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Large reorganizations in butterfly communities during an extreme weather event

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Drought events are projected to increase in frequency and magnitude, which may alter the composition of ecological communities. Using a functional community metric that describes abundance, life history traits and conservation status, based upon Grime's *CSR* (Competitive – Stress tolerant – Ruderal) scheme, we investigated how British butterfly communities changed during an extreme drought in 1995. Throughout Britain, the total abundance of these insects had a significant tendency to increase, accompanied by substantial changes in community composition, particularly in more northerly, wetter sites. Communities tended to shift away from specialist, vulnerable species, and towards generalist, widespread species and, in the year following, communities had yet to return to equilibrium. Importantly, heterogeneity in surrounding landscapes mediated community responses to the drought event. Contrary to expectation, however, community shifts were more extreme in areas of greater topographic diversity, whilst land-cover diversity buffered community changes and limited declines in vulnerable specialist butterflies.

One of the greatest threats from climate change is an increase in the frequency and magnitude of extreme events (Schär et al. 2004). Drought events have impacts on ecological communities that are vastly disproportionate to their duration (Jentsch et al. 2007, De Boeck et al. 2011). The impacts can span extremely large spatial and temporal scales (Haddad et al. 2002, Breshears et al. 2005), and can affect many levels of biodiversity, from individual responses to driving speciation (Gutschick and BassiriRad 2003, Bellard et al. 2012). Understanding the potential for management to enable communities to cope with such perturbations is a high priority, yet there is little consensus on the most effective approaches (Morecroft et al. 2012). There is a policy need highlighted at global (Convention on Biological Diversity (CBD) 2010) and national scales (Smithers et al. 2008, Dept for Environment Food and Rural Affairs 2013) for management actions that increase the resilience of ecosystems; i.e. the ability of a system to withstand or recover rapidly from disturbance (Holling 1973, Hodgson et al. 2015).

The enhancement or protection of landscape heterogeneity may promote resilient communities through increasing microclimatic variability and thus the provision of refugia under extreme weather events (Dobkin et al. 1987, Scheffers et al. 2014). Landscape heterogeneity can indeed provide very different microclimates: in Britain, for example, open habitats such as grassland and heathland can experience temperatures 5°C higher than woodlands, whilst differences in aspect can alter the temperature by 7°C (Suggitt et al. 2011). Enhanced microclimatic variability may be particularly important for invertebrates, which often respond to environmental change by altering their distribution or phenology (Van Dyck et al. 2015), rather than adapting in situ (Hill et al. 2002). Even to cope with daily variation in weather conditions, butterflies have been shown to require a diversity of habitats (Dennis and Sparks 2006), just as arboreal insects alter their positions in the canopy throughout the day (Dixon 1976). As climatic variability increases, it is likely that greater resource and microclimate variability will be needed (Davies et al. 2006, Dennis and Sparks 2006, Suggitt et al. 2015). Indeed, predictions of butterfly species turnover under climate change are vastly improved by including topographic heterogeneity in statistical models (Luoto and Heikkinen 2008). In addition, topographic heterogeneity and habitat diversity have been shown to reduce population variability (e.g. in butterflies, Oliver et al. 2010). This may be particularly important in the context of extreme events, as more stable populations with lower variability will be less likely to suffer local extinction (Pimm et al. 1988, Inchausti and Halley 2003, Oliver et al. 2012a).

In this paper, we identify which sites are most vulnerable to large community reorganizations, in terms of the drought intensity experienced during an extreme weather event, and determine whether landscape heterogeneity mediates these impacts. We focus on butterfly communities in Great Britain using the UK Butterfly Monitoring Scheme (UKBMS), which holds an extensive dataset on butterfly populations. Butterflies are an ideal taxon for this type of analysis as their ecology and taxonomy are both well studied. In addition, Great Britain is an appropriate study system as the gradient of rainfall from the north-west to south-east has been amplified in recent times, with changes of up to 20% in daily maximum rainfall, but also increased drought frequency (Marsh 1996, Rodda et al. 2010). This study focuses on an extreme drought event in 1995. The summer of 1995 was particularly hot for the UK – with the second highest mean maximum summer temperature on record, at 22.5°C (Parker et al. 1992) – and was the driest summer on record, with less than half the average rainfall across the UK (Met Office 2015). These conditions were particularly extreme in the south and east of England, although more northerly and westerly areas also experienced higher than usual temperatures and low levels of rainfall (The Parliamentary Office of Science and Technology 1995).

