Natural England Commissioned Report NECR149

The role of landscape and site scale characteristics in making species populations resilient to climate change and extreme events

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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 already affecting England's biodiversity and all the indications are that these impacts will increase in future. Adaptation to reduce adverse impacts of climate change is essential and must be based on the best available evidence. A necessary step in this process is to better understand the potential for landscape characteristics to influence species' population responses to climate change.

Increases in the occurrence of extreme events may be one of the most important aspects of climate change and this project investigates the resilience of bird and butterfly populations to drought and extremes of winter cold. The focus is on differences between species in terms of their sensitivity and recovery and the potential for population responses to be influenced by land cover and management, including the effects of agri-environment schemes, semi-natural habitat and designated Sites of Special Scientific Interest. One of the most important findings is that larger areas of semi-natural habitat promote the resilience of butterfly populations during drought years. Modelling shows that these impacts would increase under future climate change scenarios and having a sufficiently large area of habitat may make the difference between survival and localised extinction.

Understanding the factors that modify the responses of different species to climate change will support the development of adaptation measures to reduce vulnerability to extreme events, including through our designation strategy and agri-environment schemes. We also hope that the results will inform the work partnerships working at a landscape scale, such as Nature Improvement Areas. This project will therefore be followed up with work to integrate this new knowledge into our practical conservation work and advice, including through future versions of the *Natural England Climate Change Adaptation Manual*.

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The role of landscape and site scale characteristics in making species populations resilient to climate change and extreme events

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Executive summary

This project assessed the responses of UK bird and butterfly populations to a number of winter cold and summer drought events between 1981 and 2010. We assessed the sensitivity of populations (i.e. the extent to which they crashed) in addition to any subsequent recovery. Key results are summarised below:

Winter cold sensitivity

1. Bird species tend to decline following very cold winters. In contrast, most butterfly species increase. Whereas birds need food over the winter, butterflies exist in dormant stages that may actually benefit from cold (e.g. reduced pathogens).
2. In terms of variation across species within these groups- birds that feed on invertebrates in the soil tend to suffer most from extreme winter cold, whilst fruit and seed feeders are better off. Butterflies overwintering as adults and pupae, and in particular migrant species, are relatively more susceptible to winter cold.

Drought sensitivity

3. Both birds and butterflies can decrease significantly in abundance following drought events, although there is much variation across different drought events (i.e. each drought event is unique), probably due to variation in the timing and duration of high temperatures and rainfall deficits which affect groundwater and soil moisture levels.

Population recovery

4. Many bird and butterfly populations do not show population increases in the four year period following an extreme event and even those that do take several years (3-5 on average) to regain pre-event population levels.

Landscape effects on species responses

5. Area and configuration of semi-natural habitat affects species responses to extreme events. This is most detectable for butterfly species. Where there is less semi-natural habitat around monitoring sites, butterfly species tend to be more sensitive to summer droughts. Habitat fragmentation also affects recovery rates, making recovery slower.

Projected changes

6. Under future climate scenarios, significant adverse impacts are projected for the ten drought sensitive butterflies that we investigated. By 2050 the probability of populations persisting is only 10% unless large areas of unfragmented semi-natural habitat can be achieved (well above the current levels in England).

Introduction

Climate change is projected to have increasing impacts on England's biodiversity in coming decades (IPCC, 2007; UK NEA, 2011; Morecroft & Speakmann 2012). Increases in the occurrence of extreme events may be one of the most important components of climate change (Peterson, Stott & Herring, 2012). Adaptation to reduce adverse impacts of climate change is essential and robust evidence is necessary to 'provide advice and information for advisers and land managers on climate change adaptation through land management' (Natural England, 2012).

A necessary step in this process is to better understand the potential for landscape characteristics to influence species' population responses to climate change. This project extends work carried out in Oliver et al. (2012) and Oliver, Roy & Brereton (2012) to consider the resilience of species' populations to extreme climatic events in terms of their sensitivity and recovery rates. We focus on butterflies and birds as only for these groups are adequate spatial and temporally replicated monitoring data available. However, we expect them to be reasonable indicators for the effects of environmental change on many other species groups (e.g. Thomas, 2005).

This project considers years of extreme drought and winter cold in Britain. The focus is on differences between species in terms of their sensitivity and recovery and the potential for population responses to be influenced by land cover and management (e.g. agri-environment schemes, semi-natural habitat and SSSIs). Understanding how these factors modify the responses of different species to climate change will support the development of adaptation measures to reduce vulnerability to extreme events. Finally, for butterflies only we estimate the projected effects of drought under future climate scenarios.

The project results contribute to the evidence base on the influence of landscapes on the impact of climate change on biodiversity and associated ecosystem services.

Chapter 1 - Species' sensitivity and recovery to drought and winter cold

Lead organisation: CEH

Objective: The aim of this analysis was to assess the overall sensitivity and recovery of bird and butterfly species to several recent drought and winter cold events.

Methods

Climate data

We used UKCP09 Met office datasets to identify years of extreme drought and winter cold in the UK. These data provide monthly climatic measures for all 5km grid squares up to 2012. The level of drought in each year for each site was measured using an aridity index (adapted from Marsh, 2004, equation 1; also see Fig 5a) for the months April to September.

$$\text{Aridity index} = -(P_{ij}-P_{mean})/\sigma_P+0.5(T_{ij}-T_{mean})/\sigma_T \qquad [1]$$

Where $P_{i\,j}$ is the total April-Sept precipitation in year i for 5km grid cell j, P_{mean} is the mean total April-Sept precipitation across all years and all 5km grid cells and σ_P is the standard deviation about this mean. $T_{i\,j}$ is the mean monthly April-Sept temperature in year i for 5km grid cell j, T_{mean} is the mean April-Sept temperature across all years and all 5km grid cells and σ_T is the standard deviation about this mean. Hence, for each 5km cell, temperature and precipitation anomalies were standardised by standard deviations and combined giving precipitation double the weight in the final aridity index (Marsh, 2004).

Plotting aridity indices for all 5km cells and years led to the identification of 1990, 1995, and 2006 as drought years which were extreme, within the period for which there were sufficient bird and butterfly species data for analysis (1977 onwards). All these events are also highlighted in a summary of recent major droughts in England and Wales (Marsh, Cole & Wilby, 2007; Box 1)

Winter cold severity in each year was measured by the mean winter temperature recorded across all grid squares (winter being defined as December, January and February). This led to identification of the winters of 1981-1982, 1984-1985 and 2009-2010 (subsequently referred to as 1982, 1985 and 2010) as extreme winters, which also had sufficient species data for analysis.

Box 1, Descriptions of the different UK drought events, as detailed by Marsh, Cole and Wilby (2007)

1990–1992 Spring 1990–summer 1992 Major drought. Widespread and protracted rainfall deficiencies- reflected in exceptionally low groundwater levels (in summer 1992, overall groundwater resources for England and Wales probably at their lowest for at least 90 years). Intense phase in the summer of 1990 in southern and eastern England. Exceptionally low winter flows in 1991/1992.

1995–1997 Spring 1995–summer 1997 Major drought. Third-lowest 18-month rainfall total for England and Wales (1800–2002). Long-duration drought with intense episodes (affecting eastern Britain in the hot summer of 1995). Initial surface water stress, then very depressed groundwater levels and much diminished lowland stream network.

2004-6 This drought was not exceptional in duration or intensity at the national scale, but drought severity in the summers of 2005 and 2006 was greatest in the English Lowlands, the South-East especially. Here, depressed groundwater levels led to widespread spring failures and a major contraction in the stream network. November–April rainfall deficiencies for the Thames catchment; the deficiency for 2004–2006 is the greatest since the early 1890s. The drought continued to intensify through the early summer of 2006; June and July, taken together, were the second driest in 23 years for England and Wales. Correspondingly soil moisture deficits increased steeply and the regions subject to drought stress extended. Weather patterns became very unsettled through the late summer and early autumn but flows in many spring-fed streams continued to decline; the September mean flow for the River Mimram (north of London) was the lowest in a 53-year record.

Population Data

The population data we used were from the UK Butterfly Monitoring Scheme (UKBMS; http://www.ukbms.org/), Common Birds Census (CBC, for events before 2000; http://www.bto.org/survey/complete/cbc.htm) and Breeding Bird Survey (BBS, for events after 2000; http://www.bto.org/volunteer-surveys/bbs). For each event (e.g. 1995 drought) species were selected for analysis if there were complete time series available from at least ten sites. Following Oliver et al (2012), a complete time series consisted of ten years of non-zero values at a site: six years before, and four years after and including the expected impact year of the event. For cold winters, this impact year immediately follows the winter (e.g. 1985 for the winter of 1984/85) but for droughts we used the subsequent year (e.g. 1996 for the drought of 1995).

This delayed effect was chosen as the basis for analysis, as preliminary analyses showed that most species suffering a negative impact from the drought do so in the subsequent year. In Chapter 3 we relax this assumption and consider species declining in either the current year of the drought or the subsequent year.

BBS time series were also excluded if they had a median count of less than five to further minimise the risk of spuriously identifying a decline in this data set. As no data are available in the BBS data set for 2001 due to the foot and mouth disease outbreak, which prevented access to many recording locations, the period before the 2006 drought in these time series was extended to an extra year to 2000 for the analysis of bird sensitivity and recovery.

Statistical analysis

A) Population responses at the site-level

These site-level analyses follow the method in Oliver et al (2012) and are summarised below.

Testing for density dependence

Before analysing the effect of each climatic event on the selected time series, each time series was first analysed for any density dependent effects using two tests. The first test regressed $\log(N_t/N_{t+1})$ versus N_t (where Nt is population abundance in year t) and found evidence for a density dependent growth rate in 40% of time series across events. The second test fitted a quadratic model to the time series which was statistically significant in a median of 9% of time series across events. These results suggested that although density dependence is a relevant process in butterfly and bird population dynamics, in the six years prior to the extreme events that we studied there was little evidence of non-linear population trends and so a linear regression model was adequate.

Site-level effect of climatic event

In each time series (i.e. the population of a species at a site), sensitivity to a climatic event was measured as the difference between the expected and observed count in the year of impact (e.g. 1985 for the winter of 1984/85 or 1996 for the 1995 drought). The expected count was predicted by a linear model fitted to the counts from the six years preceding the climatic event. For example, for the 1995 drought a linear model was fitted to the time series between 1990 and 1995, and then used to predict the expected count in 1996. Where the linear model predicted a negative expected count, i.e. where the population trend prior to the climatic event had been sharply negative, the expected count was set to zero.

Where the time series showed a negative impact of the climatic event (i.e. observed count less than expected), recovery was measured as the slope of a linear model fitted to the four counts after the climatic event (1996 to 1999 for the 1995 drought). The 2010 winter cold event is too recent for four years of data to be available and so recovery was not analysed in this case.

B) Assessment of sensitivity and recovery at the species-level

Measures of individual species' sensitivities to and recovery from each extreme climatic event were calculated as the median values across all sites. Wilcoxon signed rank tests were used to test if these species sensitivity and recovery measures significantly differed from zero. Here, species' sensitivity measures used the percentage difference at each site (the difference between the expected and observed count relative to the expected count) to control for larger populations being likely to have larger increases/decreases in absolute terms.

Results

Butterfly sensitivity to the three drought events are shown in Table 1, and sensitivity to the three winter cold events in Table 2. Bird sensitivity to the three drought events are shown in Table 3, and sensitivity to the three winter cold events in Table 4. A summary of these results is shown in Table 5 and discussed in the next section.

Butterfly recovery rates following the three drought events are shown in Table 6 and recovery rates to two winter cold events in Table 7. Note that it was not possible to look at recovery from the 2009-10 winter cold event because it was too recent. Recovery rates were only assessed for populations that showed population declines following the extreme events. Bird recovery rates following the three drought events are shown in Table 8 and recovery rates to two winter cold events in Table 9.

Recovery times of butterflies from all events are shown in Table 10. These recovery times are influenced by both the extent of population crashes (i.e. population sensitivity) in addition to recovery rates. Recovery times of birds to all events are shown in Table 11. A summary of recovery times across species is shown in Table 12.

Table 1, Butterfly responses to three drought events in terms of percentage population change across monitoring sites with changes tested by Wilcoxon signed ranks tests for each species. Species are ranked by sensitivity to the 1995 drought event. Negative percentage change numbers indicate a lower than expected population the year after the drought year, positive numbers indicate a higher than expected population.

	1990 drought sensitivity					1995 drought sensitivity					2006 drought sensitivity				
Common name	Rank	Median % change	n	V	p	Rank	Median % change	n	V	p	Rank	Median % change	n	V	P
Large white	5	-33.58	48	879	0.00	1	-66.06	95	4096	0.00	14	-45.43	71	2094	0.00
Green hairstreak	NA	NA	NA	NA	NA	2	-58.41	17	122	0.03	10	-50.41	10	42	0.16
Small white	6	-31.34	47	863	0.00	3	-56.16	97	4364	0.00	8	-51.45	86	3245	0.00
Ringlet	NA	NA	NA	NA	NA	4	-51.28	79	2732	0.00	25	-1.61	60	796	0.38
Green-veined white	3	-37.20	48	982	0.00	5	-45.45	87	3227	0.00	18	-23.91	79	1953	0.07
Speckled wood	NA	NA	NA	NA	NA	6	-40.96	89	3391	0.00	15	-34.39	94	3442	0.00
Large skipper	NA	NA	NA	NA	NA	7	-23.84	83	2461	0.00	23	-5.96	55	617	0.20
Small/ Essex skipper	NA	NA	NA	NA	NA	8	-20.26	68	1429	0.12	NA	NA	NA	NA	NA
Small skipper	NA	NA	NA	NA	NA	9	-18.73	63	1236	0.12	7	-53.61	25	290	0.00
Small tortoiseshell	7	5.00	45	378	0.12	10	-11.84	80	1446	0.41	22	-18.15	42	491	0.63
White admiral	NA	NA	NA	NA	NA	11	-5.26	19	104	0.74	4	-65.91	15	117	0.00
Purple hairstreak	NA	NA	NA	NA	NA	12	1.94	11	31	0.90	NA	NA	NA	NA	NA
Dingy skipper	NA	NA	NA	NA	NA	13	9.09	19	54	0.10	21	-19.47	12	60	0.11
Small copper	4	-35.28	20	144	0.15	14	17.35	27	136	0.21	9	-51.11	29	326	0.02
Silver-washed fritillary	NA	NA	NA	NA	NA	15	17.61	28	95	0.01	13	-47.08	15	109	0.00
Meadow brown	9	27.25	55	381	0.00	17	21.12	112	1862	0.00	16	-27.86	87	2965	0.00
Comma	NA	NA	NA	NA	NA	18	21.21	51	330	0.00	12	-48.59	74	2563	0.00
Common blue	2	-45.01	36	506	0.01	19	30.84	70	681	0.00	2	-77.44	68	2346	0.00
Gatekeeper	NA	NA	NA	NA	NA	20	41.21	97	846	0.00	11	-49.17	76	2719	0.00
Orange tip	8	7.78	28	125	0.08	21	42.81	56	354	0.00	19	-23.44	20	139	0.22
Marbled white	NA	NA	NA	NA	NA	22	43.04	44	160	0.00	17	-26.66	39	500	0.13
Brimstone	11	75.12	34	66	0.00	23	48.12	75	265	0.00	20	-19.83	48	808	0.02
Chalk-hill blue	NA	NA	NA	NA	NA	24	49.56	20	50	0.04	1	-79.62	18	171	0.00

Peacock	10	45.35	35	89	0.00	25	62.79	85	580	0.00	28	85.47	54	108	0.00
Grizzled skipper	NA	NA	NA	NA	NA	26	125.96	12	4	0.00	26	9.96	12	27	0.38
Brown argus	NA	NA	NA	NA	NA	27	130.07	22	21	0.00	3	-66.28	19	168	0.00
Small heath	NA	NA	NA	NA	NA	28	152.28	32	29	0.00	5	-65.17	36	582	0.00
Red admiral	NA	NA	NA	NA	NA	29	185.71	79	192	0.00	24	-1.77	58	673	0.16
Holly blue	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	27	23.33	20	40	0.01
Painted lady	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	6	-58.90	13	91	0.00
Wall brown	1	-48.80	16	133	0.00	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA

Table 2, Butterfly responses to three extreme winter cold events in terms of percentage population change across monitoring sites with changes tested by Wilcoxon signed ranks tests for each species. Species are ranked by sensitivity to the 2010 winter cold event. Negative percentage change numbers indicate a lower than expected population the year after the drought year, positive numbers indicate a higher than expected population.

