

# **Extinction risk from climate change is reduced by microclimatic buffering**

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1 **Protecting biodiversity against the impacts of climate change requires effective**  
2 **conservation strategies that safeguard species at risk of extinction<sup>1</sup>. Microrefugia**  
3 **allowed populations to survive adverse climatic conditions in the past<sup>2,3</sup>, yet their**  
4 **potential to reduce extinction risk from anthropogenic warming is poorly understood<sup>3-5</sup>,**  
5 **hindering our capacity to develop robust in situ measures to adapt conservation to**  
6 **climate change<sup>6</sup>. 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 regions<sup>7</sup>. 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 change<sup>8</sup>  
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 warming<sup>4</sup>. 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<sup>1,9</sup>.  
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 species<sup>10</sup>.

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 warming<sup>11</sup>. 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 surface<sup>12</sup> 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 variation<sup>13</sup>, 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 latitudes<sup>14</sup>. However, to further  
59 demonstrate the validity of our proxy of microclimate, we compared it with modelled fine-  
60 scale temperature across 261 km<sup>2</sup> 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 (95<sup>th</sup> and 5<sup>th</sup> 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 change<sup>15</sup>, and 20<sup>th</sup> century agricultural

101 intensification has been greatest in flat, lowland areas of England<sup>16</sup>, 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 vegetation<sup>17</sup>) can have a  
104 substantial effect on the temperatures that organisms experience<sup>18</sup>, 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 cover<sup>19</sup>. 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 change<sup>19</sup> or show that habitat  
120 heterogeneity buffers populations against environmental variability<sup>20</sup>, 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 populations<sup>21</sup>. 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 conditions<sup>22</sup>. Another  
137 potential reason is that microclimatically heterogeneous regions are also associated with  
138 atypical climatic conditions<sup>23</sup> that are more resistant to invasion<sup>24</sup>. 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 warming<sup>12</sup>. 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<sup>25,26</sup>,  
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 elsewhere<sup>27</sup>.  
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<sup>8,17</sup> 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 restoration<sup>15</sup>, the redesign of protected  
159 area networks<sup>9</sup>, and assisted colonisation<sup>28</sup>, 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 solutions<sup>4</sup>. 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 observed<sup>29</sup>. The magnitude of anthropogenic  
173 warming to date is approximately half that expected by 2050<sup>30</sup>, and biodiversity losses are  
174 predicted to accelerate with increased warming<sup>7</sup>. 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 term<sup>4</sup>.

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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  
267 R.J.W. wrote the manuscript with contributions from the whole team. C.M.B., A.G.A., T.A.,  
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269

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271

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## 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 veracity<sup>31</sup>. We analysed data on 430 species identified as ‘climate-  
285 threatened’ in a recent climate change risk assessment for our study region<sup>11</sup> 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 fauna<sup>32-35</sup>, 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 Office<sup>36</sup> 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 ( $\Delta$  °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 ( $\Delta$  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 Mission<sup>37</sup> 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 shading<sup>12</sup>. 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 intervals<sup>12</sup> (mean error of  
345 model = 1.21 °C). For a 225 km<sup>2</sup> 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<sup>17, 18</sup>,  
360 and that increases in vegetation cover can dampen the effects of warming on species<sup>38</sup>. 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 warming<sup>12</sup> (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 Administration<sup>39</sup> 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) map<sup>40</sup> 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<sup>41,42</sup>. 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 1948<sup>43</sup> compared with land cover information from 1990<sup>44</sup>, 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 2007<sup>45</sup> (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 change<sup>16</sup>.

414 Because anthropogenic nitrogen deposition has been responsible for changes in  
415 community composition<sup>42</sup>, and can also modify species' responses to climate change<sup>19</sup>, 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) model<sup>46</sup> 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 equations<sup>47</sup>, 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.*<sup>48</sup> and Carl & Kühn<sup>49</sup>.