The impact of the extreme drought in 1995 on UK butterfly species has been studied previously using ten Environmental Change Network sites (Morecroft et al. 2002). This showed that mobile butterfly species with a southern distribution tended to increase in abundance from 1994 to 1996, whilst species with low mobility and a northern distribution tended to decline (Morecroft et al. 2002). In the current study, we used a considerably larger dataset of 122 sites across Great Britain (Fig. 1). We focused on the community level because community metrics can be efficient and statistically-powerful tools for linking change to environmental factors (Ferrier and Guisan 2006). In addition, we used a novel community metric, based upon Grime's (1974) *CSR* (Competitive – Stress-tolerant – Ruderal) classification scheme. Although this scheme was originally developed for plant communities, it has been extended to describe butterfly life history-traits and conservation status (Dennis et al. 2004).

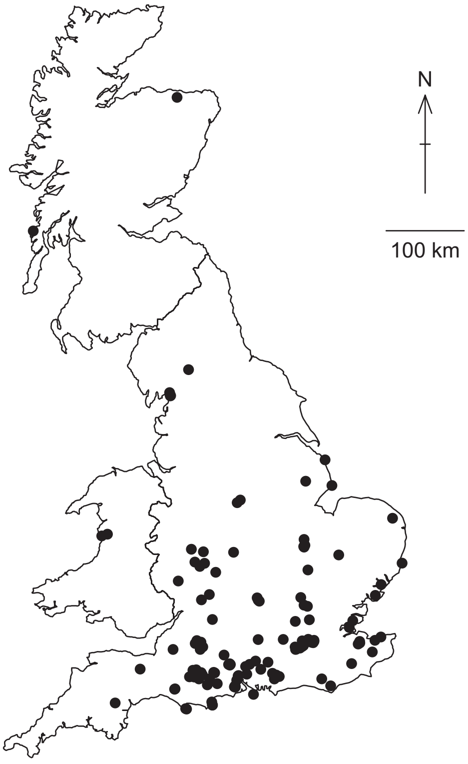

Figure 1. Map of Great Britain, showing the location of the 122 UKBMS sites used in the analysis.

We predict that during the drought year, communities will shift away from lower-mobility, host-plant specialist species (often of conservation concern) and towards more mobile, generalist species. In general, we expect the most extensive community change to be observed at sites of high drought intensity; we predict, however, that heterogeneity of the local landscape will promote resilience to these community shifts.

Material and methods

Data collation

Species abundance data were derived from the UKBMS; for a detailed methodology, see Pollard and Yates (1993). Briefly, data are collected along defined transect routes; an annual index of abundance for each species at each site is then calculated using a log-linear Poisson regression model, providing a relative index of population size (Rothery and Roy 2001). Recording coverage within the UKBMS dataset varies across time and space, and it is important to use only sites that are well sampled to ensure that the community metric will be as accurate as possible in representing the actual community composition. We therefore only included years at a site where at least ten species were recorded and representing at least 75% of the complete species list at the site, and where there were data for all years from 1992–2000. This resulted in a dataset comprising a total of 122 sites (Fig. 1) and 53 species (Supplementary material Appendix 3).

Community metrics

The community metric is based upon Grime's (1974) *CSR* (Competitive – Stress-tolerant – Ruderal) classification scheme, developed for plant communities. This theory posits that the presence of stress and disturbance in natural habitats drives plant evolution towards three functional groups: 1) competitive plants (*C*), which live in environments with low stress and low disturbance; 2) stress-tolerant plants (*S*); which grow in environments with high stress and low disturbance; and 3) ruderal plants (*R*), which exist in environments with low stress and high disturbance (Grime 1974, Hodgson et al. 1999). Dennis et al. (2004) found that the life history traits and conservation status of UK butterfly species are related to the average *C*-, *S*- and *R*-scores of their larval host plants (Table 1 and Supplementary material Appendix 1 and 2).

Using the *C*-, *S*- and *R*-scores for British butterfly species (Dennis 2010), we can describe the structure of a butterfly community by the mean *C*-, *S*-, and *R*-score across all individuals at a given location, as follows (community *C*-scores are given as the example):

$$\text{Community } C\text{ - score} = \left(\sum_{k=1}^{n} C_k \cdot N_k \right) \Bigg/ \sum_{k=1}^{n} N_k \tag{1}$$

Table 1. Life history traits of UK butterflies that are strongly correlated with the average *C, S,* and *R*-scores of their larval host plants (full list of traits including those with weaker correlations with *CSR* scores can be found in Supplementary material Appendix 1). Adapted from Dennis et al. (2004).

