

PHILOSOPHICAL TRANSACTIONS B

Climate change, climatic variation, and extreme biological responses

Journal:	<i>Philosophical Transactions B</i>
Manuscript ID	RSTB-2016-0144.R1
Article Type:	Research
Date Submitted by the Author:	n/a
Complete List of Authors:	Palmer, Georgina; University of York, Department of Biology Platts, Philip; University of York, Department of Biology Brereton, Tom; Butterfly Conservation, Chapman, Jason; Rothamsted Research, Plant & Invertebrate Ecology; University of Exeter Centre for Ecology and Conservation Dytham, Calvin; University of York, Department of Biology Fox, Richard; Butterfly Conservation, Pearce-Higgins, James; British Trust for Ornithology; University of Cambridge, Conservation Science Group, Department of Zoology Roy, D; Centre for Ecology & Hydrology, BRC Hill, Jane; University of York, Biology Department Thomas, Chris; University of York, Department of Biology
Issue Code: Click here to find the code for your issue.:	CLIMATIC
Subject:	Ecology < BIOLOGY
Keywords:	Aves, Climatic risk, Population dynamics, Weather, Moth, Butterfly

SCHOLARONE™
Manuscripts

Climate change, climatic variation, and extreme biological responses

Georgina Palmer^{1*}, Philip J. Platts¹, Tom Brereton², Jason W. Chapman^{3,4},
Calvin Dytham¹, Richard Fox², James W. Pearce-Higgins^{5,6}, David B.
Roy⁷, Jane K. Hill¹ & Chris D. Thomas^{1*}

¹Department of Biology, University of York, Wentworth Way, York, YO10 5DD, UK.

²Butterfly Conservation, Manor Yard, East Lulworth, Wareham, Dorset BH20 5QP, UK.

³AgroEcology Department, Rothamsted Research, Harpenden, Hertfordshire AL5 2JQ, UK.

⁴Centre for Ecology and Conservation, and Environment and Sustainability Institute, University of Exeter, Penryn, Cornwall TR10 9EZ, UK.

⁵British Trust for Ornithology, The Nunnery, Thetford, IP24 2PU, UK.

⁶Conservation Science Group, Department of Zoology, University of Cambridge, Downing Street, Cambridge CB2 3EJ, UK

⁷Centre for Ecology & Hydrology, Wallingford, Oxfordshire OX10 8BB, UK

Keywords: Aves, butterfly, climatic risk, Lepidoptera, moth, weather

1 Extreme climatic events could be major drivers of biodiversity change, but it is unclear whether
2 extreme biological changes are (i) individualistic (species- or group-specific), (ii) commonly
3 associated with unusual climatic events and/or (iii) important determinants of long-term population
4 trends. Using population time series for 238 widespread species (207 Lepidoptera and 31 birds) in
5 England since 1968, we found that population ‘crashes’ (outliers in terms of species’ year-to-year
6 population changes) were 46% more frequent than population ‘explosions’. (i) In every year, at least
7 three species experienced extreme changes in population size, but these were expressed in different
8 directions in 41 of the 44 years considered, suggesting individualistic responses to different, short-
9 term events, most likely associated with climatic variability. We found some degree of synchrony
10 (crash or explosion in a given year) within Lepidoptera, but not among bird species, and we found no
11 agreement between the two groups. (ii) Six out of 44 years showed a significant excess of species
12 experiencing crashes (four years for Lepidoptera, one for birds) or explosions (one year for
13 Lepidoptera). These ‘consensus years’ were associated with climatically-extreme years, consistent
14 with a link between extreme population responses and climatic variability, although not all
15 climatically-extreme years generated excess numbers of extreme population responses. (iii) Links
16 between extreme population changes and long-term population trends were absent in Lepidoptera and
17 modest (but significant) in birds. We conclude that extreme biological responses are
18 individually linked to climate, but that long-term trends of widespread species have not, to date,
19 been dominated by these events.

*Authors for correspondence (chris.thomas@york.ac.uk and georgina.palmer@york.ac.uk).

1. Introduction

Climate is an important determinant of species range, population change, abundance, phenology and biotic interactions (1-4). The precise sequence of climatic events and the time of year when these events occur may affect whether a species' biological response is rapid lifecycle development and increased reproduction leading to population growth, or increased mortality leading potentially to extinction. In the context of this paper, climate change represents a change to the frequency, severity and sequences of different weather events, which may lead to increases in the frequency of some forms of extreme events such as those associated with heat, drought or flooding, but decreases in others, such as those associated with cold (5). It has been suggested that such extreme events may generate substantial population responses and community transitions, and that these rare events could be as important in determining ecological responses to climate change as are long-term changes to the average climatic conditions that a population experiences (6). However, rigorous assessment of the frequencies and impacts of extreme population responses are constrained by the limited availability and spatial/taxonomic coverage of long-term population data (7), and also because a given sequence of climatic events will not necessarily generate a consensus response in organisms (6) due to inter-specific differences in species' ecological traits and sensitivity to climate. Previous studies have highlighted the individualistic nature of species' responses to different aspects of the climate at different times of year (8-11) although, in general, such studies have focussed on describing responses to climatic means, rather than extremes. Here, we assess the extent to which extreme population responses are individualistic, and evaluate whether they are important determinants of long-term population trends.

Extreme climatic events (ECEs), by their very nature, are outside of the norm experienced by organisms and to which species may be (locally) adapted. As such, we hypothesise that extreme events are more likely to drive negative rather than positive population changes. Therefore, we also assess whether extreme species' responses are more frequently negative, and whether these events are commonly associated with unusual climatic conditions. Previous approaches to understanding the importance of ECEs for biological communities have been either to identify such an event (e.g. a drought) and then see if some or many species responded to it or, alternatively, to seek an explanation for one-off extreme population changes that have been observed (12). Such studies have provided strong evidence of population crashes in response to unusual climatic conditions, especially in relation to extreme droughts, winter freezing, unseasonal cold and excessive heat (5, 13-19, cf. coral reef bleaching and anoxia in aquatic systems [20, 21]). However, there is potential that the results could be unrepresentative if the choice of year, climatic event or species under consideration have

1
2
3
4 53 been influenced by the events themselves. Hence, the choice of study species may not be appropriate
5 54 to elucidate the frequencies of rare events or their long-term importance during a period of climatic
6 55 change. As Bailey & van de Pol (6) and van de Pol et al. (22) discuss, a major drawback of many
7 56 studies linking ecological and climatic extremes has been a focus on the impacts of single climatic
8 57 events, over short time periods, leaving questions remaining about the long-term implications of
9 58 extreme events (but see 23). Here, we remove these potential biases by taking a multi-species
10 59 approach, analysing data over a relatively long, continuous time period to find out whether extreme
11 60 population changes tend to take place in years that are also climatically extreme. To do this, we
12 61 utilise long-running population dynamic data at a national scale for 238 species from two broad
13 62 taxonomic groups (31 birds and 207 Lepidoptera in England), to identify group- and species-specific
14 63 differences in population responses to ECEs. We identify years when species show unusually high
15 64 levels of population growth or decline, and assess whether those years are associated with particular
16 65 climatic conditions in the same and/or in the previous year(s).

17 66 Population growth rates of species with similar life histories (e.g. clutch sizes or survival rates) have
18 67 the potential to be highly synchronised (24, 25), while differences in life history can desynchronise
19 68 dynamics across species (24, 25). Thus, we contrast the timing of extreme responses of birds and
20 69 Lepidoptera, with the expectation that we will observe similar temporal responses within, but not
21 70 between, these two taxonomic groups. We also identify years where an unusually large proportion of
22 71 species exhibit extreme population changes, and investigate the role of climate in driving these
23 72 community-wide responses. Although the importance of ECEs to population dynamics is widely
24 73 discussed in the ecological and climate change literatures (6), the extent to which these events do or
25 74 do not predict long-term population trends has not been assessed robustly. There is no necessary link
26 75 between the two, although there is certainly the potential for ECEs to cause long-term population
27 76 changes (e.g. 26). There may be no link because extreme events, by definition, are rare, and an
28 77 extreme change in one year may have very little impact on the average rate of population growth or
29 78 decline over a longer period. Alternatively, it is possible that the cessation of some kinds of ECEs
30 79 (which previously either constrained populations, or generated periodic increases in reproduction)
31 80 may be as important to long-term population changes as an increased frequency of previously-rare or
32 81 wholly novel conditions. The influence of such events may only be seen in population time-series of
33 82 long duration. Therefore, we consider empirically whether the long-term population trends of species
34 83 (over four decades) are linked to the extreme population responses that they exhibit over the entire
35 84 period.

1
2
3
4 85 For linguistic simplicity, throughout this article we refer colloquially to population ‘crashes’ (steep
5 86 year-to-year national population declines – see *Methods*), population ‘explosions’ (rapid increases),
6
7 87 ‘bad years’ (years in which crashes take place), ‘good years’ (years in which explosions take place),
8
9 88 ‘consensus bad years’ and ‘consensus good years’ (years with a significant excess of population
10 89 crashes or explosions, respectively). We consider the hypotheses that:

- 11
12
13 90 i. most years are associated with extreme population changes in some species (because
14 91 biological responses to the environment differ among individual species and between higher
15 92 taxonomic groups);
16
17
18 93 ii. population crashes tend to be more frequent than population explosions during periods of
19 94 rapid climatic change (as new environments are experienced), and crashes are more extreme
20 95 than explosions (because the latter are constrained by the intrinsic rate of population growth
21 96 whereas, in principle, all individuals could die simultaneously);
22
23
24
25 97 iii. consensus years are associated with unusual climatic conditions in the same or previous year;
26 98 and
27
28
29 99 iv. long-term population trends are correlated with extreme population responses.
30
31
32
33
34
35
36
37
38
39
40
41
42
43
44
45
46
47
48
49
50
51
52
53
54
55
56
57
58
59
60

101 2. Material and Methods

102 We define our study area as mainland England, chosen because a large quantity of reliable, long-
103 running annual count data for birds and Lepidoptera (butterflies and macro-moths) are available at
104 this spatial extent. Although Lepidoptera data are also available from the rest of the United Kingdom,
105 we restricted our analyses to match the spatial extent of the bird data, so that the two groups could be
106 directly compared. We conducted our analyses using *R*, version 3.1.0 (27).

108 (a) *Species data*

109 We obtained species data for butterflies, moths and birds from the UK Butterfly Monitoring Scheme
110 (UKBMS; 28), the Rothamsted Insect Survey (RIS; 29), the Common Bird Census (CBC; 30) and the
111 Breeding Bird Survey (BBS; 31). These schemes are national networks of standardised count
112 surveys using either territory mapping (CBC), fixed-location line transects (UKBMS and BBS) or
113 fixed-location light traps (RIS). Butterfly count data (species' abundances for individual sites each
114 year) were collected from 1665 sites spanning the years 1976–2012. Macro-moth count data
115 (species' abundances for individual sites each year) were from 295 sites spanning the years 1968–
116 2012. National population indices of birds spanned the years 1968–2012, combining data from the
117 CBC, which ended in 2000, with data from the BBS which started in 1994 (see 10). There were no
118 bird data for the year 2001 because foot-and-mouth disease severely restricted access in that year.

120 We included butterfly and moth species for which there were at least five sites with non-zero counts
121 in every year of the time series (37 years for butterflies and 45 for macro-moths), and birds which
122 were sufficiently well monitored by both CBC and BBS surveys. Migrant birds and true-migrant
123 Lepidoptera were excluded, because extreme population changes of such species may not be a result
124 of climate experienced solely in our study area, although the English populations of the most mobile
125 species will still experience some exchanges with regions outside the study region. Thus, we included
126 178 macro-moth species, 29 butterfly species and 31 bird species in our analyses (listed in
127 Supplementary Table 1). Butterflies and moths were analysed together as they belong to one
128 taxonomic order (Lepidoptera), while we hypothesise that birds will differ in their response to
129 climate, and so they were analysed separately.

