determining population resilience to climate variables, we would expect a site in ‘favourable’ condition to support larger and therefore more resilient populations, but this is as yet untested.

A fundamental limitation of the present study is its focus on birds and butterflies. They were selected for analysis because of the quality of the data sets available, however, caution needs to be exercised in extrapolating the results from these groups more widely. In particular both birds and butterflies are relatively mobile groups of species. Future work will need to investigate the relevance of the findings to other groups.

Another issue which will require a different approach, is that large scale analyses of the sort reported here, do not lend themselves to testing the importance of small scale variation, for example in sward height and soil moisture. Much site scale heterogeneity cannot be adequately assessed by national scale datasets and will require a more targeted follow up in specific locations.

The establishment of the NIAs provides an opportunity to test whether the enhancements they bring have an impact on the resilience of populations. Building in appropriate monitoring from the start and identifying appropriate control areas would allow the opportunity to test some of these ideas in a rigorous experimental way.

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Testing the effectiveness of climate change adaptation principles for biodiversity conservation

Contract report for Natural England

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General introduction, aims and hypotheses[1,3]

1.1 Climate change and biodiversity loss

Biodiversity loss is one of the most serious environmental threats facing the world today and is inextricably linked with climate change. Following the failure by 2010 to halt biodiversity loss in Europe and significantly reduce the global rate of biodiversity loss, international agreement was reached at the CBD's COP-10 in Nagoya in October of that year on a new 2050 vision for biodiversity conservation, alongside a strategic plan for 2011-2020. The strategic plan is organised around five headline goals, with 20 specific targets to be achieved by 2020. Target 15 is of particular relevance to this study: *"By 2020, ecosystem resilience and the contribution of biodiversity to carbon stocks has been enhanced, through conservation and restoration, including restoration of at least 15 per cent of degraded ecosystems, thereby contributing to climate change mitigation and adaptation and to combating desertification".*

Also in 2010, a new European target to *"halt the loss of biodiversity and ecosystem services in the EU by 2020 and restore them insofar as possible, and step up the EU's contribution to averting global biodiversity loss"* was agreed. The accompanying biodiversity strategy will be published in May 2011 and will cite climate change (along with pollution) as a key pressure.

The UK has the opportunity to show leadership on the international stage, both through its responses to CBD's strategic plan and its actions to conserve biodiversity at home - where it faces some significant challenges. In England, the new England Biodiversity Strategy, to be published this year (2011), will be framed in the context of the five headline goals of CDB's strategic plan. Its 'vision' (which will run to 2060) is likely to include reference to the restoration of England's ecosystems to ensure their resilience to change, whilst its 'mission' (which will run to 2020) is likely to highlight the establishment of a resilient and coherent ecological network.

The Natural Environment White Paper is the main vehicle for setting out government's vision for the natural environment for the next 50 years. Biodiversity is central to this vision and it is, therefore, essential that the new EBS is guided by and consistent with the White Paper. Key elements include CBD's strategic plan, the EU 2020 target and other sector/cross-sector policy issues, and the major actions needed to deliver the recommendations made in *Making Space for Nature* (Lawton *et al*., 2010).

Lawton stresses the need for a more integrated, larger-scale approach to biodiversity conservation. The overarching aim is for ecological networks to deliver a natural environment where *"biodiversity is enhanced and the diversity, functioning and resilience of ecosystems re-established in a network of spaces for nature that can sustain these levels into the future, even given continuing environmental change and human pressures".* It supports the call to 'rebuild nature' through:

- Improving the quality of existing wildlife habitat
- Increasing the size of existing habitat patches
- Enhancing the connections between habitat patches
- Creating new habitat
- Reducing pressures on biodiversity and ecosystems by buffering protected areas and improving the wider environment.

Lawton recognises that the achievement of a coherent and resilient ecological network throughout England will require a number of inter-related approaches, including the establishment of Ecological Restoration Zones (ERZs) as ‘flagship’ means of engaging the Big Society in large scale restoration actions at local and national levels.

1.2 Climate change adaptation principles for biodiversity

A combination of climate change and other drivers of change threaten many species and habitats, and will have potentially serious consequences for the delivery of ecosystem services that are the cornerstone of human existence and well-being. There is, therefore, an urgent need to identify possible policy and practical responses to observed and projected climate change impacts on biodiversity in order to avoid the degradation and loss of natural ecosystems and their species.

Heller and Zaveleta (2009) reviewed 112 papers published in peer-reviewed journals and books over a period of 22 years, and from 524 records listed 113 recommendations. These were ranked according to their frequency of citation (increasing connectivity was the highest ranking measure) and synthesised with respect to delivery pathways (for example, landscape-scale and site-based). The need for improved institutional coordination, broader spatial and temporal perspectives, integration of climate change scenarios into conservation planning and action, and greater effort to mitigate other threats was recognised; major gaps were also identified. These include the need for principles and practical guidance to facilitate the integration of adaptation into existing policies and programmes.

In the UK, in a report for Defra in relation to the England Biodiversity Strategy (EBS), Mitchell *et al.* (2007) reviewed the impacts (direct and indirect) of climate change on biodiversity within each of the five EBS sectors and identified four generic principles and six implementation measures for adaptation. The principles are aimed at reducing sensitivity and managing for uncertainty, and include: reducing direct impacts; reducing indirect impacts; increasing resilience; and accommodating change. The implementation measures include:

- Direct management to reduce impacts
- Promote dispersal of species (for example, corridors, stepping stones, quality of matrix)
- Increase available habitat
- Promote conditions for natural ecosystem functioning
- Optimise responses to climate change for biodiversity
- Continue to reduce pressures not linked to climate change.

In a guidance document published by Defra on behalf of the UK Biodiversity Partnership, Hopkins *et al.* (Hopkins *et al*., 2007) describe six guiding principles on how to reduce the impacts of climate change on biodiversity and adapt existing plans and projects in the light of climate change:

- Conserve existing biodiversity
- Reduce sources of harm not linked to climate
- Develop ecologically resilient and varied landscapes
- Establish ecological networks through habitat protection, restoration and creation
- Make sound decisions based on analysis
- Integrate adaptation and mitigation measures into conservation management, planning and practice.

The guidance is aimed at conservation practitioners and does not make recommendations for policy change (although it acknowledges the need to review and strengthen policy). Building on this guidance, a report published by Defra on behalf of the EBS (Smithers *et al.*,

2008) sets out adaptation principles for those responsible for planning and delivering actions across all sectors identified in the EBS. It draws extensively on peer-reviewed and grey literature, as well as on ideas from individuals and organisations in the UK and elsewhere.

A parallel study for the Bern Convention's 'Group of Experts on Biodiversity and Climate Change' (Harley & Hodgson, 2008) provided an extensive and systematic review of published international, European and national (EU Member State) guidance on adaptation to climate change, with a focus on biodiversity and its conservation. The findings were synthesised and seven overarching adaptation principles identified:

- *Take action now* - uncertainties surrounding the precise nature of future climate change and its impacts on biodiversity should not delay practical conservation action.
- *Maintain and increase ecosystem resilience* - the ability of ecosystems to absorb and recover from change should be enhanced to enable the widest range of biodiversity to survive and adapt to climate change.
- *Accommodate the impacts of climate change* - an increasingly dynamic and innovative approach to biodiversity conservation is needed to address the impacts of both gradual changes in climate and extreme weather events.
- *Facilitate knowledge transfer and action between partners, sectors and countries* - successful adaptation requires biodiversity conservation to be integrated with other land and water management activities across relevant sectors and the wider ecosystem service benefits to be recognised.
- *Develop the knowledge/evidence base and plan strategically* - the best available evidence should be used to make decisions that will allow biodiversity to adapt in an uncertain future.
- *Use adaptive conservation management* - effective conservation in a changing climate requires continual evaluation and review to progressively increase resilience and reduce sensitivity.
- *Undertake monitoring and identify indicators* - monitoring using robust indicators will provide essential knowledge of impacts, help shape adaptive management and measure outcomes.

These principles were derived from pre-existing guidance, are supported by more detailed measures, and can help inform the development of adaptation strategies and actions to conserve species, habitats and ecosystems and the services that they provide. The principles have also been used in the development of adaptation indicators for biodiversity (Harley & van Minnen, 2009 & 2010). They are linked to a range of generic conservation activities that relate to policies, measures and actions from which both process-based indicators (policies/measures) and outcome-based indicators (actions) have been derived.

1. 3 Use of empirical research to verify adaptation principles

A number of common themes have emerged from the body of international literature and range of guidance principles on the adaptation of biodiversity and conservation strategies to climate change. These include both site-based and landscape-scale approaches to increasing connectivity of habitat networks, buffering and enlarging protected areas, and conserving topographic and habitat heterogeneity. Conceptual concerns have been expressed about the efficacy of some of these (for example, Hodgson *et al.*, 2009 & 2011), argue that the importance of connectivity is being over-emphasized) and empirical evidence is required to test and evaluate their effectiveness.

In the course of this project, it was not feasible to examine the full range of published principles or indeed all of those of specific relevance to England/ the UK. The priority was, therefore, to focus on those principles that are most relevant to the emergent themes listed above: *Develop ecologically resilient and varied landscapes - conserve and enhance local variation within sites and habitats* (3a) and *Establish ecological networks through habitat protection, restoration and creation* (4) (Hopkins *et al.*, 2007). These principles are also reflected in Smithers *et al.* (2008) and Harley & Hodgson (2008): *Maintain and increase ecological resilience - conserve the range and ecological variability of habitats and species* and *Accommodate the impacts of climate change - establish ecological networks through habitat restoration and creation*.

We analysed long-term monitoring data for a range of bird and butterfly species in the UK to determine whether site and landscape attributes influenced population responses to climate change and extreme climatic events. We also tested whether there was evidence for changes in community composition and whether these were influenced by site and landscape attributes. In doing this we used year-to-year variations in weather as well as long-term climate patterns, both as an indicator of broader climate sensitivity and to provide an insight into the effects of extreme events.

The main response variables used in the analyses were as follows:

1. Indices of mean population density (calculated from abundance indices standardised for areas sampled; **Parts 1-4**).
2. Population resilience to interannual variability in climate. We derived three variables (illustrated in Figure 1): (a) p*opulation sensitivity*- the extent of perturbation of species populations from a long term trajectory after an extreme climatic event (for example, a drought year, an exceptionally cold winter etc.), (b) *recovery time*- the rate of recovery of species populations after an extreme climatic event, and (c) *stability*- the lack of variability in long term population time series (i.e. the inverse of inter-annual variability). Understanding the effects of site- and landscape- attributes on population sensitivity may allow the detrimental effects of extreme climate events to be reduced, whilst analyses of effects on recovery time will inform the potential for such attributes to facilitate long-term persistence in the face of climate change. In addition, the three measures, population sensitivity, recovery time and stability are related, with stability a summary measure at least partly derived from the previous two mechanisms (Fig. 1; **Parts 1-4**).
3. Trends in the total density of cold- and warm- associated species assemblages under a period of incremental climate change over three decades (**Part 5**).

Box 1

Definitions

***Resilience*:** The amount of disturbance a system can absorb and still remain in the same state or domain of attraction (Holling, 1973); or, alternatively, the ability of a system to return to a pre-disturbed state (Pimm, 1984).

***Population sensitivity*:** the extent of perturbation of species populations from a long term trajectory after an extreme climatic event (for example, a drought year, an exceptionally cold winter etc.)

R*ecovery time*: the rate of recovery of species populations after an extreme climatic event, and

***Stability*:** the lack of variability in long term population time series (i.e. the inverse of inter-annual variability).

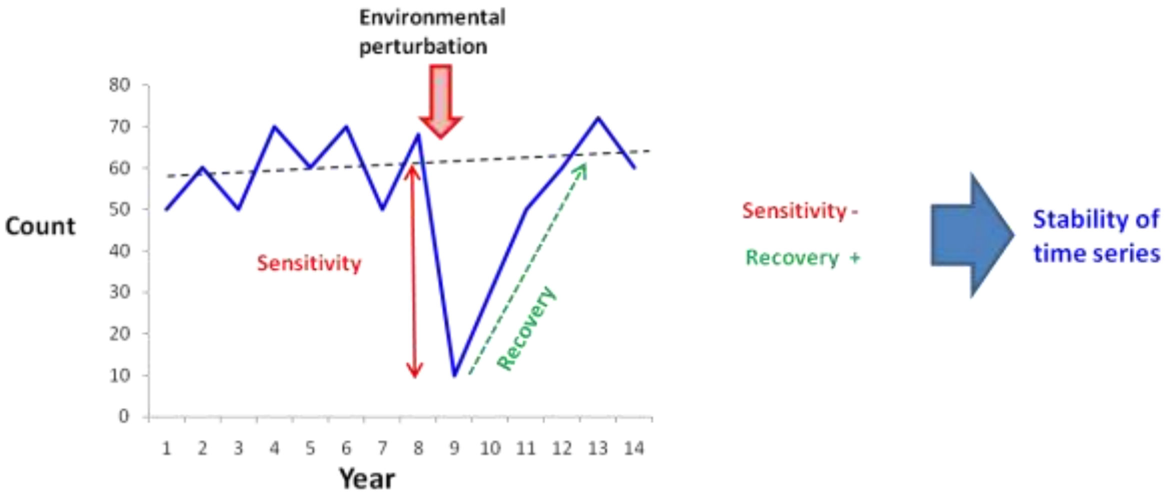

Figure 1: Investigating the resilience of populations through population sensitivity and recovery from extreme climatic events. These two measures influence the stability of population time series (measured as the inverse of the inter-annual variability).

These response variables were selected because larger populations have lower extinction risk, whilst smaller populations are more vulnerable to demographic and environmental stochasticity driving them to local extinction (Pimm *et al*., 1988, Thomas *et al*., 2011). Similarly, there is theoretical (Lande, 1993, Inchausti and Halley, 2003) and empirical evidence (Karr, 1982, Pimm *et al*., 1988) that more variable (less stable) populations also suffer greater extinction risk. The IUCN Red List criteria for classifying species' extinction risk include both small population size and the observation of extreme population fluctuations (IUCN, 2001, Mace *et al*., 2008).

Whilst we present 'population density' and resilience characteristics separately to aid the interpretation of results, it should be borne in mind that they are not truly independent variables – larger populations can promote increased resilience. It should also be noted that we are using the term *resilience* in a restricted sense but it has a much wider usage in the scientific literature. There are two main senses in which the term is used: 1) the amount of disturbance a system can absorb and still remain in the same state or domain of attraction (Holling, 1973); 2) the ability of a system to return to a pre-disturbed state (Pimm, 1984). These are both systems-level definitions, but in practice it is difficult to measure a whole system simultaneously; individual populations are components of the system which can be feasibly measured, for example, through long-term species monitoring schemes.

At present, knowledge of the factors promoting population resilience is limited. In addition to local factors such as site habitat heterogeneity, a landscape-scale perspective may often be necessary. For example, the diversity of broad habitat types at distances up to 5km around monitoring sites has been found to affect the stability of butterfly populations over time (Oliver *et al*., 2010). However, more work is required to understand the exact landscape features that promote population resilience. For example, reduced sensitivity to drought events, which are projected to increase in frequency in the UK with climate change, might be facilitated by the existence of cooler, damper habitat types or topographies. In contrast, the recovery of populations that have declined after drought years might be facilitated by an increased connectivity of the habitat types used in non-drought years. In the longer term, differences between species in their resilience to climatic variability and incremental climate change may ultimately lead to changes in species composition. Such community changes may potentially be influenced by both site and landscape attributes.

Long-term monitoring data are an essential resource to test these questions. Butterflies and birds are ideal study organisms as they are sensitive to environmental change and are commonly used as indicators of ecosystem health (Gregory *et al*., 2005, Van Swaay *et al*., 2010), whilst also providing direct cultural and aesthetic ecosystem services. These two taxonomic groups have among the best and longest running monitoring schemes of any UK taxa and offer the widest geographic scope for considering these questions. Furthermore, within and between these taxa there are a wide range of contrasts in life history offering the potential to assess the functional basis of apparent patterns. On this basis, these datasets offer one of the best opportunities to provide evidence to assess climate change adaptation principles. In this report, we have compiled the best available datasets and analysed them to test whether they provide evidence to support climate change adaptation principles. We critically assess our results for the associated certainty of the outcome. In some cases, the uncertainty in our results may affect policy implications.

We address the following general questions and specific hypotheses:

Question 1. Do site-scale attributes enhance resilience of species populations and ultimately community composition?

Hypothesis 1- Local (site) variation in habitat, soil type and topography are positively correlated with the mean density (Hypothesis 1a) and resilience (H1b) of populations as measured during recent periods of relative climatic variability and incremental change.

H2- Area of key habitat types for species' will be positively correlated with the mean density (H2a) and resilience (H2b) of populations.

H3- Under incremental climate warming, declines in cold-loving species assemblages will be least marked in sites with a broad diversity of habitat, soil type and topography (because a broad microclimatic range may allow species to persist as viable populations for longer; H3a). In contrast, species assemblages of warmth-loving species (which are expected to increase under incremental climate change) will increase most in sites which are more heterogeneous (a greater range of habitats and resources are likely to be suitable) and with more semi-natural habitat available (allowing greater potential for population growth; H3b).

Q2. Do landscape-scale attributes enhance resilience of species populations and ultimately community composition?

H4- Landscape-scale variation in habitat, soil type and topography are positively correlated with the mean density (H4a) and resilience (H4b) of populations of populations as measured during recent periods of relative climatic variability and incremental change.

H5- The area of species' key habitat types in the local landscape will be positively correlated with the mean density (H5a) and resilience (H5b) of populations.

H6- Ecological networks defined by the connectivity of species' key habitats also increase the mean density (H6a) and resilience (H6b) of populations as measured during recent periods of relative climatic variability and incremental change.

Q3. Are site or landscape factors more important and what life history characteristics interact with population resilience and site/ landscape attributes?

The relative importance of different site and landscape attributes for population robustness will vary between taxa and functional types of organisms. More specifically:

H7- Area and connectivity of key habitat types in landscapes will be more important for specialist rather than generalist species.

H8- For each species, the key site and landscape attributes that reduce sensitivity to extreme climatic events may be different to those that promote recovery from such events. More specifically, sensitivity may be reduced by site and landscape heterogeneity (‘environmental buffering’), whilst recovery may be better facilitated by habitat connectivity (‘ecological coherence’).

These hypotheses are addressed in five empirical chapters (Parts 1-5). Each chapter deals with a different set of hypotheses and uses different analytical techniques. Results are synthesised in a final chapter, summarising evidence for and against the various hypotheses.

General methodology[1]

2.1 Bird and butterfly population monitoring surveys

For this project, we used bird and butterfly population time-series data from the UK Butterfly Monitoring Scheme (UKBMS) and the BTO/JNCC/RSPB Breeding Bird Survey (BBS) and Common Bird Census (CBC). The datasets were selected as they are the most comprehensive population monitoring data across space and time available for Great Britain.

The UKBMS scheme, which has been running since 1976, comprises fixed 5m wide belt transect routes between 1.5km and 3km in length (Pollard and Yates, 1993). These transects are walked up to 26 weeks of the year throughout the main flight period of UK butterflies. An estimate of the annual abundance of each butterfly species is calculated at each site allowing for missing counts (Rothery and Roy, 2001). An index of density can be calculated by dividing the annual abundance index by the length of the transect route. The sites were subjectively chosen but are distributed across the country and conservation sites make up a relatively larger proportion of the sites. In this study, we calculated site and landscape attribute metrics for all UKBMS sites in Britain (n = 1387). However, we restricted our population analyses to a smaller subset of sites which met minimum criteria for data quality (see relevant analyses for details).

The BBS comprises a random sample, stratified by observer density, of 1km squares, each containing two 1km transects from which birds are counted twice per spring (Risely *et al*., 2010). The maximum count from the two visits was used as the index of annual population size of each bird species. Because all transect routes are the same length, no further standardisation is required to produce a density index. The BBS survey has run from 1995. We calculated site and landscape attribute metrics for all BBS sites in Britain (n = 4112).

We also used data from a different bird survey, the CBC. This survey ran from 1965 – 2000 and was a predecessor of the BBS. Although these data do not include the most recent years of warming, being a longer time-series than the BBS data for birds, they do cover periods of significant climate variability, including both severe winters and summer droughts and are subject to less inter-annual stochasticity at the site level than BBS data because of more thorough sampling at each location each year. Although these match the timing of our land cover data, which is from the end of the CBC period, less closely than the other surveys, we included them because data quality (for our purposes) is higher, so they provide a valuable additional test of our hypotheses. The survey method involved 10 visits to each woodland site between March and July. The entire survey area of a site was walked, mapping all encounters with all individual birds and recording their behaviour. Data from all annual survey visits were then collated to reveal the number of breeding territories occupied by each species, and this number of territories provided the annual datum for a species at a site. A density index was then calculated by dividing this abundance index by the total area of the study site. In this study we calculated site and landscape attribute metrics for all woodland CBC sites in Britain (n = 1184).

2.2 Collating site and landscape attribute data

We calculated a number of site and landscape attributes comprising land cover type, topography, soil type and soil moisture. These variables were selected because they present ways of measuring site and landscape attributes that are relevant to the UK Biodiversity Partnership adaptation principles (Hopkins *et al*., 2007) (Table 1). In this report, 'site-attributes' refer to the character of the local landscape 0.5km radius around the central point of a monitoring site. This allows a standardised definition of 'site' between monitoring schemes where transects are different lengths and configurations and the habitat units covered vary in size. 'Landscape-attributes' refer to areas of greater radius around sites (i.e. 2, 5 and 10km radii). Hence, the definition or site and landscape is not truly a dichotomy and in our statistical analyses we treat spatial scale as a continuous measure that reflects the UK's landscape. Each class of attributes is detailed below. Correlations between all the attributes can be found in Appendix P1B Table S2.

Habitat area: The 26 classes of land cover from the CEH LCM2000 land cover map (Fuller *et al*., 2002) were aggregated into 13 distinct broad habitat categories (Table 2). This aggregation was performed to reduce the total number of land cover classes into a manageable amount and also because the LCM2000 map does not always provide accurate distinctions between grassland types (for example, calcareous versus neutral versus improved grassland types). Because calcareous grassland is very important for many British butterflies we obtained three extra grassland data layers from the Natural England GIS Digital Boundary Datasets (http://www.gis.naturalengland.org.uk/pubs/gis/GIS_register.asp). These were lowland calcareous grasslands, lowland meadows and 'network grasslands'. These habitat types were chosen because they might be important semi-natural grassland types for birds and butterflies. Network grasslands are defined as the combined area of a number of semi-natural grassland types (rough calcareous grassland, rough acid grassland and rough neutral grassland) with an added 0.5km buffer to represent the movement potential of a generic focal species with limited dispersal ability (Catchpole, 2006, Catchpole, 2007).

The total area of each of the 13 broad habitat types was calculated in landscape buffers of 0.5, 2, 5 and 10km radius around all bird and butterfly monitoring sites.

Table 1: The two key UKBP (Hopkins *et al*., 2007) adaptation principles tested in this report and the site and landscape attributes used to measure these aspects. Further details of the attributes can be found in the main text.

Establish ecological networks	**Conserve and enhance variation within sites and landscapes**
Habitat area – 12 broad types	Habitat heterogeneity
Habitat configuration – 3 metrics	Topographic heterogeneity
	Soil heterogeneity
	Soil moisture

Table 2: Land cover categories used in the analysis with codes used in later results tables.

Broad habitat	**Code**	**Aggregated LCM 2000 categories**	**LCM 2000 categories**
Arable	A	Arable cereals, arable horticulture, non-rotational horticulture	4.1, 4.2, 4.3
Bare ground and quarries	BgRo	Inland bareground	16.1
Bracken	Br		9.1
Broadleaved woodland	BW		1.1
Coastal	C	Supra-littoral rock and sediment, littoral rock and sediment, saltmarsh	18.1, 19.1, 20.1, 21.1, 21.2
Coniferous woodland	CW		2.1
Fen	F	Fen, bog, marsh, swamp	12.1, 11.1
Grassland	G	Improved grassland, setaside grass, neutral grass, calcareous grass, acid grass	5.1, 5.2, 6.1, 7.1, 8.1
Heath	H	Dwarf shrub heath, open dwarf shrub heath	10.2, 10.2
Inland water	R		13.1
Montane	M		15.1
Urban/ suburban garden	UG	continuous urban, suburban/ rural developed	17.1, 17.2
Sea/ estuary	S	sea or estuary	22.1

Habitat configuration: For each of the 13 broad land cover types (hereon 'broad habitat' types) detailed above we also calculated metrics on the configuration of patches in landscapes around all monitoring sites. Three metrics were selected after a review of a wide range of available measures provided by the software Fragstats (McGarigal *et al*., 2002); those chosen are easily interpretable and measure complementary aspects of landscape composition. The three configuration metrics calculated at scales of 0.5, 2, 5 and 10km radii around sites were: 1) number of patches (converted to patch density when results were compared across spatial scales), 2) mean Euclidean nearest neighbour distance, based on shortest edge-edge distances, and 3) mean shape index, based on a standardised perimeter-area ratio, where actual perimeter length is considered relative to the minimum possible perimeter length for a given habitat area, i.e. larger values indicate more 'edgy' habitat patches. In later tables they are indicated by prefixes of 'NP_', 'ED_' and 'SHP_' respectively. For example, the mean Euclidean distance between patches of broadleaved woodland in a landscape buffer would be coded in tables as 'ED_BW'.

Habitat heterogeneity: For each site we calculated a Shannon Index of all broad habitat types excluding sea ($-\Sigma p.\log_n(p)$ where p is the proportional representation of each habitat type). We also calculated a Shannon Index using only semi-natural habitat types (i.e. excluding urban garden and arable habitats).

Topographic heterogeneity: Using a 50m resolution digital elevation map of Britain (DEM; Morris and Flavin, 1990) we calculated the mean slope, aspect and altitude of the landscape at 0.5, 2, 5 and 10km radius around all bird and butterfly monitoring sites. We also calculated the standard deviation of mean slope, aspect and altitude values within landscape buffers to give a measure of topographic heterogeneity. Altitude values in landscape buffers were obtained directly from the DEM using ArcGIS v.9.3.1. Slope and topographic aspect values were calculated using the spatial analyst toolbox. Slope values ranged from 0 to 90˚. Aspect values ranged from 0 to 360˚. Because these aspect values are circular the raw values were converted into an ‘eastness’ and a ‘northness’ vector using the formulas below:

$$\text{Eastness} = \sin((\text{Aspect} \times \pi)/180)$$

$$\text{Northness} = \cos((\text{Aspect} \times \pi)/180)$$

The converted values range from -1 (due East or North) to 1 (due West or South).

Soil heterogeneity: British soils were previously classified by physical properties into 29 hydrological classes at 1km resolution (HOST database; Boorman *et al*., 1995). We used ArcGIS 9.3.1 to calculate the dominant soil type in landscape buffers of 0.5, 2, 5 and 10km radius around all bird and butterfly monitoring sites. A Shannon Index was used to calculate the heterogeneity of hydrological soil type in each landscape buffer.

Soil moisture: We used the outputs from a recently developed hydrological CEH dynamic grid-based model which can estimate soil moisture deficit at daily intervals at 1km resolution (Bell *et al*., 2009). The daily estimates were used to calculate minimum, mean and maximum seasonal values. In this study, we focussed on maximum soil moisture deficit (i.e. drought) in spring (March-May) and summer (June-August) for the years 1986-2000. For each season, in each year, the mean soil deficit value was calculated for landscape buffers around sites at scales of 0.5, 2, 5 and 10km radius.

Part 1: The ability of different site and landscape attributes to explain population density and inter-annual variability in birds and butterflies[1]

3.1 Introduction

In this analysis, we consider how site and landscape attributes affect the mean density and inter-annual population variability of bird and butterfly populations. Both density and inter-annual variability are thought to be important indicators of the probability of persistence of species populations. Larger populations are known to suffer from lower extinction risk, whilst smaller populations are more vulnerable to both demographic and environmental stochasticity driving them to local extinction (Pimm *et al*., 1988, Thomas *et al*., 2011). In addition, there is both theoretical (Lande, 1993, Inchausti and Halley, 2003) and empirical evidence (Karr, 1982, Pimm *et al*., 1988) that populations that are more variable over time also suffer greater extinction risk. Hence, a primary aim of conservation is to produce large and resilient species populations that are buffered from environmental change and therefore more likely to persist. For example, the IUCN Red List criteria for classifying species' extinction risk include both small population size and the observation of extreme population fluctuations (IUCN, 2001, Mace *et al*., 2008).

Understanding the site and landscape attributes that promote larger, more stable populations provides the opportunity to manipulate landscape characteristics to create populations that are more resilient to environmental change. In this analysis, we consider the association of 81 landscape attributes with population density and inter-annual variability of butterflies and birds. We use data from the UKBMS, BBS and CBC population monitoring schemes. In this analysis, we focussed on lowland sites (<300m altitude), where the majority of monitoring sites occur, because associations with landscape variables at upland sites were expected to be qualitatively different, due to the potentially confounding effects of latitude and climate. For example, population density and inter-annual variability often show trends with latitude as do a range of landscape variables (Thomas *et al*., 1994). Upland sites in Scotland will tend to have very different land cover from lowland sites (for example, large expanses of grassland and fen/bog occur in upland areas), but also differ markedly in latitude and local climate. Therefore, including outlying upland sites in the analysis would potentially result in significant associations for land cover variables that simply reflect broad latitudinal patterns. This is less of a problem when focussing only on lowland sites because they span a smaller latitudinal (and climatic) gradient.

Due to the large number of landscape attributes and the number of spatial scales to be tested (landscape attributes were each calculated at 0.5, 2, 5 and 10km around sites), fitting multivariate models was not feasible (for example, each single landscape variable could be combined with up to 80 others, with each variable measured at any of four spatial scales). Therefore, we fitted univariate models and results should be interpreted with potential interactions between landscape attributes (and other unmeasured variables) in mind. Of course, the inability to infer causality is a perennial problem with all regression analyses. Even in multivariate analyses, strong associations with explanatory variables may occur, but unmeasured variables correlated with these (for example, habitat quality, presence of other species, climate, latitude etc.) might ultimately drive observed changes in response variables. Significant associations from regression analyses, therefore, should not be taken as proof of causality, but we can infer that landscape attributes with strong associations are potentially important determinants of population density and inter-annual variability and are thus good candidates for further investigation (for example, using controlled experimental manipulations).

Finally, we also considered the spatial scale at which each landscape attribute best explained population density and inter-annual variability. This should help to inform the most appropriate spatial scale for the manipulation of landscapes if this is appropriate. This analysis specifically addresses the following hypotheses, based on the UKBP adaptation principles (Hopkins *et al*., 2007; and numbered in the same order as in the General Introduction section):

- **Hypothesis 1-** Local (site) variation in habitat, soil type and topography are positively correlated with the mean density (Hypothesis 1a) and resilience (H1b) of populations as measured during recent periods of relative climatic variability and incremental change.
- **H2-** Area of key habitat types for species' will be positively correlated with the mean density (H2a) and resilience (H2b) of populations.
- **H4**- Landscape-scale variation in habitat, soil type and topography are positively correlated with the mean density (H4a) and resilience (H4b) of populations of populations as measured during recent periods of relative climatic variability and incremental change.
- **H5-** The area of species' key habitat types in the local landscape will be positively correlated with the mean density (H5a) and resilience (H5b) of populations.
- **H6-** Ecological networks defined by the connectivity of species' key habitats also increase the mean density (H6a) and resilience (H6b) of populations as measured during recent periods of relative climatic variability and incremental change.

3.2 Methods

We carried out a large number of univariate mixed model regressions relating site and landscape attributes to bird and butterfly population density or inter-annual population variability. Population time-series for birds from the BBS survey ran from 1994 to 2008. Therefore we used butterfly data from the UKBMS survey from the same period. This also matched well with the land cover data which was obtained from satellite imagery in the year 2000. As mentioned in the general methodology, we used data from the CBC bird survey (1965 – 2000). These data span a longer recording period than the BBS survey, even though they do not provide as good a match with the timing of our land cover data. However, changes in land cover in the 35 years pre-2000 are most likely to have been in finer landscape features such as hedgerows rather than the broad habitat categories we examined here, although some changes may have occurred, for example, in coniferous woodland cover.

We only analysed population time-series that had met a minimum criteria for data quality: each site had to be recorded for more than eight years and have less than 25% of the time series consisting of zero counts (McArdle *et al*., 1990, Thomas *et al*., 1994). Previous authors have also limited analysis to time-series with a minimum mean abundance (Lepš, 1993, Thomas *et al*., 1994). We chose not to do this because preliminary analyses showed that time-series with low abundance did not significantly contravene the assumptions of a linear relationship between log mean abundance and log variability (Appendix 1; Lepš, 1993). We limited our analyses to species that had at least 5 sites fulfilling the above criteria, because species with less than five sites had insufficient spatial replication to contribute useful data to the analysis. Hence, we analysed 48 butterfly species from 369 sites (mean = 127 ± 16.1 sites). These UKBMS sites were recorded for an average of 12.2 ± 0.01 years (range 9 -14). From the BBS survey for birds, we analysed 107 species from 1762 sites (mean = 360.0 ± 46.8 sites). These BBS sites were recorded for an average of 11.8 ± 0.004 years (range 9 -14). For the CBC bird survey, we analysed 56 species from 119 sites (mean = 48.5 ± 5.2 sites).These CBC sites were recorded for an average of 17.2 ± 0.07 years (range 9 to 36).

3.2.1 Calculating population density and inter-annual variability

Population data for each survey comprised an index of abundance for each year. For the UKBMS and CBC surveys, which had transects of different lengths, these were standardised to produce annual density indices (see General Methodology)**.** The BBS scheme had fixed transect lengths, so we simply used counts per 1km survey square. We calculated a mean annual population density as the mean for each site over all years surveyed. Mean population densities were then log transformed before analysis to improve normality.

To calculate the temporal variability of time-series we used the coefficient of variation (CV = standard deviation of annual abundance values / mean). However, as a measure of inter-annual variability CV suffers from a number of biases. Firstly, the length of time series can affect CV, with longer time series showing greater variability (Pimm and Redfearn, 1988, Curnutt *et al*., 1996, Cyr, 1997, Inchausti and Halley, 2003). Secondly, long term trends in abundance alter values of CV (Lepš, 1993). Finally, the mean abundance of time-series is often still related to CV (McArdle *et al*., 1990). Scaling the standard deviation of time-series by the mean (i.e. to calculate CV), accounts for a Power Law relationship between variability and mean abundance with a specific scaling exponent of 2 (i.e. variability = $\alpha.\text{mean}^2$) (Taylor, 1961). However, other values for the scaling exponent often occur in emiprical data (Hanski and Tiainen, 1989, Kilpatrick and Ives, 2003).

To account for these biases we can include the relevant parameters as covariates in our statistical models. This accounts for their effect and allows us to relate landscape variables to population inter-annual variability. Hence, in order to account for the first two biases described above, we included time series duration and the magnitude of the log-linear population trends as covariates. From visual inspection of our population time series, a log-linear trend captured much of the change in abundance with year. To test this more formally, we fitted a quadratic relationship between log abundance and year for every bird and butterfly population time series. There was evidence of significant curvature ($p < 0.05$) beyond a simple log-linear relationship for only 12.3% of UKBMS time-series ($n = 6073$), 12.2% of BBS time-series ($n = 41584$) and 25.4% of CBC time-series ($n = 2734$). In addition, for the cases where curvature is present, it is unlikely to show a systematic bias with regards to landscape structure. Finally, we accounted for the Power Law relationship between mean abundance and variability by logging the response variable (CV) and including log mean abundance as a covariate in our statistical models.

3.2.2 Statistical analysis

A. Multispecies analysis

We carried out a separate analysis for each survey, but all species from a survey were analysed together. For each survey, we carried out 81 mixed effects regressions relating population density to each of the landscape attributes listed in the general methodology section. The landscape attributes were calculated initially at 0.5km radius around sites. For specific habitat types, if there was no habitat in the landscape buffer around the site, then the total area was treated as zero. For configuration metrics, however, the site was treated as missing data, because the site gives no information of the configuration of that habitat type. In addition to a single fixed effect explanatory variable in each model (for example, total area of arable at 0.5km radius around each site), we included *Site* and *Species* as crossed random effects, to account for the non-independence of data recorded at the same site or recorded from the same species. It was not possible to include a random slope whereby the species were allowed individually different relationships with the explanatory variable due to a small sample size at the species level. The model formula is summarised below:

$$\check{N}_{ij} = \alpha + \beta LA_j + \text{species}_i + \text{site}_j \qquad [1]$$

Where $\check{N}$ is the mean annual abundance of $species_i$ at $site_j$, and LA is the landscape attribute value at $site_j$. The coefficient β gives the relationship between the landscape attribute and mean annual density of the 'average' butterfly or bird species. More specifically, each species contributes to the model in proportion to the number of sites occupied. This weighted average is appropriate because species with small sample sizes will give less reliable estimates of trends. The downside is that restricted species (which may also be ecologically different) are less represented. Further work might consider splitting analyses for wider countryside and more specialist species (if sufficient data is available to model them separately). However, in some cases modelling the response of the 'average' species is appropriate if, for example, an aim is to increase the density of butterflies for pollination services where we have no information on species-specific pollination ability.

Due to the large number of statistical tests carried out, we did not assess significance of individual tests using model p-values. Instead, we used a weight of evidence approach whereby we asked if the total number of tests with magnitudes of t-value > 2 was greater than expected by chance. With a large sample size per test as in this study, one would expect type 1 error rates of < 0.05 when $|t| = 2$, i.e. a 5% chance of wrongly rejecting the null hypothesis (Crawley, 1993). Hence, given the total number of tests, we calculated the expected number of tests with $|t| > 2$ versus the number actually observed. We compared these proportions using a proportion test to infer overall whether our landscape attributes measured at the 0.5km spatial scale could significantly explain population density. We repeated this process for each spatial scale (i.e. 2, 5 and 10km radius around sites).

To ascertain which landscape attributes were most important in explaining population density we ranked each attribute by the largest absolute t-value at any spatial scale. As mentioned above, a small number of landscape attributes will have $|t| > 2$ in the absence of any strong relationship. We therefore took a conservative approach and only treated a landscape attribute as having an important relationship if it had $| t | > 3$ at any spatial scale (which would be expected to give error rates of < 0.005). This produced a list of the most important landscape attributes ranked by their ability to explain population density. All the steps above were then repeated with log(CV) as the response variable. In this case, because we were interested in inter-annual population variability, we included time series duration, log mean abundance and the magnitude of the log-linear trend in abundance as additional covariates to control for these biases (see *Calculating population density and inter-annual variability* section above). The model formula is summarised below:

$$\check{N}_{ij} = \alpha + \beta LA_j + tsDur_{ij} + tsMeanAb_{ij} + tsTrend_{ij} + species_i + site_j \qquad [2]$$

Where $\check{N}$ is the mean annual abundance of $species_i$ at $site_j$, and LA is the landscape attribute value at $site_j$. The control variables $tsDur_{ij}$, $tsMeanAb_{ij}$ and $tsTrend_{ij}$ relate to time series duration, log mean abundance and the magnitude of the log-linear trend in abundance. The coefficient β gives the relationship between the landscape attribute and inter-annual variability of the 'average' butterfly or bird species.

To consider at which spatial scale landscape attributes best predicted population density and inter-annual variability we used the AIC (Aikaike Information Criterion; Akaike, 1974). To compare goodness of fit using AIC it is necessary that models are based on the same size of dataset to be comparable. However, for many landscape attributes (in particular area and configuration of broad habitat types), more sites are available for analysis at larger spatial scales, as these are more likely to contain the patches of the focal land cover type. Therefore, first, we repeated the above analyses for each landscape attribute, constraining the number of sites to the number available for analysis at the smallest spatial scale. AIC values were then used to rank models fitted at the different spatial scales. Landscape attributes measured at the site level were often the best predictor (see Results). Therefore, in order to compare which landscape scale (2, 5 or 10km radius) best predicted population density and inter-annual variability, in a second analysis, we excluded results from the analyses of attributes at 0.5km radius (site level) and picked the best landscape attributes from landscape scales of 2, 5 and 10km radii.

B. Single species analysis

In practice, analysing individual species separately would be a large undertaking, and for rare and localised species there will often be insufficient data from monitored sites to achieve this. However, to demonstrate the application of our methods to single species, we analyse one example species- the Speckled Wood butterfly, *Pararge aegeria*. This species was chosen because it is a common widespread species with well-known habitat associations (Thomas and Lewington, 2010).

3.3 Results and discussion

In this results section, we first summarise evidence for the overall effects of site and landscape attributes on butterfly and bird density and population inter-annual variability. We then address each of the hypotheses described in the introduction, with a separate section for each hypothesis.

3.3.1 Overall effects of landscape metrics on bird and butterfly density

There was strong evidence that the landscape attributes that we tested were significantly associated with population density for both butterflies and birds. The total number of slopes across all tests where |t| > 2 in all cases exceeded that expected by chance from the number of tests conducted (Table 1). Differences were more significant at larger spatial scales (generally 2km and above), probably because of the smaller sample sizes and ranges of variation for tests at small spatial scales. Landscape variables were significantly associated with population density at two or more spatial scales for all groups tested, with the exception of the CBC survey data, for which there was no overall significant association between landscape structure and population density (Table 1).The most important metrics for explaining density in birds and butterflies are discussed in more detail in the appropriate hypotheses sections below.

The relationships between each landscape attribute and density can be found in Appendix P1B Table S3 for butterflies, Appendix P1B Table S4 for birds from the BBS scheme and Appendix P1B Table S5 for birds from the CBC scheme. For all surveys, a table of landscape attributes ranked by the frequency with which they have a relationship with density of | t |> 2 can be found in Appendix P1B Table S6.

For butterflies, a summary of the most important landscape attributes for explaining density (where | t | > 3) is provided in Table 2 below. These results indicate the degree of association between various landscape variables and the density of the ‘average’ butterfly species (an ‘average’ to which each species contributes in proportion to the total number of sites occupies as explained in the Methods section). For birds in the BBS scheme, a number of landscape variables were strongly associated with bird density. A summary of the most important landscape attributes for explaining bird density (where | t | > 3) from analysis of the BBS survey can be found in Table 3.

The landscape variables tested were poor predictors of bird density from the CBC scheme. No landscape attributes has strong relationships with bird density measured from the CBC survey (i.e. with | t | >3). There are a number of possible reasons for the lack of strong associations for the CBC data, compared with the BBS data. One is that the CBC data comprise a far smaller number of sites (only 119 CBC sites were analysed compared to 1762 BBS sites), therefore statistical power is much lower. A second is that the CBC sites we used measured bird densities only in woodland and so would not capture information about other habitats in the local area.

