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Extinction risk from climate change is reduced by microclimatic buffering

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

Bioclimate modelling predicts that anthropogenic climate change will increase extinction risk for a wide range of taxa and regions[7]. However, there is a marked discrepancy between the coarse spatial scales at which geographic range contractions are commonly modelled, and the fine spatial scales at which most organisms respond to climatic variation. This has important implications for estimating the vulnerability of species to climate change[8] and, in consequence, for developing effective adaptation measures. Coarse-scale models fail to identify the localised effects of topography and vegetation on climate that were vital for sustaining refugial populations during past periods of climate change, and which could influence biological responses to current warming[4]. 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 species[10].

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[11]. 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

gridded data from the UK Met Office. To represent microclimatic heterogeneity arising from

the topography (hereafter simply 'microclimatic heterogeneity'), we calculated the proportion

of direct beam solar radiation incident on the surface[12] of each component 100 x 100 m cell,

before computing the standard deviation in these values across each 10 km grid square. The

use of solar radiation as a proxy for thermal microclimate is a well-established means of

analysing wildlife responses to fine-scale temperature variation[13], because variation in the

radiation budget associated with topography is one of the most important determinants of the

temperature of terrestrial ecosystems at temperate latitudes[14]. However, to further

demonstrate the validity of our proxy of microclimate, we compared it with modelled fine-

scale temperature across 261 km^2 of south-western England, showing that the two are closely

related (Supplementary Figs. 3 & 4). We modelled persistence versus extirpation for each

species in each 10 km square as a function of warming rate, microclimatic heterogeneity, and

the interaction between these factors. All our models also included controls for recorder

effort, agricultural intensity, nitrogen deposition, mean elevation, precipitation change, and

spatial autocorrelation (see Methods).

      To assess the importance of microclimatic heterogeneity in buffering extirpations

from climate change, we classified each species by its responses to warming, microclimatic

heterogeneity and their interaction (Fig. 1). Of the plant species showing effects of warming,

more than two thirds responded negatively (Fig. 1a). In contrast, most insect species

responded positively to warming (Fig. 1a). Of those species that responded negatively to

warming, the majority responded positively to microclimatic heterogeneity (Fig. 1b).

Crucially, 59% of species affected by an interaction between warming and microclimatic

heterogeneity benefitted from the microclimatic buffering effect (Fig. 1c). Species that were

negatively affected by warming were also more likely to benefit (Fig. 1c). In contrast, for

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 change[15], and 20th century agricultural

101 intensification has been greatest in flat, lowland areas of England[16], 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[17]) can have a

104 substantial effect on the temperatures that organisms experience[18], 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[19]. 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[19] or show that habitat

120 heterogeneity buffers populations against environmental variability[20], 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[21]. 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[22]. Another

137   potential reason is that microclimatically heterogeneous regions are also associated with

138   atypical climatic conditions[23] that are more resistant to invasion[24]. 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[12]. 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 elsewhere[27].

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 restoration[15], the redesign of protected

159 area networks[9], and assisted colonisation[28], 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[4]. 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[29]. The magnitude of anthropogenic

173 warming to date is approximately half that expected by 2050[30], and biodiversity losses are

174 predicted to accelerate with increased warming[7]. In consequence, the results of our study

9

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[4].

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264

265 **Author Contributions** A.J.S. conducted the analyses. I.M.D.M., N.J.B.I., N.A.M., M.D.M.,

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.,

268 J.J.B., J.J.H., R.F. and K.J.W. provided data and expert guidance.

269

270 **Competing financial interests** The authors have no competing financial interests to declare.

271

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Methods

Biological response data

We obtained data on the distribution of species from the Botanical Society of Britain and Ireland, the British Bryological Society, Butterflies of the New Millennium, the National Moth Recording Scheme, and the National Recording Schemes for Ground Beetles, Soldier Beetles, Longhorn Beetles, and Ladybirds. All these organisations accept records from either taxonomic specialists or the general public, and any unusual records undergo a vetting process to establish their veracity[31]. We analysed data on 430 species identified as 'climate-threatened' in a recent climate change risk assessment for our study region[11] in which projected responses to future climate change to 2100 were assessed, and for which adequate data were available (see below).

To establish patterns of extirpation over a period of warming, we aggregated the data into two time periods. For vascular plants and bryophytes these periods were 1970-1986 and 1987-2009, and for the lepidopterans and coleopterans, 1970-1989 and 1990-2009. These periods correspond to comprehensive national coverage, often associated with the production of atlases for the corresponding flora and fauna[32-35], during which coordinators sought to maximise observer coverage of 10 km x 10 km grid squares (hectads). We restricted our analysis to species which were recorded in more than 100 of the 10 km grid squares in the first time period, as long as the same 10 km square was visited by recorders for that taxonomic group's recording scheme in the second time period. Absences are not explicitly recorded within these schemes, so 'extirpations' from grid squares are here defined as a species being recorded as present during the first period, but not in the second.

To account for possible influences of variation in recorder effort on patterns of apparent extirpation, we calculated the number of unique recorder visits to each 10 km grid 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

Climate change variables

319 Monthly mean 5 x 5 km gridded temperature data were obtained from the UK Met Office[36] 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 ºC / 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 Mission[37] 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[12]. 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[12] (mean error of

345 model = 1.21 ºC). For a 225 km^2 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 species[38]. 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[12] (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[39] 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[40] 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 1948[43] compared with land cover information from 1990[44], 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[45] (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[16].

