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

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2   **Abstract**

3   Most studies on the biological impact of climate change have focussed on incremental

4   climate warming, rather than extreme events. Yet responses of species' populations to

5   climatic extremes may be one of the primary drivers of ecological change. We assess the

6   resilience of individual populations in terms of their sensitivity to- and ability to recover

7   from- environmental perturbation. We demonstrate the method using a model species, the

8   Ringlet butterfly *Aphantopus hyperantus*, and analyse the effects of an extreme drought event

9   using data from 79 British sites over 10 years. We find that populations crashed most

10   severely in drier regions but, additionally, the landscape structure around sites influenced

11   population responses. Larger and more connected patches of woodland habitat reduced

12   population sensitivity to the drought event and also facilitated faster recovery. Having

13   enough, sufficiently connected habitat appears essential for species' populations to be

14   resilient to the increased climatic variability predicted under future scenarios.

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Introduction

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 Haddi 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 Institute 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

1 as the ability to withstand and recover from environmental perturbation; specifically, in this

2 case, an extreme drought event in 1995.

3   To increase population resilience, one strategy is to alter land management at a landscape

4 scale; because effects of environmental change on species operate not only locally but also at

5 broader spatial scales (Tscharntke et al. 2005; Heard et al. 2007; Oliver et al. 2010).

6 However, to do this, we need to understand how landscape structure can influence resilience

7 to extreme events such as drought. To date, there has surprisingly been little research in this

8 area.

9   Here, we consider a model species, the ringlet butterfly *Aphantopus hyperantus*, a grass-

10 feeding lepidopteran commonly found close to woodland edges and known to be susceptible

11 to drought effects (Sutcliffe et al. 1997; Morecroft et al. 2002). For the 1995 UK drought

12 event, we quantify how the area and configuration of woodland in local landscapes influence

13 population resilience, in terms of sensitivity to drought (the magnitude of population decline

14 following the drought) and recovery from drought (the rate of population increase following

15 the crash). Previous work on this species showed that an extreme drought event in 1976

16 caused retractions from open non-wooded sections of a single site (Sutcliffe et al. 1997). We

17 predict that populations across 79 different sites will be more resilient to drought when

18 landscapes have a greater total area of- and less fragmented- woodland. These landscapes are

19 expected to provide a broader range of resources and microclimates that are accessible to

20 individuals (Oliver et al. 2010; Hodgson et al. 2011) as well as improved functional

21 connectivity allowing rescue effects (Hanski 1999).

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1 **Materials and Methods**

2 *Data collation*

3 *Aphantopus hyperantus* populations in the UK suffered delayed responses to the 1995

4 drought and crashed in 1996 (Morecroft et al. 2002). We extracted annual abundance indices

5 for *A. hyperantus* from the UK Butterfly Monitoring Scheme for the years 1990-1999 (i.e. six

6 years before 1996 drought impact and three years after). We selected 10 years of data to

7 obtain a balance between more years per site to accurately assess a pre-drought population

8 trend and a higher sample size of UKBMS sites with sufficient temporal coverage for

9 analysis. We repeated our results with different time windows to test for sensitivity to the

10 temporal window selected for analysis.

11   The transect methodology involves counting butterflies for up to 26 weeks per year at

12 each site in conditions suitable for butterfly activity (Pollard and Yates 1993). For sites with

13 sufficient data, an annual index of abundance was calculated for each year (Rothery and Roy

14 2001). In this study, we only analysed sites which had a complete set of annual indices

15 between 1990 and 1999.

16   Drought conditions in 1995 were not uniform across the UK and we expected that

17 butterflies at less droughted sites might respond differently. Therefore, we assessed the 1995

18 APET value of each site ('APET', the ratio of actual to potential evapotranspiration, gives an

19 estimate of annual drought conditions at each site). Annual APET values were obtained from

20 10km interpolation on a GB Ordnance Survey grid from the CRU ts2.1 dataset (Mitchell and

21 Jones 2005).

22   We quantified the structure of broadleaved woodland at 0.5 and 2km around the centroid

23 of butterfly monitoring sites using 25m resolution remotely sensed land cover data (LCM

24 2000; Fuller et al. 2002). These spatial scales were chosen because local landscape attributes

25 have been found to have stronger associations with population dynamics in this species

1   (Oliver et al. 2010). However, for completeness we also tested for effects of landscape

2   attributes at wider scales of 5 and 10km around sites (Table S2 & S3). For each landscape

3   buffer, we calculated the total area of woodland, the number of individual patches, the mean

4   'edginess' of patches (based on a standardised perimeter-area ratio, where actual perimeter

5   length is considered relative to the minimum possible perimeter length for a given habitat

6   area, i.e. larger values indicate more 'edgy' habitat patches), and the mean isolation of

7   patches (defined as the mean Euclidean distance nearest neighbour distance based on shortest

8   edge-edge distances). Metrics were calculated using the software FRAGSTATS (McGarigal

9   et al. 2002).

