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Contact CEH NORA team at
noraceh@ceh.ac.uk

1 Microclimate affects landscape level 2 persistence in the British Lepidoptera

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4

5 Andrew J. Suggitt^{1,2,*}, Robert J. Wilson², Tom A. August³, Richard Fox⁴, Nick J.B. Isaac³, Nicholas A.

6 Macgregor⁵, Michael D. Morecroft⁵ and Ilya M.D. Maclean¹.

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10 1 Environment and Sustainability Institute, University of Exeter - Penryn Campus, Penryn, Cornwall, UK.

11 2 Department of Biosciences, University of Exeter - Streatham Campus, Exeter, Devon, UK.

12 3 Centre for Ecology and Hydrology, Maclean Building, Benson Lane, Crowmarsh Gifford, Oxfordshire,
13 UK.

14 4 Butterfly Conservation, Manor Yard, East Lulworth, Wareham, Dorset, UK.

15 5 Natural England, Nobel House, 17 Smith Square, London, UK.

16

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

18 **Abstract**

19

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

35

36 **Keywords**

37

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

39 Introduction

40

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

49

50 A small but growing body of literature suggests that microclimate (fine-scale climate, and its spatial variation)
51 may play an important role in modifying species' responses to climatic change. Microclimate has been known to
52 be an important modifier of the broader macroclimate for some time (Kraus 1911, Geiger 1927), but measuring
53 it (Chen et al. 1999) and modelling it (Gillingham et al. 2012) at fine spatial and temporal resolutions has not
54 been possible until recent advances in microchip technology and computing. Fortunately, comprehensive
55 databases of high resolution natural history records, such as those in the Butterflies for the New Millennium
56 (BNM) and National Moth Recording Scheme (NMRS) datasets, present the means to identify associations of
57 species with local habitat features like microclimate. Although some studies have tested these fine-scale
58 species data for a response to temporal variability in the climate (e.g. Suggitt et al. 2012, Letten et al. 2013,
59 Oliver et al. 2013), the microclimatic features of landscapes or regions that can help species persist under
60 climatic change have rarely been tested (but see Suggitt et al. 2014). While our mechanistic understanding of
61 microclimate is improving (Wang et al. 2013), deployment of this type of model is often limited to resolutions of
62 1 km or coarser, and to limited spatial extents (for which ground-truthing data are required for validation
63 purposes). Statistical downscaling (e.g. Haylock et al. 2008) offers a useful proxy for climatic conditions on the
64 ground, but its reliability is constrained by the quality and density of meteorological observations, which will not
65 be available for all landscapes of interest (Ashcroft and Gollan 2012).

66

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

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

- 78
- 79 1) Patterns of persistence and extinction in the Lepidoptera have responded to spatial variation in the
80 microclimate.
- 81 2) Patterns of persistence and extinction in the Lepidoptera have responded to spatial extremity in the
82 microclimate.
- 83 3) Responses consistent with 1) or 2) were stronger in heterogeneous landscapes where spatial variation
84 in the climate was larger.

85

86 **Methods**

87

88 **Biological data**

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

96

97 Records from the BNM & NMRS are tagged with a location on the Ordnance Survey of Great Britain (OSGB)
98 national grid. Since 2000, most records are located to a resolution of 100 m x 100 m grid squares, but coarser
99 resolutions (up to 10 km x 10 km) were common in earlier years. We conducted our analysis at 1 km precision
100 to maximise the inclusion of older records whilst minimizing the probability that records were assigned to the

101 wrong grid square. Records were sorted into two temporal groupings 1971-1990, and 1991-2010, which were
102 treated as pre- and post-climatic warming conditions. We classified each occupied 1 km grid square in the first
103 time period as either a 'persistence' or an 'extinction' depending on whether the species was also recorded
104 during the second time period. Extinctions were only confirmed if the corresponding grid square had been
105 visited by a (Lepidoptera) recorder in the second time period. For each 20 km landscape, we included only
106 those species for which persistence or extinction could be classified in at least fifteen separate 1 km grid
107 squares.

108

109 **Microclimate data**

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

114

115 *1) Temperature proxy- Summer solar index*

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

128

129 *2) Water availability proxy- Topographic wetness index*

130 The topographic wetness index provides a proxy of fine-scale variations in water availability. Basin flow
131 accumulation was calculated from the DEM, which in turn was used to define the contributing area (the property
132 known as a , Equations 1 and 2) for each grid square. This was combined with information on slope angle to

133 generate the index (following Beven and Kirkby 1979). Using this approach, valley bottoms (which have a high
134 contributing area) are considered to be wetter than mountain tops, and flat areas (which have low surface run-
135 off) are considered to be wetter than areas with steep slopes.

136

Equations 1 and 2 Calculating the topographic wetness index

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

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

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

137

138

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

145

Control variables

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

158

Statistical modelling framework

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

171
172 Fitting models to the data permitted the testing of hypotheses 1) and 2), namely a response of persistence to
173 spatial variation or extremity in the microclimate (in a manner that was statistically detectable). However, to test
174 how useful this information could be in a conservation sense, we generated model predictions of persistence in
175 response to an example microclimate measure. If the relationships described above (Figure 4, Appendix 3)
176 were apparent in these predictions once the control effects of levels of recording and agricultural intensity had
177 been included, then it can be inferred that the effect in question is driving differences in rates of persistence in
178 that landscape, over and above the controls. For example, a model fitted with a microclimate variable could still
179 achieve an AIC improvement of more than two over the controls-only model even if patterns of agricultural
180 intensity were actually the dominant driver of persistence in that landscape. In this case, the relationship to a
181 particularly variable or extreme microclimate could be a genuine one, but its effect would be overwhelmed by a
182 response to the other measure. Model predictions for persistence at the 1 km level were generated using the
183 'predict' function within lme4 (Bates et al. 2014). Agreement between these predictions and the corresponding
184 observations was assessed by calculating the degree of covariance (σ) between the two.

