

Extinction risk from climate change is reduced by microclimatic buffering

Andrew J. Suggitt^{1,2,*}, Robert J. Wilson^{3,*}, Nick J.B. Isaac⁴, Colin M. Beale², Alistair G. Auffret^{5,6}, Tom August⁴, Jonathan J. Bennie¹, Humphrey Q. P. Crick⁷, Simon Duffield⁷, Richard Fox⁸, John J. Hopkins¹, Nicholas A. Macgregor^{7,9}, Mike D. Morecroft⁷, Kevin J. Walker¹⁰ and Ilya M. D. Maclean^{1,*}.

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Andrew J. Suggitt^{1,2,*}, Robert J. Wilson^{3,*}, Nick J.B. Isaac⁴, Colin M. Beale², Alistair G. Auffret^{5,6}, Tom August⁴, Jonathan J. Bennie¹, Humphrey Q. P. Crick⁷, Simon Duffield⁷, Richard Fox⁸, John J. Hopkins¹, Nicholas A. Macgregor^{7,9}, Mike D. Morecroft⁷, Kevin J. Walker¹⁰ and Ilya M. D. Maclean^{1,*}.

* Corresponding authors: andrew.suggitt@york.ac.uk, r.j.wilson@exeter.ac.uk,

i.m.d.maclean@exeter.ac.uk.

1 Environment and Sustainability Institute, College of Life and Environmental Sciences, University of Exeter, Penryn Campus, Penryn, Cornwall, TR10 9FE, UK.

2 Department of Biology, University of York, Wentworth Way, York, YO10 5DD, UK.

3 Biosciences, College of Life and Environmental Sciences, University of Exeter, Prince of Wales Road, Exeter, EX4 4PS, UK.

4 Centre for Ecology and Hydrology, Maclean Building, Benson Lane, Crowmarsh Gifford, Wallingford, Oxfordshire, OX10 8BB, UK.

5 Department of Ecology, Swedish University of Agricultural Sciences, 750 07 Uppsala, Sweden.

6 Biogeography and Geomatics, Department of Physical Geography, Stockholm University, 10691 Stockholm, Sweden.

7 Natural England, Cromwell House, 15 Andover Road, Winchester, Hampshire, SO23 7BT, UK.

8 Butterfly Conservation, Manor Yard, East Lulworth, Wareham, Dorset, BH20 5QP, UK.

9 Durrell Institute of Conservation and Ecology, School of Anthropology and Conservation, University of Kent, Canterbury, Kent, CT2 7NR, UK.

10 Botanical Society of Britain and Ireland, 57 Walton Road, Shirehampton, Bristol, BS11 9TA, UK.

1 **Protecting biodiversity against the impacts of climate change requires effective**
2 **conservation strategies that safeguard species at risk of extinction¹. Microrefugia**
3 **allowed populations to survive adverse climatic conditions in the past^{2,3}, yet their**
4 **potential to reduce extinction risk from anthropogenic warming is poorly understood³⁻⁵,**
5 **hindering our capacity to develop robust in situ measures to adapt conservation to**
6 **climate change⁶. Here we show that microclimatic heterogeneity strongly buffered**
7 **species against regional extirpations linked to recent climate change. Using more than**
8 **five million distribution records for 430 climate-threatened and range-declining species,**
9 **population losses across England are found to be reduced in areas where topography**
10 **generated greater variation in the microclimate. The buffering effect of topographic**
11 **microclimates was strongest for those species adversely affected by warming, and in**
12 **areas that experienced the highest levels of warming: in such conditions, extirpation**
13 **risk was reduced by 22% for plants and by 9% for insects. Our results indicate the**
14 **critical role of topographic variation in creating microrefugia, and provide empirical**
15 **evidence that microclimatic heterogeneity can substantially reduce extinction risk from**
16 **climate change.**

17 Bioclimate modelling predicts that anthropogenic climate change will increase
18 extinction risk for a wide range of taxa and regions⁷. However, there is a marked discrepancy
19 between the coarse spatial scales at which geographic range contractions are commonly
20 modelled, and the fine spatial scales at which most organisms respond to climatic variation.
21 This has important implications for estimating the vulnerability of species to climate change⁸
22 and, in consequence, for developing effective adaptation measures. Coarse-scale models fail
23 to identify the localised effects of topography and vegetation on climate that were vital for
24 sustaining refugial populations during past periods of climate change, and which could
25 influence biological responses to current warming⁴. If landscape features promoting

26 microclimatic heterogeneity allow species to persist under current climate change *in situ*, then
27 protection and appropriate management of such features is likely to be an important
28 complement to conservation approaches, such as enhanced landscape connectivity or species
29 translocations, that have been more widely advocated to accommodate range shifts^{1,9}.
30 However, the potential role of microclimatic heterogeneity to act as a buffer against the
31 adverse effects of climate change is yet to be established for a wide range of species¹⁰.