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11   *Population sensitivity to drought*

12   To assess the extent of *A. hyperantus* population crashes, whilst taking into account long-

13   term population trajectories at each site, we fitted a linear model to the yearly counts,

14   excluding the year 1996. Population trends varied between sites, with a large number of

15   populations (71%) showing increases, possibly due to recent increases in mean temperatures

16   (i.e. incremental warming) or improved habitat management (Roy *et al.* 2001). In preliminary

17   analyses, we tested for effects of density dependence on population growth rates (regression

18   of log(N_t/N_{t-1}) versus N_{t-1}, where N is population density in year t; Schtickzelle and

19   Baguette 2004). We found only a small proportion of the population time series (18%)

20   showed significant density dependence (at $p<0.05$). In addition, in an analysis comparing

21   linear and quadratic models to explain population trends over time (i.e. regression of N_t on

22   year), we found that linear models produced the best fit population trends (in 95% of cases;

23   Table S1). This is not to say that density dependence is not an important regulatory

24   demographic process for this species, but over the time periods and range of densities on our

25   sites, and relative to other factors (e.g. weather and habitat quality), there is little evidence of

1   curvature in population trends expected under a strong influence of density dependence. We

2   therefore used a linear model to predict the expected count in 1996 had no drought event

3   occurred (Fig. 1). The difference between the expected count and the observed count in 1996

4   gives an indication of local butterfly sensitivity to the drought event (hereon referred to as

5   '$\Delta_{1995\text{-}6}$'). Sites with higher mean abundance are likely to have greater $\Delta_{1995\text{-}6}$ scores for the

6   same percentage decline than sites with lower mean abundance. Therefore, in our statistical

7   models of population sensitivity with $\Delta_{1995\text{-}6}$ as a response variable we included the expected

8   count in 1996 as a control explanatory variable in order to model relative population decline

9   adjusted for population size. However, for ease of interpretation, when plotting our results we

10 use percentage change. Because the level of drought at each site was likely to affect the

11 extent of population change we also included the 1995 APET value of each site as a control

12 covariate in our models of population sensitivity. We initially fitted a linear regression model

13 with these two control variables as the explanatory variables and $\Delta_{1995\text{-}6}$ as the response using

14 the program R (R Development Core Team 2009). Taking residuals from this model allowed

15 us to assess the sensitivity of each population to the drought event. We mapped these

16 sensitivity scores and there was no strong spatial patterning across Southern Britain (Fig. 2a).

17   Next, we included woodland cover explanatory variables (area, number of patches,

18 'edginess' and patch isolation) in the statistical models along with the control covariates

19 described above. We fitted a separate model for woodland cover assessed at 0.5, 2, 5 and

20 10km scales. Only sites with woodland present in the selected landscape buffer could be used

21 to assess woodland spatial configuration, so sample sizes were smaller for the 0.5km

22 landscape radius. Significance of woodland explanatory variables was obtained by stepwise

23 deletion but always keeping the control covariates in the statistical model. A separate model

24 was fitted for woodland data at each spatial scale. For all models, we tested for collinearity

25 between explanatory variables using a Pearson's correlation test. At spatial scales of 0.5 and

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1   2km radius all correlation coefficients between explanatory variables were less than 0.7. At

2   spatial scales of 5 and 10km radius the isolation of woodland patches was negatively

3   correlated with the number of patches (Pearson's r <0.7). Therefore, it was necessary to retain

4   only one of these variables and we chose to retain number of woodland patches because this

5   variable had greater explanatory power than patch isolation for the models fitted at smaller

6   spatial scales.

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9   *Population recovery from drought*

10   To assess *A. hyperantus* population recovery from drought we fitted a linear model to the

11   population count in 1996 and the subsequent three years (Fig. 1). We only assessed recovery

12   for populations that suffered a decline following the drought event (i.e. 'Δ_{1995-6}' > 0), hence

13   sample sizes are slightly smaller than in our analysis of sensitivity to drought. We used the

14   rate of change in this linear model as our measure of population recovery. We also assessed

15   whether population recovery was complete within the three year period by comparing the

16   expected abundance in 1999 from our pre-drought population model versus the expected

17   abundance in 1999 from this post drought model.

18   Due to density dependence in butterfly growth rates, the extent of the population crash

19   following the drought event would be likely to affect recovery rates (e.g. smaller populations

20   further from carrying capacity would be expected to recover fastest). Therefore, with

21   recovery rate as our response variable in a linear regression model, we included the

22   magnitude of the crash following the drought event (Δ_{1995-6}) and the absolute abundance in

23   1996 as control covariates (these two variables were only weakly correlated with each other;

24   Pearson's $r = 0.30$, $n = 66$). Taking residuals from this model allowed us to assess the

1   recovery of each population from the drought event. We mapped these recovery scores and

2   there was no strong spatial patterning across Southern Britain (Fig. 2b).

3   Next, we included the woodland cover explanatory variables in the statistical models, in

4   addition the control covariates described above. We fitted a separate model for woodland data

5   at each spatial scale.

