

# Population resilience to an extreme drought is influenced by habitat area and fragmentation in the local landscape

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Most studies on the biological impact of climate change have focussed on incremental climate warming, rather than extreme events. Yet responses of species' populations to climatic extremes may be one of the primary drivers of ecological change. We assess the resilience of individual populations in terms of their sensitivity to- and ability to recover from- environmental perturbation. We demonstrate the method using a model species, the ringlet butterfly *Aphantopus hyperantus*, and analyse the effects of an extreme drought event using data from 79 British sites over 10 yr. We find that populations crashed most severely in drier regions but, additionally, the landscape structure around sites influenced population responses. Larger and more connected patches of woodland habitat reduced population sensitivity to the drought event and also facilitated faster recovery. Having enough, sufficiently connected habitat appears essential for species' populations to be resilient to the increased climatic variability predicted under future scenarios.

Around the world, local climates are changing with measurable impacts on biodiversity (Root et al. 2003). In understanding and predicting the effects of climate change most studies focus on average changes in temperature and rainfall as these are easier to assess (Jentsch et al. 2007). However, marked increases in climatic variability are also predicted under climate change scenarios, leading to an increased frequency of climatic extremes (IPCC 2007). Extreme climatic events, such as intense prolonged drought, can have drastic effects on the structure of species communities (Tilman and Haddad 1992, Morecroft et al. 2002, Archaux and Wolters 2006, Jiguet et al. 2011). For example, in the UK, an intense summer drought in 1995 (the driest April–August in England and Wales since records began in 1800; NERC Inst. of Hydrology 1996) led to marked declines in insect species associated with cooler and wetter microclimates, whilst other types of species benefited (Morecroft et al. 2002).

Long term effects on biodiversity as a consequence of more frequent drought events are little understood. However, they are likely to have subsequent effects on the ecosystem services provided by biodiversity and, hence, have immediate relevance to human well being (Archaux and Wolters 2006). Under global warming, the frequency of summer droughts is likely to increase (IPCC 2007). Given the potential negative impacts and increasing risk of droughts, it is imperative to pre-emptively identify ways to improve resilience to extreme events. 'Resilience' is often defined as the amount of disturbance a system can absorb and still remain in the same

state or domain of attraction (Holling 1973), or the ability of a system to return to a pre-disturbed state (Pimm 1984). These are both systems-level definitions, but in practice it is difficult to measure a whole system simultaneously; individual populations are components of the system which can be feasibly measured, for example, through long-term species monitoring schemes. In this study we propose to measure population resilience as the ability to withstand and recover from environmental perturbation; specifically, in this case, an extreme drought event in 1995.

To increase population resilience, one strategy is to alter land management at a landscape scale; because effects of environmental change on species operate not only locally but also at broader spatial scales (Tscharntke et al. 2005, Heard et al. 2007, Oliver et al. 2010). However, to do this, we need to understand how landscape structure can influence resilience to extreme events such as drought. To date, there has surprisingly been little research in this area.

Here, we consider a model species, the ringlet butterfly *Aphantopus hyperantus*, a grass-feeding lepidopteran commonly found close to woodland edges and known to be susceptible to drought effects (Sutcliffe et al. 1997, Morecroft et al. 2002). For the 1995 UK drought event, we quantify how the area and configuration of woodland in local landscapes influence population resilience, in terms of sensitivity to drought (the magnitude of population decline following the drought) and recovery from drought (the rate of population increase following the crash). Previous work on this species showed that an extreme drought event in 1976

caused retractions from open non-wooded sections of a single site (Sutcliffe et al. 1997). We predict that populations across 79 different sites will be more resilient to drought when landscapes have a greater total area of – and less fragmented – woodland. These landscapes are expected to provide a broader range of resources and microclimates that are accessible to individuals (Oliver et al. 2010, Hodgson et al. 2011) as well as improved functional connectivity allowing rescue effects (Hanski 1999).