32 Here, we provide an empirical test of the extent to which microclimatic heterogeneity
33 arising from landscape topography has buffered plants and insects in England against
34 extirpations associated with recent climate change. To establish patterns of extirpation for
35 each species during a period of warming, we compared distributions between two periods
36 with comprehensive recording effort (1970-1986 and 1987-2009 for plants; 1970-1989 and
37 1990-2009 for insects). Our analyses focused on the well-recorded groups of Tracheophyta
38 (vascular plants), Bryophyta (mosses and liverworts), Lepidoptera (butterflies and moths) and
39 Coleoptera (beetles), and were restricted to recently declining species that have also been
40 identified as being vulnerable to future climate warming¹¹. We selected only species with
41 records of persistence or extirpation in more than 100 unique 10 x 10 km grid squares (the
42 common unit of UK distribution atlases, and our unit of analysis – see Methods), giving a
43 total of 430 species (316 plants and 114 insects). We defined the ‘extirpation’ of a species
44 from a grid square if that species was recorded as present during the first period but not the
45 second. Because we were only analysing persistence and extirpation (and not colonisations),
46 we do not expect an observed increase in recorder effort through time to have biased our
47 results. Nevertheless, to account for spatial variation in recorder effort, we included the total
48 number of unique recorder visits to each grid square as a control in all models
49 (Supplementary Figs. 1 & 2). To represent the warming rate in each 10 km grid square we
50 calculated change in summer temperature over the study period (1970-2009), using monthly

51 gridded data from the UK Met Office. To represent microclimatic heterogeneity arising from
52 the topography (hereafter simply ‘microclimatic heterogeneity’), we calculated the proportion
53 of direct beam solar radiation incident on the surface¹² of each component 100 x 100 m cell,
54 before computing the standard deviation in these values across each 10 km grid square. The
55 use of solar radiation as a proxy for thermal microclimate is a well-established means of
56 analysing wildlife responses to fine-scale temperature variation¹³, because variation in the
57 radiation budget associated with topography is one of the most important determinants of the
58 temperature of terrestrial ecosystems at temperate latitudes¹⁴. However, to further
59 demonstrate the validity of our proxy of microclimate, we compared it with modelled fine-
60 scale temperature across 261 km² of south-western England, showing that the two are closely
61 related (Supplementary Figs. 3 & 4). We modelled persistence versus extirpation for each
62 species in each 10 km square as a function of warming rate, microclimatic heterogeneity, and
63 the interaction between these factors. All our models also included controls for recorder
64 effort, agricultural intensity, nitrogen deposition, mean elevation, precipitation change, and
65 spatial autocorrelation (see Methods).

66 To assess the importance of microclimatic heterogeneity in buffering extirpations
67 from climate change, we classified each species by its responses to warming, microclimatic
68 heterogeneity and their interaction (Fig. 1). Of the plant species showing effects of warming,
69 more than two thirds responded negatively (Fig. 1a). In contrast, most insect species
70 responded positively to warming (Fig. 1a). Of those species that responded negatively to
71 warming, the majority responded positively to microclimatic heterogeneity (Fig. 1b).
72 Crucially, 59% of species affected by an interaction between warming and microclimatic
73 heterogeneity benefitted from the microclimatic buffering effect (Fig. 1c). Species that were
74 negatively affected by warming were also more likely to benefit (Fig. 1c). In contrast, for
75 those species positively affected by warming, the relationships with microclimatic

76 heterogeneity were more idiosyncratic (Fig. 1c), emphasising that microclimatic
77 heterogeneity did not necessarily reduce probability of extirpation unless there was an
78 adverse effect of warming.