6   In all statistical models, the model residuals were assessed for normality and we tested

7   for spatial autocorrelation using the *ncf* package in R (Bjornstad 2009). Spatial

8   autocorrelation was only evident for the population recovery model with woodland structure

9   assessed at 2km radius (Figs. S1-S4). In this case, we fitted the same explanatory variables

10   but in a mixed effects model with 10km neighbourhood as a random effect (using the *lme4*

11   package in R; Bates et al. 2008). This removed the significant spatial autocorrelation and we

12   present results of both the standard linear and the mixed effect model. Significance values of

13   model coefficients in the mixed effects model were estimated using Markov Chain Monte

14   Carlo simulations with 10^4 iterations.

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16   **Results**

17   *Population sensitivity to drought*

18   Across all sites tested, the majority of *A. hyperantus* populations showed marked declines

19   between 1995 and 1996. Δ_{1995-6} scores tended to be positive, indicating that observed counts

20   in 1996 were lower than expected had the drought not occurred (Wilcoxon signed ranks test

21   to show that median Δ_{1995-6} scores were significantly different from zero: V = 2952, p <

22   0.001, n = 79). In 1996, populations declined in 66 out of 79 sites. However, the degree of

23   population decline tended to vary across the species range. In locations that suffered less

24   drought in 1995 (higher APET values), population declines were often less marked. Hence, in

25   our linear regressions explaining Δ_{1995-6} scores, site APET value had a negative coefficient

1   (for the statistical model assessing woodland cover at 0.5km radius: APET coefficient = -

2   502.1, se = 228.6, t = -2.197, p = 0.033; at 2km radius: APET coefficient = -137.3, se =

3   253.5, t = -0.54, p = 0.59).

4   The expected count on a site in 1996 was also strongly correlated to the absolute decline

5   in 1996 (Δ_{1995-6}). Sites with larger mean populations tended to suffer larger absolute declines

6   (for the statistical model assessing woodland cover at 0.5km radius: expected count in 1996

7   coefficient = 0.37, se = 0.06, t = 6.39, p <0.001; at 2km radius: expected count in 1996

8   coefficient = 0.33, se = 0.06, t = 5.84, p <0.001). Hence, including the expected count in 1996

9   as a covariate was important and allowed us to consider the relative decline in populations

10   adjusting for mean size.

11   Regarding the effect of woodland cover, there was a strong association between

12   woodland area and population sensitivity to drought, whereby populations in more wooded

13   landscapes suffered smaller population declines (Fig. 3a). This effect was strongest for

14   woodland assessed at 0.5km around sites but was also highly significant for woodland cover

15   assessed at 2km radius around sites (Table 1). The spatial configuration of woodland patches

16   in the local landscape also influenced sensitivity of butterfly populations to drought. Where

17   woodland was fragmented into a larger number of separate patches and where patches were

18   more 'edgy' i.e., greater perimeter-area ratio, population crashes were more marked. These

19   spatial configuration effects were significant when woodland was assessed at 2km radius

20   around sites but not 0.5km radius (Table 1). For both spatial scales, we tested model residuals

21   and found no evidence of spatial autocorrelation.

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23   *Population recovery from drought*

24   Of the 66 population crashes following the drought event, 54 populations showed positive

25   recovery in the subsequent 3 years, whilst 12 populations continued to decline. Only 22 out

1 of the 66 populations recovered completely to expected pre-drought population levels. Both

2 the magnitude of the crash following the drought event (Δ_{1995-6}) and the absolute abundance

3 in 1996 (Obs_{1996}) had an effect on the rate of population recovery in the subsequent three

4 years following the drought impact. Populations that suffered larger declines following the

5 drought event and those that resulted in lower abundance showed faster rates of recovery (e.g.

6 in the 2km radius model where n = 66, Δ_{1995-6} effect on recovery rate: coefficient = 0.12, se =

7 0.04, t = 3.02, p = 0.004; Obs_{1996} effect on recovery rate: coefficient = -0.06, se = 0.03, t = -

8 2.8, p = 0.042). This suggests a negative density dependent growth rate, with more rapid

9 growth in smaller populations.

10   Regarding the effect of woodland cover, sites with a greater area of woodland (measured

11 at 0.5km radius) showed faster population recovery, although this association was not

12 significant for woodland area measured at 2km radius (Table 2). In contrast, the spatial

13 configuration of woodland patches was important for population recovery and the effect was

14 strongest at the larger spatial scale of 2km radius. When woodland in the local landscape was

15 fragmented, in terms of an increased number of patches and increased distances between

16 patches, recovery rates were slower (Table 2, see figure 3b for an example of the effect of

17 number of patches, the variable with the strongest association).

18   Some spatial autocorrelation was evident in the model residuals for the population

19 recovery model with woodland structure assessed at 2km radius. Fitting a mixed effects

20 model with 10km neighbourhood as a random effect removed this spatial autocorrelation

21 (Fig. S4), and we obtained qualitatively similar results for the effects of our explanatory

22 variables on population recovery (Table 2).

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24 **Discussion**

1   We have shown that, for a drought susceptible species, habitat area and configuration in the

2   local landscape can influence population sensitivity to- and recovery from- drought events.

