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Microclimate affects landscape level persistence in the British Lepidoptera

Andrew J. Suggitt[1,2,*], Robert J. Wilson[2], Tom A. August[3], Richard Fox[4], Nick J.B. Isaac[3], Nicholas A. Macgregor[5], Michael D. Morecroft[5] and Ilya M.D. Maclean[1].

1 Environment and Sustainability Institute, University of Exeter - Penryn Campus, Penryn, Cornwall, UK.
2 Department of Biosciences, University of Exeter - Streatham Campus, Exeter, Devon, UK.
3 Centre for Ecology and Hydrology, Maclean Building, Benson Lane, Crowmarsh Gifford, Oxfordshire, UK.
4 Butterfly Conservation, Manor Yard, East Lulworth, Wareham, Dorset, UK.
5 Natural England, Nobel House, 17 Smith Square, London, UK.

* Corresponding author: a.suggitt@exeter.ac.uk.

Abstract

Microclimate has been known to drive variation in the distribution and abundance of insects for some time. Until recently however, quantification of microclimatic effects has been limited by computing constraints and the availability of fine-scale biological data. Here, we tested fine-scale patterns of persistence/extinction in butterflies and moths against two computed indices of microclimate derived from Digital Elevation Models: a summer solar index, representing fine-scale variation in temperature, and a topographic wetness index, representing fine-scale variation in moisture availability. We found evidence of microclimate effects on persistence in each of four 20 x 20 km British landscapes selected for study (the Brecks, the Broads, Dartmoor, and Exmoor). Broadly, local extinctions occurred more frequently in areas with higher minimum or maximum solar radiation input, while responses to wetness varied with landscape context. This negative response to solar radiation is consistent with a response to climatic warming, wherein grid squares with particularly high minimum or maximum insolation values provided an increasingly adverse microclimate as the climate warmed. The variable response to wetness in different landscapes may have reflected spatially variable trends in precipitation. We suggest that locations in the landscape featuring cooler minimum and/or maximum temperatures could act as refugia from climatic warming, and may therefore have a valuable role in adapting conservation to climatic change.

Keywords

Global change, topoclimate, microrefugia, range shift, habitat, topography.

Introduction

British butterflies and moths have been the subject of a rich history of research into their relationship to climate, and particularly their response to recent climatic change (e.g. Pollard 1988, Warren et al. 2001). This research has helped conservation organisations plan for and manage future change. However, as the focus shifts towards conducting conservation at the landscape level (Lawton et al. 2010, Ellis et al. 2012), these organisations need to know where in the landscape species stand the best chance of persisting, so that the protection of these areas can be prioritised (Lawson et al. 2012, 2014). If these more resilient locations can be determined, and the specific attributes of the land that lead to their high quality ascertained, then the performance of spatial prioritisation undertaken across the wider landscape can be improved.

A small but growing body of literature suggests that microclimate (fine-scale climate, and its spatial variation) may play an important role in modifying species' responses to climatic change. Microclimate has been known to be an important modifier of the broader macroclimate for some time (Kraus 1911, Geiger 1927), but measuring it (Chen et al. 1999) and modelling it (Gillingham et al. 2012) at fine spatial and temporal resolutions has not been possible until recent advances in microchip technology and computing. Fortunately, comprehensive databases of high resolution natural history records, such as those in the Butterflies for the New Millennium (BNM) and National Moth Recording Scheme (NMRS) datasets, present the means to identify associations of species with local habitat features like microclimate. Although some studies have tested these fine-scale species data for a response to temporal variability in the climate (e.g. Suggitt et al. 2012, Letten et al. 2013, Oliver et al. 2013), the microclimatic features of landscapes or regions that can help species persist under climatic change have rarely been tested (but see Suggitt et al. 2014). While our mechanistic understanding of microclimate is improving (Wang et al. 2013), deployment of this type of model is often limited to resolutions of 1 km or coarser, and to limited spatial extents (for which ground-truthing data are required for validation purposes). Statistical downscaling (e.g. Haylock et al. 2008) offers a useful proxy for climatic conditions on the ground, but its reliability is constrained by the quality and density of meteorological observations, which will not be available for all landscapes of interest (Ashcroft and Gollan 2012).

Hence tests involving a combination of fine-scale, multispecies datasets and microclimate beyond the boundaries of wildlife sites are rare (see Bennie et al. 2013 and Ashcroft et al. 2014 for single species examples). Here, we attempt such a test. We assembled fine-scale records of a well-recorded species group

(Lepidoptera) for four British landscapes whose topographic and land cover features were identified as providing potentially refugial conditions from climatic change for species at a national level (Suggitt et al. 2014). The landscapes were 20 x 20 km grid squares in two upland landscapes of south-west England (Dartmoor and Exmoor in the county of Devon), and two lowland landscapes of eastern England (The Brecks and The Broads in Suffolk and Norfolk). We tested recent (~ 40 year) patterns of persistence in the Lepidoptera for a signature of microclimate, while controlling for other effects (e.g. agricultural intensity) that may have modified responses at this scale. We used simple, topographically-derived indices of microclimate to represent spatial variation in temperature and wetness at this scale. We tested the following hypotheses:

1) Patterns of persistence and extinction in the Lepidoptera have responded to spatial variation in the microclimate.
2) Patterns of persistence and extinction in the Lepidoptera have responded to spatial extremity in the microclimate.
3) Responses consistent with 1) or 2) were stronger in heterogeneous landscapes where spatial variation in the climate was larger.

Methods

Biological data

Butterfly (BNM) and macromoth (NMRS) data were obtained from Butterfly Conservation and the Centre for Ecology and Hydrology's (CEH) Biological Records Centre for four 20 km x 20 km landscapes (Table 1, Appendix 1 and 2). Two of these (The Brecks, The Broads) have low topographic heterogeneity, while the other two have high topographic heterogeneity (Dartmoor, Exmoor). This provided a test of the microclimate indices in both types of landscape. The four landscapes offered different mixes of species: The Broads records included moth species, and with Dartmoor also had more records of habitat specialists than Exmoor or the Brecks (Appendix 2).

Records from the BNM & NMRS are tagged with a location on the Ordnance Survey of Great Britain (OSGB) national grid. Since 2000, most records are located to a resolution of 100 m x 100 m grid squares, but coarser resolutions (up to 10 km x 10 km) were common in earlier years. We conducted our analysis at 1 km precision to maximise the inclusion of older records whilst minimizing the probability that records were assigned to the wrong grid square. Records were sorted into two temporal groupings 1971-1990, and 1991-2010, which were treated as pre- and post-climatic warming conditions. We classified each occupied 1 km grid square in the first time period as either a ‘persistence’ or an ‘extinction’ depending on whether the species was also recorded during the second time period. Extinctions were only confirmed if the corresponding grid square had been visited by a (Lepidoptera) recorder in the second time period. For each 20 km landscape, we included only those species for which persistence or extinction could be classified in at least fifteen separate 1 km grid squares.

Microclimate data

NEXTMap Digital Elevation Models (DEMs, Intermap Technologies 2007) for the four study landscapes were obtained from NERC’s Earth Observation Data Centre. These report terrain elevation at the 5 m grid square level. For each of these 5 m grid squares in each study landscape, we calculated two indices of microclimate (also see Figure 1 panels a,b):

1) Temperature proxy- Summer solar index

To provide a proxy of fine-scale variations in surface temperature, we calculated a solar index. This index measures the proportion of direct beam solar radiation (i.e. that which is not reflected or scattered – also termed insolation) that reaches a surface. Although differences between fine-scale surface and regional temperatures are also affected strongly by factors such as cloud cover and wind speed, direct beam radiation has been shown to serve as a useful proxy of fine-scale variations in surface temperatures (Bennie et al. 2008) and concomitant variations in the biota (Bennie et al. 2006). Topography influences direct beam radiation by affecting the incidence angle between the sun and surface, and can be calculated from the slope inclination and aspect and from the solar altitude and azimuth, which are themselves contingent on the time of day and year and geographic location of the surface. Because different species of Lepidoptera are sensitive to temperature at different times of year, we calculated this index for Midsummer’s day (21st June) to approximate mid-season conditions. Our algorithm, based on that provided in Šúri and Hofierka (2004), also accounted for shading, whereby the direct radiation may be obscured by topographic features at certain times of day.

2) Water availability proxy- Topographic wetness index

The topographic wetness index provides a proxy of fine-scale variations in water availability. Basin flow accumulation was calculated from the DEM, which in turn was used to define the contributing area (the property known as *a*, Equations 1 and 2) for each grid square. This was combined with information on slope angle to generate the index (following Beven and Kirkby 1979). Using this approach, valley bottoms (which have a high contributing area) are considered to be wetter than mountain tops, and flat areas (which have low surface run-off) are considered to be wetter than areas with steep slopes.