131 For each macro-moth and butterfly species, we obtained national indices of abundance in two steps:
132 first, for each species, we related the species' annual count data per site to year (as a fixed factor) in a
133 generalised mixed effects model with site as a random intercept, and a Poisson error distribution. We

1
2
3
4 134 then took the fixed (year) coefficients from each species' model, which quantify the relative
5 135 abundance of species each year.
6
7 136

8
9 137 We calculated year-to-year changes in the index by subtracting the \log_{10} index value in year_t from the
10 138 \log_{10} index value in year_{t+1} (Figure 1C-D). We also calculated each species' long-term change in
11 139 abundance over the four decades of our study period as the slope of a linear model relating national
12 140 indices of abundance against year.
13
14 141

142 *(b) Climate data*

143 We downloaded gridded climate data for the period 1965–2011 from the UK Met Office website
144 (www.metoffice.gov.uk/climatechange/science/monitoring/ukcp09); supplemented with data for
145 2012 obtained directly from the Met Office. These data provide daily estimates of minimum and
146 147 maximum temperature, and monthly rainfall estimates, at a spatial resolution of 5 km × 5 km on the
148 Ordnance Survey National Grid reference system. From these data, we derived a set of 13 annual
149 climate variables that may correlate either directly (physiological limits) or indirectly (i.e. relevance
150 for habitat, food or host plants) with the population dynamics of our study species (Supplementary
151 Tables 1 and 2). Further analyses were conducted on spatial mean values, calculated across England,
152 for each year in the population time series.

153 We reduced levels of collinearity in the climate data using the following procedure, whereby highly
154 correlated variables (Pearson's $|r| > 0.7$) were sequentially removed. For each pair of correlated
155 variables in turn, starting with the most strongly correlated pair, the variable that was collinear with
156 the greatest number of other climate variables was removed; where a pair of variables was collinear
157 with the same number of other variables, the one with the largest mean absolute correlation was
158 removed. The seven retained climate variables included measures of rainfall seasonality, drought,
159 temperature range, growing degree days as well as coolness and hotness (Table 1).
160

161 We summarised temporal variation in these variables by plotting the first three axes of a principle
162 components analysis, using the 'PCA' function of the 'FactoMineR' package in R (32). For
163 comparison with the species data, we computed the 3-dimensional Euclidian distance of each year
164 from the origin of the PCA, which is a measure of how unusual a year was in terms of the unique
165 combinations of climate in that year.
166

1
2
3
4 167 (c) *Statistical analyses*

5 168

6
7 169 *Defining and describing extreme events*

8
9 170 There are many different approaches to defining an extreme event, including identifying observations
10 171 at the tails of a given frequency distribution (typically, and arbitrarily, selecting 5 or 10% of the
11 172 data), or those above or below an absolute critical threshold (see e.g. 22, 23, 33, 34, 35). In the
12 173 context of our study species, the percentile approach would mean all species would be assigned at
13 174 least one good year and one bad year, irrespective of the spread of year-to-year changes in index
14 175 across their study periods. We therefore identified extreme changes as those beyond species-specific
15 176 thresholds, defined by the median value over the study period \pm two median absolute deviations
16 177 (MAD) (36), according to Equation 1:

17 178

18 179

$$\{|x_t - \text{median}(x)| / \text{MAD}\} > 2 \quad \text{Equation 1}$$

19 180

20 181 where x_t is a species' year-to-year change in index in year t , and x is the full time series of the
21 182 species' year-to-year changes in index. Thus, we defined explosions and crashes relative to the
22 183 median in a symmetrical fashion (see e.g. Figure 1), because we found no consistent asymmetries in
23 184 species' changes in index (robust measure of skewness (37): mean across all species = -0.02 [range, -
24 185 0.47 to 0.44]). We used this same approach to define extreme climate years, according to the seven
25 186 climate variables in Table 1.

26 187

27 188 We investigated the degree of association between the occurrences of explosions / crashes across all
28 189 years by correlating the proportion of Lepidoptera (or birds) experiencing population crashes each
29 190 year to the proportion of Lepidoptera (or birds) experiencing population explosions, using
30 191 Spearman's rank correlations. We then identified 'consensus' years, during which more species
31 192 experienced extremes in the same direction (crash or explosion) than would have been expected by
32 193 chance, based on a one-tailed exact binomial test using the observed frequencies of crashes and
33 194 explosions within each group (Lepidoptera or birds, with Bonferroni correction for multiple-year
34 195 testing).

35 196

36 197 To investigate whether population trends were related to extreme population responses, each species'
37 198 long-term change in abundance was plotted against the maximum absolute population crash or
38 199 explosion (that qualified as an extreme) for that species, and also against the mean of all extreme
39 200 crash or explosion events experienced by that species during the study period. These two metrics

1
2
3
4 201 should reveal whether extreme population changes have a long-term effect on population size (e.g., if
5 202 numbers were high and crashed in year 5, and stayed low thereafter, there would be a negative
6 203 relationship between year and population size; but if there was density-dependent recovery, there
7 204 would be no relationship, or even a positive relationship). Species that did not show any extreme
8 205 population change values ($n = 2$ birds, 27 moths and 3 butterflies) were excluded from this analysis.
9 206

10
11
12
13 207 *Linking population extremes to climate*

14
15 208 Each period of population change refers to the change in index values (counts) between years, for
16 209 example between 1968 and 1969. Each climatic year also corresponds to a 12-month period (with
17 210 the exception of drought index), such that the climate referred to as ‘1969’ refers to the climatic
18 211 period from September 1 1968 to August 31 1969 (see Table 1). The data for these two years would
19 212 be compared to consider direct (lag 0) effects of climate on population change (e.g. the 1969 climate
20 213 compared to the 1968-1969 population change). Population crashes and explosions were also related
21 214 to climatic conditions in the previous year (climatic year ‘1968’, lag 1). We considered lagged
22 215 effects because impacts of ECEs can be direct (e.g., population growth in response to a warm
23 216 summer), or delayed by a year or more due to species’ long generation times or through altered
24 217 natural enemy or food abundances.
25 218

26
27
28
29
30
31
32
33 219 First, we investigated whether consensus years corresponded to extreme climate years, as defined in
34 220 Table 1. Then, in order to investigate more generally if extreme population responses were associated
35 221 with ECEs, the summed number of Lepidoptera or bird species experiencing an extreme event (crash
36 222 or explosion) each year was plotted against (i) the 3-dimensional Euclidian distance from the PCA
37 223 origin, (ii) drought index and (iii) daily minimum temperature of coldest 30 days, as we hypothesised
38 224 these would be the main drivers of population change for our focal species groups. In each case we
39 225 accounted for a direct and a lagged effect. As such, statistical inference was Bonferroni-corrected for
40 226 multiple ($n = 12$) tests.
41
42
43
44
45
46
47
48
49
50
51
52
53
54
55
56
57
58
59
60

228 **Results**

229 *(a) Extreme population changes*

230

231 At least three extreme population changes took place in every year, revealing that every year in our
232 four-decade study period was unusual from the perspective of some species (Figure 2A-B). The
233 majority of species experienced at least one extreme population change during their study periods:
234 86% of Lepidoptera (177 out of 207 species), and 93% of birds (29 of 31).

235

236 We detected a significant negative association between the proportion of Lepidoptera experiencing
237 population crashes and the proportion experiencing population explosions across years (Spearman's
238 rank correlation: $S = 22284.09$, $r_s = -0.57$, $p < 0.0001$), indicating that when multiple species did
239 exhibit extreme changes in the same year, they tended to respond in the same direction. This was not
240 significant for birds ($S = 13689.1$, $r_s = -0.11$, $p = 0.49$). Extreme population changes were,
241 nonetheless, expressed in different directions in 41 of the 44 years considered (i.e. the populations of
242 some species crashed and others exploded in the same year). Furthermore, even in the most extreme
243 years (see below), most species did not exhibit extreme population responses, demonstrating the
244 individualistic nature of the extreme population changes exhibited by species.

245

246 Out of a possible 10,178 species-by-year combinations, 374 (3.7%) population crashes and 257
247 (2.5%) population explosions were detected: an excess of crashes over explosions (two-tailed exact
248 binomial test, $n = 631$, $p < 0.001$). Crashes also tended to be larger in their absolute magnitudes than
249 explosions in both Lepidoptera (Welch two-sample t-test: $t = -3.82$, d.f. = 454.05, $p < 0.001$) and
250 birds ($t = -2.41$, d.f. = 116.71, $p < 0.02$). For Lepidoptera, crashes (mean = -0.52, range -1.03 to -
251 0.22) were on average around 13% greater in magnitude than explosions (mean = 0.46, range 0.21 to
252 1.30). Similarly for birds, crashes (mean = -0.13, range -0.48 to -0.03) were on average 18% greater
253 in magnitude than explosions (mean = 0.11, range 0.04 to 0.23).

254

255 The numbers of extreme population changes in a given year for moths were strongly positively
256 correlated with the numbers of extreme population changes in the same year for butterflies
257 (Spearman's correlation: $S = 3098.72$, $r_s = 0.60$, $p < 0.0002$; Figure 2C), suggesting that common
258 external drivers were responsible for population crashes and explosions in Lepidoptera. However,
259 comparing Lepidoptera and birds revealed a negative correlation ($S = 16433.1$, $r_s = -0.33$, $p = 0.03$;
260 Figure 2D), suggesting that birds and Lepidoptera are responding to different external drivers, or to
261 similar events but with different lagged responses.

1
2
3
4 262

5 263 The existence of common drivers that acted across multiple species was supported by the detection of
6 264 five ‘consensus’ years for Lepidoptera (1975/76, 1976/77, 1992/93, 2006/07, and 2011/12) during
7 265 which statistically-unusual numbers of species showed population explosions or crashes (at $p < 0.05$,
8 266 after Bonferroni correction). Only one of these (1975/76) was a consensus good year, while the other
9 267 consensus years were bad years, during which nearly all extreme population changes (54 out of 59 in
10 268 1976/77, 25 out of 26 in 1992/93, 30 out of 32 in 2006/07 and 42 out of 42 in 2011/12) were negative
11 269 (Figure 2A). However, even during their largest consensus years, only 26% of Lepidoptera species
12 270 and 32% of bird species experienced extreme population responses.

13
14
15
16
17 271

18 272 In contrast, for birds, only one consensus year was detected (1981/82) as statistically significant
19 273 ($p < 0.05$, after Bonferroni correction; 1990/91 was significant prior to correction), during which ten
20 274 of the 31 species crashed (Figure 2B). The lower numbers of bird species compared with Lepidoptera
21 275 in our analyses (31 rather than 207 species) may explain this apparent difference between taxa, and
22 276 so it should not be deduced that birds necessarily experienced fewer consensus years than
23 277 Lepidoptera.

24
25
26
27
28
29
30
31 278

32 279 *(b) Associations between biological and climatic extremes*

33
34
35 280

36 281 Five of the six consensus years for extreme population change coincided with one of the extreme
37 282 climate years, either directly ($n = 3$) or with a one-year lag, which is consistent with the hypothesis
38 283 that there is a positive association between population consensus years and extreme climatic
39 284 conditions (Fisher's Exact-Boschloo test, one-sided $p = 0.015$). The sixth consensus year for
40 285 population change (1992/93), which was the smallest of the consensus population crashes (Figure 2),
41 286 was not associated with any climatic extremes (Table 1).

42
43
44
45
46 287

47 288 In the only consensus year for birds (1981/82), 32% (10 of 31 species) of species crashed during
48 289 exceptionally cold winter weather in that year (Table 1; Figures 2 and 3). In 2006/07, the large
49 290 consensus year for Lepidoptera coincided with high growing degree days in that year, as well as an
50 291 extremely summer in the previous year (i.e. 2005/06; Table 1; Figures 2 and 3). The large number of
51 292 Lepidoptera crashing in 2011/12 followed an extreme cold in the previous winter.

52
53
54
55
56 293
57
58
59
60

1
2
3
4 294 The one consensus good year for populations was 1975/76, when 9% ($n = 16$) of moths were
5 295 positively affected (butterflies could not be considered because data collection did not start until the
6 296 following year). The climate in 1975 was relatively dry, with the summer of 1976 being extremely
7 297 hot and dry (Table 1, Figure 3C-D) with a drought index nearly double the median over the study
8 298 period (Figures 2A, 3D, Table 1). Subsequently, significant numbers of Lepidoptera (54 of 207
9 299 species, 26%) experienced population crashes between 1976 and 1977. However, while 1976/77 was
10 300 the largest consensus year for Lepidopteran crashes, a few Lepidoptera (4 of 207 species)
11 301 experienced population explosions in the same year. This suggests that there can be cumulative
12 302 effects, and that some climatic extremes may generate opposite direct and lagged effects (in this case,
13 303 increase followed by crash).