79 To establish the extent to which microclimatic buffering modified extirpation risk, we
80 used the full models for each species to estimate the effect of high vs. low microclimatic
81 heterogeneity (95th and 5th percentiles respectively) on the likelihood of extirpation across the
82 range of warming rates experienced in the study region (Fig. 2a). We found that the reduction
83 in modelled extirpation risk between low and high microclimatic heterogeneity was greater
84 with higher rates of warming, and for species showing stronger negative effects of warming
85 (Fig. 2b, c, g, h). Microclimatic heterogeneity was estimated to have no effect on extirpation
86 risk where warming was low (Fig. 2f, k; a median change in risk of 0% for both plants and
87 insects). With the highest observed rates of warming, microclimatic heterogeneity was
88 estimated to reduce extirpation risk of plants by a median of 16%, though no such effect was
89 predicted for insects (median 0%; Fig. 2g). However, for the subset of species that responded
90 negatively to warming, high microclimatic heterogeneity reduced extirpation risk by a
91 median of 22% for plants and 9% for insects relative to low microclimatic heterogeneity.
92 These estimated reductions in extirpation risk at high levels of warming suggest that
93 microclimatic buffering is greatest for species and regions with greater exposure to climate
94 warming, and implies that the effects of topographic microclimates on persistence will
95 become more important as temperatures increase over time.

96 While the patterns of extirpations observed in this study are associated with a variety
97 of drivers of environmental change, none of these drivers explain the disproportionate benefit
98 of heterogeneous topographic microclimates for species negatively affected by warming, and
99 at locations experiencing higher rates of warming. For example, though availability of semi-
100 natural habitat affects exposure to climate change¹⁵, and 20th century agricultural

101 intensification has been greatest in flat, lowland areas of England¹⁶, our results were robust to
102 the inclusion of an agricultural intensity control in all analyses. Other drivers of
103 microclimatic variability (such as the structure and cover of vegetation¹⁷) can have a
104 substantial effect on the temperatures that organisms experience¹⁸, and thus also have the
105 potential to buffer species against macroclimatic change. Nitrogen deposition is hypothesised
106 to induce microclimatic cooling through promoting increased vegetation cover¹⁹. However,
107 our results were robust to the inclusion of a nitrogen deposition control; and changes in Leaf
108 Area Index over the study period were not sufficiently correlated with heterogeneity in
109 topographic microclimates to confound our results, nor did they explain a substantial amount
110 of variation in overall extirpation probability (Methods, Supplementary Table 2). Although
111 temporary extirpations of local populations within metapopulations are an important
112 component of the distribution dynamics for many of our study species, this type of
113 extirpation occurs over finer spatial and temporal scales than we analyse here (10 km x 10 km
114 squares, and ~ 20 years). Therefore, a microclimatic buffering effect arising from topography
115 remains the most plausible explanation for the results we describe.

116 Our study suggests that microclimatic heterogeneity buffers species against the
117 deleterious effects of climate warming, providing refugial locations in which populations of
118 species are more likely to persist. While previous studies highlight the importance of
119 microclimate in moderating ecological responses to climate change¹⁹ or show that habitat
120 heterogeneity buffers populations against environmental variability²⁰, ours is the first to
121 demonstrate that it is microclimate heterogeneity in the presence of warming that is
122 important, rather than environmental heterogeneity *per se*. Moreover, our results show that
123 microclimatic heterogeneity plays a greater role for species that are more sensitive to
124 warming, and in regions experiencing greater exposure to warming.

125 There are several reasons why microclimatic heterogeneity could be of
126 disproportionate benefit to populations most vulnerable to warming. First, for species in parts
127 of their geographic ranges with conditions close to their thermal optima, or where warming is
128 increasing the availability of optimal thermal environments, greater spatial variation in
129 microclimate could reduce the absolute availability of thermally suitable conditions,
130 decreasing the viability of regional populations. In contrast, for species where warming is
131 reducing the availability of thermally suitable conditions, microclimatic heterogeneity could
132 benefit species, by providing sufficient spatial variation in climatic conditions to ensure that
133 thermally suitable conditions are maintained in close proximity to existing populations²¹. The
134 magnitude of warming that has occurred over the duration of our study is exceeded by fine-
135 scale spatial differences in temperature (Supplementary Fig. 4), suggesting that localised
136 movement would be sufficient for species to track changes in climatic conditions²². Another
137 potential reason is that microclimatically heterogeneous regions are also associated with
138 atypical climatic conditions²³ that are more resistant to invasion²⁴. Populations in such
139 locations may thus experience reduced competitive exclusion. A further reason is that, even
140 within relatively small regions, contrasting terrain results in remarkably variable rates of
141 warming, implying that heterogeneity in microclimate is also associated with heterogeneity in
142 rates of warming¹². In consequence, species threatened by climate change in regions of high
143 microclimatic variability may be more likely to persist for longer in localities experiencing
144 reduced rates of warming.