## Material and methods

### Data collation

*Aphantopus hyperantus* populations in the UK suffered delayed responses to the 1995 drought and crashed in 1996 (Morecroft et al. 2002). We extracted annual abundance indices for *A. hyperantus* from the UK Butterfly Monitoring Scheme for the years 1990–1999 (i.e. six years before 1996 drought impact and three years after). We selected 10 yr of data to obtain a balance between more years per site to accurately assess a pre-drought population trend and a higher sample size of UKBMS sites with sufficient temporal coverage for analysis. We repeated our results with different time windows to test for sensitivity to the temporal window selected for analysis.

The transect methodology involves counting butterflies for up to 26 weeks  $\text{yr}^{-1}$  at each site in conditions suitable for butterfly activity (Pollard and Yates 1993). For sites with sufficient data, an annual index of abundance was calculated for each year (Rothery and Roy 2001). In this study, we only analysed sites which had a complete set of annual indices between 1990 and 1999.

Drought conditions in 1995 were not uniform across the UK and we expected that butterflies at less droughted sites might respond differently. Therefore, we assessed the 1995 APET value of each site ('APET', the ratio of actual to potential evapotranspiration, gives an estimate of annual drought conditions at each site). Annual APET values were obtained from 10 km interpolation on a GB Ordnance Survey grid from the CRU ts2.1 dataset (Mitchell and Jones 2005).

We quantified the structure of broadleaved woodland at 0.5 and 2 km around the centroid of butterfly monitoring sites using 25 m resolution remotely sensed land cover data (LCM 2000, Fuller et al. 2002). These spatial scales were chosen because local landscape attributes have been found to have stronger associations with population dynamics in this species (Oliver et al. 2010). However, for completeness we also tested for effects of landscape attributes at wider scales of 5 and 10 km around sites (Supplementary material Appendix 1, Table A2, A3). For each landscape buffer, we calculated the total area of woodland, the number of individual patches, the mean 'edginess' of patches (based on a standardised perimeter-area ratio, where actual perimeter length is considered relative to the minimum possible perimeter length for a given habitat area, i.e. larger values indicate more 'edgy' habitat patches), and the mean isolation of patches (defined as the mean Euclidean distance nearest neighbour distance based on shortest edge–edge distances).

Metrics were calculated using the software FRAGSTATS (McGarigal et al. 2002).

### Population sensitivity to drought

To assess the extent of *A. hyperantus* population crashes, whilst taking into account long-term population trajectories at each site, we fitted a linear model to the yearly counts, excluding the year 1996. Population trends varied between sites, with a large number of populations (71%) showing increases, possibly due to recent increases in mean temperatures (i.e. incremental warming) or improved habitat management (Roy et al. 2001). In preliminary analyses, we tested for effects of density dependence on population growth rates (regression of  $\log(N_t/N_{t-1})$  versus  $N_{t-1}$ , where  $N$  is population density in year  $t$ ; Schtickzelle and Baguette 2004). We found only a small proportion of the population time series (18%) showed significant density dependence (at  $p < 0.05$ ). In addition, in an analysis comparing linear and quadratic models to explain population trends over time (i.e. regression of  $N_t$  on year), we found that linear models produced the best fit population trends (in 95% of cases; Supplementary material Appendix 1, Table A1). This is not to say that density dependence is not an important regulatory demographic process for this species, but over the time periods and range of densities on our sites, and relative to other factors (e.g. weather and habitat quality), there is little evidence of curvature in population trends expected under a strong influence of density dependence. We therefore used a linear model to predict the expected count in 1996 had no drought event occurred (Fig. 1). The difference between the expected count and the observed count in 1996 gives an indication of local

