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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 extinction¹. 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 understood³⁻⁵, hindering our capacity to develop robust in situ measures to adapt conservation to climate change⁶. 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

climate change.

Bioclimate modelling predicts that anthropogenic climate change will increase extinction risk for a wide range of taxa and regions⁷. 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 change⁸ 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 warming⁴. If landscape features promoting

evidence that microclimatic heterogeneity can substantially reduce extinction risk from

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

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Here, we provide an empirical test of the extent to which microclimatic heterogeneity arising from landscape topography has buffered plants and insects in England against extirpations associated with recent climate change. To establish patterns of extirpation for each species during a period of warming, we compared distributions between two periods with comprehensive recording effort (1970-1986 and 1987-2009 for plants; 1970-1989 and 1990-2009 for insects). Our analyses focused on the well-recorded groups of Tracheophyta (vascular plants), Bryophyta (mosses and liverworts), Lepidoptera (butterflies and moths) and Coleoptera (beetles), and were restricted to recently declining species that have also been identified as being vulnerable to future climate warming¹¹. We selected only species with records of persistence or extirpation in more than 100 unique 10 x 10 km grid squares (the common unit of UK distribution atlases, and our unit of analysis – see Methods), giving a total of 430 species (316 plants and 114 insects). We defined the 'extirpation' of a species from a grid square if that species was recorded as present during the first period but not the second. Because we were only analysing persistence and extirpation (and not colonisations), we do not expect an observed increase in recorder effort through time to have biased our results. Nevertheless, to account for spatial variation in recorder effort, we included the total number of unique recorder visits to each grid square as a control in all models (Supplementary Figs. 1 & 2). To represent the warming rate in each 10 km grid square we 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 surface¹² 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 variation¹³, because variation in the radiation budget associated with topography is one of the most important determinants of the temperature of terrestrial ecosystems at temperate latitudes¹⁴. However, to further demonstrate the validity of our proxy of microclimate, we compared it with modelled fine-scale temperature across 261 km² 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

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

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

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

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

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

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

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

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

The prediction that species will be extirpated from large parts of their range is prevalent in the scientific literature, leading to debate regarding approaches to avert species loss from climate change. Proposals include habitat restoration ¹⁵, the redesign of protected area networks⁹, and assisted colonisation ²⁸, but competing demands on land-use and on economic resources render such approaches difficult to achieve. *In situ* conservation measures are typically easier to implement, and if targeted at refugial locations with high microclimatic heterogeneity, could help to reduce extinction risk as regional climates become unsuitable. While management at these locations will require many of the same approaches used to conserve species as elsewhere, placing greater emphasis on enhancing local persistence gains time for systems to adapt, and for managers and society to develop longer-term solutions⁴. Ultimately, the protection of microrefugia is a way to prioritise locations for management given limited resources. What will differ is the emphasis on protecting, maintaining, and fostering the features that create microclimate heterogeneity, and on enhancing the local persistence of species in the face of ongoing climate change, alongside those regional actions that may already be in place.

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

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

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Correspondence and requests for materials should be addressed to A.J.S., R.J.W. or 252 I.M.D.M. 253 254 **Acknowledgements** We thank the many people, predominantly volunteers, who submitted 255 data to the Botanical Society of Britain and Ireland, British Bryological Society, Butterfly 256 Conservation, the Ground Beetle Recording Scheme, the Soldier Beetle Recording Scheme, 257 Longhorn Beetle Recording Scheme and the UK Ladybird Survey, as well as the co-258 ordinators of those schemes. Thanks also to the UK Met Office, Natural England, 259 260 Environment Agency, CEH, Defra and NASA for data access. Iain Stott, Richard Inger, América Paz Durán, Kevin Gaston and five referees provided helpful comments on drafts of 261 the manuscript. The work was funded by Natural England, and by NERC grant 262 263 NE/L00268X/1 to RJW and IMDM. 264 Author Contributions A.J.S. conducted the analyses. I.M.D.M., N.J.B.I., N.A.M., M.D.M., 265 S.D., H.Q.P.C. and R.J.W. conceived the work and supervised analyses. A.J.S, I.M.D.M. and 266 R.J.W. wrote the manuscript with contributions from the whole team. C.M.B., A.G.A., T.A., 267 J.J.B., J.J.H., R.F. and K.J.W. provided data and expert guidance. 268 269 **Competing financial interests** The authors have no competing financial interests to declare. 270 271 Orc IDs AJS: 0000-0001-7697-7633, AGA: 0000-0002-4190-4423, CMB: 0000-0002-2960-272 5666, JJB: 0000-0003-4394-2041, HQPC: 0000-0002-5136-378X, SD: 0000-0003-3364-273 9255, RF: 0000-0001-6992-3522, NJBI: 0000-0002-4869-8052, MDM: 0000-0002-7978-274 5554, KJW: 0000-0002-5751-8623, RJW: 0000-0003-4477-7068, IMDM: 0000-0001-8030-275 9136. 276

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 veracity³¹. We analysed data on 430 species identified as 'climate-threatened' in a recent climate change risk assessment for our study region¹¹ 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 fauna³²⁻³⁵, 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

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

Climate change variables

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

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

Microclimatic heterogeneity

To derive a proxy for landscape heterogeneity in topographically-driven temperature microclimates, a three-arc second (~90 m) horizontal resolution Digital Elevation Model (DEM) was obtained from the Shuttle Radar Topography Mission³⁷ and resampled and coarsened to 100 x 100 m resolution using bilinear interpolation. The proportion of direct beam radiation incident on the surface of each grid square of the DEM, hereafter referred to as the solar index, was calculated using a method that accounts for slope, aspect, and topographic shading ¹². The mean of hourly values over the 24 hours of 21st June was used as this provides a good proxy of near-ground daily mean and maximum temperatures across the growing season (see below). Third and finally, the standard deviation of solar index values in each 10 km grid square was calculated to represent heterogeneity in the thermal microclimate.