14 304
15 305 Five of the ten climatically-extreme years did not coincide, with or without lag, with any of the
16 306 consensus population change years in either Lepidoptera or birds. Given that extreme events tended
17 307 to happen in different years for Lepidoptera and birds (Figure 2D), it is possible that other taxa
18 308 responded strongly in these years. The pattern of apparently mixed responses is also exhibited by
19 309 individual species. For example, the mottled grey moth *Colostygia multistrigaria* population crashed
20 310 after the 1976 drought, but not after other dry years, and the tree sparrow *Passer montanus* declined
21 311 in association with some, but not all, cold winters (Figure 1).

22 312
23 313 We then considered extreme population changes in all years in relation to PCA scores, drought and
24 314 winter cold. There was no correlation between 3D distance from the PCA origin (a measure of how
25 315 climatically-unusual a year was) and the proportion of species experiencing an extreme event (Figure
26 316 4). The relationships between species' responses, drought and winter cold were also noisy for both
27 317 Lepidoptera and birds (Figure 4), with only two significant relationships detected after Bonferroni
28 318 correction. The first significant relationship was for drought index of the previous year and the
29 319 proportion of Lepidoptera species experiencing an extreme change ($t_{41} = 3.30$, $r = 0.48$, $p = 0.002$;
30 320 Figure 4D). The second was a significant negative correlation between the proportion of birds
31 321 experiencing an extreme population change and daily minimum temperature of the coldest 30 days
32 322 ($t_{39} = -3.48$, $r = -0.49$, $p = 0.001$; Figure 4E). However, in both cases, the correlations ceased to be
33 323 significant (after Bonferroni correction) once the largest consensus year was removed (1976/77 for
34 324 Lepidoptera, $t_{40} = 1.45$, $r = 0.22$, $p = 0.15$; 1981/82 for birds, $t_{38} = -2.81$, $r = -0.41$, $p = 0.01$). This
35 325 reinforces the view that consensus years are genuinely unusual. In the analyses above we reported the
36 326 proportion of species experiencing an extreme change (both explosion and crash), but results were

1
2
3
4 327 qualitatively the same when analysing those experiencing crashes or explosions, separately (see
5 328 Supplementary Figures 1 and 2, respectively).
6

7 329

8
9 330 *(c) Extremes and long-term population trends*

10 331

11 332 Overall, there was little relationship between the extreme population changes that a species exhibited
12 333 and species' long-term population trends (Figure 5). Extreme population events are modest predictors
13 334 of long-term trends, at best, and for the Lepidoptera in our study may not be linked at all.
14 335

15 336

16 337 For Lepidoptera, we first compared two groups of species: those for which the single most extreme
17 338 event was a crash, and those for which the single most extreme event was a population explosion. We
18 339 found no association between extreme population change and trend (one-tailed Wilcoxon rank sum
19 340 test: $W = 3439.5$, $p = 0.19$; Figure 5A). We then took the mean of all extreme events exhibited by
20 341 each species. Again, there was no difference between the long-term population trends of 'crashing'
21 342 and 'exploding' species ($W = 3583$, $p = 0.45$; Figure 5C). Regardless of the direction and magnitude
22 343 of the extreme, some species showed long-term increases, and others showed long-term declines.
23 344

24 345

25 346 When we repeated this analysis for birds, we did find an effect of extreme events. We found that bird
26 347 species experiencing population explosions (as single events, or the mean of their species-specific
27 348 extremes) tended to have more positive long-term population trends than bird species that exhibited
28 349 crashes (for single events, $W = 144.5$, $p = 0.005$ [significant after Bonferroni correction]; average of
29 350 all extremes, $W = 128.5$, $p = 0.02$ [n.s. after Bonferroni correction]; Figure 5). As in the Lepidoptera,
30 351 some crashing bird species showed long-term population increases and others decreases. The
31 352 different results for Lepidoptera and birds suggest that there may be taxonomic differences (perhaps
32 353 linked to generation times) in the association between extreme events and long-term trends.
33 354
34 355
35 356
36 357
37 358
38 359
39 360
40
41
42
43
44
45
46
47
48
49
50
51
52
53
54
55
56
57
58
59
60

3. Discussion

(a) *The frequencies and magnitudes of extreme population events*

Extreme population responses were observed in all years, and in at least one year for the majority of species: moths, butterflies and birds. Furthermore, in the majority of years, one or more species showed extreme positive population growth (explosions) while others showed rapid declines (crashes). These findings show that extreme population changes are individualistic among species; an extreme event for one species is not necessarily an extreme event for another. Individualism can be expressed not only in the particular climate variables (or other drivers) that a species responds to, but also in the time delays between an event and the population response. The observed effects can be direct (e.g., population growth within a warm year), delayed by a year (e.g., drought-induced mortality of Lepidoptera that is not recorded until adults fail to emerge the next year), or delayed by two or more years via community interactions (e.g., through altered natural enemy or food abundances) (38). Delayed density dependence (population crash following a ‘good’ year, or vice versa) may add further lags to the system. Across all 238 species, a combination of delayed community and density-dependent effects could mean that extreme population responses are more evenly spread across years than the ECEs that may trigger these changes. The longer generation times, larger body size, higher trophic level (on average) and homeothermic biology of birds, compared to Lepidoptera, may tend to spread their observed responses more evenly across the years, as we observed. The (weak) negative correlation between the responses of birds and Lepidoptera (Figure 2D) may stem from different lag times, differences in which aspects of environmental variation they respond to, and different overall sensitivities to the climate.

Although species were generally individualistic in their responses to extreme events, there was some agreement across species. First, there was evidence that species groups as a whole tended to respond in the same direction in a given year (i.e. experiencing either crashes or explosions), presumably in response to the same (climatic) drivers. Second, we detected six ‘consensus years’ in which a statistically-significant excess of species exhibited crashes or population explosions. Furthermore, each of these years was characterised by near unanimity in the direction of the extreme population response. Although we should be cautious in interpreting five consensus bad years to one consensus good year as an excess of negative extreme events, we also found significantly more (by 46%) crashes than population explosions across the entire data set. These observations are consistent with the hypothesis that more bad than good events are expected when the climate is changing rapidly. If populations show some degree of local adaptation to historical conditions, they may show extreme

1
2
3
4 386 population collapses under novel conditions (even if they subsequently recover through adaptation to
5 387 the new conditions).

6
7 388
8
9 389 There was also a tendency for the magnitudes of crashes to be greater than the magnitudes of
10 390 increases. We interpret this as arising because it is, in principle, possible for all individuals within a
11 391 large population to die simultaneously when they experience an extreme event, whereas population
12 392 growth is constrained by the intrinsic rate of increase of a species. Nonetheless, for insects, the
13 393 potential fecundity of individuals is high, and so extreme population growth can occasionally be
14 394 achieved, especially for species that can accomplish multiple generations within a single year.

15 395
16
17 396 Overall, we conclude that a few species exhibit extreme population changes in most years, and that
18 397 most species show extreme population changes in some years, but that there are some years that are
19 398 characterised by excesses of dramatic population changes. Furthermore, there is an excess of
20 399 population crashes, relative to explosions and there is a tendency for crashes to be larger in
21 400 magnitude than increases.

22 401
23
24 402 *(b) The link to climate*

25 403
26
27 404 Linking all of these extreme population changes to variation in the climate is difficult, given that
28 405 extreme population responses took place in every year and lagged responses can occur. Moreover,
29 406 some population explosions and crashes may have nothing to do with the climate, or with the
30 407 interaction between the climate and other species. Biological interactions that take place within
31 408 communities, including exaggerated (over-compensating) responses to density-dependent
32 409 interactions, can potentially generate population fluctuations in the absence of external drivers.

33 410
34
35 411 However, there are several lines of evidence that lead us to suggest that the majority of the rapid
36 412 changes observed here do stem from a geographically-widespread external driver, with climate the
37 413 most likely candidate. First, the year-to-year population crashes and explosions that we detected took
38 414 place at a national-scale (England). These are unlikely to be driven by more local factors, such as
39 415 local habitat change, or local interactions between species that are unrelated to a widespread driver.
40 416 Second, we found a strong positive correlation between the responses of our two groups of
41 417 Lepidoptera (butterflies and moths) across years (Figure 2C), and a negative correlation between
42 418 Lepidoptera and birds (Figure 2D). Given that the recording schemes for these three groups are
43 419 independent, these correlations imply responses to climate events that are both geographically

1
2
3
4 420 widespread and capable of generating between-year changes. Thirdly, the existence of statistically-
5 421 significant consensus years (and agreement on whether these years are good or bad) again implies
6
7 422 that some relatively fast-acting underlying causation is operating at the geographic scale of the whole
8
9 423 of England. Changes in land use and habitat management (which affect micro-climate), pesticides,
10 424 the arrival of invasive species, and other drivers that contribute to longer-term trends are unlikely to
11
12 425 act so broadly in a single year; it is only their interactions with widespread climatic factors that are
13
14 426 likely to drive such effects (39). We conclude that most (but not all) of the extreme population
15 427 crashes and explosions that we have detected stem directly or indirectly from a near-synchronous,
16
17 428 geographically widespread process, which is most likely to be the climate.
18
19 429

20 430 In general, we demonstrated an overall lack of association between climate and population responses
21 431 across all years. However, we did find that consensus years (when many species showed extreme
22 432 changes) were more likely to occur in years that were also extreme from a climatic perspective. With
23 433 such rare events (six consensus years), we should be cautious about attributing them to specific
24 434 climatic conditions. Nonetheless, five of the six consensus years, appear to be associated with either
25 435 cold winters (historic extremes that may be becoming less frequent and extreme), and with hot and
26 436 dry summers (extremes that may increase in frequency and strength). Similarly, when we looked
27 437 across all extreme responses rather than just the consensus years, we found positive associations with
28 438 drought (for Lepidoptera) and winter cold (for birds). It should be noted that there were some years
29 439 which were climatically extreme but did not generate biological consensus years; but given that birds
30 440 and Lepidoptera differed in their dynamics (i.e., responding most strongly in different years) it is
31 441 entirely feasible that other taxa that we did not study responded strongly in those years.
32
33 442

34
35 443 Three of the six biological consensus years took place in the same year as a climatic extreme, but the
36 444 negative effects of hot and dry conditions in 1976, and of extreme winter cold in 2010/11, were
37 445 mainly observed as lagged population responses (around a quarter of the Lepidoptera species crashed
38 446 in 1976/77). The summer of 1976 was hot, and also experienced the greatest drought index in the 45-
39 447 year time series, owing to hot and dry conditions stretching back to the spring/summer of 1975
40 448 (Figure 1). This apparent lag in Lepidoptera response may be an issue of detection rather than a true
41 449 biological phenomenon; individuals may have died in the summer of 1976, but it was not until the
42 450 1977 generation failed to emerge that this was noticed. For example, numbers of the Adonis blue
43 451 butterfly *Polyommatus bellargus* crashed after its hostplant *Hippocrepis comosa* dried up and
44 452 caterpillars then starved (40); and other species with summer-feeding larvae were also negatively
45 453 affected (41). The ringlet butterfly *Aphantopus hyperantus* also crashed (42) and so it seems likely
46
47
48
49
50
51
52
53
54
55
56
57
58
59
60

1
2
3
4 454 that direct effects of the 1976 drought were largely responsible for the subsequent population crashes
5 455 of other Lepidoptera. Impacts of summer drought conditions upon birds are likely to be weaker than
6
7 456 for Lepidoptera (bird populations did not change abnormally in 1975/76 or 1976/77), although there
8
9 457 is some previously-documented evidence for lagged effects on some bird species that feed on soil-
10 458 invertebrates (e.g. 38) as well as on those that are migrants (10).
11

12 459

13
14 460 *(c) Are population trends determined by extreme events?*
15

16 461

17 462 It would seem reasonable to suppose that populations exhibiting major crashes would tend to decline
18 463 in the long term, and those experiencing population explosions would increase. However, extreme
19
20 464 events are rare, and many smaller population changes in ‘normal’ years might fully compensate for
21 465 such extreme events. Density-dependent responses to extremes may also prevent any long-term
22 466 consequences of extreme events from being realised. Our data suggest that any impact of single
23 467 extreme events on long-term trends is limited (Figure 5). In particular, for Lepidoptera and bird
24 468 species experiencing population crashes (either as the most extreme event they experienced or as the
25 469 average of all extreme events), some of them showed long-term declines and others showed long-
26 470 term increases. The same was true for Lepidoptera that experienced population explosions. It was
27 471 only in birds where species explosions tended to be linked to more positive long-term population
28 472 trends.
29
30 473