145 Given finite resources, conservation practitioners are urgently assessing the relative
146 vulnerability of species to climate change. Assessments of species vulnerability have
147 focussed on comparisons of sensitivity, adaptive capacity and exposure to climate change^{25,26},
148 but have often omitted the potential for local variation in climate to reduce exposure to
149 adverse climatic changes. Variation in rates of warming and increased availability of suitable

150 local climates associated with microclimatic heterogeneity could potentially reduce exposure
151 to climate change. Species identified as being most vulnerable are typically those that are
152 predicted to have narrow climatic associations and little or no capacity to expand elsewhere²⁷.
153 However, modelled estimates of climatic associations, range shifts and extirpation risk made
154 using coarse-resolution climate data inevitably fail to account for fine-scale variation in
155 climate^{8,17} and may thus over-estimate the distance over which species must move.

156 The prediction that species will be extirpated from large parts of their range is
157 prevalent in the scientific literature, leading to debate regarding approaches to avert species
158 loss from climate change. Proposals include habitat restoration¹⁵, the redesign of protected
159 area networks⁹, and assisted colonisation²⁸, but competing demands on land-use and on
160 economic resources render such approaches difficult to achieve. *In situ* conservation
161 measures are typically easier to implement, and if targeted at refugial locations with high
162 microclimatic heterogeneity, could help to reduce extinction risk as regional climates become
163 unsuitable. While management at these locations will require many of the same approaches
164 used to conserve species as elsewhere, placing greater emphasis on enhancing local
165 persistence gains time for systems to adapt, and for managers and society to develop longer-
166 term solutions⁴. Ultimately, the protection of microrefugia is a way to prioritise locations for
167 management given limited resources. What will differ is the emphasis on protecting,
168 maintaining, and fostering the features that create microclimate heterogeneity, and on
169 enhancing the local persistence of species in the face of ongoing climate change, alongside
170 those regional actions that may already be in place.

171 Nevertheless, estimates of extinction risk from climate change demonstrate that high
172 population-level losses have already been observed²⁹. The magnitude of anthropogenic
173 warming to date is approximately half that expected by 2050³⁰, and biodiversity losses are
174 predicted to accelerate with increased warming⁷. In consequence, the results of our study

175 should not be interpreted to imply that safeguarding species against the effects of climate
176 change is any less urgent, but rather that protection and appropriate management of
177 microrefugia could form important elements of wider efforts to adapt nature conservation to
178 climate change, at least in the short term⁴.

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252 **Correspondence and requests for materials** should be addressed to A.J.S., R.J.W. or
253 I.M.D.M.

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264

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266 S.D., H.Q.P.C. and R.J.W. conceived the work and supervised analyses. A.J.S, I.M.D.M. and
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269

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271

272 **Orc IDs** AJS: 0000-0001-7697-7633, AGA: 0000-0002-4190-4423, CMB: 0000-0002-2960-
273 5666, JJB: 0000-0003-4394-2041, HQPC: 0000-0002-5136-378X, SD: 0000-0003-3364-
274 9255, RF: 0000-0001-6992-3522, NJBI: 0000-0002-4869-8052, MDM: 0000-0002-7978-
275 5554, KJW: 0000-0002-5751-8623, RJW: 0000-0003-4477-7068, IMDM: 0000-0001-8030-
276 9136.

277 **Methods**

278 *Biological response data*

279 We obtained data on the distribution of species from the Botanical Society of Britain and
280 Ireland, the British Bryological Society, Butterflies of the New Millennium, the National
281 Moth Recording Scheme, and the National Recording Schemes for Ground Beetles, Soldier
282 Beetles, Longhorn Beetles, and Ladybirds. All these organisations accept records from either
283 taxonomic specialists or the general public, and any unusual records undergo a vetting
284 process to establish their veracity³¹. We analysed data on 430 species identified as ‘climate-
285 threatened’ in a recent climate change risk assessment for our study region¹¹ in which
286 projected responses to future climate change to 2100 were assessed, and for which adequate
287 data were available (see below).

288 To establish patterns of extirpation over a period of warming, we aggregated the data
289 into two time periods. For vascular plants and bryophytes these periods were 1970-1986 and
290 1987-2009, and for the lepidopterans and coleopterans, 1970-1989 and 1990-2009. These
291 periods correspond to comprehensive national coverage, often associated with the production
292 of atlases for the corresponding flora and fauna³²⁻³⁵, during which coordinators sought to
293 maximise observer coverage of 10 km x 10 km grid squares (hectads). We restricted our
294 analysis to species which were recorded in more than 100 of the 10 km grid squares in the
295 first time period, as long as the same 10 km square was visited by recorders for that
296 taxonomic group’s recording scheme in the second time period. Absences are not explicitly
297 recorded within these schemes, so ‘extirpations’ from grid squares are here defined as a
298 species being recorded as present during the first period, but not in the second.