3   The 1995 drought event had a large impact on *Aphantopus hyperantus*, with 84% of

4   populations having lower abundance in the following year. Smaller population declines

5   occurred on sites nested in landscapes with a greater total area of woodland and where

6   woodland was less fragmented. Following these population crashes, 18% of populations

7   continued to decline in the subsequent three years. The majority of populations showed

8   positive recovery, although only 33% of populations showed complete recovery to pre-

9   drought population levels within three years. In Europe, previously infrequent extreme

10   summer heatwaves and prolonged droughts are expected to become the norm, with summer

11   temperature extremes that previously once occurred every 500 years are now projected to

12   occur every other year (Stott et al. 2004). We found that 66% of *A. hyperantus* populations

13   did not show complete recovery within three years, suggesting that this species is likely to

14   suffer long-term declines under such an altered climate. Population recovery of the species

15   was affected by woodland structure, with recovery facilitated by larger and less fragmented

16   surrounding woodlands. Hence, fragmented landscapes are clearly affecting the resilience of

17   this species.

18   These effects of habitat area and configuration on population sensitivity and recovery fit

19   with previous ecological theory because larger areas of habitat are likely to provide a broader

20   range of resources and microclimates (Oliver et al. 2010; Hodgson et al. 2011). Increased

21   heterogeneity in larger habitat patches mean that there are more likely to be refuge

22   microclimates where butterflies and their host plants can survive (or at least remain as high

23   quality food sources, under the 'plant vigour' hypothesis; Price 1991; Gutbrodt et al. 2011).

24   Larger habitat patches may also offer a greater total amount of resource, facilitating rapid

25   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 (Δ_{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

(unpublished data).

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 0.5km radius but not

2km radius). One reason for this may be the low resolution of the APET data, obtained from

10km 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 5m-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

1   standard errors about slopes), whilst still giving high sample sizes for analysis. Using longer

2   or shorter time windows, our results were qualitatively similar but the statistical power to

3   detect significant effects of landscape variables gradually declined.

4   Clearly, it would be useful to extend these analyses to other species susceptible to

5   droughts. Other landscape variables might also be considered; for example, topographically

6   diverse landscapes might harbour species more resilient to extreme events such as drought

7   (Weiss et al. 1988). In addition, habitat quality is likely to be important and may explain

8   variation in population responses for habitat patches of similar size (Thomas et al. 2001;

9   Matter et al. 2009).

10   Given the many sources of error in macroecological analyses such as these (e.g. local

11   climate, habitat assessment, population sampling), it is impressive that we found such a

12   marked effect of habitat area and configuration on population sensitivity to- and recovery

13   from drought. We have provided the first clear evidence that landscape structure can

14   influence population resilience to extreme climatic events. Our results are consistent with

15   hypotheses that central portions of environmental gradients provide higher resilience to

16   environmental stochasticity (Pulliam 1988; Sutcliffe et al. 1997), and that species'

17   populations respond to not just local environments but also those in the surrounding

18   landscape (Andrén 1994; Opdam and Wascher 2004; Heard et al. 2007; Oliver et al. 2010).

19   Anthropogenic land use change is broadly acknowledged to have had the greatest impact

20   on biodiversity to date, although climate change is projected to have greater effects in the

21   future (Millennium Ecosystem Assessment 2005; UK National Ecosystem Assessment 2011).

22   However, land use and climate change are likely to interact in their effects on species

23   populations (Warren et al. 2001; Travis 2003; Hof et al. 2011). In addition to gradual effects

24   of incremental climate change, we have shown that extreme climatic events can interact with

25   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.

Acknowledgements

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SUPPLEMENTARY MATERIAL

Additional supplementary material can be found in the online appendix of this article.

Table S1 Regressions of population count on year comparing a linear model with a quadratic
model

Table S2 Association between woodland area and fragmentation (5km and 10km radius) and
butterfly population sensitivity

Table S3 Association between woodland area and fragmentation (5km and 10km radius) and
butterfly population recovery

Figure S1 Spatial correlogram for residuals of the population *sensitivity* model fitted to
woodland cover data at 0.5km radius.

Figure S2 Spatial correlogram for residuals of the population *recovery* model fitted to
woodland cover data at 0.5km radius.

Figure S3 Spatial correlogram for residuals of the population *sensitivity* model fitted to
woodland cover data at 2km radius.

Figure S4 Spatial correlograms for residuals of the population *recovery* model fitted to
woodland cover data at 2km radius.

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3 **Table 1**, Association between woodland area and fragmentation and the sensitivity of

4 *Aphantopus hyperantus* populations to an extreme drought event. The sign of the coefficients

5 indicate that the decline in butterflies following the drought event is less marked when there

6 is more broadleaved woodland around surrounding monitoring sites and where woodland is

7 less fragmented (in terms of number of patches and the 'edginess' of each woodland patch).

8

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	

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1 **Table 2**, Association between woodland area and fragmentation and the recovery of

2 *Aphantopus hyperantus* populations from an extreme drought event. The sign of the

3 coefficients indicate that recovery is fastest when there is more broadleaved woodland

4 surrounding the monitoring sites and where woodland is less fragmented (in terms of number

5 of patches and the average isolation of each woodland patch). Models highlighted with the

6 symbol † indicate mixed effects models with a random term for 10km neighbourhood to

7 account for spatial autocorrelation.