	1982 cold sensitivity					1985 cold sensitivity					2010 cold sensitivity				
Common name	Rank	Median % change	n	V	p	Rank	Median % change	n	V	p	Rank	Median % change	n	V	p
Painted lady	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	1	-97.16	20	210	0.00
Large white	1	-15.85	13	65	0.19	20	67.02	19	20	0.00	2	-40.23	124	7509	0.00
Red admiral	NA	NA	NA	NA	NA	3	-50.85	15	120	0.00	3	-18.66	94	3525	0.00
Peacock	9	27.78	17	4	0.00	18	6.05	27	164	0.56	4	-17.49	97	3548	0.00
Speckled wood	7	26.53	14	20	0.04	4	-48.15	21	216	0.00	5	-14.92	135	7790	0.00
Comma	NA	NA	NA	NA	NA	10	-29.18	11	56	0.04	6	-13.43	118	4454	0.01
Meadow brown	6	24.62	17	33	0.04	11	-28.94	28	368	0.00	7	-12.04	139	6701	0.00
Grizzled skipper	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	8	-0.66	16	73	0.82
Green-veined white	3	11.07	16	39	0.14	17	1.44	28	171	0.48	9	-0.46	120	3469	0.67
Marbled white	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	10	2.44	55	713	0.64
Ringlet	NA	NA	NA	NA	NA	7	-30.83	15	120	0.00	11	4.08	97	2149	0.41
Small white	2	9.85	17	48	0.19	12	-24.70	21	158	0.15	12	6.54	124	3043	0.04
Small skipper	NA	NA	NA	NA	NA	9	-29.46	11	59	0.02	13	8.56	35	182	0.03
Dark green fritillary	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	14	9.33	17	43	0.12
Pearl-bordered fritillary	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	15	9.64	11	21	0.32
Brimstone	5	18.31	12	14	0.05	16	-13.25	16	97	0.14	16	11.25	80	1152	0.02
Gatekeeper	11	53.11	21	6	0.00	6	-36.42	25	299	0.00	17	14.82	111	1738	0.00
Silver-washed fritillary	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	18	20.13	27	47	0.00
Orange tip	NA	NA	NA	NA	NA	19	8.03	14	37	0.36	19	22.27	45	234	0.00
Purple hairstreak	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	20	22.67	10	22	0.63
High brown fritillary	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	21	23.46	14	23	0.07
Green hairstreak	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	22	25.77	16	15	0.00
Large skipper	4	17.41	13	7	0.00	15	-20.41	24	223	0.04	23	27.86	94	818	0.00
Dingy skipper	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	24	30.23	27	28	0.00

Small copper	NA	NA	NA	NA	NA	14	-21.64	13	75	0.04	25	33.33	61	269	0.00
Small tortoiseshell	12	60.59	19	1	0.00	5	-38.88	28	357	0.00	26	34.57	63	353	0.00
Holly blue	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	27	35.46	36	139	0.00
Small blue	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	28	35.61	13	14	0.03
Wall brown	NA	NA	NA	NA	NA	1	-76.51	10	55	0.00	29	38.01	13	8	0.01
Brown argus	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	30	40.10	42	131	0.00
Grayling	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	31	40.83	12	11	0.03
Small heath	10	41.04	11	9	0.03	8	-29.60	20	191	0.00	32	48.19	66	118	0.00
Chalk-hill blue	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	33	50.61	25	12	0.00
White admiral	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	34	55.72	22	9	0.00
Adonis blue	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	35	65.31	14	6	0.00
Common blue	NA	NA	NA	NA	NA	2	-54.92	18	171	0.00	36	71.88	107	175	0.00
Small/ Essex skipper	8	27.76	11	8	0.02	13	-22.43	10	41	0.19	NA	NA	NA	NA	NA

Table 3, Bird responses to three drought events in terms of percentage population change across monitoring sites with changes tested by Wilcoxon signed ranks tests for each species. Species are ranked by sensitivity to the 1995 drought event. Negative percentage change numbers indicate a lower than expected population the year after the drought year, positive numbers indicate a higher than expected population.

	1990 drought sensitivity					1995 drought sensitivity					2006 drought sensitivity				
Common name	Rank	Median % change	n	V	p	Rank	Median % change	n	V	p	Rank	Median % change	n	V	p
Wren	2	-42.80	41	840	0.00	1	-30.99	43	889	0.00	41	4.72	651	78557	0.00
Goldcrest	1	-50.82	11	62	0.01	2	-21.83	14	60	0.67	42	12.00	29	139	0.09
Magpie	25	9.82	24	105	0.21	3	-20.75	24	211	0.08	24	-7.49	233	13697	0.95
Coal Tit	16	-6.25	27	179	0.82	4	-19.79	27	251	0.14	29	-4.29	34	247	0.40
Dunnock	11	-19.64	32	380	0.03	5	-11.76	30	305	0.14	18	-9.68	215	12138	0.56
Chiffchaff	5	-27.08	27	355	0.00	6	-11.02	33	335	0.34	38	2.69	85	1516	0.17
Robin	9	-21.16	42	745	0.00	7	-10.89	44	707	0.01	37	1.45	547	64396	0.00
Green Woodpecker	24	7.69	14	32	0.22	8	-7.67	16	72	0.86	NA	NA	NA	NA	NA
Jackdaw	8	-21.87	10	34	0.56	9	-5.66	12	45	0.68	36	0.75	308	21373	0.12
Blackbird	14	-10.36	43	717	0.00	10	-3.61	44	434	0.48	35	-0.51	744	127121	0.05
Song Thrush	4	-28.14	28	347	0.00	11	-3.54	34	277	0.74	23	-7.49	135	4877	0.53
Stock Dove	21	-1.10	11	29	0.76	12	-0.66	12	46	0.62	1	-36.56	12	67	0.03
Great Tit	27	13.07	41	255	0.02	13	0.00	43	456	0.84	31	-3.31	339	30445	0.37
Great Spotted Woodpecker	18	-3.23	17	57	0.59	14	0.00	21	77	0.19	NA	NA	NA	NA	NA
Treecreeper	7	-22.32	16	83	0.46	15	3.45	21	83	0.27	NA	NA	NA	NA	NA
Willow Warbler	12	-15.13	28	238	0.44	16	5.05	26	160	0.71	40	3.24	128	3345	0.06
Chaffinch	19	-2.17	41	403	0.73	17	5.18	42	329	0.13	25	-5.84	740	145553	0.15
Blackcap	10	-21.05	35	435	0.05	18	6.06	39	345	0.54	17	-10.26	91	2361	0.29
Carrion/Hooded Crow	13	-11.76	21	115	1.00	19	7.14	23	105	0.33	NA	NA	NA	NA	NA
Greenfinch	NA	NA	NA	NA	NA	20	10.02	10	23	0.70	7	-23.58	291	29097	0.00
Jay	20	-2.17	22	98	0.55	21	13.21	21	53	0.03	NA	NA	NA	NA	NA

Pheasant	23	6.18	14	37	0.36	22	15.05	16	46	0.27	22	-7.55	222	11764	0.52
Woodpigeon	17	-4.91	16	68	1.00	23	15.38	23	74	0.05	26	-4.86	815	162826	0.61
Blue Tit	22	5.41	39	266	0.08	24	16.83	43	242	0.00	16	-10.99	588	103526	0.00
Long-tailed Tit	15	-10.27	12	57	0.18	25	25.00	21	75	0.17	NA	NA	NA	NA	NA
Bullfinch	29	20.81	18	46	0.09	26	28.57	18	38	0.04	NA	NA	NA	NA	NA
Nuthatch	26	12.16	18	57	0.23	27	66.67	20	19	0.00	NA	NA	NA	NA	NA
Garden Warbler	3	-33.65	12	40	0.97	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA
Yellowhammer	6	-22.78	10	52	0.01	NA	NA	NA	NA	NA	20	-7.62	119	3579	0.98
Marsh Tit	28	19.40	10	17	0.32	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA
Mistle Thrush	30	25.00	13	22	0.11	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA
Sedge Warbler	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	43	38.61	13	23	0.13
Meadow Pipit	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	39	3.15	130	3695	0.19
Shelduck	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	34	-0.88	11	28	0.70
Starling	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	33	-2.44	345	26500	0.07
Feral Pigeon	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	32	-2.86	85	1733	0.68
Skylark	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	30	-4.24	286	21186	0.63
Carrion Crow	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	28	-4.35	584	80974	0.28
Rook	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	27	-4.52	160	5723	0.22
Mallard	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	21	-7.62	138	4718	0.87
Black-headed Gull	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	19	-8.79	31	243	0.93
House Sparrow	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	15	-12.90	387	46630	0.00
Whitethroat	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	14	-20.07	78	1872	0.10
Canada Goose	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	13	-20.77	35	407	0.14
Coot	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	12	-20.99	21	149	0.26
Swallow	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	11	-21.96	271	22474	0.00
Herring Gull	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	10	-23.28	49	829	0.03
Lesser Black-backed Gull	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	9	-23.40	35	348	0.60
Collared Dove	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	8	-23.47	167	10236	0.00
Goldfinch	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	6	-24.04	90	2476	0.09

Swift	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	5	-24.73	75	1815	0.04
Linnet	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	4	-25.33	92	2606	0.07
House Martin	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	3	-27.88	75	1802	0.05
Greylag Goose	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	2	-32.27	11	39	0.64

Table 4, Bird responses to three extreme winter cold events in terms of percentage population change across monitoring sites with changes tested by Wilcoxon signed ranks tests for each species. Species are ranked by sensitivity to the 2010 winter cold event. Negative percentage change numbers indicate a lower than expected population the year after the drought year, positive numbers indicate a higher than expected population.

	1982 cold sensitivity					1985 cold sensitivity					2010 cold sensitivity				
Common name	Rank	Median % change	n	V	p	Rank	Median % change	n	V	p	Rank	Median % change	n	V	p
Tree Sparrow	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	58	30.08	14	13	0.01
Stock Dove	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	57	23.29	17	56	0.35
Shelduck	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	56	21.66	18	49	0.12
Blue Tit	12	-2.95	34	354	0.34	22	5.07	38	240	0.06	55	13.69	808	97062	0.00
Blackcap	16	1.94	23	110	0.41	12	-2.67	26	160	0.71	54	13.04	120	2317	0.00
Ring-necked Parakeet	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	53	9.29	11	20	0.28
Whitethroat	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	52	8.70	123	2932	0.03
House Sparrow	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	51	8.45	524	43791	0.00
Linnet	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	50	5.98	121	2702	0.01
Coot	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	49	5.84	30	222	0.84
Curlew	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	48	4.67	52	619	0.53
Dunnock	11	-4.90	28	217	0.76	10	-10.89	31	257	0.62	47	3.53	278	16469	0.03
Chaffinch	9	-9.43	36	388	0.40	21	4.60	38	371	1.00	46	3.45	1051	222348	0.00
Goldcrest	21	17.19	11	18	0.21	2	-21.83	10	49	0.03	45	2.48	37	288	0.35
Redstart	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	44	1.43	10	21	0.56
Sedge Warbler	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	43	0.00	25	166	0.94
Chiffchaff	3	-16.31	16	105	0.06	27	60.03	22	25	0.00	42	0.00	133	3806	0.14
Woodpigeon	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	41	-1.31	1140	296237	0.01
Greylag Goose	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	40	-2.93	19	79	0.54
Blackbird	19	7.14	35	252	0.31	19	3.33	40	392	0.82	39	-3.23	1071	283123	0.70
Long-tailed Tit	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	38	-3.33	10	25	0.85
Great Tit	13	-2.33	35	307	0.90	17	0.83	40	371	0.61	37	-3.45	518	60763	0.06
Red Grouse	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	36	-3.74	16	50	0.38
Reed Bunting	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	35	-4.38	15	60	1.00

Feral Pigeon	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	34	-4.43	122	3424	0.40
Willow Warbler	23	22.57	28	79	0.00	9	-11.76	35	425	0.07	33	-5.08	194	9591	0.87
Swallow	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	32	-5.46	436	44793	0.28
Meadow Pipit	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	31	-5.52	174	7503	0.87
Coal Tit	17	2.74	19	86	0.74	5	-19.27	22	115	0.73	30	-6.07	48	622	0.73
Tufted Duck	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	29	-6.74	21	108	0.81
House Martin	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	28	-6.97	110	2796	0.45
Greenfinch	2	-18.60	10	31	0.77	18	0.90	11	30	0.83	27	-7.69	383	37738	0.65
Carrion Crow	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	26	-7.69	862	182150	0.60
Magpie	6	-13.54	16	91	0.25	26	20.00	21	39	0.01	25	-7.69	306	22873	0.69
Mute Swan	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	24	-8.83	13	56	0.50
Skylark	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	23	-8.91	387	40647	0.16
Collared Dove	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	22	-9.40	221	12918	0.49
Goldfinch	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	21	-10.45	167	7111	0.88
Corn Bunting	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	20	-10.81	10	45	0.08
Herring Gull	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	19	-10.98	84	1853	0.76
Pheasant	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	18	-11.04	334	28264	0.87
Yellowhammer	5	-14.29	13	45	1.00	25	19.10	14	29	0.15	17	-11.11	160	7010	0.33
Red-legged Partridge	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	16	-11.69	30	254	0.67
Oystercatcher	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	15	-11.76	21	96	0.52
Song Thrush	18	7.14	31	149	0.05	3	-21.32	32	393	0.01	14	-12.09	192	11952	0.00
Jackdaw	NA	NA	NA	NA	NA	24	11.81	10	17	0.32	13	-14.44	516	69661	0.38
Mallard	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	12	-14.73	200	10450	0.63
Wren	7	-12.79	32	347	0.12	6	-16.03	36	517	0.00	11	-14.84	908	270820	0.00
Starling	NA	NA	NA	NA	NA	7	-14.44	11	27	0.64	10	-14.95	473	56127	0.98
Canada Goose	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	9	-16.47	52	781	0.40
Lesser Black-backed Gull	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	8	-17.82	54	831	0.45
Swift	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	7	-18.32	116	3609	0.55
Robin	1	-23.91	35	479	0.01	4	-20.82	40	650	0.00	6	-19.16	771	211948	0.00
Lapwing	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	5	-19.16	71	1473	0.27
Reed Warbler	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	4	-19.85	15	73	0.49
Rook	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	3	-23.08	285	22611	0.11
Black-headed Gull	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	2	-25.00	61	993	0.74
Moorhen	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	1	-26.83	17	114	0.08

Great Spotted Woodpecker	22	20.81	16	30	0.09	23	5.63	17	44	0.22	NA	NA	NA	NA	NA
Carrion/Hooded Crow	15	1.72	12	22	0.61	20	3.45	18	59	0.42	NA	NA	NA	NA	NA
Treecreeper	4	-14.63	10	30	0.85	16	0.00	11	28	0.70	NA	NA	NA	NA	NA
Jay	24	31.58	17	25	0.01	15	0.00	20	85	0.70	NA	NA	NA	NA	NA
Nuthatch	8	-9.64	13	57	0.45	14	-1.09	14	50	0.78	NA	NA	NA	NA	NA
Green Woodpecker	20	15.38	15	35	0.17	13	-2.22	12	27	0.38	NA	NA	NA	NA	NA
Bullfinch	10	-6.25	15	52	0.68	11	-7.22	17	63	0.82	NA	NA	NA	NA	NA
Mistle Thrush	14	0.00	19	58	0.24	8	-13.87	16	81	0.53	NA	NA	NA	NA	NA
Garden Warbler	NA	NA	NA	NA	NA	1	-26.83	11	45	0.32	NA	NA	NA	NA	NA

Table 5, Summary of responses across bird and butterfly species to each extreme climate event. Shown are the number of species which showed average population increases or decreases, along with the median % population change across all species. Asterisks indicate significant patterns across species.