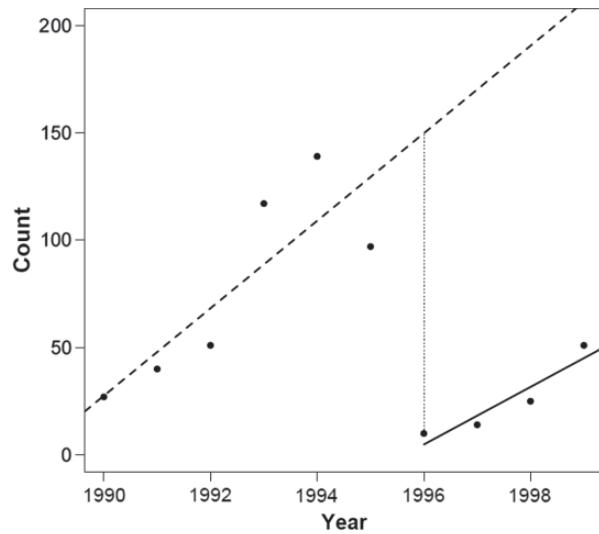


Figure 1. Demonstration of the method for assessing population sensitivity and recovery to an extreme event. A linear model (dashed line) is fitted to butterfly counts over time for the years preceding the population crash from the extreme event (1996 in this case). The sensitivity to drought is assessed as the difference between the observed count in 1996 and the expected count had no drought event occurred (dotted line;  $\Delta_{1995-6}$ ). The recovery is assessed as the rate of population growth in the three years following the crash (solid line).

butterfly sensitivity to the drought event (hereon referred to as ' $\Delta_{1995-6}$ '). Sites with higher mean abundance are likely to have greater  $\Delta_{1995-6}$  scores for the same percentage decline than sites with lower mean abundance. Therefore, in our statistical models of population sensitivity with  $\Delta_{1995-6}$  as a response variable we included the expected count in 1996 as a control explanatory variable in order to model relative population decline adjusted for population size. However, for ease of interpretation, when plotting our results we use percentage change. Because the level of drought at each site was likely to affect the extent of population change we also included the 1995 APET value of each site as a control covariate in our models of population sensitivity. We initially fitted a linear regression model with these two control variables as the explanatory variables and  $\Delta_{1995-6}$  as the response using the program R (R Development Core Team). Taking residuals from this model allowed us to assess the sensitivity of each population to the drought event. We mapped these sensitivity scores and there was no strong spatial patterning across southern Britain (Fig. 2a).

Next, we included woodland cover explanatory variables (area, number of patches, 'edginess' and patch isolation) in the statistical models along with the control covariates described above. We fitted a separate model for woodland cover assessed at 0.5, 2, 5 and 10 km scales. Only sites with woodland present in the selected landscape buffer could be used to assess woodland spatial configuration, so sample sizes were smaller for the 0.5 km landscape radius. Significance of woodland explanatory variables was obtained by stepwise deletion but always keeping the control covariates in the statistical model. A separate model was fitted for woodland data at each spatial scale. For all models, we tested for collinearity between explanatory variables using a Pearson's correlation test. At spatial scales of 0.5 and 2 km radius all correlation coefficients between explanatory variables were  $<0.7$ . At spatial scales of 5 and 10 km radius the isolation of woodland patches was negatively correlated with the number of patches (Pearson's  $r < 0.7$ ). Therefore,

it was necessary to retain only one of these variables and we chose to retain number of woodland patches because this variable had greater explanatory power than patch isolation for the models fitted at smaller spatial scales.

## Population recovery from drought

To assess *A. hyperantus* population recovery from drought we fitted a linear model to the population count in 1996 and the subsequent three years (Fig. 1). We only assessed recovery for populations that suffered a decline following the drought event (i.e. ' $\Delta_{1995-6} > 0$ '), hence sample sizes are slightly smaller than in our analysis of sensitivity to drought. We used the rate of change in this linear model as our measure of population recovery. We also assessed whether population recovery was complete within the three year period by comparing the expected abundance in 1999 from our pre-drought population model versus the expected abundance in 1999 from this post drought model.