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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†	2†	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†	2†	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'†	2†	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†	2†	66	-0.05	0.06	-0.78	0.037	*

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Figures

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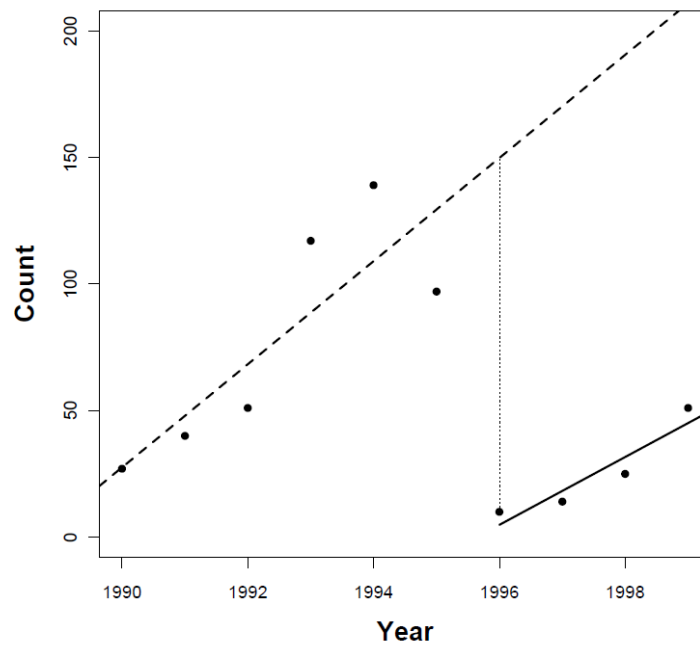
4   **Fig. 1**, Demonstration of the method for assessing population sensitivity and recovery to an

5   extreme event. A linear model (dashed line) is fitted to butterfly counts over time for the

6   years preceding the population crash from the extreme event (1996 in this case). The

7   sensitivity to drought is assessed as the difference between the observed count in 1996 and

8   the expected count had no drought event occurred (dotted line; '$\Delta_{1995\text{-}6}$'). The recovery is

9   assessed as the rate of population growth in the three years following the crash (solid line).

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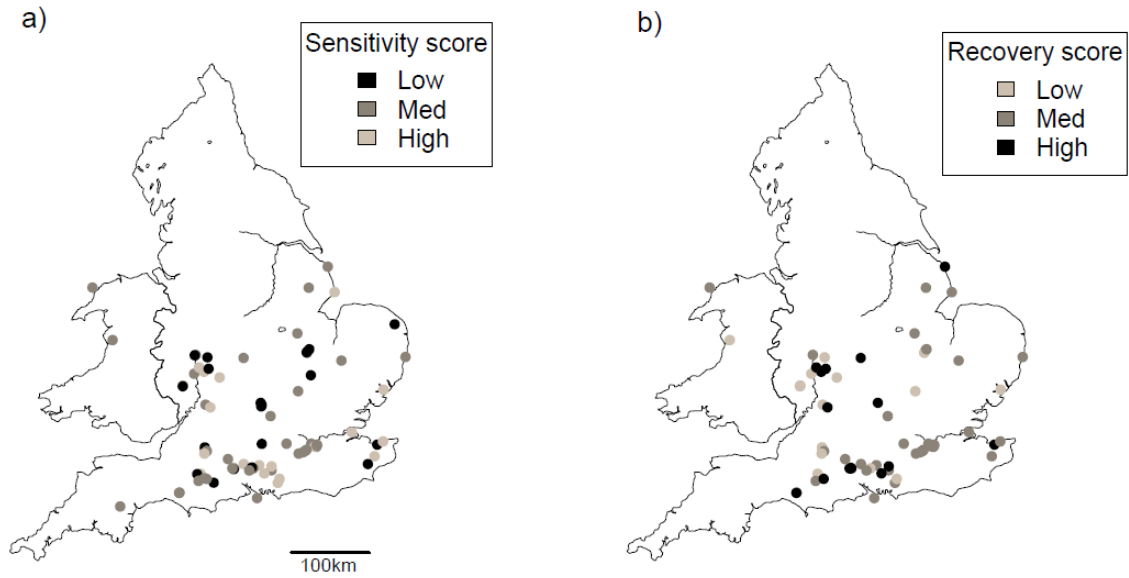
Fig. 2, Maps of a) population sensitivity to-, and b) population recovery from- the 1995

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.