31 474

32 475 There is no universal ‘best way’ to test for the effects of extremes on long-term trends, but we urge
33 476 others to test rather than assume that the two will be linked. Weak associations are not particularly
34 477 surprising. Only 6.2% of all between-year population changes qualified as extreme, and hence the
35 478 magnitude of extreme events would have to be far greater than regular population changes for such
36 479 events to leave a strong signature on the overall population trend. Reducing the threshold for
37 480 detecting ‘extremes’ (so there are many more of them) might increase the likelihood of detecting an
38 481 association, but this would be counter to the notion that extreme events are, by definition, unusual.
39 482 Altwegg et al. (this issue) report that observational studies of the impacts of extreme climatic events
40 483 have tended to investigate one extreme event during a median study duration of 11 years, which is
41 484 comparable to the frequency of extreme population responses identified here. Of course, single
42 485 events that reduce population densities by two or more orders of magnitude can happen (18, 26), but
43 486 they are very rare when considering the number of between-year population changes that we studied.
44 487 Long-term population trends are seemingly dominated by other factors, such as relatively gradual
45 488 climatic changes, or by non-climatic events that accumulate over space and time. For example, many
46 489
47 490
48 491
49 492
50 493
51 494
52 495
53 496
54 497
55 498
56 499
57 500
58 501
59 502
60 503

1
2
3
4 488 farmland birds showed declining trends during the 1970s and 1980s as a result of agricultural
5 489 intensification operating over many years (43, 44). Similarly, land-use change is the likely driver of
6
7 490 the parallel long-term declines of many Lepidoptera species in the United Kingdom (45, 46). In no
8
9 491 single year would there be sufficient intensification to cause a detectable crash at a national scale, but
10 492 the accumulation of local effects over many years seems to drive the long-term trend. Other factors
11
12 493 such as the arrival of invasive species or other locally-acting pressures can have similar effects
13
14 494 provided they operate for long enough; multiplicative effects of climatic and non-climatic factors
15 495 may also be important (39).
16
17 496

18
19 497 An additional reason why a link between extreme population events and long-term trends may not be
20 498 apparent could be related to historical extreme events (constraints) that are no longer in operation.
21
22 499 Climate warming may be just as likely to reduce or remove some historical constraints as to impose
23
24 500 new ones. For example, the insectivorous Dartford warbler *Sylvia undata* was virtually extinguished
25 501 from England by the severe winter conditions of 1961/62 (47), but this bird species has subsequently
26
27 502 increased in abundance and expanded its distribution in the absence of such a severe winter cold
28
29 503 constraint (14). Dartford warblers still do worse in cold winters, but these temperatures are now
30 504 insufficiently cold to determine the overall population trend. This phenomenon would lead to little or
31
32 505 no correlation across species in their most extreme population responses and their overall population
33
34 506 trends. Species may be released from historical constraints (including extremes), just as they may be
35 507 hampered by novel ones.
36
37 508

38 39 509 4. Conclusion

40
41 510 In every year of our 45 year time series, at least three species of Lepidoptera and/or birds showed an
42
43 511 extreme response in population size, giving support to our first hypothesis, that the responses of
44
45 512 species to climatic variability are individualistic. We also found support for our second hypothesis:
46
47 513 population crashes tended to be more frequent than population explosions during periods of rapid
48
49 514 climatic change (as new conditions are experienced by populations that are potentially locally-
50
51 515 adapted to historical conditions). Furthermore, population crashes were more extreme than
52
53 516 explosions (explosions are constrained by the intrinsic rate of population growth whereas it is
54
55 517 possible for all individuals to die). Thirdly, we did find that there were statistically-unusual
56
57 518 consensus years when many species experienced population crashes or explosions, and we obtained
58
59 519 support for the hypothesis that these events were associated with climatically extreme years. Finally,
60 520 we found only limited and weak support (among birds) for the hypothesis that long-term population
521 521 trends are correlated with extreme population responses, probably because the processes that are

1
2
3
4 522 operating in most years (which are not extreme) are usually more important determinants of long-
5 523 term trends than are rare extremes. We conclude that extreme population events are individualistic
6
7 524 despite occasional consensus years, and likely to be linked to climatic extremes (from the perspective
8
9 525 of each species), but that these extreme events are only weak predictors of long-term population
10 526 trends for the taxa we consider.
11
12 527
13
14
15
16
17
18
19
20
21
22
23
24
25
26
27
28
29
30
31
32
33
34
35
36
37
38
39
40
41
42
43
44
45
46
47
48
49
50
51
52
53
54
55
56
57
58
59
60

For Review Only

1
2
3
4
5
6
7
8
9
10
11
12
13
14
15
16
17
18
19
20
21
22
23
24
25
26
27
28
29
30
31
32
33
34
35
36
37
38
39
40
41
42
43
44
45
46
47
48
49
50
51
52
53
54
55
56
57
58
59
60

528 **Additional Information**

529 **Acknowledgments**

530 We thank the thousands of people, mainly volunteers, responsible for monitoring Lepidoptera and
531 bird populations (UKBMS, BBS, CBC and RIS surveys). The UKBMS is run by Butterfly
532 Conservation (BC), the Centre for Ecology and Hydrology (CEH) and the British Trust for
533 Ornithology (BTO), in partnership with the Joint Nature Conservation Committee (JNCC), and
534 supported and steered by Forestry Commission (FC), Natural England (NE), Natural Resources
535 Wales (NRW), Northern Ireland Environment Agency (NIEA), and Scottish Natural Heritage (SNH).
536 Light-trap data were provided by the RIS, a National Capability supported by the UK Biotechnology
537 and Biological Sciences Research Council (BBSRC); we thank P. Verrier, C. Shortall, and the survey
538 volunteers for these data. Rothamsted Research is a national institute of bioscience strategically
539 funded by BBSRC. Climate data were provided by the UK Met Office. CBC was funded by the BTO
540 and JNCC, and BBS by the BTO, RSPB and JNCC (on behalf of CCW, NE, CNCC and SNH), with
541 fieldwork conducted by BTO members and other volunteers. Bird population trends for England data
542 were provided by a partnership jointly funded by the BTO and JNCC.

543
544 **Data Accessibility**

545 The raw data for these analyses are available from the organisations listed in the acknowledgements.
546 Bird data are available via: www.bto.org/research-data-services/data-services/data-request-system,
547 and butterfly data via: www.ukbms.org/Obtaining.aspx.

548
549 **Author Contributions**

550 C.D.T. conceived, and C.D.T., G.P., C.D., P.J.P. and J.K.H. designed the study. J.W.P-H, J.W.C.,
551 T.B., D. B.R, and R.F. provided data, with additional assistance from Dario Massimino, while G.P.
552 and P.J.P. carried out the analyses. C.D.T., P.J.P. J.K.H. and G.P. drafted the manuscript, and all
553 authors contributed to revising the paper. All authors gave final approval for publication.

554
555 **Competing Interests**

556 We have no competing interests.

557
558 **Funding**

559 This research was funded by the Natural Environment Research Council (NE/K00381X/1,
560 NE/M013030/1).

561

562 References

1. Stephens PA, Mason LR, Green RE, Gregory RD, Sauer JR, Alison J, et al. Consistent response of bird populations to climate change on two continents. *Science*. 2016;352(6281):84-7.
2. Bellard C, Bertelsmeier C, Leadley P, Thuiller W, Courchamp F. Impacts of climate change on the future of biodiversity. *Ecology Letters*. 2012;15(4):365-77.
3. Parmesan C, Yohe G. A globally coherent fingerprint of climate change impacts across natural systems. *Nature*. 2003;421(6918):37-42.
4. Walther G-R. Community and ecosystem responses to recent climate change. *Philosophical Transactions of the Royal Society B: Biological Sciences*. 2010;365(1549):2019-24.
5. Easterling DR, Meehl GA, Parmesan C, Changnon SA, Karl TR, Mearns LO. Climate Extremes: Observations, Modeling, and Impacts. *Science*. 2000;289(5487):2068-74.
6. Bailey LD, van de Pol M. Tackling extremes: challenges for ecological and evolutionary research on extreme climatic events. *Journal of Animal Ecology*. 2016;85(1):85-96.
7. Amano T, Sutherland WJ. Four barriers to the global understanding of biodiversity conservation: wealth, language, geographical location and security. *Proceedings of the Royal Society B-Biological Sciences*. 2013;280(1756):20122649.
8. Mair L, Thomas CD, Anderson BJ, Fox R, Botham M, Hill JK. Temporal variation in responses of species to four decades of climate warming. *Global Change Biology*. 2012;18(8):2439-47.
9. Roy DB, Rothery P, Moss D, Pollard E, Thomas JA. Butterfly numbers and weather: predicting historical trends in abundance and the future effects of climate change. *Journal of Animal Ecology*. 2001;70(2):201-17.
10. Pearce-Higgins JW, Eglinton SM, Martay B, Chamberlain DE. Drivers of climate change impacts on bird communities. *Journal of Animal Ecology*. 2015;84(4):943-54.
11. Conrad KF, Woiwod IP, Perry JN. Long-term decline in abundance and distribution of the garden tiger moth (*Arctia caja*) in Great Britain. *Biological Conservation*. 2002;106(3):329-37.
12. Altwegg R, Visser V, Bailey L, Erni B. Learning from single extreme events. *Philosophical Transactions of the Royal Society B: Biological Sciences*. 2016.
13. Ehrlich P, Murphy D, Singer M, Sherwood C, White R, Brown I. Extinction, reduction, stability and increase: the responses of checkerspot butterfly (*Euphydryas*) populations to the California drought. *Oecologia*. 1980;46(1):101-5.
14. Gibbons DW, Wotton S. The Dartford warbler in the United Kingdom in 1994. *British Birds*. 1996;89(5):203-12.
15. Ogutu JO, Owen-Smith N. ENSO, rainfall and temperature influences on extreme population declines among African savanna ungulates. *Ecology Letters*. 2003;6(5):412-9.
16. Orsenigo S, Mondoni A, Rossi G, Abeli T. Some like it hot and some like it cold, but not too much: plant responses to climate extremes. *Plant Ecology*. 2014;215(7):677-88.
17. Oliver TH, Marshall HH, Morecroft MD, Brereton T, Prudhomme C, Huntingford C. Interacting effects of climate change and habitat fragmentation on drought-sensitive butterflies. *Nature Climate Change*. 2015;5:941 - 5.
18. Thomas CD, Singer MC, Boughton DA. Catastrophic extinction of population sources in a butterfly metapopulation. *American Naturalist*. 1996;148(6):957-75.
19. Palma AD, Dennis RLH, Brereton T, Leather SR, Oliver TH. Large reorganizations in butterfly communities during an extreme weather event. *Ecography*. 2016;39:001–9.
20. De'ath G, Lough JM, Fabricius KE. Declining Coral Calcification on the Great Barrier Reef. *Science*. 2009;323(5910):116-9.
21. Ainsworth TD, Heron SF, Ortiz JC, Mumby PJ, Grech A, Ogawa D, et al. Climate change disables coral bleaching protection on the Great Barrier Reef. *Science*. 2016;352(6283):338-42.