414   Because anthropogenic nitrogen deposition has been responsible for changes in

415 community composition[42], and can also modify species' responses to climate change[19], 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[46] 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.

Analyses

The extirpation or persistence of each species in each 10 km grid square was modelled as a

function of temperature increase, heterogeneity in topographic microclimate and an

interaction between these two variables, with agricultural intensity, nitrogen deposition,

precipitation change, the mean elevation of each grid square and recorder effort (log-

transformed) included as control variables. We modelled extirpation/persistence using

general estimating equations[47], which account for correlations within spatial clusters of data

points by parameterising a correlation matrix, while correlations between clusters are

assumed to be zero. Spatial clusters were identified automatically using the methods outlined

in Dormann *et al.*[48] and Carl & Kühn[49].

To classify species according to their response to warming, microclimate

heterogeneity and the interaction between the two (Fig. 1; Supplementary Table 1), separate

models were constructed for each species. A forward selection procedure was used to identify

the response to each term; i.e. a response to heterogeneity was assessed only for those species

responding to warming, and a response to the interaction between microclimate heterogeneity

and warming was assessed only for those species responding to both these terms individually.

We considered a species to be 'responding' to a variable (Fig. 1) only if the inclusion of that

variable resulted in improved model performance, assessed using Pan's Quasi Information

Criterion[50]. Analyses were performed using the geepack[51] and MESS[52] packages for R[53].

To test the sensitivity of our results to alternative model selection procedures, we also

conducted full multi-model inference for each species, whereby all possible responses to

climate and microclimate heterogeneity were tested. In this 'full QIC' approach, the model

with the lowest QIC was selected as the final model[54]. For species in which the best model

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

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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.
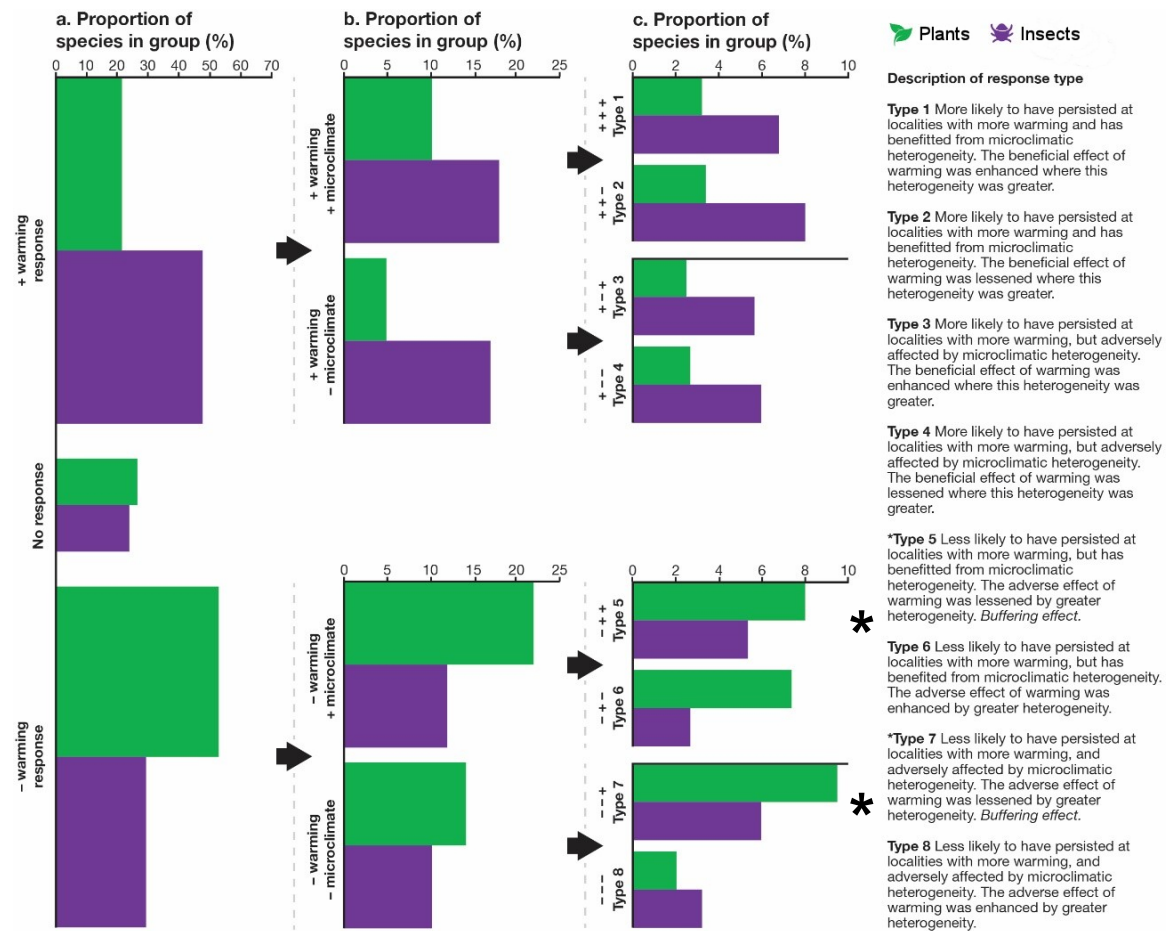
Fig. 2 Modelled change in extirpation risk for each species as a function of warming and microclimate heterogeneity. The relative frequency of warming in each grid square is shown in (a). In (b-k), the modelled differences in extirpation risk between areas of high (95th percentile) microclimatic heterogeneity 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.