Group	Event type	Year	Number species decreasing	Number species increasing	Median % change	n	V	p	
Butterflies	drought	1990	6	5	-31.34	11	40	0.577	
Butterflies	drought	1995	11	17	17.48	28	149	0.227	
Butterflies	drought	2006	25	3	-39.91	28	366	<0.001	*
Butterflies	winter cold	1982	1	11	25.56	12	3	0.002	*
Butterflies	winter cold	1985	16	4	-29.06	20	185	0.002	*
Butterflies	winter cold	2010	9	27	21.2	36	131	0.001	*
Birds	drought	1990	21	9	-8.26	30	343	0.024	*
Birds	drought	1995	12	15	0	27	148	0.710	
Birds	drought	2006	38	8	-7.55	43	832	<0.001	*
Birds	winter cold	1982	13	11	-2.64	24	154	0.630	
Birds	winter cold	1985	14	13	-1.09	27	205	0.258	
Birds	winter cold	2010	41	17	-6.41	58	1207	<0.001	*

Table 6, Butterfly recovery from three drought events in terms of rate of population change in the subsequent four year period. Only species populations showing declines following the extreme event were considered. Recovery rates significantly different to zero were tested with a Wilcoxon signed ranks tests for each species. Species are ranked by common name.

	1990 drought recovery					1995 drought recovery					2006 drought recovery				
Common name	Rank	Median recovery rate	n	V	P	Rank	Median recovery rate	n	V	P	Rank	Median recovery rate	n	V	P
Brimstone	NA	NA	NA	NA	NA	3	23.90	66	1904	0.00	2	25.90	31	431	0.00
Brown argus	3	-0.65	28	194	0.85	19	-2.50	27	130	0.16	1	74.70	68	2337	0.00
Chalk-hill blue	NA	NA	NA	NA	NA	5	10.95	74	2484.5	0.00	7	13.30	69	2286	0.00
Comma	11	-19.25	24	104	0.20	1	48.55	48	1037	0.00	28	-11.00	64	784	0.09
Common blue	4	-1.10	41	332	0.21	7	3.40	71	1707	0.01	9	9.40	51	1293	0.00
Dingy skipper	2	0.70	11	42	0.46	9	1.45	18	139	0.02	15	4.30	13	90	0.00
Gatekeeper	1	3.95	38	510	0.04	20	-3.70	85	963.5	0.00	11	7.15	76	2766	0.00
Green hairstreak	NA	NA	NA	NA	NA	22	-4.65	60	339	0.00	16	4.00	29	393	0.00
Green-veined white	6	-2.65	14	20	0.04	17	-2.20	12	6	0.01	13	5.90	21	224.5	0.00
Grizzled skipper	10	-14.20	35	36	0.00	6	3.40	87	3151	0.00	10	8.10	55	1476	0.00
Holly blue	NA	NA	NA	NA	NA	14	-1.10	15	43	0.36	26	-3.25	30	48	0.00
Large skipper	9	-8.00	20	15	0.00	23	-4.90	44	31	0.00	18	2.60	25	313	0.00
Large white	5	-1.40	9	4	0.03	16	-1.80	15	51	0.64	25	-1.40	35	252.5	0.31
Marbled white	NA	NA	NA	NA	NA	26	-8.55	28	137	0.14	12	6.80	68	1748	0.00
Meadow brown	NA	NA	NA	NA	NA	2	38.40	11	65	0.00	27	-3.90	28	135	0.13
Orange tip	NA	NA	NA	NA	NA	12	-0.30	19	82	0.62	17	2.80	68	2127	0.00
Painted lady	NA	NA	NA	NA	NA	18	-2.40	12	12	0.03	20	1.70	14	93	0.01
Peacock	NA	NA	NA	NA	NA	25	-6.50	43	215	0.00	22	1.00	22	171	0.16
Purple hairstreak	NA	NA	NA	NA	NA	27	-9.70	9	1	0.01	8	10.75	12	73	0.00
Red admiral	NA	NA	NA	NA	NA	28	-21.70	4	1	0.25	3	25.80	17	147	0.00
Ringlet	NA	NA	NA	NA	NA	8	1.50	14	67	0.39	23	0.80	7	18	0.58
Silver-washed fritillary	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	24	-1.00	7	9	0.47
Small copper	NA	NA	NA	NA	NA	29	-88.80	5	3	0.31	6	16.90	32	466	0.00
Small heath	NA	NA	NA	NA	NA	13	-0.60	7	16	0.81	21	1.70	10	48	0.04
Small skipper	NA	NA	NA	NA	NA	4	21.60	7	28	0.02	5	17.45	18	148	0.00
Small tortoiseshell	8	-6.50	8	2	0.02	11	0.70	24	169.5	0.35	19	2.60	9	35	0.16
Small white	7	-5.00	15	8	0.00	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA

Small/ Essex skipper	NA	NA	NA	NA	NA	15	-1.45	2	1	1.00	14	4.50	6	17	0.22
Speckled wood	NA	NA	NA	NA	NA	10	1.20	5	12	0.31	NA	NA	NA	NA	NA
Wall brown	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	4	20.80	13	91	0.00
White admiral	NA	NA	NA	NA	NA	21	-4.50	46	332	0.02	NA	NA	NA	NA	NA

Table 7, Butterfly recovery from two extreme winter cold events in terms of rate of population change in the subsequent four year period. Only species populations showing declines following the extreme event were considered. Recovery rates significantly different to zero were tested with a Wilcoxon signed ranks tests for each species. Species are ranked by common name.

	1982 cold recovery					1985 cold recovery				
Common name	Rank	Median recovery rate	n	V	P	Rank	Median recovery rate	n	V	P
Brimstone	1	13.30	3	6	0.25	19	-9.60	11	7	0.02
Brown argus	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA
Chalk-hill blue	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA
Comma	NA	NA	NA	NA	NA	12	0.10	7	16	0.81
Common blue	NA	NA	NA	NA	NA	13	-2.15	18	61.5	0.31
Dingy skipper	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA
Gatekeeper	5	0.30	2	2	1.00	20	-32.75	22	10	0.00
Green hairstreak	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA
Green-veined white	9	-9.10	5	3	0.31	5	3.30	13	65	0.19
Grizzled skipper	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA
Holly blue	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA
Large skipper	2	5.65	2	2	1.00	6	2.05	18	94.5	0.71
Large white	8	-3.60	9	14	0.36	3	11.90	4	10	0.13
Marbled white	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA
Meadow brown	3	4.35	6	10	1.00	9	1.00	22	149	0.48
Orange tip	NA	NA	NA	NA	NA	7	1.45	4	9	0.25
Painted lady	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA
Peacock	4	2.40	2	2	1.00	15	-3.60	10	19	0.43
Purple hairstreak	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA
Red admiral	NA	NA	NA	NA	NA	8	1.10	15	86	0.15
Ringlet	NA	NA	NA	NA	NA	2	24.40	15	76	0.39
Silver-washed fritillary	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA
Small copper	NA	NA	NA	NA	NA	4	7.40	9	32	0.30
Small heath	10	-10.65	2	0	0.50	16	-5.85	16	55	0.53
Small skipper	NA	NA	NA	NA	NA	17	-8.10	9	8	0.10
Small tortoiseshell	11	-14.20	1	0	1.00	10	0.60	21	144	0.34
Small white	7	-3.30	7	8	0.38	14	-3.00	15	30	0.09
Small/ Essex skipper	6	-1.15	2	1	1.00	18	-9.10	8	3	0.04

Speckled wood	12	-49.90	5	0	0.06	1	27.25	18	171	0.00
Wall brown	NA	NA	NA	NA	NA	11	0.25	10	30	0.85
White admiral	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA

Table 8, Bird recovery from three drought events in terms of rate of population change in the subsequent four year period. Only species populations showing declines following the extreme event were considered. Recovery rates significantly different to zero were tested with a Wilcoxon signed ranks tests for each species. Species are ranked by common name.

	1990 drought recovery					1995 drought recovery					2006 drought recovery				
Species common name	Rank	Median recovery rate	n	V	P	Rank	Median recovery rate	n	V	P	Rank	Median recovery rate	n	V	P
Blackbird	20	0.10	29	287	0.14	6	0.50	25	230.5	0.07	20	0.30	377	44034	0.00
Blackcap	10	0.30	25	235	0.05	5	0.80	17	133	0.00	10	0.70	51	1131	0.00
Black-headed Gull	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	6	0.90	17	109	0.13
Blue Tit	25	0.00	15	50	0.90	25	-0.30	13	30	0.31	15	0.40	357	40877.5	0.00
Bullfinch	13	0.30	6	17	0.21	20	0.00	5	3	0.58	NA	NA	NA	NA	NA
Canada Goose	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	13	0.50	20	119.5	0.60
Carrion Crow	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	16	0.40	309	29067.5	0.00
Carrion/Hooded Crow	14	0.30	13	65	0.05	27	-0.30	11	16	0.26	NA	NA	NA	NA	NA
Chaffinch	28	0.00	25	142	0.60	7	0.30	19	125	0.24	31	0.10	413	44911	0.06
Chiffchaff	7	0.50	23	228	0.01	10	0.30	19	125	0.09	26	0.20	38	435	0.21
Coal Tit	27	0.00	15	60.5	1.00	21	-0.10	19	83	0.93	36	-0.10	18	71	0.54
Collared Dove	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	32	0.05	116	3464	0.22
Coot	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	2	1.10	13	69	0.11
Dunnock	5	0.70	20	199	0.00	22	-0.20	21	69	0.11	19	0.30	129	5236.5	0.00
Feral Pigeon	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	25	0.20	43	501	0.54
Garden Warbler	11	0.30	7	19	0.09	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA
Goldcrest	3	0.70	9	31	0.36	16	0.00	9	24	0.44	42	-0.85	12	16	0.08
Goldfinch	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	5	1.00	57	1238	0.00
Great Spotted Woodpecker	24	0.00	9	6	0.79	15	0.00	8	17	0.21	NA	NA	NA	NA	NA
Great Tit	4	0.70	13	87	0.00	13	0.10	21	146	0.30	24	0.20	179	9356	0.01
Green Woodpecker	16	0.20	7	20	0.38	17	0.00	10	17	0.67	NA	NA	NA	NA	NA
Greenfinch	NA	NA	NA	NA	NA	24	-0.20	4	1.5	0.59	40	-0.30	206	6966	0.00
Greylag Goose	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	1	2.50	8	25	0.38
Herring Gull	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	8	0.75	34	375	0.09
House Martin	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	37	-0.10	47	610.5	0.63

House Sparrow	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	9	0.70	249	20098	0.00
Jackdaw	8	0.50	7	28	0.02	23	-0.20	7	1	0.03	4	1.05	154	8489.5	0.00
Jay	22	0.05	12	41	0.50	19	0.00	7	7	1.00	NA	NA	NA	NA	NA
Lesser Black-backed Gull	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	27	0.15	22	134.5	0.52
Linnet	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	11	0.60	61	1292	0.01
Long-tailed Tit	19	0.10	8	23	0.55	12	0.10	10	34	0.19	NA	NA	NA	NA	NA
Magpie	12	0.30	9	31	0.36	14	0.00	17	77	0.13	30	0.10	130	4537.5	0.14
Mallard	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	33	0.00	73	1506.5	0.28
Marsh Tit	18	0.10	3	6	0.25	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA
Meadow Pipit	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	21	0.30	60	876	0.88
Mistle Thrush	26	0.00	5	5.5	1.00	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA
Nuthatch	21	0.10	7	14	0.53	9	0.30	3	6	0.25	NA	NA	NA	NA	NA
Pheasant	17	0.15	6	16	0.31	26	-0.30	7	8	0.38	34	0.00	121	3650.5	0.48
Robin	1	2.60	30	451	0.00	3	1.00	31	374	0.01	35	0.00	267	17590	0.53
Rook	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	23	0.20	88	2169.5	0.38
Sedge Warbler	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	43	-1.55	6	0	0.06
Shelduck	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	22	0.25	6	12	0.28
Skylark	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	38	-0.10	160	6105.5	0.76
Song Thrush	23	0.00	22	127.5	0.41	18	0.00	19	89	0.57	29	0.10	77	1387.5	0.53
Starling	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	39	-0.15	176	6767	0.25
Stock Dove	15	0.25	6	11	1.00	4	0.80	6	21	0.03	14	0.45	10	32.5	0.26
Swallow	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	18	0.30	173	10059.5	0.00
Swift	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	12	0.50	51	889	0.03
Treecreeper	9	0.40	11	54	0.07	8	0.30	8	29	0.15	NA	NA	NA	NA	NA
Whitethroat	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	7	0.80	49	978.5	0.00
Willow Warbler	29	-0.10	17	71.5	0.83	11	0.20	13	51	0.74	17	0.35	62	1242	0.03
Woodpigeon	6	0.55	10	37	0.38	2	1.00	6	17	0.22	3	1.10	441	67306	0.00
Wren	2	2.00	38	690	0.00	1	2.00	41	830	0.00	41	-0.40	291	15483.5	0.00
Yellowhammer	30	-0.60	9	7	0.07	NA	NA	NA	NA	NA	28	0.10	68	1162	0.89

Table 9, Bird recovery from two extreme winter cold events in terms of rate of population change in the subsequent four year period. Only species populations showing declines following the extreme event were considered. Recovery rates significantly different to zero were tested with a Wilcoxon signed ranks tests for each species. Species are ranked by common name.