Traits	*C*-score	*S*-score	*R*-score
Fecundity	Short early stages; rapid development	Univoltine; fewer eggs; longer developmental time	Multivoltinism; higher egg load; rapid development
Adult life	Long lived; low adult hardiness	Short lived; adult hardiness	Short lived; adult hardiness
Mobility	Higher mobility	Lower mobility	Higher mobility
Resource use	More host plants; associated with tall plants, particularly trees	Monophagy; fewer host plants and biotope occupancy; associated with short plants	Polyphagy; more host plants; higher biotope occupancy; associated with annual, short plants
Population characteristics	Open, areally expansive, patchy population structures; relatively dense distributions	Closed, areally limited populations with typical metapopulation structures; sparse distributions; limited geographical ranges	Dense distributions and wide geographical ranges
Vulnerability	Resistance to range retractions and increasing rarity; low conservation concern	Range retractions, increasing rarity; high conservation concern	Resistance to range retractions and increasing rarity; low conservation concern

where n is the number of species in a community, C is the *C*-score of species k, and N is the number of individuals within species k. In addition, total abundance and species richness were calculated for each site.

The *CSR* metric we use here is useful because it summarises numerous functional response and effect traits into just three (non-independent) axes (Díaz et al. 2013). For example, increasing *S*-scores are highly correlated with higher conservation concern (Dennis et al. 2004), including many specialist univoltine and lower mobility species that tend to be more susceptible to environmental change (e.g. habitat fragmentation, Ockinger et al. 2010). Species with higher *R*-scores tend to be Pierids that use a number of common, ruderal plant species, while increasing *C*-scores are associated with a broader range of longer-lived butterfly species. Although simpler categorization can be informative (e.g. specialist vs generalist species; Charrette et al. 2006, Debinski et al. 2013), information is lost on other features that may influence species' responses to disturbance (e.g. adult hardiness, which tends to be associated with higher *S*- and *R*-scores but not *C*-scores). Another alternative is to use dimension reduction methods (e.g. principal component analysis) to capture the varied trait information. However, the link between butterfly life-history traits and those of their host plants are then lost, making it difficult to interpret to what extent changes in butterfly community composition may be driven by shifts in vegetation.

Environmental data

Environmental data characterizing local climate, land cover diversity and topographic heterogeneity were related to change in the community balance of *C*-, *S*- and *R*-scores during the 1995 drought. Data on landscape heterogeneity were derived from the Landcover Map 2000 (25 m resolution, Fuller et al. 2002) for four spatial extents: 0.5, 2, 5, and 10 km radii around the UKBMS transect centroid. Using information on the area of 12 land-cover types within the buffer (excluding the area of sea), a Shannon–Wiener diversity index, *H'*, was calculated (vegan package, Oksanen et al. 2011); hereafter referred to as land cover diversity. The land-cover types included the area of: arable land, bareground/rock, bracken, broadleaved woodland, coastal region, coniferous woodland, fen/bog, grassland, heathland, montane regions, river or other inland water, and the area of urban/suburban/gardens in the landscape. Topographic heterogeneity variables included standard deviations of: slope (degrees from horizontal; range 0–90), elevation (m), and northerly aspect (cos((aspect × pi)/180), where aspect ranges from 0–360°; the transformation linearises this circular variable). North-south aspect rather than east-west aspect was considered as the former is expected to have greater microclimatic variation at higher latitudes.

Three climatic variables related to moisture availability were initially investigated. Summer soil moisture deficit (mm) data were obtained from a grid-to-grid hydrological model, calculated as the difference between the field capacity of soil moisture and the actual soil moisture (Bell et al. 2009). Summer rainfall (mm) data and annual actual-to-potential evapotranspiration ratio data (APET) were interpolated to the 10 km GB Ordnance Survey grid using data from CRU TS 2.1 (Mitchell and Jones 2005) and CRU 61-90 climate (New et al. 1999) datasets. Preliminary analysis revealed that annual APET was the most appropriate variable for predicting shifts in the butterfly community composition during the extreme weather event (see Supplementary material Appendix 4 and 5 for detailed methodology and results). Results are therefore reported for APET only. As the absolute ranges of the above explanatory variables differed considerably, they were standardized to have a mean of zero and a standard deviation of one.