Due to density dependence in butterfly growth rates, the extent of the population crash following the drought event would be likely to affect recovery rates (e.g. smaller populations further from carrying capacity would be expected to recover fastest). Therefore, with recovery rate as our response variable in a linear regression model, we included the magnitude of the crash following the drought event ( $\Delta_{1995-6}$ ) and the absolute abundance in 1996 as control covariates (these two variables were only weakly correlated with each other; Pearson's  $r = 0.30$ ,  $n = 66$ ). Taking residuals from this model allowed us to assess the recovery of each population from the drought event. We mapped these recovery scores and there was no strong spatial patterning across southern Britain (Fig. 2b).

Next, we included the woodland cover explanatory variables in the statistical models, in addition the control covariates described above. We fitted a separate model for woodland data at each spatial scale.

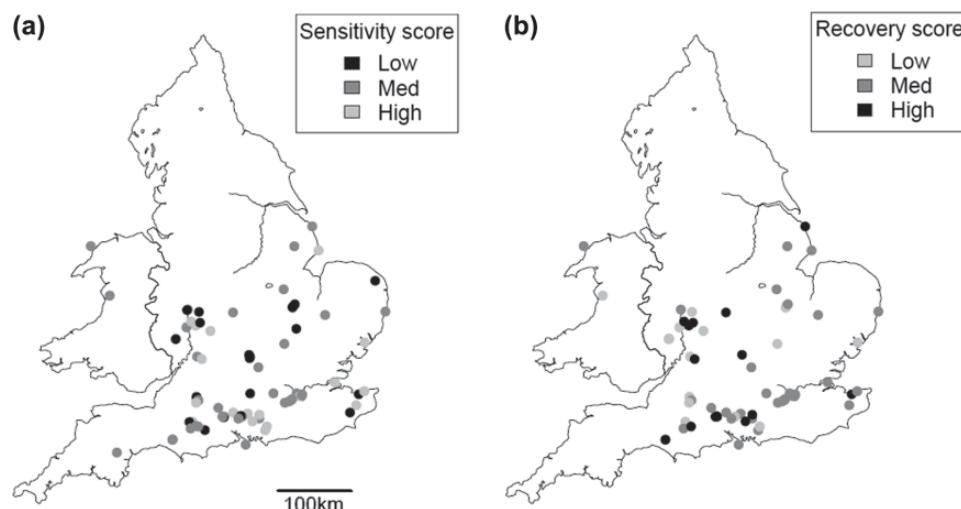


Figure 2. Maps of (a) population sensitivity to –, and (b) population recovery from – the 1995 drought event. Population scores for sensitivity and recovery were grouped into three classes based on score quartiles: Low = bottom quartile; Medium = middle quartiles; High = upper quartile. Shading indicates the level of population resilience, with black circles indicating sites greater resilience to the extreme event.

In all statistical models, the model residuals were assessed for normality and we tested for spatial autocorrelation using the ncf package in R (Bjornstad 2009). Spatial autocorrelation was only evident for the population recovery model with woodland structure assessed at 2 km radius (Supplementary material Appendix 1, Fig. A1–A4). In this case, we fitted the same explanatory variables but in a mixed effects model with 10 km neighbourhood as a random effect (using the lme4 package in R; Bates et al. 2008). This removed the significant spatial autocorrelation and we present results of both the standard linear and the mixed effect model. Significance values of model coefficients in the mixed effects model were estimated using Markov Chain Monte Carlo simulations with  $10^4$  iterations.

## Results

### Population sensitivity to drought

Across all sites tested, the majority of *A. hyperantus* populations showed marked declines between 1995 and 1996.  $\Delta_{1995-6}$  scores tended to be positive, indicating that observed counts in 1996 were lower than expected had the drought not occurred (Wilcoxon signed ranks test to show that median  $\Delta_{1995-6}$  scores were significantly different from zero:  $V = 2952$ ,  $p < 0.001$ ,  $n = 79$ ). In 1996, populations declined in 66 out of 79 sites. However, the degree of population decline tended to vary across the species range. In locations that suffered less drought in 1995 (higher APET values), population declines were often less marked. Hence, in our linear regressions explaining  $\Delta_{1995-6}$  scores, site APET value had a negative coefficient (for the statistical model assessing woodland cover at 0.5 km radius: APET coefficient =  $-502.1$ , SE =  $228.6$ ,  $t = -2.197$ ,  $p = 0.033$ ; at 2 km radius: APET coefficient =  $-137.3$ , SE =  $253.5$ ,  $t = -0.54$ ,  $p = 0.59$ ).