185
186 We used a number of techniques to measure and account for spatial autocorrelation in the data, including
187 repeating analyses at the 2 km grid square level. The 2 km analyses also provided a check of the sensitivity of
188 our results to potential false absences in the second period.

189

190 **Results**

191

192 **Temperature proxy- Summer solar index**

193 We estimated larger levels of variability in summer insolation in the two more topographically heterogeneous
194 landscapes (Dartmoor, Exmoor) than in the flatter landscapes (Brecks, Broads; Figure 2). Exmoor seemed to
195 generate the widest range of solar index values of all the landscapes, with the Brecks being the least variable.
196 These differences were apparent in all three measures of insolation at the 1 km level: low (5th percentile, Figure
197 2 panels a,b), low (95th percentile, Figure 2e,f) and variable (SD, Figure 2c,d) insolation. The standard deviation
198 in solar index was an order of magnitude greater in the more variable landscapes than in the less variable
199 landscapes.

200

201 **Water availability proxy- Topographic wetness index**

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

206

207 **Statistical modelling of persistence**

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

214

215 *Brecks*

216 For the Brecks data, a single model performed better ($\Delta AIC < 2$) than the controls-only model. This model was
217 fitted with the 5th percentile topographic wetness index values, and the response was positive, indicating that
218 persistence responded positively to higher minimum wetness conditions (Appendix 3). The slope value of 0.67
219 (Table 2) can be interpreted thus: every unit increase in the 5th percentile of our topographic wetness measure
220 (calculated per 5 m grid square in each 1 km grid square) increased the log odds of a typical species of
221 butterfly persisting by a factor of 0.67 (holding all other effects constant). By taking the exponent of this value, a
222 unit increase in the 5th percentile of our topographic wetness measure increased the odds of a butterfly or moth

223 persisting by a factor of 1.96, or in other words, for every unit increase in wetness, a typical species was almost
224 twice as likely to persist in 1 km grid squares with fewer areas of extreme dry conditions as go extinct. In terms
225 of the control variables, agricultural intensity had a predictably negative effect on persistence. Here, a unit
226 increase in agricultural intensity decreased the odds of butterfly persistence by a factor of 0.17 (an 83%
227 decrease in the odds). Given that our measure represents the proportion of the land occupied by arable and
228 horticultural land, ranging between 0 and 1 (i.e. an entire 'unit'), this effect could be interpreted as being
229 relatively modest: a 1% increase in agricultural intensity reduced the odds of persistence by 0.83%.

230

231 *Broads*

232 Lepidoptera in the Broads showed the widest range of responses to microclimate of all the study landscapes,
233 with five of the six microclimate models performing better than control (Table 2). Models built with the 5th
234 percentile topographic wetness index values and the 95th percentile summer solar index values performed
235 notably better than other types of microclimate model, however. These models implied a negative response to
236 high maximal solar index values and a positive response to higher minimum wetness (Figure 4a,b, Appendix 3).
237 These results suggest that species were less likely to have persisted in 1 km grid squares that contained either
238 the driest or hottest conditions in the landscape. Note that parameter estimates for all models containing the
239 summer solar index (Appendix 3) were divided by 100 prior to calculating the probabilities in Figure 4a, to aid
240 readability and ensure the resulting ratios have more 'real world' relevance. Hence, for example, the Dartmoor
241 5th percentile probability of 0.48 in Figure 4a represents a decrease in the probability of persistence by 0.02, or
242 2% (0.5-0.48), for every increase of 0.01 in the 5th percentile summer solar index.

243

244 *Dartmoor*

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

253

254 *Exmoor*

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

261

262 **Testing model predictions**

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

269

270 Evidence for the signature of microclimate effects on lepidopteran persistence in the four landscapes was
271 mixed (Figure 5), although the beneficial effect of extreme low wetness in Dartmoor was apparent (Figure 5c),
272 with a close fit between the observed and modelled probability of persistence for species in the landscape.
273 Observed and predicted persistence values exhibited positive covariance in two landscapes (Dartmoor σ :
274 0.0700; Broads σ : 0.0300) and negative covariance in the other two landscapes (Brecks σ : -0.0040; Exmoor σ :
275 -0.0003), indicating that established relationships to topographic wetness were more likely to be the dominant
276 driver of persistence in these former two landscapes (Dartmoor, Broads) than in the latter two (Brecks,
277 Exmoor). Results from analyses at 2 km grid square level were consistent with those conducted at 1 km grid
278 square level (Appendix 4).

279

280 **Discussion**

281

282 **Did patterns of persistence and extinction in the Lepidoptera respond to spatial variation in, or** 283 **extremity of, the microclimate?**

284 We detected a number of effects of spatial variation and extremity in the microclimate on persistence patterns
285 in the Lepidoptera (Table 2, Appendix 3). Our model selection criteria identified that 11 of the 24 possible model

286 combinations of microclimate variable and landscape performed better than control, and in all these cases, the
287 microclimate effect was statistically significant. In terms of Hypothesis 1 (namely: “Patterns of persistence and
288 extinction in the Lepidoptera have responded to spatial variation in the microclimate”), standard deviation in
289 solar index was (jointly) responsible for the ‘best’ model in the Dartmoor landscape, and 3 of the 8 possible
290 models for microclimate variability across the four landscapes performed better than the controls-only
291 equivalent. In three landscapes (and jointly in Dartmoor, Table 2) ‘best’ models comprised responses to
292 extreme microclimate, and models fitted with measures of extreme microclimate outperformed the controls-only
293 model in 8 of 16 cases, offering support for Hypothesis 2 (“Patterns of persistence and extinction in the
294 Lepidoptera have responded to spatial extremity in the microclimate”).