Statistical analysis

Long-term trends in community composition

The data were assessed for long-term trends in community composition, to ensure that this did not confound inferences about the discrete event (Magurran et al. 2010). Linear mixed effects models were constructed for the community *C*-, *S*-, and *R*-scores (lme4 package, Bates et al. 2015) with year as a fixed continuous effect and site as a random effect. Significance values were calculated using Statterthwaite's approximation (lmerTest package, Kuznetsova et al. 2015). For total abundance and species richness, similar models were constructed, but a Poisson error distribution and canonical log-link were specified and for species richness, year was scaled prior to modelling to allow model convergence.

Calculating the community change in 1995 and 1996

The year 1995 was taken as the drought year; there was no documented drought during 1994, so this was taken as the pre-drought reference year (The Parliamentary Office of Science and Technology 1995). This was confirmed statistically using the APET time-series (Fig. 2; Supplementary material Appendix 4). The change in butterfly community composition was calculated as the difference (Δ) in the community *C-*, *S-*, and *R*-scores, total abundance and species richness, between the pre-drought year and the drought year. We similarly assessed community change between the reference year (1994) and the year after the drought (1996); however, it should be noted that the autumn and winter of 1995 were exceptionally wet (Marsh 1996, Roy et al. 2001), and the year 1996 was also drier than usual (Fig. 2), hence communities were unlikely to have returned to equilibrium (Supplementary material Appendix 6).

A Wilcoxon signed rank test was performed to examine whether the central tendency of the Δ values were significantly different from zero, with a continuity correction applied for Δ species richness to account for values with tied ranks. In addition, we assessed whether the most extreme shifts in community composition in 1995 occurred in sites with intense drought as predicted, by splitting the dataset by the median value of APET in 1995 and carrying out Wilcoxon's signed rank tests on both subsets.

Landscape heterogeneity and community change in 1995

Explanatory variables were assessed for co-linearity using Pearson's product moment correlation test (Pearson's $R \geq 0.6$ was taken as evidence of strong co-linearity). No variables showed evidence of strong co-linearity except for APET and standard deviation of elevation (at 10 km: Pearson's $R = 0.61$, $p < 0.0001$). Variables were also assessed against northing, which has been found previously to have a relationship with landscape heterogeneity in Britain (Oliver et al. 2010): only APET showed strong significant correlation with northing (at 10 km: $R = 0.63$, $p < 0.0001$).

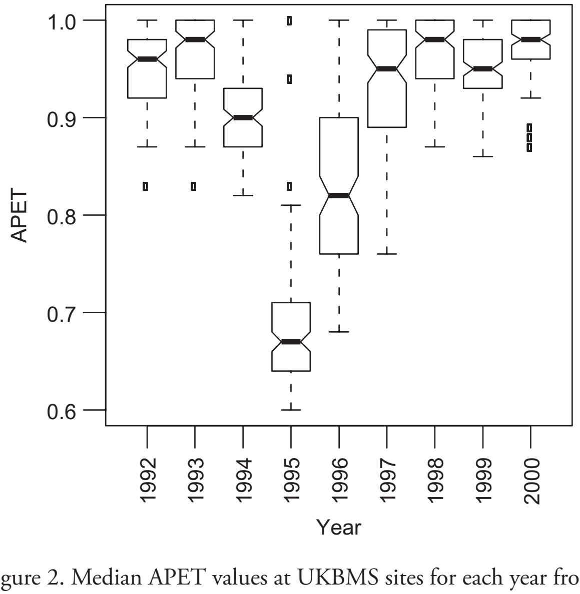

Figure 2. Median APET values at UKBMS sites for each year from 1992–2000 (n = 122).

For each spatial extent (0.5, 2, 5 and 10 km radius around sites), the change (Δ) in community *C*-, *S*- and *R*-score, total abundance and species richness, were each assessed as a function of APET (included in the models to account for spatial patterns in rainfall and mean elevation with northing), along with land cover diversity, heterogeneity of northness (aspect), and heterogeneity of slope (topography), using linear models. Δ species richness did not conform to the assumptions of normality, so was transformed using the log-modulus transformation, which maintains zero values (John and Draper 1980). Backwards stepwise model simplification was used to determine the minimum adequate model for each response variable at each spatial extent, using Akaike's information criterion corrected for small sample sizes (AICc; note that using the standard AIC metric did not change results). Furthermore, to determine at which spatial extent landscape heterogeneity has the greatest influence on community change, the models at all four spatial extents (0.5, 2, 5 and 10 km radius) were compared for each response variable using AICc. To account for multiple comparisons, we adjusted p-values using the false discovery rate method (Benjamin and Hochberg 1995, Pike 2011). There was no strong evidence of spatial autocorrelation in the residuals of any model, as assessed using Moran's *I*, nor was there evidence of overdispersion for models including a Poisson error term. All analyses were carried out using *R* ver. 3.2.2 (R Core Team). We repeated the above analysis on Δ abundance for dietary specialists and generalists separately, in order to investigate this alternative species classification (Supplementary material Appendix 9). Note that this categorisation is correlated with habitat generalism in UK butterflies (number of main biotypes used: two sample t-test, $t = -3.24$, $p < 0.01$, $n = 54$).