For the single species analysis of the Speckled Wood butterfly, *P. aegeria*, the relationships between each landscape attribute and *P. aegeria* population density can be found in Appendix P1B Table S11. A summary of the most important landscape attributes (where | t | > 3) for explaining Speckled Wood population density can be found in Table 4.

3.3.2 Overall effects of landscape metrics on bird and butterfly inter-annual population variability

There was some evidence that the landscape attributes that we tested were significantly associated with inter-annual population variability for both butterflies and birds, although results varied across surveys and spatial scales. There were generally fewer significant relationships than for analyses of population density (Table 1). For the UKBMS and CBC surveys, the total number of relationships where | t | > 2 was significantly greater than that expected by chance only for landscape attributes calculated at 5km or 10km radius around sites. Rather than larger spatial scales being the best scale at which to measure landscape attributes, these differences are probably caused by differences in the number of landscape buffers with habitat present at different spatial scales. Larger landscape buffers are more likely to contain the patches of the focal land cover type. Therefore, for the configuration metric, where no habitat present in a landscape buffer leads to a site being treated as a missing value, there will be greater number of sites for analysis at larger spatial scales (for example, see sample sizes in the different landscape buffers in Appendix P1B Tables S3-S5 & S7-S9). For a comparison of the best spatial scale at which to measure landscape attributes (where sample size is standardised to the number of sites at the smallest spatial scale) see the later results section. For the BBS survey (which often had a large number of sites analysed at all spatial scales) there was a significant overall effect of landscape attributes on inter-annual population variability at spatial scales of 2-10km radius around sites (Table 1).

The relationships between each landscape attribute and inter-annual population variability can be found in Appendix P1B Table S7 for butterflies, Appendix P1B Table S8 for birds from the BBS survey and Appendix P1B Table S9 for birds in the CBC survey. For all surveys, a table of landscape attributes ranked by the frequency with which they have a relationship with density of | t |> 2 can be found in Appendix P1B Table S10.

For butterflies, a summary of the most important landscape attributes for explaining inter-annual population variability can be found in Table 5. For birds in the BBS survey, a summary of the most important landscape attributes for explaining bird inter-annual population variability can be found in Table 6.For birds in the CBC survey, a summary of the most important landscape attributes for explaining bird inter-annual population variability can be found in Table 7.

For the single species analysis of the Speckled Wood butterfly, *P. aegeria*, the relationships between each landscape attribute and *P. aegeria* inter-annual population variability can be found in Appendix P1B Table S12. A summary of the most important landscape attributes (where | t | > 3) for explaining Speckled Wood population density can be found in Table 8.

3.3.3 Evidence for Hypotheses based on the UKBP adaptation principles

We discuss evidence for each of the hypotheses we cited in the introduction using results from the multispecies analysis of butterflies and the two bird recording schemes. We also include the results from our single species analysis of the Speckled Wood butterfly, *P. aegeria.*

3.3.3.1 Evidence for Hypotheses 1a and 4a: Association between population densities and site and landscape heterogeneity

These hypotheses suggested that variation in habitat, soil type and topography would be positively correlated with the mean density of populations. Hypothesis 1a pertains to site heterogeneity (0.5km radius) and hypothesis 4a to landscape heterogeneity (2, 5 and 10km radius).

All butterflies
Habitat heterogeneity: Shannon index of semi-natural habitat was a highly important land cover variable explaining butterfly density (Table 2). This effect was apparent only when habitat heterogeneity was assessed at a large spatial scale (2km and above). Landscapes with a broad diversity of semi-natural landcover types were associated with lower butterfly densities. This highlights that having a variety of different habitat types does not necessarily lead to larger populations (although they may be more stable populations- see hypotheses 1b and 4b below).
*Soil Type: H*eterogeneity and dominance of soil type were not strongly associated with butterfly density (Table 2 and Appendix P1B Table S4).
Topography: No topographic landscape metrics were strongly associated with butterfly density (Table 2 and Appendix P1B Table S4).

Speckled wood butterfly, P. aegeria
Neither habitat, soil or topographic heterogeneity had strong associations with mean density of *P. aegeria* populations (Table 7).

Birds (BBS scheme)
Habitat heterogeneity: There was a strong positive association between bird density and the Shannon Index of all land cover types . There was also a (weaker) association between bird density and the Shannon Index of only semi-natural habitat types . This reflects the importance of a diversity of land cover types in landscapes for higher bird densities. The fact that the Shannon Index of all land cover types was a better predictor of bird density than semi-natural habitats alone probably reflects the fact that urban/ garden habitats were associated with higher bird densities (Table 3).
Soil Type: Dominant hydrological soil type of Shannon Index of hydrological soil types was not a strong predictor of bird density (Table 3).
Topography: There were was a negative relationship between mean altitude and bird density (Table 3). Hence higher altitudes (up to 300m tested) tended to have lower bird densities. This relationship reflects the lower bird densities as upland areas are approached towards the north of Britain.

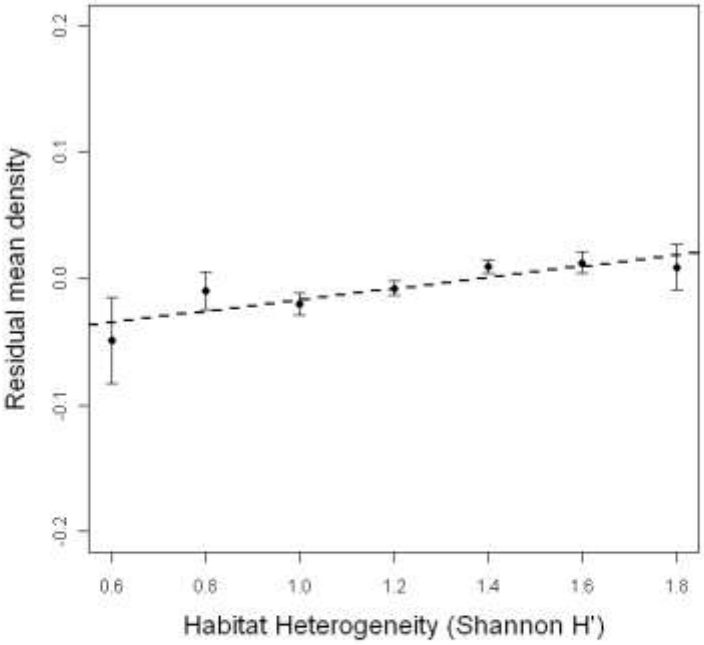

Figure 1: Relationship between (BBS) bird density and the heterogeneity of land cover types in the landscape around monitoring sites (10km radius). Bars represent standard errors of interval means. Results are plotted for all 107 bird species across 1762 sites (total n = 38525). Mean density was calculated by taking residuals from equation [1] (see Methods), but without the landscape attribute variable (LA_i).

Birds (CBC scheme)
All site and landscape attributes tested were poor predictors of bird density from the CBC scheme.

3.3.3.2 Evidence for Hypotheses 1b and 4b: Association between population resilience and site and landscape heterogeneity

These hypotheses suggested that variation in habitat, soil type and topography are positively correlated with population resilience. In this analysis, we assessed the inter-annual variability of populations, which is inversely related to stability (a measure of population resilience). Hypothesis 1b pertains to site heterogeneity (0.5km radius) and hypothesis 4b to landscape heterogeneity (2, 5 and 10km radius).

All butterflies
Habitat heterogeneity: There was a strong negative association between the Shannon Index of all land cover types and butterfly inter-annual variability, indicating butterfly populations are more stable in landscapes with a diversity of land cover types (Figure 2, Table 5). This effect was strongest when habitat heterogeneity was assessed at the site level (0.5km radius). These results are consistent with previous studies highlighting the importance of local and landscape habitat heterogeneity for population stability (Oliver *et al*., 2010). A Shannon Index of only semi-natural land cover types a less strong predictor of butterfly inter-annual variability, indicating that the presence of urban/ garden and arable habitats make a contribution to butterfly population stability.
Soil Type: Dominant hydrological soil type or Shannon Index of hydrological soil types was not a strong predictor of the inter-annual variability of butterfly populations (Table 5).

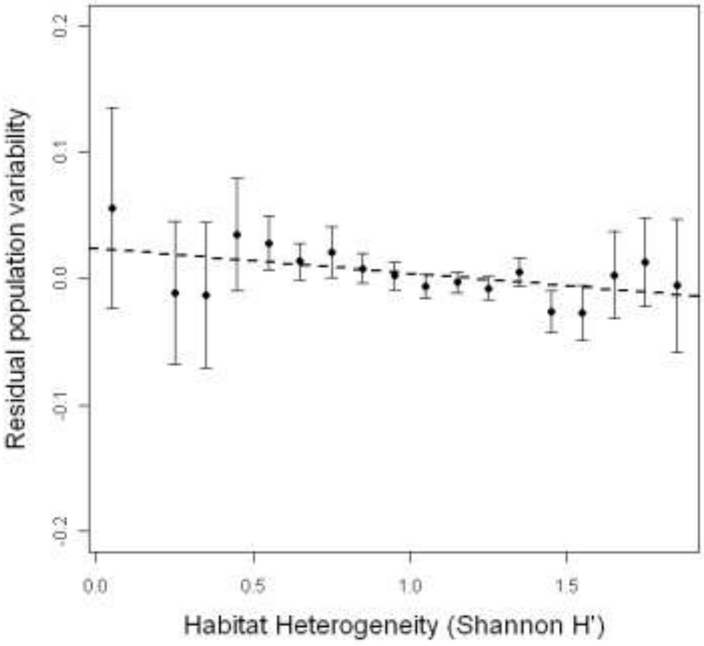

Figure 2: Relationship between butterfly inter-annual population variability and the heterogeneity of land cover types around monitoring sites (0.5km radius). Bars represent standard errors of interval means. Results are plotted for all 48 butterfly species across 369 sites (total n = 6076). Inter-annual population variability was calculated by taking residuals from equation [2] (see Methods), but without the landscape attribute variable (LA_i).

Topography: Topographical land cover variables did not emerge as strong predictors of butterfly inter-annual variability in this analysis (Table 5).

Speckled wood butterfly, P. aegeria

Neither habitat, soil or topographic heterogeneity had strong associations with inter-annual variability of *P. aegeria* populations (Table 8).

Birds (BBS scheme)

Neither habitat, soil or topographic heterogeneity had strong associations with inter-annual variability of bird populations from the BBS scheme (Table 6).

Birds (CBC scheme)

Neither habitat, soil or topographic heterogeneity had strong associations with inter-annual variability of bird populations from the CBC scheme (Table 7).

3.3.3.3 Evidence for Hypotheses 2a and 5a *Association between population densities and site and key habitat areas*

These hypotheses suggested that the area of key habitat types for species' will be positively correlated with mean density. Hypothesis 2a pertains to the site level (0.5km radius around monitoring sites) and hypothesis 5a to the landscape scale (2, 5 and 10km radius).

Butterflies

There was a negative association between areas of heathland, coniferous woodland, urban/ garden, coastal and fen/bog habitats and butterfly density (Table 2). The result implies that in these habitats lower densities of butterflies will be found than in other habitat types. Many of these results are expected as these habitat types have fewer resources for butterflies and less suitable microclimates; only a small number of specialised species generally thrive in these habitat types (Settele *et al.*, 2009, Thomas and Lewington, 2010). The exception is urban/ garden habitats in which more generalist species tend to be found. However, our result suggests that they are not found at high densities in these habitat types relative to others. In many cases the negative effect of these habitat types is most apparent at larger spatial scales (for example, greater than 2km radius around sites). This suggests that the presence of these habitat types, even at large distances from monitoring sites, can depress local butterfly densities. In certain cases (for example coniferous woodland and fen/bog habitats), the negative effect is markedly lower or non-existent when the habitat types are assessed at the site level (0.5km around sites). This might reflect the fact that transect locations are non-random and avoid habitats known to be poor butterfly habitat; therefore, there are only very few sites with habitat present on which to base tests.

The area of arable habitat and lowland calcareous grassland was positively associated with butterfly density. The effect of lowland calcareous grassland fits with our expectations because many British butterflies depend on host plants limited to chalk grasslands (Asher *et al*., 2001, Fox *et al*., 2006). This result for arable land was unexpected, however, as intensive agriculture is often associated with lower insect densities (New, 2009). However, the area of arable land cover also correlates with the ‘edginess’ of arable habitat (Appendix P1B Table S2) and this had a stronger association with butterfly density. Therefore, the relationship with arable area may be an artefact of this covariation between landscape variables (i.e. arable edges are good habitat for the average butterfly). It should be noted that butterfly transects in arable areas typically follow field boundaries, so edge habitat will be preferentially sampled. It is also possible that intensive arable farming areas with poor edge habitats are under-represented in the BMS. This is therefore a result which needs to be interpreted with care and investigated further.

Speckled wood butterfly, *P. aegeria*

As expected the area of broadleaved woodland on sites (0.5km radius) was positively associated with *P. aegeria* densities (Table 4). As an example, a figure of this relationship is shown in Figure 3. Surprisingly, however, there was a suggestion that large areas of broadleaved woodland up to 10km around sites had a negative effect on the density of this butterfly. This may reflect the butterfly preference for woodland edge habitat, rather than large expanses of woodland at a landscape scale. Network grasslands were negatively associated with Speckled Wood density, which is unexpected as the butterfly is sometimes found in more open grassland.

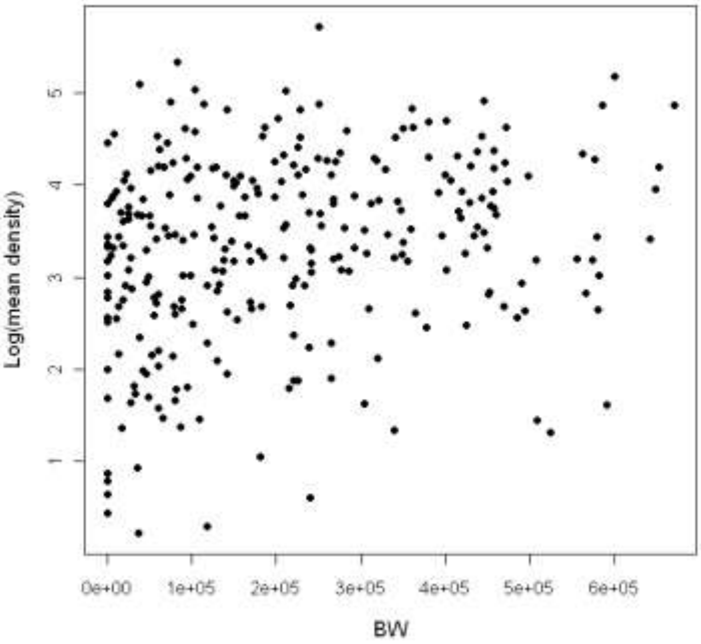

Figure 3: Relationship between *Pararge aegeria* butterfly density and area of broadleaved woodland (BW; m^2) at 0.5km radius around monitoring sites and. Summary statistics for the relationship can be found in Appendix P1B Table S11.

Birds (BBS scheme)

The area of urban/ garden land cover had the strongest association with bird density (Table 3). Landscapes with more urban/ garden areas were associated with higher bird densities (especially if the urban has lots of interfaces with other landcover types- see next section). Larger areas of broadleaved woodland, undetermined grassland and inland water were also associated with higher bird densities. In contrast, large areas of arable, bracken and heathland were associated with lower bird densities. These results do not imply that these habitats are poor for all species, but simply that they have lower overall densities of birds regardless of species-type.

Birds (CBC scheme)

All site and landscape attributes tested were poor predictors of bird density from the CBC scheme.

3.3.3.4 Evidence for Hypotheses 2b and 5b *Association between population resilience and site and key habitat areas*

These hypotheses suggest that the area of key habitat types for species' will be positively correlated with population resilience. In this analysis, we assessed the inter-annual variability of populations, which is inversely related to stability (a measure of population resilience). Hypothesis 2b pertains to the site level (0.5km radius around monitoring sites) and hypothesis 5b to the landscape scale (2, 5 and 10km radius).

Butterflies

Areas of urban/ garden habitat and grassland (from LCM2000) were negatively associated with the inter-annual variability of butterfly populations (Table 5). Landscapes with large areas of urban/ garden habitat tended to have less variable populations. This may reflect the fact that butterfly populations show latitudinal gradients in population variability, with increased population variability towards northern range margins (where there are fewer urban areas; Thomas *et al*., 1994). Alternatively urban areas may harbour less variable populations due to the higher local temperatures (i.e. the urban heat island effect). They may also have a greater range of flowering resources throughout the year compared to the wider countryside. Encouragingly, the result suggests that urban expansion is not associated with reduced stability of butterfly populations. It may be, however, that sites with urban habitats contain a different species assemblage of more widespread species, which tend to be less variable over time (i.e. the more sensitive specialist species having already disappeared from these areas: 'the ghost of habitat degradation past'). There are also likely to be differences across urban area types, with few butterfly transects located close to city centre areas compared to suburban ones.

Speckled wood butterfly, P. aegeria

For no habitat types was total area strongly correlated with *P. aegeria* inter-annual population variability (Table 8).

Birds (BBS scheme)

Area of urban/ garden, arable, broadleaved woodland and fen/ bog land cover types all had a strong association with the inter-annual variability of bird populations (Table 6). Landscapes with large areas of urban/ garden and broadleaved habitat tended to harbour more stable bird populations with lower inter-annual variability. Landscapes with large areas of arable and fen/ bog land cover tended to have less stable bird populations with greater inter-annual variability. One possible reason for this relationship might be the fact that fen habitats tend to have a greater proportion of long-distance migrants birds. These might have more variable populations because of the larger impact of density independent factors influencing them.

Birds (CBC scheme)

Area of arable land cover had a strong positive relationship with bird population inter-annual variability from the CBC survey (Table 7). This suggests bird populations are more stable in landscapes with less arable area. The effect was strongest at 2km radius around sites. In contrast, larger proportions of semi-natural habitat around sites was associated with more stable bird populations. This effect was strongest at the largest spatial scale tested (10km radius).

3.3.3.5 Evidence for Hypothesis 6a: Ecological connectivity leads to increases in mean density

This hypothesis suggests that ecological networks defined by the connectivity of species' key habitats will promote larger mean population densities. In this study, we assessed connectivity using three configuration metrics, applied to each of the 13 broad land cover types (see General Methodology for configuration metric and land cover descriptions).

Butterflies

A greater 'edginess' of arable land cover, grassland (LCM category) and lowland calcareous grassland was associated with higher butterfly densities (Table 2). The edges of arable and grassland fields can often provide shelter and resources for butterflies (Critchleya *et al*., 2003, Haaland *et al*., 2011). This result may indicate the beneficial effect of arable and grassland interface habitats. For the LCM classified grassland (all types) and arable fields the amount of edge habitat was most significant at the largest spatial scale of 10km radius around sites. This suggests that the presence of these edge habitats at a landscape scale can be beneficial for butterflies. In contrast, the positive effect of lowland calcareous grassland edges was only apparent at the site level (0.5km). This makes sense as many calcareous species only have limited dispersal distances (Cowley *et al*., 2001).

The ‘edginess’ of fen/ bog habitats, lowland meadow, broadleaved and coniferous woodland had a negative association with butterfly density. The effect of fen/ bog and lowland meadow edges was apparent only at the site level, whereas broadleaved and coniferous woodland edges had the strongest negative associations when they were measured at the largest spatial scale (10km radius).

These results imply that fen/ bog and lowland meadow interface habitats do not make for good butterfly sites (in terms of overall butterfly density), whilst woodland edge habitats have a negative influence at the landscape level. The result for broadleaved woodland is slightly surprising as broadleaved woodland might be though of as useful movement routes for butterflies creating functional connectivity at the landscape level (for example, Powney *et al*., 2011). However, this may only be true for a small number of specialist woodland species.

The mean nearest neighbour distance between arable fields and bracken habitats were negatively associated with butterfly density. Landscapes with arable patches separated by larger distances tended to have lower butterfly densities. Hence, although arable edges seem to provide good habitat for butterflies, the patches of arable field must be close enough together, which might indicate that these edges are important for promoting functional connectivity across landscapes.

Finally, the number of patches of bare ground/ exposed rock habitats and lowland calcareous grassland were positively associated with butterfly density. However for each habitat the strength of the effect was weak and with a $| t | >3$ only at one spatial scale, therefore results should be interpreted with caution. Bare ground/ exposed rock habitats are known to have positive effects on butterflies, providing particularly warm microclimates (Thomas and Lewington, 2010). The number of patches of bare ground/ exposed rock habitat was strongly correlated with the total area of this habitat type (Appendix P1B Table S2). Hence, it is difficult to separate the importance of these two metrics for butterfly density, but we can infer that even small patches of bare ground/ exposed rock seem to be good for promoting butterfly density. For lowland calcareous grassland the result is counterintuitive as fragmentation of grassland patches are expected to lead to lower butterfly densities. However, this result may be due to the fact that landscape with a large number of lowland calcareous grassland also tend to have larger total areas of this habitat type (Pearson’s correlation coefficient = 0.45; Appendix P1B Table S2).

Speckled wood butterfly, P. aegeria

The ‘edginess’ of urban/ garden and broadleaved woodland habitat were associated with Speckled Wood density (Table 4). High densities of the butterfly were found where sites had a large amount of urban/ garden edge habitat (0.5km radius). This butterfly is a common visitor to gardens. Woodland edges were positively associated with density at the site level, but there was actually a negative relationship with density at the 10km scale.

The number of patches of arable and grassland (LCM categorisation) has a positive association with butterfly density. Small patches of arable and grassland habitat might be expected to benefit this species which is primarily a woodland edge species.

Birds (BBS scheme)

The most important land cover configuration variables for explaining bird density were the number of patches of urban/garden, arable, grassland, inland water, broadleaved woodland, heathland and bare ground/ exposed rock habitat (Table 3). In all cases, except heathland, an increased number of patches were associated with higher densities. In some cases, these associations may arise due to correlations between number of patches and total area habitat types. For example, for arable habitat, a greater number of arable patches are associated with less total area of arable cover (Appendix P1B Table S2). Hence, this result is consistent with arable generally being poor a habitat for birds. For urban/ garden habitats, however, the number of patches was not correlated with total habitat area. Hence, this result may be a genuine effect of urban/ garden configuration on bird density.

The ‘edginess’ of certain habitat types also affect bird densities. Edges of arable were negatively associated with effect on bird density. However the ‘edginess’ of arable habitat was also positively correlated with total area of arable field (Pearson’s correlation coefficient = 0.71; Appendix P1B Table S2). Area of arable had a stronger effect on population density (Table 3), therefore this is probably most likely the causal factor affecting bird density. Edges of urban/ garden habitats were positively associated with bird population density. Once again, this configuration variable was positively correlated with the total area of the land cover type. So landscapes with large areas of urban/ garden landcover tend also to have greater amount of urban/ garden edges, and these landscapes are associated with higher bird density. The ‘edginess’ of bareground/ exposed rock habitats, grassland (LCM categorisation) and broadleaved woodland also affected bird density. Edges of bareground/ exposed rock habitats had negative effects on bird density but only when assessed at larger landcape scales (>2km radius around sites). The same was true for grassland habitat. Broadleaved woodland edges were positively associated with bird density, mostly strongly at the site level (0.5km radius).

Isolation of some habitat types also affected bird density. Landscapes with urban/ garden patches separated by large distances tended to have lower densities as did landscapes with isolated patches of broadleaved woodland, and inland water habitats. In some cases, the total area of these habitat types is correlated with isolation, and it may be total area of habitat that is primarily driving associations with density. For example, area of woodland is negatively correlated with woodland isolation (Pearson’s correlation coefficient = -0.44; Appendix P1B Table S2). Woodland area had a strong positive associated with bird density and this may also explain the (weaker) association between woodland isolation and density.

Birds (CBC scheme)
All site and landscape attributes tested were poor predictors of bird density from the CBC scheme.

3.3.3.6 Evidence for Hypothesis 6b: Ecological connectivity leads to increases in population resilience

This hypothesis suggests that ecological networks defined by the connectivity of species’ key habitats will promote more resilient populations. In this analysis, we assessed by the inter-annual variability of populations, which is inversely related to stability (a measure of population resilience). We assessed connectivity in the same way as for Hypothesis 6a, above.

Butterflies
The number of patches of urban/ garden, grassland (LCM2000) habitat were associated with the inter-annual variability of butterfly populations (Table 5). Butterfly populations were less variable in landscapes with many patches of urban/ garden habitat. This may reflect the fact that urban/ garden habitats can provide benefits to butterflies (as evidenced by the area result above), but only if they a suitably interspersed with semi-natural habitat (i.e. a large number of smaller patches of urban/garden habitat will be more beneficial than large conurbations). An alternative explanation is that landscapes with large numbers of urban/ garden patches also tended to have higher habitat heterogeneity (Pearson’s correlation coefficient = 0.44; Appendix P1B Table S2); hence, they are very mixed landscapes, which supports hypotheses that habitat heterogeneity can promote more stable populations (see relevant section below).

Speckled wood butterfly, *P. aegeria*

The number of patches of urban/ garden habitat was the only landscape attribute strongly associated with *P. aegeria* inter-annual population variability (Table 8). When sites had fewer patches of urban/ garden habitat, populations were more stable. This relationship is illustrated in Figure 4.

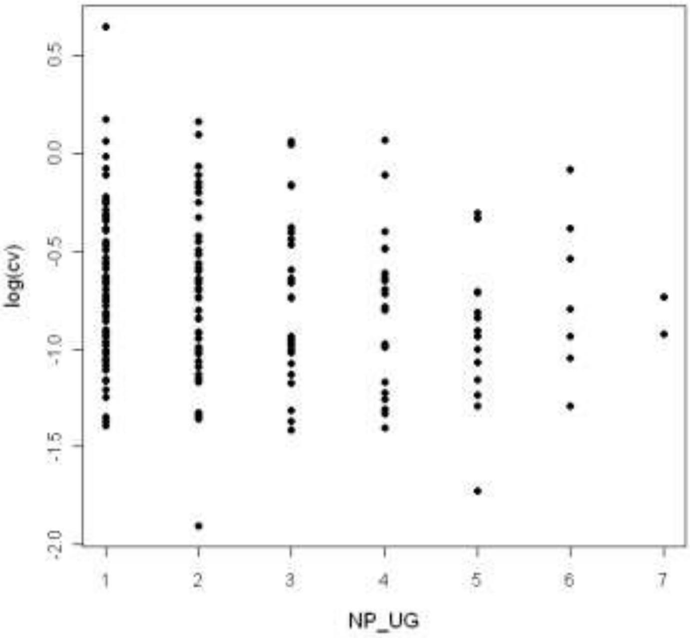

Figure 4: Relationship between *Pararge aegeria* butterfly population variability (log(cv)) and number of patches of urban/garden habitat (NP_UG) at 0.5km radius around monitoring sites. Summary statistics for the relationship can be found in Appendix P1B Table S12.

Birds (BBS scheme)

The most important configuration metrics for the inter-annual variability of bird populations were the ‘edginess’ of urban/ garden, arable and bareground/ exposed rock habitats. Landscapes with more urban/ garden edge habitats had more stable bird populations. The ‘edginess’ of urban/garden habitats was negatively correlated with the total area of this habitat type (Pearson’s correlation coefficient = -0.41; Appendix P1B Table S2). Area of urban/ garden also had a (stronger) negative association with the inter-annual variability of bird populations (Table 6). Hence, if the result for urban/ garden edginess was purely a result of covariation with the total area of this habitat type, then we would expect the opposite effect (where sites with large urban/ garden areas, which tend to have fewer edges, have more stable populations). Hence, there appears to be an additional independent effect of urban/garden edges, which may imply that this interface habitat is particularly important for bird population stability.

In contrast to the positive effect of urban/ garden edges, landscapes with more arable and bareground/ exposed rock edge habitats, bird populations tended to be less stable. In this case, covariation between habitat edginess and total area may explain the result adequately. For example, edginess of arable habitat was positively correlated with arable area, which had a (stronger) negative impact on bird population stability.

The number of patches of broadleaved woodland was associated with lower inter-annual variability of bird populations. However, interpreting this effect is difficult as this configuration metric was highly correlated with many other land cover metrics, in particular the total area of broadleaved woodand which also had a positive effect on population stability (Pearson's correlation coefficient = 0.45; Appendix P1B Table S2). In contrast, the number of patches of heathland and bracken was positively with lower inter-annual variability of bird populations. For these habitat types, the total area of the habitat did not have strong associations with inter-annual variability, suggesting a possible genuine effect of configuration. Potentially, the the fragmentation of these habitats may lead to less stable populations, although there were are probably few large unfragmented patches of these habitat types on which to base comparisons.

Finally, isolation of broadleaved woodland and urban/ garden habitats was associated with larger inter-annual variability of bird populations. Populations were less stable when patches of woodland and urban/ garden habitat were separated by large distances. Again, potentially these results may be due to covariation between total habitat area and configuration. For example, larger patches of urban/ garden habitat tend to house less variable bird populations (Table 6), and in these landscapes, urban/ garden patches tend to be less isolated (Pearson's correlation coefficient = -0.41; Appendix P1B Table S2).

Birds (CBC scheme)
The configuration of arable patches, coastal and lowland calcareous grassland had associations with bird population inter-annual variability from the CBC survey (Table 7). Increased 'edginess' of arable and lowland calcareous grassland patches were associated with more variable populations. Again, this effect was strongest at intermediate spatial scales (5 and 2km radius respectively). In contrast to butterflies, birds do not seem to benefit as much from arable and grassland interface habitats. In contrast, the presence of coastal edge habitat on sites (0.5km radius) was associated with more stable bird populations.

3.3.3.7 Explanatory power of landscape attributes at different spatial scales

For the UKBMS butterfly survey and for both bird surveys (BBS & CBC), the spatial scale at which landscape metrics best explained both population density and inter-annual variability was 0.5km radius around monitoring sites (Table 9). However, there was also substantial number of metrics at which larger spatial scales were the best predictor (up to 10km radius around sites). If we excluded results from the analyses of attributes at 0.5km radius (site level) and identify the best landscape attributes from landscape scales of 2, 5 and 10km radii, then there were still clear differences in explanatory power between spatial scales (Table 10). Most landscape attributes were had most explanatory power when assessed at the smallest landscape scale of 2km, whilst for others the largest landscape scale was best. There were fewest landscape metrics that had had the strongest explanatory power at the intermediate landscape scale of 5km radius around sites.

For the single species analysis of the Speckled Wood butterfly, *Pararge aegeria,* the spatial scale at which landscape metrics best explained both population density and inter-annual variability was, again, 0.5km radius around monitoring sites, although the results were not significant (Table 11). There was a high frequency of landscape attributes for which larger spatial scales were the best predictor of population density and inter-annual variability, as would be expected for a relatively mobile species (Cowley *et al*., 2001).

3.4 General discussion

Many of the landscape attributes had strong associations with the density and inter-annual variability of butterfly and bird populations. A list of the landscape attributes that had consistent strong associations with population density across spatial scales and across species groups are listed in Table S6. A list of the landscape attributes that had consistent strong associations with population interannual-variability across spatial scales and across species groups are listed in Table S10. In both cases, a wide range of landscape attributes, including habitat area, configuration and heterogeneity, had strong associations these response variables.

In this analysis we specifically addressed the the following hypotheses, based on the UKBP adaptation principles (Hopkins *et al*., 2007; and numbered in the same order as in the General Introduction section). Below we summarise the evidence for and against each of the hypotheses:

Hypothesis 1- Local (site) variation in habitat, soil type and topography are positively correlated with the mean density (Hypothesis 1a) and resilience (H1b) of populations as measured during recent periods of relative climatic variability and incremental change.

Hypothesis 1a**:** There was a strong positive association between average bird density and habitat heterogeneity on monitoring sites. In contrast, we found no significant effect of site habitat heterogeneity on butterflies. Soil and topographic heterogeneity of sites similarly had no apparent effect on average butterfly density. Topography did have some effect on birds however, with lower bird densities on higher altitude sites.

Hypothesis 1b**:** Habitat heterogeneity on monitoring sites had a strong association with the inter-annual variability of butterfly populations. Sites with higher habitat heterogeneity tended to have more stable butterfly populations. A similar result was found by Oliver *et al.* (2010), who used a species-specific measure of habitat heterogeneity (i.e. excluding those land cover types rarely used by a species). In this study, we used a generic measure of habitat heterogeneity (including all land cover types), which might be expected to be less sensitive as a measure of site quality. However, there are clearly strong associations between butterfly population stability and habitat heterogeneity even with this generic measure. Notably, we also tested an index of habitat heterogeneity which excluded arable and urban/ garden land cover types. This index was not strongly associated with butterfly population inter-annual variability, suggesting that the presence of these land cover types may help promote population resilience.

For birds, there was no evidence that site habitat heterogeneity affected population stability. Similarly, for both species groups, butterflies and birds, there was little evidence for associations between soil and topographic heterogeneity on population stability. A study by Oliver *et al.* (2010) found that variation in topographic aspect can help promote stability in butterfly populations, although the strength of the association was weaker than that between habitat heterogeneity and population stability. The results of this study reinforce the strong importance of habitat heterogeneity on (butterfly) population resilience, whilst the effects of topographic heterogeneity on population resilience appear weaker.

H2- Area of key habitat types for species’ will be positively correlated with the mean density (H2a) and resilience (H2b) of populations.

Hypothesis 2a**:** The area of certain habitat types on monitoring sites was not often strongly associated with average butterfly density. Stronger associations occurred more frequently at larger spatial scales, although this may be partly due to larger sample sizes at these scales (see Hypothesis 5a). There were some weak associations between butterfly and heathland and arable area on sites. Heathland was associated with lower average butterfly densities, whilst, surprisingly, larger areas of arable land cover were associated with higher average butterfly densities. For the speckled wood butterfly, *Pararge aegeria*, broadleaved woodland area on sites was positively associated with butterfly density. For birds, assessed using the BBS survey, the area of certain habitat types on monitoring sites had much stronger associations with average density. Larger areas of urban/ garden, broadleaved woodland and inland water on sites were all associated with higher average bird densities. In contrast, larger areas of arable land cover had a strong negative correlation with bird density. Using the CBC, survey no associations between site attributes and population density were found.

Hypothesis 2b: There was some evidence that the area of certain habitat types on monitoring sites was related to bird and butterfly population stability, although associations were less strong than for density relationships. Both butterfly and bird populations were, on average, more stable between years when more urban/ garden habitat was present on monitoring sites. For birds, assessed using the BBS survey, there was also a relationship between population stability and area of arable field; bird populations were less stable when larger areas of arable land cover were present on monitoring sites.

H4- Landscape-scale variation in habitat, soil type and topography are positively correlated with the mean density (H4a) and resilience (H4b) of populations of populations as measured during recent periods of relative climatic variability and incremental change.

***Hypothesis 4a*:** Although population density was best predicted by attributes measured at the site scale (when comparing site and landscape attributes using the same complement of sites), there tended to be a greater number of attributes emerging as significant predictors at the landscape level (due to the greater number of sites available for analysis when considering attributes at larger spatial scales). Hence, the heterogeneity of semi-natural habitat types had strong associations with butterfly density when measured at the landscape level. Landscapes with a greater diversity of semi-natural habitat types had lower butterfly densities. This highlights that although habitat heterogeneity can promote population resilience (measured by stability; Hypothesis 4b), it can also lead to lower mean densities. Hence there may be a trade off between resilience and mean density when trying to promote robustness of populations. Other measures of landscape heterogeneity (soil type and topography) were not strongly associated with butterfly density.

For birds, using the BBS survey, there were strong positive associations between habitat heterogeneity at the landscape scale and average population density (i.e. the opposite results to butterflies). Incidentally, an index of habitat heterogeneity including urban/ garden and arable land cover was a better predictor of bird density than an index of semi-natural habitats only. This probably reflects the fact that urban/ garden habitats can have positive effects on average bird density (see Hypotheses 2 and 5). Soil and topographic heterogeneity variables did not have strong associations with bird density. However, there was a negative association between mean altitude and bird density.

***Hypothesis 4b*:** Habitat heterogeneity at the landscape level was associated with butterfly population stability, although effects were generally stronger at the site level (Hypothesis 1b). For birds (BBS and CBC survey), there was no evidence of association between habitat heterogeneity and population stability. Similarly, for both butterflies and birds there was little evidence that landscape-level soil or topographic heterogeneity are important for population stability.

H5- The area of species' key habitat types in the local landscape will be positively correlated with the mean density (H5a) and resilience (H5b) of populations.

Hypothesis 5a: The area of certain habitat types at a landscape level were strong predictors of both bird and butterfly density. For butterflies, heathland, fen/ bog, coastal and coniferous woodland all had negative associations with average butterfly density. In contrast, larger areas of arable land cover in the landscape were associated with higher average butterfly density. For birds, using the BBS survey, urban/ garden and broadleaved woodland were strongly associated with higher average bird density. Arable, bracken and heathland land cover were all associated with lower average bird density. Using the CBC survey, no associations between landscape attributes and population density were found.

Hypothesis 5b: The area of certain habitat types at a landscape level were associated with both bird and butterfly stability, although the number of significant associations was generally less than with population density as a response variable. Larger areas of urban/ garden habitat in the landscape were associated with more stable populations of both butterflies and birds (BBS survey only). In contrast, large areas of arable land cover were associated with less stable bird populations (both BBS and CBC surveys). Using the BBS survey, there were additional associations with the area of broadleaved woodland (promoting stability) and the area of fen (reducing stability).

H6- Ecological networks defined by the connectivity of species' key habitats also increase the mean density (H6a) and resilience (H6b) of populations as measured during recent periods of relative climatic variability and incremental change.

Hypothesis 6a: The configuration of certain habitat types had strong associations with population density of both birds and butterflies. In some cases, habitat configuration was correlated with total habitat area. If population density was more strongly related to habitat area, then this suggests that correlations with habitat configuration may be an artefact of the previous relationship. In contrast, there were occasions when configuration metrics had stronger effects on population density than total habitat area. For example, the mean shape index ('edginess') of arable habitat had a positive association on butterfly density that was stronger than the positive association with total arable area. This suggests that the configuration effect may be genuine; arable edge habitats appear important for average butterfly density. All three configuration metrics that we tested had strong associations with bird and butterfly density for one or more habitat types, although the mean shape index ('edginess') metric appeared to be a stronger predictor of butterfly density.

Hypothesis 6b: As with habitat area attributes, there were generally fewer significant associations with configuration of certain habitat types with population stability, rather than density, as the response variable. In many cases, covariation between habitat configuration and area (of the same habitat type and others) confounded interpretation. However, there were cases where there appeared to be genuine effects of habitat configuration on population stability. For example, the mean shape index ('edginess') of urban garden habitats was associated with more stable bird populations, a result that was unlikely to arise from simply due to covariation with the area of this habitat type.

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Table 1: The overall ability of landscape attributes to explain population density and inter-annual variability. Given are the observed number of the relationships with a magnitude of t-value > 2 and the number expected by chance with a type 1 error rate of 0.05. A proportion test was used to compare if these were significantly different.

Survey	Response	Spatial scale (km radius)	Observed number relationships where t > 2	Expected number relationships where t > 2	Total number of tests	X2	df	p
Butterflies (UKBMS)	Density	0.5	11	4	73	2.67	1	0.102
Butterflies (UKBMS)	Density	2	17	4	77	7.94	1	**0.005**
Butterflies (UKBMS)	Density	5	23	4	77	14.55	1	**<0.001**
Butterflies (UKBMS)	Density	10	31	4	77	24.99	1	**<0.001**
Butterflies (UKBMS)	Inter-annual variability	0.5	7	4	73	0.39	1	0.531
Butterflies (UKBMS)	Inter-annual variability	2	12	4	77	3.42	1	0.065
Butterflies (UKBMS)	Inter-annual variability	5	13	4	77	4.23	1	**0.040**
Butterflies (UKBMS)	Inter-annual variability	10	13	4	77	4.23	1	**0.040**
Birds (BBS)	Density	0.5	20	4	73	11.22	1	**0.001**
Birds (BBS)	Density	2	33	4	79	27.67	1	**<0.001**
Birds (BBS)	Density	5	37	5	81	30.89	1	**<0.001**
Birds (BBS)	Density	10	42	5	81	38.84	1	**<0.001**
Birds (BBS)	Inter-annual variability	0.5	11	4	73	2.67	1	0.102
Birds (BBS)	Inter-annual variability	2	17	4	79	7.91	1	**0.005**
Birds (BBS)	Inter-annual variability	5	19	5	81	8.27	1	**0.004**
Birds (BBS)	Inter-annual variability	10	22	5	81	11.38	1	**0.001**
Birds (CBC)	Density	0.5	4	3	57	0.00	1	1.000
Birds (CBC)	Density	2	6	4	77	0.11	1	0.744
Birds (CBC)	Density	5	5	4	77	0.00	1	1.000
Birds (CBC)	Density	10	5	4	77	0.00	1	1.000
Birds (CBC)	Inter-annual variability	0.5	5	3	57	0.13	1	0.714
Birds (CBC)	Inter-annual variability	2	9	4	77	1.34	1	0.246
Birds (CBC)	Inter-annual variability	5	13	4	77	4.23	1	**0.040**
Birds (CBC)	Inter-annual variability	10	12	4	77	3.42	1	**0.065**

Table 2: The most important landscape attributes for explaining butterfly density. Listed are the t-values for the relationship between each landscape attribute and butterfly density at four spatial scales around sites. Relationships with |t| > 3 have cells highlighted (blue for positive relationships, red for negative). The table is ordered with strongest relationships (across all spatial scales for a given landscape attribute) listed first. Descriptions of landscape attributes are given in the General Methodology section.