295
296 Taking the measure with the most evidence of an effect on persistence across the Lepidoptera group in our
297 study landscapes (5th percentile measure of topographic wetness index), the ability of these models to predict
298 persistence was mixed (Figure 5). It is perhaps relevant that the microclimate effects were more evident in the
299 predicted values for the landscapes that offered more records for model fit (Dartmoor and the Broads, $n =$
300 1719, 2133 respectively), while the microclimate effects were less apparent in landscapes that were less well
301 observed (Exmoor and the Brecks, $n = 538, 1051$). Positive covariance between observed and predicted
302 persistences in the Broads and Dartmoor landscapes lends weight to the predictive ability of these models. The
303 (weakly negative) covariance observed in the other two landscapes (Brecks, Exmoor) may however reflect a
304 lack of statistical power in their respective datasets, which would reduce the likelihood of discerning a
305 microclimate effect. There may also be a genuinely diminished effect of microclimate in these landscapes
306 (Brecks, Exmoor), variation in the hydrological requirements of the constituent species within each landscape,
307 or differential patterns of rainfall change, which are often variable in space (Jenkins et al. 2008). It is also
308 important to remember that the microclimatic conditions created by topography interact with habitat
309 management to determine both the probability of population presence, and vulnerability to change. If the
310 populations of many Lepidoptera are associated with relatively warm or dry pockets of the landscape at their
311 northern range limits (e.g. Lawson et al. 2012, Suggitt et al. 2012), then populations in precisely such locations
312 could be vulnerable to climatic variability, or to changes in management.

313

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

316 Solar index heterogeneity was estimated to be an order of magnitude greater in Dartmoor and Exmoor than in
317 the Brecks and Broads (Figure 2c,d), while heterogeneity in topographic wetness in these landscapes was

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

328

329 **Conservation implications**

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

347

348 Responses to wetness were both positive and negative, depending upon the context. This could reflect the
349 varying patterns (and indeed direction) of change in precipitation that landscapes in Britain have experienced

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

367

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369

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375

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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.