299 To account for possible influences of variation in recorder effort on patterns of
300 apparent extirpation, we calculated the number of unique recorder visits to each 10 km grid
301 square across the period of our study (1970-2009) and included this as a control for relative

302 recorder effort in all analyses (Supplementary Fig. 1a). The risk that extirpations were an
303 artefact of recorder effort was reduced by the fact that there were 3.5 times more records
304 submitted for the second period than the first (Supplementary Fig. 1b, c). To reduce the risk
305 of falsely assigned absences further, we only included grid squares in analysis if at least one
306 species within a respective taxon's recording scheme was recorded in the target grid square
307 during the second time period (i.e. inferred extirpation required other species from the same
308 taxonomic group to have been recorded). For the vast majority of grid squares and taxa, the
309 number of distribution records was higher in the second period than the first (Supplementary
310 Fig. 2). In addition to using recorder effort as a control, we checked whether changes to
311 recorder effort could have confounded our analyses, by assessing correlations between
312 recording change over time and microclimatic heterogeneity (Supplementary Table 2). Seven
313 of the eight recording schemes showed a weak negative correlation, suggesting that recorder
314 effort tended to increase more in grid squares with lower microclimatic heterogeneity. In
315 other words, a loss of species from the *less* microclimatically heterogeneous grid squares
316 would be very unlikely to result from variation in detection over time.

317

318 *Climate change variables*

319 Monthly mean 5 x 5 km gridded temperature data were obtained from the UK Met Office³⁶ to
320 calculate the mean summertime (June, July, August) temperature of each 10 km x 10 km grid
321 square in each year within the period of study (1970-2009). Summertime temperatures were
322 selected to represent the main influences of climate on the population dynamics of our study
323 species. Linear models were then fitted to the climate data for each grid square and the slopes
324 of these regressions (Δ °C / year) were derived and utilised for subsequent analyses. The same
325 methods were used to derive the change in total summertime precipitation in each grid square
326 (Δ mm / year), which was included as a control variable. Although we did not limit our

327 analysis to grid squares in which the climate has warmed, in practice almost all grid squares
328 did experience a warming trend over our study period.

329

330 *Microclimatic heterogeneity*

331 To derive a proxy for landscape heterogeneity in topographically-driven temperature
332 microclimates, a three-arc second (~90 m) horizontal resolution Digital Elevation Model
333 (DEM) was obtained from the Shuttle Radar Topography Mission³⁷ and resampled and
334 coarsened to 100 x 100 m resolution using bilinear interpolation. The proportion of direct
335 beam radiation incident on the surface of each grid square of the DEM, hereafter referred to
336 as the solar index, was calculated using a method that accounts for slope, aspect, and
337 topographic shading¹². The mean of hourly values over the 24 hours of 21st June was used as
338 this provides a good proxy of near-ground daily mean and maximum temperatures across the
339 growing season (see below). Third and finally, the standard deviation of solar index values in
340 each 10 km grid square was calculated to represent heterogeneity in the thermal
341 microclimate.

342 To verify that solar index values are a good proxy for the effects of topography on
343 fine-scale microclimatic temperatures, we tested them against the outputs of a microclimate
344 model that accurately estimates near-ground temperatures at hourly intervals¹² (mean error of
345 model = 1.21 °C). For a 225 km² part of our study region (The Lizard Peninsula in Cornwall),
346 we derived surface temperatures over a 20 year period (1990-2009) at a spatial resolution of
347 100 x 100 m and at hourly temporal resolution, before calculating the mean and mean daily
348 maximum temperature of each 100 m grid square across the growing season of April to
349 September (Supplementary Figs. 3 & 4). We calculated the standard deviation in
350 temperatures of all the 100 m grid squares (n = 100) in each 1 x 1 km square (separately for

351 maximum and mean temperatures) and compared these values to the standard deviation in
352 solar index values in corresponding grid cells.

353 We found the solar index to be a reliable proxy of both mean and maximum
354 temperatures across the growing season. More than half of the spatial variation in the mean
355 ($r^2 = 0.72$, $p < 0.0001$) and maximum ($r^2 = 0.73$, $p < 0.0001$) temperature anomalies is
356 explained by the solar index, our proxy for the thermal microclimate (Supplementary Figs. 3
357 & 4).