Equations 1 and 2 Calculating the topographic wetness index

$$\text{Topographic wetness index} = \log_e\left(a / \tan \beta \right) \quad (1)$$

Where β is the slope angle and a is the contributing area, which can be derived from flow accumulation as follows:

$$a = (\text{flow accumulation} + 1) \times \text{grid square resolution}^2 \quad (2)$$

Both microclimate indices rely on information from the surrounding landscape to calculate values for the target grid square robustly. We therefore included a five kilometre buffer around our landscapes to ensure that estimates of topographic shading and basin flow were accurate (this was checked via watershed analysis). To summarise the 5 m indices at the 1 km level, we calculated measures of variation (standard deviation, hypothesis 1) and extremity (5th and 95th percentiles, hypothesis 2) within each 1 km grid square for the landscape (i.e. drawing from 200 x 200 = 40,000 observations in each 1 km square, Figure 1 panels c, d).

Control variables

The persistence or extinction of species can respond to multiple drivers of change. Perhaps most prominent among these, habitat change and loss have been a key driver of biodiversity loss worldwide, notably so in British butterflies (Warren et al. 2001) and moths (Fox et al. 2014). We used the CEH Land Cover Map (Morton et al. 2011) to calculate the proportion of each 1 km grid square containing arable land, horticultural land, or improved pasture (unfortunately a national dataset of habitat change- specifically agricultural intensification- is not available, Mair et al. 2014). This measure of agricultural intensity was inserted into our statistical models as a control. Because recorder effort in almost all large biological datasets is variable, and low effort increases the chance of determining the false absence of (any) species, we also calculated the recorder effort (total number of recorder visits between 1971 and 2010) for each 1 km grid square to include as a control. Because this recorder effort has increased over time, both in Britain and in our four study landscapes (Asher et al. 2001), apparent extinctions are more likely to be genuine (although this is an implicit assumption of our analyses).

Statistical modelling framework

For each landscape, we matched the 1 km records of Lepidoptera to the microclimatic indices and control variables in R (R Core Team 2013), before constructing logistic regression models to test our hypotheses. We fitted Generalised Linear Mixed Models (GLMMs) to our binomial (Persist/Extinct) response data using the 'lme4' package (Bates et al. 2014) with a 'logit' link function. Species identity was treated as a random intercept; hence models were built on all the species records within a landscape. We built 24 separate models to test each microclimate measure (n=6) in each study landscape (n=4). Conventional (Wald-type) means of estimating 95% confidence intervals for parameter estimates within a GLMM framework may not be robust for lower sample sizes. Here, we used the (more conservative) profile log-likelihood method (Venzon and Moolgavkar 1988). Akaike's Information Criterion (AIC, Burnham and Anderson 2002) was calculated for each model to assess the performance of models including microclimate against models including only control variables (recorder effort, agricultural intensity), in an information-theoretic approach.

Fitting models to the data permitted the testing of hypotheses 1) and 2), namely a response of persistence to spatial variation or extremity in the microclimate (in a manner that was statistically detectable). However, to test how useful this information could be in a conservation sense, we generated model predictions of persistence in response to an example microclimate measure. If the relationships described above (Figure 4, Appendix 3) were apparent in these predictions once the control effects of levels of recording and agricultural intensity had been included, then it can be inferred that the effect in question is driving differences in rates of persistence in that landscape, over and above the controls. For example, a model fitted with a microclimate variable could still achieve an AIC improvement of more than two over the controls-only model even if patterns of agricultural intensity were actually the dominant driver of persistence in that landscape. In this case, the relationship to a particularly variable or extreme microclimate could be a genuine one, but its effect would be overwhelmed by a response to the other measure. Model predictions for persistence at the 1 km level were generated using the 'predict' function within lme4 (Bates et al. 2014). Agreement between these predictions and the corresponding observations was assessed by calculating the degree of covariance (σ) between the two.

We used a number of techniques to measure and account for spatial autocorrelation in the data, including repeating analyses at the 2 km grid square level. The 2 km analyses also provided a check of the sensitivity of our results to potential false absences in the second period.

Results

Temperature proxy- Summer solar index

We estimated larger levels of variability in summer insolation in the two more topographically heterogeneous landscapes (Dartmoor, Exmoor) than in the flatter landscapes (Brecks, Broads; Figure 2). Exmoor seemed to generate the widest range of solar index values of all the landscapes, with the Brecks being the least variable. These differences were apparent in all three measures of insolation at the 1 km level: low (5th percentile, Figure 2 panels a,b), low (95th percentile, Figure 2e,f) and variable (SD, Figure 2c,d) insolation. The standard deviation in solar index was an order of magnitude greater in the more variable landscapes than in the less variable landscapes.

Water availability proxy- Topographic wetness index

The flatter landscapes were estimated to be (topographically) wetter than the heterogeneous landscapes (Figure 3a,b,e,f), particularly so for 1 km grid squares with extremely dry conditions (5th percentile wetness). Although median variability in topographic wetness was broadly similar across both types of landscape, the range of standard deviation values in the heterogeneous landscapes was larger (Figure 3c,d).

Statistical modelling of persistence

There was evidence that variability and extremity in the microclimate affected persistence in all landscapes (Table 2, Figure 4, Appendix 3). Models including some measure of microclimate performed better than controls-only models (including land cover and recording effort effects) in 7 of the 8 combinations of landscape and microclimate proxy. Broadly, responses to higher minimum and maximum values of solar index were negative (Figure 4), while responses to wetness differed between the landscapes. We proceed with detailed descriptions of the model results by landscape.

Brecks

For the Brecks data, a single model performed better (Δ AIC < 2) than the controls-only model. This model was fitted with the 5th percentile topographic wetness index values, and the response was positive, indicating that persistence responded positively to higher minimum wetness conditions (Appendix 3). The slope value of 0.67 (Table 2) can be interpreted thus: every unit increase in the 5th percentile of our topographic wetness measure (calculated per 5 m grid square in each 1 km grid square) increased the log odds of a typical species of butterfly persisting by a factor of 0.67 (holding all other effects constant). By taking the exponent of this value, a unit increase in the 5th percentile of our topographic wetness measure increased the odds of a butterfly or moth persisting by a factor of 1.96, or in other words, for every unit increase in wetness, a typical species was almost twice as likely to persist in 1 km grid squares with fewer areas of extreme dry conditions as go extinct. In terms of the control variables, agricultural intensity had a predictably negative effect on persistence. Here, a unit increase in agricultural intensity decreased the odds of butterfly persistence by a factor of 0.17 (an 83% decrease in the odds). Given that our measure represents the proportion of the land occupied by arable and horticultural land, ranging between 0 and 1 (i.e. an entire ‘unit’), this effect could be interpreted as being relatively modest: a 1% increase in agricultural intensity reduced the odds of persistence by 0.83%.

Broads

Lepidoptera in the Broads showed the widest range of responses to microclimate of all the study landscapes, with five of the six microclimate models performing better than control (Table 2). Models built with the 5th percentile topographic wetness index values and the 95th percentile summer solar index values performed notably better than other types of microclimate model, however. These models implied a negative response to high maximal solar index values and a positive response to higher minimum wetness (Figure 4a,b, Appendix 3). These results suggest that species were less likely to have persisted in 1 km grid squares that contained either the driest or hottest conditions in the landscape. Note that parameter estimates for all models containing the summer solar index (Appendix 3) were divided by 100 prior to calculating the probabilities in Figure 4a, to aid readability and ensure the resulting ratios have more ‘real world’ relevance. Hence, for example, the Dartmoor 5th percentile probability of 0.48 in Figure 4a represents a decrease in the probability of persistence by 0.02, or 2% (0.5-0.48), for every increase of 0.01 in the 5th percentile summer solar index.

Dartmoor

Dartmoor was the only landscape in which Lepidoptera responded negatively to wetness, with species persistence higher in grid squares with a lower minimum (5th percentile) wetness score (Figure 4b) i.e. the driest parts of the squares appeared to favour persistence. Species also responded negatively to higher minimum insolation, and positively to heterogeneity in solar regime (Figure 4a). These models could not be separated based on our performance criterion (Table 2): the former model suggested that species had a greater chance of persistence in 1 km squares where some very cool conditions were available; while the latter, potentially related, model suggested that a wide variety of levels of solar insolation favoured persistence in 1 km squares.

Exmoor

Microclimate models performed better than control in two of the six combinations of microclimate index and measure, although the improvement in AIC was marginal in both cases (Δ AIC < 4). These implied responses were a negative response to extremely high solar index values (Figure 4a; note that the confidence intervals are masked by the plot symbol), and a positive response to higher minimum wetness (Figure 4b). The direction of the responses was thus similar to that estimated for the Broads, with species less likely to persist in squares containing the hottest or driest conditions in the landscape.

Testing model predictions

Models including the 5th percentile measure of topographic wetness index were responsible for the 'best' model in two of the four landscapes (Brecks and Dartmoor), and had an AIC score of only 1.1 and 3.2 above the 'best' model in the other two landscapes (Exmoor and Broads, respectively). The 5th percentile topographic wetness measure was also the only variable to achieve an AIC score improvement in all four landscapes relative to the controls-only model (Table 2). Therefore, for consistency we proceeded with this variable to assess the predictive ability of models fitted with microclimate in each landscape.