- 1 22. Van de Pol M, Jenouvrier S, Visser ME. Ecological and evolutionary response to extreme
2 climatic events: challenges and research directions. *Philosophical Transactions of the Royal Society*
3 *B: Biological Sciences*. 2016.
- 4 23. Bailey L, Ens BJ, Both C, Heq D, Oosterbeek K, Van de Pol M. Phenotypic plasticity in nest-
5 site selection as a response to extreme flooding events. *Philosophical Transactions of the Royal*
6 *Society B: Biological Sciences*. 2016.
- 7 24. Loreau M, de Mazancourt C. Species synchrony and its drivers: neutral and nonneutral
8 community dynamics in fluctuating environments. *The American Naturalist*. 2008;172(2):E48-E66.
- 9 25. Sæther BE, Grøtan V, Engen S, Noble DG, Freckleton RP. Rarity, life history and scaling of
10 the dynamics in time and space of British birds. *Journal of Animal Ecology*. 2011;80(1):215-24.
- 11 26. Cavin L, Mountford EP, Peterken GF, Jump AS. Extreme drought alters competitive
12 dominance within and between tree species in a mixed forest stand. *Functional Ecology*.
13 2013;27(6):1424-35.
- 14 27. R Core Team. R: A language and environment for statistical computing. R Foundation for
15 Statistical Computing, Vienna, Austria. www.R-project.org. 2013.
- 16 28. Brereton T, Roy DB, Middlebrook I, Botham M, Warren M. The development of butterfly
17 indicators in the United Kingdom and assessments in 2010. *Journal of Insect Conservation*.
18 2011;15(1-2):139-51.
- 19 29. Fox R, Parsons MS, Chapman JW, Woiwod LP, Warren MS, Brooks DR. The state of
20 Britain's larger moths 2013: Butterfly Conservation and Rothamsted Research, Wareham, Dorset,
21 U.K.; 2013. 1-29 p.
- 22 30. Marchant JH, Hudson R, Carter SP, Whittington P. *Population Trends in British Breeding*
23 *Birds*: BTO, Tring; 1990.
- 24 31. Gregory RD, Baillie SR. Large-scale habitat use of some declining British birds. *Journal of*
25 *Applied Ecology*. 1998;35(5):785-99.
- 26 32. Husson F, Josse J, Le S, Mazet J. FactoMineR: Multivariate Exploratory Data Analysis and
27 Data Mining with R. R package version 1.25. <http://CRAN.R-project.org/package=FactoMineR>.
28 2013.
- 29 33. Ummenhofer C, Mehl J. Extreme weather and climate events with ecological relevance - a
30 review. *Philosophical Transactions of the Royal Society B: Biological Sciences*. 2016.
- 31 34. Pardo D, Jenouvrier S, Weimerskirch H. Modelling the effect of extreme sea temperature
32 events on the demography of an age-structured albatross population. *Philosophical Transactions of*
33 *the Royal Society B: Biological Sciences*. 2016.
- 34 35. McDermott Long O, Warren R, Price J, Brereton TM, Botham MS, Franco AMA. Sensitivity
35 of UK butterflies to local climatic extremes: which life stages are most at risk? *Journal of Animal*
36 *Ecology*. 2016:n/a-n/a.
- 37 36. Leys C, Ley C, Klein O, Bernard P, Licata L. Detecting outliers: Do not use standard
38 deviation around the mean, use absolute deviation around the median. *Journal of Experimental Social*
39 *Psychology*. 2013;49(4):764-6.
- 40 37. Brys G, Hubert M, Struyf A. A Robust Measure of Skewness. *Journal of Computational and*
41 *Graphical Statistics*. 2004;13(4):996-1017.
- 42 38. Pearce-Higgins JW, Dennis P, Whittingham MJ, Yalden DW. Impacts of climate on prey
43 abundance account for fluctuations in a population of a northern wader at the southern edge of its
44 range. *Global Change Biology*. 2010;16(1):12-23.
- 45 39. Dinh KV, Janssens L, Stoks R. Exposure to a heat wave under food limitation makes an
46 agricultural insecticide lethal: a mechanistic laboratory experiment. *Global Change Biology*.
47 2016;22(10):3361-72.
- 48 40. Thomas J. The ecology and conservation of *Lysandra bellargus* (Lepidoptera: Lycaenidae) in
49 Britain. *Journal of Applied Ecology*. 1983:59-83.
- 50 41. Thomas J, Merrett P. Observations of butterflies in the Purbeck Hills in 1976 and 1977. *Proc*
51 *Dorset Nat Hist Archaeol Soc*. 1980;99:112-9.

- 1 42. Sutcliffe OL, Thomas CD, Yates TJ, Greatorex Davies JN. Correlated extinctions,
2 colonizations and population fluctuations in a highly connected ringlet butterfly metapopulation.
3 *Oecologia*. 1997;109(2):235-41.
- 4 43. Eglinton SM, Pearce-Higgins JW. Disentangling the relative importance of changes in
5 climate and land-use intensity in driving recent bird population trends. *Plos One*. 2012;7(3).
- 6 44. Chamberlain DE, Fuller RJ, Bunce RG, Duckworth JC, Shrubbs M. Changes in the
7 abundance of farmland birds in relation to the timing of agricultural intensification in England and
8 Wales. *Journal of Applied Ecology*. 2000;37(5):771-88.
- 9 45. Warren MS, Hill JK, Thomas JA, Asher J, Fox R, Huntley B, et al. Rapid responses of British
10 butterflies to opposing forces of climate and habitat change. *Nature*. 2001;414(6859):65-9.
- 11 46. Fox R, Oliver T, Harrower C, Parsons MS, Thomas CD, Roy DB. Long-term changes to the
12 frequency of occurrence of British moths are consistent with opposing and synergistic effects of
13 climate and land use changes. *Journal of Applied Ecology*. 2014;51(4):949 - 57.
- 14 47. Tubbs C. Numbers of Dartford warblers in England during 1962-66. *Brit Birds*. 1967;60:87-9.
- 15 48. Walsh R, Lawler D. Rainfall seasonality: description, spatial patterns and change through
16 time. *Weather*. 1981;36(7):201-8.
- 17
18
19
20
21
22
23
24
25
26
27
28
29
30
31
32
33
34
35
36
37
38
39
40
41
42
43
44
45
46
47
48
49
50
51
52
53
54
55
56
57
58
59
60

Tables

Table 1. Climate variables used in the analyses. The plus and minus columns identify ‘extreme’ years in which the England-wide average conditions were greater than (+) or less than (-) twice the median absolute deviation from the median. With the exception of the drought index, each variable was calculated over the 12-month period from September 1 to August 31 (i.e., 1979 corresponds to the period September 1st 1978 to August 31st 1979). For the drought index, calculations ran over an 18-month period (beginning March 1) in order to capture water deficit accumulated over successive hot and dry springs/summers.

Variable	Abbreviation	Units	+	-	Description
Rainfall wettest month	<u>WETTEST</u>	mm			Rainfall of the wettest calendar month
Rainfall seasonality	<u>RAINSEASON</u>	mm	1979, 1990, 1995		Rainfall contrast across seasons (48): $\sum s = 1.4 R_s - RT/4 /RT$, where R_s is rainfall in season s , and RT is total annual rainfall
Drought index	<u>DROUGHT</u>	mm	1976, 1996		Accumulated water deficit, where a deficit is defined by monthly Hargreaves PET > monthly rainfall. Months with excess rainfall reduce the deficit, but only up to field capacity. The drought index is the maximum water deficit recorded during spring/summer of the reference year
Growing degree days	<u>GDD5</u>	°C	2007		Annual sum of degrees by which daily mean air temperature exceeds 5 °C
Annual temperature range	<u>TEMPRANGE</u>	°C			Annual maximum air temperature minus annual minimum air temperature
Daily minimum temperature of coldest 30 days	<u>COLD30</u>	°C		1979, 1982, 1986, 2011	Mean of daily minima over coldest consecutive 30-day period
Daily maximum temperature of hottest 30 days	<u>HOT30</u>	°C	1976, 1995, 2006		Mean of daily maxima over hottest consecutive 30-day period

Figures

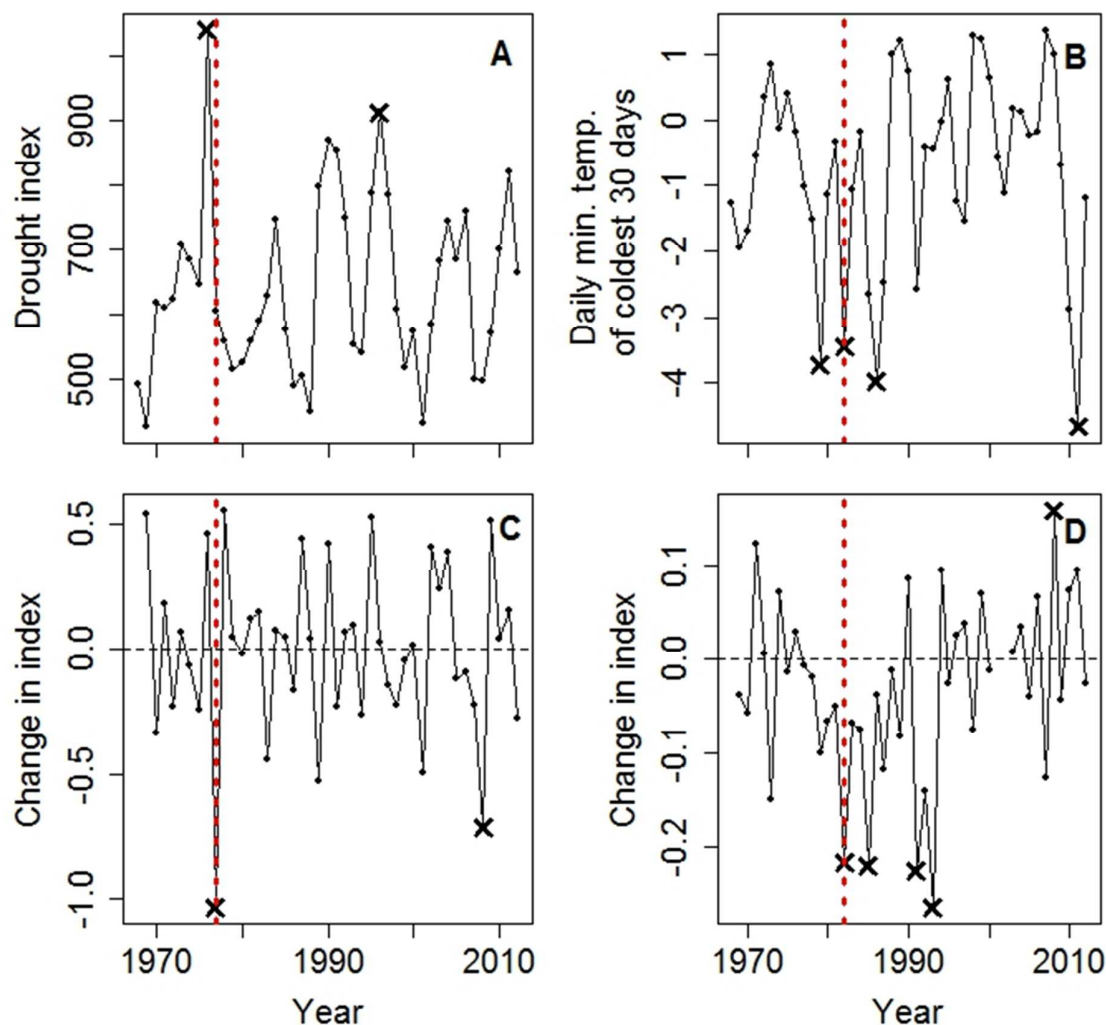


Figure 1. Exemplar climatic variables and species to illustrate our approach. The plots show how we identified extreme climatic events (A and B) and species responses (C and D). The vertical (red) dashed lines represent the largest consensus year, where an extreme number of Lepidoptera (A and C) and birds (B and D) experienced population crashes. Panels C and D represent year-to-year changes in index of two example species, chosen as they experienced the greatest crashes in the largest consensus year for each species' group: in C, the mottled grey moth *Colostygia multistrigaria* and in D, the tree sparrow *Passer montanus*. Values below zero in C and D indicate negative population growth, and values above zero indicate positive growth. In each panel, extreme years (outliers) for climate and species are represented by black crosses.