358 However, it should be noted that the microclimates experienced by organisms are
359 influenced both by the effects of topography and by the effects of vegetation structure^{17, 18},
360 and that increases in vegetation cover can dampen the effects of warming on species³⁸. Whilst
361 our main aim was to address the possible buffering effects of topographic microclimates over
362 the scales which they are likely to have the dominant effects on rates and patterns of
363 warming¹² (100 m – 10 km), we conducted a supplementary analysis to examine possible
364 confounding effects of changes in vegetation cover on our results. We used the 0.05 degree
365 (~ 5 km) dataset of daily Leaf Area Index (LAI) from the National Oceanic and Atmospheric
366 Administration³⁹ to calculate the mean LAI in each 10 km grid square from 1982 (the earliest
367 date for which it is available) until 1989, and for 1990 to 2009, and calculated the log
368 proportional change between the two periods (Supplementary Fig. 5). The weak positive
369 correlation between change in LAI and modelled heterogeneity in topographic microclimate
370 ($r = +0.07$, d.f. = 1300, $p = 0.02$; Supplementary Table 2) suggests that changes to vegetation
371 cover have not confounded our results. As a further check we also tested the ability of change
372 in LAI to explain the overall pattern of extirpations observed. We fitted Generalised Linear
373 Mixed Models (GLMMs) to the datasets from plant and insect groups separately, with LAI
374 change included as a fixed effect, and species identity included as a random intercept. LAI
375 change explained less than 0.04% of the variation in extirpation probability in either group

376 (the ‘marginal r-squared’ statistic), giving us further confidence that our conclusions are
377 robust.

378

379 *Control variables*

380 As well as the control for recorder effort, we included a set of control variables in all of our
381 analyses to account for additional factors which could have influenced the patterns of
382 persistence and extirpation observed across 10 km grid squares. We note that species could
383 have been lost from 10 km grid squares because of a range of independent or interacting
384 factors, including climate change, habitat loss and pollution.

385 To control for possible confounding effects of greater agricultural intensity in flatter
386 landscapes (with lesser heterogeneity in topographic microclimates) we calculated a measure
387 of agricultural intensity for all 10 km grid squares. The Centre for Ecology and Hydrology’s
388 2007 land cover (vector) map⁴⁰ was sampled to a grid square resolution of 1 x 1 km, and the
389 proportion of each 10 x 10 km grid square that was ‘Arable and horticulture’ or ‘Improved
390 grassland’ calculated. Determining change in these land cover classes was not possible for the
391 period of time covered by our analyses, as the classification method used to derive successive
392 land-cover maps of the same region has been modified substantially over time^{41,42}. As an
393 indication that our measure of agricultural intensity is representative of spatial patterns in
394 land-use intensification over a time period relevant to the changes observed to species
395 distributions, we also calculated a measure of land development (proportion land cover
396 change to arable or urban) for each 10 km grid square (Supplementary Fig 5c). The land
397 development measure was based on a digitisation of land cover maps using data from 1925-
398 1948⁴³ compared with land cover information from 1990⁴⁴, and was positively correlated
399 with our measure of agricultural intensity ($r = 0.52$, d.f. = 1300, $p < 0.00001$). Most of the
400 patterns in land development from 1948-1990 comprise conversion of land to agricultural (r

401 = 0.72, d.f.= 1300, $p < 0.00001$), with the patterns only weakly correlated with changes to
402 urban ($r = 0.15$, d.f. = 1300, $p < 0.00001$). In addition, the majority of this intensification of
403 land use in England and Wales is estimated to have occurred between 1925 and 1978, based
404 on a comparison of the 1925-1948 land cover data and surveys conducted in the UK
405 Countryside Survey in 1978, 1990, 1998 and 2007⁴⁵ (Note: the 1978-2007 data cannot be
406 used to estimate change in all 10 km grid squares, as the surveys were not exhaustive). Given
407 that most land cover changes pre-dated our period of study, we use agricultural intensity as
408 the control that is most likely to be relevant for distribution changes observed between the
409 two *c.* 20 year distribution recording periods before and after the end of the 1980s. Although
410 the land cover categories included in agricultural intensity represent the classes we expect to
411 be most deleterious to our study taxa, it is important to emphasise that they are only
412 simplified representations of the effects we seek to control for, and do not represent all the
413 components of land-use intensification that could potentially be drivers of change¹⁶.

414 Because anthropogenic nitrogen deposition has been responsible for changes in
415 community composition⁴², and can also modify species' responses to climate change¹⁹, we
416 also included estimates of nitrogen deposition as a control in our models. Spatial data for
417 England are available via outputs from Defra's Concentration Based Estimated Deposition
418 (CBED) model⁴⁶ from 2004 onwards, which we used to calculate the mean annual total
419 nitrogen deposition (kg N / hectare / year) between 2004 to 2009 in each 10 km grid square.