Results

Long-term trends in butterfly community composition

Between 1992 and 2000 (across all 122 sites), there were no trends in community *C*-scores ($t = -1.22$, $p = 0.22$), *R*-scores ($t = -1.40$, $p = 0.16$), or in species richness ($z = -0.77$, $p = 0.44$). There was very slight evidence for an upward trend in *S*-scores ($t = 1.9$, $p = 0.06$) and there was a significant negative trend in total butterfly abundance ($z = -54.98$, $p < 0.0001$).

APET and community change

In the drought year (1995), community *R*-scores and total abundance tended to increase while community *S*-scores decreased (Table 2 and Fig. 3). These changes were most pronounced in wetter sites, although total abundance tended to increase at both dry and wet sites (Table 2). By 1996, communities had not yet reached equilibrium; community *C*-scores and total abundance showed significant increases relative to the pre-drought year (1994), while community *S*-scores continued to decline (Table 2).

Table 2. Results of Wilcoxon's signed rank test, testing whether there was a significant change in community *C*, *S*, *R*-scores, total abundance and species richness between the pre-drought year (1994) and the drought (1995) or post-drought year (1996).

	Change between the pre-drought year (1994) and:			
	The drought year			The post-drought year
Metric	All sites ($n = 122$); Fig. 3	Wetter sites ($n = 54$)	Drier sites ($n = 68$)	All sites ($n = 122$)
C	No change $V = 3791$, $p = 0.92$	No change $V = 619$, $p = 0.29$	No change $V = 1370$, $p = 0.23$	Increase $V = 5502$, $p < 0.001$
S	Decline $V = 2108$, $p < 0.001$	Decline $V = 253$, $p < 0.001$	No change $V = 919$, $p = 0.12$	Decline $V = 2313$, $p < 0.001$
R	Increase $V = 5609$, $p < 0.001$	Increase $V = 1381$, $p < 0.001$	No change $V = 1299$, $p = 0.44$	No change $V = 3818$, $p = 0.87$
Total abundance	Increase $V = 5265.5$, $p < 0.001$	Increase $V = 1534$, $p < 0.05$	Increase $V = 1127$, $p < 0.001$	Increase $V = 6164$, $p < 0.001$
Species richness	No change $V = 522.4$, $p = 0.22$	No change $V = 83$, $p = 0.77$	No change $V = 194$, $p = 0.21$	No change $V = 470.5$, $p = 0.40$

Landscape heterogeneity and community change in 1995

After simplifying models, we found that the change in community *C*-scores tended to increase on sites with greater topographic heterogeneity, but tended to decline on sites with greater land cover diversity (Table 3), perhaps explaining the lack of overall change across all sites (Fig. 3). Community *S*-scores had the opposite relationship: increased topographic heterogeneity exacerbated declines in community *S*-scores, whilst increased land cover diversity mitigated declines (Table 3). Species richness and abundance also tended to decline on sites with greater topographic heterogeneity. In contrast, we did not find a significant effect of north-south aspect for any response variable. These results were maintained after accounting for multiple comparisons, except for the effect of topographic heterogeneity on ΔC scores. The best spatial extent, i.e. the model with the lowest AICc score, differed among response variables, with the largest extent preferred for models of ΔS scores and Δ abundance, and the smallest extent preferred for models of ΔC scores and Δ species richness (Table 3). However, in general larger spatial extents (5–10 km) produced models with high goodness of fit and showed consistent results within response variables. For brevity, results are only given for the two best fitting models for each response variable (Table 3, see Supplementary material Appendix 7 for full results).