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 Criterion<sup>50</sup>. Analyses were performed using the *geepack*<sup>51</sup> and *MESS*<sup>52</sup> packages for R<sup>53</sup>.

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 model<sup>54</sup>. 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

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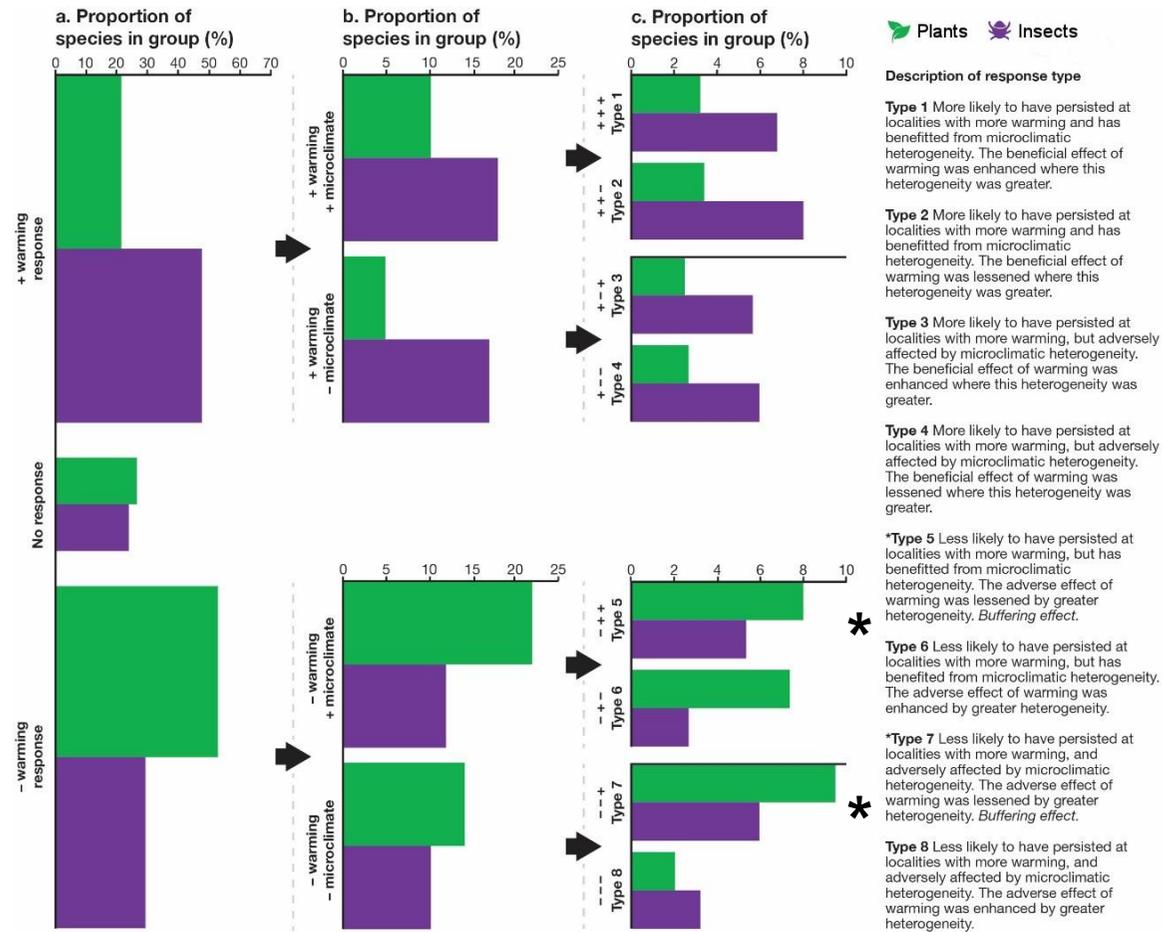
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**Fig. 1** Classification of plants (green) and insects (purple) by responses to warming and microclimatic heterogeneity. Species (n = 430) were initially classified by their response to warming (panel a). For those species affected by warming (n = 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.