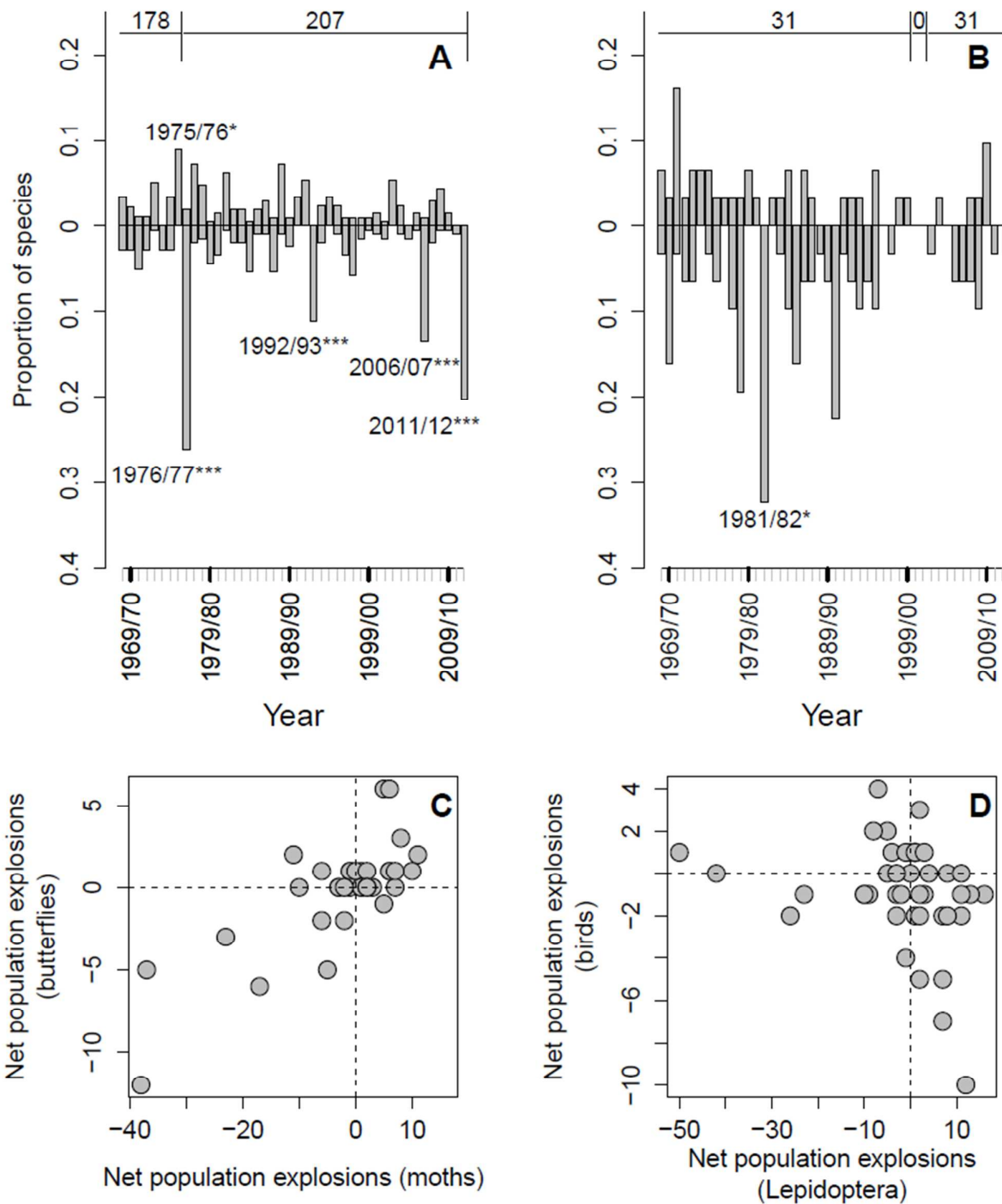


Figure 2. Annual extreme population changes of English Lepidoptera and birds. Upper panels: proportion of Lepidoptera (A; butterflies and macro-moths) and bird species (B) experiencing a population explosion (upwards bars) or crash (downwards bars). Asterisks denote significance of consensus years (*, $p < 0.05$; ***, $p < 0.0001$; Bonferroni-corrected for multiple-year testing); numbers at the top of the plots represent the number of species included in that year. Lower panels: relationships within (C) and between (D) higher taxonomic groups are significant ($p \leq 0.03$). Each filled circle represents one year. ‘Net population explosions’ represents the difference in numbers of species showing population explosions and crashes in a given year (e.g., if there are five species with an explosion and 15 with a crash in the same year, that year scores -10).

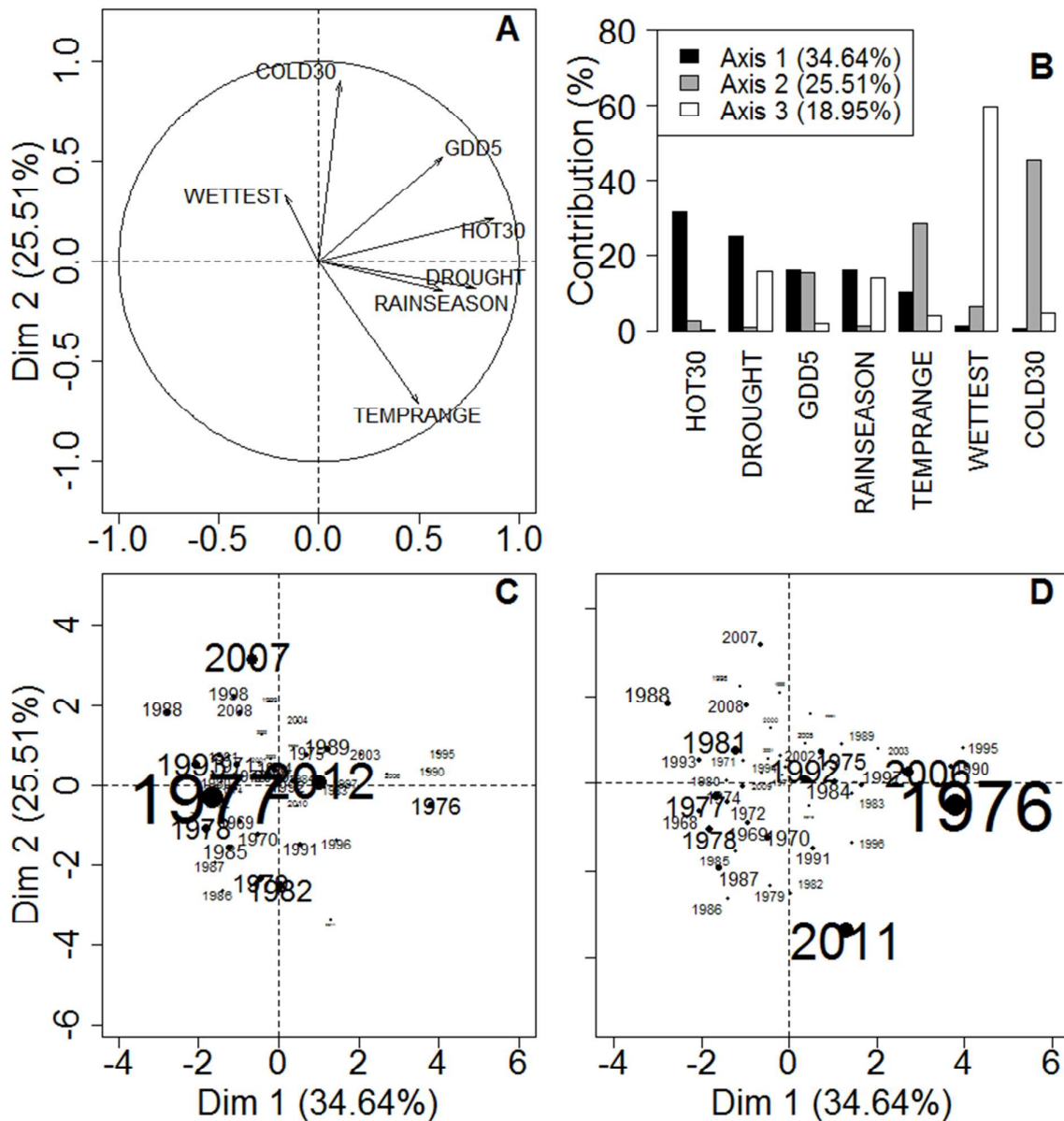


Figure 3. Principal components analysis (PCA) illustrating the variation in the seven climate variables (Table 1) across our study period. Panel A shows vectors for individual climate variables associated with the first two PCA axes (i.e. dimensions, labelled ‘Dim’); Panel B shows the percentage contributions of each variable to the first three PCA axes. Panels C and D show the positions for each year on the first two axes; the size of the text reflects the relative size of the consensus year (i.e. the number of species experiencing an extreme population change) in either the year during which the population change was measured (panel C) or in the previous year (i.e. accounting for a one-year population lag, panel D).

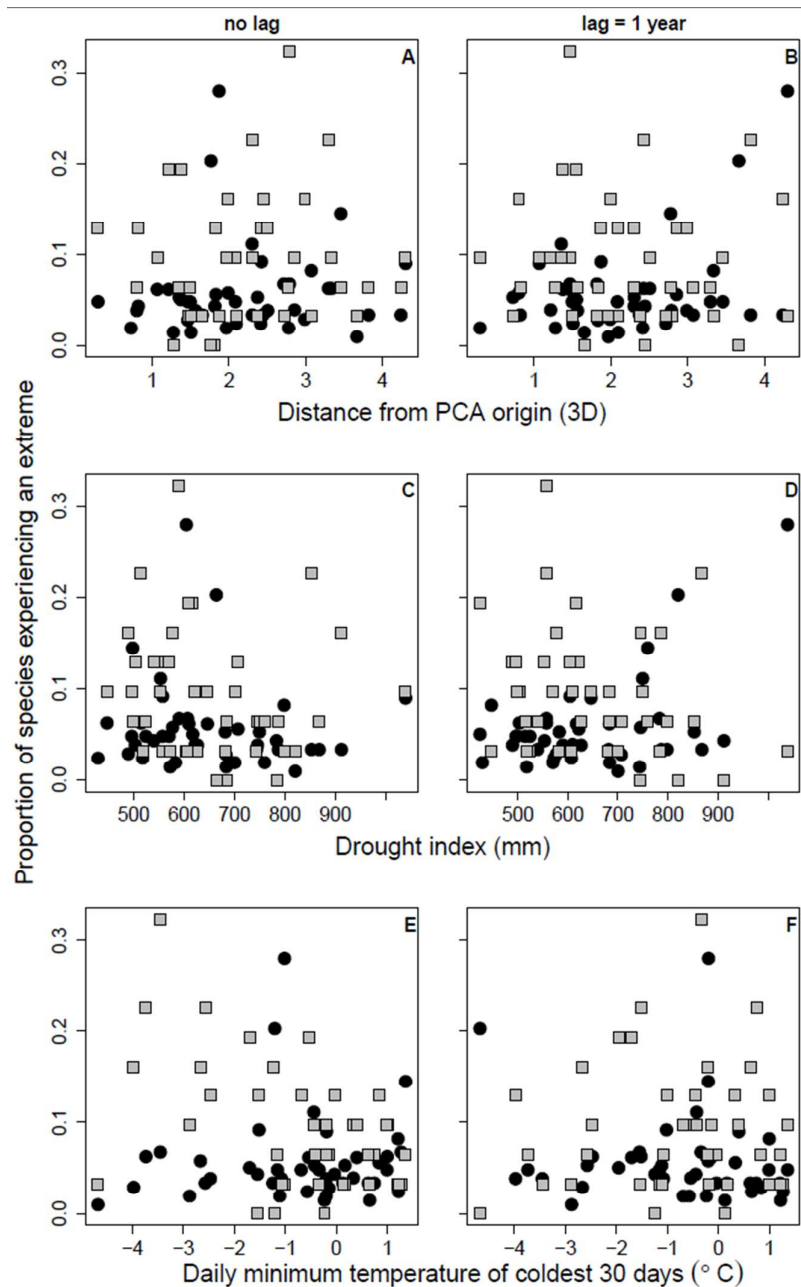


Figure 4. No overall relationship was observed between climatic conditions and the numbers of species showing extreme population responses. Relationships between the proportion of species experiencing an extreme response (either population crashes or explosion) in each year and 3D distance from the climate-PCA origin (A, B), drought index (C, D) and daily minimum temperature of the coldest 30 days (E, F) are shown. Lepidoptera are represented by black circles and birds by grey squares; each symbol represents one year. The lags are measured in years, with lag 0 representing the climate measured in the current year i.e. population changes from 1968 – 1969 were related to the climate in 1968 (lag = 1 year) and/or 1969 (no lag).