	1982 cold recovery					1985 cold recovery				
Species common name	Rank	Median recovery rate	n	V	P	Rank	Median recovery rate	n	V	P
Blackbird	9	0.20	15	70	0.59	3	0.70	19	147	0.04
Blackcap	21	-0.30	11	24	0.45	11	0.10	13	52	0.33
Black-headed Gull	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA
Blue Tit	3	0.80	20	155.5	0.02	27	-0.60	15	25.5	0.10
Bullfinch	12	0.10	9	26.5	0.26	22	-0.20	9	8.5	0.20
Canada Goose	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA
Carrion Crow	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA
Carrion/Hooded Crow	10	0.15	4	3	0.37	12	0.05	6	7.5	1.00
Chaffinch	4	0.50	21	138	0.44	5	0.35	18	118	0.05
Chiffchaff	6	0.30	13	42.5	0.42	4	0.70	4	9	0.25
Coal Tit	19	-0.20	9	22	1.00	20	-0.10	12	34	0.72
Collared Dove	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA
Coot	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA
Dunnock	24	-0.95	16	27	0.04	9	0.20	18	92	0.48
Feral Pigeon	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA
Garden Warbler	NA	NA	NA	NA	NA	6	0.30	9	28	0.55
Goldcrest	14	0.10	5	7	0.58	13	0.00	8	16	0.83
Goldfinch	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA
Great Spotted Woodpecker	15	0.10	5	7	0.58	17	0.00	7	4.5	0.59
Great Tit	17	0.05	18	89	0.29	24	-0.40	20	86.5	0.75
Green Woodpecker	13	0.10	6	7.5	0.46	14	0.00	6	4	0.85
Greenfinch	18	-0.20	6	4	0.42	16	0.00	5	4.5	0.59
Greylag Goose	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA
Herring Gull	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA
House Martin	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA
House Sparrow	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA

Jackdaw	NA	NA	NA	NA	NA	25	-0.40	3	1	0.50
Jay	11	0.15	4	3	0.37	18	-0.05	10	21.5	0.95
Lesser Black-backed Gull	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA
Linnet	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA
Long-tailed Tit	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA
Magpie	2	0.85	10	51	0.02	19	-0.05	4	3	1.00
Mallard	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA
Marsh Tit	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA
Meadow Pipit	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA
Mistle Thrush	20	-0.25	8	3	0.07	21	-0.10	11	21	0.91
Nuthatch	7	0.25	8	23	0.15	15	0.00	7	9	0.20
Pheasant	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA
Robin	8	0.20	25	193.5	0.41	1	1.05	26	233	0.15
Rook	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA
Sedge Warbler	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA
Shelduck	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA
Skylark	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA
Song Thrush	22	-0.50	15	40.5	0.28	8	0.20	21	107.5	0.15
Starling	NA	NA	NA	NA	NA	7	0.25	6	9	0.79
Stock Dove	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA
Swallow	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA
Swift	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA
Treecreeper	16	0.05	6	9.5	0.68	23	-0.20	5	4	0.85
Whitethroat	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA
Willow Warbler	23	-0.75	10	15	0.22	26	-0.45	26	134.5	0.30
Woodpigeon	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA
Wren	1	0.90	20	155	0.06	2	0.95	28	317	0.01
Yellowhammer	5	0.40	7	14	0.53	10	0.20	5	8	1.00

Table 10, Butterfly recovery times from the extreme events, combining both sensitivity and recovery rates to give the time to reach expected population levels had the extreme event not occurred. Only species populations showing declines following the extreme event were considered. Species are ranked by common name.

	1982 cold recovery time			1985 cold recovery time			1990 drought recovery time			1995 drought recovery time			2006 drought recovery time		
Species common name	Median recovery time	n recovering	n not recovering	Median recovery time	n recovering	n not recovering	Median recovery time	n recovering	n not recovering	Median recovery time	n recovering	n not recovering	Median recovery time	n recovering	n not recovering
Brimstone	2.00	3	0	135.00	1	10	2.50	2	7	3.00	4	11	3.50	10	25
Brown argus	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	0	3	3.50	14	2
Chalk-hill blue	NA	NA	NA	NA	NA	NA	NA	NA	NA	2.00	3	3	6.00	9	9
Comma	NA	NA	NA	6.50	2	5	NA	NA	NA	4.00	8	11	4.00	39	29
Common blue	NA	NA	NA	4.00	4	13	5.50	4	24	3.00	8	19	4.00	62	3
Dingy skipper	NA	NA	NA	NA	NA	NA	NA	NA	NA	1.50	4	3	3.00	6	4
Gatekeeper	3.00	1	1	6.00	1	21	NA	NA	NA	3.00	7	20	6.00	33	34
Green hairstreak	NA	NA	NA	NA	NA	NA	NA	NA	NA	5.00	8	6	4.50	2	5
Green-veined white	6.00	1	4	3.00	8	4	2.00	15	26	3.00	41	30	2.00	45	6
Grizzled skipper	NA	NA	NA	NA	NA	NA	NA	NA	NA	1.00	1	1	2.50	4	2
Holly blue	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	12.00	2	5
Large skipper	3.00	1	1	4.00	9	8	NA	NA	NA	5.00	8	52	3.00	19	8
Large white	3.50	4	5	1.50	4	0	1.00	2	33	3.00	66	19	2.00	42	12
Marbled white	NA	NA	NA	NA	NA	NA	NA	NA	NA	1.00	10	1	4.50	6	22
Meadow brown	2.50	2	4	2.50	8	12	3.50	8	16	3.00	38	10	3.00	17	46
Orange tip	NA	NA	NA	3.00	3	1	5.50	6	5	3.00	13	5	3.00	10	3
Painted lady	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	1.00	11	0
Peacock	1.50	2	0	6.50	2	8	1.00	1	7	10.00	9	15	2.00	7	2
Purple hairstreak	NA	NA	NA	NA	NA	NA	NA	NA	NA	4.00	2	3	NA	NA	NA
Red admiral	NA	NA	NA	3.00	9	6	NA	NA	NA	4.00	3	12	6.00	3	27
Ringlet	NA	NA	NA	5.50	6	9	NA	NA	NA	4.00	38	27	2.00	21	9

Silver-washed fritillary	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	0	9	5.00	7	5
Small copper	NA	NA	NA	3.00	5	4	8.50	2	12	5.00	3	9	5.00	12	8
Small heath	9.00	1	1	2.00	5	11	NA	NA	NA	2.00	2	3	5.00	18	12
Small skipper	NA	NA	NA	16.00	1	8	NA	NA	NA	4.50	10	32	3.00	11	10
Small tortoiseshell	NA	0	1	3.00	9	11	3.50	2	18	1.00	5	39	3.00	24	1
Small white	2.00	5	2	1.00	7	8	3.00	18	20	2.00	13	72	4.00	61	15
Small/ Essex skipper	1.00	1	0	18.00	1	7	NA	NA	NA	5.00	13	32	NA	NA	NA
Speckled wood	NA	0	5	2.00	17	0	NA	NA	NA	5.00	46	26	3.00	52	17
Wall brown	NA	NA	NA	9.00	6	4	NA	0	15	NA	NA	NA	NA	NA	NA
White admiral	NA	NA	NA	NA	NA	NA	NA	NA	NA	3.00	4	8	9.00	7	7

Table 11, Bird recovery times from the extreme events, combining both sensitivity and recovery rates to give the time to reach expected population levels had the extreme event not occurred. Only species populations showing declines following the extreme event were considered. Species are ranked by common name.

	1982 cold recovery time			1985 cold recovery time			1990 drought recovery time			1995 drought recovery time			2006 drought recovery time		
Species common name	Median recovery time	n recovering	n not recovering	Median recovery time	n recovering	n not recovering	Median recovery time	n recovering	n not recovering	Median recovery time	n recovering	n not recovering	Median recovery time	n recovering	n not recovering
Blackbird	2.00	9	6	4.50	10	9	4.50	12	17	3.00	15.00	10	3.00	175	197
Blackcap	6.00	2	9	2.50	4	8	4.00	12	13	3.00	13.00	4	4.00	34	17
Black-headed Gull	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	3.00	6	9
Blue Tit	3.00	13	7	11.00	1	14	2.50	6	9	2.00	3.00	10	4.00	190	163
Bullfinch	1.00	5	4	NA	0	9	1.00	3	3	4.00	1.00	4	NA	NA	NA
Canada Goose	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	6.00	11	9
Carrion Crow	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	4.00	167	142
Carrion/Hooded Crow	3.00	3	1	4.00	3	3	3.00	9	4	6.00	3.00	8	NA	NA	NA
Chaffinch	5.50	8	13	3.00	9	9	4.00	14	11	3.00	8.00	11	4.00	169	237
Chiffchaff	9.00	7	6	7.00	3	1	12.00	8	15	2.50	10.00	9	3.00	19	19
Coal Tit	4.00	2	7	10.00	5	7	9.50	4	11	4.00	10.00	9	5.00	7	11
Collared Dove	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	4.00	55	61
Coot	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	3.00	8	5
Dunnock	2.00	3	13	4.00	10	7	4.00	11	9	5.00	7.00	14	4.00	59	68
Feral Pigeon	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	3.00	19	24
Garden Warbler	NA	NA	NA	6.00	4	5	8.00	4	3	NA	NA	NA	NA	NA	NA
Goldcrest	2.50	2	3	21.00	2	6	5.00	5	4	9.00	3.00	6	5.00	3	9
Goldfinch	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	4.00	33	24
Great Spotted Woodpecker	4.00	1	4	2.00	3	4	5.50	4	5	2.00	3.00	5	NA	NA	NA
Great Tit	4.00	6	12	8.00	7	13	3.00	8	5	2.50	8.00	13	5.00	79	97
Green Woodpecker	4.00	3	3	3.50	4	2	2.50	4	3	3.00	5.00	5	NA	NA	NA
Greenfinch	13.50	2	4	2.50	4	1	NA	NA	NA	3.00	3.00	1	6.00	68	136
Greylag Goose	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	3.00	4	4
Herring Gull	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	5.50	14	17

House Martin	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	3.50	20	27
House Sparrow	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	4.00	130	117
Jackdaw	NA	NA	NA	2.00	1	2	3.00	3	4	4.00	1.00	6	3.00	80	70
Jay	2.00	3	1	13.50	2	8	5.00	6	6	1.50	2.00	5	NA	NA	NA
Lesser Black-backed Gull	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	3.00	10	12
Linnet	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	3.00	27	34
Long-tailed Tit	NA	NA	NA	NA	NA	NA	3.00	3	5	5.00	5.00	5	NA	NA	NA
Magpie	3.00	6	3	3.00	1	3	3.00	7	2	3.00	8.00	9	3.00	61	68
Mallard	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	5.00	31	41
Marsh Tit	NA	NA	NA	NA	NA	NA	15.00	1	2	NA	NA	NA	NA	NA	NA
Meadow Pipit	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	4.50	30	26
Mistle Thrush	NA	0	8	2.50	4	7	4.00	3	2	NA	NA	NA	NA	NA	NA
Nuthatch	9.00	4	4	11.50	2	5	21.00	4	3	3.00	2.00	1	NA	NA	NA
Pheasant	NA	NA	NA	NA	NA	NA	4.50	4	2	10.00	2.00	5	4.00	43	78
Robin	4.00	7	18	6.00	14	12	7.00	17	13	4.00	17.00	14	3.00	118	144
Rook	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	3.00	34	51
Sedge Warbler	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	7.00	1	5
Shelduck	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	2.00	3	3
Skylark	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	4.00	73	85
Song Thrush	3.00	7	8	2.00	7	13	8.00	10	12	3.00	8.00	11	4.00	35	41
Starling	NA	NA	NA	7.00	3	3	NA	NA	NA	NA	NA	NA	4.00	75	97
Stock Dove	NA	NA	NA	NA	NA	NA	10.00	1	5	3.00	5.00	1	4.00	6	4
Swallow	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	4.00	73	99
Swift	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	3.50	30	21
Treecreeper	2.00	2	4	2.00	1	4	7.00	8	3	2.00	5.00	3	NA	NA	NA
Whitethroat	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	4.00	34	15
Willow Warbler	3.00	2	8	3.50	8	18	5.00	9	8	5.00	9.00	4	3.00	31	29
Woodpigeon	NA	NA	NA	NA	NA	NA	7.50	4	6	11.00	1.00	5	3.00	221	213
Wren	2.50	12	8	7.50	14	14	10.00	21	17	6.00	33.00	8	3.00	113	175
Yellowhammer	23.00	5	2	2.00	2	3	2.00	1	8	NA	NA	NA	4.00	34	34

Table 12, Summary of recovery times across bird and butterfly species to each extreme climate event. Shown are the median of the species median recovery times (from Tables 11 and 12) for species which had sufficient data for analysis and had some populations showing positive recovery. Also shown are the median percentage of populations not recovering across all species and the number of species which had sufficient data for analysis.

Group	Event type	Year	Median recovery time (years)	n	Median percentage of populations not recovering	n
Butterflies	drought	1990	3.3	10	81.74	11
Butterflies	drought	1995	3.0	26	61.25	28
Butterflies	drought	2006	3.5	28	40	28
Butterflies	winter cold	1982	2.8	10	50	12
Butterflies	winter cold	1985	3.5	20	57.5	20
Birds	drought	1990	4.8	30	48.5	30
Birds	drought	1995	3.0	27	52.9	27
Birds	drought	2006	4.0	43	53.5	43
Birds	winter cold	1982	3.0	23	56.7	24
Birds	winter cold	1985	4.0	26	60	27

Discussion

The aim of this analysis was to assess the overall sensitivity and recovery of bird and butterfly species to several recent drought and winter cold events. We found that species' responses varied across extreme events of the same type. For example, the Common blue butterfly *Polyommatus icarus* populations significantly declined following the droughts in 1990 and 2006, but actually increased following droughts in 1995 (Table 1). This reflects the broader pattern across butterfly species where species declined severely following the 2006 drought event (25 species decreased and only 3 increased) whilst trends were very mixed in 1990 and 1995 droughts (e.g. six species decreased and five increased in 1990, whilst 11 species decreased and 17 increased in 1995, with no significant trend across species in either year; Table 5).

Similarly, butterfly species responses to winter cold also varied between specific events. There were significant declines across species after the winter of 1984-5, whilst winters of 1981-2 and 2009-10 resulted in significant increases across butterfly species (Table 5).

These results suggest caution in trying to generalise responses of species to extreme events- each event appears to be quite unique in its effect. In retrospect, this makes sense as the exact weather conditions during each extreme event vary (e.g. in terms of location, timing and protraction of rainfall deficiencies, groundwater and soil moisture levels; see Box 1 and also Marsh, Cole & Wilby, 2007 for a comparison of different historic droughts in England and Wales). In addition, other factors may affect species during each event. These may include weather conditions subsequent to the extreme event (i.e. favouring or hindering recovery), but also other factors such as variation in predator/ pathogen intensity and levels of habitat extent and quality during the focal period.