Evidence for the signature of microclimate effects on lepidopteran persistence in the four landscapes was mixed (Figure 5), although the beneficial effect of extreme low wetness in Dartmoor was apparent (Figure 5c), with a close fit between the observed and modelled probability of persistence for species in the landscape. Observed and predicted persistence values exhibited positive covariance in two landscapes (Dartmoor σ: 0.0700; Broads σ: 0.0300) and negative covariance in the other two landscapes (Brecks σ: -0.0040; Exmoor σ: -0.0003), indicating that established relationships to topographic wetness were more likely to be the dominant driver of persistence in these former two landscapes (Dartmoor, Broads) than in the latter two (Brecks, Exmoor). Results from analyses at 2 km grid square level were consistent with those conducted at 1 km grid square level (Appendix 4).

Discussion

Did patterns of persistence and extinction in the Lepidoptera respond to spatial variation in, or extremity of, the microclimate?

We detected a number of effects of spatial variation and extremity in the microclimate on persistence patterns in the Lepidoptera (Table 2, Appendix 3). Our model selection criteria identified that 11 of the 24 possible model combinations of microclimate variable and landscape performed better than control, and in all these cases, the microclimate effect was statistically significant. In terms of Hypothesis 1 (namely: "Patterns of persistence and extinction in the Lepidoptera have responded to spatial variation in the microclimate"), standard deviation in solar index was (jointly) responsible for the 'best' model in the Dartmoor landscape, and 3 of the 8 possible models for microclimate variability across the four landscapes performed better than the controls-only equivalent. In three landscapes (and jointly in Dartmoor, Table 2) 'best' models comprised responses to extreme microclimate, and models fitted with measures of extreme microclimate outperformed the controls-only model in 8 of 16 cases, offering support for Hypothesis 2 ("Patterns of persistence and extinction in the Lepidoptera have responded to spatial extremity in the microclimate").

Taking the measure with the most evidence of an effect on persistence across the Lepidoptera group in our study landscapes (5th percentile measure of topographic wetness index), the ability of these models to predict persistence was mixed (Figure 5). It is perhaps relevant that the microclimate effects were more evident in the predicted values for the landscapes that offered more records for model fit (Dartmoor and the Broads, *n* = 1719, 2133 respectively), while the microclimate effects were less apparent in landscapes that were less well observed (Exmoor and the Brecks, *n* = 538, 1051). Positive covariance between observed and predicted persistences in the Broads and Dartmoor landscapes lends weight to the predictive ability of these models. The (weakly negative) covariance observed in the other two landscapes (Brecks, Exmoor) may however reflect a lack of statistical power in their respective datasets, which would reduce the likelihood of discerning a microclimate effect. There may also be a genuinely diminished effect of microclimate in these landscapes (Brecks, Exmoor), variation in the hydrological requirements of the constituent species within each landscape, or differential patterns of rainfall change, which are often variable in space (Jenkins et al. 2008). It is also important to remember that the microclimatic conditions created by topography interact with habitat management to determine both the probability of population presence, and vulnerability to change. If the populations of many Lepidoptera are associated with relatively warm or dry pockets of the landscape at their northern range limits (e.g. Lawson et al. 2012, Suggitt et al. 2012), then populations in precisely such locations could be vulnerable to climatic variability, or to changes in management.

Were responses to microclimate stronger in landscapes where microclimatic heterogeneity was greater?

Solar index heterogeneity was estimated to be an order of magnitude greater in Dartmoor and Exmoor than in the Brecks and Broads (Figure 2c,d), while heterogeneity in topographic wetness in these landscapes was estimated to be broadly similar (Figure 3c,d). Models containing some measure of solar index were the 'best' models for both Dartmoor and Exmoor, according to AIC. In Exmoor, the AIC values would suggest that this was predominantly a negative response to extremely high insolation values, rather than heterogeneity *per se*. The Lepidoptera in Dartmoor seemed to respond both: a) negatively where local availability of 'cooler' solar index values was low, and b) positively where local heterogeneity in solar index was high. This is the type of response that could be expected for any temperature-sensitive species subject to warming at a given location, with availability of the coolest microclimates increasingly important in hotter years. In these cases, such habitats may offer an escape from hotter conditions, with heterogeneity being of benefit to any species that can modify its habitat association to dampen the extremes of macroclimate fluctuation (Krämer et al. 2012, Suggitt et al. 2012, Oliver et al. 2013).

Conservation implications

We found evidence for microclimatic effects in all our study landscapes, but these effects were not necessarily consistent in their direction. Species can respond to extremely high or low temperatures, or neither; for our study, this will have depended on the position of our study landscapes within the species' thermal niches (Settele et al. 2008), and the thermal requirements of the study species during midsummer. Responses to extreme levels of higher incoming solar radiation were mostly negative (Figure 4), while in Dartmoor, species seemed to benefit from higher levels of heterogeneity in local solar regime. Although there is little that conservationists can do at the site level to alter the solar regime, at a regional level, landscape-scale conservation projects could incorporate microclimatic diversity (especially ensuring protections of habitats or locations supporting cooler microclimates) into approaches to spatial prioritisation. In areas lacking this heterogeneity (in this study the Brecks and Broads), an alternative approach could be slope creation, which has already been implemented successfully in a number of conservation projects elsewhere (e.g. in Wiltshire, RSPB 2010; Sussex, Danahar 2011), Managing the height and density of vegetation may also be an option, and indeed some lepidopterans have already demonstrated that they can shift into taller vegetation if required (*Polyommatus bellargus*, cf. Roy and Thomas 2003). Such interventions should always form part of a wider consideration of species' habitat requirements, and although we exclude new colonisations from our analysis, the conditions necessary to encourage such colonisations (thereby enhancing the probability of successful range shifting) must also be preserved and encouraged wherever possible.

Reponses to wetness were both positive and negative, depending upon the context. This could reflect the varying patterns (and indeed direction) of change in precipitation that landscapes in Britain have experienced over the last 40 years (Jenkins et al. 2008), making a generic prescription for hydrological management for the benefit of Lepidoptera more difficult. Future rainfall in Britain, as in many mid-latitude regions, is projected to become more erratic and more intense. The likely effect of these projected trends on the conservation of Lepidoptera and insects generally is unclear. Nevertheless, the impact of any shift towards less reliable rainfall and a greater prevalence of drought-type conditions is likely to negate any benefit for Lepidoptera from a broader shift in the climate towards warmer mean temperatures (Oliver et al. 2013), despite many species being at the northern limits of their distributions and hence expected to be limited by the availability of warm conditions. Given the drying trend already observed and expected under future warming for the East of England region (Jenkins et al. 2008, Murphy et al. 2009), the negative effects of extreme dryness we discerned for the Brecks and Broads are likely to become more pronounced in the future. Prioritisation of wetter areas for conservation will in fact be easier to achieve than a prioritisation of heterogeneity, as mapping them does not require fine-scale analyses of the type required to adequately capture topographic heterogeneity. The likelihood of a positive regional or landscape-level response by Lepidoptera to climatic change is mitigated by the size, quality and configuration of suitable habitat (Oliver et al. 2013, Mair et al. 2014), meaning that adapting our conservation approach to climatic change cannot proceed without a broader approach that also addresses these factors. However, our observations suggest that the underlying effects of microclimate need to be taken account when planning conservation measures to enhance connectivity or local habitat quality.

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Fig. 1 Indices of microclimate were calculated for every 5 m OSGB square in the study landscapes. Panels (a) and (b) show an example calculation of summer solar index values for Dartmoor at the 5 m level. Summary measures of the microclimate within each 1km square were derived from these data (c), while retaining spatial information (d). This process was repeated across each landscape (example of the standard deviation in summer solar index for Dartmoor, panel e; see also Fig. 2). These values were matched to data describing persistence and extinction in the Lepidoptera (e.g. Green hairstreak, panel f) for statistical analysis.