		Strength of association with density (t- value) at different spatial scales			
Landscape attribute	**Explanation**	**0.5km**	**2km**	**5km**	**10km**
Shan.LCM.habitat.SN.only	Shannon Index of semi-natural habitats	0.33	-2.78	-4.86	-5.35
SHP_A	Edginess of arable	-0.11	2.68	3.73	5.24
ED_A	Mean nearest neighbour distance of arable	-1.15	-3.29	-4.19	-5.09
H	Heathland area	-2.70	-4.36	-4.66	-4.52
A	Arable area	2.89	4.61	4.37	4.27
CW	Coniferous woodland area	0.34	-1.32	-2.78	-4.57
ED_Br	Mean nearest neighbour distance of broadleaved woodland	-4.45	1.40	1.97	1.81
SHP_G	Edginess of grassland (LCM)	0.48	1.14	2.22	3.93
LC	Area of lowand calcareous grassland	2.03	1.09	1.49	3.90
BgRo	Area of bareground/ exposed rock	1.62	3.09	2.95	3.58
UG	Area of urban/ garden	-0.05	-2.11	-2.92	-3.41
NP_BgRo	Number of patches of bareground/ exposed rock	0.48	3.39	2.56	2.64
C	Area of coastal	-1.16	-2.44	-3.33	-2.99
F	Area of fen/ bog	0.47	-0.87	-3.32	-2.79
SHP_F	Edginess of fen/ bog	3.23	-0.07	-1.65	-1.54
NP_LC	Number of patches of lowland calcareous grassland	-1.22	0.64	1.48	3.22
SHP_LM	Edginess of lowland meadows	-3.20	-1.05	-1.27	1.03
SHP_LC	Edginess of lowland calcareous grassland	3.17	0.16	0.21	-0.57
SHP_BW	Edginess of broadleaved woodland	0.89	-2.62	-2.34	-3.02
SHP_CW	Edginess of coniferous woodland	-0.22	0.02	-0.69	-3.02

Table 3: The most important landscape attributes for explaining bird density from the BBS survey. Listed are the t-values for the relationship between each landscape attribute and butterfly density at four spatial scales around sites. Relationships with |t| > 3 have cells highlighted (blue for positive relationships, red for negative). The table is ordered with strongest relationships (across all spatial scales for a given landscape attribute) listed first. Descriptions of landscape attributes are given in the General Methodology section.

		Strength of association with density (t- value) at different spatial scales			
Landscape attribute	**Explanation**	**0.5km**	**2km**	**5km**	**10km**
UG	Area or urban/ garden	12.12	11.80	11.15	10.84
A	Area of arable	-10.85	-8.85	-8.21	-7.44
BW	Area of broadleaved woodland	6.69	7.10	7.98	8.78
NP_UG	Number of patches of urban/ garden	2.43	6.29	7.73	7.86
NP_A	Number of patches of arable	4.37	5.75	7.72	7.46
ED_UG	Mean nearest neighbour distance of urban/garden	-2.53	-7.62	-5.77	-6.43
Shan.LCM.habitat.all	Shannon Index of all habitat types	5.13	7.18	7.55	7.36
NP_G	Number of patches of grassland (LCM)	4.10	6.80	5.85	4.96
SHP_A	Edginess of arable	-6.18	-6.54	-5.58	-3.45
SHP_UG	Edginess of urban/ garden	4.93	5.99	6.22	4.49
NP_R	Number of patches of inland water	0.98	3.37	4.37	6.15
NP_BW	Number of patches of broadleaved woodland	2.69	5.91	5.82	5.85
ED_BW	Mean nearest neighbour distance of broadleaved woodland	-0.65	-4.80	-2.20	-4.44
DEM_MEAN	Mean altitude	-4.34	-4.69	-4.50	-4.34
SHP_BgRo	Edginess of bareground/ exposed rock	-0.68	-2.05	-3.23	-4.57
UDG	Area of undetermined grassland	0.99	2.09	3.68	4.46
NP_H	Number of patches of heathland	-0.33	-2.53	-4.03	-4.39
Br	Area of bracken	-2.92	-3.85	-4.13	-4.38
SHP_BW	Edginess of broadleaved woodland	3.74	2.44	2.92	2.82
SHP_Br	Edginess of bracken	-1.19	-0.32	-3.51	-2.38
SHP_G	Edginess of grassland	-1.56	-3.10	-3.47	-2.80
Shan.LCM.habitat.SN.only	Shannon index of semi-natural habitat	2.26	3.28	3.46	2.79
ED_F	Mean nearest neighbour distance of fen/ bog	0.59	1.15	3.46	-0.58
H	Area of heathland	-2.46	-3.20	-3.22	-3.40
NP_BgRo	Number of patches of bareground/ exposed rock	0.62	-0.28	2.71	3.40
ED_BgRo	Mean nearest neighbour distance of bareground/ exposed rock	0.20	2.08	-0.37	-3.27
ED_R	Mean nearest neighbour distance of inland water	-0.02	-1.12	-0.34	-3.27
R	Area of inland water	3.18	2.91	2.70	2.76
SHP_F	Edginess of fen/ bog	-0.01	-2.69	-2.69	-3.17

Table 4: The most important landscape attributes for explaining *Pararge aegeria* butterfly density. Listed are the t-values for the relationship between each landscape attribute and butterfly density at four spatial scales around sites. Relationships with |t| > 3 have cells highlighted (blue for positive relationships, red for negative). The table is ordered with strongest relationships (across all spatial scales for a given landscape attribute) listed first. Descriptions of landscape attributes are given in the General Methodology section.

		Strength of association with density (t- value) at different spatial scales			
Landscape attribute	**Explanation**	**0.5km**	**2km**	**5km**	**10km**
BW	Area of broadleaved woodland	3.98	0.70	-0.96	-2.44
SHP_UG	Edginess of urban/ garden	3.61	0.97	0.73	-0.51
NP_A	Number of patches of arable	3.30	1.69	0.92	0.77
SHP_BW	Edginess of broadleaved woodland	2.38	-1.03	-2.58	-3.20
NG	Area of network grasslands	-2.86	-3.12	-3.06	-0.87
SHP_S	Edginess of sea	3.07	1.07	-1.18	0.68
NP_G	Number of patches of grassland (LCM)	3.05	1.34	-0.52	-1.75

Table 5: The most important landscape attributes for explaining butterfly inter-annual population variability. Listed are the t-values for the relationship between each landscape attribute and butterfly density at four spatial scales around sites. Relationships with |t| > 3 have cells highlighted (blue for positive relationships, red for negative). The table is ordered with strongest relationships (across all spatial scales for a given landscape attribute) listed first. Descriptions of landscape attributes are given in the General Methodology section.

		Strength of association with inter-annual variability (t- value) at different spatial scales			
Landscape attribute	**Explanation**	**0.5km**	**2km**	**5km**	**10km**
NP_UG	Number of patches of urban/ garden	-5.23	-2.79	-2.18	-1.58
UG	Area of urban/ garden	-3.51	-4.59	-3.58	-3.23
ED_UG	Mean nearest neighbour distance of urban/ garden	1.62	1.90	4.07	3.20
NP_G	Number of patches of grassland	-2.15	-3.78	-2.67	-1.77
Shan.LCM.habitat.all	Shannon Index of all habitat types	-3.69	-2.65	-2.56	-2.29
SHP_G	Edginess of grassland	3.30	3.29	2.18	1.66

Table 6: The most important landscape attributes for explaining bird inter-annual population variability from the BBS survey. Listed are the t-values for the relationship between each landscape attribute and butterfly density at four spatial scales around sites. Relationships with |t| > 3 have cells highlighted (red for positive relationships, blue for negative). The table is ordered with strongest relationships (across all spatial scales for a given landscape attribute) listed first. Descriptions of landscape attributes are given in the General Methodology section.

		Strength of association with inter-annual variability (t- value) at different spatial scales			
Landscape attribute	**Explanation**	**0.5km**	**2km**	**5km**	**10km**
UG	Area of urban/ garden	-7.15	-6.41	-5.23	-4.47
A	Area of arable	5.91	4.50	3.70	2.99
SHP_UG	Edginess of urban/ garden	-3.33	-4.44	-3.25	-1.31
NP_BW	Number of patches of broadleaved woodland	-1.87	-2.96	-4.06	-4.31
ED_BW	Mean nearest neighbour distance of broadleaved woodland	0.94	1.74	2.31	4.23
BW	Area of broadleaved woodland	-4.02	-3.69	-3.56	-4.16
ED_UG	Mean nearest neighbour distance of urban/ garden	0.95	3.28	3.76	3.58
NP_H	Number of patches of heathland	1.11	3.08	3.42	3.69
SHP_A	Edginess of arable	3.28	3.58	2.35	0.51
SHP_BgRo	Edginess of bareground/ exposed rock	0.92	1.16	2.26	3.43
F	Area fen/ bog	1.38	2.45	2.50	3.18
NP_Br	Number of patches of bracken	1.84	2.11	2.84	3.11

Table 7: The most important landscape attributes for explaining bird inter-annual population variability from the CBC survey. Listed are the t-values for the relationship between each landscape attribute and butterfly density at four spatial scales around sites. Relationships with |t| > 3 have cells highlighted (red for positive relationships, blue for negative). The table is ordered with strongest relationships (across all spatial scales for a given landscape attribute) listed first. Descriptions of landscape attributes are given in the General Methodology section.

		Strength of association with inter-annual variability (t- value) at different spatial scales			
Landscape attribute	**Explanation**	**0.5km**	**2km**	**5km**	**10km**
A	Area of arable	2.66	4.33	4.04	3.65
SHP_A	Edginess of arable	-0.54	3.53	3.93	2.85
SHP_C	Edginess of coastal	-3.59	-0.74	0.76	-0.76
SHP_LC	Edginess of lowland calcareous grassland	0.96	3.28	3.15	2.39
prop.semi.natural	Proportion of semi-natural habitat	-2.38	-2.77	-2.61	-3.01

Table 8: The most important landscape attributes for explaining *Pararge aegeria* butterfly inter-annual population variability. Listed are the t-values for the relationship between each landscape attribute and butterfly density at four spatial scales around sites. Relationships with |t| > 3 have cells highlighted (red for positive relationships, blue for negative). The table is ordered with strongest relationships (across all spatial scales for a given landscape attribute) listed first. Descriptions of landscape attributes are given in the General Methodology section.

		Strength of association with inter-annual variability (t- value) at different spatial scales			
Landscape attribute	**Explanation**	**0.5km**	**2km**	**5km**	**10km**
NP_UG	Number of patches of urban/ garden	-3.05	-1.88	-1.93	-1.51

Table 9: Frequency table of the best spatial scale for which landscape attributes can explain population density and inter-annual variability. A chi-squared test was to consider whether the frequency distribution was significantly different from that expected by chance.

		Frequency best scale						
Survey	**Response**	**0.5km**	**2km**	**5km**	**10km**	**X2**	**df**	**p**
Butterflies (UKBMS)	Density	34	9	11	19	21.19	3	<0.001
Birds (BBS)	Density	34	14	9	16	19.55	3	<0.001
Birds (CBC)	Density	29	8	8	12	21.11	3	<0.001
Butterflies (UKBMS)	Interann. variability	34	14	11	15	17.78	3	<0.001
Birds (BBS)	Interann. variability	41	5	6	23	46.12	3	<0.001
Birds (CBC)	Interann. variability	22	9	9	18	8.90	3	<0.001

Table 10: Omitting results at 0.5km, frequency table of the best spatial scale between 2km -10km for which landscape attributes can explain population density and inter-annual variability. A chi-squared test was to consider whether the frequency distribution was significantly different from that expected by chance.

		Frequency best scale					
Survey	**Response**	**2km**	**5km**	**10km**	**X2**	**df**	**p**
Butterflies (UKBMS)	Density	35	13	25	9.97	2	0.007
Birds (BBS)	Density	38	15	20	12.03	2	0.002
Birds (CBC)	Density	29	13	15	8.00	2	0.018
Butterflies (UKBMS)	Interann. variability	44	12	17	24.36	2	<0.001
Birds (BBS)	Interann. variability	35	9	29	15.23	2	<0.001
Birds (CBC)	Interann. variability	27	10	20	7.68	2	0.021

Table 11: Frequency table of the best spatial scale for which landscape attributes can explain population density and inter-annual variability for the] butterfly *Pararge aegeria*. A chi-squared test was to consider whether the frequency distribution was significantly different from that expected by chance.

	Frequency best scale						
Response	**0.5km**	**2km**	**5km**	**10km**	**X2**	**df**	**p**
Density	27	16	11	17	7.59	3	0.055
Interann. variability	22	16	18	19	1.00	3	0.801

Part 2: Exploring interactions between the area and configuration of broadleaved woodland on population density and inter-annual variability in birds and butterflies[1]

4.1 Introduction

Landscape-scale approaches are increasingly recognised as vital to successful conservation efforts (Lawton *et al*., 2010). Where habitat patches are too small or isolated, populations face increased extinction risk and there is an increased chance than meta-populations will not be able to persist (Hanski, 1999). The configuration of habitat patches is important through the facilitation or hindering of 'ecological connectivity' (Crooks and Sanjayan, 2006, Doerr *et al*., 2011). Well-connected populations allow rescue effects to occur when certain populations become locally extinct, thereby maintaining persistent meta-populations (Hanski, 1999). This has led to an emphasis on 'connectivity conservation'- promoting the 'joining up' of habitat patches through habitat corridors or by reducing the hostility of intervening landscapes (Crooks and Sanjayan, 2006, Lawton *et al*., 2010). Increasing ecological connectivity is the most commonly cited conservation action to adapt to climate change (Heller and Zavaleta, 2009, Hodgson *et al*., 2011).

However, some researchers disagree on such a strong focus on promoting ecological connectivity, at the expense of other conservation actions. For example, simply increasing the quality and area of habitat patches has many clear benefits (Hill *et al*., 2001, Krauss *et al*., 2003, Krauss *et al*., 2004, Hodgson *et al*., 2009, Powney *et al*., 2011). From a meta-analysis of published evidence, increasing habitat area has been suggested to have greater effects on population viability than the configuration of habitat patches (Hodgson *et al*., 2011). In most previous published studies, however, population viability has only been assessed in terms of population density and species richness (for example, see Hodgson *et al*., 2001, for a summary of landscape-scale studies related to population viability). The stability of populations over time has been relatively neglected, even though this is an important factor determining the extinction risk of populations. (Karr, 1982, Pimm *et al*., 1988, Lande, 1993, Inchausti and Halley, 2003). In addition, many studies have focussed exclusively on habitat area *or* habitat configuration, rather than their combined effects. Some researchers have suggested that interaction effects may occur between habitat area and configuration (Andrén, 1994, Opdam and Wascher, 2004). For example, the spatial configuration of habitat patches may only be important when there is a low proportion of habitat available in landscapes. In a review of studies on birds and mammals, Andrén (1994) suggested that habitat configuration may only be important where the proportion of suitable habitat in landscapes is less than 30%. In addition to limited number of studies in which this conclusion was based, population viability was again only assessed through population density. Hence, there is a strong need for further information on the relative importance of habitat area and configuration on population viability to inform conservation policy and land management.

We conducted an analysis of the combined effects of woodland area and configuration on the population density and inter-annual variability of 82 bird and 32 butterfly species. Woodland cover was assessed at a radius of 2km around population monitoring sites. This spatial scale was chosen because landscape structure generally has the strongest effect on population parameters at smaller spatial scales (Chapter 1), but we wanted a landscape scale large enough that an interaction between area and configuration might occur. A spatial scale of 2km around sites is one at which landscape scale conservation might feasibly be considered. Configuration of woodland was assessed using three metrics: ED- mean Euclidean nearest neighbour distance between woodland patches, SHP- mean shape index or PD- patch density (see General Methodology for further description). These metrics were chosen because they are easily interpretable and capture different aspects (albeit inter-related) of spatial configuration that are known to be important to many species populations: isolation, edge effects and fragmentation (Hanski, 1999). We tested for an interaction effect between area and configuration metrics and we also considered the relative ability of these two variables to predict population density and inter-annual variability. Using expert opinion, we categorised species *a priori* depending on their perceived association with broadleaved woodland (specialist, generalist and 'non-woodland' species) because we might expect differences in the responses of these groups (M. Botham, S. Gillings, S. Newson, *pers. comm.*; Appendix P2). We tested the following hypotheses:

1. There will be an interaction effect between woodland area and configuration on the population density and inter-annual variability, whereby configuration is has a stronger effect when total area of the woodland is small.
2. After controlling for area of woodland, landscapes where woodland patches are fragmented (in terms of isolation, 'edginess' and number of patches) will be associated with smaller and less stable populations (related to **Hypotheses 6a and 6b** in the General Introduction).
3. Increased areas of woodland will benefit woodland specialist and, to a lesser degree, woodland generalist species, and have no effect on 'non-woodland' species (related to **Hypotheses 5a, 5b and 7** in the General Introduction).
4. Area of woodland will be a better predictor of population viability, assessed through mean density and inter-annual variability, than configuration metrics.

4.2 Materials and methods

4.2.1 Calculating population density and inter-annual variability

We used the same methodology as used in Part 1 to calculate the density and temporal variability (CV) of bird and butterfly species. The only difference was that we limited our analysis to species with data available for > 30 sites because a relatively large number of sites is required to test for an interaction effect between two explanatory variables with reasonable statistical power. This resulted in 79 bird species from the BBS scheme, 29 bird species from the CBC scheme (with the exception of three, a subset of the BBS species) and 32 butterfly species. Each species was classified by expert opinion into three groups of broadleaved woodland association: specialist (broadleaved woodland as primary habitat), generalist (broadleaved woodland as a marginal habitat) and 'non-woodland' species (rarely found in broadleaved woodland; Appendix P2).

4.2.2 Calculating landscape woodland metrics

We calculated the area of broadleaved woodland in 2km radii around bird and butterfly monitoring sites. For each site we also calculated three configuration metrics: ED- mean Euclidean nearest neighbour distance between woodland patches, SHP- mean shape index (perimeter of patch divided by the minimum possible perimeter given the patch area) and PD- patch density. We tested for collinearity between woodland area and the different configuration metrics and in no case did it prohibit including the variables as regression covariates (Pearsons R: area-ED = -0.44; area-SHP = 0.55; area-PD = 0.47).

4.2.3 Statistical analysis

For each species, we fitted three separate regression models with woodland area and woodland configuration measured by one of the three metrics as explanatory variables, along with an interaction term (see equation [1] for an example). Due to the large number of statistical tests carried out, we did not assess significance of interaction terms using model p-values. Instead, we used a weight of evidence approach whereby we asked if the total number of interaction terms with magnitudes of t-value > 2 was greater than expected by chance. With a reasonable sample size per test as in this study, one would expect type 1 error rates of 0.05 when $|t| = 2$, i.e. a 5% chance of wrongly rejecting the null hypothesis. Hence, given the total number of tests, we calculated the expected number of interaction terms with $|t| > 2$ versus the number actually observed. We compared these proportions using a proportion test (Crawley, 2007) to consider whether there was good evidence for an interaction effect between woodland area and configuration on population density. We repeated the analyses with inter-annual population variability as a response variable.

$$N \sim \alpha + \beta_1 \mathrm{AreaBW} + \beta_2 \mathrm{ConfigBW} + \beta_3 \mathrm{AreaBW{:}ConfigBW} \qquad [1]$$

Where N = mean population density, AreaBW = area of broadleaved woodland in 2km radius and ConfigBW = configuration of broadleaved woodland in 2km radius measured by one of three metrics (ED, SHP or PD). The coefficient β_3 and its associated t-value indicates the evidence for an interaction effect between woodlan area and configuration on population density.

In the absence of strong evidence for interaction effects (see Results), for each species, we fitted three separate additive regression models with woodland area and woodland configuration as explanatory variables, with population density as the response variable (i.e. one model for each different configuration metric). To assess the main effects of woodland area and the different configuration metrics across species, we again used a weight of evidence approach. We tallied the number of positive slope coefficients versus negative slope coefficients across species and tested whether they were significantly different using a binomial test. We repeated the analyses with log(CV) variability as a response variable. In this case, because we were interested in inter-annual population variability, we included time series duration, log mean abundance and the magnitude of the log-linear trend in abundance as additional covariates to control for these biases (see *Calculating population density and inter-annual variability* section in Part 1).

Finally, to compare the relative importance of woodland area and configuration metrics as predictors of population density, we considered the magnitude of t-values for these variables from the additive mode described above. We compared the number of cases where the magnitude of t-value for the area variable was greater than then for the configuration variable using a binomial test (Crawley, 2007). We then repeated the analysis with inter-annual population variability as a response variable.

4.3 Results

4.3.1 Interaction effect between woodland area and configuration on population density

There was little evidence for an interaction effect between woodland area and configuration on the population density of butterflies and birds. The number of interaction slopes with $|t|>2$ was never significantly greater than that expected from the number of tests conducted (Table 1). In total, across butterflies and birds (BBS and CBC surveys), 420 single-species models were fitted to test for an interaction between woodland area and configuration on the population density. Of these tests, only 34 had an interaction term with $|t|>2$, which was not significantly greater from the 33 expected under the null hypothesis (Table 1).

4.3.2 Interaction effect between woodland area and configuration on inter-annual variability

There was little evidence for an interaction effect between woodland area and configuration on the inter-annual variability of butterfly and bird populations. The number of interaction slopes with $|t|>2$ was never significantly greater than that expected from the number of tests conducted (Table 1). In total, across butterflies and birds (BBS and CBC surveys), 420 single-species tests were made for an interaction between woodland area and configuration on inter-annual population variability. Of these tests, only 21 had an interaction term with |t|>2, which was not significantly different from the 33 expected under the null hypothesis (Table 1).

4.3.3 Main effects of woodland area on population density

In additive models with woodland area and configuration as explanatory variables (i.e. holding the effect on woodland configuration constant) there was a strong positive association between woodland area and population density for woodland specialist species (summary results across both birds and butterflies can be found in Table 2). This result mainly arose from the response of bird species in the BBS survey (Table 3). In contrast, there were no clear associations between woodland area and population density for butterfly woodland specialists nor for bird woodland specialists using data from the CBC survey.

For woodland generalist species there was also some evidence of a positive association between woodland area and population density (Table 2). Once again, this pattern was driven by the strong relationships for bird species in the BBS survey (Table 3). There were no clear associations between woodland area and population density for butterfly woodland generalists or for bird woodland generalists using data from the CBC survey.

For species previously classified as ‘non-woodland’ species, there was a strong negative association between woodland area and population density (Table 2). This relationship was strongest and most consistent for bird species in the BBS survey (Table 3). For ‘non-woodland’ butterflies and birds using the CBC data, there was also some evidence of negative relationships between woodland area and population density. For each species group, the number of negative relationships was significantly greater than positive relationships for only one out of three models (the additive model with the nearest neighbour configuration metric as a covariate for butterflies and patch density configuration metric as a covariate for CBC birds. However, models with other configuration metrics as covariates showed qualitatively similar, but non-significant, trends.

4.3.4 Main effects of woodland area on inter-annual population variability

In additive models with woodland area and configuration as explanatory variables (i.e. holding the effect on woodland configuration constant), for woodland specialist species, across all species groups, there was no evidence for a consistent association between woodland area and inter-annual population variability (Table 2), nor were any trends for individual species groups significant (Table 3). For woodland generalists, there was a significant negative association between woodland area and inter-annual population variability, suggesting large areas of woodland can promote more stable populations (Table 2). This negative relationship was strongest for birds using data from the CBC survey. Butterflies and birds using the BBS survey did not show significant effects individually, although trends in these groups were qualitatively similar (Table 3).

Across all species groups, for ‘non-woodland species’, there was no evidence for a consistent association between woodland area and inter-annual population variability (Table 2). However, considering the species groups individually, butterflies showed some evidence for a positive relationship between woodland area and inter-annual population variability (Table 3).

4.3.5 Main effects of woodland configuration on population density

In additive models with woodland area and configuration as explanatory variables (i.e. holding the effect on woodland area constant), for woodland specialist species, across all species groups, there was no evidence for a consistent association between the configuration of woodland patches and population density (Table 2). However, considering the species groups individually, significant relationships did occur for birds using data from the CBC survey (Table 4). For this group the direction of effect differed depending on the configuration metric used. There was a strong negative relationship between both mean nearest neighbour distance (ED) and mean shape index (SHP) on bird population density, i.e. higher bird densities were associated with landscapes with less isolated woodland patches and those with a lower perimeter to area ratio (less ‘edgy’ patches). In contrast, there was a strong positive association between the density of woodland patches (PD) and population density, i.e. higher bird densities occurred when the woodland in landscapes was fragmented into many smaller woodland patches.

Across all species groups, for woodland generalist species, there was no evidence for a consistent association between the configuration of woodland patches and population density (Table 2). However, considering the species groups individually, significant relationships did occur for two of the groups. Once again, the direction of the effect differed depending on the configuration metric used. For butterflies, there was a significant negative relationship between mean shape index and population density, i.e. smaller populations were found in landscapes where the woodland was more ‘edgy’ (Table 4). In contrast, there was a strong positive association between the density of woodland patches and population density. For birds using data from the CBC survey, there was also a strong positive association between the density of woodland patches and population density. These results for butterfly and bird generalists mirror those found for specialist bird species (CBC data) described above. Also the bird generalists using data from the BBS survey showed qualitatively similar trends, although these were not significant (Table 4).

For ‘non-woodland’ species, there was no consistent association between woodland configuration and population density across all species groups (Table 2), nor were trends significant for any individual species group (Table 4).

4.3.6 Main effects of woodland configuration on inter-annual population variability

In additive models with woodland area and configuration as explanatory variables (i.e. holding the effect on woodland area constant), for woodland specialist species, across all species groups, there was a negative association between the configuration of woodland patches and population inter-annual variability (Table 2). However, the only group with individually significant trends were the birds using data from the CBC survey. For this group, there was a strong negative association between woodland patch density and population inter-annual variability, i.e. landscapes with a greater number of woodland patches were associated with less variable bird populations.

Across all species groups, for woodland generalist species, there was no evidence for a consistent relationship between the configuration of woodland patches and inter-annual population variability (Table 2). However, considering the species groups individually, significant relationships did occur for birds using data from the CBC survey (Table 4). For these species, there was a significant positive relationship between the mean shape index of woodland and inter-annual population variability, i.e. landscapes where woodland is more ‘edgy’ were associated with more variable populations. In contrast, there was a negative relationship between woodland patch density and inter-annual population variability, i.e. populations were less variable where woodland was fragmented into many smaller patches.

For ‘non-woodland’ species, there was no consistent association between woodland configuration and inter-annual population variability across all species groups (Table 2), nor were trends significant for any individual species group (Table 4).

4.3.7 Comparison of the explanatory power of area and configuration metrics

Across species groups, for woodland specialist and woodland generalist species, there were no clear differences in the ability of woodland area and configuration metrics in explaining population density (Table 5). However, there were differences between in the relative explanatory power between species groups. For birds using the BBS survey, woodland area was most often the best predictor of population density (Table 6). This was particularly apparent when the ED metric was used to assess woodland configuration. For specialist and generalist butterflies and CBC birds there were no clear differences in the explanatory power of area and configuration metrics.

Across species groups, for ‘non-woodland’ species, woodland area was significantly better in predicting population density than the configuration metrics (Table 5). All individual species groups with all configuration metrics tested showed this qualitative pattern, although only for CBC birds was it individually significant (Table 6).

Across species groups, there were no clear differences in the explanatory power of woodland area and configuration metrics with regards to inter-annual population variability, regardless of species woodland associations (i.e. specialist, generalist or ‘non-woodland’ species; Table 5). There were also no clear differences when species groups and the different configuration metrics were considered separately (Table 6).

4.4 Discussion

In this study, we found evidence for additive effects of broadleaved woodland area and configuration on the population density and inter-annual variability of bird and butterfly populations, but no evidence for an interaction effect. Previous studies have suggested that the configuration of habitat may only be relevant when there are small amounts of habitat in the landscape (Andrén, 1994, Opdam and Wascher, 2004). Testing across a large number of bird and butterfly species (113 in total) we found little evidence for such interaction effects. Of course, we have only tested three configuration metrics in this study at a range of 2km around sites. Further work might consider other metrics at other spatial scales. However, the configuration metrics that were chosen are based on sound ecological theory to have effects on species’ populations, and were therefore good candidate metrics to test for interactions with area (Hanski, 1999).

In the absence of an interaction effect, there were still strong main effects of both woodland area and configuration on the population density and inter-annual variability of bird and butterfly populations. As expected, woodland area had positive effects on the density of woodland specialist and generalist species, particularly for birds in the BBS survey. This supports **Hypothesis 5a** (Report Introduction) suggesting that the area of species’ key habitat types in the local landscape will be positively correlated with the mean density. Larger areas of woodland in landscapes around sites are likely to provide more resources and a greater number of good quality nest sites. Woodland area also had an effect on species that were *a priori* classified as ‘non-woodland’ species. For these species, large areas of woodland in landscapes were associated with lower densities. Although we initially expected no strong effect of woodland area on these species, the results make sense because large areas of woodland mean a reduction in the amount of suitable habitat for non-woodland species. This result highlights that, despite Britain having low overall broadleaved woodland cover (6 % in 2007; Countryside Survey, 2008), high woodland cover locally can be detrimental for species not adapted to it.

As well as promoting larger populations, the area of woodland in landscapes was also associated with more stable populations (lower inter-annual variability). This supports **Hypothesis 5b** suggesting that the area of species’ key habitat types in the local landscape will be correlated with population resilience. Interestingly this pattern was much more evident for woodland generalist than specialist species. This counters **Hypothesis 7,** which suggested that the area and connectivity of key habitat types in landscapes will be more important for specialist rather than generalist species. It may be that woodland facilitates movement of generalist species, thereby allowing recovery from local population declines on sites. Alternatively, large areas of woodland may provide buffers to generalist species in reducing sensitivity to extreme weathers (for example, woodland habitats are cooler and might provide shelter and resources in drought years; Suggitt *et al*., 2011). The fact that a marginal (non-primary) habitat type is important for population stability fits with the contention that a diverse range of broad habitat types (of those used by species) can be important for maintaining stable populations (Oliver *et al*., 2010).

In addition to the effect of woodland area, the configuration of woodland patches was also sometimes correlated with population density and inter-annual variability. However, the direction of the relationship varied depending on the configuration metric used. Hence, there was equivocal support for **Hypotheses 6a and 6b** suggesting that ecological networks defined by the connectivity of species' key habitats are associated with increases mean density and population resilience. Increased isolation and 'edginess' of woodland patches was associated with lower population densities and more variable populations. In contrast, an increased density of woodland patches (independent of woodland area) was associated with larger and more stable populations. Such opposing effects of configuration metrics were unexpected. Many species are known to be sensitive to edge effects, where an increased perimeter to area ratio reduces habitat quality (Paton, 1994, Owens and Wilson, 1999, Fahrig *et al*., 2010). Also, isolated of habitat patches are often less likely to be used due to reduced connectivity (Thomas *et al*., 2001). However, usually the fragmentation of patches (here defined as the number of patches for a given area of habitat) is expected to lead to lower densities (Andrén, 1994). Our results suggest that, for butterflies and birds, landscapes with more patches of woodland tend to have higher densities (and for birds the populations tend to be more stable). One possible reason for higher population densities measured in landscapes with smaller woodland patches might be sampling bias, where individuals are more apparent when woodland patches are smaller. However, this fails to explain why population inter-annual variability shows a negative relationship with patch density. Alternatively, our result may suggest that fragmentation is not necessarily detrimental to bird and butterfly populations, as long as patches are not too isolated or with too great a degree of 'edginess'. The relationship between patch density, 'edginess' and isolation and their combined effects on population density would make for interesting further work. Our results do suggest, however, that configuration of habitats *can* be important for population viability. Hodgson *et al*. (2011) stated that although habitat configuration has been shown to increase dispersal rates, this does not necessarily lead to increases in population variability. Here, we show habitat configuration can be important for maintaining stable populations, which are likely to be more persistent over time.

Finally, when comparing the relative importance of woodland area and configuration as predictors of population density we found that area was most often the best predictor of population density. This fits with the contention that habitat area has greater effects on population viability (at least measured by population density; Hodgson *et al*., 2011). However, with inter-annual population variability as the response variable there were no clear differences in the explanatory power of habitat area versus configuration.

In summary, this study suggests that both area and configuration are (additively) associated with the density and inter-annual variability of bird and butterfly populations, although area was most frequently the best predictor of population density (see Figure 1 for an example). Increasing habitat area is likely to be a win-win solution, increasing both population density and stability, with consequent reductions in population extinction risk. Configuration of woodland patches did affect populations but effects varied depending on the metric used.

Our results suggest that increasing habitat area will be the most reliable and effective way to increase population viability. It should be kept in mind, however, that this conclusion is based on a generalisation of results across species. Depending on their particular ecology, for certain individual species, habitat configuration may be more important than habitat area (see Figure 2 for an example). But, in general, and where conservation actions are aimed at multiple species, focussing on habitat area, rather than connectivity, would appear to offer greater returns.

Of course, when new habitat is created this alters the configuration of the existing habitat. So through new habitat creation, land managers have an opportunity to influence both metrics. Our results suggest that for bird and butterfly conservation, new woodland patches should not be too isolated from existing woodland and edge effects should be minimised (for example, avoiding thin linear stretches of woodland). From the perspective of conserving butterfly and bird populations, land managers should not necessarily be afraid of creating many patches of woodland, rather than single large patches, as long as the patches are not so small that they are mostly ‘edge’ habitats. Other types of species may of course have other habitat requirements. To conclude, this study supports the view that creating *more* (good quality) habitat should be a priority in conservation (Lawton *et al*., 2010). Spatially targeting new habitat can further increase benefits, but should be avoided if involves large costs that would reduce the total area of habitat able to be created.

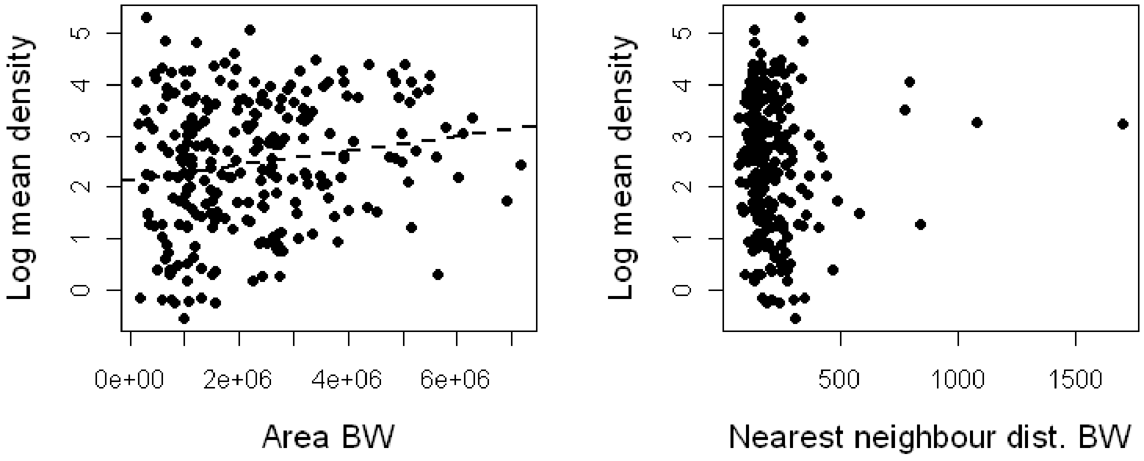

Figure 1: Individual species relationship between a) area of broadleaved woodland (BW; m^2), and b) nearest neighbour distance between woodland patches (ED; m) and mean population density of the brimstone butterfly *Gonepteryx rhamni* (L.). Woodland area had a significant association with log mean population density ($F_{1,246} = 6.85$, $p < 0.001$), whilst the configuration metric did not ($F_{1,246} = 0.09$, $p = 0.76$). Hence, it appears that the brimstone responds to woodland area more strongly than isolation.

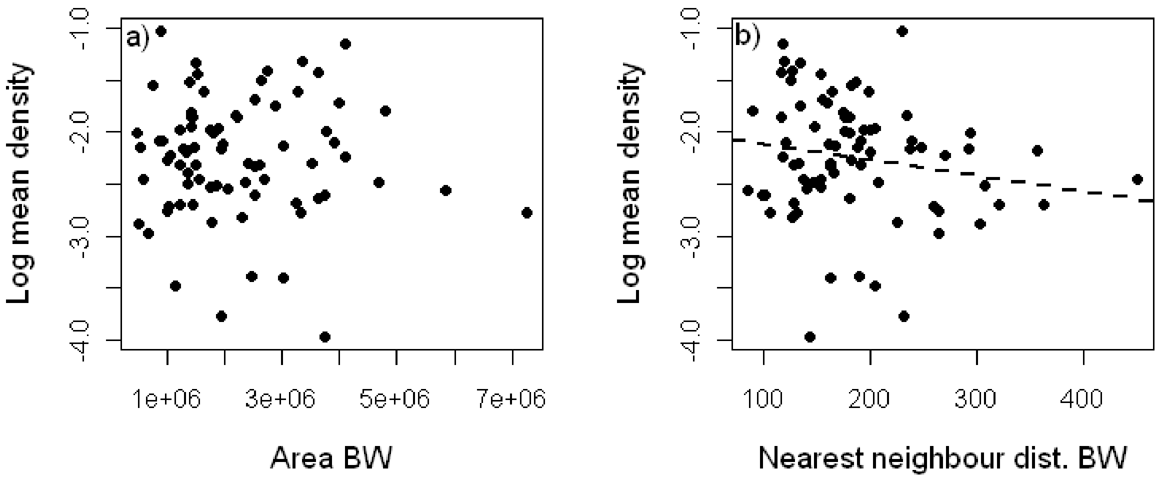

Figure 2: Individual species relationship between a) area of broadleaved woodland (BW; m^2), and b) nearest neighbour distance between woodland patches (ED; m) and mean population density of the long tailed tit *Aegithalos caudatus* L. from the CBC survey. Woodland area did not have a significant association with log mean population density ($F_{1,75} = 2.88$, $p = 0.093$), whilst the configuration metric did ($F_{1,75} = 5.45$, $p = 0.022$). Hence, it appears the long tailed tit responds to woodland isolation more strongly than woodland area.

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Table 1: Frequency of interaction effects between woodland area and configuration (2km radius around sites) on population density or inter-annual variability of bird and butterfly species. Woodland configuration was assessed using three metrics: ED- mean Euclidean nearest neighbour distance between woodland patches, SHP- mean shape index or PD- patch density in the 2km radius around sites. A separate model was fitted to each species in each group for each response variable. The total number of tests per group is listed along with the expected number of tests with |t|>2 under a null hypothesis of no interaction effect between the explanatory variables. The observed number of species' models with |t|>2 is compared to the expected number using a proportion test.

Species group	**Response variable**	**Woodland association**	**Configuration metric**	**Total number of tests**	**Observed |t|>2**	**Expected |t|>2**	χ^2	**df**	**p**
Birds (BBS)	Specialist	Density	ED	10	1	1	0	1	1
Birds (BBS)	Specialist	Density	SHP	10	2	1	0	1	1
Birds (BBS)	Specialist	Density	PD	10	0	1	0	1	1
Butterflies (UKBMS)	Specialist	Density	ED	5	0	1	0	1	1
Butterflies (UKBMS)	Specialist	Density	SHP	5	0	1	0	1	1
Butterflies (UKBMS)	Specialist	Density	PD	5	0	1	0	1	1
Birds (CBC)	Specialist	Density	ED	10	0	1	0	1	1
Birds (CBC)	Specialist	Density	SHP	10	0	1	0	1	1
Birds (CBC)	Specialist	Density	PD	10	0	1	0	1	1
Birds (BBS)	Specialist	Inter-annual variability	ED	10	0	1	0	1	1
Birds (BBS)	Specialist	Inter-annual variability	SHP	10	0	1	0	1	1
Birds (BBS)	Specialist	Inter-annual variability	PD	10	0	1	0	1	1
Butterflies (UKBMS)	Specialist	Inter-annual variability	ED	5	0	1	0	1	1
Butterflies (UKBMS)	Specialist	Inter-annual variability	SHP	5	0	1	0	1	1
Butterflies (UKBMS)	Specialist	Inter-annual variability	PD	5	0	1	0	1	1
Birds (CBC)	Specialist	Inter-annual variability	ED	10	0	1	0	1	1
Birds (CBC)	Specialist	Inter-annual variability	SHP	10	1	1	0	1	1
Birds (CBC)	Specialist	Inter-annual variability	PD	10	2	1	0	1	1
Birds (BBS)	Generalist	Density	ED	13	3	1	0.30	1	0.59
Birds (BBS)	Generalist	Density	SHP	13	6	1	3.13	1	0.08

Table continued…

Species group	**Response variable**	**Woodland association**	**Configuration metric**	**Total number of tests**	**Observed $\lvert t\rvert>2$**	**Expected $\lvert t\rvert>2$**	χ^2	**df**	**p**
Birds (BBS)	Generalist	Density	PD	13	3	1	0.30	1	0.59
Butterflies (UKBMS)	Generalist	Density	ED	16	1	1	0	1	1
Butterflies (UKBMS)	Generalist	Density	SHP	16	0	1	0	1	1
Butterflies (UKBMS)	Generalist	Density	PD	16	0	1	0	1	1
Birds (CBC)	Generalist	Density	ED	12	0	1	0	1	1
Birds (CBC)	Generalist	Density	SHP	12	0	1	0	1	1
Birds (CBC)	Generalist	Density	PD	12	0	1	0	1	1
Birds (BBS)	Generalist	Inter-annual variability	ED	13	4	1	0.99	1	0.32
Birds (BBS)	Generalist	Inter-annual variability	SHP	13	1	1	0	1	1
Birds (BBS)	Generalist	Inter-annual variability	PD	13	1	1	0	1	1
Butterflies (UKBMS)	Generalist	Inter-annual variability	ED	16	0	1	0	1	1
Butterflies (UKBMS)	Generalist	Inter-annual variability	SHP	16	0	1	0	1	1
Butterflies (UKBMS)	Generalist	Inter-annual variability	PD	16	0	1	0	1	1
Birds (CBC)	Generalist	Inter-annual variability	ED	12	1	1	0	1	1
Birds (CBC)	Generalist	Inter-annual variability	SHP	12	0	1	0	1	1
Birds (CBC)	Generalist	Inter-annual variability	PD	12	2	1	0	1	1
Birds (BBS)	Non-woodland species	Density	ED	56	5	3	0.13	1	0.71
Birds (BBS)	Non-woodland species	Density	SHP	56	6	3	0.48	1	0.49
Birds (BBS)	Non-woodland species	Density	PD	56	3	3	0	1	1
Butterflies (UKBMS)	Non-woodland species	Density	ED	11	1	1	0	1	1
Butterflies (UKBMS)	Non-woodland species	Density	SHP	11	0	1	0	1	1
Butterflies (UKBMS)	Non-woodland species	Density	PD	11	2	1	0	1	1
Birds (CBC)	Non-woodland species	Density	ED	7	0	1	0	1	1
Birds (CBC)	Non-woodland species	Density	SHP	7	1	1	0	1	1
Birds (CBC)	Non-woodland species	Density	PD	7	0	1	0	1	1
Birds (BBS)	Non-woodland species	Inter-annual variability	ED	56	1	3	0.26	1	0.61

Table continued…

Species group	Response variable	Woodland association	Configuration metric	Total number of tests	Observed |t|>2	Expected |t|>2	χ^2	df	p
Birds (BBS)	Non-woodland species	Inter-annual variability	SHP	56	4	3	0	1	1
Birds (BBS)	Non-woodland species	Inter-annual variability	PD	56	3	3	0	1	1
Butterflies (UKBMS)	Non-woodland species	Inter-annual variability	ED	11	0	1	0	1	1
Butterflies (UKBMS)	Non-woodland species	Inter-annual variability	SHP	11	0	1	0	1	1
Butterflies (UKBMS)	Non-woodland species	Inter-annual variability	PD	11	0	1	0	1	1
Birds (CBC)	Non-woodland species	Inter-annual variability	ED	7	0	1	0	1	1
Birds (CBC)	Non-woodland species	Inter-annual variability	SHP	7	1	1	0	1	1
Birds (CBC)	Non-woodland species	Inter-annual variability	PD	7	0	1	0	1	1

Table 2: Summary table for the frequency of positive and negative relationships between woodland area or configuration and population density or inter-annual variability of birds and butterflies. A binomial test was used to test whether the relationships were evenly distributed between positives and negatives. Also listed are the number of individually significant species relationships where |t|>2.