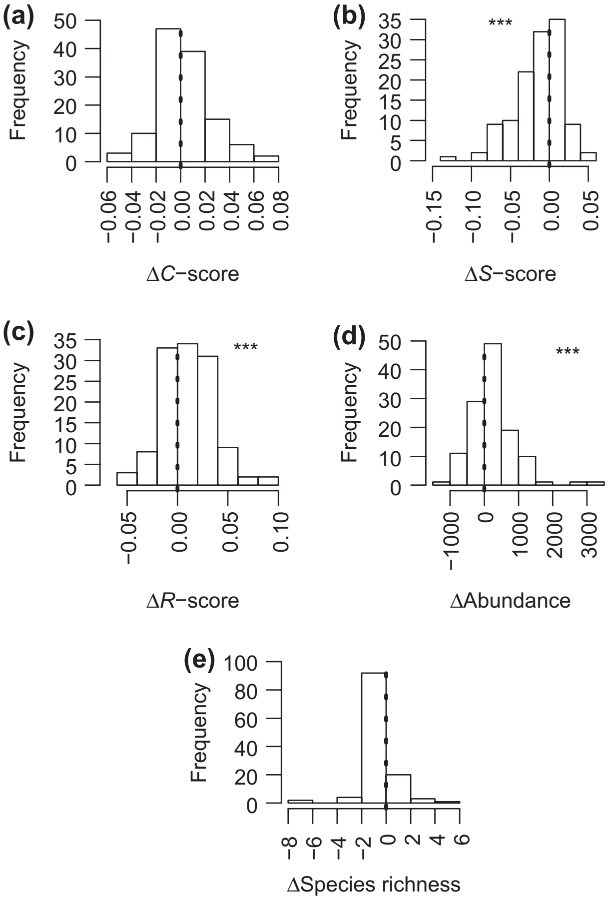

Figure 3. Frequency distributions of the change in (a–e) *C*-score, *S*-score, *R*-score, total abundance and species richness, between the pre-drought year (1994) and the drought year (1995) for all sites ($n = 122$). Asterisks indicate whether the central tendency of change was significantly different from zero ($p < 0.05$*, $p < 0.01$**, $p < 0.001$***). Position of asterisks indicates whether the direction of the central tendency of change was positive or negative.

When the dataset was split into dietary generalists and specialists, we could not detect many of the effects of landscape heterogeneity on change in abundance during the drought year, particularly for generalist species (Supplementary material Appendix 9). This is not surprising given the different responses of species with higher *C*- and *R*-scores; although these species tend to be dietary generalists, they also differ in many life-history traits as well as in their preferred larval host plants (Table 1).

Discussion

We have demonstrated that during the extreme drought of 1995, Britain saw significant shifts in butterfly community structure, moving away from univoltine, monophagous, early successional species of high conservation concern (species with higher *S*-scores; Table 1) and towards multivoltine, short-lived, generalist species (species with higher *R*-scores), as predicted. By 1996, butterfly communities had still not reached equilibrium; communities continued to show shifts away from species of higher conservation concern, but with shifts towards highly mobile, longer-lived species (associated with higher *C*-scores). Such shifts away

Table 3. Coefficient estimates for effects of landscape heterogeneity on the change in community structure during an extreme drought event ($n = 122$). Significance is indicated by asterisks ($p < 0.05$*, $p < 0.01$**, $p < 0.001$***); statistics are emboldened when statistical significance was supported after correction for multiple comparisons. Note that for Δ *R*, only results for one spatial extent are given as all models were identical.

Response	Intercept	APET	*H′*	Std aspect	Std slope	Buffer size	AICc
Δ *C*	–0.0023	–	–	–	0.088**	0.5 km	–575.82
	0.0032	–	**–0.0060****	–	0.0041*	10 km	–574.65
Δ *S*	**–0.034*****	**–0.0080***	**0.0077****	–	**–0.0065***	10 km	–514.81
	–0.034***	**–0.0089****	0.0063*	–	–0.0063*	5 km	–512.93
Δ *R*	**0.035*****	**0.011*****	–		–	5 km	–567.87
Δ abundance	**220.41*****	–	–	–	**–129.24***	10 km	1927.2
	227.65***	–	–	–	–86.26	5 km	1930.39
Δ species richness	**0.066***	–	–	–	**–0.89***	0.5 km	15.32
	–0.096	–0.056*	–	–0.059	–	10 km	17.65

from specialist species of conservation concern are even more marked given there was no long-term trend (but very slight evidence of a positive trend) in community *S*-scores. Extreme drought is known to have severe impacts on certain butterflies (Oliver et al. 2015), but anecdotal evidence also suggests that these impacts can have long lasting effects on communities. For example, historical UK biological records show that many UK butterflies suffered steep declines following a severe drought in 1976, from which they have yet to recover (Fox et al. 2015). A lack of spatially- and temporally-replicated monitoring data over that early period, however, prevents quantitative analysis linking community changes to landscape heterogeneity as we present here.