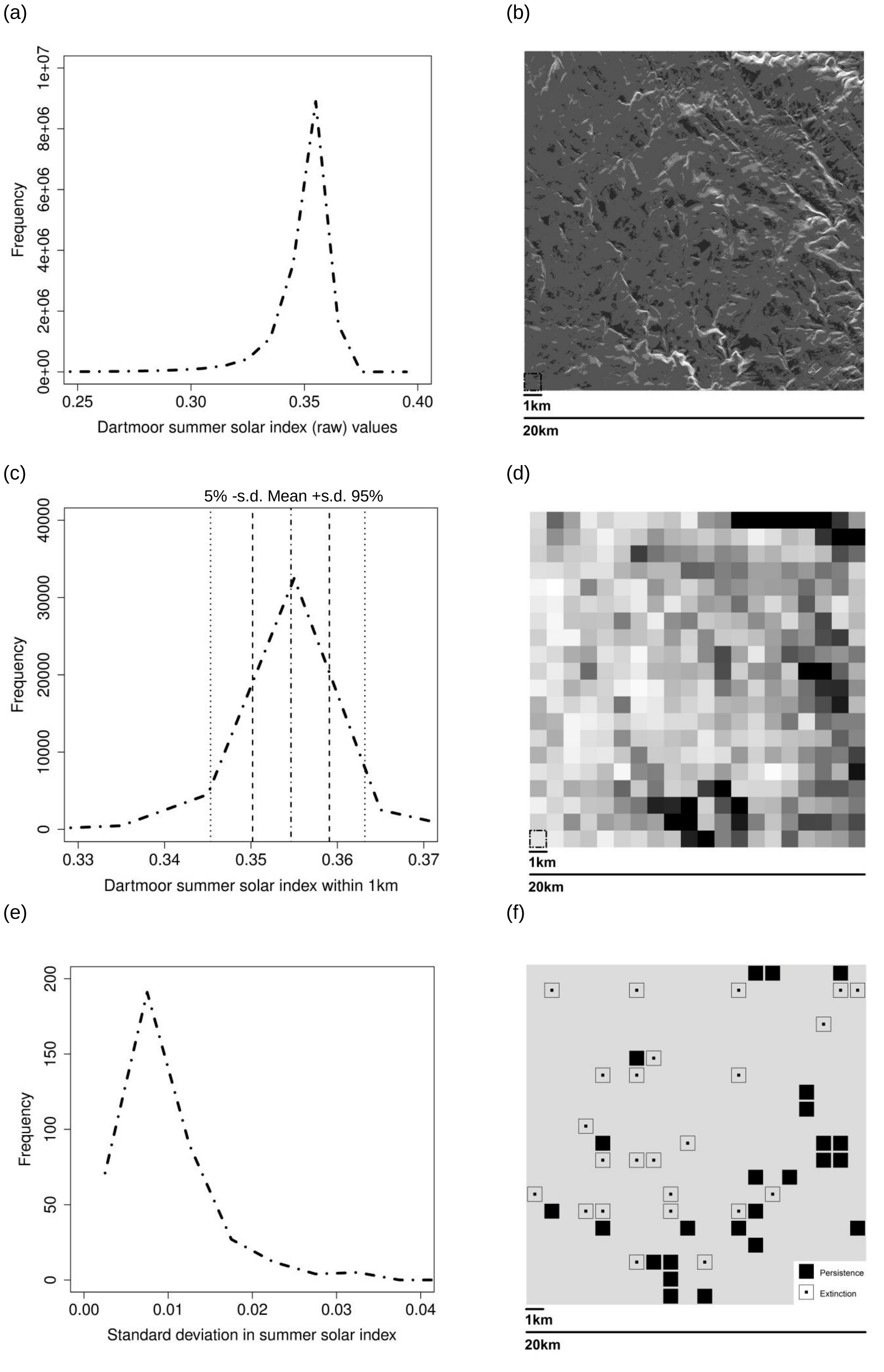


Fig. 2 Values of the summer solar index used in analyses. First, summer solar index was calculated for every 5 m grid square in each landscape. Second, these data were summarised at the 1 km grid square level by calculating the 5th percentile (panels a and b), standard deviation (c and d), and 95th percentile (e and f) the 5 m values within that square. Landscapes selected for study offered both low topographic heterogeneity (panels a,c,e) and high topographic heterogeneity (b,d,f).

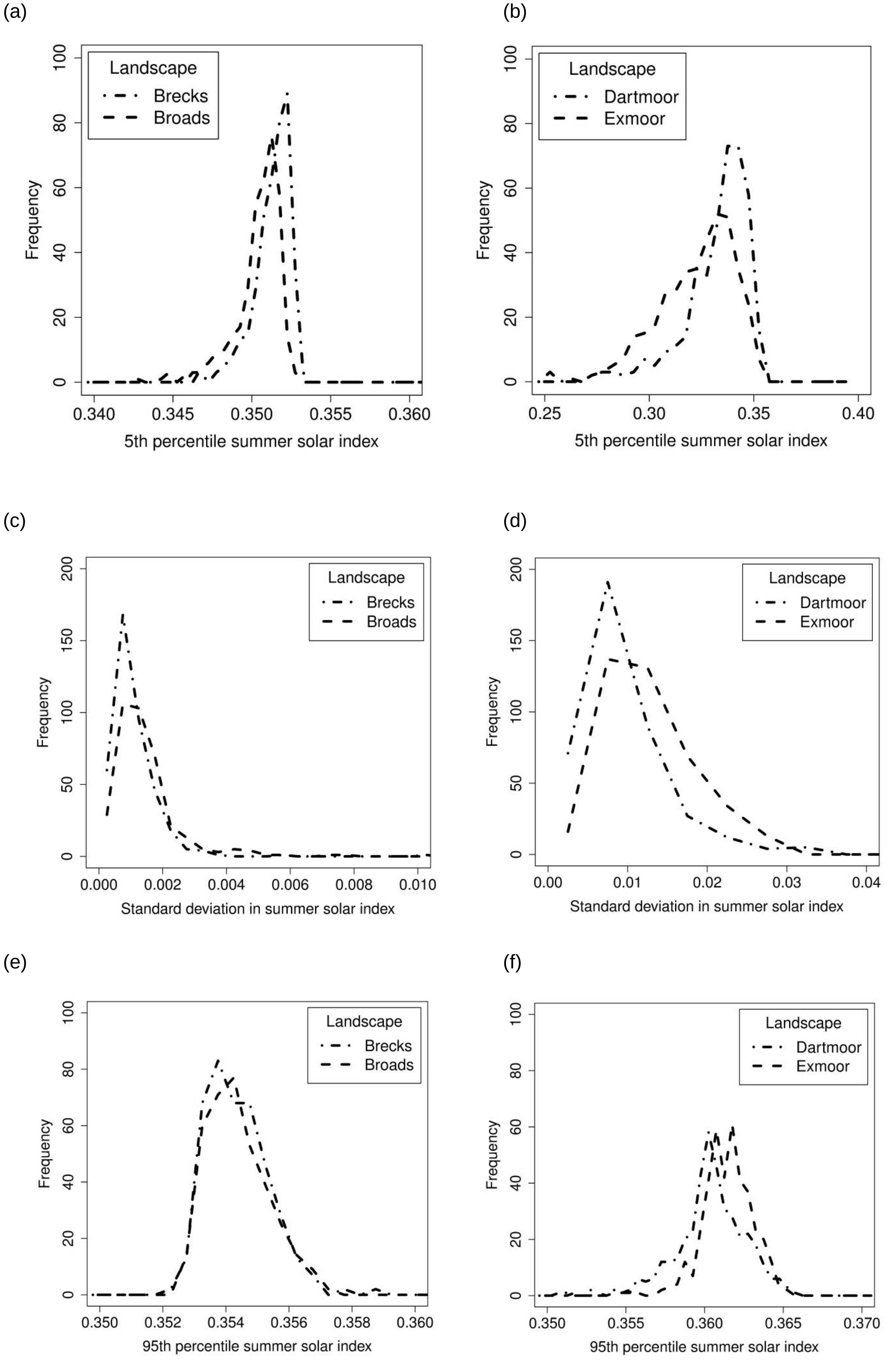


Fig. 3 Values of the topographic wetness index used in analyses. First, topographic wetness index was calculated for every 5 m grid square in each landscape. Second, these data were summarised at the 1 km grid square level by calculating the 5th percentile (panels a and b), standard deviation (c and d), and 95th percentile (e and f) of the 5 m values within that square. Landscapes selected for study offered both low topographic heterogeneity (panels a,c,e) and high topographic heterogeneity (b,d,f).