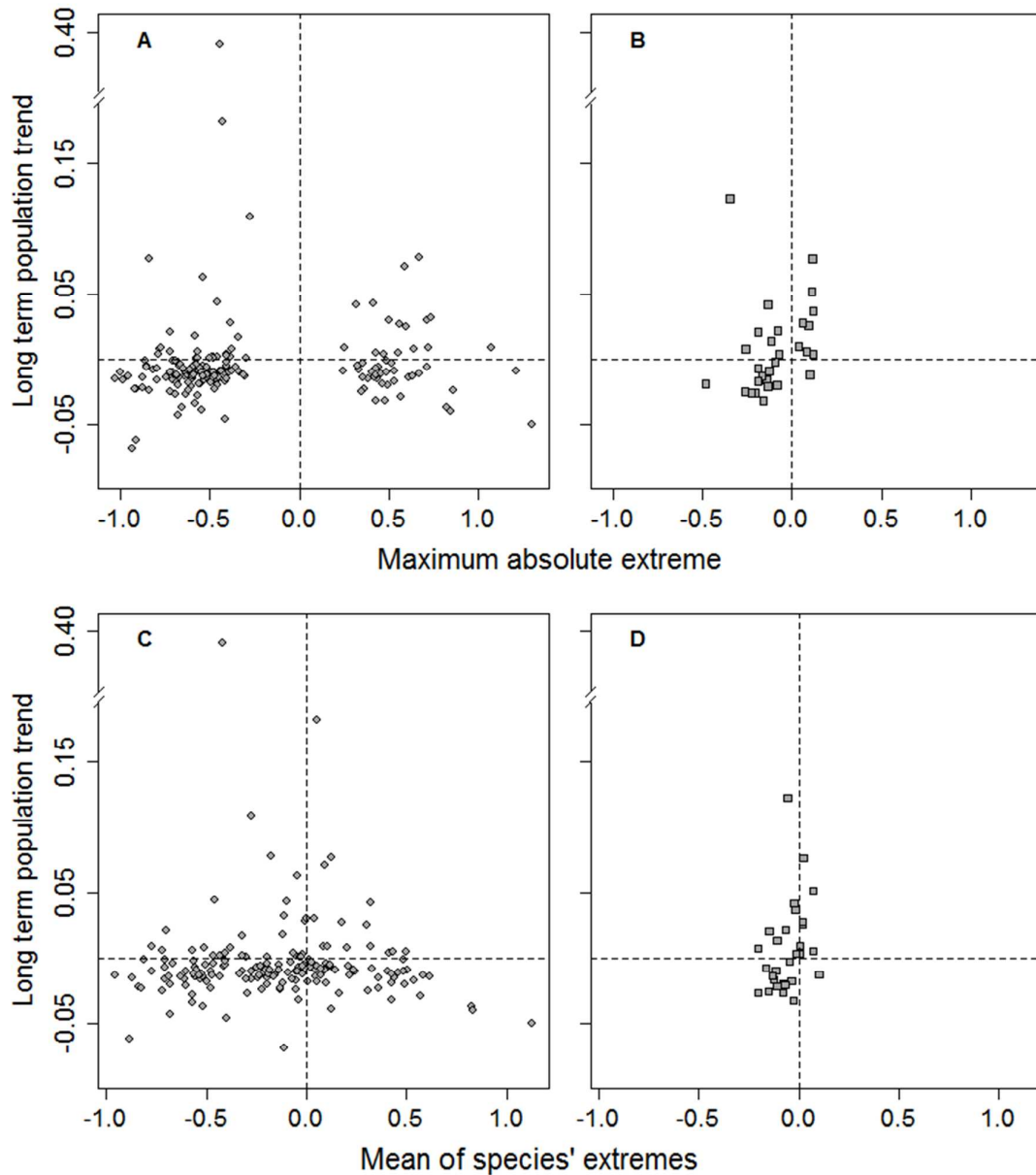
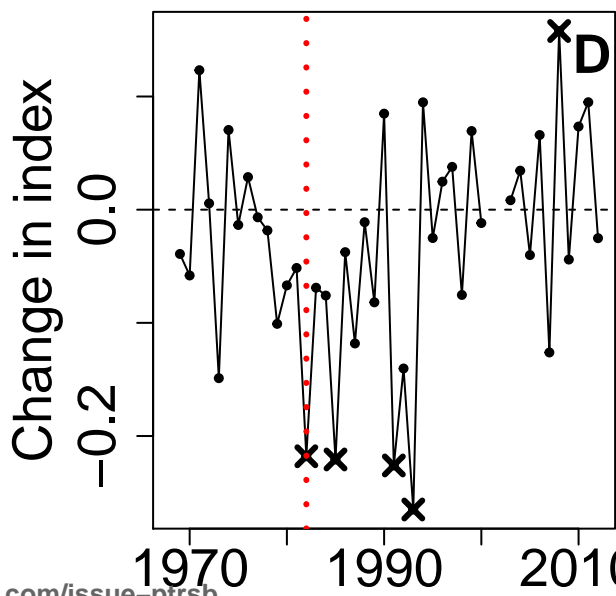
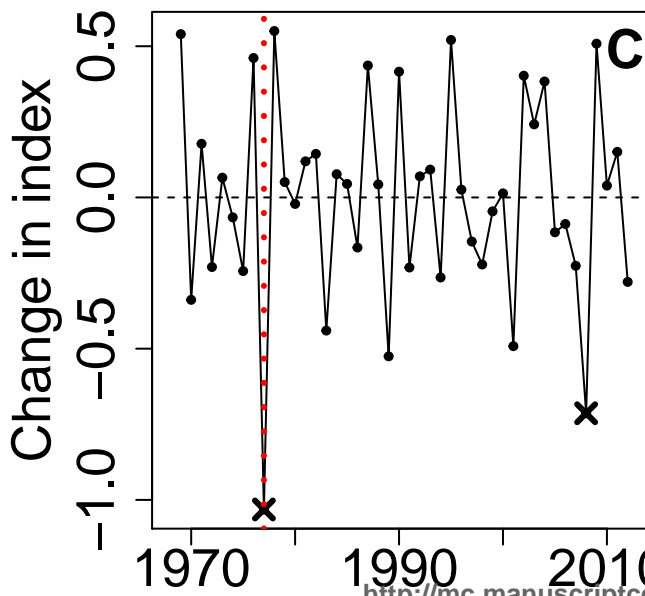
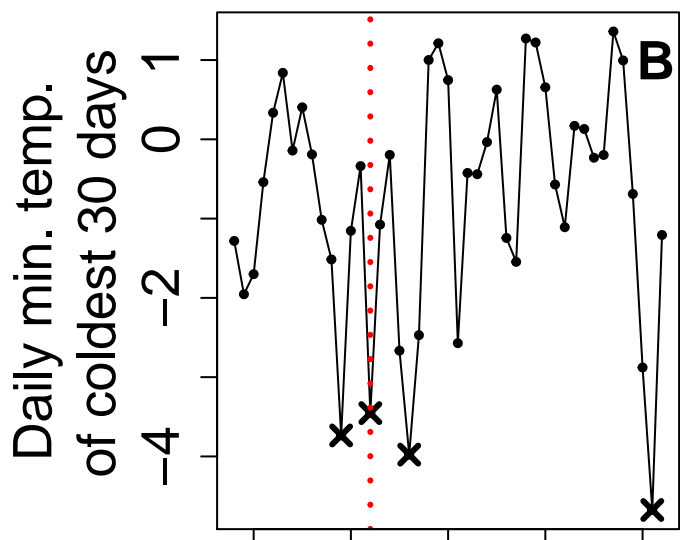
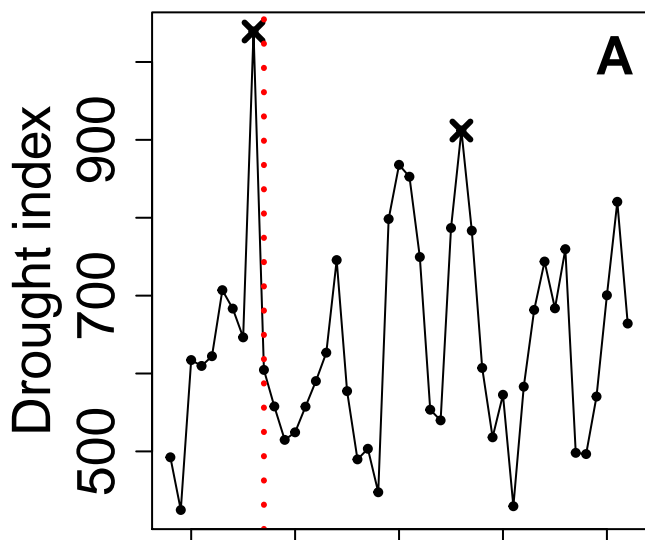
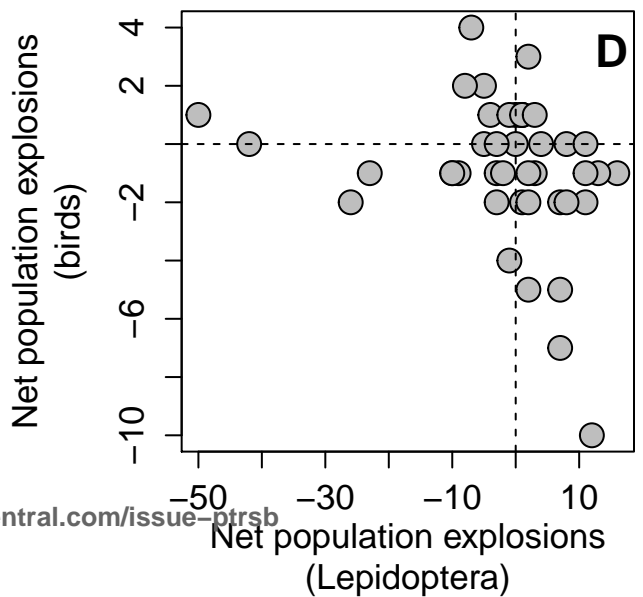
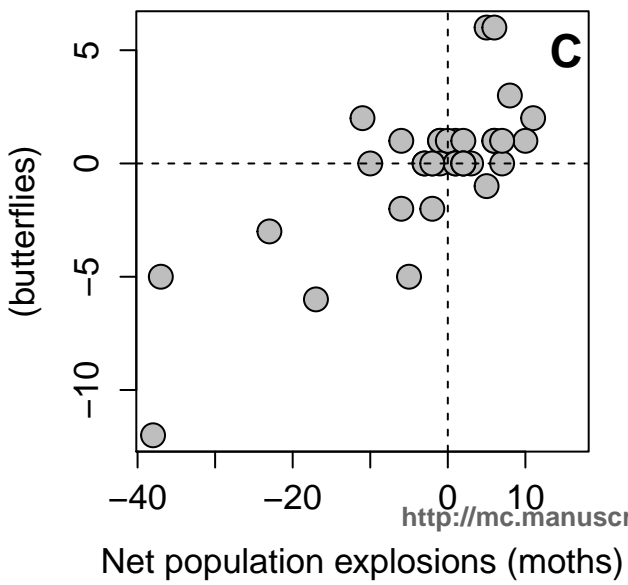
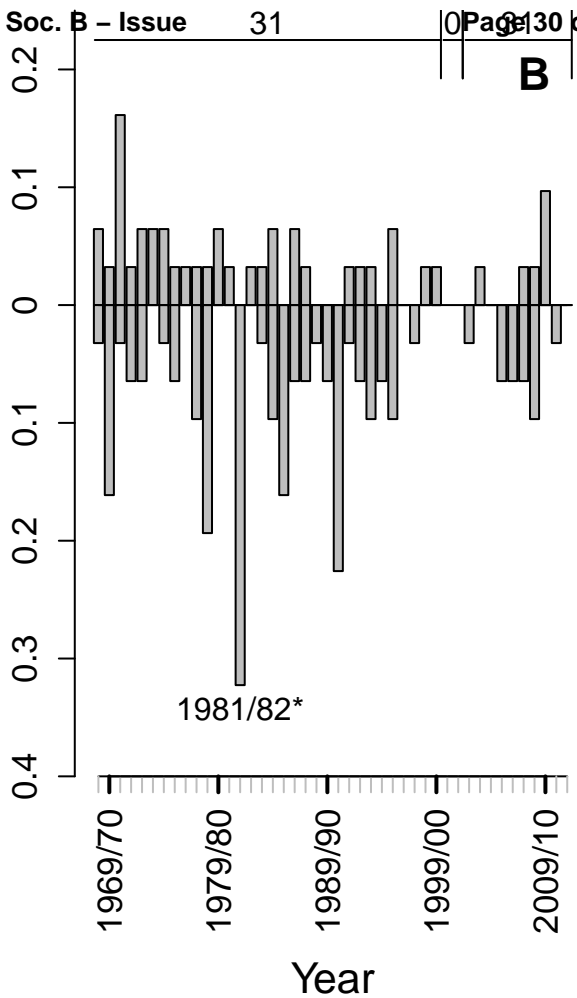
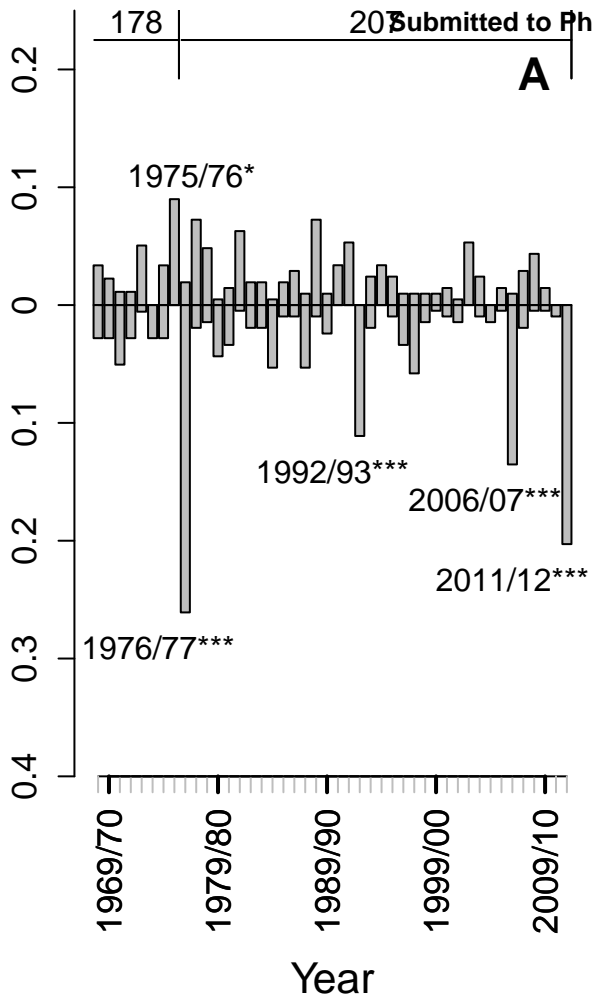


Figure 5. Relationships between Lepidoptera (A and C) and bird (B and D) species' long-term abundance trend and: the maximum absolute extreme value for a species during the study period (panels A and B) and mean over all extreme events experienced by that species during the study period (panels C and D). Note the broken y-axes.