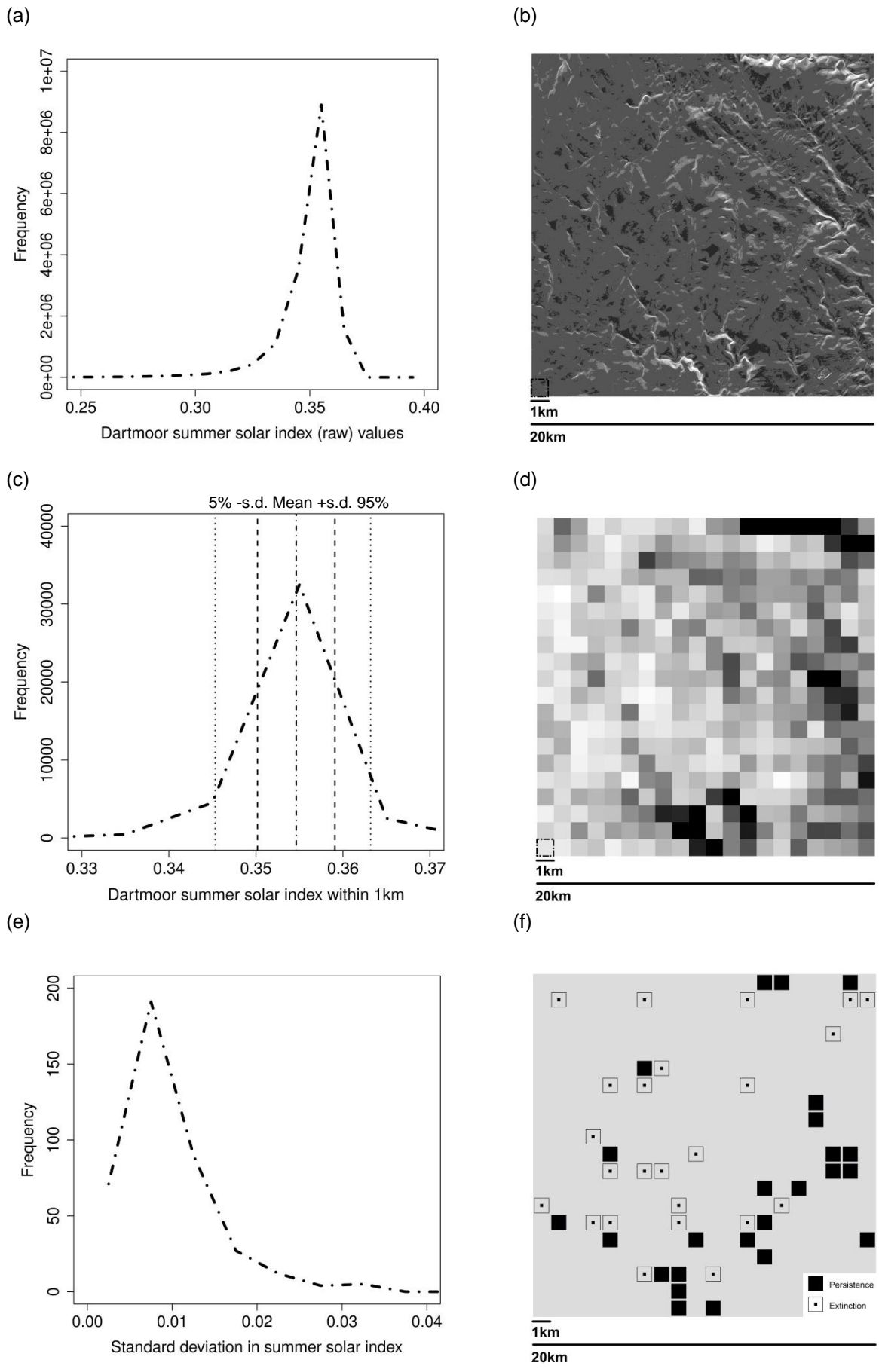


Fig. 2 Values of the summer solar index used in analyses. First, summer solar index was calculated for every 5 m grid square in each landscape. Second, these data were summarised at the 1 km grid square level by calculating the 5th percentile (panels a and b), standard deviation (c and d), and 95th percentile (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).

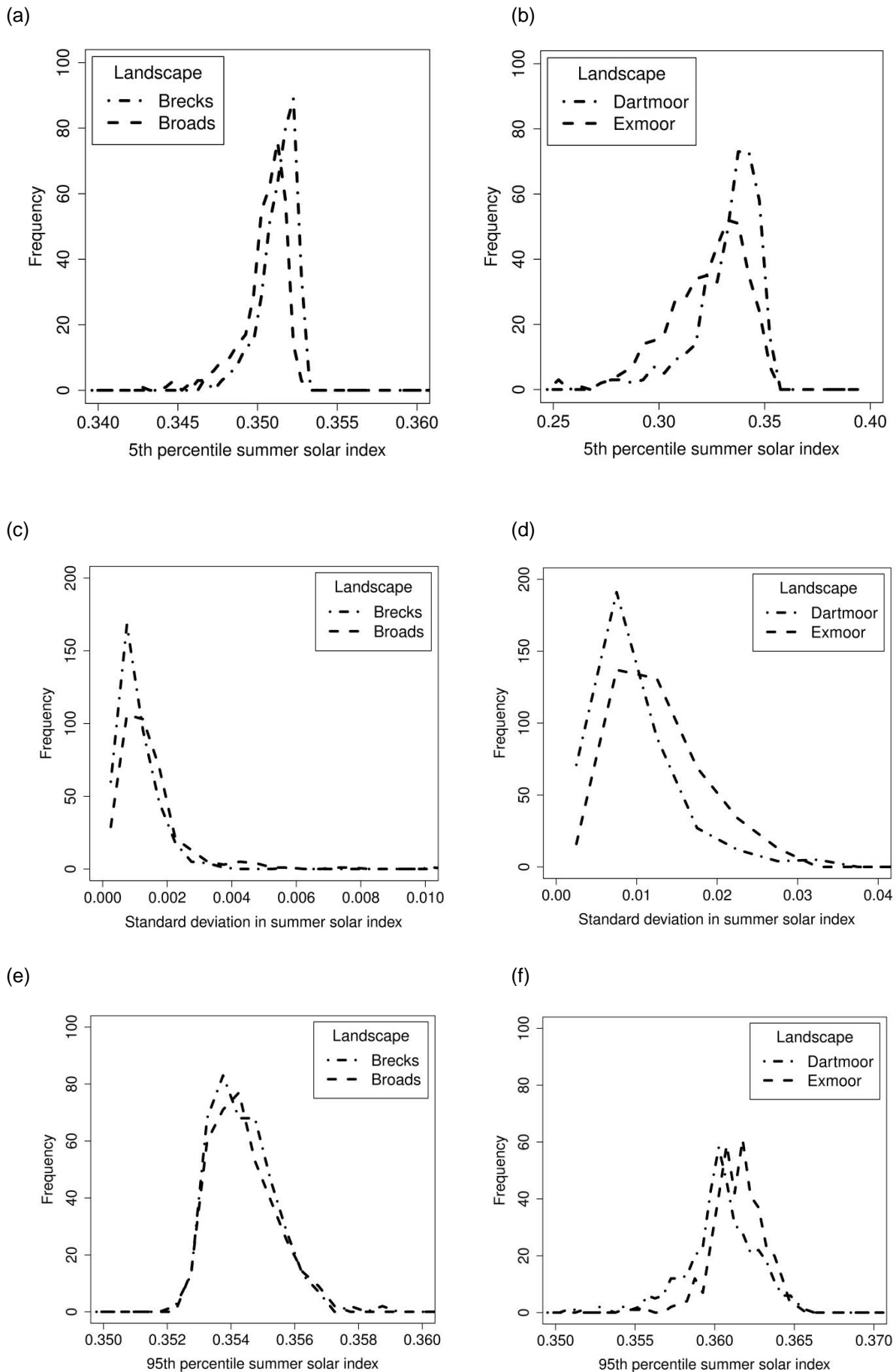
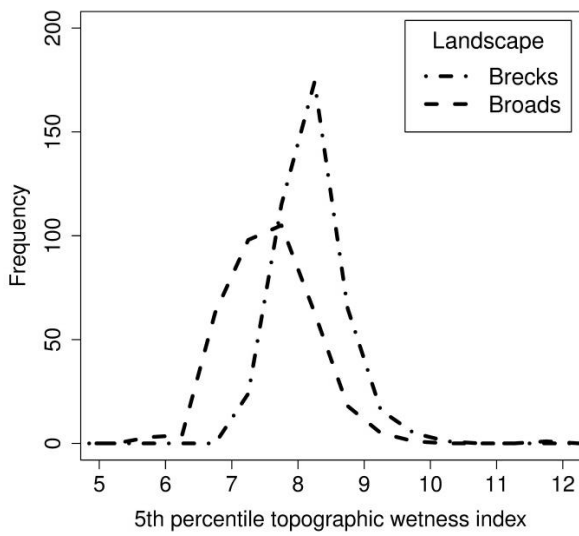
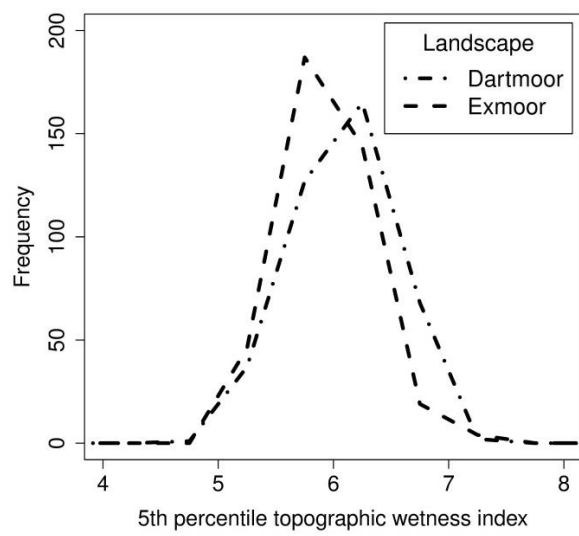