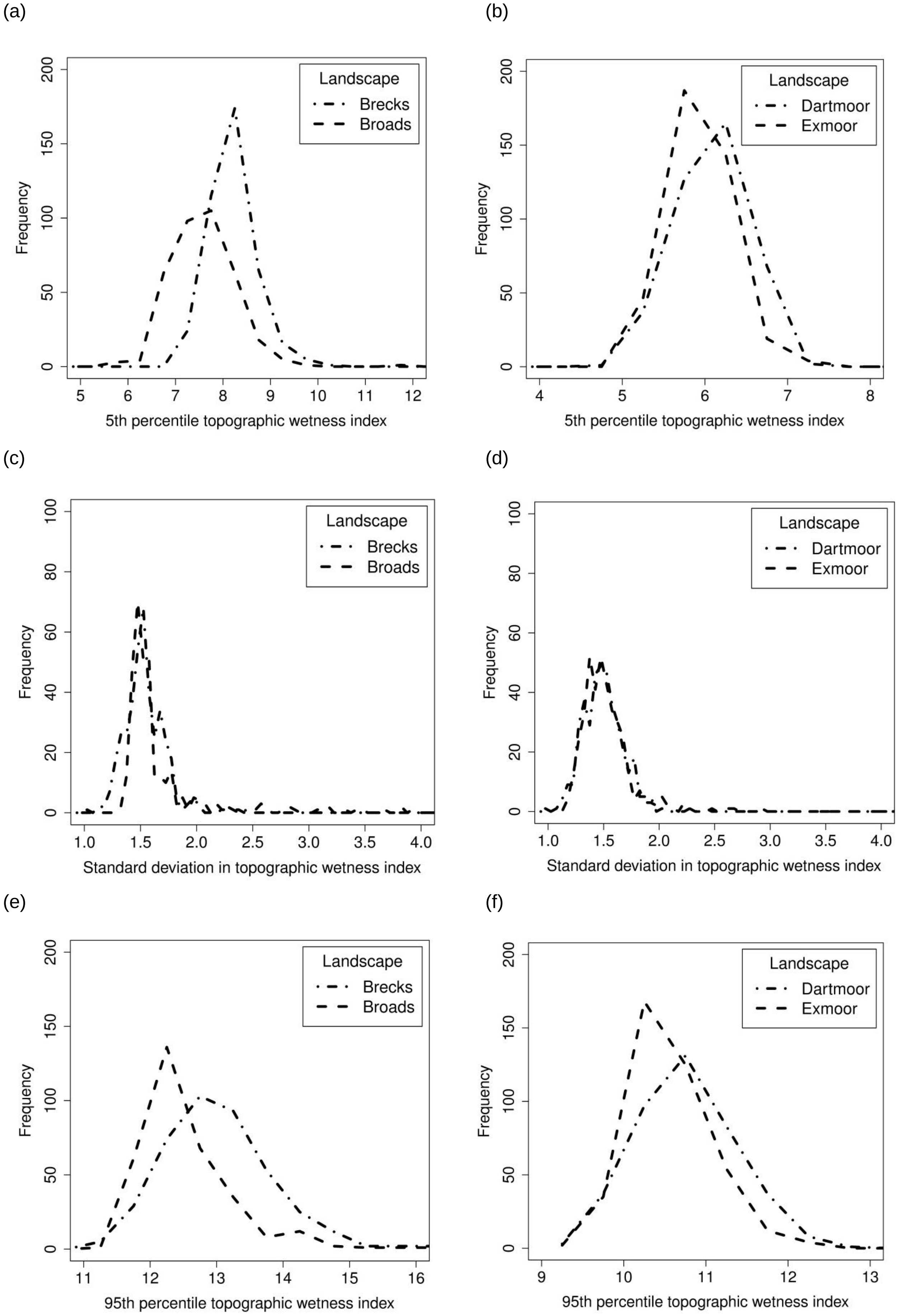
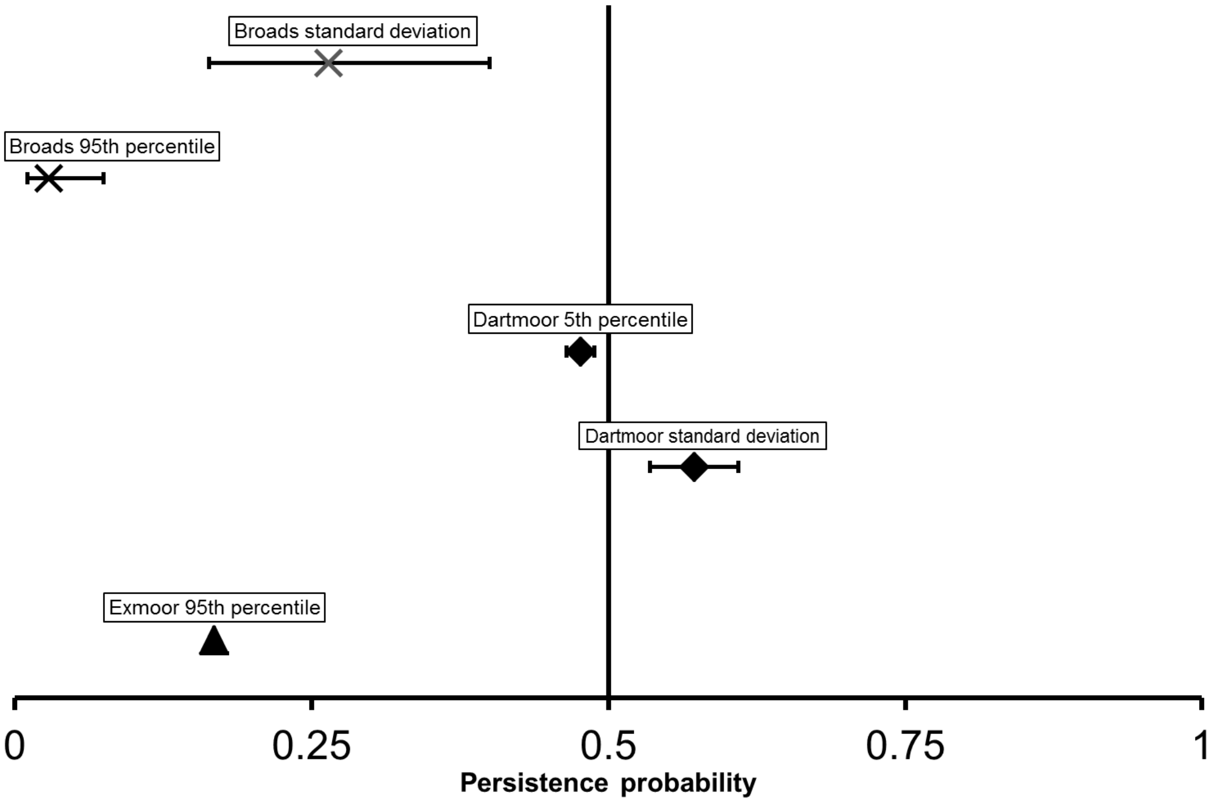

(a) (b) (c) (d) (e) (f)

Fig. 4 Effects of microclimate on the probability of persistence in Lepidoptera. Effects are only included if the GLMM it was built with achieved an AIC of more than two points below the control model. The effects of: (a) a 0.01 unit increase in summer solar index measures, and (b) a unit increase in topographic wetness index measures on persistence probability are presented. The ‘best’ model for each landscape (lowest AIC) is coloured in black, with other models coloured in grey. The two Dartmoor solar index models differed by less than two in their AIC score, and hence a ‘best’ model could not be determined. See Appendix 3 for full models.