The above conclusions also hold true to birds. Many species varied in their responses across events (Tables 3 &4). However, across species, there was more consistency in patterns. Birds, as a group, showed significant decline in response to drought events of 1990 and 2006, although no significant response in 1995. They also showed consistent declines to winter cold events, although this was only significant for the last winter of 2009-10.

One of the key messages from this work is that every drought or cold winter is different and it is important to exercise caution in making generalisations. The drought of 1995 seems to have had positive or negligible effects across most butterflies and birds respectively. In contrast, the more recent 2006 drought had severe significant impacts across both birds and butterflies. For example, in 2006, 25 out of 28 butterfly species declined along with 38 out of 43 bird species. In contrast, the 2009-10 winter saw large differences between the groups with 27 out of 26 butterflies increasing, whilst 41 out of 58 bird species declined (Table 5). From these results we might tentatively conclude that drought tends to have negative impact on both species groups, whilst winter cold has an adverse impact on birds, but a positive effect on butterflies.

These results are consistent with what our understanding of species biology. Regarding winter cold, birds are warm-blooded species and cold winters can increase mortality due to lack of food (especially over extended cold periods), or may be killed directly due to extremely low temperatures (Cawthorne & Marchant, 1980). Previous analyses of both population trends (Greenwood and Baillie 1991) and ringing data (Robinson et al. 2007), have identified declines in abundance or survival following cold (and in particular, snowy or frosty) winters. In contrast, butterflies are ectothermic animals that are in a dormant stage overwinter. Many species are adapted to tolerate extremes of cold (e.g. 'antifreeze' chemicals in haemolymph), and metabolic rates are lowered so that no feeding is required (Leather, Walters & Bale, 1993). Indeed, it has been suggested that warmer winters may actually be more harmful to insects because they increase metabolic rates meaning food reserves become exhausted faster and can also increase susceptibility to pathogens (Harvell *et al.*, 2002).

Regarding drought, extreme air temperatures may have direct effects by reducing butterfly longevity and aridity can lead to desiccation of immature (caterpillar and pupal) stages. There are also indirect effects mediated through changes in host plant availability or quality (Talloen, Van Dyck & Lens, 2004). Similarly, for birds, drought may mean that less food is available in terms of fruit, seeds and invertebrates (Pearce-Higgins et al. 2010).

In terms of recovery following extreme events, it is clear that many populations do not show immediate recovery and a large proportion of populations (sometimes the majority) continue to decline (Tables 6-11, with summary on Table 12). Such declines may be due to other factors irrespective of the extreme event itself, e.g. subsequent poor weather, changes to resources, or increased in predators or pathogens; but there are also likely to be historic influences of the event due to reductions in population density. When populations crash to small numbers we would expect release from density dependent population feedback to mean that numbers increase rapidly, especially in short-lived organisms such as insects. However, there may other density dependent effects at play in small populations, so called 'Allee effects', where growth is slower than expected. These can be caused by mate-finding difficulties, elevated exposure to predators through reduced aggregation, and decreased cluster induced thermoregulation (Kuusaari et al., 1998; Berec et al., 2007). The current study does not inform on the mechanism behind these population changes, but it is clear that whatever the mechanism, there are no large qualitative differences in the proportion of populations recovering or in recovery times between butterflies and birds. On average, less than half of populations show positive recovery in the subsequent four years following the extreme events studied here. For those populations that that do show positive recovery, recovery times vary across species but on average range between 3-5 years (Table 6). Of course, these averages can mask large differences between individual species. In some cases, differences may be caused by small sample sizes (i.e. rates of recovery may only be available from a few monitoring sites). But in other cases there may be sufficient sample sizes to suspect that differences reflect some genuine ecological differences. For example, whereas the marbled white butterfly showed very poor and slow recovery following the extended 2006 drought (22 out of 28 populations continued to decline with the 6 recovering populations taking 4.5 years on average to recover), other species such as the large white and green veined white showed rapid recovery (42 out of 54 and 45 out of 51 respectively showing recovery rather than continued decline; with average recovery times of 2 years for both species). The two whites have multiple generations per year and so may be able to recover population levels more rapidly than the marbled white which only has one generation per year. However, we should be cautious in such speculations because many traits co-vary in species and are also confounded with phylogeny; therefore, rigorous statistical tests are necessary (see Chapter 3) and more detailed studies of ecological processes.

To conclude, in terms of sensitivity to extreme events the patterns that we observed across butterflies and birds do generally confirm anecdotal knowledge of the impacts of drought and winter cold. In terms of recovery, many bird and butterfly populations do not show population increases in the subsequent four year period and even those that do take several years to regain pre-event population levels. However, as we have discussed, extreme events can have idiosyncratic effects, probably due to their uniqueness in terms of timing, intensity and duration of various climatic variables. Further work would benefit from identifying the exact climatic variables and periods during which species are most sensitive, in order to allow analysis of responses across multiple events. This would also help to remove the potential confounding effects of any non-climatic factors on declines.

Chapter 2 - Comparative analysis of species traits

Lead organisation: BTO

Objective: The aim of this analysis was to explain variation between species in terms of their responses to extreme climatic events

Introduction
There is increasing understanding of how variation in precipitation and temperature may affect species' populations. As shown in Chapter 1, fluctuations in the abundance of butterfly species vary with respect to temperature and precipitation, with generally positive effects of summer temperature, but evidence for detrimental effects of drought being apparent in the following year in some species (Roy *et al.* 2001; Chapter 1, this report). Populations of birds also tend to vary in relation to the weather, with fluctuations of resident passerines being strongly driven by winter weather severity (Greenwood & Baillie 1991), results which are supported by subsequent analyses of survival rates (Robinson *et al.* 2007). Further analyses of these and other time-series are being conducted through the BICCO-Net project to document the impacts of climate change in UK biodiversity. These analyses are focussed on average population responses to annual variation in temperature and precipitation, but there is some evidence that extreme climatic events may result in more dramatic ecological consequences (Morecroft *et al.* 2002, Jiguet *et al.* 2006). In this analysis, we have therefore focused on analyses of long-term population monitoring data to examine the response of birds and butterflies to specific extreme climatic events, focusing on population responses to summer drought and severe winter events.

Specifically, we examined whether the response of species to summer drought and winter cold and their recovery from summer drought could be predicted by functional species traits. Responses are described by the degree of decline in a population following an extreme climatic event ('population sensitivity'), and then the subsequent speed of population recovery after that decline (See Chapter 1). Analyses focused on population declines and recovery from the 1995 drought and 2009-10 winter. It was therefore not possible to describe population recovery following the extreme winter event. After consideration of available species' trait data, the following hypotheses were generated (the abbreviation used in Table 13 to display the result of each hypothesis is shown in brackets):

A. The location of the European distribution of the species across climate space (i.e. species temperature index; sensu Devictor *et al.*, 2008; Devictor *et al.*, 2012) will correlate with sensitivity to climatic extremes. High STI species (species which experience high average temperatures across their range) will be more susceptible to cold winters as they are more poorly adapted for colder temperatures than low STI species. High STI species will be less susceptible to summer drought. (TABLE CODE: STI)

B. Sensitivity to cold winters will be affected by over-wintering strategies.

I. Early stage (egg) hibernating butterflies will be less adversely affected by cold winter weather than adult hibernators because they are in a more stable dormant stage.

II. Long-distance migratory birds and butterflies will be un-affected by extreme winters. Species that migrate to southern Europe will show some sensitivity to extreme winters.

(TABLE CODE: Hibernation stage / Migration)

C. In birds, body size will be negatively correlated with sensitivity to cold winters because of a decreasing surface area to volume ratio allowing larger birds to retain heat more efficiently (Cawthorne & Marchant 1980). (TABLE CODE: Body mass)

D. Species with high behavioural adaptability will be less sensitive to extreme weather conditions. There have been some indications that birds with larger brains are able to adapt better to change than those with small relative brain sizes, and will therefore be less sensitive to extreme weather (Thaxter *et al*., 2010; Schultz *et al*., 2005). (TABLE CODE: Brain)

E. Mobile species will show higher recovery rates because they can disperse from climate refugia more quickly than other species. In birds this will be measured as natal dispersal (Jiguet *et al*., 2007), while Wilson *et al*. (2004) provide mobility measures for butterflies. (TABLE CODE: Mobility/ Natal dispersal)

F. Species with large populations will show higher recovery rates as there will be greater probability of immigration into sites from other populations following local declines. (TABLE CODE: No. 10km sqs/ 1km sqs) and a lower probability of localised extinctions.

G. Species with longer generation times (k-selected species) can generally outcompete those with shorter generation times (r-selected species) when resources are scarce and may therefore be less sensitive to climatic extremes (Townsend *et al*., 2008). However, where populations of both groups do crash, species with shorter generation times (measured as voltinism in butterflies and age at first breeding for birds; Jiguet *et al*., 2010) will recover more rapidly from extreme events. (TABLE CODE: Voltinism/ Age 1st breed)

H. Sensitivity and recovery from extreme weather events will be linked to the response of food species.

I. Butterflies with high host-plant specificity and nectar specificity will be more sensitive to extreme weather events than those with low host-plant and nectar specificity (Tudor *et al*., 2004). (TABLE CODES: No. of host plants, No. nectar sources)

II. Insectivore birds will be more sensitive to cold winters than granivorous and frugivorous species because their food supply will be more adversely affected by cold weather. (TABLE CODE: Winter diet type)

Methods
We tested which traits correlated with butterflies' and birds' sensitivity to winter cold, summer drought and their recovery from summer drought. The STIs of species have been previously derived by combining species' European range with the mean temperature across their range (sensu Devictor et al. 2008; Devictor et al. 2012). To test the effect of body mass on sensitivity to winter cold we used a log-transformed mass based on Ringing Scheme data from the British Trust for Ornithology. The relative brain size was calculated as the residuals of a linear relationship between the natural log of the brain mass modelled against the natural log of the body mass (Thaxter et al. 2010). Information from Jiguet *et al*. (2007) and Wilson *et al*. (2004) were used to determine the natal dispersal of birds, mobility of butterflies and the number of broods per year of bird species. The number of 10 km squares across Britain that butterfly species occurred in was taken from Asher *et al*. (2001). For each of these six response variables (butterflies' sensitivity to winter cold and summer drought; recovery from summer drought; birds' sensitivity to winter cold and summer drought; recovery from summer drought) we tested explanatory variables based on the hypotheses above simplifying maximal linear models to the minimum adequate model. Factors in discrete variables were combined where appropriate in step-wise model simplification, using an ANOVA test to compare models before and after combining factors (Crawley, 2007). The maximal models with all explanatory variables included are shown in Box 2. Phylogenetic autocorrelation was tested for prior to modelling and if found we tested the models with and without phylogenetic structure incorporated into the model (Kunin 2008; Box 3). We did not include any interactions between explanatory variables except the interaction between migration and all other variables when modelling birds' sensitivity to winter cold. This interaction was included because without it variables that affect resident species' response to winter cold but not migratory species' response could be missed. There were only two migratory species of butterfly, both of which were very sensitive to winter cold. We therefore carried out the analysis of butterfly response to winter cold with and without the migratory species included.

Box 2. Maximal models

Butterflies:
Summer drought sensitivity ~ STI + voltinism (single or multi-brood) + no. host plants + no. nectar sources
Winter cold sensitivity ~ STI + voltinism (single or multi-brood) + no. host plants + hibernation stage (egg, caterpillar, chrysalis and adult, all initially as separate factors)
Recovery from drought ~ voltinism (single or multi-brood) + mobility + no. 10 km UK sqs + specialist (+ or -)

Birds:
Summer drought sensitivity ~ STI + age of 1st breed + relative brain mass
Winter cold sensitivity ~ STI + age of 1st breed + relative brain mass + log (body mass) + winter diet (fruit, invertebrates, omnivorous, seeds, other plant material) + migratory (non, European or long distance) + migratory:STI + migratory:age + migratory:brain + migratory:mass + migratory:diet
Recovery from drought ~ age of 1st breed + natal dispersal + no. 1 km UK sqs + specialist (+ or -)

Box 3. Phylogenetic autocorrelation

We checked for phylogenetic autocorrelation between the six response variables, explanatory variables and residuals of linear models of the response variable against each explanatory variable. This was done in the R "ape" package using Moran's I-test with Geary randomizations (1000 iterations) (Dray & Dufour 2007). A consensus tree was produced for butterflies from 1000 phylogenetic trees and the branch lengths computed using Grafen's method (1989) in the R "ape" package.

Where phylogenetic autocorrelation was found GLS's were used, and the best correlation structure was selected by comparing the AIC of maximal models with no correlation structure and three correlation structures based on Brownian motion (Felsenstein 1985), and covariance matrices defined in Martins and Hansen (1997) and in Freckelton et al. (2002).

Results

No phylogenetic autocorrelation was found except in the recovery of butterflies to summer drought (P = 0.036). This was due to significant phylogenetic variation in the residuals of linear models of butterfly recovery for specialisation, voltinism and the number of 10 km squares (P = 0.026, 0.014 & 0.037 respectively).

No traits were found to correlate with sensitivity to, or recovery from, summer drought for either taxon (Table 13). Impacts and responses to drought therefore seemed to be unpredictable in both groups.

Table 13, Minimal adequate models (MAM) of species traits in relation to sensitivity to summer drought, winter cold, and recovery from drought. * $p < 0.05$; ** $p < 0.01$; *** $p < 0.001$. ns – not included in MAM: these non-significant variables were then modelled against the response variable with any significant explanatory variables, in order to provide the direction of relationship (+ or -) which is displayed before the trait name or, for non-significant results, displayed before the 'ns'. Only relationships with *a priori* hypotheses (white cells) were tested.

	Butterflies			**Birds**		
Trait	**Drought sensitivity**	**Cold Sensitivity**[a]	**Drought recovery**[b]	**Drought sensitivity**	**Cold sensitivity**	**Drought recovery**
STI	-ns: P=0.527	-ns: P=0.839		-ns: P=0.352	+ns: P=0.640	
Voltinism/ Age 1st breed	-ns: P=0.216	-ns: P=0.200	-ns: P=0.125	+ns: P=0.654	+ns: P=0.280	-ns: P=0.145
No. of host plants	+ns: P=0.074	+ns: P=0.743				

No. nectar sources	+ns: P=0.390					
Hibernation stage / Migration		**+ migratory species ±adult & chrysalis; - egg & caterpillar*** **			ns: -resident, +migrant P = 0.626	
Winter diet type					**+invert, omniv, plant; -fruit, seeds** **	
Relative brain mass				+ns: P=0.816	+ns: P=0.588	
Body mass					+ns: P=0.345	
Mobility/ Natal dispersal			+ns: P=0.178			+ns: P=0.252
No. 10km sqs/ 1km sqs			-ns: P=0.238			+ns: P=0.194
Specialist (Y or N)			ns: -Specialists, P = 0.201			ns: +Specialists, P = 0.668
Migration : other explanatory variables					ns	

[a] The two migrant species were very sensitive to cold winters. However, with migratory species excluded from analysis hibernation stage was again the only significant explanatory variable.
[b] Phylogenetic auto-correlation was found. The results above were found with or without phylogeny included in the model.