Fig. 3 Values of the topographic wetness index used in analyses. First, topographic wetness index was calculated for every 5 m grid square in each landscape. Second, these data were summarised at the 1 km grid square level by calculating the 5th percentile (panels a and b), standard deviation (c and 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).

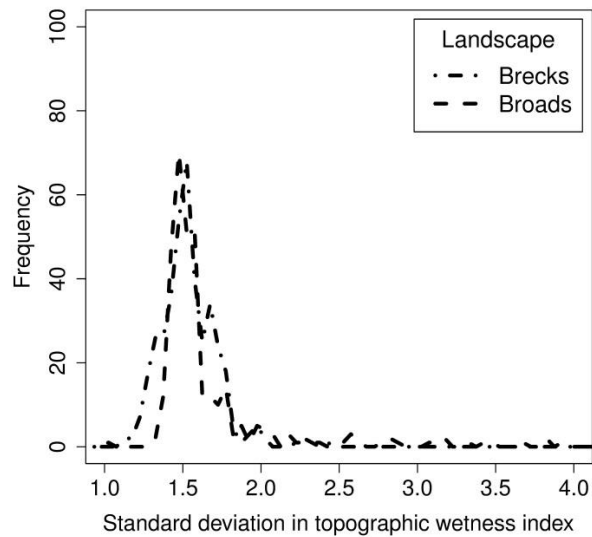
(a)



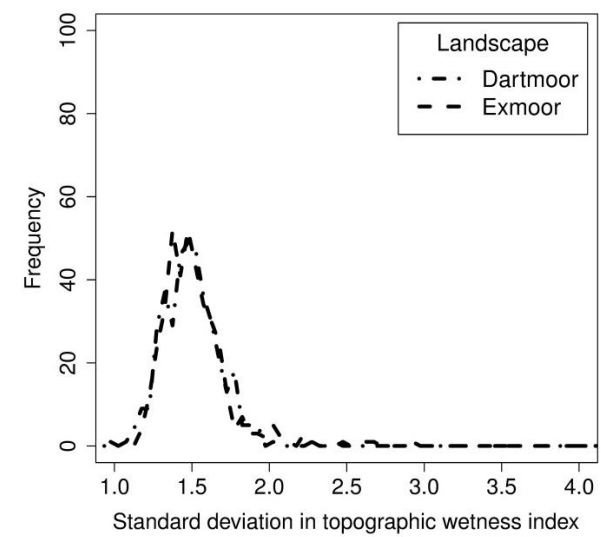
(b)



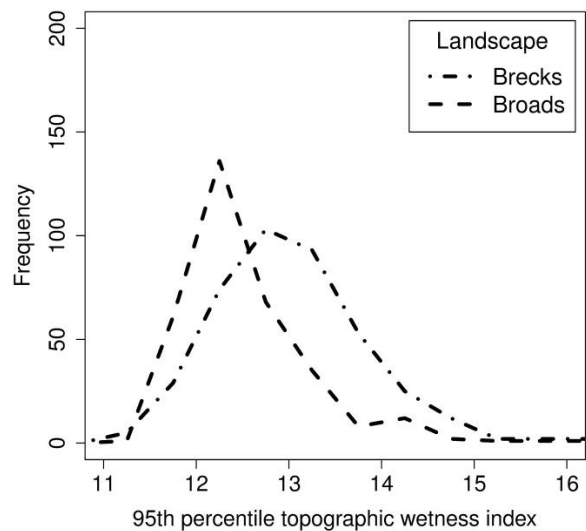
(c)



(d)



(e)



(f)