The expected count on a site in 1996 was also strongly correlated to the absolute decline in 1996 ( $\Delta_{1995-6}$ ). Sites with larger mean populations tended to suffer larger absolute

declines (for the statistical model assessing woodland cover at 0.5 km radius: expected count in 1996 coefficient =  $0.37$ , SE =  $0.06$ ,  $t = 6.39$ ,  $p < 0.001$ ; at 2 km radius: expected count in 1996 coefficient =  $0.33$ , SE =  $0.06$ ,  $t = 5.84$ ,  $p < 0.001$ ). Hence, including the expected count in 1996 as a covariate was important and allowed us to consider the relative decline in populations adjusting for mean size.

Regarding the effect of woodland cover, there was a strong association between woodland area and population sensitivity to drought, whereby populations in more wooded landscapes suffered smaller population declines (Fig. 3a). This effect was strongest for woodland assessed at 0.5 km around sites but was also highly significant for woodland cover assessed at 2 km radius around sites (Table 1). The spatial configuration of woodland patches in the local landscape also influenced sensitivity of butterfly populations to drought. Where woodland was fragmented into a larger number of separate patches and where patches were more ‘edgy’ i.e. greater perimeter-area ratio, population crashes were more marked. These spatial configuration effects were significant when woodland was assessed at 2 km radius around sites but not 0.5 km radius (Table 1). For both spatial scales, we tested model residuals and found no evidence of spatial autocorrelation.

### Population recovery from drought

Of the 66 population crashes following the drought event, 54 populations showed positive recovery in the subsequent 3 yr, whilst 12 populations continued to decline. Only 22 out of the 66 populations recovered completely to expected pre-drought population levels. Both the magnitude of the crash following the drought event ( $\Delta_{1995-6}$ ) and the absolute abundance in 1996 ( $Obs_{1996}$ ) had an effect on the rate of population recovery in the subsequent three years following the drought impact. Populations that suffered larger declines following the drought event and those that resulted in lower abundance showed faster rates of recovery (e.g. in the 2 km radius model where  $n = 66$ ,  $\Delta_{1995-6}$  effect on recovery

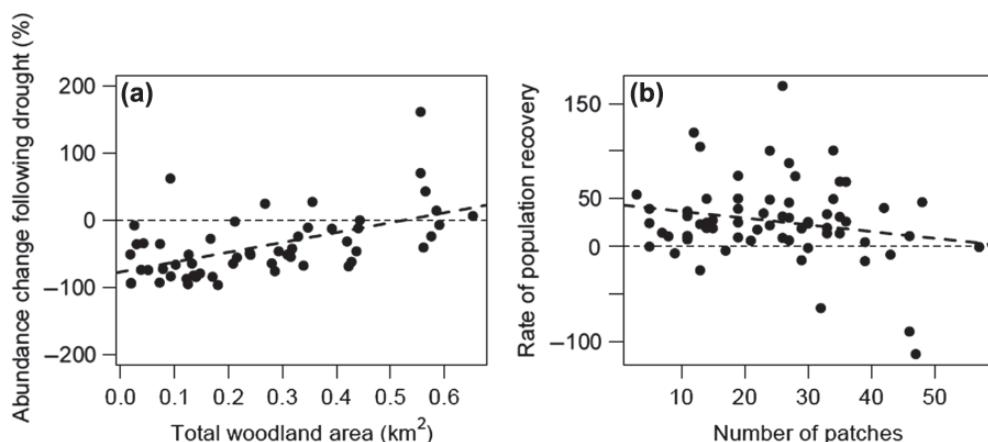


Figure 3. Population resilience of *Aphantopus hyperantus* to an extreme drought event in terms of (a) sensitivity and (b) recovery in relation to woodland habitat area and configuration in the local landscape. Panel (a) shows that populations are most sensitive to drought events where there is less woodland in the surrounding area (0.5 km radius). Panel (b) shows that population recovery is fastest where woodland patches are not fragmented (2 km radius).