In response to the impact of the 2010 extreme winter, resident butterflies were more likely to increase in abundance in 2011, whilst it was migratory species who appeared most cold sensitive. The magnitude of these population increases were greater in butterflies that overwintered as eggs or caterpillars, whilst those which overwintered as adults or chrysalis showed a much smaller increase (Fig 1). The two migrant species were very sensitive to winter cold (mean median change = 57.91 % decrease; P = 0.000). If the two migratory species were excluded, hibernation stage remained the only significant explanatory variable for butterflies (P = 0.003). Further analyses were therefore carried out excluding the two migratory butterfly species.

The response of bird populations to the 2010 extreme winter varied significantly with winter diet. As expected, frugivorous and granivorous species declined less than invertivorous, omnivorous and other herbivorous bird species (P = 0.008; Fig 2).

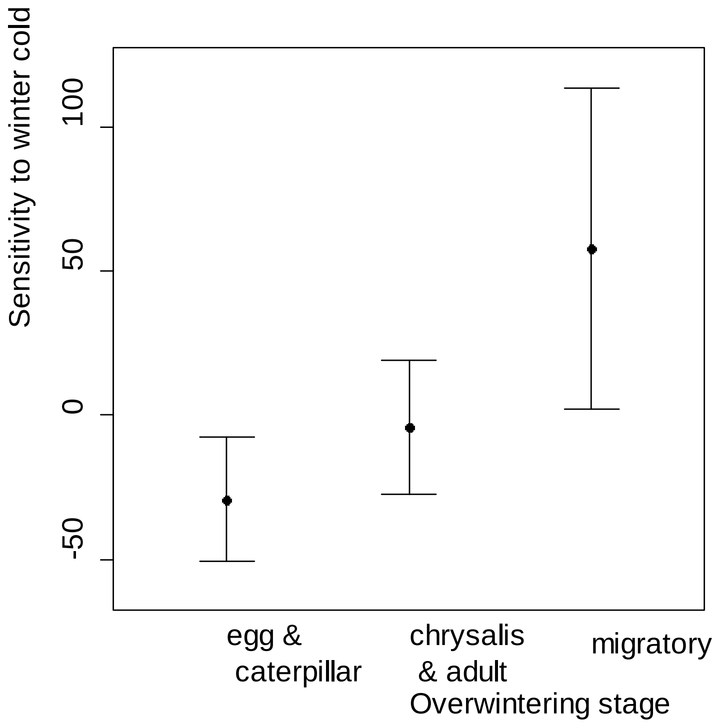

Figure 1, Mean sensitivity of butterflies to winter cold based on overwintering stage and standard deviation. Positive values indicate greater declines and sensitivity to the extreme event.

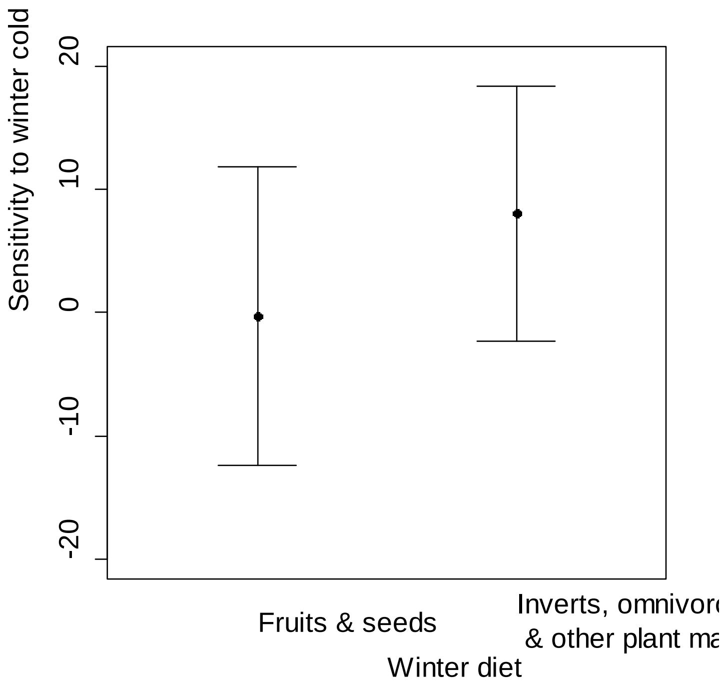

Figure 2, Mean sensitivity of birds to winter cold based on winter diet and standard deviation. Positive values indicate greater declines and high sensitivity.

Discussion

We found evidence for very few of the proposed hypotheses. In particular, no ecological traits were found to explain between-species variation in sensitivity to or recovery from summer drought. The lack of significant traits could be partly due to small sample sizes: there were only 27 or 28 species assessed for response to summer drought for birds and butterflies respectively (Table 5). An alternative explanation is that the effect of drought may be largely site specific (see Chapter 3) rather than species specific or an interaction between the two. Below, we review the evidence in support of each of our initial hypotheses.

Contrary to expectation, species' responses to climatic extremes were not affected by their Species Temperature Index (STI), suggesting that climatic ranges may not be limited by resilience to extreme events. This result was surprising, given that bird populations towards the cool margin of a species' range have shown more positive trends in response to warming than populations at warmer locations (Jiguet et al. 2010). Further, Jiguet *et al*. (2006) showed that the response of bird populations to the French summer heat waves of 2003 was correlated with the thermal range (the range of temperature over which a species' occurs) of each species. Further, Morecroft et al. (2002) examined the sensitivity of butterflies to the 1995 summer drought and found that southern distributed butterflies increased in abundance while declining species were generally more northern species. We expected that STI would be a good indication of physiological adaptations to avoid desiccation and reduced adult longevity, two mechanisms that can drive butterfly population declines after drought. Both 2003 and 1995 were warm and dry and this correlation between summer temperature and low rainfall makes it difficult to determine whether species' fluctuations are due to temperature or precipitation. This difference in results could reflect a difference between measures of thermal range and STI. Although both are based on functions of the temperatures in species' geographical range, they differ slightly in their calculation, and further work to compare what these, and other related measures, including thermal maxima, mean would be useful. This discrepancy in results of Morecroft *et al* (2002) might be because species' trends preceding the drought were not taken into account in the former analysis: southerly distributed species were increasing both before and after the drought event. The effect of drought on butterflies in the year of the drought and the following year was examined in this study and by Morecroft *et al*. (2002). However, the effect of drought on species is often mediated by food availability (Talloen et al. 2004; Pearce-Higgins et al. 2010) It could take more than a year for species to respond to drought if their growth is linked to food plants which may have a lagged response and the lagged effect of climatic events on species could be examined further.

The increased survival of resident overwintering butterflies (slight in adult and chrysalis hibernators, stronger in egg and caterpillar hibernators) was in line with our hypotheses and the results from the BICCO-Net Phase I project, which suggested that butterfly populations in general tended to increase following cold winter weather (Pearce-Higgins *et al.* 2011). A negative correlation between Lepidoptera survival and winter temperatures has previously been noted (Beirne, 1955) and may be because of reduced pressure from pathogen infection or predation by vertebrates, or reduced food requirements after hibernation because of lower metabolic rates in the cold. If this is the case, our results may suggest that the decreased energy requirement in early in the Lepidoptera life-stages has a beneficial impact on survival in warmer winters. However, in a different previous study, egg-larva hibernating butterflies were more adversely affected by cold winters than adult-pupa hibernators, although this was attributed to a following cold spring (Wallisdevries & van Swaay 2006). There has been very little research on the relative cold tolerance of overwintering stages in butterflies and further research could confirm our findings.

The high sensitivity of migratory species was also expected since they are generally adapted to warmer conditions. In mild winters some migrant species may survive overwintering. However, in colder winters migrant butterflies are less likely to survive and rely on recolonisation the subsequent spring from mainland Europe (Thomas & Lewington, 2010). However, as there were only two migratory species included in this analysis this conclusion remains tentative and there is limited scope to test further on UK butterflies alone.

The difference in bird species' sensitivity to winter cold based on winter food was as expected, and follows the inference from previous analyses of overwinter survival rates (Robinson *et al.* 2007). Access to fruits and seeds will be less affected by cold weather than access to other food sources, such as invertebrates. Indeed, we might expect that ground feeders may be particularly sensitive to such extreme winter weather as frost and snow cover may reduce access to food, although further work is required to examine precisely how foraging behaviour affects species' sensitivity to weather. Other mechanisms that lead to bird declines after cold winters include food shortages later in the year because of delayed plant growth and death directly caused by cold (Cawthorne and Marchant 1980). We found no evidence for these factors affecting bird populations; smaller birds or species with southerly ranges (ones with a high STI) were expected to be more at risk from death directly caused by cold. The winter of 2010 was not only cold but also particularly snowy, which may have led to these mechanisms being masked by the larger impact of winter food accessibility.

The resilience and recovery of birds and butterflies were analysed separately because there were a number of traits that were not applicable to both taxa. This analysis showed that cross-taxa analysis of functional traits is likely to require multiple tests, and therefore an increased chance of false positive results. Models including both taxa but with interactions between traits and taxa could have been carried out, increasing the sample size for traits applicable to both taxa and decreasing the total number of tests carried out. However, this would still have limited the number of traits that could have been examined.

To conclude, there are some difficulties in assessing species' ecological response to particular climatic extremes making it difficult to reject hypotheses about the factors affecting species responses to extreme events from this analysis, although we do find evidence that overwinter strategy affects butterfly sensitivity to winter cold events, and that diet affects the response of birds to winter weather. Both results are supported by other studies, and therefore can be regarded with a reasonable degree of confidence.

Chapter 3- Interactions with landscape and habitat availability

Lead organisation: CEH, assisted by FERA with land cover configuration analysis.

Objective: The aim of this analysis was to assess whether different attributes within landscapes can influence species' responses to extreme events, to contribute to our understanding of the role of landscape scale management in climate change adaptation.

Methods

Land cover data collation

We collated data on 'semi-natural habitat' extent around bird and butterfly population monitoring sites. Semi-natural habitat was defined as all CEH Landcover Map (LCM) land cover types apart from urban, arable, improved grassland and sea. For analyses linking landscape structure to population responses to the 1995 drought event we used the LCM 2000 map, which is based on satellite imagery from the year 2000 (Fuller *et al.*, 2002). For analyses linking landscape structure to population responses to the 2010 winter cold event we used the LCM 2007 map (Centre for Ecology and Hydrology, 2011). For each monitoring site we calculated the total area of semi-natural habitat in hectares in 3km buffer around it. We also assessed configuration of this habitat in terms of mean 'shape index', mean nearest neighbour distance between habitat patches and patch density (number of patches per m^2). 'Shape index' is the ratio of the total habitat patch perimeter compared to the minimum possible perimeter for the habitat area, and so is a measure of 'edginess' with higher values indicating a greater amount of habitat patch edge. More information on these metrics can be found at in Appendix 4.

For the analysis of bird responses, the area of selected agri-environment options that may provide winter bird food was also included. We used Natural England data sets to assess the total area of the ES scheme options in Table 14. All analyses were carried out in ArcGIS.

Table 14, Agri-environment scheme options assessed which might provide winter bird food.

Code	Agri-environment Option
EB3	Enhanced hedgerow management
EC24	Hedgerow tree buffer strips on cultivated land
EF2	Wild bird seed mixture
EF6	Over-wintered stubbles
EG4	Cereals for whole crop silage followed by over-wintered stubbles
OF2	Wild bird seed mixture
OB3	Enhanced Hedgerow management
OF6	Over-wintered stubbles
OG4	Cereals for whole crop silage followed by over-wintered stubbles

Preliminary analyses suggested that population responses across multiple species were best determined by land cover assessed at the 3km buffer scale, so we only present these results here.

Statistical analysis

We analysed the effect of semi-natural habitat on bird and butterfly sensitivity and recovery to extreme events. For these analyses we used the site-level measures of sensitivity and recovery calculated in Chapter 1 and corresponding data on semi-natural habitat area and configuration in a 3km buffer around each site. As the timing of the impact of drought on butterflies may vary between species, we measured each species response to the 1995 drought with a one year lag (population change in 1996) and with no lag (population change in 1995). The site-level sensitivity and recovery measures used for each species in our analyses were then determined by the data set (with or without lag) in which each species showed the greatest decline.

The analyses described here generally follow the method developed by Oliver et al (2012). The conceptual framework is shown in figure 3 and explained below. All models exploring the predictors of population sensitivity, as measured by the difference between the observed and expected population (Figure 3), included expected population size and a measure of the site's drought (aridity index) or winter cold (mean winter temperature) as control explanatory variables. All models exploring the predictors of recovery rates included the size of the initial population change (difference between observed and expected population) and population size after the drought or cold event. Our analyses took two parts. First, we analysed the overall effect of semi-natural habitat on bird and butterfly population resilience (sensitivity and recovery) to drought and winter cold across all species ('multi-species analyses'). Second, we analysed the effect of semi-natural habitat on population resilience to drought and winter cold for each species separately ('single-species analyses').

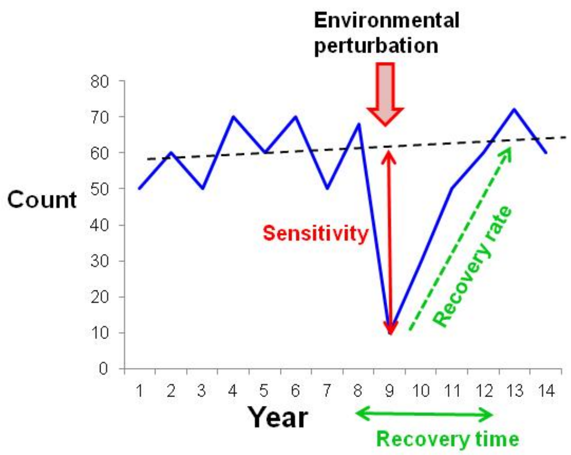

Figure 3, Conceptual framework for investigating species non-linear responses to extreme events. Sensitivity is measured as the relative population change following perturbation. The recovery rate is the post-perturbation population trajectory. Both these measures allow calculation of a recovery time – the time to return to expected population levels had the environmental pertubation not occurred. This is a measure of population 'resilience'- the ability to withstand and recover from perturbation.

The multi-species analyses involved, for each taxonomic group and event combination (e.g. butterflies and drought), fitting one linear mixed-effects model (LMM) exploring the predictors of population sensitivity and one LMM exploring the predictors of population recovery. In addition to the control variables described above, each of these models included the following fixed effects in the full model describing the characteristics of semi-natural habitat in a 3km buffer around each site: area (ha), mean 'shape index' (a measure of edginess), mean nearest neighbour distance between habitat patches and patch density (number of patches per m^2). Models analysing bird population responses to cold also included agri-environment scheme area (ha). To control for species-specific effects of these habitat variables, each mixed model included a species-specific random slope for each habitat variable (i.e. allowing the fitted relationships between habitat variables and response variables to vary between species). They also included site and species as random intercepts to control for repeated measures from the same site and the same species. All habitat variables were standardised to have a mean of zero and standard deviation of one (i.e. by subtracting the mean and dividing by standard deviation). To find the minimum adequate model the least significant habitat variable was sequentially dropped until no more could be dropped without losing a significant amount of explanatory power, determined by using a χ^2 test to compare the model residual variances (Crawley, 2007). This multi-species analysis only used data from species which had been identified as sensitive to each event, (i.e defined as showing a significant decline across sites as in Chapter 1, but considering both impacts in the drought year of 1995 as well as the subsequent year, 1996).