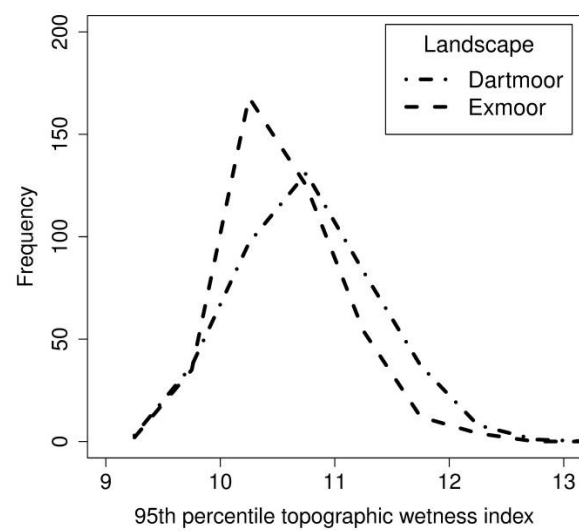
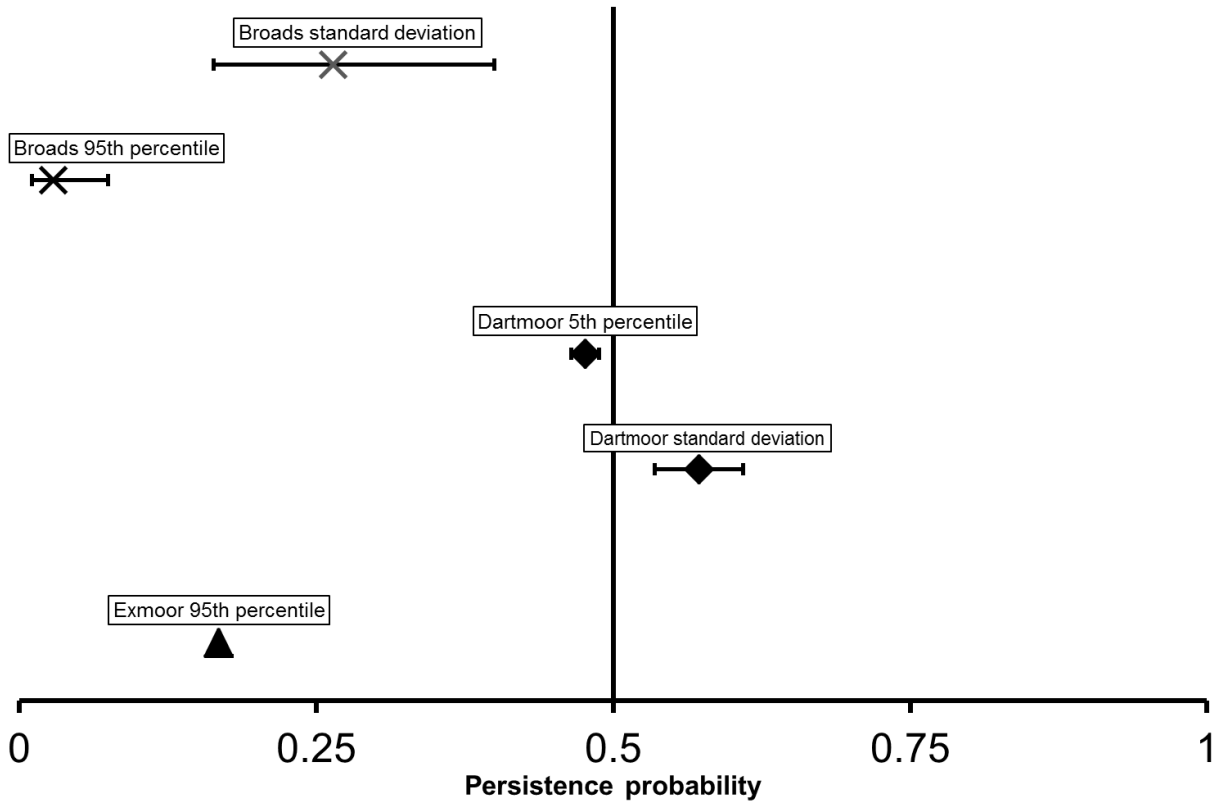


Fig. 4 Effects of microclimate on the probability of persistence in Lepidoptera. Effects are only included if the GLMM it was built with achieved an AIC of more than two points below the control model. The effects of: (a) a 0.01 unit increase in summer solar index measures, and (b) a unit increase in 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