The changes in community composition that we document from the 1995 drought were accompanied by increased total abundance relative to the pre-drought reference year. Given the significant negative long-term trend in abundance, this suggests, on balance, a substantial benefit of increased temperatures for these insects (Pollard and Moss 1995, Roy et al. 2001, Morecroft et al. 2002). The shifts in community composition during the drought year were most extensive at wetter, cooler sites (with high actual-to-potential evapotranspiration ratio, APET). Whilst counter to our prediction, this result is consistent with previous research: Debinski et al. (2006, 2013) found that the most prominent changes in butterfly communities during a drought were in wet rather than dry meadows, potentially driven by shifts in vegetation towards drought-tolerant plants. Indeed, plant community change in response to climatic perturbations can be more extreme in wetter rather than drier sites (Kardol et al. 2010), while the condition of plants and their suitability as butterfly host-plants may also be affected (Gibbs et al. 2012). It is likely that the observed changes in butterfly communities were similarly driven by shifts in vegetation composition or condition (Dennis 2010). Annual plants tend to be the preferred host plant of the generalist, short-lived butterflies associated with high *R*-scores. The increased abundance of annual plants (especially those that were not moisture limited) during the 1995 drought (Morecroft et al. 2002, 2004) may therefore have mediated the shift in community composition towards these butterfly species and, as a result, away from species with higher *S*-scores, which as larvae more often feed on plants growing in open short-turf habitats (Dennis et al. 2004, Kemp et al. 2008). In addition, wetter sites may have seen increased survival of the subsidiary host plants of generalist species associated with higher *R*-scores (Kardol et al. 2010) resulting in greater dominance of these species at wetter sites (Supplementary material Appendix 8).

Concurrent declines in more specialist, threatened species through increased mortality and/or emigration may have also contributed to community shifts (away from community *S*-scores) at wetter sites. During the drought-year, the increased vegetative growth of annual plants that were not moisture-limited (Morecroft et al. 2002, 2004) could result in microclimatic cooling; this can reduce habitat availability for insects associated with open, short-turf habitats, typical of species with high *S*-scores (Wallisdevries and Van Swaay 2006, Oliver et al. 2012b, Supplementary material Appendix 2).

The propensity for strong community changes in these wetter sites may also be because they are more northerly. At range margins, populations tend to be more sensitive to climate and are characterized by high temporal variability and synchronous dynamics across space (Thomas et al. 1994, Powney et al. 2010, Oliver et al. 2012b). Increased synchrony in more northerly sites could therefore correspond to less stable metapopulations with greater susceptibility to extreme weather conditions. This could be particularly relevant for specialist species of conservation concern (with high *S*-scores), which often have metapopulations (Table 1, Dennis et al. 2003, 2004) and synchronous dynamics (Franzén et al. 2013).

It is important to note that our sample does not include many western and northern sites where there are extreme specialists for wet sites, such as *Erebia aethiops* and *Coenonympha tullia*, which also have high *S*-scores. Community shifts may therefore be different in these areas. Additionally, we cannot discount that our results could in part be affected by differences in species detectability during the drought year (i.e. differences between species in the way drought affects individual movement rates; Dennis et al. 2006, Dennis and Sparks 2006). Movement of individuals across landscapes and concentration into wetter sites could also explain some of these changes in abundance (Debinski et al. 2001). In addition, it is not possible to attribute shifts in community composition to the drought event with complete certainty; a number of other environmental changes could have affected species in that year.

Nonetheless, our results suggest that although policy makers are concerned about the ecological effects of extreme drought in already dry locations, in butterfly communities at least, wetter locations may be just as or even more vulnerable to large community reorganizations. Policy makers and land managers may therefore want to consider ways to promote resilience in these regions, which may in turn promote ecosystem stability.