The single-species analyses involved fitting separate linear models for each species that showed a decline in response to the drought and cold events in Chapter 1. For each species, we fitted a linear model exploring how semi-natural habitat area and (birds and cold only) agri-environment scheme area (both ha) predicted a population's sensitivity and recovery to cold and drought. These models also included the same control variables for models exploring population sensitivity and recovery as detailed above.

All multi- and single species analyses were carried out in R version 2.15.2 (R Core Development Team 2012) and the mixed-effects models in the multi-species analyses were fitted using the package lme4 version 0.999999-0 (Bates et al. 2012).

Results

Ten butterfly species were found to be significantly sensitive to the 1995 drought event, showing a significant population crash in either 1995 or 1996. In a multispecies model including all these species an investigating how responses were affected by landscape structure, we found that larger areas of semi-natural habitat around monitoring sites were associated with less sensitive populations (Table 15). In the single species models, eight out of the ten species had negative slope coefficients indicating decreased sensitivity where sites were surrounded by more semi-natural habitat (Table 16, figure 4a). Recovery rates were also affected by landscape attributes; in this case, not the total area of semi-natural habitat but by its configuration. Recovery rates were higher where semi-natural habitat had a lower shape index (i.e. was less 'edgy'; Table 15, figure 4b). For birds, only two species (the wren and robin) showed significant sensitivity to the 1995 drought therefore we did not fit a multispecies model but only single species analyses (Table 17). The only significant result was that for wren where, non-intuitively, populations tended to show increased sensitivity in areas where there was a greater total area of semi-natural habitat.

With regards to the effects of winter cold, the extent or configuration of semi-natural habitat had no effect on population sensitivity or recovery rates across butterfly species (Table 15). Some individual species results were significant. For example, the speckled wood and red admiral were less sensitive to winter cold where semi-natural habitat extent was greater (Table 18). Due to the lack of sufficient data after such a recent event, it was not possible to investigate landscape effects on recovery to winter cold.

For birds, there were also no significant effects of winter cold on sensitivity across species (Table 15). However, the statistical model which retained a term for AES area was significantly better, indicating that this variable may be important (with a negative co-efficient indicating larger AES areas could reduce population sensitivity to winter cold). Considering the single species results, it is clear that this relationship is driven by the woodpigeon, whereby larger areas of AES significantly reduced sensitivity to the 2009-10 winter cold event (Table 19).

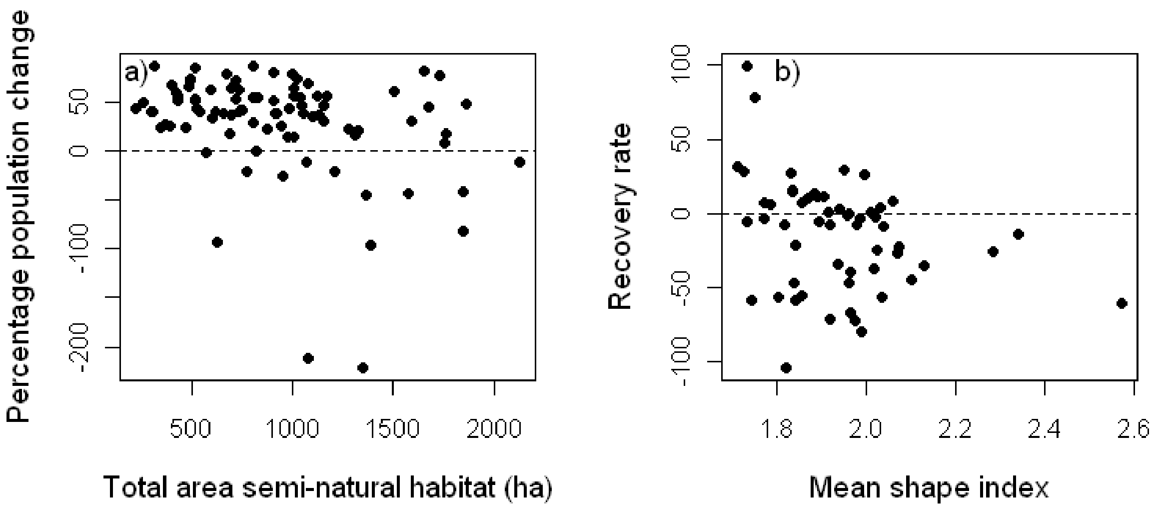

Figure 4, Examples of relationships between butterfly population resilience and landscape characteristics. Panel a shows the relationship between sensitivity to 1995 drought and area of semi-natural habitat for the speckled wood butterfly (coefficient = -0.017 ± 0.01 (s.e), t = -1.8, n = 88, p = 0.07). Panel b shows a relationship between recovery time and mean shape index of semi-natural habitat for the gatekeeper butterfly (coefficient = -90.6 ± 28.5, t = -3.2, n = 88, p= 0.0025). These species were chosen as they demonstrate key relationships that were significant in the multispecies analysis.

Table 15, Results from multispecies analysis assessing the effects of semi-natural habitat on bird and butterfly responses to drought and winter cold. Presented are beta co-efficients are from models using landscape variables scaled to mean=0 and s.d. = 1. Negative beta coefficients indicate that an increase in the landscape variable is associated with reduced sensitivity or lower recovery rates.

		Sensitivity					Recovery				
Event	Taxonomic group	Explanatory variable	beta	s.e.	t	p	Explanatory variable	beta	s.e.	t	p
1995 drought	Butterflies	**SNH area**	**-9.34**	**3.65**	**-2.56**	**0.02**	**SNH shape**	**-3.80**	**1.66**	**-2.28**	**0.03**
2010 cold	Butterflies	None significant									
	Birds	AES area	-0.39	0.81	-0.49	0.35					

Table 16, Results from single species analyses assessing the effects of semi-natural habitat on butterfly responses to the 1995 drought event. Negative beta coefficients indicate that an increase in the landscape variable is associated with reduced sensitivity or lower recovery rates. The symbol $ indicates species where sensitivity and recovery data were calculated from the drought year itself rather than a one year lag.

		Sensitivity				**Recovery**				
Common name	Latin name	beta	s.e.	t	p	beta	s.e.	t	p	
Ringlet	*Aphantopus hyperantus*	-0.080	0.041	-1.93	0.06	-0.0076	0.0142	-0.54	0.59	
Green hairstreak	*Callophrys rubi*	0.010	0.010	1.02	0.33	-0.0002	0.0030	-0.08	0.94	
White admiral	*Limenitis camilla*	-0.004	0.007	-0.66	0.52	-0.0015	0.0036	-0.42	0.69	$
Gatekeeper	*Pyronia tithonus*	-0.015	0.023	-0.64	0.53	-0.0137	0.0111	-1.23	0.22	$
Marbled white	*Melanargia galathea*	-0.024	0.046	-0.52	0.61	0.0229	0.0240	0.96	0.35	$
Large skipper	*Ochlodes venata*	-0.015	0.009	-1.59	0.12	-0.0047	0.0025	-1.86	0.07	
Speckled wood	*Pararge aegeria*	-0.017	0.010	-1.82	0.07	-0.0089	0.0056	-1.59	0.12	
Large white	*Pieris brassicae*	-0.009	0.007	-1.25	0.21	-0.0042	0.0024	-1.75	0.08	
Green-veined white	*Pieris napi*	0.003	0.011	0.29	0.77	-0.0172	0.0055	-3.13	0.00	
Small white	*Pieris rapae*	-0.006	0.017	-0.36	0.72	0.0060	0.0111	0.54	0.59	

Table 17, Results from single species analyses assessing the effects of semi-natural habitat on bird responses to the 1995 drought event. Negative beta coefficients indicate that an increase in the landscape variable is associated with reduced sensitivity or lower recovery rates.

		Sensitivity				Recovery			
Common name	Species	beta	s.e.	t	p	beta	s.e.	t	p
Wren	*Troglodytes troglodytes*	0.0083	0.0038	2.20	0.03	-0.0022	0.0024	-0.93	0.37
Robin	*Erithacus rubecula*	0.0039	0.0036	1.10	0.28	0.0013	0.0025	0.53	0.61

Table 18, Results from single species analyses assessing the effects of semi-natural habitat on butterfly sensitivity to the 2009-10 winter cold event. Negative beta coefficients indicate that an increase in the landscape variable is associated with reduced sensitivity.

		Sensitivity			
Common name	Latin name	beta	s.e.	t	p
Meadow brown	*Maniola jurtina*	0.0127	0.0334	0.38	0.70
Peacock	*Inachis io*	0.0017	0.0102	0.17	0.87
Speckled wood	*Pararge aegeria*	-0.0213	0.0075	-2.84	0.01
Large white	*Pieris brassicae*	-0.0063	0.0046	-1.36	0.18
Comma	*Polygonum c-album*	-0.0028	0.0026	-1.07	0.29
Red admiral	*Vanessa atalanta*	-0.0031	0.0015	-2.11	0.04
Painted lady	*Vanessa cardui*	-0.0026	0.0030	-0.86	0.40

Table 19, Results from single species analyses assessing the effects of semi-natural habitat on bird sensitivity to the 2009-10 winter cold event. Negative beta coefficients indicate that an increase in the landscape variable is associated with reduced sensitivity.

		SNH AREA				AES AREA			
Common name	Species	beta	s.e.	t	p	beta	s.e.	t	p
Robin	*Erithacus rubecula*	0.0005	0.0005	1.14	0.25	0.0058	0.0070	0.82	0.41
Song Thrush	*Turdus philomelos*	0.0007	0.0005	1.24	0.22	0.0139	0.0117	1.19	0.24
Woodpigeon	*Columba palumbus*	0.0024	0.0021	1.13	0.26	-0.0960	0.0256	-3.75	0.00
Wren	*Troglodytes troglodytes*	0.0005	0.0004	1.14	0.26	0.0052	0.0058	0.91	0.37

Discussion

The aim of this analysis was to assess whether different aspects of landscape structure influence species' responses to extreme events. We found that butterfly sensitivity and recovery from the 1995 drought event was affected by the total area and configuration (shape index) of semi-natural habitat. This result is in line with our original hypotheses and also supports results from a previous study considering effects of woodland area and configuration on the Ringlet butterfly (Oliver, Brereton & Roy, 2012). For the Ringlet butterfly, we suggested that larger woodlands are more likely to contain microclimates and soil conditions that can provide refugia during a drought event. In contrast, smaller woodlands may be are more susceptible to drying out at woodland edges (Morecroft, Taylor & Oliver, 1998; Herbst *et al.* 2007; Rowe, 2007; Riutta, 2012). Results from the current study suggest that a more generic measure of total area of a semi-natural habitat gives a similar result across many species, and we can speculate that the mechanisms are similar- large habitat areas provide more varied microclimatic conditions and also a more varied resource base.

We found that analysis of multiple species in the same statistical model appears to confer much greater statistical power to detect relationships. For example, from the single species models considering effects of habitat area, most (8 out of the 10 butterflies) showed relationships with negative coefficients indicating lower sensitivity in areas with more semi-natural habitat, although none of these relationships were individually significant (two were marginal; Table 16). This is probably due to lower sample sizes in these tests, resulting in less statistical power to detect an effect of habitat in addition to other control variables in the model (e.g. the local aridity around the site) and other factors not assessed (e.g. demographic stochasticity). The multispecies model allows greater statistical power, and using this model there was an overall significant effect of semi-natural habitat area on sensitivity of butterfly populations across the 10 species. These results suggest that retaining sufficient semi-natural habitat in landscapes may be vital in allowing species to persist in the face of extreme climate events such as the 1995 drought.

Recovery of butterfly populations following the drought was not significantly affected by the total area of semi-natural habitat, but was related to the configuration of semi-natural habitat. Specifically, where semi-natural habitat had a higher shape index (i.e. was more 'edgy') recovery rates were slower.

Both the above results suggest that landscapes where semi-natural habitat is highly fragmented are likely to harbour populations that are less resilient (in terms of increased sensitivity and slower recovery rates) to extreme climate events such as the 1995 drought. If patterns in butterflies reflect those of other invertebrates, then this highlights the importance of maintaining sufficient amounts of unfragmented semi-natural habitat in landscapes to promote climate change adaptation (Hopkins *et al.*, 2007; Mitchell *et al.*, 2007; Smithers *et al.*, 2008; Lawton *et al.*, 2010). Butterflies are generally considered as good indicators of population trends in wider insect biodiversity (Thomas, 2005). However, it is not clear to what extent this extends to more complex interaction relationships between population trends and landscape attributes. Butterflies are a relatively mobile group compared to many others and, therefore, our results could potentially underestimate the importance of habitat connectivity for other invertebrates.

For birds, fewer species suffered significant crashes after the 1995 drought, and so there were only two species available for analysis. For sensitivity, there was a non-intuitive result whereby wren populations seemed to be more sensitive to drought on sites surrounded by more semi-natural habitat. More investigation is needed to check whether this relationship is genuine or spurious. There was little evidence for effects of semi-natural habitat area on population recovery in the two bird species.

Considering the winter cold event in 2009-10, we found no evidence for effects of semi-natural habitat on butterflies or birds. However, for birds, we also tested the relationship between total area of specific agri-environment scheme (AES) options, hypothesised to provide winter feeding resources, and population sensitivity and recovery. Before we discuss these results, it is worth emphasising that given the relative insensitivity of granivorous species to the extreme cold winter (Chapter 2), the species for which agri-environment scheme provision would be most likely to be effective in providing winter food resources were the ones that appeared relatively unaffected by cold winter weather. It is therefore likely that the benefits of AES options for these species accrue across all years (Baker *et al.* 2012). We did find one significant result, driven by woodpigeons, whereby greater total areas of AES options in surrounding landscapes was associated with higher recovery rates following population crashes. We had expected that the sensitivity of populations would more be affected, i.e. where more winter food available means higher bird survival rates and less sensitive populations. Instead, the significant association was with woodpigeon recovery rates. We might speculate that woodpigeon populations suffer significant mortality regardless of winter food availability, but in areas where there is more winter food available birds are fitter and more able to make a rapid population recovery through better fledgling success rates. An alternative explanation is that, following cold winter population declines, sites are recolonised from other refugia and sites with more AES schemes are more likely to be recolonised first. However, given that woodpigeon populations have increased in response to increases in arable yields (Eglington and Pearce-Higgins 2012), as they are a significant pest of arable crops, this result may equally be spurious and further research would be useful.

Overall, our results indicate that population crashes and recovery following drought, rather than following particularly cold winters, are more likely to be mediated by landscape attributes. Future work, could consider more species (e.g. considering other extreme events) and look at specific land cover types tailored to species' specific habitat associations. However, from the current body of work, there is good evidence to conclude that, at least for butterflies, the area and configuration of semi-natural habitat has a key role in mediating species responses to extreme drought events.

Chapter 4- Projected drought impacts under future climate scenarios

Lead organisation: CEH

Objective: The aim of this analysis was to assess what future climate projections might mean for butterfly species which showed significant sensitivity to drought events.