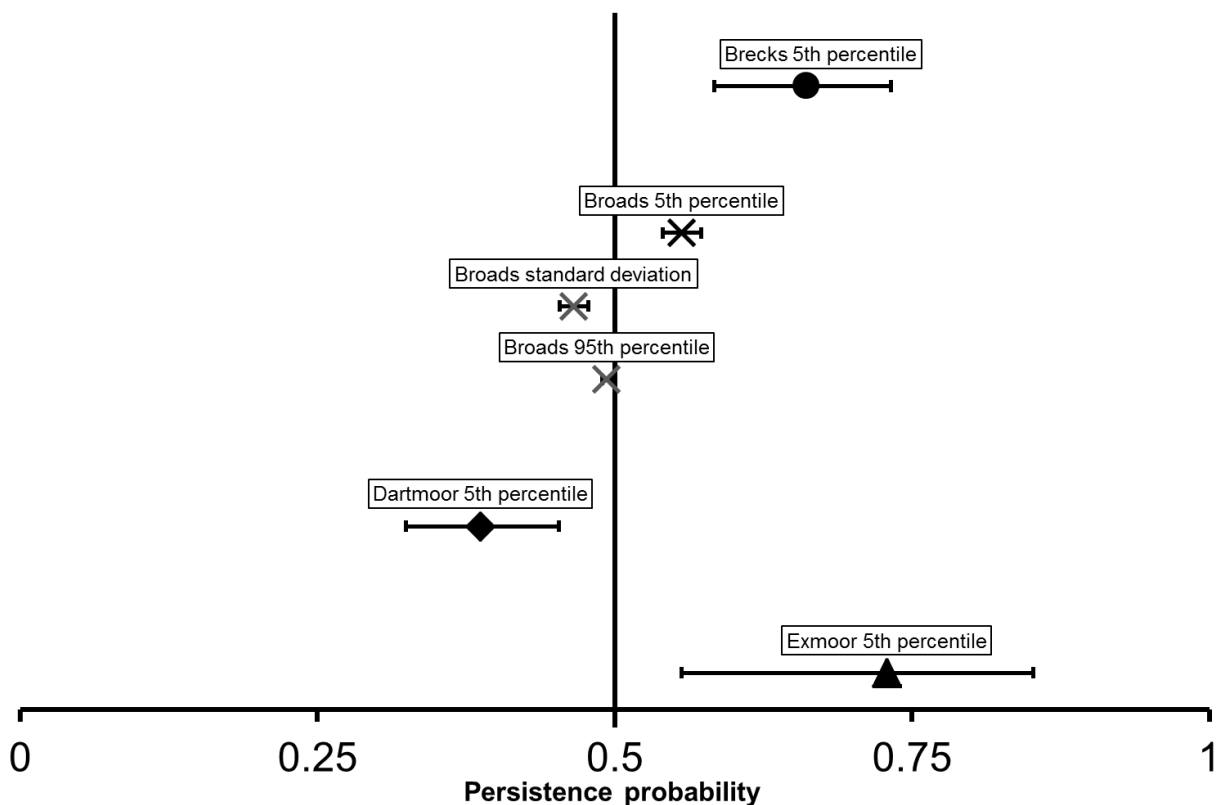
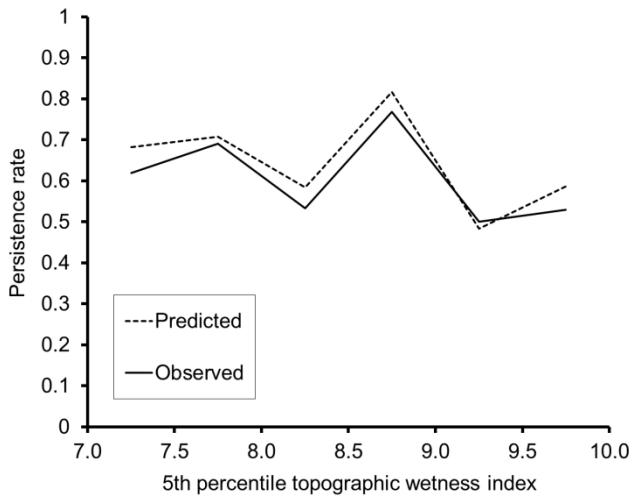
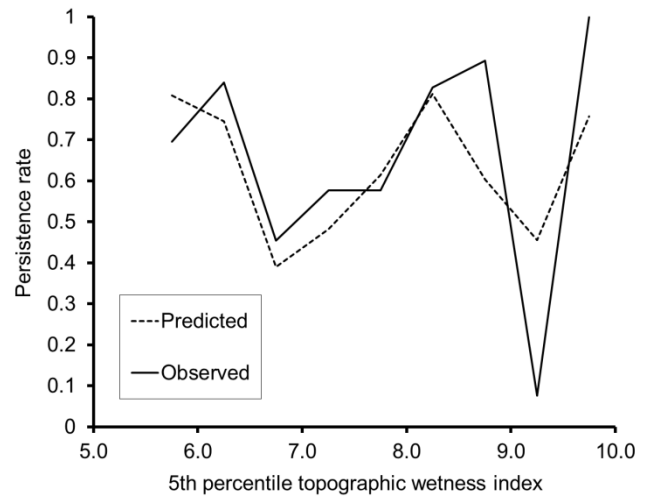


Fig. 5 Predicted and observed persistence in the Lepidoptera at various levels of the 5th percentile topographic wetness index measure (calculated at the 1 km level). Solid lines indicate mean persistence observed in the raw data at each level of wetness. Dotted lines indicate model predicted persistence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

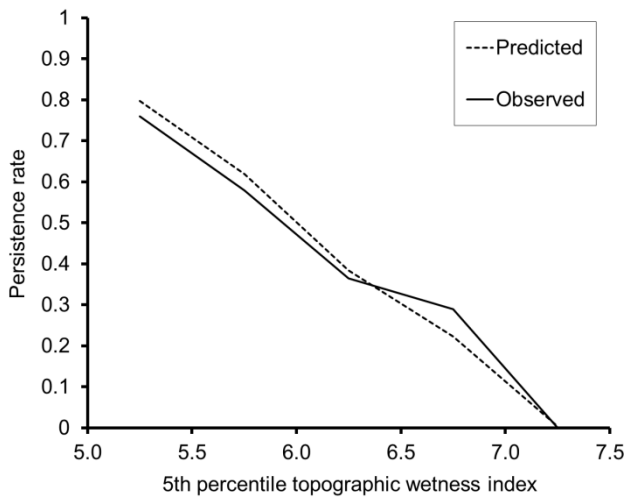
(a) Brecks ($\sigma = -0.0040$)



(b) Broads ($\sigma = 0.0300$)



(c) Dartmoor ($\sigma = 0.0700$)



(d) Exmoor ($\sigma = -0.0003$)