It is still unclear how best to manage these landscapes in order to promote resilient ecosystem functions, however. One suggestion is to promote (or prioritise) landscape heterogeneity (Smithers et al. 2008, Oliver et al. 2010). Our results suggest that land cover diversity and topographic heterogeneity may have mediated community change in the drought event but with varying effects on different components of the butterfly community. Topographic heterogeneity promoted a shift during the drought year towards long-lived, highly mobile species (with higher *C*-scores) and away from shorter-lived, specialist species of high conservation concern (with higher *S*-scores), along with declines in species richness and abundance. One possible explanation for this is as follows. Steep slopes are generally more resistant to invasion by competitive plant species (the host plants of butterfly species with high *C*-scores) due to nutrient limitation (Bennie et al. 2006). In drought years, however, they may become inhospitable even for stress-tolerant (*S*-score) plant species, due to their thinner soils, with implications for the butterflies they support. In areas with higher topographic heterogeneity, competitive plants may still thrive leading to a greater balance of butterfly species with higher *C*-scores as these disperse outwards from the microclimatic refugia (McLaughlin et al. 2002, Oliver et al. 2010).

Increased land cover diversity on the other hand, was correlated with shifts away from long-lived, mobile species (associated with higher *C*-scores), but mitigated the relative declines in community *S*-scores, perhaps by providing increased resource availability, which may enable persistence of specialist, monophagous species (associated with higher *S*-scores) through the extreme weather event (Shreeve and Dennis 2011). These species may disproportionally benefit from local land cover diversity given their limited dispersal ability (Menéndez et al. 2007). At the landscape scale, land cover diversity may increase the resilience of metapopulations to perturbation by providing refugia and reducing widespread synchronized extinctions driven by extreme weather (Powney et al. 2010).

The effects of landscape heterogeneity on community change were not apparent across all spatial extents tested. Statistical models fitted to environmental data at larger spatial extents (between 5 and 10 km) most often had the highest goodness of fit (based on Akaike's information criterion corrected for small sample sizes), and results were consistent at these extents. This suggests that enhancing or prioritizing land cover diversity will be needed at relatively large spatial scales, even though the butterflies most likely to benefit tend to have low mobility (higher *S*-scores). There were, however, some inconsistencies among spatial extents. The smallest spatial extent had the highest goodness of fit (lowest AICc score) for two response variables (change in community *C*-scores and species richness), where strong effects of heterogeneity of slope but not land cover diversity were evident, although these were only marginally better than the largest extent. It is possible that our measure of land cover diversity is too coarse, limiting our ability to detect relationships at smaller spatial extents. For instance, the importance of land cover diversity is likely to have been underestimated in this study; the identity of elements that comprise the diversity index were not investigated and neither was the quality and diversity within these elements. These data are currently not available across multiple widespread sites, but such refined measures would help to identify more specific management options at appropriate scales that improve the ability of butterfly communities to cope with extreme weather events. It is also possible that landscape heterogeneity may have greater effects on the recovery of communities from extreme weather events, but this was not explored here. Such research could further enhance our understanding of the ecological impacts of extreme weather events (Nimmo et al. 2015).

The CSR-community metric used here has proven useful for linking ecological traits (including trophic interactions) and responses to external drivers. The metric could be used to investigate changes in ecosystem functioning with climatic variation if the community *C*-, *S*- and *R*-scores are also functional effect types, that is, types that differentially influence ecosystem properties or services (Díaz et al. 2013). Our results indicate that the community metric is more sensitive to change than species richness and perhaps abundance, although an evaluation of its robustness to using presence only data would be useful. Many previous studies have used a categorization that separates butterflies out into specialist and generalist categories to assess responses to habitat fragmentation or environmental change (Warren et al. 2001, Menéndez et al. 2006). Here, we tested a classification based on dietary breath (that strongly correlated with habitat breadth) with regards to community responses to drought, but found it lacked the sensitivity to detect the effects of landscape heterogeneity on responses (Supplementary material Appendix 9). Dietary breadth is only one aspect of butterfly life-history that can influence response to disturbance, failing to incorporate explicit links to host plant traits and may therefore reduce power to detect correlates of vulnerability or resistance to extreme weather events.

Our investigation provides insight into what factors contribute to the resilience of communities under extreme weather events. We show that the extreme drought of 1995 resulted in significant shifts in butterfly community composition, particularly in wetter sites, and that by 1996, communities had yet to return to equilibrium. Furthermore, our results suggest that the promotion of landscape-level land cover diversity may enhance the resilience of communities. The results for topographic heterogeneity were however, counter to our expectations; perhaps because, compared with land cover diversity, the two states do not provide the same opportunities or lack of them from a resource-based habitat viewpoint. Further research into this, and alternative management options, is vital if we are to maintain resilient ecological communities in a future of more frequent extreme weather events.

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Supplementary material (Appendix ECOG-02228 at <www.ecography.org/appendix/ecog-02228>). Appendix 1–9.