Table 1. Association between woodland area and fragmentation and the sensitivity of *Aphantopus hyperantus* populations to an extreme drought event. The sign of the coefficients indicate that the decline in butterflies following the drought event is less marked when there is more broadleaved woodland around surrounding monitoring sites and where woodland is less fragmented (in terms of number of patches and the ‘edginess’ of each woodland patch).

BW variable	Spatial scale (km radius)	n	Coefficient	SE	t	p
Area	0.5	56	-414.70	84.63	-4.90	<0.001 ***
Area	2	79	-38.53	10.52	-3.66	<0.001 ***
Number of patches	0.5	56	12.86	8.84	1.46	0.152
Number of patches	2	79	3.14	1.33	2.35	0.022 *
Patch ‘edginess’	0.5	56	46.6	80.7	0.58	0.566
Patch ‘edginess’	2	79	217.9	105.6	2.06	0.043 *
Patch isolation	0.5	56	-0.12	0.14	-0.91	0.369
Patch isolation	2	79	-0.14	0.15	-0.92	0.360

rate: coefficient = 0.12, SE = 0.04, t = 3.02, p = 0.004; Obs<sub>1996</sub> effect on recovery rate: coefficient = -0.06, SE = 0.03, t = -2.8, p = 0.042). This suggests a negative density dependent growth rate, with more rapid growth in smaller populations.

Regarding the effect of woodland cover, sites with a greater area of woodland (measured at 0.5 km radius) showed faster population recovery, although this association was not significant for woodland area measured at 2 km radius (Table 2). In contrast, the spatial configuration of woodland patches was important for population recovery and the effect was strongest at the larger spatial scale of 2 km radius. When woodland in the local landscape was fragmented, in terms of an increased number of patches and increased distances between patches, recovery rates were slower (Table 2, see Fig. 3b for an example of the effect of number of patches, the variable with the strongest association).

Some spatial autocorrelation was evident in the model residuals for the population recovery model with woodland structure assessed at 2 km radius. Fitting a mixed effects model with 10 km neighbourhood as a random effect removed this spatial autocorrelation (Supplementary material Appendix 1, Fig. A4), and we obtained qualitatively similar results for the effects of our explanatory variables on population recovery (Table 2).

## Discussion

We have shown that, for a drought susceptible species, habitat area and configuration in the local landscape can influence population sensitivity to – and recovery from – drought events.

The 1995 drought event had a large impact on *Aphantopus hyperantus*, with 84% of populations having lower abundance in the following year. Smaller population declines occurred on sites nested in landscapes with a greater total area of woodland and where woodland was less fragmented. Following these population crashes, 18% of populations continued to decline in the subsequent three years. The majority of populations showed positive recovery, although only 33% of populations showed complete recovery to pre-drought population levels within three years. In Europe, previously infrequent extreme summer heatwaves and prolonged droughts are expected to become the norm, with summer temperature extremes that previously once occurred every 500 yr are now projected to occur every other year (Stott et al. 2004). We found that 66% of *A. hyperantus* populations did not show complete recovery within three years, suggesting that this species is likely to suffer long-term declines under such an altered climate. Population recovery of the species was affected by woodland structure, with

Table 2. Association between woodland area and fragmentation and the recovery of *Aphantopus hyperantus* populations from an extreme drought event. The sign of the coefficients indicate that recovery is fastest when there is more broadleaved woodland surrounding the monitoring sites and where woodland is less fragmented (in terms of number of patches and the average isolation of each woodland patch). Models highlighted with the symbol † indicate mixed effects models with a random term for 10 km neighbourhood to account for spatial autocorrelation.