(a) Summer solar index



(b) Topographic wetness index

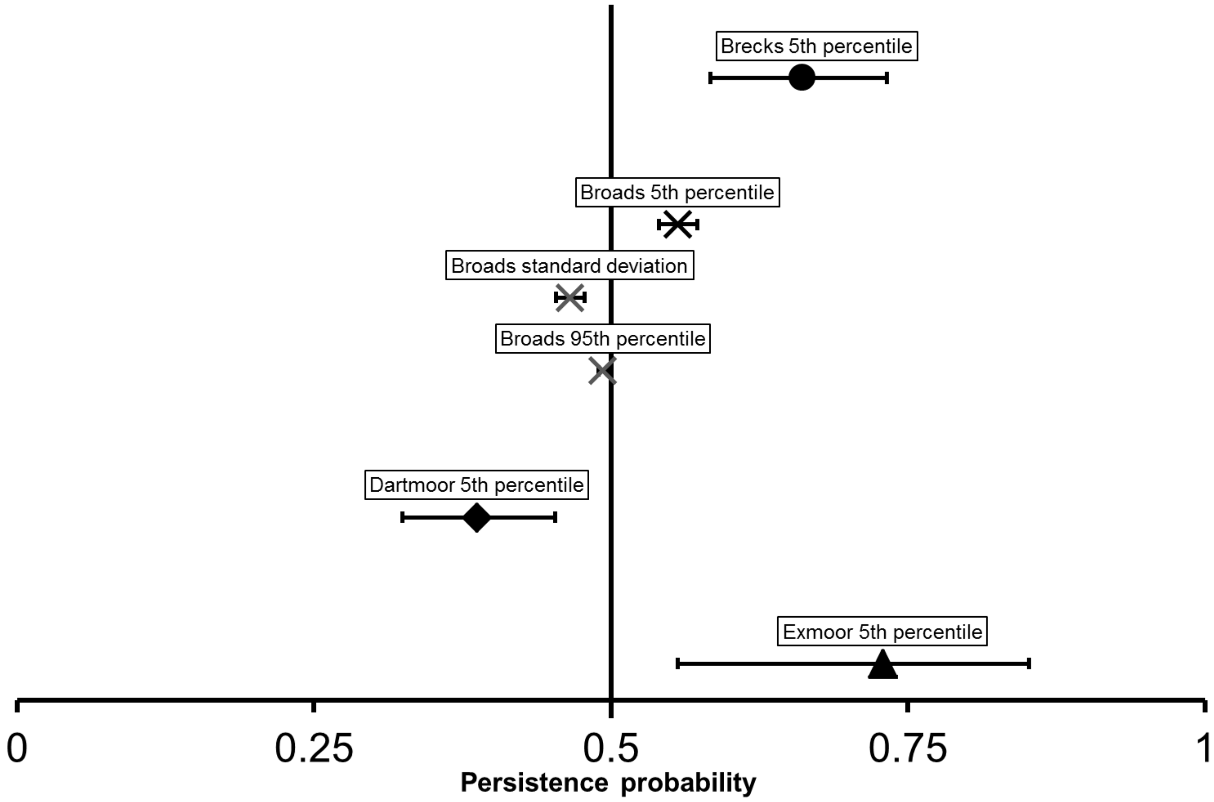
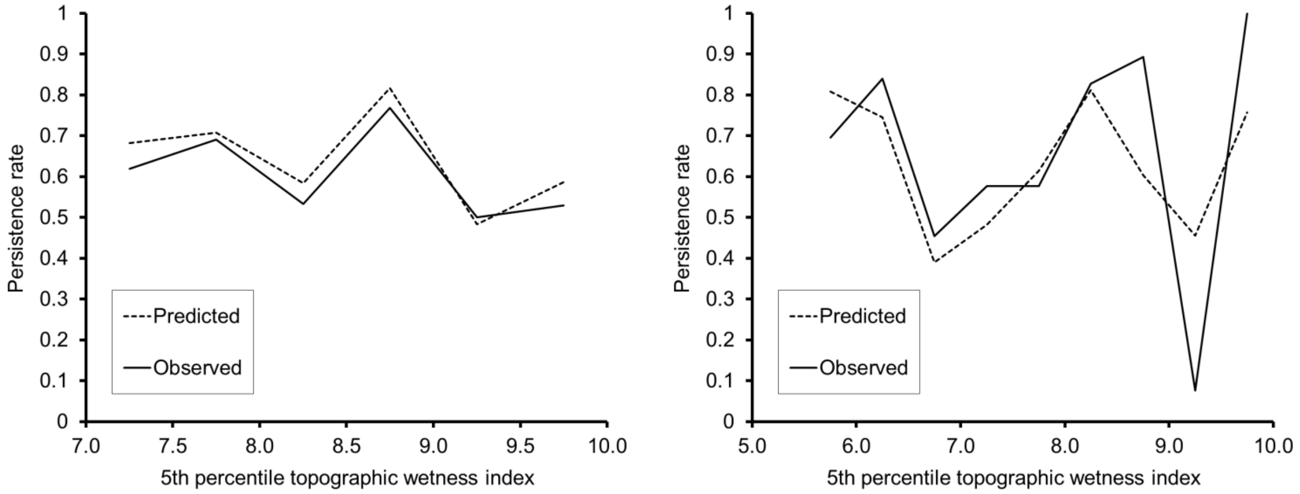
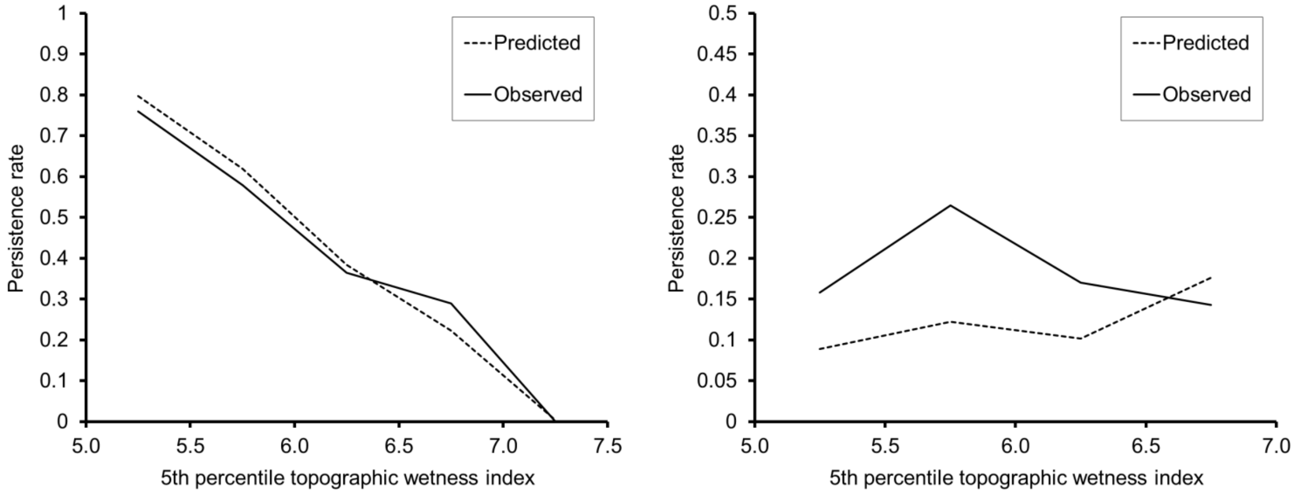


Fig. 5 Predicted and observed persistence in the Lepidoptera at various levels of the 5th percentile topographic wetness index measure (calculated at the 1 km level). Solid lines indicate mean persistence observed in the raw data at each level of wetness. Dotted lines indicate model predicted persistence at the corresponding level of wetness. Values for the level of covariance between observed and predicted persistence in each landscape appear in brackets.



(a) Brecks (σ = -0.0040)

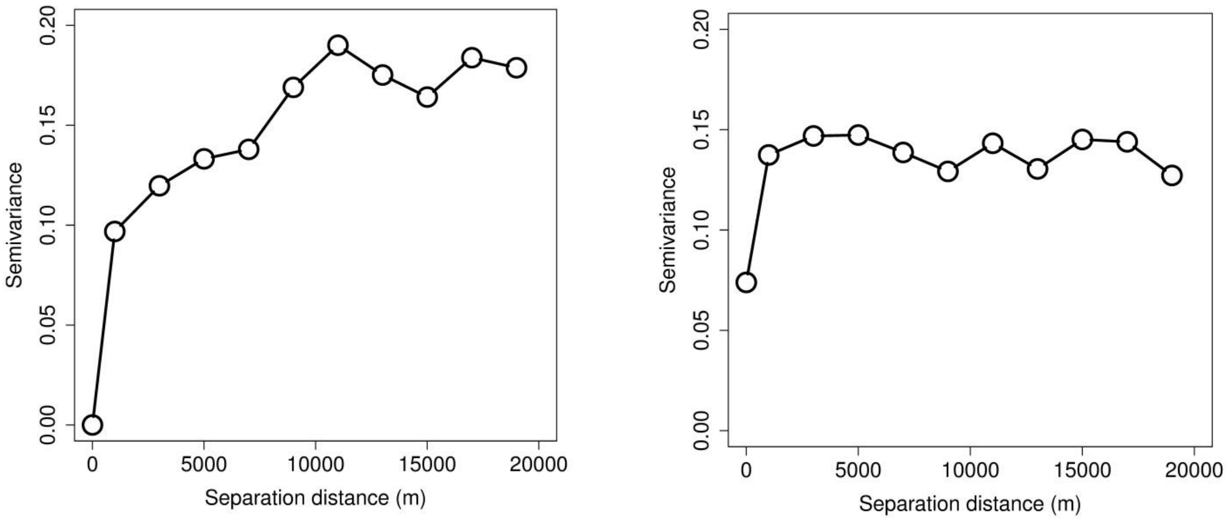
(b) Broads (σ = 0.0300)



(c) Dartmoor (σ = 0.0700)

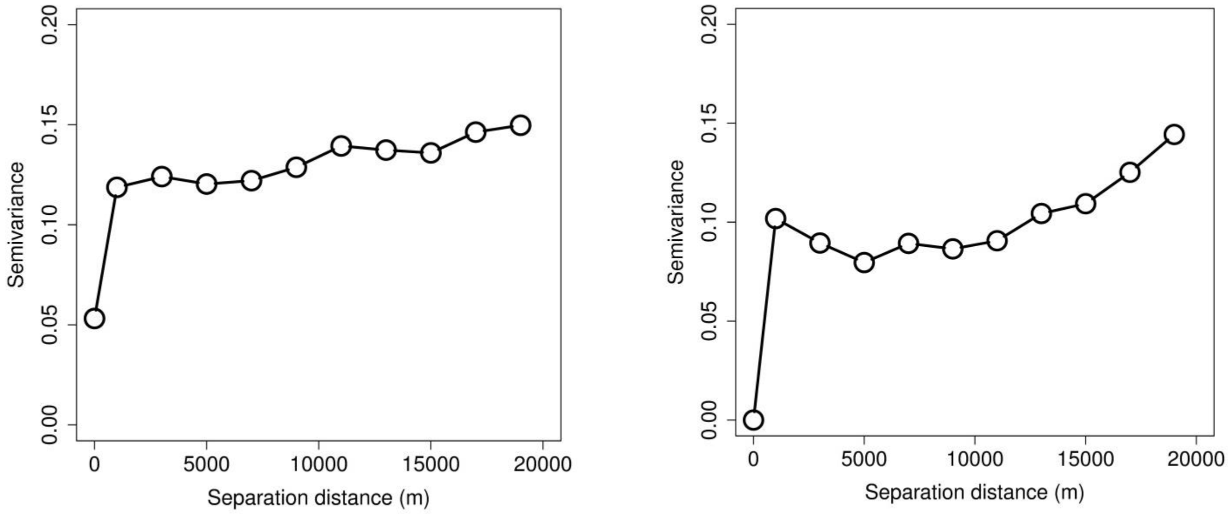
(d) Exmoor (σ = -0.0003)

Fig. S1 Semivariograms for values of species persistence recorded across the four study landscapes. Semivariance (y-axis) was calculated between pairs of points at separation distances (x-axis) of up to 20km.



(a) Brecks

(b) Broads



(c) Dartmoor

(d) Exmoor

Table 1 Lepidoptera species data included in statistical models. Here, we use the word ‘record’ to represent the recorded persistence or extinction of a species in a 1 km grid square. Species lists for each landscape are included in Appendix 2.

Landscape	n (species)	n (records)	n (persistences)	n (extinctions)
Brecks	22	1051	647	404
Broads	88	2133	734	1399
Dartmoor	30	1719	901	818
Exmoor	9	538	118	420

Table 2 Change in information theoretic estimates of Akaike's Information Criterion ('ΔAIC', Burnham and Anderson 2002) for Generalised Linear Mixed Models (GLMMs) fitted with indices of microclimate, relative to those fitted solely with control variables. Values in bold highlight models including microclimate that achieved an improvement in AIC of more than 2 points. A star indicates the microclimate variable was statistically significant ($p < 0.05$).