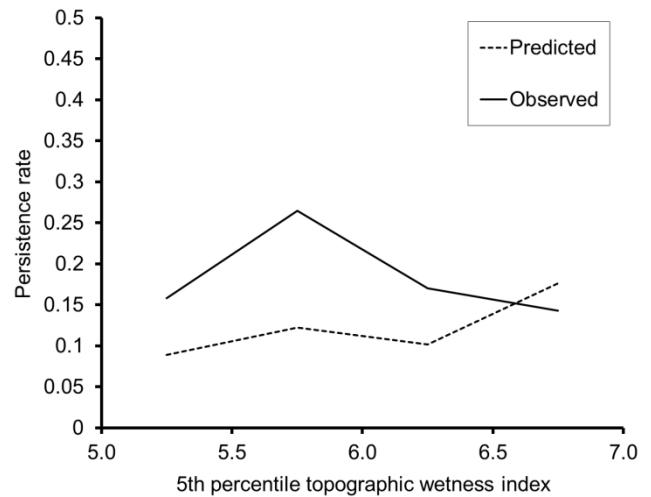
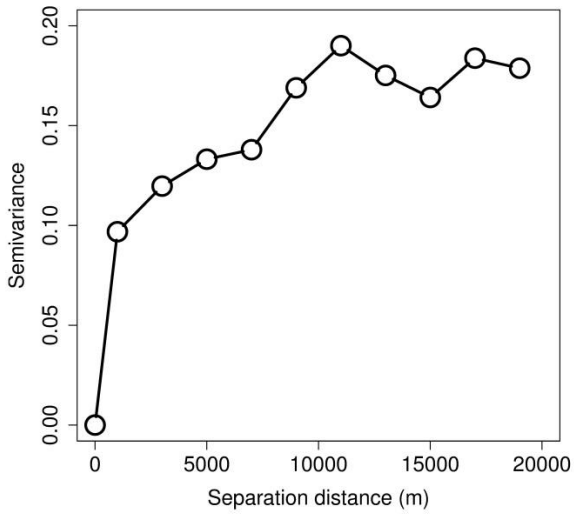
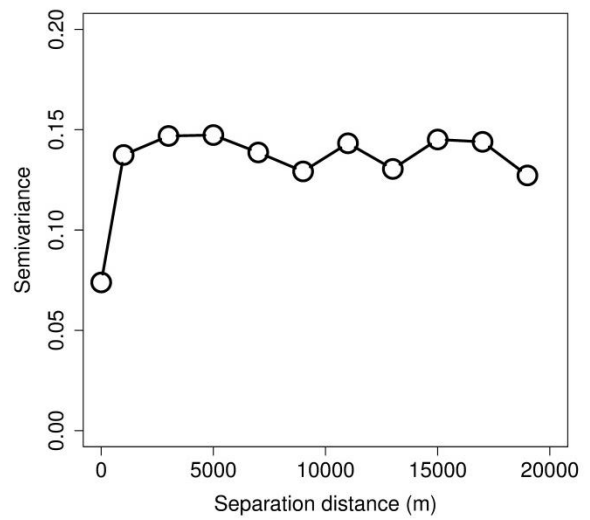


Fig. S1 Semivariograms for values of species persistence recorded across the four study landscapes. Semivariance (y-axis) was calculated between pairs of points at separation distances (x-axis) of up to 20km.

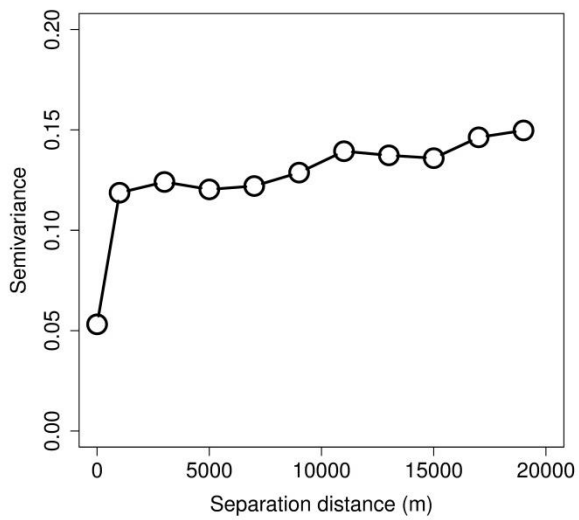
(a) Brecks



(b) Broads



(c) Dartmoor



(d) Exmoor

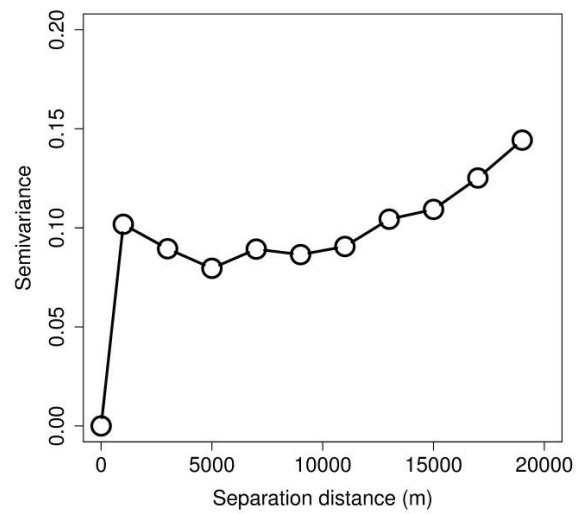


Table 1 Lepidoptera species data included in statistical models. Here, we use the word ‘record’ to represent the recorded persistence or extinction of a species in a 1 km grid square. Species lists for each landscape are included in Appendix 2.

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

(b) Broads (n=88)

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

Broads species list continued...

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

Broads species list continued...

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

(c) Dartmoor (n=30)

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

Dartmoor species list continued...

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

(d) Exmoor (n=9)

Scientific name	Common name
<i>Aglais urticae</i>	Small Tortoiseshell
<i>Anthocharis cardamines</i>	Orange-tip
<i>Aphantopus hyperantus</i>	Ringlet
<i>Maniola jurtina</i>	Meadow Brown
<i>Pararge aegeria</i>	Speckled Wood
<i>Pieris brassicae</i>	Large White
<i>Pieris napi</i>	Green-veined White
<i>Pyronia tithonus</i>	Gatekeeper
<i>Vanessa atalanta</i>	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 (Ribeiro 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	0.011101

(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