Explanatory variable	Response variable	Woodland association	Positive slopes	Negative slopes	p	Significant positive slopes	Significant negative slopes
Area of woodland	Density	Specialist	51	24	0.002	21	2
Area of woodland	Density	Generalist	69	54	0.207	32	16
Area of woodland	Density	Non-woodland species	55	167	<0.001	9	50
Area of woodland	Inter-annual variability	Specialist	40	35	0.644	0	3
Area of woodland	Inter-annual variability	Generalist	45	78	0.003	4	10
Area of woodland	Inter-annual variability	Non-woodland species	109	113	0.840	5	8
Configuration of woodland	Density	Specialist	37	38	1	6	5
Configuration of woodland	Density	Generalist	57	66	0.471	13	20
Configuration of woodland	Density	Non-woodland species	108	114	0.737	13	12
Configuration of woodland	Inter-annual variability	Specialist	28	47	0.037	2	2
Configuration of woodland	Inter-annual variability	Generalist	61	62	1	5	9
Configuration of woodland	Inter-annual variability	Non-woodland species	116	106	0.596	11	6

Table 3: Frequency of positive and negative relationships between woodland area and population density or inter-annual variability of bird and butterfly species. Additive models were fitted to each species in each group with broadleaved woodland area and woodland configuration (2km radius around sites) as explanatory variables (i.e. controlling for the effect of configuration to assess the effects of woodland area). Woodland configuration was assessed using three metrics: ED- mean Euclidean nearest neighbour distance between woodland patches, SHP- mean shape index or PD- patch density in the 2km radius around sites. A binomial test was used to test whether the relationships were evenly distributed between positives and negatives. Also listed are the number of individually significant species relationships where |t|>2.

Species group	**Response variable**	**Woodland association**	**Configuration metric**	**Positive slopes**	**Negative slopes**	**p**	**Significant positive slopes**	**Significant negative slopes**
Birds (BBS)	Density	Specialist	ED	9	1	0.021	6	0
Birds (BBS)	Density	Specialist	SHP	8	2	0.109	4	0
Birds (BBS)	Density	Specialist	PD	9	1	0.021	6	0
Butterflies (UKBMS)	Density	Specialist	ED	1	4	0.375	1	0
Butterflies (UKBMS)	Density	Specialist	SHP	4	1	0.375	1	0
Butterflies (UKBMS)	Density	Specialist	PD	3	2	1.000	1	0
Birds (CBC)	Density	Specialist	ED	3	7	0.344	0	1
Birds (CBC)	Density	Specialist	SHP	8	2	0.109	1	0
Birds (CBC)	Density	Specialist	PD	6	4	0.754	1	1
Birds (BBS)	Inter-annual variability	Specialist	ED	6	4	0.754	0	2
Birds (BBS)	Inter-annual variability	Specialist	SHP	5	5	1.000	0	0
Birds (BBS)	Inter-annual variability	Specialist	PD	5	5	1.000	0	1
Butterflies (UKBMS)	Inter-annual variability	Specialist	ED	2	3	1.000	0	0
Butterflies (UKBMS)	Inter-annual variability	Specialist	SHP	3	2	1.000	0	0
Butterflies (UKBMS)	Inter-annual variability	Specialist	PD	4	1	0.375	0	0
Birds (CBC)	Inter-annual variability	Specialist	ED	6	4	0.754	0	0
Birds (CBC)	Inter-annual variability	Specialist	SHP	4	6	0.754	0	0
Birds (CBC)	Inter-annual variability	Specialist	PD	5	5	1.000	0	0
Birds (BBS)	Density	Generalist	ED	12	1	0.003	8	0
Birds (BBS)	Density	Generalist	SHP	11	2	0.022	9	0
Birds (BBS)	Density	Generalist	PD	12	1	0.003	8	0
Butterflies (UKBMS)	Density	Generalist	ED	6	10	0.454	2	5
Butterflies (UKBMS)	Density	Generalist	SHP	8	8	1.000	3	3

Table continued…

Species group	Response variable	Woodland association	Configuration metric	Positive slopes	Negative slopes	p	Significant positive slopes	Significant negative slopes
Butterflies (UKBMS)	Density	Generalist	PD	6	10	0.454	2	6
Birds (CBC)	Density	Generalist	ED	4	8	0.388	0	1
Birds (CBC)	Density	Generalist	SHP	7	5	0.774	0	0
Birds (CBC)	Density	Generalist	PD	3	9	0.146	0	1
Birds (BBS)	Inter-annual variability	Generalist	ED	4	9	0.267	1	1
Birds (BBS)	Inter-annual variability	Generalist	SHP	5	8	0.581	1	1
Birds (BBS)	Inter-annual variability	Generalist	PD	4	9	0.267	1	3
Butterflies (UKBMS)	Inter-annual variability	Generalist	ED	5	11	0.210	0	1
Butterflies (UKBMS)	Inter-annual variability	Generalist	SHP	8	8	1.000	1	1
Butterflies (UKBMS)	Inter-annual variability	Generalist	PD	6	10	0.454	0	1
Birds (CBC)	Inter-annual variability	Generalist	ED	6	6	1.000	0	0
Birds (CBC)	Inter-annual variability	Generalist	SHP	2	10	0.039	0	2
Birds (CBC)	Inter-annual variability	Generalist	PD	5	7	0.774	0	0
Birds (BBS)	Density	Non-woodland species	ED	14	42	<0.001	3	14
Birds (BBS)	Density	Non-woodland species	SHP	17	39	0.005	4	15
Birds (BBS)	Density	Non-woodland species	PD	13	43	<0.001	2	13
Butterflies (UKBMS)	Density	Non-woodland species	ED	1	10	0.012	0	1
Butterflies (UKBMS)	Density	Non-woodland species	SHP	4	7	0.549	0	1
Butterflies (UKBMS)	Density	Non-woodland species	PD	3	8	0.227	0	2
Birds (CBC)	Density	Non-woodland species	ED	2	5	0.453	0	1
Birds (CBC)	Density	Non-woodland species	SHP	1	6	0.125	0	2
Birds (CBC)	Density	Non-woodland species	PD	0	7	0.016	0	1
Birds (BBS)	Inter-annual variability	Non-woodland species	ED	26	30	0.689	0	1
Birds (BBS)	Inter-annual variability	Non-woodland species	SHP	23	33	0.229	1	4
Birds (BBS)	Inter-annual variability	Non-woodland species	PD	23	33	0.229	1	2
Butterflies (UKBMS)	Inter-annual variability	Non-woodland species	ED	10	1	0.012	1	0
Butterflies (UKBMS)	Inter-annual variability	Non-woodland species	SHP	9	2	0.065	1	0
Butterflies (UKBMS)	Inter-annual variability	Non-woodland species	PD	8	3	0.227	1	0
Birds (CBC)	Inter-annual variability	Non-woodland species	ED	3	4	1.000	0	0
Birds (CBC)	Inter-annual variability	Non-woodland species	SHP	3	4	1.000	0	1
Birds (CBC)	Inter-annual variability	Non-woodland species	PD	4	3	1.000	0	0

Table 4: Frequency of positive and negative relationships between woodland configuration and population density or inter-annual variability of bird and butterfly species. Additive models were fitted to each species in each group with broadleaved woodland area and woodland configuration (2km radius around sites) as explanatory variables (i.e. controlling for the effect woodland area to assess effects of configuration). Woodland configuration was assessed using three metrics: ED- mean Euclidean nearest neighbour distance between woodland patches, SHP- mean shape index or PD- patch density in the 2km radius around sites. A binomial test was used to test whether the relationships were evenly distributed between positives and negatives. Also listed are the number of individually significant species relationships where |t|>2.

Species group	Response variable	Woodland association	Configuration metric	Positive slopes	Negative slopes	p	Significant positive slopes	Significant negative slopes
Birds (BBS)	Density	Specialist	ED	5	5	1.000	0	0
Birds (BBS)	Density	Specialist	SHP	8	2	0.109	1	1
Birds (BBS)	Density	Specialist	PD	6	4	0.754	2	1
Butterflies (UKBMS)	Density	Specialist	ED	3	2	1.000	0	0
Butterflies (UKBMS)	Density	Specialist	SHP	1	4	0.375	0	0
Butterflies (UKBMS)	Density	Specialist	PD	3	2	1.000	0	0
Birds (CBC)	Density	Specialist	ED	1	9	0.021	0	1
Birds (CBC)	Density	Specialist	SHP	1	9	0.021	0	2
Birds (CBC)	Density	Specialist	PD	9	1	0.021	3	0
Birds (BBS)	Inter-annual variability	Specialist	ED	3	7	0.344	1	0
Birds (BBS)	Inter-annual variability	Specialist	SHP	5	5	1.000	0	0
Birds (BBS)	Inter-annual variability	Specialist	PD	7	3	0.344	1	0
Butterflies (UKBMS)	Inter-annual variability	Specialist	ED	0	5	0.063	0	1
Butterflies (UKBMS)	Inter-annual variability	Specialist	SHP	2	3	1.000	0	0
Butterflies (UKBMS)	Inter-annual variability	Specialist	PD	1	4	0.375	0	0
Birds (CBC)	Inter-annual variability	Specialist	ED	5	5	1.000	0	0
Birds (CBC)	Inter-annual variability	Specialist	SHP	4	6	0.754	0	0
Birds (CBC)	Inter-annual variability	Specialist	PD	1	9	0.021	0	1
Birds (BBS)	Density	Generalist	ED	3	10	0.092	1	6
Birds (BBS)	Density	Generalist	SHP	3	10	0.092	0	4
Birds (BBS)	Density	Generalist	PD	9	4	0.267	8	2
Butterflies (UKBMS)	Density	Generalist	ED	9	7	0.804	1	1
Butterflies (UKBMS)	Density	Generalist	SHP	1	15	0.001	0	5

Table continued…

Species group	**Response variable**	**Woodland association**	**Configuration metric**	**Positive slopes**	**Negative slopes**	**p**	**Significant positive slopes**	**Significant negative slopes**
Butterflies (UKBMS)	Density	Generalist	PD	13	3	0.021	1	0
Birds (CBC)	Density	Generalist	ED	4	8	0.388	0	0
Birds (CBC)	Density	Generalist	SHP	4	8	0.388	0	2
Birds (CBC)	Density	Generalist	PD	11	1	0.006	2	0
Birds (BBS)	Inter-annual variability	Generalist	ED	5	8	0.581	0	1
Birds (BBS)	Inter-annual variability	Generalist	SHP	8	5	0.581	1	0
Birds (BBS)	Inter-annual variability	Generalist	PD	5	8	0.581	1	1
Butterflies (UKBMS)	Inter-annual variability	Generalist	ED	6	10	0.454	0	2
Butterflies (UKBMS)	Inter-annual variability	Generalist	SHP	7	9	0.804	0	1
Butterflies (UKBMS)	Inter-annual variability	Generalist	PD	9	7	0.804	1	1
Birds (CBC)	Inter-annual variability	Generalist	ED	9	3	0.146	2	0
Birds (CBC)	Inter-annual variability	Generalist	SHP	11	1	0.006	0	0
Birds (CBC)	Inter-annual variability	Generalist	PD	1	11	0.006	0	3
Birds (BBS)	Density	Non-woodland species	ED	21	35	0.081	4	7
Birds (BBS)	Density	Non-woodland species	SHP	34	22	0.141	3	2
Birds (BBS)	Density	Non-woodland species	PD	26	30	0.689	5	2
Butterflies (UKBMS)	Density	Non-woodland species	ED	2	9	0.065	0	0
Butterflies (UKBMS)	Density	Non-woodland species	SHP	5	6	1.000	0	1
Butterflies (UKBMS)	Density	Non-woodland species	PD	6	5	1.000	0	0
Birds (CBC)	Density	Non-woodland species	ED	4	3	1.000	1	0
Birds (CBC)	Density	Non-woodland species	SHP	4	3	1.000	0	0
Birds (CBC)	Density	Non-woodland species	PD	6	1	0.125	0	0
Birds (BBS)	Inter-annual variability	Non-woodland species	ED	27	29	0.894	0	1
Birds (BBS)	Inter-annual variability	Non-woodland species	SHP	31	25	0.504	3	1
Birds (BBS)	Inter-annual variability	Non-woodland species	PD	33	23	0.229	3	2
Butterflies (UKBMS)	Inter-annual variability	Non-woodland species	ED	6	5	1.000	0	0
Butterflies (UKBMS)	Inter-annual variability	Non-woodland species	SHP	2	9	0.065	1	1
Butterflies (UKBMS)	Inter-annual variability	Non-woodland species	PD	6	5	1.000	2	0
Birds (CBC)	Inter-annual variability	Non-woodland species	ED	5	2	0.453	1	0
Birds (CBC)	Inter-annual variability	Non-woodland species	SHP	5	2	0.453	1	0
Birds (CBC)	Inter-annual variability	Non-woodland species	PD	1	6	0.125	0	1

Table 5: Comparison of woodland area and configuration as predictors of population density and inter-annual variability across bird and butterfly species. Both area and configuration were predictors in an additive model for each bird and butterfly species. The predictive power of each was assessed by the magnitude of the respective t-value in the model. Detailed are the number of species for which each variable was the best predictor along with the p-value from a binomial test on the ratio.

Response variable	Woodland association	Number of cases area best predictor	Number cases configuration best predictor	p
Density	Specialist	43	32	0.248
Density	Generalist	68	55	0.279
Density	Non-woodland species	134	88	0.002
Inter-annual variability	Specialist	34	41	0.489
Inter-annual variability	Generalist	63	60	0.857
Inter-annual variability	Non-woodland species	107	115	0.636

Table 6: Comparison of woodland area and configuration as predictors of population density and inter-annual variability for birds and butterflies. Both area and configuration were predictors in an additive model for each bird and butterfly species. The predictive power of each was assessed by the magnitude of the respective t-value in the model. Detailed are the number of species for which each variable was the best predictor, along with the p-value from a binomial test on the ratio.

Species group	Response variable	Woodland association	Configuration metric	Number of cases area best predictor	Number of cases configuration best predictor	p
Birds (BBS)	Specialist	Density	ED	10	0	0.002
Birds (BBS)	Specialist	Density	SHP	7	3	0.344
Birds (BBS)	Specialist	Density	PD	9	1	0.021
Butterflies (UKBMS)	Specialist	Density	ED	3	2	1.000
Butterflies (UKBMS)	Specialist	Density	SHP	1	4	0.375
Butterflies (UKBMS)	Specialist	Density	PD	2	3	1.000
Birds (CBC)	Specialist	Density	ED	4	6	0.754
Birds (CBC)	Specialist	Density	SHP	4	6	0.754
Birds (CBC)	Specialist	Density	PD	3	7	0.344
Birds (BBS)	Specialist	Inter-annual variability	ED	4	6	0.754
Birds (BBS)	Specialist	Inter-annual variability	SHP	5	5	1.000
Birds (BBS)	Specialist	Inter-annual variability	PD	5	5	1.000

Table continued…

Species group	Response variable	Woodland association	Configuration metric	Number of cases area best predictor	Number of cases configuration best predictor	p
Butterflies (UKBMS)	Specialist	Inter-annual variability	ED	1	4	0.375
Butterflies (UKBMS)	Specialist	Inter-annual variability	SHP	3	2	1.000
Butterflies (UKBMS)	Specialist	Inter-annual variability	PD	3	2	1.000
Birds (CBC)	Specialist	Inter-annual variability	ED	2	8	0.109
Birds (CBC)	Specialist	Inter-annual variability	SHP	7	3	0.344
Birds (CBC)	Specialist	Inter-annual variability	PD	4	6	0.754
Birds (BBS)	Generalist	Density	ED	11	2	0.022
Birds (BBS)	Generalist	Density	SHP	10	3	0.092
Birds (BBS)	Generalist	Density	PD	9	4	0.267
Butterflies (UKBMS)	Generalist	Density	ED	11	5	0.210
Butterflies (UKBMS)	Generalist	Density	SHP	7	9	0.804
Butterflies (UKBMS)	Generalist	Density	PD	12	4	0.077
Birds (CBC)	Generalist	Density	ED	4	8	0.388
Birds (CBC)	Generalist	Density	SHP	2	10	0.039
Birds (CBC)	Generalist	Density	PD	2	10	0.039
Birds (BBS)	Generalist	Inter-annual variability	ED	10	3	0.092
Birds (BBS)	Generalist	Inter-annual variability	SHP	8	5	0.581
Birds (BBS)	Generalist	Inter-annual variability	PD	10	3	0.092
Butterflies (UKBMS)	Generalist	Inter-annual variability	ED	4	12	0.077
Butterflies (UKBMS)	Generalist	Inter-annual variability	SHP	8	8	1.000
Butterflies (UKBMS)	Generalist	Inter-annual variability	PD	6	10	0.454
Birds (CBC)	Generalist	Inter-annual variability	ED	5	7	0.774
Birds (CBC)	Generalist	Inter-annual variability	SHP	8	4	0.388
Birds (CBC)	Generalist	Inter-annual variability	PD	4	8	0.388
Birds (BBS)	Non-woodland species	Density	ED	32	24	0.350
Birds (BBS)	Non-woodland species	Density	SHP	31	25	0.504
Birds (BBS)	Non-woodland species	Density	PD	31	25	0.504
Butterflies (UKBMS)	Non-woodland species	Density	ED	9	2	0.065
Butterflies (UKBMS)	Non-woodland species	Density	SHP	7	4	0.549
Butterflies (UKBMS)	Non-woodland species	Density	PD	8	3	0.227
Birds (CBC)	Non-woodland species	Density	ED	5	2	0.453

Table continued…

Species group	Response variable	Woodland association	Configuration metric	Number of cases area best predictor	Number of cases configuration best predictor	p
Birds (CBC)	Non-woodland species	Density	SHP	4	3	1.000
Birds (CBC)	Non-woodland species	Density	PD	7	0	0.016
Birds (BBS)	Non-woodland species	Inter-annual variability	ED	27	29	0.894
Birds (BBS)	Non-woodland species	Inter-annual variability	SHP	30	26	0.689
Birds (BBS)	Non-woodland species	Inter-annual variability	PD	25	31	0.504
Butterflies (UKBMS)	Non-woodland species	Inter-annual variability	ED	7	4	0.549
Butterflies (UKBMS)	Non-woodland species	Inter-annual variability	SHP	6	5	1.000
Butterflies (UKBMS)	Non-woodland species	Inter-annual variability	PD	6	5	1.000
Birds (CBC)	Non-woodland species	Inter-annual variability	ED	3	4	1.000
Birds (CBC)	Non-woodland species	Inter-annual variability	SHP	2	5	0.453
Birds (CBC)	Non-woodland species	Inter-annual variability	PD	1	6	0.125

Part 3: Are populations in well-connected sites protected from environmental change? A test using bird and butterfly monitoring data[2]

5.1 Introduction

Over recent years many forecasted maps of potential species distribution under different scenarios of climate change have been produced (for example, Huntley *et al*. 2007). The fact that predicted future ranges are remote from current ranges has prompted renewed interest in how species move though landscapes. Conservation practioners are keen to manage landscapes to promote such movements to enable species to respond to climate change. However, opinion is divided as the best way to achieve this. Proponents of connectivity conservation contend that for species to colonise their potential future range (for example, as predicted by a climate envelope model: Huntley *et al*. 2007) the landscape needs to support movement from occupied sites, potentially through unfavourable matrix habitat or linear features of favourable habitat (for example, Doerr *et al*. 2011). Others (for example, Hodgson *et al*. 2011) argue that management to maintain or create large patches of high quality habitat is the key to producing the population pressure needed to generate long distance dispersal. Larger, higher quality sites with a variety of local conditions may also support populations that are more resilient to climate extremes and change. These differing management options may all have value and were summarised in a series of principles (the “UK Biodiversity Partnership principles”, Hopkins *et al*. 2007) to guide UK conservation policy. A range of similar sets of principles have also been published internationally (Heller & Zavaleta 2009) and Smithers *et al*. (2008) have produced an expanded set for the England Biodiversity Strategy. Faced with the need to undertake potentially expensive management involving a multitude of landowners and occupiers there is a pressing need for empirical evidence to support the use of these principles and to help prioritise them.

Unfortunately, acquiring such evidence is difficult owing to the contemporary nature of the issue and the variable scale over which the processes may operate (for example, see Part 1). One approach to providing this evidence is to analyse long-term monitoring data and assess whether populations’ responses to recent weather patterns are mediated by the natural variation in landscape structure we see in the British countryside. In this study we consider two factors affecting population resilience: population sensitivity and recovery time. We define sensitivity as the extent of the site-specific perturbation of a species’ local population size from its long-term trajectory, for example due to an extreme climatic event (for example, a drought year, an exceptionally cold winter etc.); we define the recovery time (hereafter “recovery”) as the time taken for the population size to return to its previous trajectory. By assessing whether a population’s response to such events is limited or facilitated by aspects of the site and surrounding landscape, we hope to draw parallels with how similar aspects could limit or facilitate future resilience to incremental climate change. For example, if bird populations in woodlands with many nearby woodland patches recover more rapidly (shorter recovery time) than populations in isolated woodlands, this would suggest that promoting local habitat availability and connectivity will facilitate resilience and perhaps dispersal in response to future climate change. Also, considering extreme events has direct relevance because climate change scenarios include an increasing incidence of extreme events.

In this study, we examine the population changes on individual sites of UK bird and butterfly monitoring schemes and relate measures of population resilience to estimates of the extent, diversity and configuration of the environment at the site and landscape scale. Specifically we test five hypotheses (note: numbering is consistent with other report sections):

H_{1b} Local (site) variation in habitat, soil type and topography are positively correlated with the resilience of populations as measured during recent periods of relative climatic variability and incremental change.

H_{2b} Area of key habitat types for species’ will be positively correlated with population resilience.

H_{4b} Landscape-scale variation in habitat, soil type and topography are positively correlated with the resilience of populations as measured during recent periods of relative climatic variability and incremental change.

H_{5b} The area of species' key habitat types in the local landscape will be positively correlated with population resilience.

H_{6b} Ecological networks defined by the connectivity of species' key habitats also increase the resilience of populations as measured during recent periods of relative climatic variability and incremental change.

Note that by our definition of sensitivity and recovery time, many of the expected relationships are actually negative. For example, more habitat should reduce sensitivity and reduce recovery time. The exception is isolation: more isolated patches should be more sensitive.

5.2 Methods

5.2.1 Data Sources

5.2.1.1 Time series data

Monitoring data were taken from two long running time series: bird data from the BTO Common Bird Census (CBC, Marchant *et al*. 1990) and butterfly data from the UK Butterfly Monitoring Scheme (UKBMS, Pollard & Yates 1993). Both schemes contain at least 20 years of data from the mid-1960s/1970s to at least 2000 and include several extremely cold winters and extreme drought summers which could have impacted on the two taxa in question. For both schemes, annual site-specific abundance estimates are based on intensive fieldwork throughout the spring and summer months. These multiple visits reduce the probability of missing individuals entirely and, whilst it is difficult to entirely rule out sampling error, the high intensity of fieldwork gives us confidence that observed changes in abundance closely reflect local population changes.

5.2.1.2

CBC sites were categorised as "woodland", "farmland" or "special", the last being a miscellaneous group of wetland and scrub sites. For the purposes of this analysis we needed to be able to identify similar habitat patches from remote sensed landcover data in order to assess configuration. We therefore concentrated this analysis on "woodland" CBC sites; "specials" were too few and of variable habitat composition and it was unclear how to treat "farmland" sites within the farmland matrix. CBC coverage of woodland plots ran from 1965 to 2000 but individual sites were surveyed for shorter periods (see below for minimum time series considerations). We concentrated on 24 bird species (Table 1) with known woodland associations ranging from woodland generalists such as Blackbird to woodland specialists such as Nuthatch (Newson *et al*. 2009). Our selection excluded species if there was uncertainty over data quality (for example, nocturnal species likely to have high sampling error) or if they were present on fewer than 20 sites. Sites with fewer than eight years of data or more than 25% missing values between the first and last year of the site's coverage were omitted. Further, random fluctuations of very scarce or difficult to detect species could mask subtle effects of quality and connectivity. For this reason, species were deleted from sites if during the course of the site's monitoring history the mean count was less than one individual per year.

UKBMS sites span a range of woodland, grassland and heathland habitats. Owing to this variable habitat composition, known associations of butterfly species and differences in the mean level of occupancy of sites between birds and butterflies, different rules were needed to determine which UKBMS sites and butterfly species could be analysed. Butterfly species were considered for analysis if they were present on at least 100 UKBMS sites and if on those sites they were present in at least 50% of surveyed years. This gave a set of 36 species with varying prevalence and specialism (Table 2).

5.2.1.3 Environmental data

To characterise environmental conditions at and around the monitoring sites we extracted data from three main sources (see General Methodology). For all variables we extracted data at four spatial scales using circles of radius 0.5km, 2km, 5km and 10km centred on each monitoring site in order to quantify the environment in the immediate vicinity of the site (0.5km radius) scaling up to the environment of the wider landscape. For assessing the diversity, availability and configuration of broad habitat types we used the 25m resolution parcel data from the Land Cover Map 2000 (LCM2000, Fuller *et al*. 2002). These data describe the location and size of contiguous patches of land of relatively uniform habitat or land use. LCM2000 contains 26 habitat types but for the purposes of this analysis we simplified these to 13 biotopes defined on more biological grounds (Table 3; see part 0 General Methodology for background). Within a GIS the boundaries between adjacent patches of the same biotope were dissolved and then for each biotope, within each circular buffer, the following were calculated: total % cover; number of distinct patches as a measure of patch density (*PATCHES(x)*), mean of nearest neighbour (Euclidean) distances for patches as a measure of patch isolation (*ISOLATION(x)*); mean shape index as a measure of the influence of edge habitat on interior habitat (*SHAPE(x)*). The last three metrics were calculated using the package Fragstats (McGarigal *et al*., 2002). Within each circular buffer size the % cover of the 13 biotopes were combined in to an index of biotope diversity using the Shannon-Weiner diversity index (*DIV*). In some respects the LCM2000 dataset is rather crude for this type of analysis. It has high spatial precision but its ability to discern subtle biological differences in habitats, to measure habitat quality, or to quantify linear features, is limited. These limitations must be borne in mind when interpreting the results.

For many invertebrate species microclimatic conditions can be important for survival. Data on microclimate were not available but since altitude and aspect are major determinants of variation in microclimate, we quantified these around each site using a 50m resolution Digital Elevation Model (DEM, Morris & Flavin 1990). After calculating aspect at each 50m interval we calculated the standard deviation of aspect at all points within the respective buffers to give measures of variation in aspect. Processing of aspect was undertaken in ArcGIS (version 9.3.1) with the easting component defined as sin((aspect×π)/180) and ranging from 1 (due East) to -1 (due West); similarly the northing component was defined as cos((aspect×□π)/180).

For certain terrestrial-foraging bird species, and invertebrates that rely on humid microclimatic conditions, variation in soil type with respect to their hydrological characteristics could be an important determinant of resilience to extreme temperatures. We used the 1-km resolution HOST dataset, a spatially referenced categorisation of soil by hydrology to determine a Shannon diversity index of soil types within the buffers as a quantitative measure of spatial variation in microclimate humidity. Note that it was not possible to calculate diversity at the site scale because the 500m buffer was smaller than the 1-km resolution of the HOST data (see General Methodology section of the Report).

5.2.2 Characterising local population changes

Two methods were adopted for identifying extreme events: “weather-derived” and “trend-derived”. For weather derived events and bird populations we considered cold winters. Birds are known to respond markedly to extreme winters and the period of CBC coverage was punctuated by several cold winters documented to have affected bird populations (for example, Marchant *et al*. 1990). We objectively identified the cold winters as the six greatest negative anomalies in the winter season daily minimum Central England Temperature series: 1969/70, 1978/79, 1981/82, 1984/85, 1990/91 and 1995/96 (see Figure 1a for an example). For butterflies we considered summer drought because rainfall is known to affect population growth rates in some butterfly species (Pollard *et al*. 1997; Roy *et al*. 2001). Recently the best documented summer drought with impacts on butterflies was the drought of 1995 and its impacts on butterfly populations in 1996. An earlier drought in 1976 has also received attention (Sutcliffe *et al*. 1997) but we concentrate on the later event for which we can extract contemporary soil moisture data. It should be noted that in previous analyses of these extreme events biologists have noted marked decreases in population size of some species (for example, small-bodied insectivorous birds), while other species appear largely immune or even increase (Morecroft *et al*. 2002). In this study, we initially measure sensitivity and recovery time in all species, rather than just those known to be sensitive, because it is possible that the apparent stability of the national trend conceals interesting fluctuations at the site-level.

Our second approach to identifying extreme events is an extension of this logic. Whilst biologists might note extreme weather events and effects in certain species, there may be more subtle combinations of conditions that are extreme for certain species but that escape human notice. These conditions need not necessarily be climatic. It might not be apparent what caused a significant drop in the national trend, but how the magnitude of the drop is manifested at the site level, and how quickly local populations recover, can still be informative for the wider question of how local and landscape features affect resilience. For a given species, these “trend-derived events” were identified as follows. First, an unsmoothed national trend was produced using a generalised linear model (Poisson errors and log link function) with site and year factors. Inter-annual changes were calculated as the arithmetic difference between consecutive year parameters. Extreme event years were defined as those in which the change in trend was negative and deviated by at least 1.5 standard deviations from the mean inter-annual change. An example of this process is shown in Figure 1b. Note that for some species this approach did not identify any events (for example, for a species showing a year on year increase) and for others one or more events were identified.

Once events had been identified, whether from weather data or from analysis of national trends, the following process was used to derive metrics of site-level population resilience. For species j at site i, counts were standardised by subtracting annual counts from the site’s mean count and dividing by its standard deviation so that changes could be compared among sites. Sensitivity, V_{ij}^{t}, was defined as the size of the decrease in observed count from the year prior to the event (year t-1) to the year following (or during) the event year (year t) at site i for species j. For example, for a severe event in winter 1969/70 we would assess the change in population size from breeding season 1969 to 1970. By this definition, a large decrease in population size is recorded as a large positive number; if the local population actually increased, the sensitivity would be recorded as negative, i.e. not sensitive. Monitoring sites are rarely surveyed for the whole duration of a monitoring scheme so inevitably some sites were not surveyed in year t or t-1 and it was not possible to calculate V_{ij}^{t} for all t and all j.

The calculation of Recovery time, R_{ij}^{t}, was slightly more involved due to the need to estimate the trend at a site in the absence of an extreme event, to allow the estimation of the time when a population could be said to have recovered. In the absence of any long-term trend this calculation would be simply the delay until the post-event count equalled or exceeded the pre-event count. However, many sites showed evidence of long-term population change. For this analysis we assumed that the count in each event year and its subsequent year (i.e. all t and t+1) were likely to be suppressed by the severe events. We estimated the site-specific long-term trend in the absence of these influential years by fitting a smoothing spline through the remaining standardised counts at each site. Smoothing was performed using a Generalised Additive Model (SAS/STAT Proc GAM) with the degrees of freedom set to the number of years surveyed divided by 4. Initial tests showed that this degree of smoothing produced a moderately smoothed trend that described the general long term trend without too closely following annual fluctuations (Figure 1). R_{ij}^{t} was defined as the number of years from the event year until the observed count was equal to or greater than the smoothed trend. Note that there were instances where R_{ij}^{t} was zero because the count in the event year was already greater than the smoothed trend. Note also that it made little sense to calculate recovery time if the population did not decrease. Therefore, R_{ij}^{t} was only calculated in those cases where V_{ij}^{t} was greater than zero. Due to this, and the fact that R_{ij}^{t} could not be calculated if the site ceased to be monitored in year t+1, the sample size for recovery time analyses was lower than for sensitivity analyses. We could have included all sites and set R_{ij}^{t} to zero for $V_{ij}^{t} \leq 0$ but to do so would have duplicated much of the variation already measured in V_{ij}^{t}. An example site-specific trend with each V_{ij}^{t} and R_{ij}^{t} illustrated is shown in Figure 1. These methods for measuring V_{ij}^{t} and R_{ij}^{t} were repeated for each event year t identified in each time series.

5.2.3 Statistical analysis

Species were said to be sensitive if V_{ij}^{t} was greater than zero in at least 50% of events (summed across all *j* sites and all *t* events). For all sensitive species a series of generalised linear models were undertaken to test the overall level of evidence for diversity and configuration influences on resilience. For CBC woodland bird species we separately related sensitivity and recovery time to habitat diversity, woodland cover, woodland patch density, woodland isolation and woodland shape index. For UKBMS butterfly species, in addition to habitat diversity we also tested soil diversity and variation in altitude and aspect. Separately for butterfly species defined as woodland species, grassland species, or heathland species, we related sensitivity and recovery time to cover, patch density, isolation and shape of the corresponding biotype.

For completeness, covariates were tested at all scales but only those covariates and scales relevant to the hypotheses were summarised. For example, hypothesis 1 concerned diversity/heterogeneity at the site-scale and correspondingly only tests performed on 500m buffer covariates are reported. For the landscape scale there was potentially a choice of three buffer sizes. Preliminary correlations of the explanatory variables showed that values in the 5000m buffer were moderately to highly correlated with the 2000m and 10000m buffers (Table S1). Therefore, for subsequent tabulations the 5000m buffer values were taken to represent landscape covariates (with 2000m and 10000m analyses presented in supplementary material for completeness).

Although the emphasis was on univariate tests of each diversity or configuration metric, other variables had to be included in models to control for certain patterns in the data. For instance, preliminary analyses revealed that sensitivity was correlated with count in the previous year suggesting some degree of density dependence. Greenwood and Baillie (1991) demonstrated density dependence in woodland bird populations from analyses of CBC data. To control for this potential density-dependence the count in the previous year was included in all models. Similarly, recovery time was positively correlated with sensitivity in some species because a greater fall in population size took longer to recover from. It was therefore, necessary to include the sensitivity term in GLMs testing recovery time.

The sensitivity index was symmetrically distributed and approached normality for all species, so could be modelled with an identity link and normal errors model structure. Recovery time, which was a count of the number of years to recovery, was more appropriately modelled with a log link and Poisson errors. The following four classes of model were produced:

Model V0: Sensitivity ~ count in previous year
Model V1: Sensitivity ~ count in previous year + *VAR*

Model R0: Recovery ~ Sensitivity
Model R1: Recovery ~ Sensitivity + *VAR*

where *VAR* is one of the n habitat or landscape covariates (for example, habitat diversity index). For each the correlation coefficient between observed values and predicted values was computed and the changes in correlation coefficient from V0 to V1 and from R0 to R1 were calculated to give an indication of the improvement in explanatory power with the addition of habitat or landscape covariates. More formally, the addition of covariates was tested using likelihood ratio tests and these are reported as $P>0.10$ non-significant; $0.10>P<0.05$ non-significant (marginal); $P<0.05$; $P<0.01$ and $P<0.001$.

For both indices of resilience there were potentially multiple measures for each site. For example, some sites were monitored through up to five focal cold winters, giving five estimates of sensitivity that could not be considered statistically independent. Rather than combine all data into a single mixed model, thereby potentially masking opposing, species-specific signals, we instead performed separate analyses for each species and for each detected event and then tallied the number of relationships by the direction and strength of the association. Results were summarised for each hypothesis by calculating t-values (parameter estimate divided by its standard error) and using the conventional threshold of |2| for significance. The number of positive relationships ($t \geq 2$), number of negative relationships ($t \leq -2$), and all remaining relationships was tallied for each variable, across species. For each hypothesis we also determined how many significant t-values would be expected by chance. Assuming $\alpha = 0.05$ we would expect 5% of the relationships to return a significant t-value in support of the hypothesis. This figure is tabulated to indicate whether more relationships were in agreement with the hypothesis than would be expected by chance.

5.3 Results

After the necessary filtering of data according to time series length, missing data, minimum abundance and prevalence of species we were left with 10 woodland specialist and 14 woodland generalist bird species (Table 1) on 153 CBC sites and 36 butterfly species (Table 2) on 548 UKBMS sites.

5.3.1 Quantifying resilience by estimating sensitivity and recovery time

Bird population resilience to weather-defined events

Of the 24 bird species considered five showed a decrease in population size in at least 50% of the measured events (Table 5, Figure 2). For example, across all the sites considered and the six winter events tested, Wren populations decreased (i.e. $V_{ij}^{t} > 0$) in 328 (80%) of the 412 changes considered. In 89% of the instances where a decrease occurred it took between two and five years for local populations to recover to pre-event levels. Similar patterns were apparent for the other four species showing significant sensitivity to cold winters. There was a significant negative correlation between the percentage of changes that were negative (i.e. sensitive species) and body mass ($r_s = -0.50$, P = 0.024, N = 20) indicating that small birds suffered more in cold winters. After controlling for body mass there was a significant effect of specialisation, with generalists showing a greater degree of sensitivity than specialists (binomial model of number of decrease events out of all events tested: likelihood ratio test of effect of specialisation $F_{1,17} = 11.1$, P=0.004).

5.3.2 Bird population resilience to trend-defined events

When events were defined from national trends, 13 species showed sensitivity on at least 50% of sites (Table 6, Figure 3). These 13 included the five species that responded to the cold winters, though only for Wren, Robin and Goldcrest did the event years detected from national trends include the known winter events, and then not exclusively. This suggests that there were other causes of events that were more important biologically than the perceived cold winters. This also indicates that results from trend-defined events are worthy of consideration in addition to those from known events. The year most commonly identified with events was 1973 (9 species), followed by 1982 and 1991 (both 6 spp) and 1979 and 1986 (both 5 spp). A repeat of the correlation between the percentage of changes that were negative and body mass was again significant (rs = -0.57, P = 0.004, N = 24) indicating that small-bodied bird species showed greater sensitivity than large-bodied species.

5.3.3 Butterfly population resilience to the 1995 drought

Twelve butterfly species showed significant sensitivity to the 1995 drought (Table 7, Fig 4). Of these the Ringlet, Specked Wood and the three “whites” were particularly sensitive with decreases detected in 72%, 67% and 75-90% of site-specific changes respectively (Table 7). Of these, Ringlet, Speckled Wood and Large White are accepted as being drought-intolerant. Conventionally, Small Tortoiseshell is also included in this category (Pollard *et al*. 1997) but in our analysis this was more moderately sensitive (52% of changes negative).

5.3.4 Butterfly population resilience to trend-defined events

When butterfly trends were analysed for trend-determined events we found significant sensitivity in all but 4 species (Table 8, Fig 5). The year most commonly identified with events was 1977 (11 species), followed by 1985 (9 spp), 1993 (8 spp), 1983 and 1998 (both 5 spp). In only two species did 1996 appear as a significant event when defined from the trends, suggesting that the 1995 drought was not necessarily the most important event, in terms of inter-annual changes, in the period under consideration. It is worth noting that a severe drought occurred in 1976 (Rodda & Marsh 2011), one year prior to the year when the largest number of species showed an event. Unfortunately, the UKBMS data only start in 1976 so do not allow us to test for a change from pre-1976 drought levels.

5.3.5 Predictors of population resilience

The majority of tests performed between sensitivity and local and landscape covariates were non-significant: for butterfly events determined from weather 90% of tests were non-significant ($P > 0.05$); 83% of tests resulted in $P > 0.1$. Equivalent figures for butterfly events determined from trends were: ns $P > 0.05$ = 90%, ns $P>0.1$ = 83%; figures for birds and weather events were: ns $P > 0.05$ = 92%, ns $P>0.1$ = 87%. Finally, figures for birds and trend-defined events were: ns $P > 0.05$ = 89%, ns $P>0.1$ = 81%. Results were similar when considering the performance of tests of recovery time and covariates. These figures indicate that there were few near-significant results. The following sections consider each hypothesis in turn.

Note that hypotheses 1 versus 4 and 2 versus 5 attempt to separate local from landscape effects. For the main analyses we chose the 500m and 5000m scales to reflect site and landscape. As illustrated by Table S1, most variables differed more between these scales than among the 2000m, 5000m and 10000m scales. The exceptions were altitude variation which was correlated at $r > 0.9$ across scales and habitat cover which was moderately correlated ($0.52 < r < 0.65$) between 500m and 5000m scales. Nevertheless, with the exception of altitude there was sufficient variation across scales to warrant considering the importance of local and landscape scales separately.

H_{1b} – *site-scale variation enhances resilience*

For H_1 we expected a negative relationship between sensitivity (or recovery time) and each of the measures of diversity or heterogeneity (i.e. variation in habitat, altitude, aspect and soil) . Across variables, species and methods in only five of 193 tests of sensitivity were the t-values greater than $|2|$ and in the expected direction; similarly only six of 156 tests of recovery time were in the expected direction (Table 9). In those cases where t-values were in the expected direction, the increase in predictive power between models with and without a diversity or heterogeneity variable was small (Table S5). For each variable, we expected one or two spurious results by chance and the degree of support was largely consistent with this (Table 9).

These results could be considered conservative if, for example, sampling error diminished our ability to detect effects using threshold-based tests. As a counter to that we also tallied the proportion of tests in the expected direction regardless of P-value or t-value threshold. Overall, 50% of the sensitivity tests, and 50% of the recovery time tests in Table 9 had parameter estimates in the expected direction. In conclusion, there was no appreciable support for heterogeneity in habitat, altitude, aspect or soil increasing resilience in species showing significant sensitivity.

When the analysis was broadened to include all species (i.e. not just those showing sensitivity on at least 50% of occasions) the results were similar. The only exception was some evidence for variation in northing aspect influencing butterfly recovery time from drought (Table S10).