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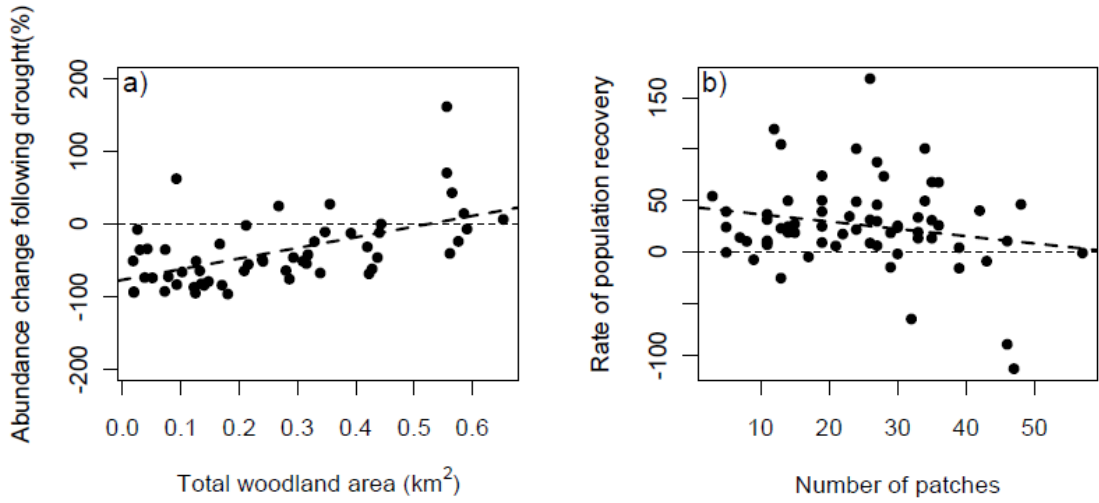**Fig. 3**, Population resilience of *Aphantopus hyperantus* to an extreme drought event in terms

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 (0.5km radius). Panel b shows that population

recovery is fastest where woodland patches are not fragmented (2km radius).

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Appendix 1

This appendix contains the following:

| | **Model 1** | | | | **Model 2** | | | |
| | Year | | | | Year^2 | | | |
Site	coefficient	SE	t	p	coefficient	SE	t	p
1	89.69	47.78	1.88	0.134	50.68	23.89	2.12	0.124
2	86.51	26.94	3.21	**0.033**	3.75	21.19	0.18	0.871
3	78.74	8.84	8.91	**0.001**	-5.41	6.25	-0.87	0.450
4	77.29	24.15	3.20	**0.033**	28.34	9.83	2.88	0.063
5	66.43	17.34	3.83	**0.019**	2.73	13.62	0.20	0.854
6	65.37	41.50	1.58	0.190	-19.11	30.90	-0.62	0.580
7	64.06	45.34	1.41	0.231	39.38	27.72	1.42	0.251
8	61.69	39.88	1.55	0.197	36.73	23.32	1.57	0.213
9	51.09	11.60	4.40	**0.012**	-5.70	8.56	-0.67	0.553
10	48.43	36.55	1.32	0.256	36.00	20.08	1.79	0.171
11	44.83	51.91	0.86	0.437	-3.68	40.99	-0.09	0.934
12	41.20	21.76	1.89	0.131	-26.84	7.48	-3.59	**0.037**
13	39.31	61.18	0.64	0.555	-32.93	44.47	-0.74	0.513
14	36.63	9.06	4.04	**0.016**	6.79	5.99	1.13	0.340
15	35.43	37.29	0.95	0.396	-35.14	21.39	-1.64	0.199
16	32.34	15.35	2.11	0.103	-5.20	11.76	-0.44	0.689
17	31.31	11.08	2.83	**0.048**	-6.95	7.79	-0.89	0.438
18	29.03	13.95	2.08	0.106	-7.93	10.04	-0.79	0.487
19	27.14	6.05	4.49	**0.011**	1.95	4.65	0.42	0.704
20	26.51	5.53	4.80	**0.009**	-5.96	2.69	-2.22	0.113
21	24.17	17.15	1.41	0.231	-20.57	6.53	-3.15	0.051
22	23.54	9.75	2.42	0.073	-2.89	7.52	-0.38	0.726
23	23.26	22.76	1.02	0.365	-25.75	10.13	-2.54	0.085
24	23.14	12.32	1.88	0.133	-13.52	5.82	-2.32	0.103
25	22.83	10.25	2.23	0.090	1.23	8.07	0.15	0.888
26	21.74	7.16	3.04	**0.039**	-3.93	5.19	-0.76	0.504
27	21.71	45.23	0.48	0.656	-20.34	33.78	-0.60	0.590
28	20.37	6.67	3.05	**0.038**	-4.13	4.70	-0.88	0.445
29	18.06	4.41	4.10	**0.015**	0.88	3.45	0.25	0.816
30	17.31	16.64	1.04	0.357	7.86	12.35	0.64	0.570
31	16.54	2.36	7.02	**0.002**	0.54	1.84	0.29	0.789
32	14.49	12.59	1.15	0.314	-16.32	3.20	-5.11	**0.015**
33	14.26	8.83	1.61	0.182	-5.23	6.29	-0.83	0.467
34	14.17	21.80	0.65	0.551	-5.82	16.90	-0.34	0.753
35	13.29	4.99	2.66	0.056	-1.98	3.77	-0.53	0.636
36	12.40	7.79	1.59	0.186	-8.80	3.47	-2.54	0.085
37	11.89	23.15	0.51	0.635	-13.05	16.68	-0.78	0.491
38	10.57	12.61	0.84	0.449	2.68	9.85	0.27	0.803
39	9.17	3.78	2.42	0.073	3.45	2.23	1.54	0.221

1 **Table S1**, Regressions of population count on year comparing a linear model (model 1) with
2 a quadratic model (model 2; only the coefficient for the quadratic term is shown). There was
3 little evidence for curvature in population trajectories in the six years prior to the drought
4 event. Significant p values (p < 0.05) are highlighted in bold font.