420 Because there is a relative lack of flatter areas on higher ground in the English
421 landscape, heterogeneity in topographic microclimates could also be confounded by
422 elevation. Hence, the mean elevation of each 10 x 10 km grid square, derived from the 100 x
423 100 m resolution DEM, was also included as a control variable in models. Finally, to account
424 for extirpations driven by moisture changes, the annual change in total precipitation for each
425 10 km grid square was also included as a control.

426

427 *Analyses*

428 The extirpation or persistence of each species in each 10 km grid square was modelled as a
429 function of temperature increase, heterogeneity in topographic microclimate and an
430 interaction between these two variables, with agricultural intensity, nitrogen deposition,
431 precipitation change, the mean elevation of each grid square and recorder effort (log-
432 transformed) included as control variables. We modelled extirpation/persistence using
433 general estimating equations⁴⁷, which account for correlations within spatial clusters of data
434 points by parameterising a correlation matrix, while correlations between clusters are
435 assumed to be zero. Spatial clusters were identified automatically using the methods outlined
436 in Dormann *et al.*⁴⁸ and Carl & Kühn⁴⁹.

437 To classify species according to their response to warming, microclimate
438 heterogeneity and the interaction between the two (Fig. 1; Supplementary Table 1), separate
439 models were constructed for each species. A forward selection procedure was used to identify
440 the response to each term; i.e. a response to heterogeneity was assessed only for those species
441 responding to warming, and a response to the interaction between microclimate heterogeneity
442 and warming was assessed only for those species responding to both these terms individually.
443 We considered a species to be ‘responding’ to a variable (Fig. 1) only if the inclusion of that
444 variable resulted in improved model performance, assessed using Pan’s Quasi Information
445 Criterion⁵⁰. Analyses were performed using the *geepack*⁵¹ and *MESS*⁵² packages for R⁵³.

446 To test the sensitivity of our results to alternative model selection procedures, we also
447 conducted full multi-model inference for each species, whereby all possible responses to
448 climate and microclimate heterogeneity were tested. In this ‘full QIC’ approach, the model
449 with the lowest QIC was selected as the final model⁵⁴. For species in which the best model
450 included warming, microclimate, and/or the interaction between the two, there was a high

451 level of support for the conclusions from the forwards approach (Supplementary Fig. 6). Of
452 species responding to warming, 70% of plants were affected negatively by warming in the
453 full QIC approach, whereas only 40% of insects were affected negatively. Of species where
454 the best models for persistence versus extirpation included an interaction between
455 microclimate and warming, 69% of plants and 57% of insects showed a positive interaction,
456 suggesting a beneficial effect of microclimatic heterogeneity for species whose patterns of
457 extirpation were affected by climate change. For both plant and insect species in which the
458 lowest QIC included all predictor variables and interactions, the most prevalent response was
459 that most indicative of a buffering effect, showing a negative effect of warming, a positive
460 effect of microclimatic heterogeneity, and a positive interaction between the two (Type 5 in
461 Fig 1c and Supplementary Fig. 6).

462 Finally, to estimate the size of the microclimate buffering effect, we used the full
463 model for each species (including all variables) to predict variation in extirpation risk at
464 various levels of warming and microclimatic heterogeneity, holding the control variables at
465 their median value (Fig. 2). Grid squares that were colonised between the two time periods
466 were excluded from analyses.

467

468 ***Data availability***

469 The datasets that support this study are available from the following sources: biological
470 response data via NBN (<https://nbnatlas.org>), climate change data via the UK Met Office
471 (<http://catalogue.ceda.ac.uk/uuid/87f43af9d02e42f483351d79b3d6162a>), elevation data via
472 USGS (<https://www2.jpl.nasa.gov/srtm/cbanddataproducts.html>), LAI vegetation cover data
473 via NOAA (<https://data.nodc.noaa.gov/cgi-bin/iso?id=gov.noaa.ncdc:C00898>), land cover
474 data under licence via EDINA (<https://digimap.edina.ac.uk>), nitrogen deposition data via
475 CEH (<http://www.pollutantdeposition.ceh.ac.uk>).