H_{2b} – *site-scale area of key habitat enhances resilience*

The expectation was a negative relationship: more habitat at the site level ought to decrease sensitivity. There was no support for this hypothesis with the number of tests in the expected direction similar or less than the number of relationships expected by chance (Table 10) and relationships had poor predictive power (Table S6). Contrary to H_2, there was evidence that resilience to trend-defined events in butterfly populations decreased with increasing habitat cover (Table 10). Across all sensitivity tests, 48% of parameter estimates were in the expected direction, regardless of significance; the figure for recovery time tests was 53%. The only individual test with a high proportion of parameter estimates in the expected direction was the relationship between butterfly recovery time from weather events and habitat cover where 70% of tests were in the expected direction (but only one of which was significant: Table 10). The balance of evidence based on all species (Table S11) was similar.

H_{4b} – landscape-scale variation enhances resilience

As at the site scale, there was no evidence for or against the influence of heterogeneity in habitat, altitude, aspect or soil on sensitivity or recovery time at the landscape scale (Table 11, Table S7). These results were based on the 5000m buffer size but the same conclusion can be drawn from analyses performed at the 2000m and 10000m scale (Table S2). In general, results from all species again showed no support for hypothesis 5. The exception was three tests each showing a negative effect of altitudinal variation and northing aspect variation on butterfly sensitivity to drought (Table S12). Across sensitivity and recovery time tests, 48% and 44% of parameter estimates, respectively, were in the expected direction regardless of significance. The only examples of a strong bias in favour of parameter estimates in the expected direction was for northing aspect and butterfly recovery time from weather events (80% of parameter estimates) and soil diversity and butterfly sensitivity to weather events (73%).

H_{5b} – landscape-scale area of key habitat enhances resilience

The results at the landscape scale were identical to those at the site scale: no evidence for a beneficial effect of habitat area on resilience but some evidence for greater habitat cover leading to increased sensitivity and longer recovery time in butterfly populations (Table 12, Table S8). Again the results are robust to scale (Table S3). When analyses were broadened to all species, six butterfly species showed the expected effect of preferred habitat cover on the sensitivity to drought; all other tests were in accordance with random patterns (Table S13). Across sensitivity and recovery time tests, 42 and 49% of parameter estimates, respectively, were in the expected direction regardless of significance. Only the relationship between butterfly sensitivity to weather and habitat cover showed a strong bias in favour of negative parameter estimates (71%).

H_{6b} – landscape-scale configuration of key habitats enhances resilience

When considering only species showing sensitivity on 50% of occasions, there was little or no evidence in support of habitat configuration enhancing resilience (Table 13, Table S9) and these results were consistent across scales (Table S4). When broadened to all species there was some support for hypothesis 7, but also some evidence against (Table S14). Isolation and shape affected butterfly sensitivity to drought more often than expected; however, patch density had the opposite effect in nine species responding to drought and 14 cases of response to unknown trend-defined events (Table S14). Patch density was related to recovery time in four and five cases, respectively, in weather-defined and trend-defined events, respectively. All bird relationships in the expected direction occurred at the frequency expected by chance. Contrary to expectation, there were 13 cases of a positive effect of patch density on bird population sensitivity to weather events. Across sensitivity and recovery time tests, 34% and 52% of parameter estimates were in the expected direction regardless of significance. Of these, shape index was negatively related to butterfly sensitivity to weather events in 71% of cases; all other parameter estimates were more equivocal or tended to be in opposite direction.

5.4 Discussion

5.4.1 Characterising population resilience

These analyses were successful in so far as to characterise patterns of population change in relation to events of known and unknown cause. In this regard, it is interesting to note that for both birds and butterflies many of the trend-derived events were of equal or greater significance compared to the severe winters and droughts. The causes of these events are currently unknown but would warrant further study.

For butterflies, we concentrated on only the 1995 drought and its impact upon numbers in the 1996 breeding season. There may be other climatic events of both a negative and positive nature impacting on butterfly populations. It is noteworthy that there were extremely high counts of Peacock and Large White in 1992 which gave rise to apparent sensitivity due to the drop back down to more normal levels in 1993. Other butterfly species, for example the Green-veined and Small White, and to a lesser extent, Small Tortoiseshell, appeared to vary in a highly stochastic manner. Unlike bird populations, where the cold weather event occurred between monitoring periods, the summer drought occurred during the monitoring period. It is possible, therefore, that the butterfly counts in late spring/summer 1995 were directly affected. If this within-season impact was sufficiently large, 1995 would have arisen as one of the trend-determined events for butterfly species. In reality, this pattern was very rare and only one species (Small Blue) had a trend-determined event in 1995. Eleven species showed a trend-determined event in 1977. This is very near the beginning of the UKBMS time series but would tally with the severe drought of 1976. The collated indices of the UKBMS scheme rank 1977 as the third worst year (Botham *et al*. 2009).

For birds the known cold winters were defined objectively from temperature data and several events identified in this way agreed with previous studies of cold weather and bird population responses (for example, Marchant *et al*. 1990). The species for which weather events were identified were broadly the same as those discussed by others (Marchant *et al*. 1990; Gregory *et al*. 2007). Part of the difficulty in assessing the relationship between sensitivity and landscape as seen below may stem from differing responses to events. Although not one of the species considered here, Kingfisher was the species worst affected by the 1962/63 winter and again showed sensitivity in 1981/82 but did not do so in the winter of 1985/86 (Marchant *et al*. 1990). Marchant *et al*. (1990) discuss many features of the events (coldness, wind chill, ice) as well as their timing (for example, in relation to day length for feeding) and geographic extent (for example, in relation to refugia) which may dictate the impacts on different bird populations. Greenwood and Baillie (1991) correlated bird population changes with several weather variables and found that snow cover was often a better predictor of changes than temperature, suggesting that access to food is of critical importance. This highlights the importance, in analyses of weather effects, of choosing variables with which to define variation in weather that represent the key environmental influences on target species accurately.

Of the other events identified from bird populations, 1982, 1991 and 1979 were among the cold winter events tested separately. That these events were identified objectively from trends is reassuring. Similarly, the winter 1985/86 fell just below the threshold used here to define cold winters but this may explain why 1986 was identified as an event year for five species. The reason for the number of species showing an event in 1973 is unclear. It is also interesting to speculate what caused the events detected in trends of the four Afro-Palearctic migrants. The 1969 event for Spotted Flycatcher coincides with the largest detected spring decline in Whitethroat, which was attributed to drought in West Africa (Winstanley *et al*. 1974). Only one year was shared among migrants: 1991 for Chiffchaff and Blackcap. A small but increasing proportion of Britain's breeding populations of these species is resident. In 1991 it is unlikely that a significant proportion of Britain's breeding population remained to winter and, therefore, it is unlikely the cold 1990/91 winter was the cause of sensitivity, unless its influence extended to SW Europe where these birds may have wintered.

It is interesting to note that we found a greater degree of sensitivity among bird generalists than specialists. On the face of it this is contrary to expectation: we expected habitat specialists to be more sensitive. In reality we might expect the influence of habitat to be greater on specialists than on generalists, but we might not necessarily expect specialists to be more sensitive *per se* than generalists. Indeed other life history traits such as body size (as demonstrated) and diet (generalist/specialist, granivore/invertebrate feeder) may be more important in determining sensitivity than habitat specialism.

5.4.2 Relating resilience to local and landscape covariates

Although we were able to measure resilience successfully, we found no consistent strong support for the five hypotheses addressed. For each hypothesis, occasional individual tests were in the expected direction and, in total, equalled or slightly exceeded the number of responses expected by chance. In general, there was slightly more support for the hypotheses among butterfly populations than bird populations but this might merely reflect the greater number of variables tested for butterflies than birds (for example, landscape scale variation in altitude and aspect). It should be stressed that there are many influences on population size so the real quantitative effect of landscape variation may be small and thus difficult to detect. If this were true, one might expect a tendency for parameter estimates to be in the expected direction but non-significant. This was not the case, however: under each hypothesis tested there was an almost equal balance of positive and negative parameter estimates. On balance there appears to be little evidence for strong mediation of resilience to extreme events by local and landscape habitat diversity and configuration suggesting that there is little scope for active management to mitigate extreme events for these taxa.

5.4.3 No evidence or a failure to detect evidence?

There are several reasons why our ability to find strong support for the hypotheses may have been limited. Firstly, despite our use of intensive survey data, the population changes measured may still include stochastic variation that masks any habitat-induced signal. This is an inevitable consequence of trying to measure the response of a population, which is the summation of a variety of processes of which the mortality, movement and productivity of individual population members (and landscape influences thereon) is just one. The sensitivity to detect landscape influences may be improved by measuring individual movements directly, such as using bird ringing data or targeted field investigations.

A second problem is the difficulty in characterising the subtleties of habitat quality and configuration using remote-sensed data. For example, the remote-sensed landcover data used are undoubtedly crude for this purpose, being based on a human perception of the landscape and what constitutes and delimits patches. What we may consider two identical patches with intervening distances representing isolation may to a bird or butterfly species represent two different habitats and isolation is actually far greater. A related issue is the difficulty of measuring linear features from existing land cover data. For many woodland species hedgerows may act as a sufficiently functioning corridor as to connect some woodland patches. Currently, the presence of absence of connecting hedgerows cannot be assessed from landcover data. Other data sources such as LIDAR or the new (2007) Land Cover Map might facilitate a focused analysis of connectivity among an array of woodlands or other habitats using existing survey data. The availability and spatial coverage of LIDAR has increased and such analyses may now be feasible. However, it should be noted that the temporal mismatch between historical biodiversity data and contemporary habitat data will only increase with more recently collected habitat information and become more of a potential problem (i.e. a less reliable measure of the habitat as it affected the focal taxa historically) as newer data sources are employed. Alternatively, in conjunction with direct observation and/or ringing/tracking of individuals, LIDAR may offer a highly effective means of understanding movement through real landscapes. Such work should consider margin and hedgerow features of Environmental Stewardship which have the capacity to promote movements and may be an effective way to promote connectivity or soften the matrix of agricultural landscapes. These may also benefit species other than birds and butterflies for which we have not been able to test the importance of habitat diversity and configuration. For less mobile taxa habitat configuration may well be more important than is apparent for the mobile birds and butterflies considered here.

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Table 1: Woodland bird species used for analysis and their degree of association with broad-leaved woodland cover. JW is a Jacobs' selection index calculated from BBS data (using methods similar to Newson *et al*. 2009). Species in bold (those with JW > 0.3) were classified as woodland specialists; the remainder were classified as woodland generalists. N sites is the number of CBC plots contributing data for the species. Body mass of birds from BTO BirdFacts (www.bto.org/birdfacts)

Species	**Scientific name**	**JW**	**N sites**	**Mass (g)**
Marsh Tit	***Poecile palustris***	**0.6**	**65**	12
Nuthatch	***Sitta europaea***	**0.6**	**73**	24
Treecreeper	***Certhia familiaris***	**0.5**	**94**	10
Jay	***Garrulus glandarius***	**0.5**	**98**	170
Great Spotted Woodpecker	***Dendrocopos major***	**0.5**	**95**	85
Blackcap	***Sylvia atricapilla***	**0.5**	**123**	21
Chiffchaff	***Phylloscopus collybita***	**0.4**	**114**	9
Garden Warbler	***Sylvia borin***	**0.4**	**72**	19
Green Woodpecker	***Picus viridis***	**0.4**	**62**	190
Long-tailed Tit	***Aegithalos caudatus***	**0.4**	**97**	9
Bullfinch	*Pyrrhula pyrrhula*	0.3	93	21
Great Tit	*Parus major*	0.3	145	18
Blue Tit	*Cyanistes caeruleus*	0.3	146	11
Robin	*Erithacus rubecula*	0.3	151	18
Wren	*Troglodytes troglodytes*	0.2	150	10
Song Thrush	*Turdus philomelos*	0.2	138	83
Spotted Flycatcher	*Muscicapa striata*	0.2	29	17
Coal Tit	*Periparus ater*	0.2	120	9
Woodpigeon	*Columba palumbus*	0.2	71	450
Mistle Thrush	*Turdus viscivorus*	0.1	84	130
Chaffinch	*Fringilla coelebs*	0.1	147	24
Blackbird	*Turdus merula*	0.1	149	100
Goldcrest	*Regulus regulus*	0.1	86	6
Jackdaw	*Corvus monedula*	0.1	40	220

Table 2: Butterfly species used in the analysis and their association with broad-leaved woodland (W), grassland (G) and heathland (H). In each case values 1, 2 and 3 indicate, respectively, that the species is a specialist, generalist or rarely uses the habitat.

Species	**Scientific name**	**W**	**G**	**H**	**N sites**
Small tortoiseshell	*Aglais urticae*	2	1	2	544
Orange tip	*Anthocaris cardamines*	2	1	3	515
Ringlet	*Aphantopus hyperantus*	2	1	3	475
Dark green fritillary	*Argynnis aglaja*	2	2	3	274
Silver-washed fritillary	*Argynnis paphia*	1	2	3	268
Brown argus	*Aricia agestis*	3	1	3	332
Pearl-bordered fritillary	*Boloria euphrosyne*	2	3	3	113
Small pearl-bordered fritillary	*Boloria selene*	2	3	3	135
Green hairstreak	*Callophrys rubi*	2	2	3	301
Holly blue	*Celastrina argiolus*	2	2	3	484
Small heath	*Coenonympha pamphilus*	3	1	2	488
Small blue	*Cupido minimus*	3	1	3	133
Dingy skipper	*Erynnnis tages*	3	1	3	270
Brimstone	*Gonepteryx rhamni*	1	2	3	476
Grayling	*Hipparchia semele*	3	3	1	154
Peacock	*Inachis io*	2	2	3	540
Wall brown	*Lasiommata megara*	3	2	3	352
White admiral	*Limenitis camilla*	1	3	3	166
Small copper	*Lycaena phlaeas*	3	1	2	527
Meadow brown	*Maniola jurtina*	2	1	2	548
Marbled white	*Melanargia galathea*	3	1	3	376
Purple hairstreak	*Neozephyrus quercus*	1	3	3	267
Large skipper	*Ochlodes venata*	2	1	3	500
Speckled wood	*Pararge aegeria*	1	2	3	513
Large white	*Pieris brassicae*	2	2	3	539
Green-veined white	*Pieris napi*	2	1	3	544
Small white	*Pieris rapae*	2	1	3	535
Comma	*Polygonum c-album*	2	2	3	499
Chalk-hill blue	*Polyommatus coridon*	3	1	3	162
Common blue	*Polyommatus icarus*	3	1	2	537
Grizzled skipper	*Pyrgus malvae*	3	1	3	231
Gatekeeper	*Pyronia tithonus*	2	1	2	492
Essex skipper	*Thymelicus lineola*	3	1	3	262
Small skipper	*Thymelicus sylvestris*	3	1	3	445
Red admiral	*Vanessa atalanta*	2	2	3	543
Painted lady	*Vanessa cardui*	2	2	3	540

Table 3: Biotope categories extracted from the Landcover Map 2000 to characterise habitat and land use in and around monitoring sites.

Arable
Bare ground and quarries
Bracken
Broadleaved woodland
Coastal
Coniferous woodland
Fen
Grassland
Heath
Inland water
Montane
Urban/ suburban garden
Sea

Table 4: Environmental variables used in the analysis. Each variable was calculated separately for the four buffer sizes around each site. Note that due to the large number of potential variables the analysis was focussed on hypotheses and likely causal effects and so not all variables were used in all analyses.

Habitat Configuration variables	
COVER(x)	Percentage cover of habitat x within buffer
PATCHES(x)	Number of patches of habitat x in buffer (proportional to patch density)
ISOLATION(x)	Mean nearest neighbour distances between patches of habitat x within buffer
SHAPE(x)	Mean perimeter:area ratio across patches of habitat x in buffer
	where x = broad-leaved woodland (W); grassland (G); or heathland (G)
Diversity	
HABDIV	Shannon diversity index of biotope cover types
SOILDIV	Shannon index of 29 HOST soil classes
Altitude and Aspect	
ALT_STD	Standard deviation of altitude in buffer
EAST_STD	Standard deviation of measures of aspect within buffer
NORTH_STD	
Soil moisture deficit	
DRY_SPRING	Soil moisture deficit in spring 1995
DRY_SUMMER	Soil moisture deficit in summer 1995

Table 5: Summary of sensitivity and recovery time measures for birds in response to known severe winters. Dec, NC and Inc indicate the number of sites × events in which the species showed a decrease, no change or increase in population size. For those sites × events where the population decreased, the mean recovery time is followed by seven columns indicating the frequency with which different lengths of recovery time were observed. For species marked in bold, 50% or more of site × event changes were decreases. These species were the focus of further analysis.

Species	**Dec**	**NC**	**Inc**	**Mean R_{ij}**	**0yr**	**1yr**	**2yr**	**3yr**	**4yr**	**5yr**	**6+yr**
Woodpigeon	58	29	74	2.5	10	12	13	10	4	2	4
Green Woodpecker	35	88	47	2.7	0	14	3	4	6	3	1
Great Spotted Woodpecker	53	125	70	2.6	2	17	7	9	7	4	2
Wren	328	21	63	2.7	10	53	70	88	47	12	10
Robin	285	25	105	2.6	21	54	69	52	28	16	14
Blackbird	234	51	128	2.3	24	47	55	40	29	8	4
Song Thrush	189	89	97	2.6	8	56	30	35	24	8	9
Mistle Thrush	58	107	50	2.7	2	18	6	9	7	2	6
Blackcap	139	72	132	2.3	5	46	40	10	15	1	6
Garden Warbler	69	53	67	2.2	4	20	15	14	3	4	2
Chiffchaff	144	69	105	2.2	12	38	35	23	14	2	5
Goldcrest	116	44	46	2.4	13	24	21	19	22	7	1
Spotted Flycatcher	25	11	29	2.6	3	7	2	4	4	0	3
Long-tailed Tit	85	96	65	2.9	3	16	12	20	13	3	6
Blue Tit	167	56	182	2.0	17	50	30	20	18	4	4
Great Tit	181	65	162	2.2	17	43	45	24	16	4	4
Coal Tit	136	77	101	2.6	7	45	27	14	12	5	9
Marsh Tit	63	51	45	2.6	3	16	14	8	6	3	4
Nuthatch	56	67	66	2.5	3	12	14	7	5	5	2
Treecreeper	72	97	73	2.5	5	15	12	14	13	3	2
Jay	48	134	84	2.6	3	10	10	8	6	3	3
Jackdaw	24	43	32	2.0	3	8	3	7	2	1	0
Chaffinch	178	56	176	2.3	14	56	37	21	14	10	5
Bullfinch	82	82	81	2.1	5	22	21	7	6	5	1

Table 6: Summary of sensitivity and recovery time measures for birds in response to trend-defined events of unknown cause. Events lists the 1-5 events identified per species. Dec, NC and Inc indicate the number of sites × events in which the species showed a decrease, no change or increase in population size. For those sites × events where the population decreased, the mean recovery time is followed by seven columns indicating the frequency with which different lengths of recovery time were observed. For species marked in bold, 50% or more of site × event changes were decreases. These species were the focus of further analysis.

Species	Events	Dec	NC	Inc	Mean R_{ij}	0yr	1yr	2yr	3yr	4yr	5yr	6+yr
Woodpigeon	1966	0	0	2								
Green Woodpecker	1982, 1984	26	25	12	3.1	0	8	4	5	3	0	3
Great Spotted Woodpecker	1975, 1986	20	35	8	2.8	1	6	1	3	4	1	1
Wren	1976, 1979, 1982, 1991, 1996	308	16	35	2.6	6	56	82	70	21	29	6
Robin	1970, 1982, 1985, 1991	189	20	62	2.7	13	37	46	27	12	22	12
Blackbird	1967, 1970, 1973, 1982	109	14	62	2.3	10	27	28	18	2	7	3
Song Thrush	1973, 1991	65	18	25	2.7	5	14	9	12	4	6	5
Mistle Thrush	1966, 1973	14	13	5	3.9	0	3	2	4	1	3	1
Blackcap	1978, 1986, 1991	91	36	53	2.2	4	30	16	13	1	10	3
Garden Warbler	1973, 1975	17	12	7	4.2	1	2	1	4	2	2	3
Chiffchaff	1974, 1991, 1999	104	30	18	2.3	5	15	6	14	0	12	1
Goldcrest	1976, 1979, 1986, 1991	89	27	9	2.9	5	11	17	25	3	16	7
Spotted Flycatcher	1967, 1969	6	3	4	1.2	2	2	1	1	0	0	0
Long-tailed Tit	1979	17	12	7	2.5	0	5	3	2	0	5	0
Blue Tit	1973, 1982	63	22	40	1.9	7	27	6	10	2	3	1
Great Tit	1973, 1982, 1986	115	34	55	2.2	13	29	27	18	3	8	4
Coal Tit	1970, 1979, 1986	74	26	28	2.2	5	22	19	12	3	7	1
Marsh Tit	1966, 1972, 1997	28	16	11	1.8	2	7	9	4	0	1	0
Nuthatch	1992	15	16	5	2.5	2	3	1	1	1	5	0
Treecreeper	1973, 1979	22	26	14	3.5	1	4	3	4	3	2	2
Jay	1973, 1978	32	26	14	2.9	0	6	6	7	0	6	2
Jackdaw	1968	0	4	1								
Chaffinch	1969, 1970, 1973	61	12	27	2.8	9	15	12	6	5	3	6
Bullfinch	1966, 1968, 1978, 1998	51	33	21	1.8	4	12	8	7	1	2	0

Table 7: Summary of sensitivity and recovery time measures for butterflies in response to the spring-summer drought of 1995. Dec, NC and Inc indicate the number of sites × events in which the species showed a decrease, no change or increase in population size. For those sites × events where the population decreased, the mean recovery time is followed by seven columns indicating the frequency with which different lengths of recovery time were observed. For species marked in bold, 50% or more of site × event changes were decreases. These species were the focus of further analysis.

Species	**Dec**	**NC**	**Inc**	**Mean R_{ij}**	**0yr**	**1yr**	**2yr**	**3yr**	**4yr**	**5yr**	**6+yr**
Small Tortoiseshell	153	4	136	1.0	53	78	6	4	1	0	5
Orange Tip	91	24	132	2.1	18	27	11	15	8	1	6
Ringlet	179	24	44	2.8	9	37	27	54	31	7	9
Dark Green Fritillary	32	21	44	1.3	13	13	0	1	2	0	2
Pearl-bordered Fritillary	20	12	20	1.3	5	13	0	0	0	0	2
Silver-washed Fritillary	33	11	52	1.4	13	10	2	3	3	0	2
Small Pearl-bordered Fritillary	24	9	21	2.9	7	6	2	1	1	1	4
Brown Argus	36	14	92	2.2	14	8	2	3	1	5	3
Green Hairstreak	53	20	32	2.6	6	16	4	10	9	3	4
Holly Blue	14	36	190	1.4	4	2	7	1	0	0	0
Small Heath	71	40	127	1.8	24	18	9	7	3	2	6
Small Blue	26	6	7	2.4	3	5	4	8	2	3	0
Dingy Skipper	58	21	27	1.5	9	34	5	4	3	1	2
Grayling	28	7	19	2.8	3	3	3	8	6	3	0
Brimstone	52	11	183	1.5	15	18	9	6	1	1	2
White Admiral	18	9	47	3.0	5	1	2	3	3	1	3
Small Copper	139	29	111	1.8	50	44	6	6	7	10	12
Chalk-hill Blue	27	4	38	2.3	5	7	2	6	4	2	1
Meadow Brown	141	5	173	2.3	27	18	28	43	11	5	6
Gatekeeper	57	3	224	1.6	21	13	6	7	5	5	0
Marbled White	40	17	123	1.5	5	19	8	5	2	0	0
Peacock	54	16	215	2.0	15	12	6	7	8	1	4
Large Skipper	163	12	114	2.3	38	32	16	27	22	15	8
Speckled Wood	195	27	68	2.5	8	47	47	42	32	4	8
Wall Brown	71	45	33	3.7	5	6	6	22	7	7	15

Table continued…

Species	**Dec**	**NC**	**Inc**	**Mean R_{ij}**	**0yr**	**1yr**	**2yr**	**3yr**	**4yr**	**5yr**	**6+yr**
Large White	235	9	51	1.6	13	116	75	6	9	5	5
Green-veined White	220	12	63	1.8	17	106	44	16	20	5	6
Small White	263	2	28	2.2	39	127	13	17	12	15	32
Comma	142	26	95	1.6	46	41	8	20	20	1	2
Common Blue	124	8	157	1.5	50	36	4	10	5	3	9
Grizzled Skipper	19	9	58	1.9	4	8	4	1	0	1	1
Purple Hairstreak	38	11	33	2.3	9	5	12	2	4	1	5
Essex Skipper	17	19	27	3.2	2	2	5	3	1	1	3
Small Skipper	119	10	110	3.0	26	21	5	23	12	13	18
Red Admiral	66	9	230	3.0	13	4	9	7	20	0	10
Painted Lady	1	1	300	1.0	0	1	0	0	0	0	0

Table 8: Summary of sensitivity and recovery time measures for butterflies in response to trend-defined events of unknown cause. Events lists the 1-4 events identified per species. Dec, NC and Inc indicate the number of sites × events in which the species showed a decrease, no change or increase in population size. For those sites × events where the population decreased, the mean recovery time is followed by seven columns indicating the frequency with which different lengths of recovery time were observed. For species marked in bold, 50% or more of site × event changes were decreases. These species were the focus of further analysis.

Species	**Events**	**Dec**	**NC**	**Inc**	**Mean R_{ij}**	**0yr**	**1yr**	**2yr**	**3yr**	**4yr**	**5yr**	**6+yr**
Small Tortoiseshell	1983,1985,1998	428	5	50	3.6	47	48	34	30	100	103	45
Orange Tip	1994	139	13	48	2.7	10	24	32	32	17	11	7
Ringlet	1996,2001	323	36	112	2.5	31	65	80	63	44	9	20
Dark Green Fritillary	1977	4	2	3	4.3	0	0	0	1	1	2	0
Pearl-bordered Fritillary	1988	16	2	4	2.5	0	4	5	3	3	1	0
Silver-washed Fritillary	1977,1998,2007	150	12	13	3.3	10	13	16	13	13	17	13
Small Pearl-bordered Fritillary	1978,1979,1991	25	3	10	2.6	1	10	2	6	2	3	1
Brown Argus	1977,1998	122	20	25	4.0	3	12	24	12	11	32	22
Green Hairstreak	1986,1989	37	15	27	2.9	3	12	1	7	6	3	5
Holly Blue	1992,1999	338	28	59	3.8	23	7	28	89	64	68	38
Small Heath	1977,1991	138	7	39	3.0	29	24	9	14	21	23	18
Small Blue	1988,1995	27	6	18	2.7	5	4	5	1	8	2	2
Dingy Skipper	1977,1989	33	6	25	2.0	3	17	4	1	4	3	1
Grayling	1977,1980,1985	36	4	10	2.9	4	3	10	7	4	3	4
Brimstone	1986	57	7	10	3.5	5	2	9	8	16	12	5
White Admiral	1977,1980,1993	44	19	12	3.1	5	1	11	13	4	5	5
Small Copper	1977,1985	84	11	13	3.6	1	12	11	9	29	10	9
Chalk-hill Blue	1981,2007	55	4	1	2.4	0	5	2	1	1	0	1
Meadow Brown	1985,1993	252	5	50	3.1	22	29	46	59	28	34	26
Gatekeeper	1985,1993	240	7	38	2.8	34	20	21	96	21	23	17
Marbled White	1987	32	11	12	3.6	3	2	1	5	16	3	2
Peacock	1983,1993	218	14	51	2.5	33	30	28	82	22	8	12
Large Skipper	1985	52	10	23	1.9	11	13	13	6	3	2	2
Speckled Wood	1977,1990	130	24	32	2.6	14	12	50	21	24	3	4
Wall Brown	1977,1984,1985	141	11	16	3.8	20	2	4	9	41	48	10

Table continued…

Species	**Events**	**Dec**	**NC**	**Inc**	**Mean R_{ij}**	**0yr**	**1yr**	**2yr**	**3yr**	**4yr**	**5yr**	**6+yr**
Large White	1980,1993	265	3	15	3.4	13	27	54	25	81	41	21
Green-veined White	1983,1993	234	13	52	2.4	33	31	79	26	36	12	12
Small White	1987,1993,1996,1998	779	22	107	2.9	63	188	177	64	57	95	98
Comma	1983,1993,2007	357	42	58	2.5	17	24	123	41	43	6	10
Common Blue	1977,1985,2007	291	14	18	3.2	11	20	38	13	35	24	16
Grizzled Skipper	1978,1998	74	9	18	3.4	15	5	9	5	17	7	15
Purple Hairstreak	1979,1982	11	9	10	3.6	0	1	3	1	2	3	1
Essex Skipper	1980,1982,2006	26	9	23	2.0	2	7	5	4	3	0	0
Small Skipper	1985	53	7	13	2.4	19	9	1	2	7	3	9
Red Admiral	1983,1997,2004	625	22	44	3.2	21	80	147	130	48	45	92
Painted Lady	1997	315	0	2	5.6	2	0	0	31	8	67	191

Table 9: Summary of tests concerning hypothesis 1b (site-scale variation enhances resilience). For each taxon/method of deriving events/variable, relationships are tallied according to the magnitude and direction of t-values. Here only results from the 500m scale are included so as to assess site-scale covariates. Cells shaded in grey indicate the expected relationship according to H_1. Expected is the number of relationships expected by chance (one-tailed □ = 0.05).

Taxon	**Method**	**Variable**	**Sensitivity**				**Recovery time**			
			Expected	**Neg**	**None**	**Pos**	**Expected**	**Neg**	**None**	**Pos**
Butterfly	Weather	ALT_STD	0.55	0	11	0	0.5	1	9	0
		EAST_STD	0.55	1	10	0	0.5	0	9	1
		HABDIV	0.55	0	10	1	0.5	1	8	1
		NORTH_STD	0.55	1	9	1	0.5	3	7	0
	Trend	ALT_STD	1.35	2	22	3	1.05	0	21	0
		EAST_STD	1.35	0	26	1	1.05	0	21	0
		HABDIV	1.35	0	27	0	1.05	0	20	1
		NORTH_STD	1.35	1	25	1	1.05	1	20	0
Bird	Weather	HABDIV	1.45	0	26	3	1.05	0	21	0
	Trend	HABDIV	0.6	0	12	0	0.55	0	11	0

Table 10: Summary of tests concerning hypothesis 2b (site-scale area of key habitat enhances resilience). For each taxon/method of deriving events/variable, relationships are tallied according to the magnitude and direction of t-values. For butterflies, tests were combined across habitats, but only including species known to be associated with each habitat (i.e. tallied woodland butterflies relationships with woodland cover, etc). Here only results from the 500m scale are included so as to assess site-scale covariates. Cells shaded in grey indicate the expected relationship according to H_2. Expected is the number of relationships expected by chance (one-tailed □ = 0.05).

Taxon	**Method**	**Variable**	**Sensitivity**				**Recovery time**			
			Expected	**Neg**	**None**	**Pos**	**Expected**	**Neg**	**None**	**Pos**
Butterfly	Weather	COVER(x)	1.05	1	18	2	1	1	19	0
	Trend	COVER(x)	2.45	0	41	8	2.1	2	34	6
Bird	Weather	COVER(W)	1.45	1	26	2	1.05	1	18	2
	Trend	COVER(W)	0.6	1	10	1	0.55	0	11	0

Table 11: Summary of tests concerning hypothesis 4b (landscape-scale variation enhances resilience). For each taxon/method of deriving events/variable, relationships are tallied according to the magnitude and direction of t-values. Here only results from the 5000m scale are included so as to assess landscape-scale covariates. Cells shaded in grey indicate the expected relationship according to H_5. Expected is the number of relationships expected by chance (one-tailed □ = 0.05).

Taxon	**Method**	**Variable**	**Sensitivity**				**Recovery time**			
			Expected	**Neg**	**None**	**Pos**	**Expected**	**Neg**	**None**	**Pos**
Butterfly	Weather	ALT_STD	0.55	0	9	2	0.5	0	9	1
		EAST_STD	0.55	0	11	0	0.5	0	9	1
		HABDIV	0.55	0	10	1	0.5	0	9	1
		NORTH_STD	0.55	0	11	0	0.5	1	9	0
		SOILDIV	0.55	1	10	0	0.5	0	10	0
	Trend	ALT_STD	1.35	1	24	2	1.05	0	20	1
		EAST_STD	1.35	0	25	2	1.05	0	21	0
		HABDIV	1.35	0	24	3	1.05	1	20	0
		NORTH_STD	1.35	2	24	1	1.05	0	21	0
		SOILDIV	1.35	0	24	3	1.05	0	21	0
Bird	Weather	HABDIV	1.45	0	29	0	1.05	0	21	0
	Trend	HABDIV	0.6	1	11	0	0.55	0	9	2

Table 12: Summary of tests concerning hypothesis 5b (landscape-scale area of key habitat enhances resilience). For each taxon/method of deriving events/variable, relationships are tallied according to the magnitude and direction of t-values. For butterflies, tests were combined across habitats, but only including species known to be associated with each habitat (i.e. tallied woodland butterflies relationships with woodland cover, etc). Here only results from the 5000m scale are included so as to assess landscape-scale covariates. Cells shaded in grey indicate the expected relationship according to H_6. Expected is the number of relationships expected by chance (one-tailed □ = 0.05).

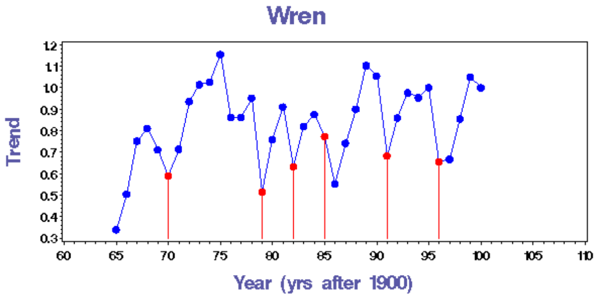
Taxon	**Method**	**Variable**	**Sensitivity**				**Recovery time**			
			Expected	**Neg**	**None**	**Pos**	**Expected**	**Neg**	**None**	**Pos**
Butterfly	Weather	COVER(x)	1.05	1	18	2	1	1	19	0
	Trend	COVER(x)	2.45	2	38	9	2.1	2	35	5
Bird	Weather	COVER(W)	1.45	2	24	3	1.05	1	20	0
	Trend	COVER(W)	0.6	1	11	0	0.55	0	10	1

Table 13: Summary of tests concerning hypothesis r (landscape-scale configuration of key habitat enhances resilience). For each taxon/method of deriving events/variable, relationships are tallied according to the magnitude and direction of t-values. For butterflies, tests were combined across habitats, but only including species known to be associated with each habitat (i.e. tallied woodland butterflies relationships with woodland isolation, etc). Here only results from the 5000m scale are included so as to assess landscape-scale covariates. Cells shaded in grey indicate the expected relationship according to H_7. Expected is the number of relationships expected by chance (one-tailed □ = 0.05).

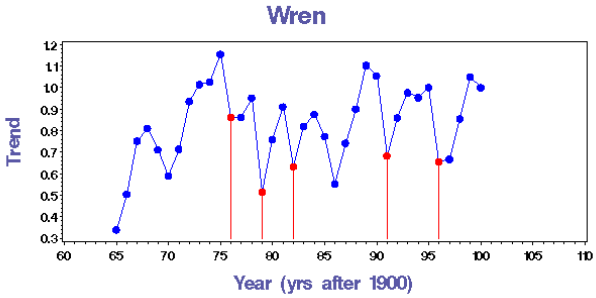
Taxon	**Method**	**Variable**	**Sensitivity**				**Recovery time**			
			Expected	**Neg**	**None**	**Pos**	**Expected**	**Neg**	**None**	**Pos**
Butterfly	Weather	ISOLATION(x)	1.05	2	18	1	1	1	19	0
		PATCHES(x)	1.05	1	15	5	1	1	19	0
		SHAPE(x)	1.05	1	19	1	1	1	19	0
	Trend	ISOLATION(x)	2.45	8	41	0	2.1	4	36	2
		PATCHES(x)	2.45	2	34	13	2.1	5	35	2
		SHAPE(x)	2.45	4	42	3	2.1	2	39	1
Bird	Weather	ISOLATION(W)	1.45	3	24	2	1.05	1	19	1
		PATCHES(W)	1.45	1	23	5	1.05	1	20	0
		SHAPE(W)	1.45	3	25	1	1.05	0	21	0
	Trend	ISOLATION(W)	0.6	1	11	0	0.55	0	11	0
		PATCHES(W)	0.6	1	11	0	0.55	1	10	0
		SHAPE(W)	0.6	0	11	1	0.55	0	10	1

Figure 1: Examples of calculation of sensitivity (V_{ij}) and recovery time (R_{ij}) for Wren. The first two graphs show the national unsmoothed trend with a) the six weather-defined extreme events and b) the five trend-defined extreme events. Note that four years are detected by both methods. Graphs b-f show the calculation of V_{ij} and R_{ij} where j = site 120. Note that site 120 was not surveyed in 1970 so resilience to that event could not be calculated at this site. Note at this site the Wren population seemingly did not respond to the 1982 event so V_{ij} = 0 and R_{ij} is null. In all other events the population decreased and took between 1 and 4 years to recover.

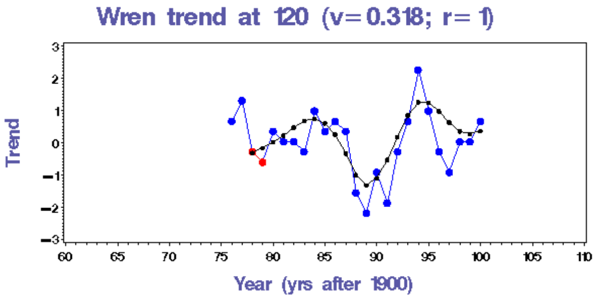
a) trend with weather-defined events



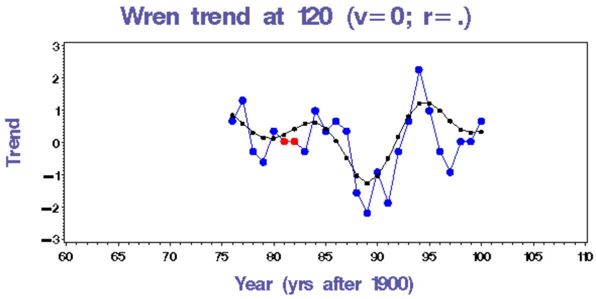
b) trend with trend-defined events



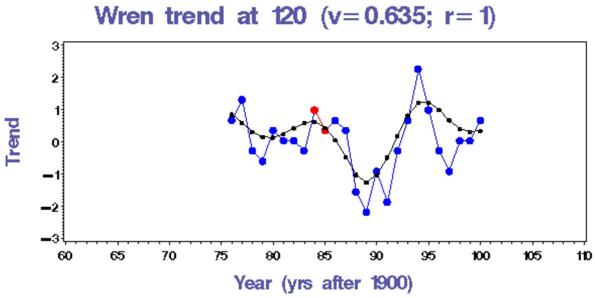
c) trend at site 120, event 1979



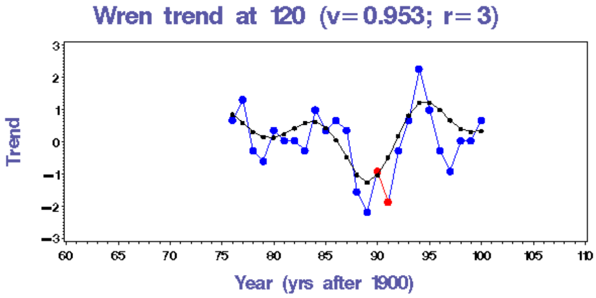
d) trend at site 120, event 1982



e) trend at site 120, event 1985



f) trend at site 120, event 1991



g) trend at site 120, event 1996

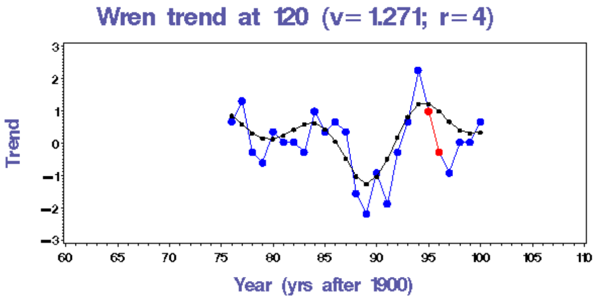


Figure 2: National trends of bird species showing significant sensitivity to known cold winters.

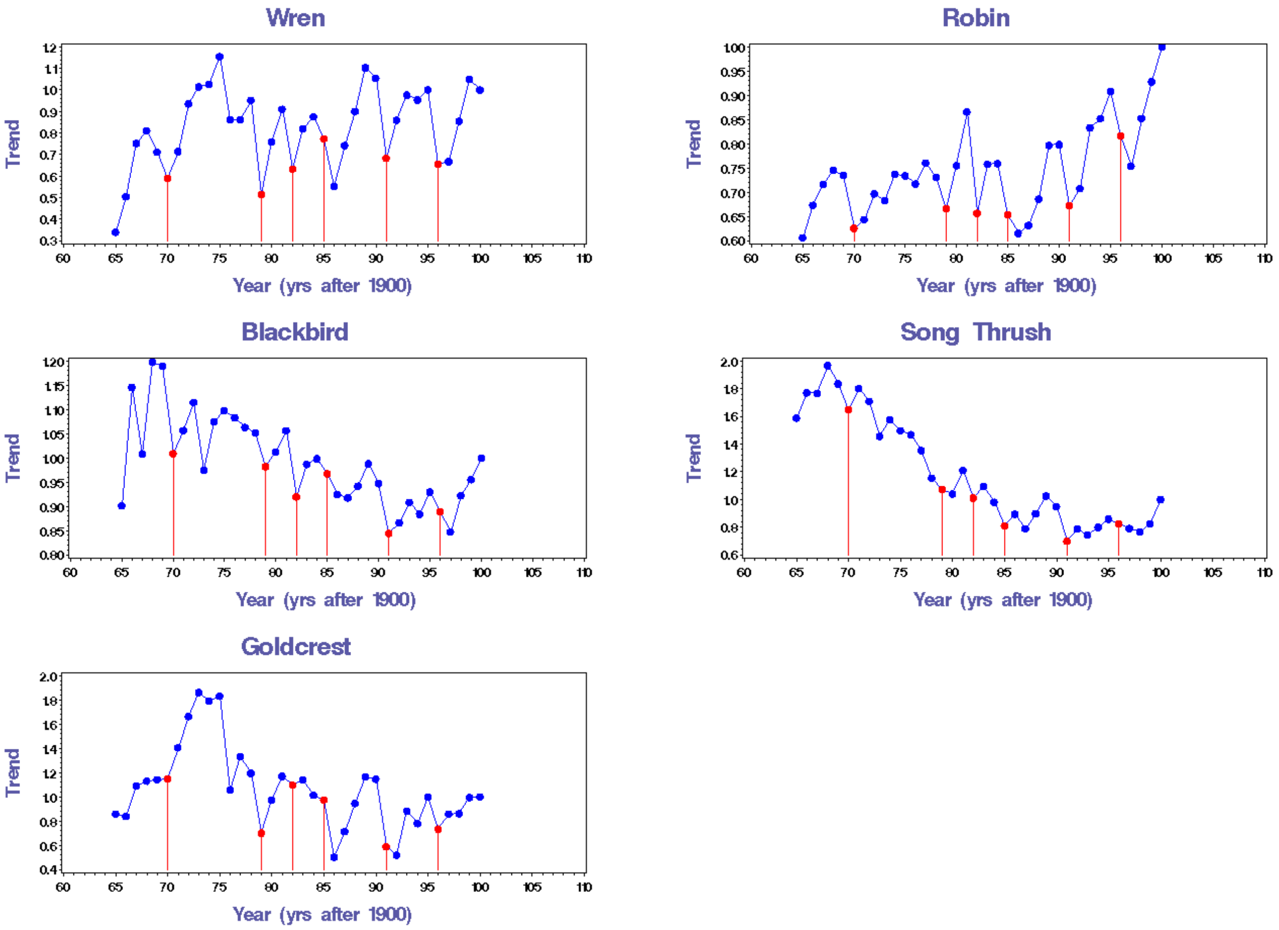


Figure 3: National trends of bird species showing significant sensitivity to unknown events derived from trends.