BW variable	Spatial scale (km radius)	n	Coefficient	SE	t	p
Area	0.5	47	114.78	42.58	2.70	0.010 *
Area	2	66	5.32	4.24	1.26	0.215
Area <sup>†</sup>	2 <sup>†</sup>	66	5.46	4.55	1.20	0.246
Number of patches	0.5	47	-3.91	3.66	-1.07	0.291
Number of patches	2	66	-1.71	0.60	-2.83	0.006 **
Number of patches <sup>†</sup>	2 <sup>†</sup>	66	-1.17	0.57	-2.05	0.006 **
Patch ‘edginess’	0.5	47	-0.5	37.0	-0.01	0.989
Patch ‘edginess’	2	66	-25.0	30.4	-0.82	0.129
Patch ‘edginess’ <sup>†</sup>	2 <sup>†</sup>	66	-54.3	34.4	-1.58	0.120
Patch isolation	0.5	47	0.08	0.05	1.80	0.079
Patch isolation	2	66	-0.14905	0.06798	-2.193	0.032 *
Patch isolation <sup>†</sup>	2 <sup>†</sup>	66	-0.05	0.06	-0.78	0.037 *

recovery facilitated by larger and less fragmented surrounding woodlands. Hence, fragmented landscapes are clearly affecting the resilience of this species.

These effects of habitat area and configuration on population sensitivity and recovery fit with previous ecological theory because larger areas of habitat are likely to provide a broader range of resources and microclimates (Oliver et al. 2010, Hodgson et al. 2011). Increased heterogeneity in larger habitat patches mean that there are more likely to be refuge microclimates where butterflies and their host plants can survive (or at least remain as high quality food sources, under the ‘plant vigour’ hypothesis; Price 1991, Gutbrodt et al. 2011). Larger habitat patches may also offer a greater total amount of resource, facilitating rapid population recovery following environmental perturbation. We found evidence for density dependent recovery rates suggesting that smaller populations are less limited by density dependent factors (such as lack of resources). The magnitude of decline caused by the drought event ( $\Delta_{1995-6}$ ) as well as the post-drought population size ( $Obs_{1996}$ ) were both significantly correlated with recovery rates. However, it was the magnitude of population decline that was a much stronger predictor, indicating that density dependence processes might vary between sites. For example, in larger habitat patches, small populations should have even more resources available to promote rapid population growth. Note that we also tested for non-linearity in density dependent effects to explore for the possibility of Allee effects (Kuussaari et al. 1998, Piessens et al. 2009), but we found no evidence for this (unpubl.).

In addition to the effects of habitat area on population sensitivity to- and recovery from- drought events we also found evidence that the spatial configuration of habitat was important. Sites surrounded by more fragmented woodland, in terms of number of patches and patch ‘edginess’, suffered larger declines as a consequence of the drought event. This suggests that smaller habitat patches may suffer from edge effects that may be exacerbated during these extreme events (Herbst et al. 2007). The denser and shadier vegetation more likely to be provided by larger habitat patches can provide cooler and moister conditions (Rowe 2007), and this appears to be particularly important with regards for *A. hyperantus* sensitivity to drought events. Butterfly population recovery was also affected by woodland spatial configuration, with a larger number of patches and increased distances between patches hampering recovery. This result fits with expectations from ecological theory that landscapes with a greater degree of ecological connectivity allow rescue effects to occur after local population crashes (Hanski 1999, Doerr et al. 2011).