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

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

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

However, it should be noted that the microclimates experienced by organisms are influenced both by the effects of topography and by the effects of vegetation structure^{17, 18}, and that increases in vegetation cover can dampen the effects of warming on species³⁸. Whilst our main aim was to address the possible buffering effects of topographic microclimates over the scales which they are likely to have the dominant effects on rates and patterns of warming 12 (100 m – 10 km), we conducted a supplementary analysis to examine possible confounding effects of changes in vegetation cover on our results. We used the 0.05 degree (~ 5 km) dataset of daily Leaf Area Index (LAI) from the National Oceanic and Atmospheric Administration³⁹ to calculate the mean LAI in each 10 km grid square from 1982 (the earliest date for which it is available) until 1989, and for 1990 to 2009, and calculated the log proportional change between the two periods (Supplementary Fig. 5). The weak positive correlation between change in LAI and modelled heterogeneity in topographic microclimate (r = +0.07, d.f. = 1300, p = 0.02; Supplementary Table 2) suggests that changes to vegetation cover have not confounded our results. As a further check we also tested the ability of change in LAI to explain the overall pattern of extirpations observed. We fitted Generalised Linear Mixed Models (GLMMs) to the datasets from plant and insect groups separately, with LAI change included as a fixed effect, and species identity included as a random intercept. LAI change explained less than 0.04% of the variation in extirpation probability in either group

(the 'marginal r-squared' statistic), giving us further confidence that our conclusions are robust.

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Control variables

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

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

= 0.72, d.f.= 1300, p < 0.00001), with the patterns only weakly correlated with changes to urban (r = 0.15, d.f. = 1300, p < 0.00001). In addition, the majority of this intensification of land use in England and Wales is estimated to have occurred between 1925 and 1978, based on a comparison of the 1925-1948 land cover data and surveys conducted in the UK Countryside Survey in 1978, 1990, 1998 and 2007^{45} (Note: the 1978-2007 data cannot be used to estimate change in all 10 km grid squares, as the surveys were not exhaustive). Given that most land cover changes pre-dated our period of study, we use agricultural intensity as the control that is most likely to be relevant for distribution changes observed between the two c. 20 year distribution recording periods before and after the end of the 1980s. Although the land cover categories included in agricultural intensity represent the classes we expect to be most deleterious to our study taxa, it is important to emphasise that they are only simplified representations of the effects we seek to control for, and do not represent all the components of land-use intensification that could potentially be drivers of change¹⁶.

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

Because there is a relative lack of flatter areas on higher ground in the English landscape, heterogeneity in topographic microclimates could also be confounded by elevation. Hence, the mean elevation of each 10 x 10 km grid square, derived from the 100 x 100 m resolution DEM, was also included as a control variable in models. Finally, to account for extirpations driven by moisture changes, the annual change in total precipitation for each 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 equations⁴⁷, 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 & Kühn⁴⁹.

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 Criterion⁵⁰. Analyses were performed using the geepack⁵¹ and MESS⁵² packages for R⁵³.

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 model⁵⁴. For species in which the best model included warming, microclimate, and/or the interaction between the two, there was a high

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

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

Data availability

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

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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.

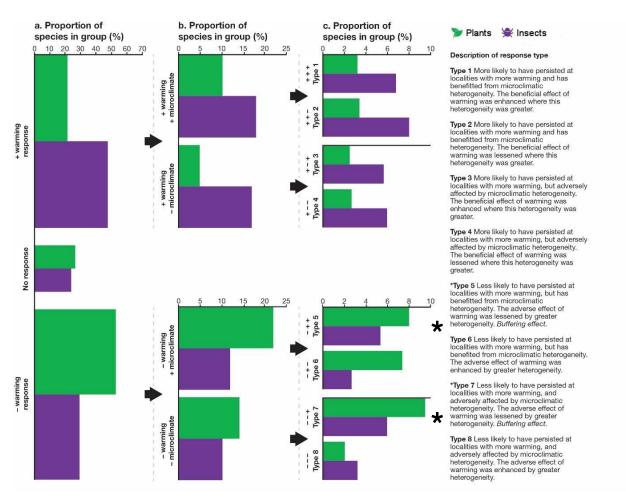


Fig. 2 Modelled change in extirpation risk for each species as a function of warming and microclimate heterogeneity. The relative frequency of warming in each grid square is shown in (a). In (b-k), the modelled differences in extirpation risk between areas of high (95th percentile) microclimatic heterogeneity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