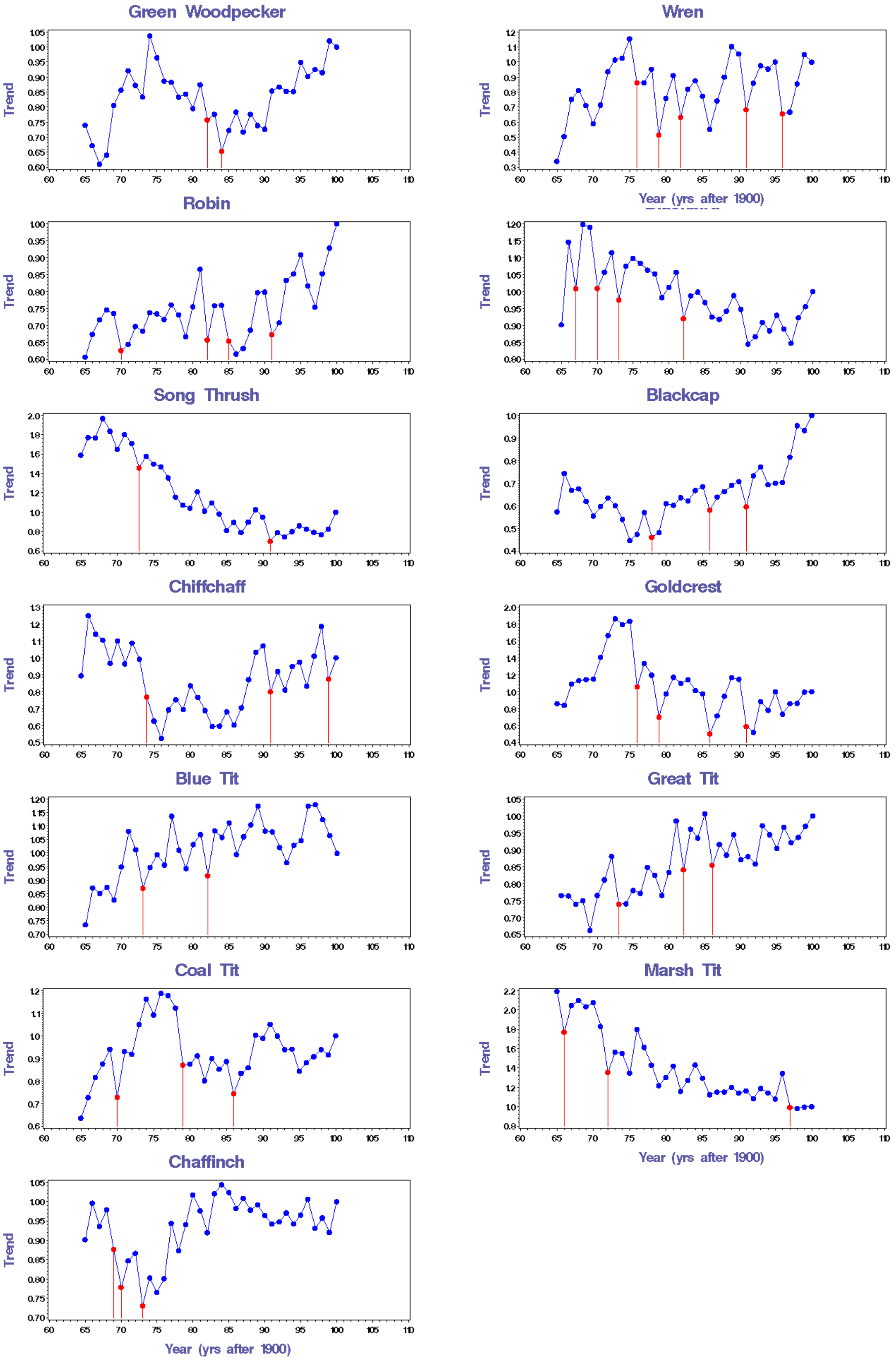


Figure 4: National trends of butterfly species showing significant sensitivity to the 1995 drought.

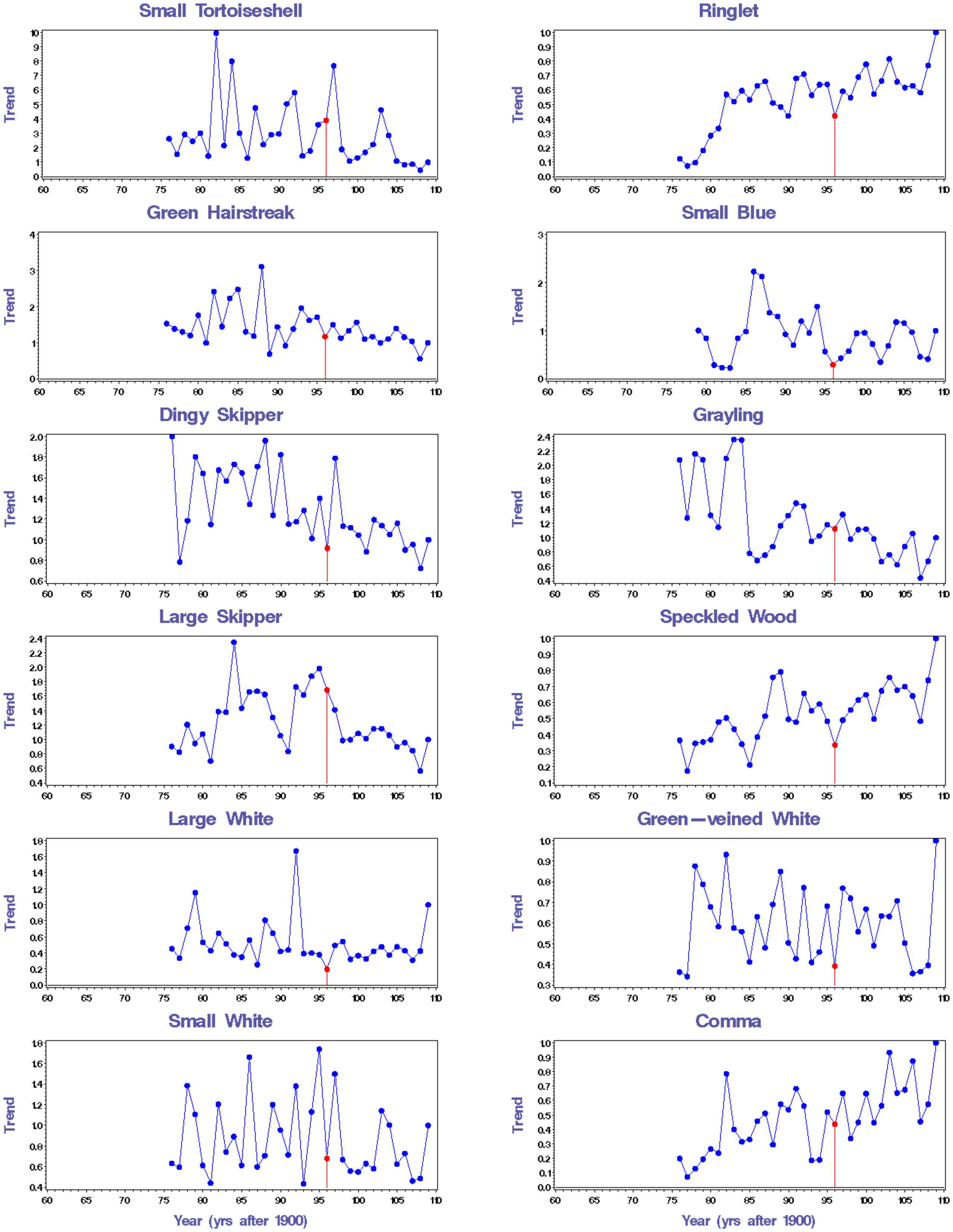
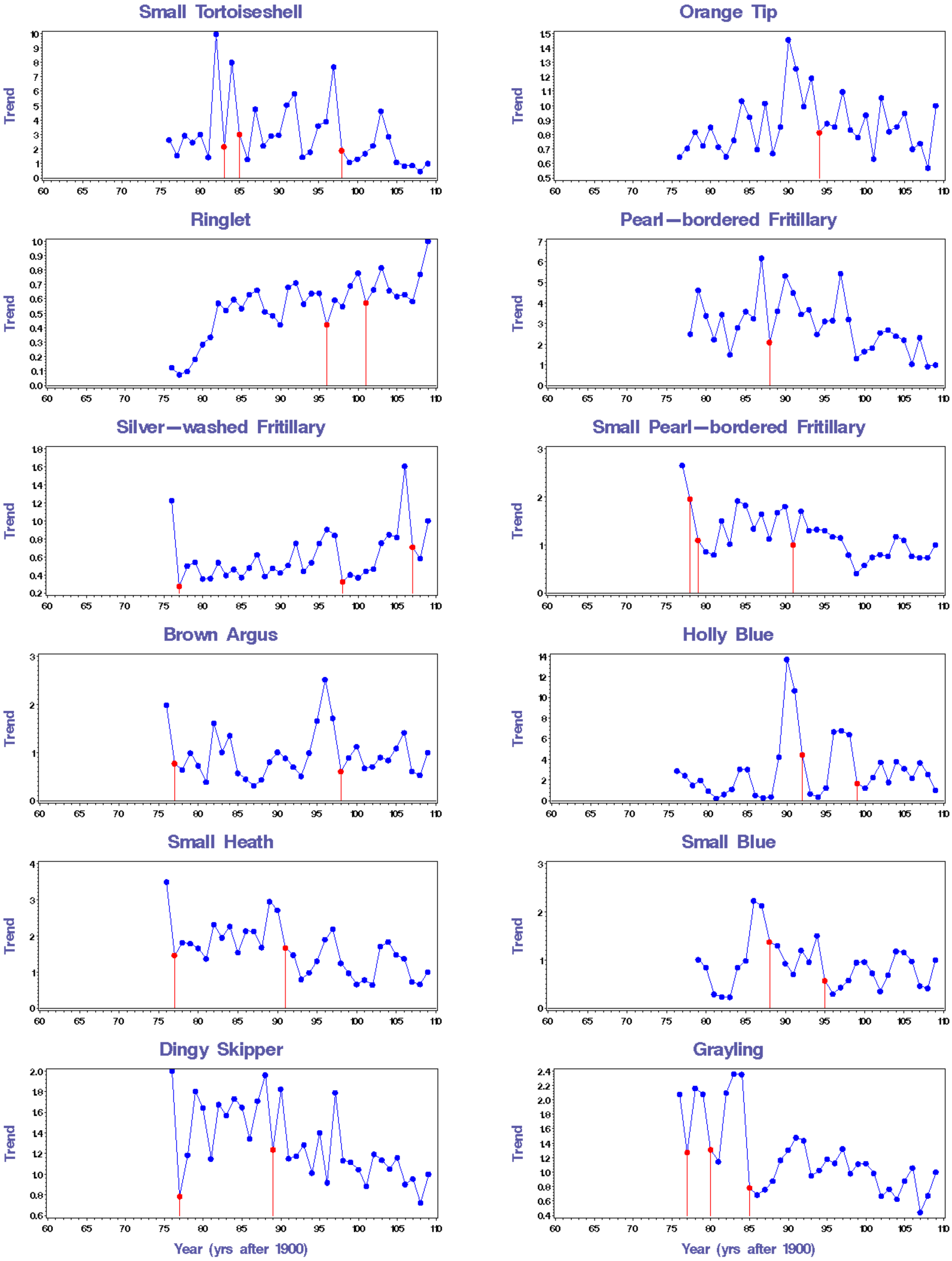


Figure 5: National trends of butterfly species showing significant sensitivity to unknown events derived from trends.



Small Tortoiseshell

Orange Tip

Ringlet

Pearl—bordered Fritillary

Silver—washed Fritillary

Small Pearl—bordered Fritillary

Brown Argus

Holly Blue

Small Heath

Small Blue

Dingy Skipper

Grayling

Figure 5 cont.

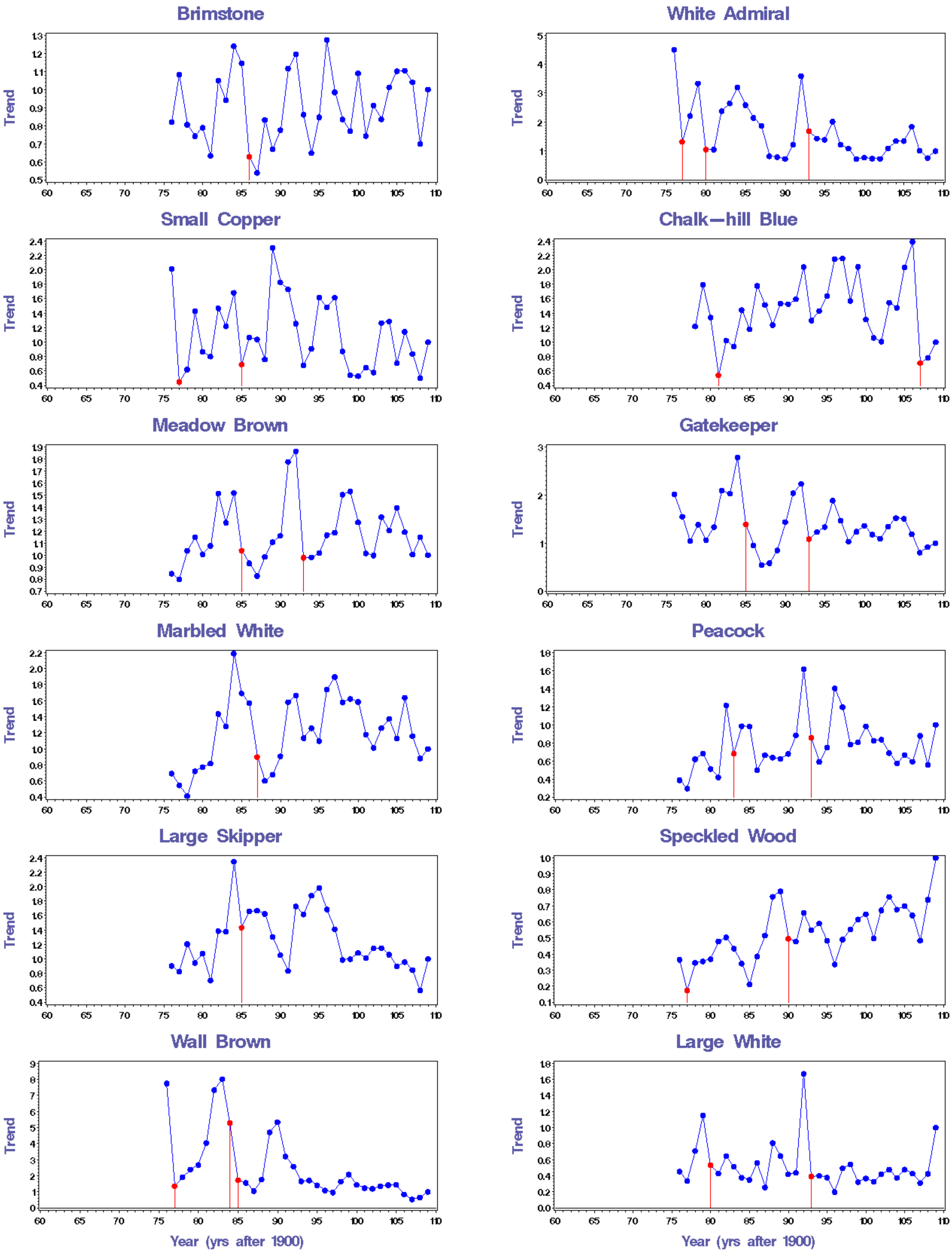
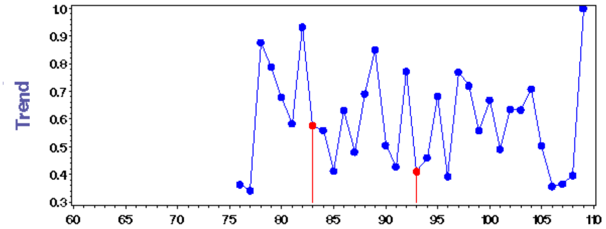
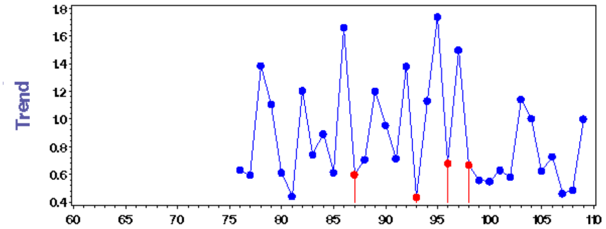
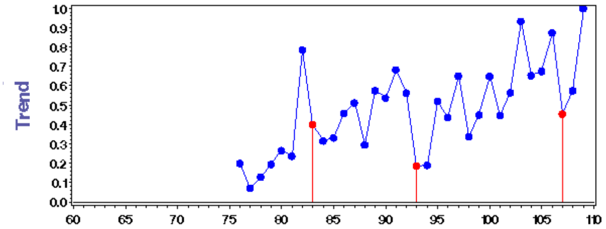
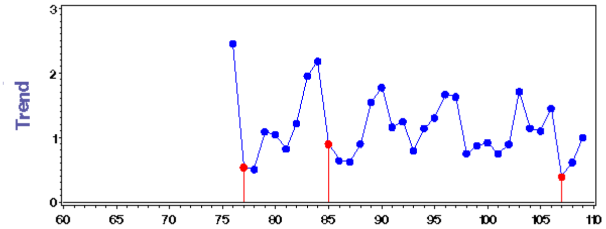


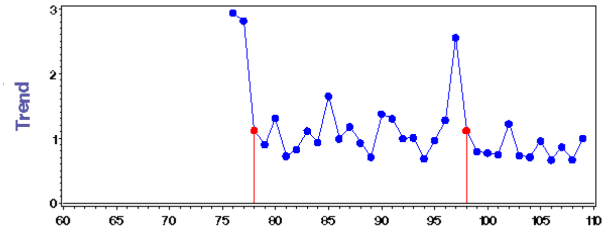
Figure 5 cont.

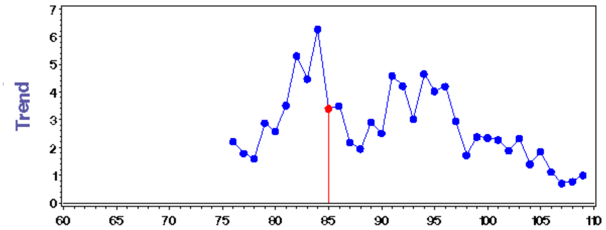

Green—veined White

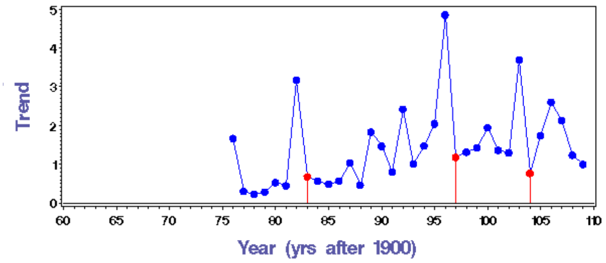

Small White

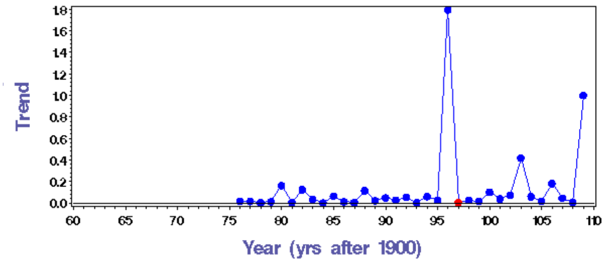

Comma


Common Blue


Grizzled Skipper


Small Skipper


Red Admiral


Painted Lady

Part 4: Can site and landscape scale attributes buffer bird populations against weather-mediated population declines and facilitate recovery?[2]

6.1 Introduction

Climate change is projected to have significant impacts upon global biodiversity through the course of this century, resulting in a significantly increased risk of extinction for many species (for example, Thomas *et al*. 2004). Indeed, there is increasing evidence that species' ranges, populations and communities are responding to recent warming (Hickling *et al*. 2006, Devictor *et al.* 2008, Gregory *et al*. 2009, Both *et al*. 2010). As a result, there is particular interest in the potential for management intervention to reduce or to negate the negative effects of climate change (adaptation). Given projected large-scale shifts in the distribution of likely suitable climate for species, it is anticipated that species' ranges will move polewards and upwards in response to climate change, driven by range expansion and colonisation at the leading edge, and population decline and extinction at the trailing edge (for example, Huntley *et al*. 2007).

Climate change adaptation may therefore focus on increasing the ability of species to respond to climate amelioration at the leading range margin, or reducing the negative effects of climate change at the trailing range margin. These two options result in different adaptation strategies, and there is considerable debate as to which may be most effective (for example, Opdam & Wascher 2004, Heller & Zavaleta 2009, Hodgson *et al*. 2009, Green & Pearce-Higgins 2010, Pearce-Higgins *et al*. 2011). As a result, a number of potential adaptation strategies could be considered. Some focus on maximising the quality of existing sites and protected areas to increase their resilience to climate change (for example, Pearce-Higgins *et al*. 2011, Carroll *et al*. 2010), whilst others are associated with large-scale management across landscapes to reduce the obstacles to species' range expansion (for example, Vos *et al*. 2008). Thus, site-based adaptation may involve the protection of large, high quality sites, whilst landscape-scale adaptation may involve the development of resilient and connected landscapes (for example, Hopkins *et al.* 2007, Hodgson *et al.* 2009). However, the evidence for the role of site-based and landscape-scale attributes in increasing the resilience of species and populations to climate change is theoretical and based upon limited empirical evidence (Natural England 2008). Given the long-term nature of climate change, collecting such evidence is difficult, although a high conservation research priority, given the requirement to implement effective adaptation strategies now.

To address this knowledge gap, we use detailed long-term monitoring data of variation in bird populations at individual sites to appraise the relative importance of site- and landscape-scale attributes in driving spatial variation in population growth. Whilst there is considerable literature on the relative importance of patch size and connectivity on the occurrence and abundance of birds (for example, Lampila *et al*. 2005), we, uniquely, test the extent to which these attributes may buffer bird populations against weather-mediated population declines or facilitate the subsequent recovery of those populations. Hence w1e provide evidence to test the following hypotheses:

H_{2b} The area of key habitat types for species' around monitoring sites will be positively correlated with population resilience.

H_{5b} The area of species' key habitat types in the local landscape will be positively correlated with population resilience.

H_{6b} Ecological networks defined by the connectivity of species' key habitats also increase the resilience of populations as measured during recent periods of relative climatic variability and incremental change.

We use past variation in both breeding season and winter weather in order to infer how populations may respond to future climatic change. The focus of our analysis is woodland birds, a group of species known to be sensitive to habitat fragmentation (for example, van Dorp & Opdam 1987, Bellamy *et al*. 2003) and both breeding season and winter weather (Greenwood & Baillie 1991, Robinson *et al*. 2007). This study therefore provides the first empirical test of the potential for site-based attributes and landscape-scale attributes to mediate the effects of weather variation upon species' populations.

6.2 Methods

6.2.1 Common Bird Census data

This study uses data from an extensive volunteer survey, the British Trust for Ornithology / Joint Nature Conservation Committee (JNCC) Common Birds Census (CBC). The CBC was introduced in 1962 to provide the first systematic monitoring of bird abundance of the UK. Under the CBC, bird territories were mapped from observations made on between seven to ten site visits per year between April and July (Marchant *et al.* 1990). This intensive methodology provides good estimates of the number of breeding territories present within each census plot, giving us confidence that observed changes in abundance closely reflect local population changes. CBC plots are largely categorised as "woodland" or "farmland". We focus here on the period 1965-2000 during which there were several extremely cold winters and extreme drought summers, and where there was a sufficient number of plots for change in relative abundance of woodland birds to be monitored over time.

In order to prevent the results being skewed by non-woodland species which may occur in woodland, we focus our analysis on species associated with woodland (specifically broad-leaved / mixed woodland). These were identified from the bird and habitat data recorded by Breeding Bird Survey (BBS) volunteers (Risely *et al*. 2010), which provides representative coverage of birds and habitats across the UK. We calculated a Jacobs' habitat preference index value (Jacobs 1974) for each species in broad-leaved / mixed woodland to match the habitat composition of woodland CBC plots. This was calculated as:

$J = (r - p) / [(r + p) - 2rp]$

where r is the used proportion and p the available proportion of habitat, using BBS bird counts and habitat data from 1994-2009. It ranges between +1 for maximum preference and -1 for maximum avoidance. From this, we selected all species (27 species in total), where the CBC sample size has been sufficient in the past to produce trends in relative abundance (Marchant *et al*. 1990) and for which broad-leaved / mixed woodland was the preferred or second most preferred habitat. Ranking these species according to their Jacobs' index value and using an arbitrary index cutpoint of greater than or less than 0.3, we further split these species into two groups, comprising woodland specialists and woodland generalists (Table 1). Whilst these species cover a large proportion of woodland bird species in Britain, there are a number of species which are too scarce, nocturnal or have territories that are too large to be surveyed adequately by this survey and are not considered here.

6.2.2 Environmental attributes of sites and the wider landscape

To reduce the degree of multiple testing, we chose to focus on a small number of key habitat variables derived from the 25-m resolution parcel data from the Land Cover Map 2000 (LCM2000, Fuller *et al*. 2002). This describes the location and size of contiguous patches of land of relatively uniform habitat or land use with a high spatial precision. The extent of broad-leaved / mixed woodland was used to derive information about both site- and landscape attributes. We used the percentage cover of woodland habitat (W0.5) and an index of site edginess (E, calculated as the total perimeter of woodland patches within 0.5 km divided by the minimum possible perimeter given the area of woodland habitat in the buffer) extracted from a 0.5km radius centred on the centre of each CBC plot to provide two site variables. The percentage cover of woodland habitat (W5) and an estimate of patch isolation (mean distance between patches, D) extracted within a 5 km radius provide two landscape variables. Two further landscape buffers of 2 and 10 km were considered at the beginning of the study, but because habitat attributes were strongly correlated across landscape scales (Gillings *pers comm.*, we chose to focus on the mid-distance 5 km landscape scale only. D and E were calculated using the package Fragstats (McGarigal & Marks 1995).

To examine whether there is evidence that site and landscape scale habitat variables can mediate the effect of weather variation upon species' populations, we consider two weather variables which have been shown in several studies to be associated with changes in avian demography (for example, Sæther *et al*. 2004, Robinson *et al*. 2007, Knape & de Valpine 2010): maximum temperature (MAX) during the preceeding breeding season (April to July, Joys & Crick 2004), and for resident species (i.e. excluding migrants which are absent from the UK during the winter months, Table 1) minimum winter temperature (MIN) from the preceding winter period (December-February), as a measure of winter severity. For these we used spatial monthly weather data provided at a 5-km resolution by the Meteorological Office through the UK Climate Impact Programme matched to the centre point of each CBC plot (UKCIP, www.ukcip.org.uk).

6.2.3 Examining importance of site and landscape variables in mediating climate response

We used a repeated measures generalized linear model (GLM) with Poisson errors and log link, applied using the GENMOD procedure in SAS (SAS Institute 2001) to look at the relationship between species counts and site, landscape and weather variables and their interactions. Non-independence of successive counts in the same CBC plots was taken into account by applying a repeated statement using plot as subject. We modelled between-year change in bird numbers by including the log of the count in the previous year as an offset. For these analyses, it was necessary to exclude all plots with zero counts in the previous year (given in Table 1). This means that the analysis does not examine the potential colonisation of unoccupied sites. The models are structured in order to examine:

i) The effects of site, landscape and weather variables in driving population growth.
ii) The effects of site and landscape variables on population sensitivity to weather, tested by the interactions between both site and landscape variables and weather.
iii) The effects of site and landscape variables on population recovery, by testing the three-way interactions between both site and landscape variables, weather and count in previous year.

For each separate analyses we calculate and present species-specific coefficients, but also use the SURVEYMEANS procedure in SAS (SAS Institute 2001) to calculate a weighted mean coefficient and standard error to summarise results across species, weighting by 1 / standard error, for woodland specialists and generalists separately as defined above. A t-test was subsequently used to test whether the weighted mean was significantly different from zero.

6.2.4 Expectations

6.2.4.1 Does weather influence population growth rates of woodland birds?

Our expectation is that growth rate of woodland birds (habitat specialists and generalists) will increase following years with higher breeding season temperature through increased productivity (number of chicks fledged) and subsequent greater recruitment. We also expect that growth rate will increase following warm winters as a result of increased over winter survival. With these expectations, we make an important assumption / caveat that productivity and survival can limit populations.

6.2.4.2 Are site or landscape variables correlated with population growth rates of woodland birds?

Whilst we would expect that sites and landscapes with more woodland would support more woodland birds (for example, Bellamy *et al*. 1996), in the absence of weather and other variables that may perturb a population, we do not have an expectation that population growth rates would vary between sites and landscapes with more woodland, or with greater distance between patches or amount of woodland edginess, on the assumption that under such circumstances, populations would be at carrying capacity. However, as many populations are likely to suffer perturbation in response to other factors, we might expect that growth rate may be more positive at sites and within landscapes where there is more woodland, and depressed at sites which are more isolated and where individual movement and the potential for recruitment is reduced. We might also expect that such effects be larger for woodland specialists, whilst the population growth of generalists may be greater where there is more edge habitat / heterogeneity.

6.2.4.3 Do site or landscape variables influence species sensitivity to and recovery from weather-mediated population declines?

We expect that woodland species will be less sensitive to weather mediated population declines at sites of higher quality (more woodland and less edge) as mortality may be lower and productivity greater at such sites. We similarly expect that woodland species will be less sensitive in more connected landscapes (with more woodland and smaller distances) as a result of increased opportunities for immigration. In all these cases, we expect that the relationship should be stronger for habitat specialists than for generalists. We may also expect that woodland generalists would respond more positively than woodland specialists at sites with greater edge habitat / heterogeneity.

6.3 Results

6.3.1 Does weather influence growth rates of woodland birds?

There was little evidence that maximum temperature during the previous breeding season had a strong or consistent impact on the growth rate of woodland bird populations (Table 2). Whilst the weighted mean calculated across species coefficients was positive and in the expected direction for habitat generalists and specialists, the weighted means were not significantly different from zero.

Similarly there was no strong evidence that the growth rates of woodland birds were consistently more positive following a warm winter, although there was some evidence that warmer winters may be important for two small-bodied species (GLM coefficient for Goldcrest 0.060, se = 0.017, P = <0.001; Long-tailed Tit 0.038, se 0.008, P = <0.001, Table 2).

6.3.2 Are site- or landscape- variables correlated with population growth rates of woodland birds?

We did not have a strong expectation that the growth rates of woodland birds (habitat generalists or specialists) would vary according to habitat attributes, although we hypothesised that growth rate might be more positive at sites and within landscapes where there is more woodland, depressed at sites which are more isolated and where movement and potential for recruitment is reduced.

We found consistent evidence that population growth rates of both habitat generalists and specialists were more positive where there was more woodland habitat at the site (0.5 km) and within the wider landscape (5 km), Table 2. One species, Lesser-spotted woodpecker, was an exception, as population growth was reduced at sites and within landscapes with more woodland habitat.

There was some evidence that the growth rate of habitat generalists and some habitat specialists were depressed where there was reduced connectivity, i.e. greater distance between woodland patches within the wider landscape (habitat generalists: weighted mean = -0.002, se = 0.001, P = <0.05. specialists = -0.0000, se = 0.001), ns, Table 2). In particular, the growth rates of Nuthatch and Wood Warbler were significantly depressed with greater distance between wood patches. However, the growth rates of three habitat specialists, Garden Warbler, Nightingale and Willow Tit were more positive at sites with reduced connectivity (Table 2).

We also hypothesised that woodland generalists and specialists would respond positively to increasing edge habitat. For many habitat generalists (10 of 12 species) and specialists (6 of 15 species) there was good evidence that growth rates were significantly more positive where there was more edge habitat (Table 2). Overall there was better evidence that habitat generalists respond more positively to increasing edge habitat (habitat generalists: weighted mean = 0.2081, se = 0.0421, P = <0.001, specialists: weighted mean = 0.0638, se = 0.0272, P = <0.05), although only the growth rate of Lesser spotted woodpecker was depressed where there was more edge habitat.

6.3.3 Do site or landscape variables influence species sensitivity to and recovery from weather-mediated population declines?

Overall we found weak evidence that either site or landscape variables interact with weather to buffer woodland bird populations against weather-mediated population declines (species sensitivity), or influence growth rate following a year with reduced numbers (three-way interaction between site or landscape variables with weather and count in the previous year; species recovery). There was some evidence that the positive effects of greater woodland area at the site level was reduced following a warmer breeding season (negative interaction between W0.5 and MAX; Table 3). We also found weak evidence that habitat generalists respond more negatively following a warmer breeding season where there was reduced habitat connectivity i.e. greater distance between woodland patches, although there was no consistent evidence for habitat specialists (Table 3). Considering the amount of woodland edge habitat around a site, there was no consistent evidence that species respond significantly more positively at sites with greater edge habitat following warmer breeding season weather (Table 3). We also found no consistent evidence that population sensitivity to winter weather is influenced by either site or landscape variables (Table 3).

In terms of species recovery, there was some weak evidence that habitat specialists and perhaps generalists were more likely to respond positively following a warmer breeding season where there was more woodland at the site level, although contrary to expectation, such effects were greater following years of high abundance (Table 4). There was also some evidence some species were less likely to recover following a warmer breeding season where woodland patches were more isolated (GLM coefficient for Nuthatch = -0.0017, se = 0.0008, *P* = <0.05; Nightingale = -0.0063, se = 0.0016, *P* = <0.001), although Wood Pigeon, Chiffchaff, Jay and Willow Tit were more likely to recover where there was greater distance between woodland patches (Table 4). There was little convincing evidence that species recovery was more positive following a warmer breeding season where there was more edge habitat or convincing evidence that recovery was more likely following a warmer winter in relation to habitat attributes (Table 4).

6.4 Discussion

Our analysis provides some evidence that reduced habitat connectivity (increased distance between woodland patches) within the landscape (5-km radii) is likely to depress habitat generalists and some habitat specialists, most notably Nuthatch and Wood Warbler, although some species (Garden Warbler, Nightingale and Willow Tit) responded positively to reduced connectivity. We also provide weak evidence that habitat generalists were more likely to be depressed and recovery less likely following a warmer breeding season where there was reduced connectivity (i.e. weak support for **Hypothesis 6**). This means that within the heavily fragmented British landscape, management to reduce the distance between woodlands, for example through the creation of new woodland stepping stones, may increase the ability of some woodland bird species to maintain populations in established areas. This matches the conclusions of Dolman *et al*. (2007), who reviewed the literature and inferred that increasing woodland connectivity may be most likely to benefit generalist species. Our results therefore suggest that such principles are likely to apply specifically to climate change adaptation, and therefore management to increase landscape connectivity is most likely to benefit generalist species which are most likely to also utilize other environments.

However, it is worth also considering the responses of individual species. One of the best studied temperate woodland bird species showed to benefit from landscape-scale attributes of woodland cover and connectivity is the European nuthatch *Sitta europaea*. The occurrence of this species within woodland patches is consistently negatively associated with the degree of isolation of those patches from others (for example, van Dorp & Opdam 1987, Bellamy *et al.* 1998, Villiard & Taylor 1994), and has been the subject of the development of a number of spatial models to explore the consequences of this (Bellamy *et al*. 1998, van Langevelde 2000, Alderman *et al*. 2005). These models indicate that isolation has restricted the occupancy of otherwise suitable habitat in eastern England, despite suitability of the climate for this species in the region (Bellamy *et al*. 1998). Bellamy *et al*. (1998) further suggests that net immigration from areas with greater woodland cover is essential to maintain the current, fragmented population. This emphasises the importance of large, good quality habitat patches within the existing range, and close to the expanding range margin, to produce large numbers of dispersers to colonise the newly suitable woodland patches. From this it could be argued that to increase the probability of persistence, a management option could be to increase the size of the largest woodland patches to a size that would be likely to support a secure population (Alderman *et al*. 2005). This is known as the 'key patch' approach to network analysis (Verboom *et al.* 2001) in which the total area of habitat required in a network to sustain a viable population is less if that network includes a key patch. For nuthatch it has been suggested that this is likely to be an area of woodland which supports more than 10 pairs (Verboom *et al.* 1993). In our study we found evidence that nuthatch population growth was positively correlated with woodland area at the site and landscape scale, negatively correlated with patch isolation and positively correlated with site-edge. More widely, there was good evidence that the growth rates of many habitat generalists and specialists were significantly more positive where there was more woodland habitat at the site and landscape scales. We also found some evidence that the growth rates of habitat generalists and specialists were less positive following a warmer breeding season. The most likely explanation for this is that woodland birds are responding more positively to warmer breeding season in small woodland patches, where there is likely to be less stability in numbers across years.

In the US, similar modelling approaches to the nuthatch work have been taken to assess the conservation of the northern spotted owl *Strix occidentalis caurina* in the boreal forests. Here, it was considered that the most important conservation priority is to develop reserves that are of sufficient size to support about 20-25 territories of the species. However, beyond that threshold, any additional resources should be used to increase the connectivity of those reserves, and increase the geographical extent of the reserve network (Lamberson *et al*. 1994). This approach has informed the Northwest Forest Plan which aims to protect old-growth forests to ensure viable spotted owl populations and protect a wide array of other forest biodiversity (Thomas *et al*. 2006). Although the current network may face increasing stress as a result of projected northward and upward shifts in the distribution of the spotted owl, and other species, by maintaining a network approach which focus on areas of topographical and climatic heterogeneity, it may be possible to design a fixed network that is robust to future climate change (Carroll *et al.* 2010).

In terms of woodland edge habitat, as expected many habitat generalists and to a lesser degree specialists appeared to benefit from increasing woodland edge habitat around the site, although little evidence that species responded more positively following a warmer breeding season or winter at sites where there was more edge habitat. This first finding provides empirical support to the literature which suggests that species diversity and population densities of birds tend to increase near habitat edges (reviewed in Sisk & Battin 2002). It may also reflect the fact that there are few real woodland specialists in the UK and those that remain are highly localised in range or nocturnal and not monitored through the CBC. The occurrence of different habitats is thought to provide more resources for birds in a smaller area than offered by one habitat alone and vegetation structure tends to be more diverse where two habitats intergrade, thus creating more nesting and feelding opportuntities for birds (Kroodsma 1984, Yahner 1988, Meunier *et al.* 1999, Flashpohler *et al.* 2001). The finding that habitat specialists appeared to benefit from increased woodland edge habitat in this study supports the idea that in our study there are few deep woodland specialists that benefit from large areas of woodland. Hence, our definition of a “specialist” here may just be one end of a cline in generalism. The only species to show a significant negative association with edge habitat here was Lesser Spotted Woodpecker. Paradoxically, the fact the Lesser Spotted Woodpecker also fared better in small woodland patches, could suggest that results from there being fewer competitors in these areas. An alternative explanation is that if this species is dependent on old trees with rotting wood, it may be that such trees are more likely to survive (i.e. less likely to be harvested) in small patches of woodland, for example in parkland or old wood pasture before getting old, than in true woodland. Another habitat specialist, for which there was inadequate data to consider here, the Pied Flycatcher *Ficedula hypoleuca* is known to strongly avoid edge habitat, because it does not forage on cleared stands (Huhta *et al*. 1999).

In conclusion, we provide evidence of the importance of habitat attributes in influencing woodland bird population growth rates. We also provide some weak empirical support for the idea that site based attributes (woodland patch size and edginess; **Hypothesis 2b and 6**) and landscape-scale attributes (patch isolation and surrounding area of habitat; **Hypothesis 5b and 6**) may influence the ability of some species of woodland bird, which are known to be sensitive to habitat fragmentation, to withstand weather-mediated population change. In terms of the potential influence of adaptation measures, it appears that woodland generalists would be most likely to benefit from changes to woodland area and configuration, in addition to one or two woodland specialists, of which the Nuthatch is probably the best example. Future studies dealing with this subject should build upon these findings to consider the effects of finer-scale habitat attributes and landscape configuration at a species-specific level. It would also be useful to consider other measures of connectivity, such as the presence of hedges and large trees, using other data sources such as Land Cover Map 2007 or LiDAR data.

Table 1: Bird species and information relevant to the analyses of CBC data. Species are grouped into broad-leaved / mixed woodland specialists and generalists and ordered within group according to declining preference (Jacobs' index) for this habitat derived from BBS data.