Landscape	ΔAIC for models featuring a microclimatic explanatory variable					
	Topographic wetness index			Summer solar index		
	Low	Variable	High	Low	Variable	High
Brecks	**-9.0***	-0.3	+1.8	+1.9	+1.5	+1.9
Broads	**-38.4***	**-20.4***	**-6.0***	-0.2	**-5.3***	**-31.7***
Dartmoor	**-5.7***	+1.0	+0.3	**-8.9***	**-8.2***	1.5
Exmoor	**-2.5***	+1.7	+0.8	-0.1	-1.1	**-3.6***

Appendix 1 OSGB 10km (hectad) codes for the study landscapes.

Landscape	10k hectad codes (grid squares)
Brecks	TL78, TL79, TL88 & TL89
Broads	TG31, TG32, TG41 & TG42
Dartmoor	SX67, SX68, SX77 & SX78
Exmoor	SS62, SS63, SS72 & SS73

Appendix 2 List of species included in statistical models (by landscape).

(a) Brecks (n=22)

Scientific name	**Common name**
Aglais urticae	Small Tortoiseshell
Anthocharis cardamines	Orange-tip
Aphantopus hyperantus	Ringlet
Aricia agestis	Brown Argus
Coenonympha pamphilus	Small Heath
Gonepteryx rhamni	Brimstone
Hipparchia semele	Grayling
Inachis io	Peacock
Lycaena phlaeas	Small Copper
Maniola jurtina	Meadow Brown
Ochlodes faunus	Large Skipper
Pararge aegeria	Speckled Wood
Pieris brassicae	Large White
Pieris napi	Green-veined White
Pieris rapae	Small White
Polygonia c-album	Comma
Polyommatus icarus	Common Blue
Pyronia tithonus	Gatekeeper
Thymelicus lineola	Essex Skipper
Thymelicus sylvestris	Small Skipper
Vanessa atalanta	Red Admiral
Vanessa cardui	Painted Lady

(b) Broads (n=88)

Scientific name	**Common name**
Abraxas grossulariata	The Magpie
Acronicta psi	Grey Dagger
Aglais urticae	Small Tortoiseshell
Agrotis exclamationis	Heart & Dart
Agrotis puta	Shuttle-shaped Dart
Anthocharis cardamines	Orange-tip
Apamea lithoxylaea	Light Arches
Apamea monoglypha	Dark Arches
Aphantopus hyperantus	Ringlet
Arctia caja	Garden Tiger
Arenostola phragmitidis	Fen Wainscot
Axylia putris	The Flame
Biston betularia	Peppered Moth
Cabera exanthemata	Common Wave
Cabera pusaria	Common White Wave
Campaea margaritata	Light Emerald
Celaena leucostigma	The Crescent
Coenonympha pamphilus	Small Heath

Broads species list continued…

Scientific name	**Common name**
Cosmia trapezina	Dun-bar
Crocallis elinguaria	Scalloped Oak
Deilephila elpenor	Elephant Hawk-moth
Diachrysia chrysitis	Burnished Brass
Diarsia rubi	Small Square-spot
Discestra trifolii	The Nutmeg
Drepana falcataria	Pebble Hook-tip
Eilema griseola	Dingy Footman
Eilema lurideola	Common Footman
Ennomos alniaria	Canary-shouldered Thorn
Epirrhoe alternata	Common Carpet
Euproctis similis	Yellow-tail
Euthrix potatoria	The Drinker
Furcula furcula	Sallow Kitten
Gonepteryx rhamni	Brimstone
Habrosyne pyritoides	Buff Arches
Hoplodrina alsines	The Uncertain
Hydriomena furcata	July Highflyer
Hypena proboscidalis	The Snout
Idaea aversata	Riband Wave
Idaea dimidiata	Single-dotted Wave
Inachis io	Peacock
Lacanobia oleracea	Bright-line Brown-eye
Laothoe populi	Poplar Hawk-moth
Lasiommata megera	Wall
Lomaspilis marginata	Clouded Border
Lycaena phlaeas	Small Copper
Maniola jurtina	Meadow Brown
Mythimna ferrago	The Clay
Mythimna impura	Smoky Wainscot
Mythimna pallens	Common Wainscot
Mythimna straminea	Southern Wainscot
Noctua comes	Lesser Yellow Underwing
Noctua fimbriata	Broad-bordered Yellow Underwing
Noctua interjecta	Least Yellow Underwing
Noctua janthe	Lesser Broad-bordered Yellow Underwing
Noctua pronuba	Large Yellow Underwing
Notodonta dromedarius	Iron Prominent
Notodonta ziczac	Pebble Prominent
Ochlodes faunus	Large Skipper
Ochropleura plecta	Flame Shoulder
Opisthograptis luteolata	Brimstone Moth
Papilio machaon	Old World Swallowtail
Pelosia muscerda	Dotted Footman
Peribatodes rhomboidaria	Willow Beauty

Broads species list continued…

Scientific name	**Common name**
Phalera bucephala	Buff-tip
Pheosia tremula	Swallow Prominent
Phlogophora meticulosa	Angle Shades
Phragmatobia fuliginosa	Ruby Tiger
Pieris brassicae	Large White
Pieris napi	Green-veined White
Pieris rapae	Small White
Polygonia c-album	Comma
Pterostoma palpina	Pale Prominent
Ptilodon capucina	Coxcomb Prominent
Pyronia tithonus	Gatekeeper
Rivula sericealis	Straw Dot
Scopula immutata	Lesser Cream Wave
Selenia dentaria	Early Thorn
Simyra albovenosa	Reed Dagger
Smerinthus ocellata	Eyed Hawk-moth
Thumatha senex	Round-winged Muslin
Thymelicus sylvestris	Small Skipper
Vanessa atalanta	Red Admiral
Vanessa cardui	Painted Lady
Xanthorhoe ferrugata	Dark-barred Twin-spot Carpet
Xanthorhoe spadicearia	Red Twin-spot Carpet
Xestia c-nigrum	Setaceous Hebrew character
Xestia triangulum	Double Square-spot
Xestia xanthographa	Square-spot Rustic

(c) Dartmoor (n=30)

Scientific name	**Common name**
Aglais urticae	Small Tortoiseshell
Anthocharis cardamines	Orange-tip
Aphantopus hyperantus	Ringlet
Argynnis adippe	High Brown Fritillary
Argynnis aglaja	Dark Green Fritillary
Argynnis paphia	Silver-washed Fritillary
Boloria euphrosyne	Pearl-bordered Fritillary
Boloria selene	Small Pearl-bordered Fritillary
Callophrys rubi	Green Hairstreak
Celastrina argiolus	Holly Blue
Coenonympha pamphilus	Small Heath
Euphydryas aurinia	Marsh Fritillary
Gonepteryx rhamni	Brimstone
Hipparchia semele	Grayling
Inachis io	Peacock
Lasiommata megera	Wall

Dartmoor species list continued…

Lycaena phlaeas	Small Copper
Maniola jurtina	Meadow Brown
Melanargia galathea	Marbled White
Neozephyrus quercus	Purple Hairstreak
Ochlodes faunus	Large Skipper
Pararge aegeria	Speckled Wood
Pieris brassicae	Large White
Pieris napi	Green-veined White
Pieris rapae	Small White
Polygonia c-album	Comma
Polyommatus icarus	Common Blue
Pyronia tithonus	Gatekeeper
Vanessa atalanta	Red Admiral
Vanessa cardui	Painted Lady

(d) Exmoor (n=9)

Scientific name	**Common name**
Aglais urticae	Small Tortoiseshell
Anthocharis cardamines	Orange-tip
Aphantopus hyperantus	Ringlet
Maniola jurtina	Meadow Brown
Pararge aegeria	Speckled Wood
Pieris brassicae	Large White
Pieris napi	Green-veined White
Pyronia tithonus	Gatekeeper
Vanessa atalanta	Red Admiral

Appendix 3 Summary tables of GLMMs including microclimate that achieved an improvement in AIC of more than 2 points relative to a model including control variables only. Models fitted with measures of low (5th percentile), variable (standard deviation) and high (95th percentile) microclimate are presented, for summer solar and topographic wetness indices.