In our analyses we included a number of control variables, such as the extent of local drought (measured by annual APET value), the expected absolute abundance given a pre-drought population trajectory and the absolute abundance after the drought event. These variables were justified in their inclusion by their significant effects. However, the effect of local drought extent (APET value) only had weak associations with our measured population sensitivity to drought (significant for models fitted to woodland cover at 0.5 km radius but not 2 km radius). One reason for this may be the low resolution of the APET data, obtained from 10 km interpolation. Fine-scale variation in topography is likely to affect local soil moisture conditions and affect population

responses to drought (Kennedy 1997). In addition, habitat structure can affect microclimatic conditions (Morecroft et al. 1998, Suggitt et al. 2011), which may partly explain our strong effect of woodland cover on population sensitivity. Other sources of error in our studies include sampling error during population counts and the error introduced when fitting models of population trend to give expected abundance values in the absence of the drought event. The UKBMS sampling technique is based on a Pollard walk method, and produces indices of abundance which are related to actual abundance by some constant value (Pollard and Yates 1993). Due to differences in butterfly detectability there is a possibility that this constant might vary between habitat types. However, this variation is minimised through the Pollard method by a relatively narrow 5 m-wide recording band (Isaac et al. 2011). Additionally, because we analysed population trends in each transect separately, this error is unlikely to present a problem. If habitat type and butterfly detectability on transects varied over time, however, this might introduce error into our estimates of sensitivity and recovery; but it is unlikely that such error would be systematic with regards to our explanatory variables of interest. In addition, due to habitat management on UKBMS transects, broad habitat compositions generally change little over time. Regarding our statistical models of population trajectories, we used data for six years before and three years after the drought event. Preliminary analysis showed that this time window produced the best balance between accuracy in our estimate of population trend (lower standard errors about slopes), whilst still giving high sample sizes for analysis. Using longer or shorter time windows, our results were qualitatively similar but the statistical power to detect significant effects of landscape variables gradually declined.

Clearly, it would be useful to extend these analyses to other species susceptible to droughts. Other landscape variables might also be considered; for example, topographically diverse landscapes might harbour species more resilient to extreme events such as drought (Weiss et al. 1988). In addition, habitat quality is likely to be important and may explain variation in population responses for habitat patches of similar size (Thomas et al. 2001, Matter et al. 2009).

Given the many sources of error in macroecological analyses such as these (e.g. local climate, habitat assessment, population sampling), it is impressive that we found such a marked effect of habitat area and configuration on population sensitivity to, and recovery from, drought. We have provided the first clear evidence that landscape structure can influence population resilience to extreme climatic events. Our results are consistent with hypotheses that central portions of environmental gradients provide higher resilience to environmental stochasticity (Pulliam 1988, Sutcliffe et al. 1997), and that species’ populations respond to not just local environments but also those in the surrounding landscape (Andrén 1994, Opdam and Wascher 2004, Heard et al. 2007, Oliver et al. 2010).

Anthropogenic land use change is broadly acknowledged to have had the greatest impact on biodiversity to date, although climate change is projected to have greater effects in the future (Millennium Ecosystem Assessment 2005, UK National Ecosystem Assessment 2011). However, land use and climate change are likely to interact in their effects on

species populations (Warren et al. 2001, Travis 2003, Hof et al. 2011). In addition to gradual effects of incremental climate change, we have shown that extreme climatic events can interact with land use to affect species populations. On the positive side, the implications of these results are that there may exist opportunities to manipulate landscape structure to promote resilience under such extreme events (cf. Hopkins et al. 2007, Lawton et al. 2010). On the negative side, our results imply that landscapes with small percentages of poorly connected suitable habitat (e.g. those dominated by intensive agriculture) will house more sensitive populations that may struggle to recover from extreme events. Hence, although there is growing political pressure to improve food security (FAO 2011), it is imperative that large enough areas of semi-natural habitat remain so that species populations are resilient to the increased climatic variability predicted under future scenarios.

To conclude, we have presented a new method to assess the resilience of populations to extreme events. We have shown that population resilience to an extreme drought can be influenced by habitat area and configuration in the local landscape. Both sensitivity to – and recovery from – drought were affected by landscape structure, suggesting that wise landscape management may promote more resilient species' populations.

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Supplementary material (Appendix E7665 at <[www.oikosoffice.lu.se/appendix](http://www.oikosoffice.lu.se/appendix)>). Appendix 1.