Species (species code)	**Status**	**Jacobs' indices**	**Sites in model (% of total)**
Broad-leaved / mixed woodland generalists			
Bullfinch, *Pyrrhula pyrrhula* (BF)	Resident	0.30	149 (68)
Great tit, *Parus major* (GT)	Resident	0.29	176 (94)
Blue tit, *Parus caeruleus* (BT)	Resident	0.27	175 (95)
Robin, *Erithacus rubecula* (R.)	Resident	0.26	178 (99)
Song thrush, *Turdus philomelos* (ST)	Resident	0.24	176 (86)
Wren, *Troglodytes troglodytes* (WR)	Resident	0.24	178 (98)
Coal tit, *Parus ater* (CT)	Resident	0.17	167 (72)
Wood pigeon, *Columba palumbus* (WP)	Resident	0.15	115 (65)
Mistle thrush, *Turdus viscivorus* (M.)	Resident	0.14	162 (61)
Chaffinch, *Fringilla coelebs* (CH)	Resident	0.11	176 (83)
Blackbird, *Turdus merula* (B.)	Resident	0.09	177 (99)
Goldcrest, *regulus regulus* (GC)	Resident	0.08	140 (61)
Broad-leaved / mixed woodland specialists			
Wood warbler, *Phylloscopus trochilus*, (WO)	Migrant	0.60	45 (54)
Marsh tit, *Parus palustris* (MT)	Resident	0.58	120 (63)
Nightingale, *Luscinia megarhynchos* (N.)	Migrant	0.57	40 (53)
Nuthatch, *Sitta europaea* (NH)	Resident	0.55	118 (69)
Lesser spotted woodpecker, *Dendrocopos minor* (LS)	Resident	0.54	52 (53)
Eurasian treecreeper, *Certhia familiaris* (TC)	Resident	0.54	145 (64)
Jay, *Garrulus glandarius* (J.)	Resident	0.47	171 (73)
Willow tit, *Parus montanus* (WT)	Resident	0.46	67 (57)
Blackcap, *Sylvia atricapilla* (BC)	Migrant	0.45	174 (85)
Great spotted woodpecker, *Dendrocopos major*(GS)	Resident	0.45	157 (70)
Chiffchaff, *Phylloscopus collybita* (CC)	Migrant	0.42	170 (78)
Garden warbler, *Sylvia borin* (GW)	Migrant	0.41	145 (60)
Green woodpecker, *Picus viridis* (G.)	Resident	0.35	132 (59)
Long-tailed tit, Aegithalos caudatus (LT)	Resident	0.35	162 (66)
Redstart, *Phoenicurus phoenicurus* (RT)	Migrant	0.33	34 (61)

Table 2: Main effects - Change in woodland bird populations in relation to environmental variables according to Common Birds Census data (1965-2000). P-values are: *<0.05, **<0.01, ***<0.001. Significant results are further highlighted in bold. Columns are weighted average coeffcients calculated across species, and their weighted standard errors in parentheses. W = percent woodland cover, D = distance between patches, E = site edgeness, MIN = minimum winter temperature during the preceding winter period, MAX = maximum temperature (MAX) during the preceeding breeding. Full species names are given in Table 1.

Species	**W0.5**	**W5**	**D5**	**E0.5**	**MIN**	**MAX**
Generalists						
B.	**0.0055 (0.0011) *** **	**0.0098 (0.0013) *** **	-0.0103 (0.0063)	**0.322 (0.0448) *** **	-0.0256 (0.0138)	0.0005 (0.014)
BF	-0.0005 (0.0006)	0.0003 (0.0009)	0.0004 (0.0013)	0.0139 (0.0241)	-0.0008 (0.0101)	**0.040 (0.0085) *** **
BT	**0.0033 (0.0007) *** **	**0.0053 (0.0012) *** **	0.0014 (0.0018)	**0.2257 (0.0361) *** **	0.0021 (0.0122)	0.007 (0.0117)
CH	**0.0048 (0.0011) *** **	**0.0091 (0.002) *** **	-0.0092 (0.0082)	**0.3279 (0.0439) *** **	-0.0087 (0.012)	0.0007 (0.0132)
CT	**0.0034 (0.0008) *** **	**0.007 (0.0012) *** **	-0.0034 (0.0029)	**0.2012 (0.0353) *** **	0.0141 (0.0091)	0.0002 (0.0102)
GC	0.0018 (0.0011)	**0.0046 (0.001) *** **	-0.0075 (0.0046)	**0.2046 (0.0495) *** **	**0.0602 (0.0166) *** **	-0.005 (0.0149)
GT	**0.0059 (0.0012) *** **	**0.0102 (0.0019) *** **	-0.0064 (0.0047)	**0.3852 (0.0552) *** **	0.0101 (0.0107)	0.0283 (0.0156)
M.	0.0004 (0.0007)	0.0013 (0.0011)	-0.0047 (0.0035)	0.0066 (0.026)	0.0105 (0.0097)	-0.0054 (0.0109)
R.	**0.0039 (0.0008) *** **	**0.0066 (0.0011) *** **	-0.0014 (0.0035)	**0.2599 (0.0333) *** **	0.0092 (0.0143)	-0.0016 (0.0114)
ST	**0.0029 (0.0005) *** **	**0.0056 (0.0011) *** **	-0.0018 (0.003)	**0.2452 (0.0395) *** **	0.007 (0.0098)	0.0017 (0.011)
WP	**0.0042 (0.0011) *** **	**0.0085 (0.0019) *** **	-0.0021 (0.0068)	**0.2628 (0.0547) *** **	0.0378 (0.0218)	0.0115 (0.0162)
WR	**0.0056 (0.0007) *** **	**0.0086 (0.0017) *** **	-0.0015 (0.0045)	**0.3401 (0.0364) *** **	-0.0342 (0.0199)	**-0.0256 (0.0106) * **
Weighted mean (se) [a]	**0.0032 (0.0006) *** **	**0.0058 (0.0010) *** **	**-0.0024 (0.0011) * **	**0.2081 (0.0421) *** **	0.0058 (0.0052)	0.0047 (0.0057)
Specialists						
BC	**0.0029 (0.0006) *** **	**0.0071 (0.0012) *** **	-0.0031 (0.0043)	**0.2604 (0.045) *** **		0.018 (0.0116)
CC	**0.0034 (0.0006) *** **	**0.0064 (0.0011) *** **	-0.0009 (0.0032)	**0.2943 (0.0406) *** **		0.0095 (0.0133)
G.	-0.0004 (0.0006)	0.0004 (0.0009)	0.0001 (0.0023)	-0.0103 (0.0285)	0.0158 (0.0113)	-0.0159 (0.0111)
GS	0.0005 (0.0004)	0.0009 (0.0007)	0.0001 (0.0014)	0.0306 (0.0209)	-0.002 (0.011)	-0.0019 (0.0084)
GW	0.0015 (0.001)	0.0012 (0.0013)	**0.0065 (0.0021) ** **	0.0591 (0.0322)		0.0108 (0.0146)
J.	**0.0012 (0.0006) * **	0.0012 (0.0009)	-0.0013 (0.0014)	0.0313 (0.0205)	-0.0067 (0.0063)	-0.0088 (0.0082)
LS	**-0.0123 (0.0028) *** **	**-0.0169 (0.0039) *** **	0.0122 (0.0127)	**-0.4339 (0.0973) *** **	0.0348 (0.0425)	-0.0206 (0.0322)
LT	0.0007 (0.0006)	0.0012 (0.001)	0.001 (0.0015)	**0.0707 (0.0251) ** **	**0.0379 (0.0086) *** **	-0.0043 (0.011)
MT	0.0016 (0.001)	0.0018 (0.0012)	-0.0013 (0.0018)	**0.0876 (0.0386) * **	0.0039 (0.0118)	**0.0244 (0.0106) * **
N.	-0.003 (0.0026)	-0.0026 (0.0038)	**0.0234 (0.0105) * **	-0.0734 (0.1177)		0.0017 (0.0485)
NH	**0.0018 (0.0007) * **	**0.0045 (0.0013) *** **	**-0.0161 (0.004) *** **	**0.1056 (0.0299) *** **	0.0003 (0.0128)	0.0051 (0.0121)
RT	0.0028 (0.003)	0.0055 (0.0048)	-0.007 (0.0184)	**0.2583 (0.1163) * **		0.0222 (0.0471)
TC	**0.0017 (0.0007) * **	**0.0021 (0.0009) * **	-0.0009 (0.0023)	0.0602 (0.0308)	0.0131 (0.0114)	0.0089 (0.0109)
WO	0.0044 (0.004)	**0.0075 (0.0036) * **	**-0.0585 (0.0238) * **	0.1842 (0.1363)		0.0442 (0.0512)
WT	-0.0055 (0.0032)	-0.0058 (0.0034)	**0.0059 (0.0021) ** **	-0.1726 (0.0914)	0.0188 (0.0369)	0.0175 (0.0213)
Weighted mean (se) [a]	0.0010 (0.0005)	**0.0019 (0.0008) * **	-0.0000 (0.0013)	**0.0638 (0.0272) * **	0.0094 (0.0063)	0.0047 (0.0037)

[a] Weighted by 1 / variance

Table 3: Measure of sensitivity - Change in woodland bird populations in relation to environmental variables according to Common Birds Census data (1965-2000). P-values are: *<0.05, **<0.01, ***<0.001. Significant results are further highlighted in bold. Columns are weighted average coeffcients calculated across species, and their weighted standard errors in parentheses. W = percent woodland cover, D = distance between patches, E = site edgeness, C = count in previous year, MIN = minimum winter temperature during the preceding winter period, MAX = maximum temperature (MAX) during the preceeding breeding. Full species names are given in Table 1.

Species	**W0.5*MAX**	**W5*MAX**	**D5*MAX**	**E0.5*MAX**	**W0.5*MIN**	**W5*MIN**	**D5*MIN**	**E0.5*MIN**
Generalists								
B.	0.0007 (0.0005)	0.0001 (0.0007)	-0.0002 (0.0013)	0.0299 (0.0293)	-0.0001 (0.0004)	0.0001 (0.0007)	0.0021 (0.0011)	0.0077 (0.0379)
BF	**-0.0009 (0.0004) ***	**-0.0012 (0.0005) ***	-0.0001 (0.0004)	-0.0086 (0.0121)	0.0002 (0.0004)	0.0005 (0.0006)	-0.0006 (0.0007)	0.0316 (0.0215)
BT	-0.0006 (0.0005)	-0.001 (0.0007)	0.0011 (0.0019)	-0.02 (0.0303)	0 (0.0004)	**-0.0016 (0.0006) ***	0.0005 (0.0012)	0.0049 (0.0331)
CH	0.0003 (0.0004)	-0.0003 (0.0006)	-0.001 (0.0022)	0.0331 (0.0326)	0.0003 (0.0006)	-0.0004 (0.0007)	0 (0.0011)	0.0173 (0.0394)
CT	**-0.0012 (0.0004) ****	-0.0005 (0.0005)	0.0001 (0.0007)	**-0.0356 (0.0167) ***	**-0.0008 (0.0004) ***	-0.0006 (0.0005)	0.0002 (0.0013)	-0.0201 (0.0155)
GC	-0.0006 (0.0006)	-0.0008 (0.0006)	-0.0002 (0.0017)	-0.0186 (0.0324)	0.0004 (0.0008)	0.0008 (0.0012)	0.001 (0.002)	-0.016 (0.0416)
GT	-0.0004 (0.0005)	-0.0007 (0.0008)	**-0.0029 (0.0013) ***	0.001 (0.0245)	-0.0002 (0.0004)	-0.0013 (0.0007)	0.001 (0.0017)	-0.0236 (0.02)
M.	0.0004 (0.0005)	0.0007 (0.0006)	0.0008 (0.0024)	0.0178 (0.0175)	-0.0005 (0.0004)	-0.0005 (0.0005)	0.0026 (0.0015)	-0.0103 (0.0196)
R.	-0.0006 (0.0004)	-0.0001 (0.0006)	-0.0008 (0.0007)	-0.0324 (0.0185)	-0.001 (0.0008)	**-0.0022 (0.0012) *****	**0.0031 (0.0015) ***	0.0094 (0.029)
ST	-0.0004 (0.0004)	0.0007 (0.0005)	-0.0014 (0.0015)	-0.0152 (0.0167)	0 (0.0003)	0.0006 (0.0005)	-0.0008 (0.0008)	-0.0159 (0.0167)
WP	0.0002 (0.0005)	-0.001 (0.001)	-0.0031 (0.0026)	0.02 (0.0282)	-0.0006 (0.0008)	-0.0015 (0.0012)	0.0035 (0.0037)	0.0417 (0.0613)
WR	-0.0003 (0.0004)	-0.0004 (0.0005)	-0.0005 (0.0004)	0.0033 (0.0266)	0.0002 (0.0008)	-0.0007 (0.001)	0.0016 (0.001)	0.0027 (0.0441)
Weighted mean (se) [a]	-0.0003 (0.0002)	-0.0003 (0.0002)	**-0.0005 (0.0002) ***	-0.0051 (0.0065)	-0.0002 (0.0001)	-0.0005 (0.0003)	0.0008 (0.0005)	-00041 (0.0066)
Specialists								
BC	**-0.0011 (0.0005) ***	-0.0012 (0.0007)	-0.0009 (0.0024)	**-0.0561 (0.0232) ***				
CC	-0.0008 (0.0005)	-0.0002 (0.0009)	**-0.0027 (0.0012) ***	0.0092 (0.0249)				
G.	0 (0.0004)	-0.0004 (0.0006)	0.0021 (0.0013)	-0.012 (0.0228)	-0.0001 (0.0004)	-0.0002 (0.0007)	-0.0007 (0.0021)	-0.0034 (0.0279)
GS	0.0004 (0.0003)	0.0007 (0.0005)	0.0002 (0.0006)	0.0084 (0.0189)	0.0006 (0.0004)	**0.0017 (0.0006) ****	-0.0007 (0.0013)	0.0337 (0.0474)
GW	-0.0004 (0.0006)	0.0005 (0.001)	-0.0005 (0.0005)	-0.0265 (0.0265)				
J.	-0.0002 (0.0003)	-0.0001 (0.0007)	0.0016 (0.0012)	-0.0115 (0.0284)	-0.0001 (0.0002)	0 (0.0004)	0.0005 (0.0005)	0.0107 (0.023)
LS	-0.0003 (0.0014)	**0.0035 (0.0016) ***	-0.0036 (0.0033)	**0.2341 (0.0918) ***	0.0023 (0.0021)	0.0016 (0.0041)	0.0002 (0.002)	0.2055 (0.1265)
LT	-0.0005 (0.0004)	-0.0003 (0.0006)	**0.0016 (0.0006) ****	-0.022 (0.0186)	0.0004 (0.0004)	0.0002 (0.0005)	0 (0.0004)	-0.0081 (0.0174)
MT	**-0.001 (0.0005) ***	0.0001 (0.0005)	0.0009 (0.0008)	0.0137 (0.018)	**-0.0013 (0.0006) ***	-0.0009 (0.0006)	**0.0038 (0.0008) *****	-0.0384 (0.0213)
N.	-0.0042 (0.0031)	0.0031 (0.0066)	0.0046 (0.0055)	0.0091 (0.2071)				
NH	-0.0003 (0.0004)	-0.0008 (0.0008)	**0.0071 (0.0023) ****	-0.0328 (0.0242)	0.0003 (0.0005)	0.0019 (0.001)	-0.0028 (0.0034)	-0.0119 (0.0333)
RT	-0.001 (0.0014)	-0.0005 (0.0015)	**0.0093 (0.0043) ***	-0.4225 (0.2527)				
TC	-0.0003 (0.0004)	0.0002 (0.0005)	**-0.0019 (0.0004) *****	0.0376 (0.0213)	0 (0.0005)	0.0006 (0.0006)	0.0016 (0.0012)	-0.0066 (0.0358)
WO	-0.0013 (0.0013)	0.0007 (0.0012)	-0.0097 (0.0112)	-0.1908 (0.2456)				
WT	-0.0008 (0.0015)	0.0005 (0.0016)	0.0001 (0.0006)	-0.0404 (0.0764)	0.0012 (0.0019)	0.0047 (0.0026)	**-0.0026 (0.0009) ****	0.0712 (0.1091)
Weighted mean (se) [a]	**-0.0004 (0.0001) ****	0.0000 (0.0002)	0.0002 (0.0005)	-0.0031 (0.0104)	0.0001 (0.0002)	0.0005 (0.0003)	0.0003 (0.0006)	0.0019 (0.0106)

[a] Weighted by 1 / variance

Table 4: Measure of recovery - Change in woodland bird populations in relation to environmental variables according to Common Birds Census data (1965-2000). P-values are: *<0.05, **<0.01, ***<0.001. Significant results are further highlighted in bold. Columns are weighted average coeffcients calculated across species, and their weighted standard errors in parentheses. W = percent woodland cover, D = distance between patches, E = site edgeness, C = count in previous year. Full species names are given in Table 1

Species	**W0.5*MAX*C**	**W5*MAX*C**	**D5*MAX*C**	**E0.5*MAX*C**	**W0.5*MIN*C**	**W5*MIN*C**	**D5*MIN*C**	**E0.5*MIN*C**
Generalists								
B.	-0.0001 (0.0002)	0 (0.0003)	0 (0.0007)	-0.0171 (0.0153)	0 (0.0002)	0.0001 (0.0007)	-0.0001 (0.0005)	0.009 (0.0153)
BF	0.0003 (0.0002)	0.0001 (0.0004)	0.0004 (0.0005)	-0.0019 (0.006)	-0.0003 (0.0002)	0.0005 (0.0006)	0.0004 (0.0003)	**-0.0234 (0.0079) ** **
BT	**0.0005 (0.0002) ** **	0.0003 (0.0003)	-0.0016 (0.0012)	0.0037 (0.0194)	0.0001 (0.0002)	**-0.0016 (0.0006) ** **	-0.0015 (0.0009)	0.0069 (0.0167)
CH	0.0003 (0.0003)	0.0003 (0.0003)	0.0007 (0.0012)	0.0211 (0.018)	0.0003 (0.0003)	-0.0004 (0.0007)	-0.0004 (0.001)	**0.048 (0.0134) *** **
CT	0 (0.0002)	-0.0003 (0.0003)	-0.0006 (0.0004)	-0.0166 (0.0114)	0.0002 (0.0002)	-0.0006 (0.0005)	-0.0008 (0.0006)	-0.0051 (0.0121)
GC	-0.0003 (0.0004)	-0.0006 (0.0005)	0.0012 (0.0018)	0.0253 (0.0232)	0.0001 (0.0003)	0.0008 (0.0012)	0.0011 (0.0009)	0.0273 (0.0194)
GT	0.0003 (0.0002)	0.0002 (0.0003)	0.0008 (0.0007)	**0.0211 (0.0092) * **	-0.0003 (0.0002)	**-0.0013 (0.0007) * **	0.0005 (0.0006)	0.0036 (0.0124)
M.	**-0.0007 (0.0003) * **	0 (0.0005)	-0.0006 (0.0017)	-0.0238 (0.0128)	**-0.0005 (0.0002) * **	-0.0005 (0.0005)	0.0012 (0.0009)	**-0.0245 (0.0098) * **
R.	-0.0003 (0.0004)	-0.0007 (0.0004)	0.001 (0.0007)	-0.0515 (0.0272)	-0.0002 (0.0002)	-0.0022 (0.0012)	0.0002 (0.0007)	-0.0032 (0.0189)
ST	0.0001 (0.0003)	0.0003 (0.0003)	-0.0003 (0.0005)	0.0146 (0.0149)	-0.0003 (0.0002)	0.0006 (0.0005)	**0.0014 (0.0006) * **	**-0.0266 (0.0112) * **
WP	0.0001 (0.0003)	0.0002 (0.0004)	**0.0026 (0.001) ** **	0.0095 (0.0157)	0.0004 (0.0003)	-0.0015 (0.0012)	-0.0009 (0.0012)	-0.0085 (0.0139)
WR	0.0001 (0.0002)	-0.0003 (0.0002)	-0.0006 (0.0004)	-0.0244 (0.0244)	-0.0002 (0.0003)	-0.0007 (0.001)	0.0007 (0.0007)	-0.03 (0.0248)
Weighted mean (se) [a]	0.0001 (0.0001)	-0.0000 (0.0001)	0.0001 (0.0003)	-0.0015 (0.0055)	-0.0001 (0.0001)	-0.0002 (0.0002)	0.0003 (0.0003)	-0.0108 (0.0052)
Specialists								
BC	0.0001 (0.0002)	-0.0003 (0.0003)	0.0005 (0.0008)	**0.0182 (0.0071) ** **				
CC	0.0005 (0.0003)	0.0006 (0.0005)	**0.0011 (0.0004) ** **	-0.0202 (0.0128)				
G.	0.0002 (0.0005)	-0.0004 (0.0007)	0.0001 (0.0015)	-0.0133 (0.0284)	-0.0003 (0.0005)	-0.0002 (0.0007)	0.0001 (0.0018)	0.0045 (0.0308)
GS	**0.0005 (0.0002) * **	0 (0.0006)	0.0004 (0.0007)	-0.0016 (0.0191)	**-0.0004 (0.0002) * **	**0.0017 (0.0006) ** **	0.0006 (0.0011)	-0.0314 (0.026)
GW	0.0001 (0.0002)	**0.001 (0.0003) *** **	0.0001 (0.0002)	0.0114 (0.0111)				
J.	-0.0001 (0.0002)	-0.0007 (0.0004)	**0.0016 (0.0005) ** **	-0.0283 (0.015)	0.0001 (0.0002)	0 (0.0004)	**0.0013 (0.0005) * **	-0.0248 (0.0158)
LS	0.0018 (0.0027)	0.0067 (0.0038)	-0.0013 (0.004)	0.138 (0.246)	-0.0007 (0.002)	0.0016 (0.0041)	0.0063 (0.0042)	0.0126 (0.2804)
LT	0.0006 (0.0003)	0.0001 (0.0004)	0.0003 (0.0007)	0.0318 (0.0291)	-0.0001 (0.0002)	0.0002 (0.0005)	0.0001 (0.0007)	0.0058 (0.0161)
MT	0.0004 (0.0004)	0.0002 (0.0004)	-0.0011 (0.0006)	-0.0443 (0.0236)	0.0003 (0.0003)	-0.0009 (0.0006)	-0.0018 (0.0011)	-0.0108 (0.0126)
N.	0.0018 (0.0011)	0.0024 (0.0019)	**-0.0063 (0.0016) *** **	**-0.1923 (0.0916) * **				
NH	0 (0.0002)	0.0004 (0.0003)	**-0.0017 (0.0008) * **	**0.0393 (0.0166) * **	0.0003 (0.0002)	0.0019 (0.001)	**-0.0041 (0.0015) ** **	**0.0563 (0.027) * **
RT	-0.0006 (0.0006)	-0.0004 (0.0007)	0.0015 (0.003)	0.1265 (0.1282)				
TC	0.0004 (0.0003)	0.0007 (0.0006)	-0.0012 (0.0008)	-0.0039 (0.0174)	0.0004 (0.0003)	0.0006 (0.0006)	-0.0006 (0.0007)	0.0178 (0.0293)
WO	-0.0016 (0.0011)	-0.001 (0.0016)	-0.0081 (0.0064)	-0.2401 (0.196)				
WT	**0.0023 (0.001) * **	-0.0017 (0.0027)	**0.0033 (0.0005) *** **	0.017 (0.0427)	0.0001 (0.0008)	**0.0047 (0.0026) * **	-0.001 (0.0009)	**-0.1521 (0.0482) ** **
Weighted mean (se) [a]	**0.0003 (0.0001) * **	0.0002 (0.0002)	0.0001 (0.0004)	-0.0006 (0.0083)	0.0000 (0.0001)	0.0001 (0.0001)	-0.0002 (0.0005)	-0.0096 (0.0122)

[a] Weighted by 1 / variance

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Part 5: Loss of cold-associated species under climate warming is exacerbated by landscape modification[1]

7.1 Introduction

Both climatic and other enviromental changes can lead to changes in the structure of species assemblages. Under climatic warming, warmth-limited species are expected to increase, whilst species intolerant of warm conditions are expected to decline. The balance of cold- and warm-associated species is captured in the community temperature index (CTI; Devictor *et al*., 2008). To calculate the CTI, each species is allocated a species temperature index (STI) based on the long-term temperature experienced by a species across its range. Species found associated with colder locations will have lower STI scores. Although absolute STI scores depend on the size and location of the study region, the relative ranking of species by STI scores is thought to remain scale-independent (Devictor *et al*., 2008). For a species assemblage at any single site, the CTI reflects the STI scores of all the species in the assemblage weighted by their relative abundance. For bird assemblages in France over the past two decades, site CTI scores have on average increased over time, fitting expectations under a warming climate. However, the increase in CTI, which reflects a shift in species range edges northwards of about 91km, has not kept pace with the northward shift in isotherms, which moved about 273km in the same time period (Devictor *et al*., 2008). This has been taken as evidence that bird communities are not tracking climate envelopes fast enough. However, a lack of change in CTI might also reflect the fact that cold-associated species are persisting longer than expected in the face of climatic warming. This could potentially occur through evolutionary adaptation, or through the use of local topographic and habitat features that provide cooler micro-climates (Weiss *et al*., 1988, Oliver *et al*., 2010, Suggitt *et al*., 2011).

Although the CTI is a useful metric to summarise the balance of warm and cold-associated species in assemblages, it loses information on which of these species types are primarily driving changes in assemblage structure. For example, an increase in CTI might correspond to a decline in the abundance of cold-associated species or an increase in warm-associated species, or both. In addition, such changes may be due to by changes in abundance of species already present, or by the addition to or loss of species from assemblages. In this study, we test for overall changes in the CTI of bird and butterfly communties in Britain over the last three decades. These species groups and region were chosen as they represent one of the best available long-term and spatially replicated datasets in the world. We consider whether changes in CTI have arisen due to increases in the abundance and/or species richness of cold- and warm-associated species. We also test whether changes in the abundance of these species groups might have been influenced by landscape structure and land-use.

Landscape structure and land-use are known to have impacts on biodiversity (Tscharntke *et al*., 2005, Öckinger *et al*., 2010). Heterogeneous landscapes often harbour higher species diversity and sometimes higher densities of species (Weibull *et al*., 2000, Benton *et al*., 2003). Although, for habitat heterogeneity, effects depend on the scale of heterogeneity (i.e. patch size) and on the habitat categories included in the measurement the heterogeneity index (Fahrig *et al*., 2010). Heterogeneous landscapes may also maintain more stable species populations by providing a variety of resources and microclimates (Oliver *et al*., 2010). The intensivity of land use also strongly affects biodiversity, with heavy modification of landscapes being associated with biodiversity declines (Tscharntke *et al*., 2005, Smart *et al*., 2006). In this study, we characterise the habitat and topography at 0.5km radius around the centroid of bird and butterfly monitoring sites. This small spatial scale was chosen as habitat effects often operate at smaller spatial scales for more sedentary specialist species, whilst more mobile species respond to habitat structure at both the site and landscape level (Oliver *et al*., 2010). We relate landscape structure and degree of landscape modification to the change in the total abundance of cold- and warm- associated species, to test the following hypotheses: a) Under incremental climate warming, declines in cold-associated species assemblages will be least marked on sites with a broad diversity of habitat, soil type and topography (because a broad microclimatic range may allow species to persist as viable populations for longer) and with more semi-natural habitat available (allowing greater potential for population growth; **Hypothesis 3a** in Report Introduction), and b) warm-associated species will experience greater increases in abundance on these sites (due to the greater range and amount of resources available; **Hypothesis 3b** in Report Introduction).

7.2 Methods

7.2.1 Species data

Data on bird and butterfly communities were obtained from the UK Butterfly Monitoring Scheme (UKBMS) and the BTO/JNCC/RSPB Common Bird Census (CBC). The UKBMS scheme, which has been running since 1976, comprises fixed 5m wide belt transect routes between 1.5km and 3km in length (Pollard and Yates, 1993). These transects are walked up to 26 weeks of the year throughout the main flight period of UK butterflies. Given a year has been sufficiently recorded (in the weeks of peak abundance for a given species), an estimate of the annual abundance of each butterfly species is calculated at each site in each year, allowing for missing counts (Rothery and Roy, 2001). For any site, we only used data for years in which at least 10 butterfly species were present and for which abundance indices could be calculated for > 75% of the species, so that our community metrics (see next section) were an accurate representation as possible of the actual species assemblages. We also restricted our analyses to sites with more than 5 years' data, because we were interested in changes in butterfly communities over time. In total 493 butterfly sites were analysed.

The CBC (bird) recording scheme involved 10 visits to each site between March and July. The entire survey area of a site was walked, mapping locations and behaviours of all UK breeding birds. Annual data were collated to estimate the total number of breeding territories of each species within each site area each year. Again, for any site, we only used data for years in which at least 10 bird species were present, and we only used sites for which more than 5 years' data were available. We used data from 1964-2000, encompassing 178 sites.

7.2.2 Community temperature metrics

Each bird and butterfly species in our analysis was previously allocated a 'species temperature index' (STI) based on the average temperature occupied across their European range (V. Devictor, *pers. comm.*). This allows species to be ranked by the degree to which they are associated with warmer or cooler places. At any given site, in any given year, a 'community temperature index' can then be calculated as the average of each individual's STI present in a bird or butterfly species assemblage, i.e. each UKBMS site has a butterfly CTI for each year, and each CBC site has a bird CTI for each year. The CTI of a site in a given year reflects the balance of low- and high- temperature-associated species (Devictor *et al*., 2008).

7.2.3 Landscape structure

For each butterfly and bird monitoring site, we assessed the heterogeneity of the site (at 0.5km radius) in terms of habitat, hydrological soil type and topography. Habitat heteregeneity was assessed using Land Cover Map 2000 with land cover types aggregated into 13 broad types (Appendix P5 Table S1). We then calculated a Shannon Index from the area of these land cover types, excluding the 'sea' category ($-\Sigma p.\log_n(p)$ where p is the proportional representation of each habitat type). To assess soil heterogeneity, we used the HOST database, whereby British soils have been previously classified by physical properties into 29 hydrological classes at 1km resolution (HOST database; Boorman *et al*., 1995). We calculated a Shannon Index of all the soil types in the landscape around sites. To assess topographic heterogeneity, we used a 50m resolution digital elevation map of Britain (DEM; Morris and Flavin, 1990) to calculate mean altitude (m), mean slope (degree differential from horizontal; range 0-90), standard deviation of slope values, mean northness of aspect (cos((aspect x pi)/180) where aspect ranges from 0-360˚), and standard deviation of northness values. We did not include standard deviation of altitude in our models as this was highly correlated with mean slope. We only included northness of aspect rather than eastness (which runs perpendicular) because a greater breadth of microclimates is expected to span this aspect gradient in temperate regions.

Finally, we also assessed the overall proportion of semi-natural habitat in around each monitoring site. Semi-natural habitat was classified as all land cover types excluding arable, urban/suburban and sea. All the landscape structure variables were standardised to zero mean and unit variance before analysis in order to better compare their relative importance in explaining changes in community structure over time. We then tested for colinearity between all of these landscape variables. In no cases did colinearity prevent inclusion of the variables as regression covariates (Table S2: UKBMS sites, Table S3: CBC sites).

7.2.4 Statistical analysis

We carried out two types of analysis. The first tested for overall change in bird and butterfly CTI over time and the second overall changes in low and high STI species. We ranked species by their STI scores to identify those particularly associated with cold places (bottom quartile of STI scores) and those particularly associated with warm places (top quartile of STI scores). To assess changes in CTI and in the total abundance of these low and high STI species groups over time, we fitted linear mixed effects models using the lme4 package in the program R (Bates *et al*., 2008, R Development Core Team, 2009). In the first instance, CTI was the response variable and year was the continuous fixed effect explanatory variable. We fitted random intercepts for *Site* and *Year* (categorical variable), to account for the non-independence of data within sites across years and across sites within years. We also included a random slope for the effect of year at each site, because model comparison using AIC suggested that the temporal trend in CTI varied between sites. To test the significance of the year effect we used a likelihood ratio test. To examine spatial patterns in CTI temporal trends we plotted the random slopes (estimated trend in CTI at each site) and tested for spatial autocorrelation by plotting spline correlograms using the *ncf* package (Bjornstad, 2009).

To consider changes in the total abundance of low or high STI species over time we used the same model structure (i.e. same fixed and random effects) but specified Poisson errors. For these generalised linear mixed models, the significance of fixed effects were obtained from model z-values. Again, we examined spatial patterns in the data and tested for spatial autocorrelation. We also tested for changes in the total species richness of low or high STI species over time using the same model and error structure.

For our second type of analysis we related temporal changes in the total combined abundance of low and high STI species to the habitat and topographic heterogeneity around monitoring sites. We used a generalised linear mixed model with Poisson error structure and fitted year and all the landscape structure variables, described above, as main effects. We also included interaction terms between year and each of the landscape variables. These interaction terms indicate whether the trends in abundance of low and high STI species vary depending on the habitat and topographic heterogeneity around monitoring sites.

Although we fitted a single, comprehensive statistical model to test our hypotheses, in order to illustrate our results, we obtained individual temporal trends for the combined total abundance of low and high STI species for each site. This was done by fitting a separate regression for each site and then plotting these regression slopes against the variables that described the landscape structure around each site. For this procedure, we omitted sites with fewer than 10 years' data because, analysed separately in this manner, these sites provide inaccurate trend estimates. However, they do still provide useful evidence for interpretation of the unified mixed model analysis (which weights the contribution of individual sites according to their the sample size).

7.3 Results

7.3.1 Changes in bird and butterfly communities over time

There was no overall significant change in the community temperature index (CTI) of butterfly species at each site between 1976 and 2009 (year coefficient = 0.013 ± 0.01, $X^2 = 1.068$, df = 1, p = 0.30; Appendix P1A Figure S1). Considering only low STI butterfly species (i.e. those 25% of British species most associated with colder places), there was sigificant change in neither the total abundance of these species at each site (year coefficient = 0.019 ± 0.05, z = 0.39, p = 0.70; Figure 1a), nor their species richness (year coefficient = -0.014 ± 0.008, z = -1.78, p = 0.08; Figure 1b). However, considering the plot of total abundance of low STI species over time (Figure 1a), there appear to be two outlying datapoints for the years 1976 and 1977. The year 1976 was a severe drought in the Great Britain, which a negative impact on the abundance of many species (Parker *et al*., 1992, Botham *et al*., 2009). It is likely that low-STI butterfly species, favouring cooler temperatures, may have been disproportionately affected, thus causing declines in their total abundance. If we re-analyse the total abundance of low STI butterfly species excluding these outlying years, then the trend coefficient does become negative, although it is still non-significant (year coefficient = -0.049 ± 0.04, z = -1.11, p = 0.267).

For high STI butterfly species, there was a significant increase in total abundance at each site (year coefficient = 0.105 ± 0.037, z = 2.79, p = 0.005; Figure 1c) and in their species richness (year coefficient = 0.037 ± 0.010, z = 3.75, p < 0.001; Figure 1d).

There was a significant increase in the CTI of bird species at each site between 1964 and 2000 (year coefficient = 0.045 ± 0.008, X^2 = 27.8, df = 1, p = <0.001; Figure S2). This change in CTI appears to be driven primarily by loss in the total abundance of low STI (cold-associated) species (year coeffficient = -0.285 ± 0.051, z = -5.60, p < 0.001; Figure 2a) and in their species richness (year coefficient = -0.141 ± 0.020, z = -7.16, p < 0.001; Figure 2b). There was no significant change in the total abundance of high STI species (year coefficient = -0.037 ± 0.062, z = -0.60, p = 0.60), but there was a significant decline in their species richness (year coefficient = -0.050 ± 0.023, z = -2.02, p = 0.043).

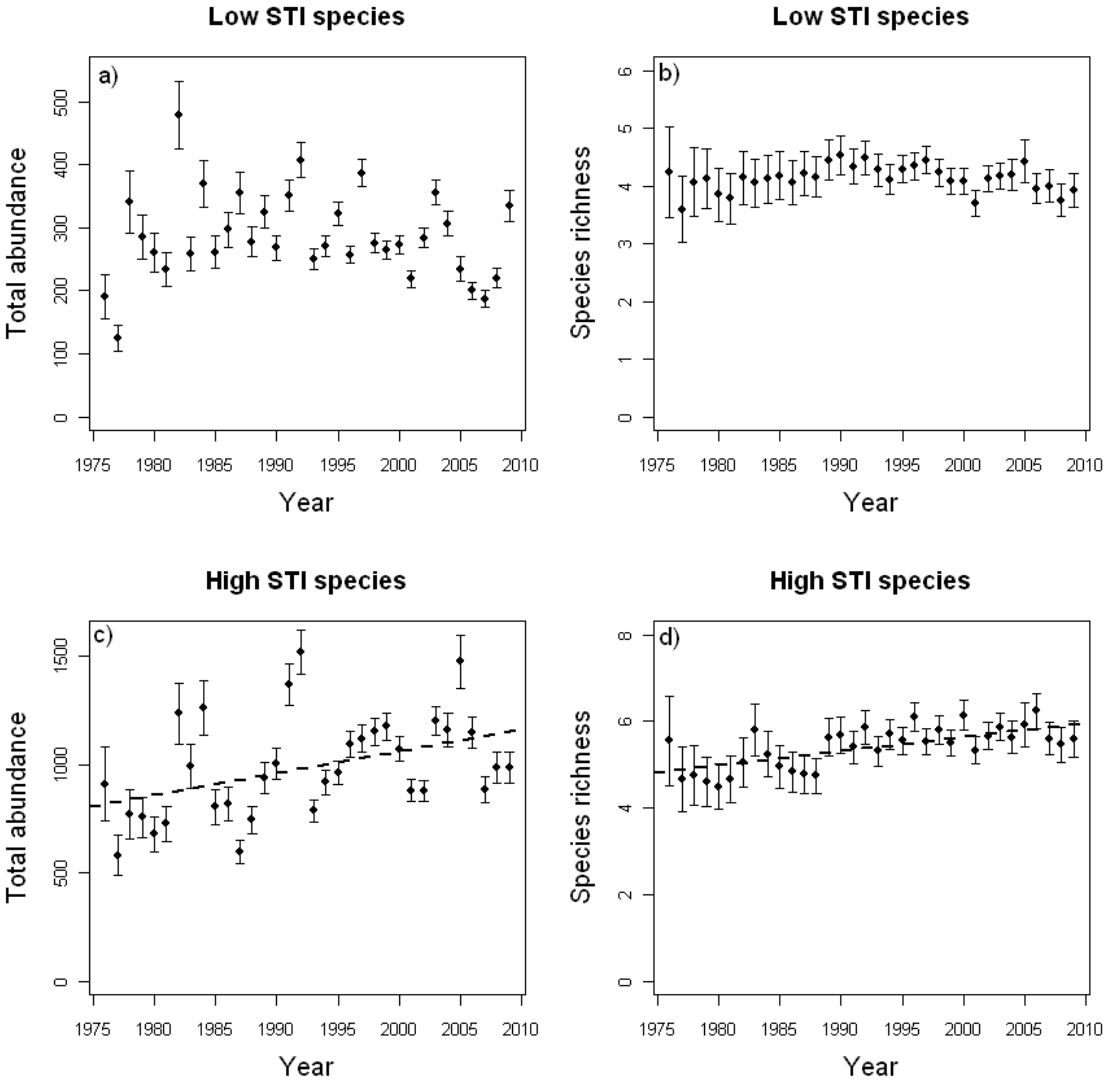

Figure 1: Trends in total abundance and species richness of low STI (cold-associated) and high STI (warmth-loving) butterfly species. Plotted are mean values for each year with standard error bars. The dashed lines indicated significant trends (see main text for summary statistics).

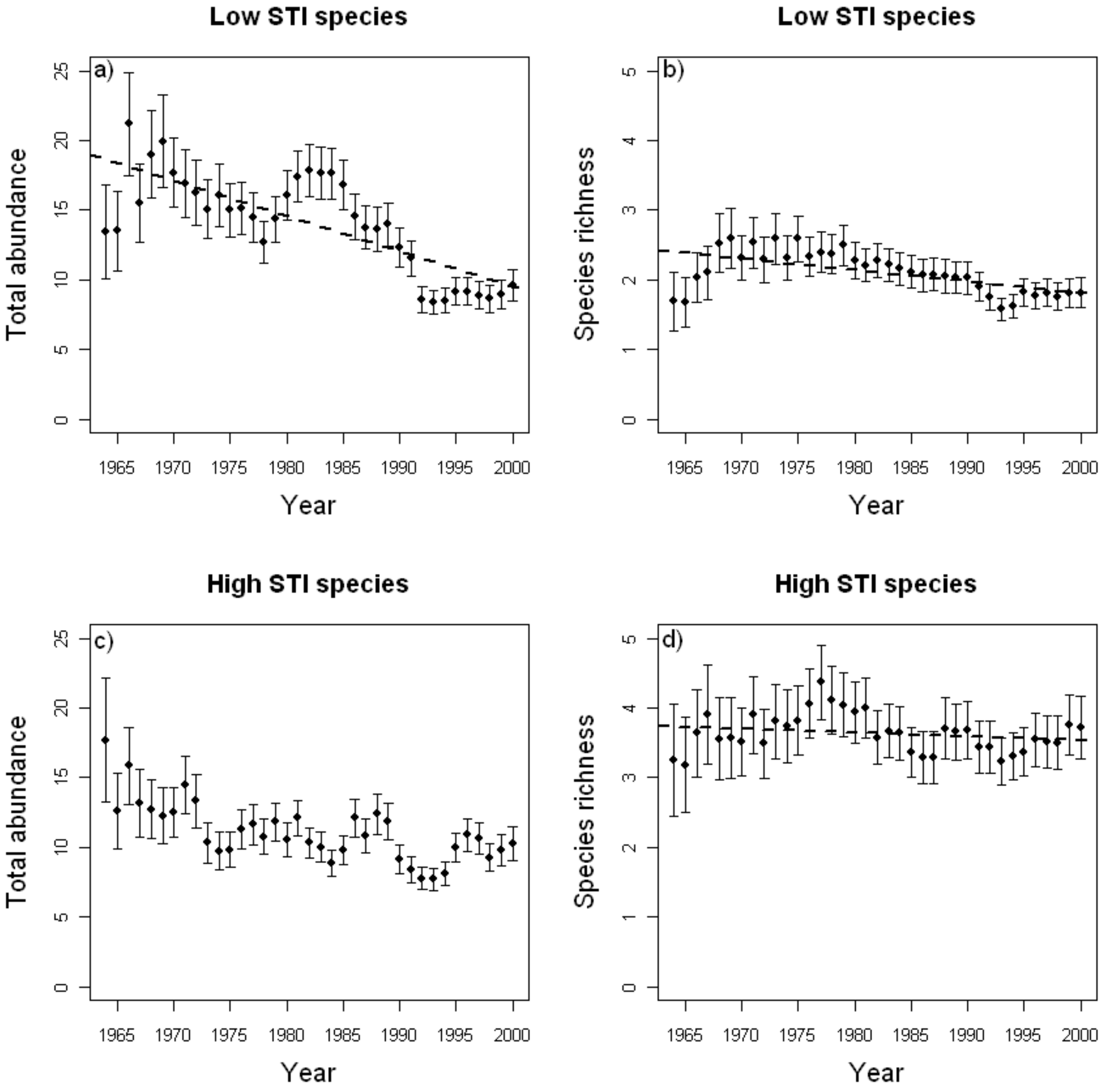

Figure 2: Trends in total abundance and species richness of low STI (cold-associated) and high STI (warmth-loving) bird species (CBC data). Plotted are mean values for each year with standard error bars. The dashed lines indicated significant trends.