(a) 5th percentile topographic wetness index, Brecks landscape

Term	Estimate	S.E.	z-value	p
Intercept	-10.55	1.79	-5.91	3.42E-09
log(records)	1.45	0.1	14.41	4.49E-47
Agricultural intensity	-1.79	0.39	-4.55	5.45E-06
5th percentile topographic wetness index	0.67	0.20	3.33	0.000867

(b) 5th percentile topographic wetness index, Broads landscape

Term	Estimate	S.E.	z-value	p
Intercept	-8.55	0.49	-17.38	1.14E-67
log(records)	1.20	0.05	22.51	3.27E-112
Agricultural intensity	0.76	0.25	3.02	0.002527
5th percentile topographic wetness index	0.23	0.04	5.59	2.26E-08

(c) Standard deviation (SD) in topographic wetness index, Broads landscape

Term	Estimate	S.E.	z-value	p
Intercept	-6.32	0.37	-17.24	1.42E-66
log(records)	1.25	0.05	22.67	7.94E-114
Agricultural intensity	-0.18	0.27	-0.69	0.492803
SD in topographic wetness index	-0.14	0.03	-4.83	1.39E-06

(d) 95th percentile topographic wetness index, Broads landscape

Term	Estimate	S.E.	z-value	p
Intercept	-6.20	0.38	-16.22	3.63E-59
log(records)	1.22	0.05	22.59	5.24E-113
Agricultural intensity	0.05	0.26	0.19	0.845971
95th percentile topographic wetness index	-0.03	0.01	-2.87	0.004078

(e) Standard deviation (SD) in summer solar index, Broads landscape

Term	Estimate	S.E.	z-value	p
Intercept	-6.50	0.36	-18.12	2.08E-73
log(records)	1.20	0.05	22.60	3.94E-113
Agricultural intensity	0.32	0.24	1.34	0.180165
SD in summer solar index	-102.30	36.31	-2.82	0.004846

(f) 95th percentile summer solar index, Broads landscape

Term	Estimate	S.E.	z-value	p
Intercept	20.86	34.96	0.60	0.55078
log(records)	0.87	0.05	18.01	1.77E-72
Agricultural intensity	1.03	0.31	3.39	0.000712
95th percentile summer solar index	-73.66	98.82	-0.75	0.456074

(g) 5th percentile topographic wetness index, Dartmoor landscape

Term	Estimate	S.E.	z-value	p
Intercept	-0.59	1.08	-0.54	0.587215
log(records)	0.90	0.05	16.76	4.50E-63
Agricultural intensity	-2.12	0.54	-3.90	9.69E-05
5th percentile topographic wetness index	-0.46	0.17	-2.78	0.005362

(h) 5th percentile summer solar index, Dartmoor landscape

Term	Estimate	S.E.	z-value	p
Intercept	-0.32	1.02	-0.31	0.756238
log(records)	0.91	0.05	17.23	1.58E-66
Agricultural intensity	-1.76	0.53	-3.34	0.000836
5th percentile summer solar index	-9.39	2.88	-3.25	0.001134

(i) Standard deviation in summer solar index, Dartmoor landscape

Term	Estimate	S.E.	z-value	p
Intercept	-3.70	0.23	-16.14	1.24E-58
log(records)	0.91	0.05	17.16	5.12E-66
Agricultural intensity	-1.78	0.53	-3.39	0.000711
Standard deviation in summer solar index	28.98	9.19	3.15	0.001616

(j) 5th percentile topographic wetness index, Exmoor landscape

Term	Estimate	S.E.	z-value	p
Intercept	-11.28	2.81	-4.02	5.79E-05
log(records)	1.52	0.16	9.47	2.75E-21
Agricultural intensity	1.60	1.17	1.37	0.171372
5th percentile topographic wetness index	0.99	0.46	2.14	0.03268

(k) 95th percentile summer solar index, Exmoor landscape

Term	Estimate	S.E.	z-value	p
Intercept	52.28	23.74	2.20	0.027673
log(records)	1.47	0.15	9.48	2.58E-21
Agricultural intensity	2.46	1.11	2.22	0.026702
95th percentile summer solar index	-159.85	65.82	-2.43	0.015155

Appendix 4 Accounting for possible effects of spatial autocorrelation.

The results of spatial analysis can be confounded by spatial autocorrelation effects (Dormann et al. 2007). We tested for the presence of this non-independence in our persistence data by the construction of semivariograms using the package 'geoR' in R (Ribero and Diggle 2001). We calculated the semivariance between pairs of points at separation distances of up to 20 km, finding no evidence of a consistent spatial autocorrelation effect across the landscapes (Figure S1). In this figure, there is not a consistent 'sill' (flattening) present across the four landscapes that would be indicative of an obvious choice of spatial scale at which to aggregate the data. In the Broads the sill is reached at 1 km separation distance (i.e. the 'range' = 1 km), while in the Brecks the curve shows some signs of change (perhaps arguably) at 10 km.

We also aggregated our data at the 2 km grid square level as a further check of the robustness of our results to a possible effect of spatial autocorrelation, finding 10 of the 11 effects presented in Figure 4 to be consistent across both grain sizes (Tables below). Furthermore, the one effect that was not consistent with the 1 km results (Standard deviation in solar index, Broads landscape) was non-significant at the 2 km level.

Appendix 4 References

Dormann, C. et al. (2007). Methods to account for spatial autocorrelation in the analysis of species distributional data: a review. Ecography 30, 609-628.

Ribeiro, P.J. & Diggle, P.J. (2001). geoR: a package for geostatistical analysis. R-NEWS 1(2), 15-18. June, 2001.

Appendix 4 Tables (Format analogous to Appendix 3 data tables, but for analyses conducted at the 2 km grid square level). Summary tables of GLMMs fitted with measures of low (5th percentile), variable (standard deviation) and high (95th percentile) microclimate are presented, for summer solar and topographic wetness indices.

(a) 5th percentile topographic wetness index, Brecks landscape

Term	Estimate	S.E.	z-value	p
Intercept	-0.34	2.03	-0.17	0.86583
log(records)	0.85	0.07	11.64	2.67E-31
Agricultural intensity	-0.09	0.47	-0.19	0.847091
5th percentile topographic wetness index	0.40	0.24	1.62	0.105454

(b) 5th percentile topographic wetness index, Broads landscape

Term	Estimate	S.E.	z-value	p
Intercept	-3.78	0.66	-5.73	9.88E-09
log(records)	0.91	0.05	17.42	6.09E-68
Agricultural intensity	0.57	0.33	1.72	0.084618
5th percentile topographic wetness index	0.18	0.07	2.54	0.01101

(c) Standard deviation (SD) in topographic wetness index, Broads landscape

Term	Estimate	S.E.	z-value	p
Intercept	-4.90	0.41	-12.03	2.34E-33
log(records)	0.90	0.05	17.77	1.16E-70
Agricultural intensity	0.55	0.36	1.53	0.126882
SD in topographic wetness index	-0.10	0.05	-2.11	0.034748

(d) 95th percentile topographic wetness index, Broads landscape

Term	Estimate	S.E.	z-value	p
Intercept	-4.77	0.44	-10.86	1.85E-27
log(records)	0.91	0.05	17.37	1.31E-67
Agricultural intensity	0.62	0.35	1.77	0.077413
95th percentile topographic wetness index	-0.03	0.02	-1.96	0.049717

(e) Standard deviation (SD) in summer solar index, Broads landscape

Term	Estimate	S.E.	z-value	p
Intercept	-5.26	0.40	-13.18	1.15E-39
log(records)	0.87	0.05	17.88	1.83E-71
Agricultural intensity	0.99	0.30	3.32	0.000896
SD in summer solar index	28.52	49.98	0.57	0.568247

(f) 95th percentile summer solar index, Broads landscape

Term	Estimate	S.E.	z-value	p
Intercept	20.86	34.96	0.60	0.55078
log(records)	0.87	0.05	18.01	1.77E-72
Agricultural intensity	1.03	0.31	3.39	0.000712
95th percentile summer solar index	-73.66	98.82	-0.75	0.456074

(g) 5th percentile topographic wetness index, Dartmoor landscape

Term	Estimate	S.E.	z-value	p
Intercept	1.31	2.37	0.55	0.581976
log(records)	0.85	0.07	11.81	3.41E-32
Agricultural intensity	-2.13	0.81	-2.63	0.008523
5th percentile topographic wetness index	-0.86	0.36	-2.42	0.015626

(h) 5th percentile summer solar index, Dartmoor landscape

Term	Estimate	S.E.	z-value	p
Intercept	7.59	2.33	3.26	0.00111
log(records)	0.81	0.07	12.27	1.27E-34
Agricultural intensity	-2.03	0.69	-2.94	0.00324
5th percentile summer solar index	-34.25	6.63	-5.16	2.43E-07

(i) Standard deviation in summer solar index, Dartmoor landscape

Term	Estimate	S.E.	z-value	p
Intercept	-4.71	0.33	-14.28	2.90E-46
log(records)	0.80	0.07	11.89	1.26E-32
Agricultural intensity	-2.21	0.70	-3.13	0.001734
Standard deviation in summer solar index	107.47	21.73	4.95	7.58E-07

(j) 5th percentile topographic wetness index, Exmoor landscape

Term	Estimate	S.E.	z-value	p
Intercept	-4.69	3.85	-1.22	0.222845
log(records)	1.18	0.14	8.50	1.95E-17
Agricultural intensity	3.67	1.52	2.41	0.016172
5th percentile topographic wetness index	0.12	0.64	0.18	0.85633

(k) 95th percentile summer solar index, Exmoor landscape

Term	Estimate	S.E.	z-value	p
Intercept	47.40	45.13	1.05	0.293619
log(records)	1.18	0.14	8.66	4.71E-18
Agricultural intensity	3.40	1.50	2.27	0.023392
95th percentile summer solar index	-145.96	124.84	-1.17	0.242334