476

477 **Methods references**

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Fig. 1 Classification of plants (green) and insects (purple) by responses to warming and microclimatic heterogeneity. Species (n = 430) were initially classified by their response to warming (panel a). For those species affected by warming (n = 321), the species' response is classified as positive or negative, and their response to microclimate heterogeneity (in addition to warming) assessed (b). For those species affected by both warming and microclimate heterogeneity (n = 228), the effects of an interaction between warming and heterogeneity were assessed, and each species exhibiting a response was assigned to one of eight response types (c). Asterisks indicate response types indicative of microclimate buffering.

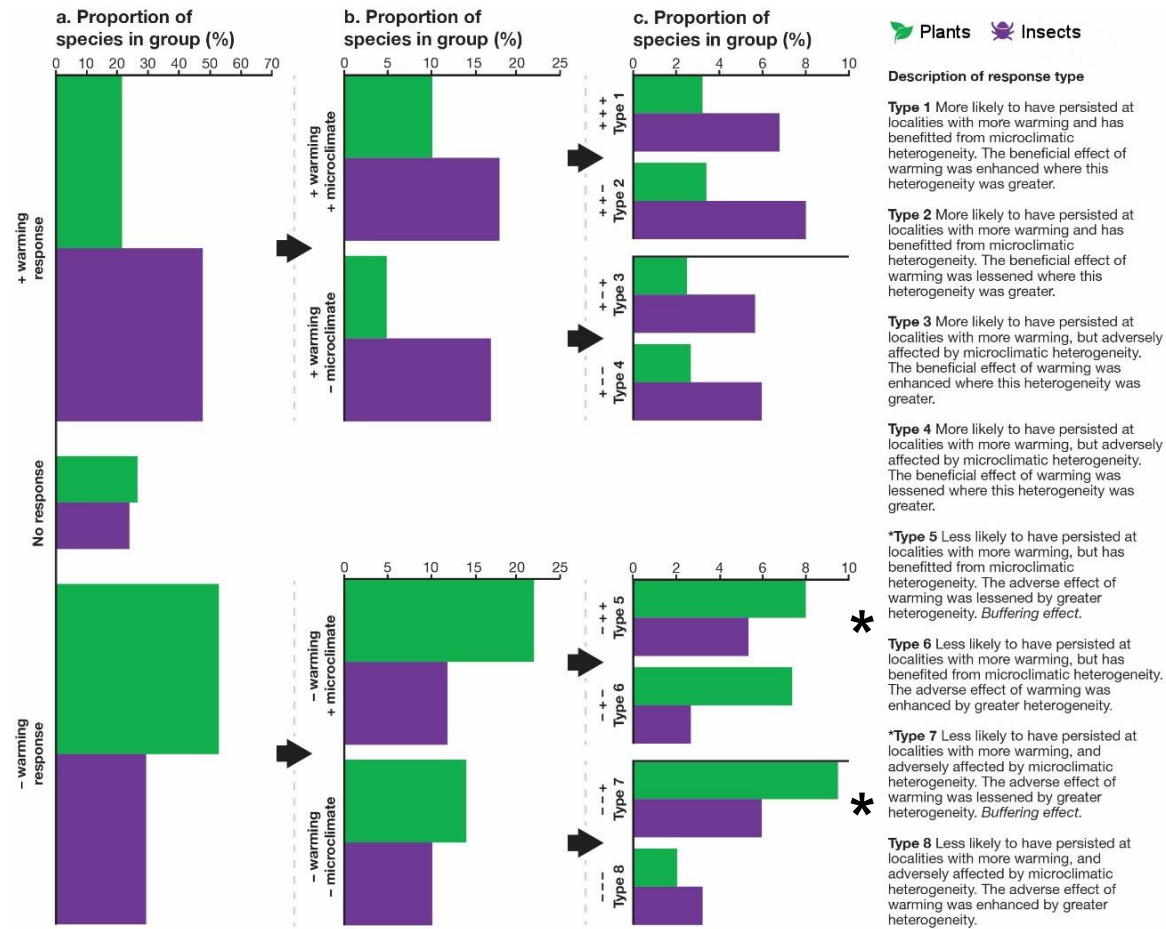


Fig. 2 Modelled change in extirpation risk for each species as a function of warming and microclimate heterogeneity. The relative frequency of warming in each grid square is shown in (a). In (b-k), the modelled differences in extirpation risk between areas of high (95th percentile) microclimatic heterogeneity and low (5th percentile) microclimatic heterogeneity are shown for various levels of warming, separately for plants (b-f) and insects (g-k). Red coloration denotes species adversely affected by warming, for which the inclusion of a warming term improved model performance. Orange coloration denotes species models that exhibited a negative response to warming, but for which the inclusion of a warming term did not improve model performance. Grey coloration denotes species that exhibited a positive relationship to warming.