Methods

We explored how projected changes in the occurrence of drought under climate change may impact butterfly population persistence and whether semi-natural habitat might moderate these impacts. This involved calculating the projected change in the occurrence of drought events under climate change with the projected butterfly population recovery time under different semi-natural habitat scenarios to investigate how the probability of a butterfly population persisting under each of these habitat scenarios changed over time.

We used the eleven component models ('members') of the Future Flows Climate models (Prudhomme *et al.*, 2012) based on the Met Office Hadley Centre's climate ensemble projection HadRM3-PPE of UK climate to project occurrence of drought events between 2010 and 2099. For each of the eleven members, we used each summer's (April to October) predicted mean temperature and total rainfall to calculate its aridity index (Marsh 2004, see equation in Chapter 1 and Fig 5a below). We then used this aridity index time series to calculate how the predicted number of years between drought events in a thirty year period changed between 2010-2039 and 2070-2099 (Fig. 5b). Drought events were defined years with aridity indices greater than or equal to 2.43, the observed aridity index in 1995.

We used the model coefficients from the multispecies model in Chapter 3 to calculate expected butterfly recovery time under different semi-natural habitat scenarios. Recovery time was calculated as the change in population in response to the drought (expected minus observed population) divided by the post-drought population recovery rate (change in population per year). These measures of expected average population change and recovery were calculated using the models we fitted in Chapter 3:

population change = 2.79
+ 0.39*expected population
+ 0.42*site aridity index
- 6.94*semi-natural habitat area

population recovery rate = 7.1
+ 0.03*population change
- 0.03*observed population
- 3.8*semi-natural habitat shape

In these models we used the mean observed expected population, site aridity index and observed population and a 'high' (mean + s.d.) and 'low' (mean – s.d.) value for semi-natural habitat area and shape. These produced predicted population recovery times under four semi-natural habitat scenarios, e.g. high area and high shape index.

We projected how the probability of the average butterfly population persisting under climate change varied over time in each of these habitat scenarios. For a given 30-year window between 2010-2039 and 2070-2099, this probability of persistence was calculated as the proportion of Future Flows Climate model members that projected drought years occurring less frequently than the predicted population recovery time for the particular habitat scenario (see Fig. 5b). We then plotted this probability of persistence over time in each of the four habitat scenarios (Fig. 5c). Note, that this method is conservative as it assumes that events are regularly spaced apart. If extreme events show clustering over time then recovery rates would potentially need to be even higher to allow population persistence.

Results

For each of the Future Flows model members we calculated April-September aridity indices for years 1950-2100. An example is shown in Figure 5a. Figures for all model members for England, Wales and Scotland can be found in Appendices 1-3. Using these data, we considered how frequently an aridity as a severe as the summer of 1995 was exceeded. We used a 30-year moving window to assess the return period for these extreme droughts. Initially, for the first 30 year window from 2010-39, we found that the return period was between four and 30 years (the maximum possible; Figure 5b). Hence, butterfly populations with a recovery time of less than four years would be predicted to be able to persist in this period under all climate scenarios, whilst butterflies with a recovery time of more than four years would not be expected to persist under some of the more arid climate scenarios. As shown in Chapter 3, recovery times depended on area and configuration of semi-natural habitat. Using empirical relationships determined from our statistical models, we calculated that recovery rates of the 'average' butterfly species (i.e. relationships from models fitted across 10 drought sensitive species) varied from between 1.6 years under landscapes of high habitat availability and low shape index, to 6 years under landscapes of low habitat availability and high shape index. 'High' and 'low' here refer to habitat availability relative to the mean in 3km landscape buffers across our population monitoring sites (specifically, one standard deviation from the mean).

Combining these estimates of recovery time under different land cover scenarios with the projected return times for '1995-like' droughts under different climate scenarios, we found that likelihood of butterfly population persistence varied both over time and depending on local land cover. In the initial 30 year period probabilities of butterfly persistence varied from 0.8 to 1. However, by the period 2041-2070 probabilities of butterfly persistence had declined to 0.1 under all but one of the land cover scenarios- the scenario of high habitat availability and low shape index which still had a probability of persistence of 0.8. Exact changes in probability are shown in Figure 5c.

Discussion

The aim of this analysis was to assess what future climate projections might mean for ten butterfly species which showed significant sensitivity to drought events. Our results demonstrate that increases in the frequency of extreme drought events (as projected by all Future Flows model members, Appendix 1), are likely to severely threaten the survival of the ten drought sensitive butterfly species that we investigated. However, interactions between resilience to extreme events and landscape attributes provide opportunities to maximise persistence by ensuring that sufficient amounts- and connectivity of- semi-natural habitat remain in landscapes. For example, under a land use scenario where landscapes have a large proportion of semi-natural habitat and where that habitat is has low shape index (i.e. is less 'edgy) then projected population persistence remained high at 0.8 by mid-century, compared with 0.1 under the other scenarios. This demonstrates the crucial importance of both land cover area and configuration in climate change adaptation.

The proportion of semi-natural habitat availability in the 3km landscape buffer under the 'high' scenario (47%; Figure 5d) might well be unrealistic in arable landscapes. They are not, however, unrealistic in less intensively managed parts of the country: these extents of semi-natural habitat do occur around some population monitoring sites. The 'high' and 'low' scenarios used here were selected as one standard deviation around the means of total semi-natural habitat area around the UKBMS sites. Our results suggest that butterflies will persist on only a small proportion of UK sites under future climate scenarios. Conservationists will want to ensure that this number of sites and their spatial arrangement is sufficient to ensure viable metapopulations can persist.

With concerns about food security, maintaining productive landscapes has risen up the political agenda, along with the recognition that increases in productivity must be ecologically sustainable. Our results suggest that land sharing approaches where small, fragmented amounts of semi-natural habitat are mixed with intensive agriculture and urban land cover are unlikely to provide long term sustainable solutions under climate change (Lawton *et al.*, 2010). Instead, it is crucial to maintain landscapes with large extents of well connected semi-natural habitat. To achieve this over large areas of the country would truly require a step change in conservation (Lawton *et al.*, 2010). It is interesting to note, however, the relatively large role played by habitat configuration for these butterflies compared with total habitat area (Fig 5c). Hence, much additional benefit may be achieved by simply making sure new habitat is in the right place (i.e. making patches large enough and reducing edge effects).

Although not studied directly in this report, topographic variability is also likely to play an important role in climate change adaptation (Hopkins *et al.*, 2007; Oliver *et al.*, 2010). Hence, areas of high topographic variability and with large extents of well connected semi-natural habitat might be identified as landscapes with high levels of population persistence. There is growing evidence that some areas can act as 'refugia' with a higher chance of species persistence under climate change; this topic is assessed in another Natural England report (Suggitt et al., 2014). These landscapes should be protected from semi-natural habitat loss. Other areas may need investment to increase extent and connectedness of semi-natural habitat to bring it in line with levels required for successful climate change adaptation. Finally, some landscapes may have already suffered such loss of semi-natural habitat that restoration would be unfeasibly expensive. These areas might be allocated to intensive food production. However, whilst this might be sensible from a large-scale ecological perspective, such questions are as much social as ecological issues and there may be valid reasons for conserving biodiversity locally, i.e. to promote cultural ecosystem services.

This report contributes to the ecological debate the finding that very large areas of semi-natural habitat might be needed to provide species populations that are resilient to climate change. This suggests that, in order to prevent widespread population extinction of drought sensitive species, large areas of high quality habitat will be a necessary part of a sustainable land use solution for the UK under climate change.

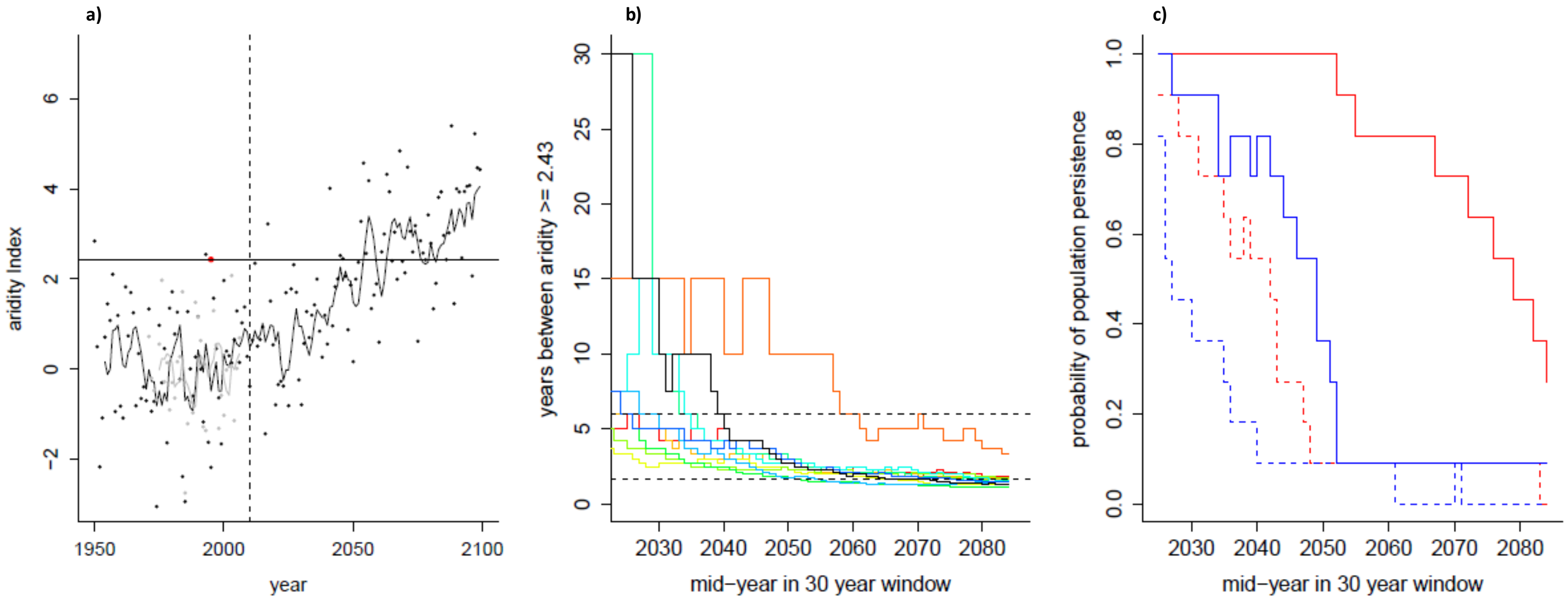

Figure 5: The impact of climate change of butterfly population persistence.

(a) Summer (Apr-Oct) aridity index in England observed (grey) and predicted by one member of the Future Flows Climate based on the Hadley climate ensemble projection HadRM3-PPE (black) with 5 year running means. The horizontal line indicated the 1995 aridity score (2.43, red dot) and dashed vertical line indicates the start of prediction period (2010).

(b) Frequency (years per event) of a 1995-level drought (aridity index >=2.43) predicted by the 11 Hadley model members in a 30-year moving window. The model member shown in (a) is in black. Horizontal dotted lines show the longest (5.97 years, low area, high shape) and shortest (1.64, high, low) population recovery time predicted by our butterfly models. Probability of persistence in under each scenario in (c) is the proportion of models at a given time that predict a frequency greater than the scenario's recovery time.

(c) Predicted probability of butterfly population persistence under four semi-natural habitat scenarios combining high and low values (± 1 s.d.) for area and 'shape' within a 3km buffer around each UK Butterfly Monitoring Scheme site. 'Shape' is a ratio of the observed length of habitat perimeter over the minimum possible perimeter for the given habitat area. See (d) for details each scenario's: area and shape values, graphical presentation of the habitat configuration each scenario represents, their predicted recovery time from a 1995-level drought and the colour and style of line used to represent each in (c).

(d) Key for (c). % cover expressed as a percentage of the total area in a 3km buffer (2827ha).

d)

key		area (ha) category	% cover	shape category	index	recovery time (years)
solid blue line		low	17	low	1.80	2.86
dashed blue line		low	17	high	2.05	5.97
solid red line		high	47	low	1.80	1.64
dashed red line		high	47	high	2.05	3.58

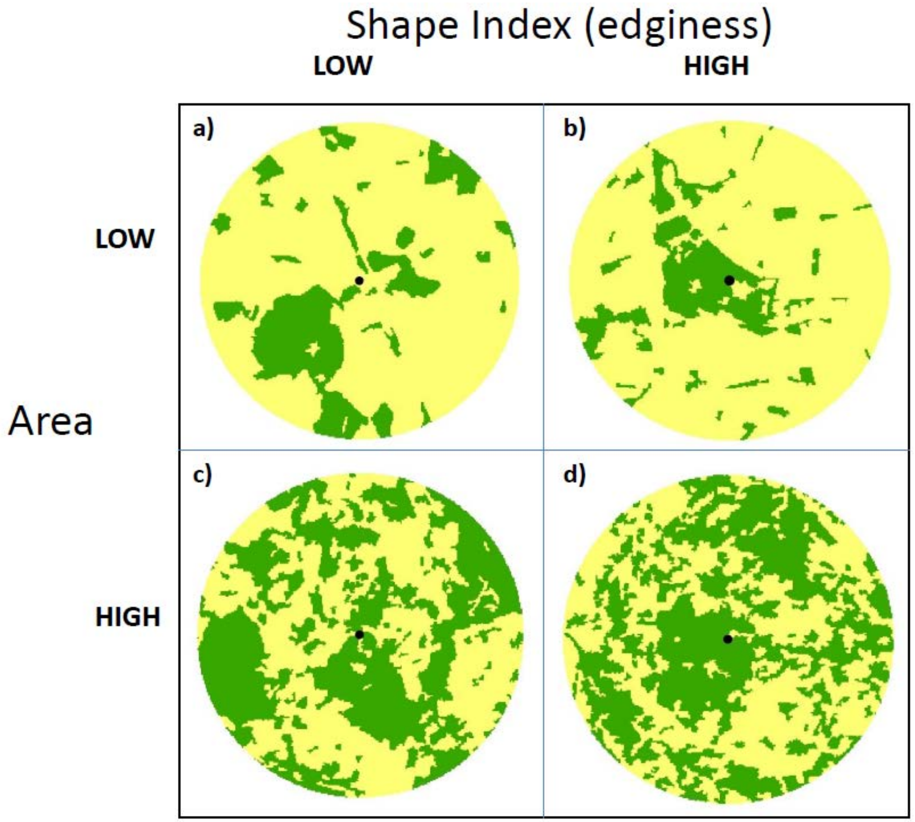

Figure 6, LCM 2000 remotely sensed land cover around centroids of four UKBMS monitoring sites (black circles). Sites were selected to demonstrate 'high' and 'low' (mean ± s.d.) values for semi-natural habitat area (shaded green) and mean shape index (edginess). Sites are as follows a: Woodwalton Fen, Cambridgeshire, OS grid reference: TL210810 , % semi-natural habitat (SNH) = 17.4% , mean shape index (MSI) = 1.80; b: Holme Fen, Cambridgeshire, TL210890, SNH = 15.2 %, MSI = 2.04; c: West Moors, Dorset, SU090045, SNH = 47.8 %, MSI = 1.88 ; d: Haugh Wood North, Herefordshire, SO595370, SNH = 45.4 %, MSI = 2.1

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