Site	Model 1 Year coefficient	SE	t	p	Model 2 Year2 coefficient	SE	t	p
40	9.14	9.93	0.92	0.409	6.54	6.88	0.95	0.412
41	8.14	7.94	1.02	0.363	-7.14	4.74	-1.51	0.229
42	5.94	3.05	1.95	0.123	1.27	2.30	0.55	0.620
43	5.89	1.59	3.70	**0.021**	0.14	1.25	0.11	0.917
44	4.57	3.36	1.36	0.246	-0.09	2.66	-0.03	0.975
45	4.57	9.74	0.47	0.663	-7.41	6.40	-1.16	0.331
46	4.11	5.55	0.74	0.499	-6.46	2.30	-2.81	0.067
47	3.86	7.31	0.53	0.625	1.84	5.68	0.32	0.767
48	3.77	15.86	0.24	0.824	-19.64	5.36	-3.67	**0.035**
49	2.69	2.65	1.01	0.368	-2.73	1.38	-1.98	0.142
50	2.20	2.50	0.88	0.428	-2.61	1.28	-2.04	0.134
51	1.97	11.28	0.17	0.870	-5.36	8.37	-0.64	0.568
52	1.94	1.89	1.03	0.362	0.21	1.49	0.14	0.895
53	1.74	4.36	0.40	0.710	0.68	3.43	0.20	0.856
54	1.63	10.53	0.15	0.885	-5.82	7.61	-0.76	0.500
55	1.57	39.91	0.04	0.970	-47.52	15.58	-3.05	0.055
56	0.77	2.06	0.37	0.727	-0.02	1.63	-0.01	0.992
57	0.63	7.65	0.08	0.938	-8.52	3.52	-2.42	0.094
58	-0.23	8.73	-0.03	0.980	-6.52	5.79	-1.13	0.342
59	-0.69	2.18	-0.31	0.769	-1.75	1.40	-1.25	0.299
60	-0.77	11.42	-0.07	0.949	-9.84	7.01	-1.40	0.255
61	-1.43	7.15	-0.20	0.851	0.86	5.63	0.15	0.889
62	-1.94	0.95	-2.04	0.111	-0.46	0.70	-0.66	0.556
63	-7.11	44.84	-0.16	0.882	-49.23	21.19	-2.32	0.103
64	-7.43	6.77	-1.10	0.334	-4.88	4.55	-1.07	0.363
65	-8.14	5.02	-1.62	0.180	5.50	2.38	2.31	0.104
66	-9.20	11.70	-0.79	0.476	-8.59	7.81	-1.10	0.352
67	-9.80	19.70	-0.50	0.645	-18.80	11.17	-1.68	0.191
68	-10.89	6.34	-1.72	0.161	-2.68	4.77	-0.56	0.614
69	-11.26	8.74	-1.29	0.267	-7.21	5.51	-1.31	0.282
70	-13.94	55.01	-0.25	0.812	-6.00	43.35	-0.14	0.899
71	-14.94	7.39	-2.02	0.113	-3.18	5.54	-0.57	0.607
72	-17.51	85.49	-0.20	0.848	14.04	67.10	0.21	0.848
73	-17.77	57.93	-0.31	0.774	28.95	42.64	0.68	0.546
74	-22.49	104.20	-0.22	0.840	3.41	82.36	0.04	0.970
75	-24.49	8.54	-2.87	**0.046**	-5.79	5.86	-0.99	0.397
76	-25.11	7.62	-3.29	**0.030**	-8.59	3.43	-2.51	0.087
77	-40.06	35.18	-1.14	0.318	-16.91	26.05	-0.65	0.562
78	-55.00	49.76	-1.11	0.331	-61.00	17.54	-3.48	**0.040**
79	-72.80	70.74	-1.03	0.362	-70.48	38.37	-1.84	0.164
80	-74.57	95.40	-0.78	0.478	-92.88	53.04	-1.75	0.178

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2 **Table S2**, Association between woodland area and fragmentation (5km and 10km radius) and
3 the sensitivity of *Aphantopus hyperantus* populations to an extreme drought event. Positive
4 coefficients indicate increased sensitivity to the drought event (i.e. greater magnitude of
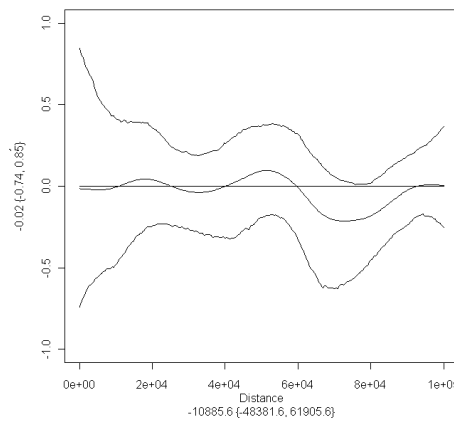5 population decline).