7.3.2 Effects of local habitat and topography structure on community change

There was no spatial autocorrelation apparent in the abundance trends over time of low or high STI species for either butterflies or birds (Figures S3-S6). For low STI (cold-dwelling) butterfly species, the habitat and topographic heterogeneity around monitoring sites appeared to moderate changes in abundance over time. The proportion of semi-natural habitat within sites had the strongest effect (Table 1). Sites with less semi-natural tended to show steeper declines in low STI butterfly species (Figure 3c). Topographic diversity of sites was also associated with changes in the abundance of low STI butterfly species. Low STI butterfly species have declined most in sites with higher slope diversity and lower aspect diversity (Figure 3a & b respectively). For high STI (warmth-loving) butterfly species, none of the landscape variables tested were significantly associated with changes in abundance over time (Table 2).

For birds, the proportion of natural habitat around sites was the only landscape variable that was significantly associated with changes in the abundance of low STI species over time (Table 3). Similar to the result for butterflies, sites with a less semi-natural habitat in the surrounding landscape tended to show steeper declines in low STI bird species (Figure 4). For high STI (warmth-loving) bird species, four landscape variables were significantly associated with changes in the abundance over time, although all effects were fairly weak (Table 4; Figure 5). Sites at higher altitude, with steeper slopes and greater slope diversity have shown the steepest declines in high STI bird species. Again the proportion of semi-natural habitat in landscapes affected abundance trends, with greater declines of high STI species in landscapes with less semi-natural habitat.

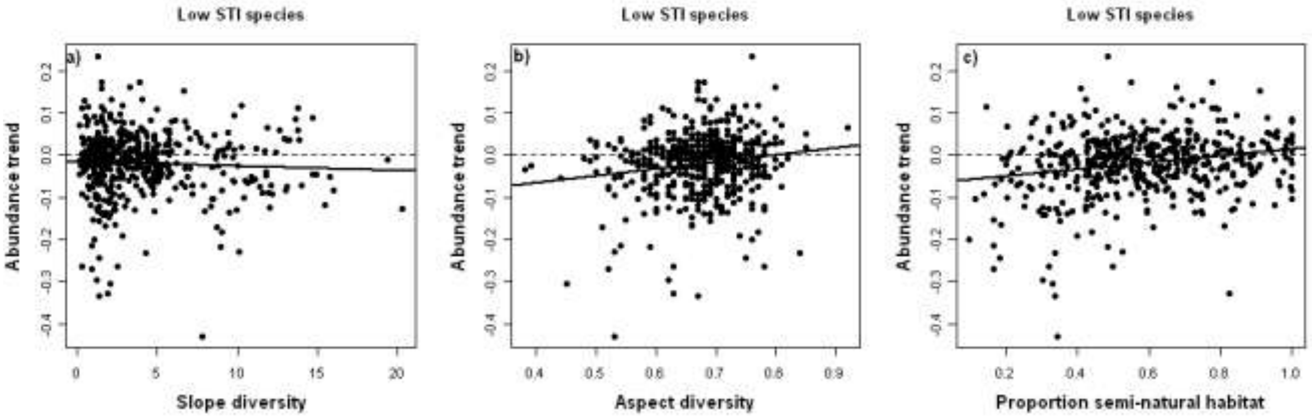

Figure 3: Relationships between landscape variables and trends in abundance of low STI (cold-associated) butterfly species.

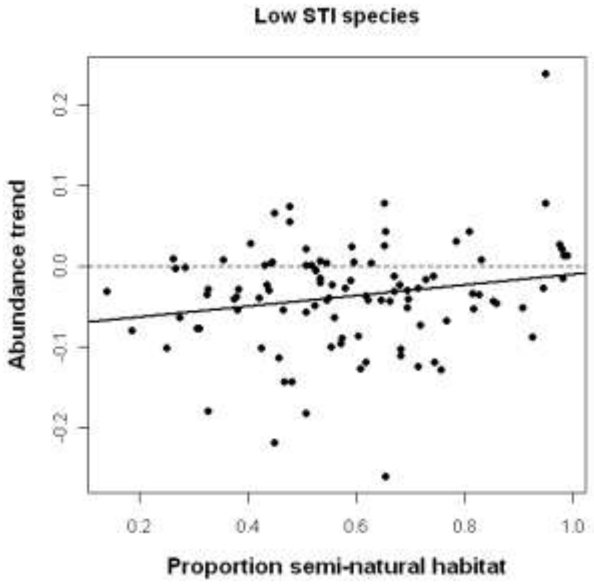

Figure 4: Relationships between proportion of semi-natural habitat in the landscape and trends in abundance of low STI (cold-associated) bird species.

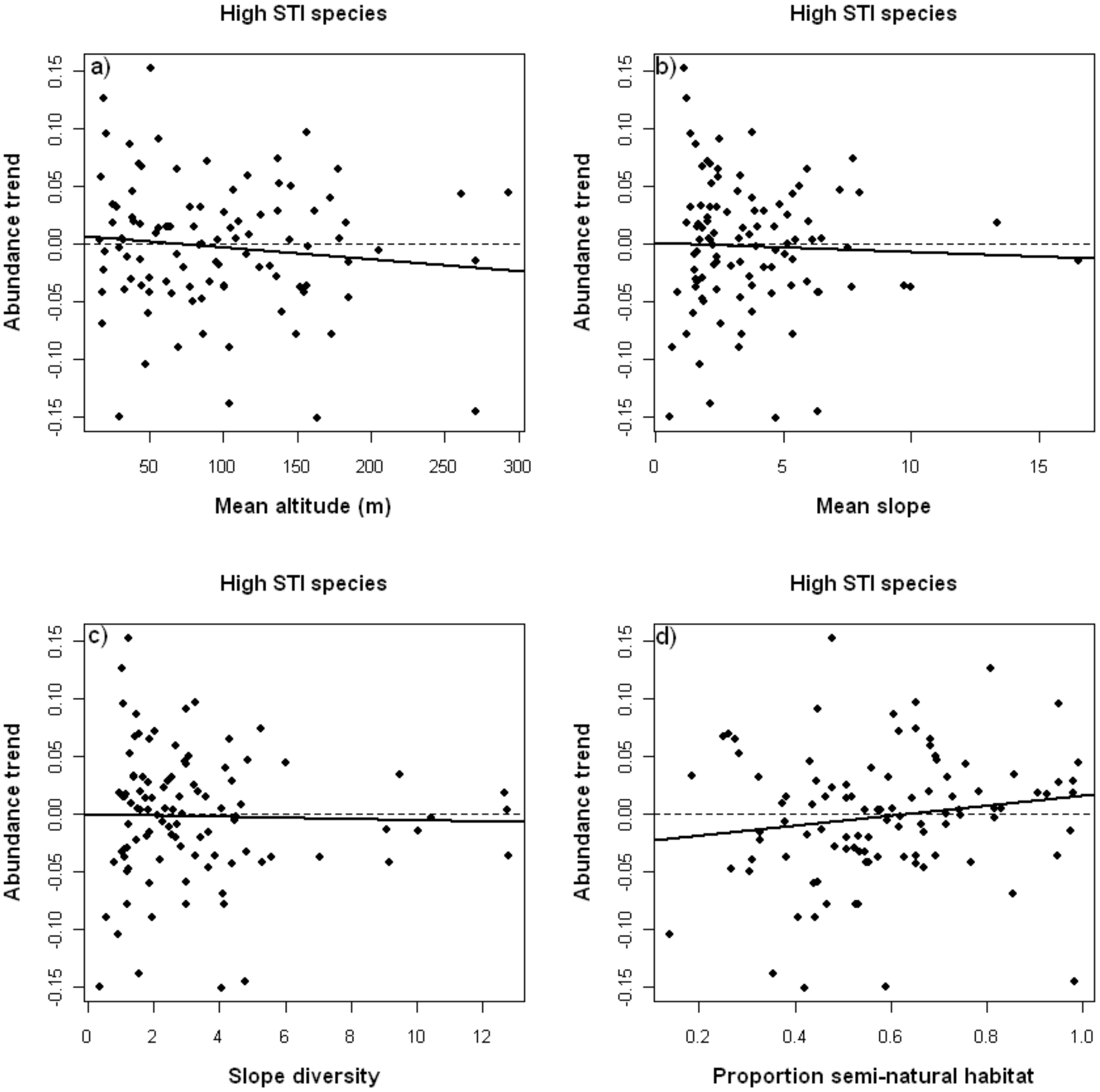

Figure 5: Relationships between proportion of semi-natural habitat in the landscape and trends in abundance of high STI (warmth-loving) bird species.

7.4 Discussion

In this study, we found that the average CTI of British birds has increased significantly over the last three decades. The average CTI of butterflies increased slightly, although the overall change was not significant. However, there were significant increases in the total abundance and species richness of warmth-loving butterfly species. For birds, the overall changes in CTI were primarily driven by the loss of cold-associated species (both in terms of species richness and total abundance). A previous study found that the CTI of French birds had increased over time, but whether this was due to loss of cold-associated species of gain of warm-associated species was not identified (Devictor *et al.*, 2008).

We found that the loss of cold-associated species was associated with local habitat and topographic heterogeneity and land use on monitoring sites. Cold-associated bird and butterfly species decreased most in areas with less semi-natural habitat present (i.e. areas where arable and urban/ suburban land cover types dominated). This variable also affected the changes in of warm-associated bird species, with increased recruitment of warm-loving species in areas with more semi-natural habitat (i.e. strong support for hypotheses **3a and 3b** with regards to amount of semi-natural habitat in landscapes). Hence, the degree of landscape modification from a semi-natural state appears to have a very strong effect in moderating community responses to climate change. Anthropogenic drivers are commonly known to interact to determine biodiversity responses (Warren *et al*., 2001, White and Kerr, 2006, Walther, 2007, Moss *et al*., 2010).

Topographic heterogeneity was also found to be an important factor associated with changes in species assemblages. An increase in aspect diversity was associated with reduced decline in cold-associate butterfly species. This result fits with our hypotheses based on existing theory (i.e. there was some evidence supporting **Hypothesis 3a** with regards to topographic heterogeneity). A large diversity of topographical aspect provides a broader range of microclimates. Butterfly species have been found to have more stable populations and to persist for longer in areas with a range of topographic aspects (Weiss *et al*., 1988, Oliver *et al*., 2010). Other topographical variables, however, had effects contrary to our expectations. Sites with higher mean altitude and slope suffered greater losses in warmth-loving bird species, although these effects were weak. However, there was a strong effect of slope diversity on both butterfly and bird assemblages, whereby sites with higher slope diversity suffered greater losses in cold-associated butterfly species and warmth-loving bird species (i.e. other evidence did not support **Hypothesis 3a and 3b** with regards to topographic heterogeneity). Previous theory would suggest that topographic diversity provides a range of microclimates that might increase the retention of cold-associated species and facilitate recruitment of warmth-loving species (Weiss *et al*., 1988, McLaughlin *et al*., 2002, Roslin *et al*., 2009). One possible reason for our result for declines in cold-associated butterflies is that high latitude sites (which tend to be more topographically diverse) have experienced the greatest warming in climate. However, there was no clear latitudinal pattern in the trends in cold-associated butterfly species over time (Figure S3) and this explanation is insufficient for the (albeit weaker) effect on warmth-loving bird species. A second possibility is that sites with low topographic diversity may already have lost their complement of cold-associated butterfly species, and hence show little overall change in the abundance of these species. In contrast, sites with high topographic diversity may have retained reasonable numbers of these species and begun to lose them rapidly over the last 30 years. We recommend further work on the importance of topography in community change because, although our results suggest prioritisation of sites topographically diverse in aspect, which may be more likely to retain cold-associated butterfly species, there were unexpected (and negative) associations of slope diversity on both cold-associated butterfly and warmth-loving bird species.

There were no strong effects of habitat or soil heterogeneity on the change in species assemblages i.e. little evidence supporting **Hypothesis 3a and 3b** with regards to habitat and soil heterogeneity). Habitat heterogeneneity is thought to play a role in a maintaining more stable and persistent species populations (Kindvall, 1996, Piha *et al*., 2007). In this study, by necessity of considering multiple species simultaneously, we only used a general measure of habitat heterogeneity (Shannon Index of all semi-natural habitat types), rather than a species-specific measure (including only habitat types frequently used by a given species), which might be expected to be more sensitive to population dynamics (Oliver *et al*., 2010). Alternatively, it may be that habitat and soil heterogeneity genuinely have little impact on community change or have effects at different spatial scales to those tested; with such coarse macroecological studies the absence of an effect does not disprove its importance.

Our results suggest that components of the environment at individual sites may affect changes in the community structure of both birds and butterflies under incremental climate warming. Increased amounts of semi-natural habitat are likely to promote the population growth of many bird species at the site-level, with population declines most rapid in more intensively managed landscapes (Chamberlain *et al*., 2000). Increasing amounts of semi-natural habitat may also improve the resilience of cold-associated butterfly populations to warming, although the population growth of warm-associated butteflies appeared little affected by habitat availability. Continuing to protect areas of semi-natural habitat is therefore likely to be a sensible conservation strategy in a changing climate, associated with reducing sources of harm from other pressures and increasing resilience to climate change. The protection of areas of high topographic diversity is also regarded as a sensible adaptation strategy (for example, Hodgson *et al*. 2009), for which there is some limited evidence from our analysis, which must be considered in the light of other, more species-specific analyses (Oliver *et al*., 2010, Bradbury *et al*., 2011).

Our results have general implications that that both landscape structure and, in particular, the cover of anthropogenically modified habitat can mediate community changes under incremental climate warming. Promoting resilience is often seen as a goal in climate change adaptation, although definitions of the term vary from the amount of disturbance a system can absorb and still remain in the same state or “domain of attraction” (Walker *et al*., 2004), to the ability of a system to return to a pre-disturbed state without incurring any lasting fundamental change (Pimm, 1984). Indeed, increasing resilience is often seen as a general target for many socioeconomic systems (Elmqvist *et al*., 2003, Walker *et al*., 2004, Fischer *et al*., 2006, Gallopin, 2006, Tschakert and Dietrich, 2010). In the context of climate change adaptation, resilience might be thought of as the ability of a species assemblage to resist incremental climate warming and ‘bounce back’ from extreme climatic events(i.e. for species composition and relative abundance to remain unchanged). Such a goal is unrealistic as we show here that the composition of our species assemblages has clearly changed in the past three decades. Maintaining cold-associated species for as long as possible in the face of climate warming might be seen as a worthwhile goal, however it may also be beneficial to recruit new warmth-loving species into communities, i.e. accommodating change (Montoya and Raffaelli, 2010, Traill *et al*., 2010, Thomas *et al*., 2011; Morecroft *et al*., in press). In the face of inevitable lossed of cold-associated species, adaptation through managing the habitat infrastructure to accommodate new species, may allow the maintanance of ecosystem services. Such a habitat-focussed approach may also facilitate the return of cold-associated species in the future, if global warming were ever reversed. Hence, the focus of climate change adaptation should be to maintain the resilience of ecosystem services but not necessarily of community structures. Species assemblages are intrinsically dynamic and, indeed, may *need* to be dynamic to maintain resilience in ecosystem services. For example, accommodating the arrival of warmth-loving insect species to communities may promote the resilience of local pollination services as cold-associated community members decline. i.e. managing to allow accomodation and transformation of systems in order to create reslience in ecosystem service provision (Morecroft *et al*. in press).

Our study suggests that adaptive responses (i.e. maintaining the complement of cold-associated species, whilst simultaneously accomodating warmth-loving species) may be hampered in landscapes that are highly modified by human land-use. Limiting the proportion of land occupied by arable and urban/suburban landcover is likely to be an important climate change adaptation strategy. If this is not possible, then modified landscapes will need to be managed creatively to ensure that, in the future, they provide better habitats than they do currently.

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Table 1: Interactions between landscape variables and year on the total abundance of low STI (cold-associated) butterfly species. Significant interactions (marked with asterisks) indicate that the landscape structure around sites is associated with the trend in species abundance over time. Each significant interaction effect plotted in Figure 3 to aid interpretation.

Interaction term	**coefficient**	**se**	**z**	**p**	
Year: Habitat diversity	0.012	0.026	0.440	0.660	
Year: Soil diversity	0.034	0.025	1.360	0.174	
Year: Mean altitude	-0.012	0.035	-0.350	0.728	
Year: Mean slope	0.070	0.051	1.380	0.168	
Year: Slope diversity	-0.156	0.046	-3.410	0.001	***
Year: Mean aspect (northness)	0.009	0.025	0.340	0.735	
Year: Aspect diversity	0.058	0.025	2.350	0.019	*
Year: Proportion S-N habitat	0.114	0.029	3.910	<0.001	***

Table 2: Interactions between landscape variables and year on the total abundance of high STI (warmth-loving) butterfly species. Significant interactions (marked with asterisks) indicate that the landscape structure around sites is associated with the trend in species abundance over time.

Interaction term	**coefficient**	**se**	**z**	**p**	
Year: Habitat diversity	0.014	0.022	0.620	0.535	
Year: Soil diversity	0.023	0.021	1.080	0.282	
Year: Mean altitude	-0.012	0.032	-0.370	0.710	
Year: Mean slope	0.026	0.044	0.590	0.553	
Year: Slope diversity	-0.003	0.039	-0.070	0.944	
Year: Mean aspect (northness)	-0.004	0.022	-0.190	0.847	
Year: Aspect diversity	-0.033	0.021	-1.550	0.121	
Year: Proportion S-N habitat	-0.024	0.025	-0.970	0.331	

Table 3: Interactions between landscape variables and year on the total abundance of low STI (cold-associated) bird species. Significant interactions (marked with asterisks) indicate that the landscape structure around sites is associated with the trend in species abundance over time. The significant interaction effect is plotted in Figure 4 to aid interpretation.

Interaction term	**coefficient**	**se**	**z**	**p**	
Year: Habitat diversity	-0.037	0.044	-0.834	0.405	
Year: Soil diversity	-0.015	0.045	-0.346	0.729	
Year: Mean altitude	-0.024	0.059	-0.406	0.685	
Year: Mean slope	0.100	0.092	1.084	0.278	
Year: Slope diversity	-0.096	0.078	-1.239	0.215	
Year: Mean aspect (northness)	-0.030	0.046	-0.660	0.509	
Year: Aspect diversity	-0.003	0.044	-0.066	0.948	
Year: Proportion S-N habitat	0.104	0.051	2.050	0.040	*

Table 4: Interactions between landscape variables and year on the total abundance of high STI (warmth-loving) bird species. Significant interactions (marked with asterisks) indicate that the landscape structure around sites is associated with the trend in species abundance over time. The significant interaction effects are plotted in Figure 5 to aid interpretation.

Interaction term	**coefficient**	**se**	**z**	**p**	
Year: Habitat diversity	-0.054	0.056	-0.968	0.333	
Year: Soil diversity	0.087	0.054	1.624	0.104	
Year: Mean altitude	-0.154	0.073	-2.116	0.034	*
Year: Mean slope	0.239	0.118	2.030	0.042	*
Year: Slope diversity	-0.195	0.095	-2.053	0.040	*
Year: Mean aspect (northness)	0.008	0.055	0.149	0.881	
Year: Aspect diversity	-0.051	0.054	-0.945	0.345	
Year: Proportion S-N habitat	0.123	0.062	1.987	0.047	*

Synthesis: Evidence for the effectiveness of climate change adaptation principles[1,2]

8.1 Summary of evidence

In the introduction to this report we discussed how there is little empirical evidence for the role of site-based and landscape-scale attributes in affecting the resilience of wildife populations to climate change. Despite this, a number of climate change adaptation principles have been proposed (Hopkins *et al*., 2007, Mitchell *et al*., 2007, Smithers *et al*., 2008), and whilst these are based on sound ecological theory, there is a crucial need to increase the evidence base to inform climate change adaptation policy and land management decisions. Here, we set out to address a number of hypotheses directly relevant to these climate change adaptation principles. We carried out analyses of data from a large number of bird and butterfly population monitoring sites (> 2000 sites in total for >150 species primarily over a period of 9-15 years, but extending in some cases up to 35 years). From these analyses, we summarise below the evidence for and against each of the hypotheses raised.

Question 1. Do site-scale (0.5km radius) attributes enhance resilience of species populations and ultimately community composition?

Hypothesis 1- Local (site) variation in habitat, soil type and topography are positively correlated with the mean density (Hypothesis 1a) and resilience (H1b) of populations as measured during recent periods of relative climatic variability and incremental change.

***Hypothesis 1a*:** There was a strong positive association between average bird density and habitat heterogeneity on monitoring sites (Part 1). In contrast, we found no significant effect of site habitat heterogeneity on butterflies. Soil and topographic heterogeneity of sites similarly had no apparent effect on average butterfly density. Topography did have some effect on birds however, with lower bird densities on higher altitude sites.

***Hypothesis 1b*:** Habitat heterogeneity on monitoring sites had a strong association with the inter-annual variability of butterfly populations (Part 1). Sites with higher habitat heterogeneity tended to have more stable butterfly populations. A similar result was found by Oliver *et al.* (2010), who used a species-specific measure of habitat heterogeneity (i.e. excluding those land cover types rarely used by a species). In this study, we used a generic measure of habitat heterogeneity (including all land cover types), which might be expected to be less sensitive as a measure of site quality. However, there are clearly strong associations between butterfly population stability and habitat heterogeneity even with this generic measure. Notably, we also tested an index of habitat heterogeneity which excluded arable and urban/ garden land cover types. This index was not strongly associated with butterfly population inter-annual variability, suggesting that the presence of these land cover types may help promote population resilience.

For birds, there was no evidence that site habitat heterogeneity affected population stability. Similarly, for both species groups, butterflies and birds, there was little evidence for associations between soil and topographic heterogeneity on population stability. A study by Oliver *et al.* (2010) found that variation in topographic aspect can help promote stability in butterfly populations, although the strength of the association was weaker than that between habitat heterogeneity and population stability. The results of this study reinforce the strong importance of habitat heterogeneity on (butterfly) population resilience, whilst the effects of topographic heterogeneity on population resilience appear weaker.

We also assessed population resilience in two other ways besides population stability: population sensitivity to- and recovery from- extreme events. There was little evidence that site-scale heterogeneity of habitat, soil or topography were consistently associated with these measures of resilience across species.

H2- Area of key habitat types for species' will be positively correlated with the mean density (H2a) and resilience (H2b) of populations.

Hypothesis 2a**:** The area of certain habitat types on monitoring sites was not often strongly associated with average butterfly density. Stronger associations occurred more frequently at larger spatial scales, although this may be partly due to larger sample sizes at these scales (Part 1; see Hypothesis 5a). There were some weak associations between butterfly and heathland and arable area on sites. Heathland was associated with lower average butterfly densities, whilst, surprisingly, larger areas of arable land cover were associated with higher average butterfly densities. For the speckled wood butterfly, *Pararge aegeria*, broadleaved woodland area on sites was positively associated with butterfly density. For birds, assessed using the BBS survey, the area of certain habitat types on monitoring sites had much stronger associations with average density. Larger areas of urban/ garden, broadleaved woodland and inland water on sites were all associated with higher average bird densities. In contrast, larger areas of arable land cover had a strong negative correlation with bird density. Using the CBC, survey no associations between site attributes and population density were found.
Hypothesis 2b: There was some evidence that the area of certain habitat types on monitoring sites was related to bird and butterfly population stability, although associations were less strong than for density relationships (Part 1). Both butterfly and bird populations were, on average, more stable between years when more urban/ garden habitat was present on monitoring sites. For birds, assessed using the BBS survey, there was also a relationship between population stability and area of arable field; bird populations were less stable when larger areas of arable land cover were present on monitoring sites.

We also assessed population resilience in two other ways besides population stability: population sensitivity to- and recovery from- extreme events. From an analysis identifying extreme events and quantifying the population responses to these (Part 3), there was little evidence that the area of key habitat types on sites were consistently associated with these measures of resilience across species. From an analysis of growth rates from entire time series (Part 4- woodland birds only), there was some evidence that for an interaction between woodland area and growth rate for specialist species. Interestingly, the positive effects of warm years were less on sites that had larger amounts of woodland. This might reflect that populations on sites with large amounts of woodland tend be more stable over time (*Part 2*). There was also some evidence that populations of specialist species on more wooded sites were more likely to maintain high abundances in subsequent years following a beneficial warm summer.

H3- Under incremental climate warming, declines in cold-associated species assemblages will be least marked on sites with a broad diversity of habitat, soil type and topography (because a broad microclimatic range may allow species to persist as viable populations for longer) and with more semi-natural habitat available (allowing greater potential for population growth; H3a). In contrast, species assemblages of warmth-associated species will increase most on these sites (due to the greater range and amount of resources available; H3b).

Hypothesis 3a**:** We found no evidence that site-level heterogeneity in habitat or soil type moderated changes in the total abundance of cold-associated bird or butterfly species (between 1964-2000 for birds and 1976-2009 for butterflies; Part 5). There was some evidence, however, for associations between topographic heterogeneity and the change in abundance of cold-associated butterfly species. For aspect diversity, the effect was in the direction expected, where a range of aspects on sites (along a north-south gradient) was associated with the retention of cold-associated species. In contrast, for slope diversity, the effect was in the opposite direction expected. Sites with a range of different slope values tended to have shown the most marked decline in cold-associated butterfly species. This may reflect the fact that sites with low topographic diversity have already lost their complement of cold-associated butterfly species, and hence show little overall change in the abundance of these species. In contrast, sites with high topographic diversity may have retained reasonable numbers of these species and begun to lose them rapidly over the last 30 years. Further work is needed to test this hypothesis. However, it should be noted that the strongest site attribute associated with change in cold-associated species was not habitat, soil or topographic heterogeneity, but the proportion of semi-natural habitat on sites (i.e. proportional total area excluding arable and urban/ garden land cover). Cold-associated butterfly species declined most on sites with less semi-natural habitat. Similarly for birds, neither habitat, soil or topographic heterogeneity explained loss in cold-associated species, but there was a strong effect whereby larger areas of semi-natural habitat ameliorated declines.

Hypothesis 3b**:** We found no evidence that site-level heterogeneity in habitat, soil type or topography moderated changes in the total abundance of warm-associated butterfly species (Part 5). There were weak associations between topographic heterogeneity and changes in the abundance of warmth associated bird species however. Sites at higher altitude and with higher slope diversity (upland sites) have shown the greatest decline in warm-associated species. The proportion of semi-natural habitat on sites was also weakly associated with changes in the abundance of warmth associated bird species, where sites with more semi-natural habitat were more likely to experience increases in the total abundance of these species.

Q2. Do landscape-scale (2km- 10km radius) attributes enhance robustness of species populations and ultimately community composition?

H4- Landscape-scale variation in habitat, soil type and topography are positively correlated with the mean density (H4a) and resilience (H4b) of populations of populations as measured during recent periods of relative climatic variability and incremental change.

Hypothesis 4a**:** Although population density was best predicted by attributes measured at the site scale (when comparing site and landscape attributes using the same complement of sites), there tended to be a greater number of attributes emerging as significant predictors at the landscape level (due to the greater number of sites available for analysis when considering attributes at larger spatial scales; Part 1). Hence, the heterogeneity of semi-natural habitat types had strong associations with butterfly density when measured at the landscape level. Landscapes with a greater diversity of semi-natural habitat types had lower butterfly densities. This highlights that although habitat heterogeneity can promote population resilience (measured by stability; Hypothesis 4b), it can also lead to lower mean densities. Hence there may be a trade off between resilience and mean density when trying to promote robustness of populations. Other measures of landscape heterogeneity (soil type and topography) were not strongly associated with butterfly density.

For birds, using the BBS survey, there were strong positive associations between habitat heterogeneity at the landscape scale and average population density (i.e. the opposite results to butterflies). Incidentally, an index of habitat heterogeneity including urban/ garden and arable land cover was a better predictor of bird density than an index of semi-natural habitats only. This probably reflects the fact that urban/ garden habitats can have positive effects on average bird density (see Hypotheses 2 and 5). Soil and topographic heterogeneity variables did not have strong associations with bird density. However, there was a negative association between mean altitude and bird density.

Hypothesis 4b**:** Habitat heterogeneity at the landscape level was associated with butterfly population stability, although effects were generally stronger at the site level (Hypothesis 1b). For birds (BBS and CBC survey), there was no evidence of association between habitat heterogeneity and population stability. Similarly, for both butterflies and birds there was little evidence that landscape-level soil or topographic heterogeneity are important for population stability.

We also assessed population resilience in two other ways besides population stability: population sensitivity to- and recovery from- extreme events. There was little evidence that landscape-level heterogeneity of habitat, soil or topography were consistently associated with these measures of resilience across species.

H5- The area of species’ key habitat types in the local landscape will be positively correlated with the mean density (H5a) and resilience (H5b) of populations.

Hypothesis 5a**:** The area of certain habitat types at a landscape level were strong predictors of both bird and butterfly density. For butterflies, heathland, fen/ bog, coastal and coniferous woodland all had negative associations with average butterfly density. In contrast, larger areas of arable land cover in the landscape were associated with higher average butterfly density. For birds, using the BBS survey, urban/ garden and broadleaved woodland were strongly associated with higher average bird density. Arable, bracken and heathland land cover were all associated with lower average bird density. Using the CBC survey, no associations between landscape attributes and population density were found.

Hypothesis 5b**:** The area of certain habitat types at a landscape level were associated with both bird and butterfly stability, although the number of significant associations was generally less than with population density as a response variable (Part 1). Larger areas of urban/ garden habitat in the landscape were associated with more stable populations of both butterflies and birds (BBS survey only). In contrast, large areas of arable land cover were associated with less stable bird populations (both BBS and CBC surveys). Using the BBS survey, there were additional associations with the area of broadleaved woodland (promoting stability) and the area of fen (reducing stability).

We also assessed population resilience in two other ways besides population stability: population sensitivity to- and recovery from- extreme events. From an analysis identifying extreme events and quantifying the population responses to these (Part 3), there was little evidence that the area of key habitat types in landscapes (5km radius) were consistently associated with these measures of resilience across species. Similarly, from an analysis of growth rates from entire time series (Part 4- woodland birds only), there was little evidence that woodland area in the landscape (5km radius) had a strong effect on the sensitivity to- and recovery from- years of climatic extreme.

H6- Ecological networks defined by the connectivity of species' key habitats also increase the mean density (H6a) and resilience (H6b) of populations as measured during recent periods of relative climatic variability and incremental change.

Hypothesis 6a**:** The configuration of certain habitat types had strong associations with population density of both birds and butterflies (Part 1). In some cases, habitat configuration was correlated with total habitat area. If population density was more strongly related to habitat area, then this suggests that correlations with habitat configuration may be an artefact of the previous relationship. In contrast, there were occasions when configuration metrics had stronger effects on population density than total habitat area. For example, the mean shape index ('edginess') of arable habitat had a positive association on butterfly density that was stronger than the positive association with total arable area. This suggests that the configuration effect may be genuine; arable edge habitats appear important for average butterfly density. All three configuration metrics that we tested had strong associations with bird and butterfly density for one or more habitat types, although the mean shape index ('edginess') metric appeared to be a stronger predictor of butterfly density.

For broadleaved woodland we carried out multivariate tests for interaction effects between woodland area and configuration on population density (Part 2). There was no evidence for interaction effects on density, but there were strong additive effects of both landscape attributes, although woodland area was generally a better predictor of density. The direction of effects differed depending on species' woodland associations (woodland specialist, generalist or 'non-woodland' species; see Hypothesis 7).

Hypothesis 6b**:** As with habitat area attributes, there were generally fewer significant associations with configuration of certain habitat types with population stability, rather than density, as the response variable (Part 1). In many cases, covariation between habitat configuration and area (of the same habitat type and others) confounded interpretation. However, there were cases where there appeared to be genuine effects of habitat configuration on population stability. For example, the mean shape index ('edginess') of urban garden habitats was associated with more stable bird populations, a result that was unlikely to arise from simply due to covariation with the area of this habitat type.

For broadleaved woodland, we carried out multivariate tests for interaction effects between woodland area and configuration on population stability. Effects of woodland configuration on population stability were generally much weaker than effects on population density. Woodland configuration was important for population stability of birds assessed using the CBC survey, but not for birds using the BBS survey or for butterflies. The effects of woodland configuration on CBC birds varied depending on species' woodland associations (see Hypothesis 7).

We also assessed population resilience in two other ways besides population stability: population sensitivity to- and recovery from- extreme events. From an analysis identifying extreme events and quantifying the population responses to these (Part 3), there was little evidence that the configuration of key habitat types were consistently associated with these measures of resilience across species. One notable exception was that the number of patches of species' key habitat types (woodland, grassland or heathland defined *a priori*) was often significantly related to species' population sensitivity to (trend-derived) extreme events. The direction of effect was opposite to that initially expected. We expected increased population sensitivity in landscapes where habitat is fragmented into lots of separate patches, yet we found tentative evidence that sensitivity in these landscapes was actually lower. In retrospect, this fits with results from our analyses on other aspects of population robustness, where we found that mean density and population stability tended to be higher when key habitat types were separate into multiple patches. An (ad hoc) explanation might be that multiple patches of habitat are less likely to be managed homogeneously and will provide more varied resources and microclimates.

From an analysis of growth rates from entire time series (Part 4- woodland birds only), there was some weak evidence that woodland configuration in the landscape (5km radius) affected sensitivity to- and recovery from- years of climatic extreme. For generalist woodland species, the positive population response following a warm breeding season was lower in sites in poorly connected landscapes (i.e. greater mean nearest neighbour distance between woodland patches). There was no analogous response for specialist species, however.

Q3. Are site or landscape factors more important and what life history characteristics interact with population robustness and site/ landscape attributes?

The relative importance of different site and landscape attributes for population resilience will vary between taxa and functional types of organisms. More specifically:
H7- Area and connectivity of key habitat types in landscapes will be more important for specialist rather than generalist species.

For broadleaved woodland, we carried out multivariate tests for the effects of woodland area and configuration on population density and stability (Part 2). We found that there were differences in the effects of both woodland area and configuration depending on species woodland association (classified *a priori* as woodland specialist, generalist or 'non-woodland' species). Specialist and generalist woodland species were found at higher densities on sites with larger areas of woodland in the landscape (2km radius). Non-woodland species tended to be found at lower densities in these landscapes. Woodland configuration had strong associations with the density of specialist birds and the density of generalist birds and butterflies (results were significant for birds only using the CBC survey). For both groups, an increased 'edginess' of woodland (mean shape index) was associated with lower population densities (controlling for the effects of woodland area). In addition, for specialist birds, increased distances between woodland patches (mean nearest neighbour distance) were associated with lower population densities, although this metric was generally a less consistent predictor of density than mean shape index. The third configuration metric tested, patch density, was also a strong predictor of population density, although the direction of effect was unexpected. Controlling for the effects of woodland area, a greater number of woodland patches in the landscape was associated with higher densities of specialist birds and generalist birds and butterflies (CBC survey for birds). This suggests that woodland fragmentation per se might not be detrimental to specialist woodland species, as long as woodland patches are not too isolated or too 'edgy' (for example, thin linear tracts of woodland).

Using population stability as a response variable, associations with woodland area and configuration were generally weaker; although, trends were qualitatively similar to the density analysis above. For example, for generalist bird species (assessed using the CBC survey) more stable bird populations tended to occur in landscapes with lower woodland 'edginess' and also in landscapes with more patches of woodland. Differences between generalist and specialist species were much less apparent, potentially due to the weaker relationships between landscape attributes and inter-annual population variability, as compared with density.

H8- For each species, the key site and landscape attributes that reduce sensitivity to extreme climatic events may be different to those that promote recovery from such events. More specifically, sensitivity may be reduced by site and landscape heterogeneity ('environmental buffering'), whilst recovery may be better facilitated by habitat connectivity ('ecological coherence').

We found little evidence that population sensitivity to- and recovery from- extreme events were consistently (across species) associated with any site or landscape attributes (Part 3). Therefore, this hypothesis was not relevant in light of these results.

8.2 Caveats and further work

These analyses revealed a number of strong associations between site and landscape attributes and mean density and resilience of butterfly and bird populations. For others, we found little evidence (for example, soil heterogeneity was found to have little effect on the mean density and resilience of butterfly and bird species). It is possible that these factors genuinely have little effect on species populations. However, alternatively, a lack of response might simply reflect inadequacy of the site and landscape data used. For example, fine-scale heterogeneity within patches (for example, soil moisture, vegetation structure, microclimatic variation) are likely to be highly important for promoting resilient populations (Kindvall, 1996; Benton *et al*., 2003), but remain untested in this macroecological study. To address this research gap, further work might attempt to quantify the quality of habitat patches through direct observation or using finer-resolution remote sensing (for example, LIDAR). However, currently such high resolution data are often lacking in sufficient spatial replication.

In some cases, we found unexpected relationships between site and landscape attributes and population density and resilience. For example, the total area of arable land cover was associated with higher butterfly densities, implying that this landscape attribute captures some aspect of a ‘key’ habitat type. Areas of intensive crop cover are well known to be hostile habitat for most (non-pest) Lepidoptera. However, it may be that arable edges (along which monitoring transects follow), may provide important nectar resources and movement routes for butterflies, making them key habitat types. Further work using finer resolution habitat data would be useful to understand these relationships better.

In addition to better-resolved and more appropriate explanatory variables, future analyses might consider other response variables. Although we considered changes in butterfly and bird population size at a community level (Part 5), such analyses could be conducted at a species level, for example, asking how do incremental climate change and habitat structure influence changes in species density over time?

Further extensions might also consider a wider range of species traits and how they influence responses to landscape structure. For example, although we investigated broad differences in response of woodland specialists, generalists and non-woodland species to woodland structure, this approach might be extended by considering traits such as mobility. We might expect species of intermediate mobility to respond most strongly to habitat configuration; very sedentary species may not benefit from changes to habitat configuration, whilst highly mobile species might need very little structural connectivity.

Finally, when considering the broader implications of the results in this report, we should remember that have studied only birds and butterflies. This was necessary as no other taxa have monitoring schemes of sufficient spatial and temporal replication. However, we should be cautious in generalising our results to other organisms, for example those that are likely to be considerably less mobile. Notwithstanding this caveat, we did find some common patterns across birds and butterflies, despite differences in the study organisms and the monitoring methods between schemes. For example, in both groups loss of cold-associated species from species assemblages was most marked on sites with less semi-natural habitat remaining. Such commonalities might represent general patterns across many organisms and, data permitting, would be worthwhile testing on other species groups.

8.3 Conclusions

In this report, we found good evidence that both the area and connectivity of key habitat types can have important effects on population density and resilience. Effects were apparent at both the site and landscape level, although controlled comparisons between the two suggested that, for the average species, attributes measured at the site level had the best predictive power. We found differences in response between species groups (birds and butterflies) and between species with different habitat associations (for example, woodland specialists versus generalists). This highlights the difficulty of generalising results across large numbers of species. We can conclude, however, that the climate change adaptation principles tested were generally supported by this analysis (much more evidence for, rather than against, the various hypotheses tested; Table 1). Notwithstanding the caveats mentioned above, such as the representativeness of birds and butterflies as study organisms, our analyses, using the best species and environmental datasets currently available, suggest that providing sufficient habitat heterogeneity and ecological connectivity at both a site- and landscape- level is warranted in order to adapt species' populations to climate change.

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Table 1: Summary of weight-of-evidence for and against the hypotheses testing climate change adaptation principles.

Hypothesis	**Method of testing**	**Birds**			**Butterflies**		
		Against	**None**	**For**	**Against**	**None**	**For**
H1 - Local (site) variation in habitat, soil type and topography are positively correlated with the mean density and resilience of populations as measured during recent periods of relative climatic variability and incremental change.	Density			xxxx		xxxx	
	Inter-annual Variability		xxxx			xx	xx
	Sensitivity & Recovery		xxxx			xxxx	
H2 - Area of key habitat types for species' will be positively correlated with mean density population resilience.	Density		x	xxx		xxx	x
	Inter-annual Variability		x	xxx		x	xxx
	Sensitivity & Recovery		xxxx			xxxx	
	Growth rates		xx	xx	▨	▨	▨
H3 - Under incremental climate warming, declines in cold-associated species assemblages will be least marked on sites with a broad diversity of habitat, soil type and topography and with more semi-natural habitat available. In contrast, species assemblages of warmth-associated species will increase most on these sites.	Loss of cold-associated species	x		xxx	x		xxx
	Gain of warm-associated species	x		xxx			xxx
H4 - Landscape-scale variation in habitat, soil type and topography are positively correlated with the mean density and resilience of populations of populations as measured during recent periods of relative climatic variability and incremental change.	Density	x		xxx	xx	xx	
	Inter-annual Variability			xxxx		xx	xx
	Sensitivity & Recovery		xxxx			xxxx	
	Growth rates				▨	▨	▨
H5 - The area of species' key habitat types in the local landscape will be positively correlated with the mean density and resilience of populations.	Density		xx	xx			xxxx
	Inter-annual Variability		x	xxx		x	xxx
	Sensitivity & Recovery		xxxx			xxxx	
	Growth rates		xxxx		▨	▨	▨
H6 - Ecological networks defined by the connectivity of species' key habitats also increase the mean density and resilience of populations as measured during recent periods of relative climatic variability and incremental change.	Density			xxx			xxx
	Inter-annual Variability		xxx	x		xxx	x
	Sensitivity & Recovery		xxx		x	xxx	
	Growth rates		xx	xx	▨	▨	▨
H7 - Area and connectivity of key habitat types in landscapes will be more important for specialist rather than generalist species.	Density	x		xx	xxx		
	Inter-annual Variability	xxx		x	x		xx
H8 - For each species, the key site and landscape attributes that reduce sensitivity to extreme climatic events may be different to those that promote recovery from such events.	Not tested	▨	▨	▨	▨	▨	▨

Evidence Key (number of statistical tests)

Strong	xxxx	Moderate	xxx	Weak	xx	Very weak	🟨	Not tested	▨