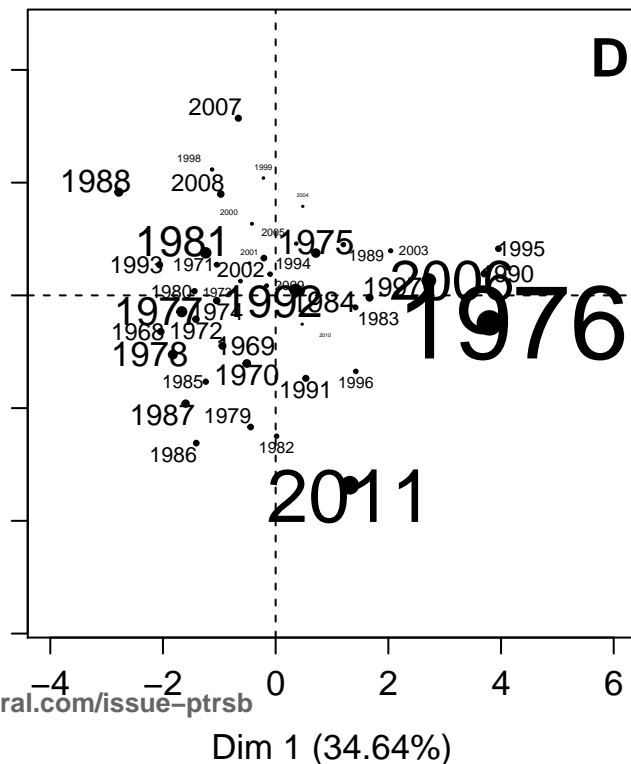
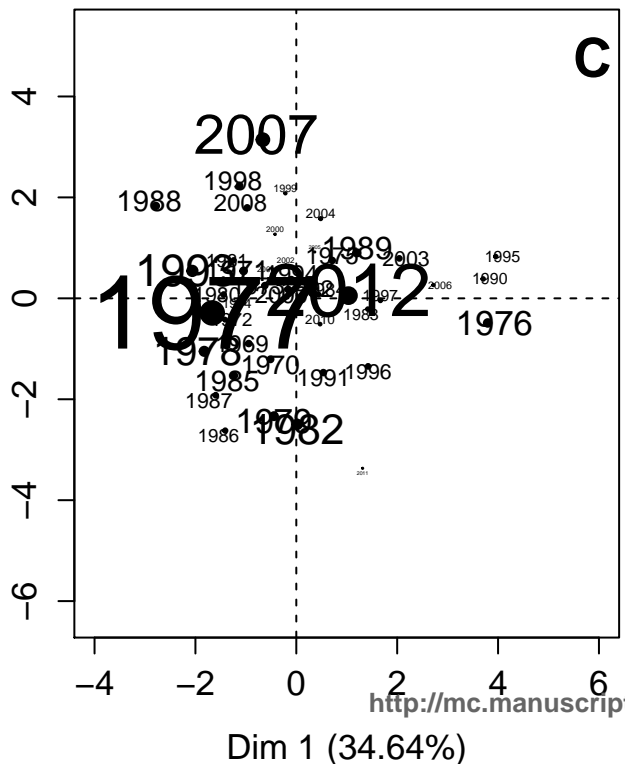
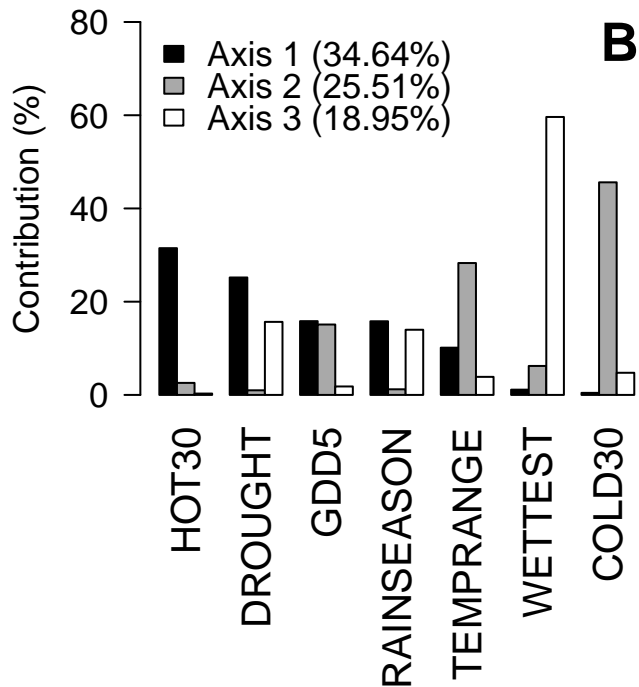
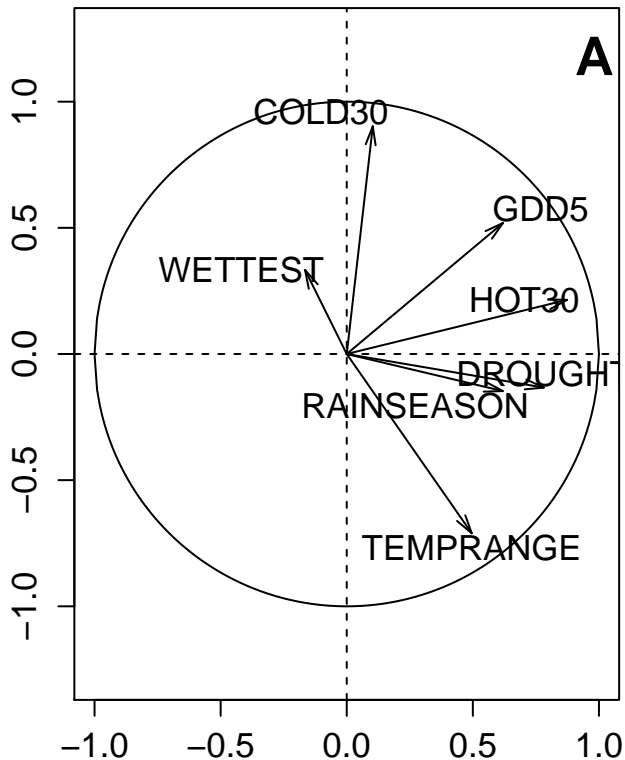
1
2
3
4
5
6
7
8
9
10
11
12
13
14
15
16
17
18
19
20
21
22
23
24
25
26
27
28
29
30
31
32
33
34
35
36
37
38
39
40
41
42



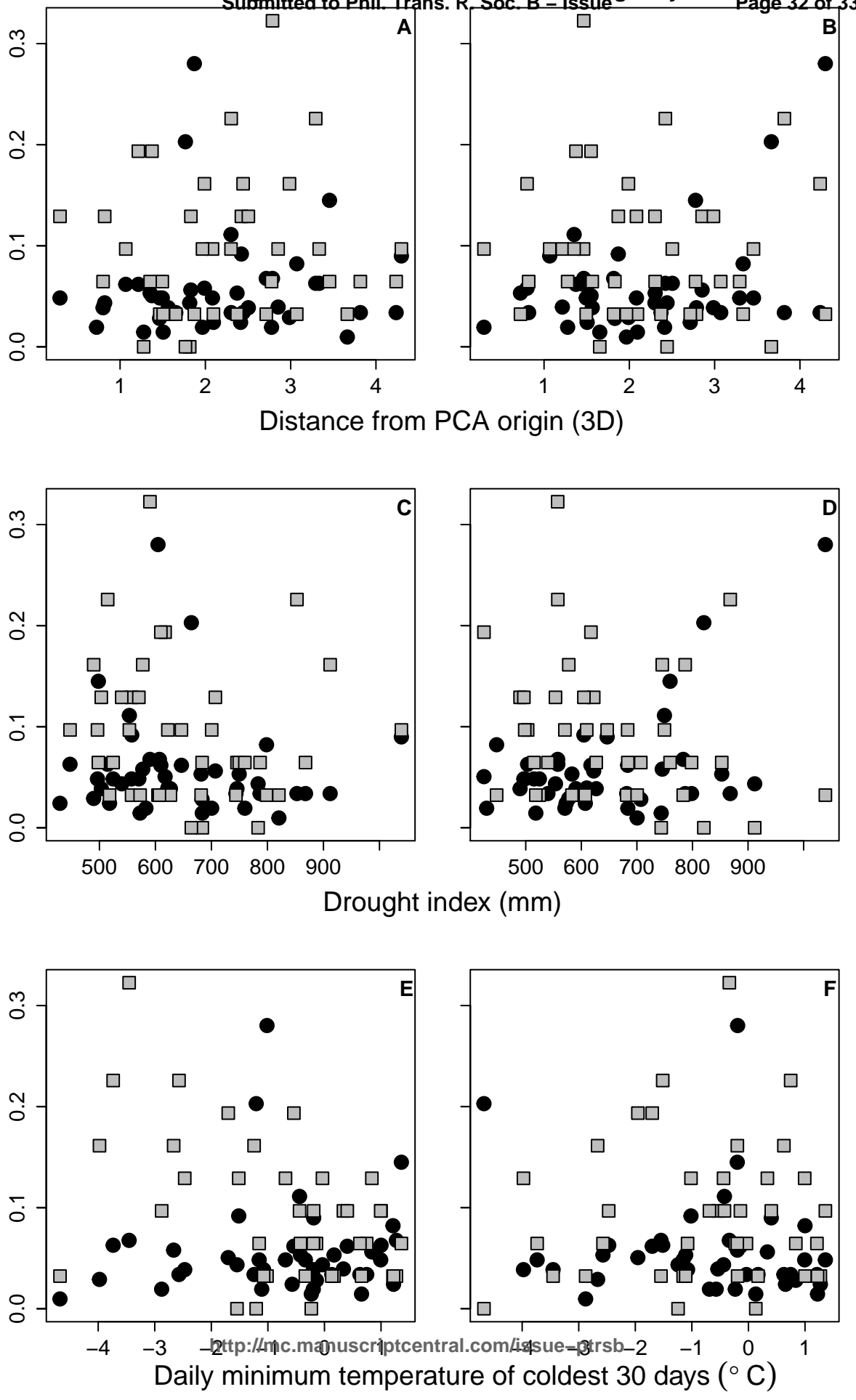
1
2
3
4
5
6
7
8
9
10
11
12
13
14
15
16
17
18
19
20
21
22
23
24
25
26
27
28
29
30
31
32
33
34
35
36
37
38
39
40
41
42
43
44
45
46
47
48
49
50



1
2
3
4
5
6
7
8
9
10
11
12
13
14
15
16
17
18
19
20
21
22
23
24
25
26
27
28
29
30
31
32
33
34
35
36
37
38
39
40
41
42
43
44
45
46
47
48
49



1
2
3
4
5
6
7
8
9
10
11
12
13
14
15
16
17
18
19
20
21
22
23
24
25
26
27
28
29
30
31
32
33
34
35
36
37
38
39
40
41
42
43
44
45
46
47
48
49
50
51
52
53
54
55
56
57
58
59
60



1
2
3
4
5
6
7
8
9
10
11
12
13
14
15
16
17
18
19
20
21
22
23
24
25
26
27
28
29
30
31
32
33
34
35
36
37
38
39
40
41
42
43