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BW Variable	Spatial scale (radius)	n	Coefficient	SE	t	p	
Area	5km	79	-12.43	4.50	-2.76	0.007	**
Area	10km	79	-0.53	1.05	-0.50	0.617	
Number of patches	5km	79	0.37	0.50	0.75	0.454	
Number of patches	10km	79	0.08	0.09	0.90	0.370	
Patch 'edginess'	5km	79	304.9	233.9	1.30	0.197	
Patch 'edginess'	10km	79	344.6	418.1	0.82	0.413	

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9 **Table S3**, Association between woodland area and fragmentation (5km and 10km radius) and
10 the recovery of *Aphantopus hyperantus* populations to an extreme drought event. Positive
11 coefficients indicate more rapid recovery from the drought event.

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BW Variable	Spatial scale (radius)	n	Coefficient	SE	t	p
Area	5km	66	0.80	0.81	0.99	0.327
Area	10km	66	0.23	0.25	0.93	0.357
Number of patches	5km	66	-0.07	0.09	-0.81	0.419
Number of patches	10km	66	-0.03	0.04	-0.83	0.412
Patch 'edginess'	5km	66	-65.3	78.3	-0.83	0.407
Patch 'edginess'	10km	66	-44.1	104.1	-0.42	0.673

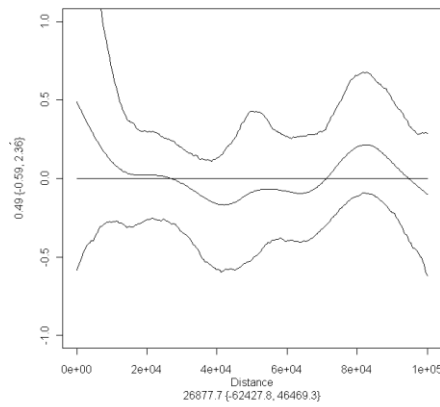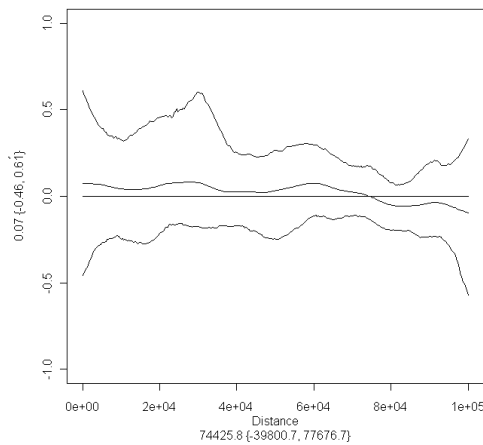14
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17 **Figure S1**, Spatial correlogram for residuals of the population sensitivity model fitted to
18 woodland cover data at 0.5km radius. The outer lines show 95% confidence intervals. Hence,
19 significant spatial autocorrelation is indicated if these lines cross the horizontal line of zero
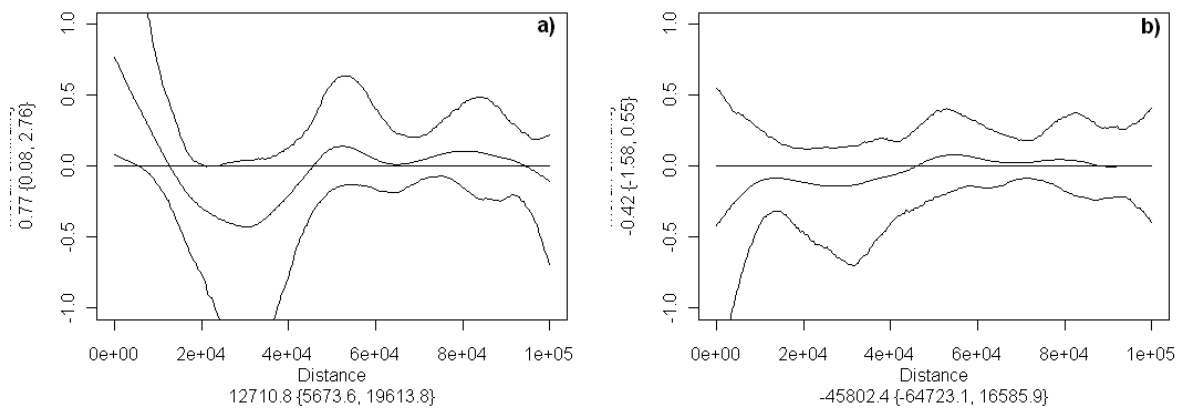20 correlation.

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2 **Figure S2**, Spatial correlogram for residuals of the population recovery model fitted to
3 woodland cover data at 0.5km radius. The outer lines show 95% confidence intervals. Hence,
4 significant spatial autocorrelation is indicated if these lines cross the horizontal line of zero
5 correlation.
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9 **Figure S3**, Spatial correlogram for residuals of the population sensitivity model fitted to
10 woodland cover data at 2km radius. The outer lines show 95% confidence intervals. Hence,
11 significant spatial autocorrelation is indicated if these lines cross the horizontal line of zero
12 correlation.
13

Figure S4, Spatial correlograms for residuals of the population recovery models fitted to woodland cover data at 2km radius. Panel a shows the statistical model without 10km neighbourhood as a random effect, panel b shows the statistical model including this term. The outer lines show 95% confidence intervals. Hence, significant spatial autocorrelation is indicated if these lines cross the horizontal line of zero correlation.