

1 **Macroclimate data over-estimate range shifts of plants in response to climate**
2 **change**

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4 Ilya M. D. Maclean^{1,2,*} and Regan Early²

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6 ¹Environment and Sustainability Institute, University of Exeter Penryn Campus, Cornwall,
7 United Kingdom, TR10 9FE.

8

9 ²Department of Ecology and Conservation, University of Exeter Penryn Campus, Cornwall,
10 United Kingdom, TR10 9FE.

11

12 *Author for correspondence. Email: i.m.d.macleam@exeter.ac.uk; Tel.: +44 (0)1326 255 968.

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14

15 **Abstract**

16 Current conservation policy has been shaped by the expectation, that for many species,
17 places with suitable climate will lie outside their current range thus leading to predictions of
18 numerous extinctions. Here we show that the magnitude of range shifts is often overestimated
19 as climate data used does not reflect the microclimatic conditions that many organisms
20 experience. We model the historic (1977-1995) distributions of 244 heathland and grassland
21 plant taxa using both macro- and microclimate data and project these distributions to present
22 day (2003-2021). Whereas macroclimate models predicted major range shifts (median 14 km
23 shift), microclimate models predicted localised shifts into favourable microclimate, generally
24 of less than 1 km, that more closely match observed patterns of establishment and extirpation.
25 Thus, improving protection of refugial populations within species' existing geographic range
26 may, for species living in environments exposed to sunlight, be more effective than assisted
27 translocations and overhaul of protected area networks.

28

29 **Main text**

30 It is widely predicted that places with suitable climate will soon lie outside the current range of
31 many species that cannot adapt¹⁻³, such that survival will depend on how rapidly populations
32 can move⁴⁻⁶. Many organisms are thought to face insurmountable range-shift barriers, leading
33 to the conclusion that the only viable option to prevent extinctions is to translocate them to
34 places where the climate is suitable⁷, or create habitat corridors that allow them to get there
35 of their own accord⁸. However, the expectation that species will have to undergo major range
36 shifts to avoid range loss is founded on the assumption of strong and smooth geographic
37 gradients in climate. These gradients would mean that temperature or precipitation changes
38 make swathes of species' current ranges unsuitable and create swathes of suitable habitat
39 elsewhere. While clear climatic gradients occur at coarse spatial resolution, at finer resolutions
40 topography, soil and vegetation exert great influence on local climatic conditions, resulting in
41 considerable microclimate heterogeneity, particularly near the ground^{9,10}. These fine-
42 resolution variations can exceed the variability that occurs over continents in coarse-resolution
43 climate, and greatly exceed the magnitude of climate change expected over the next 100
44 years¹¹. For the most part organisms experience climate at these local resolutions, which are
45 orders of magnitude finer than the scales at which shifts are measured and modelled¹².
46 Despite this, there is little consensus on the extent to which microclimate matters for species
47 range shifts. On the one hand, it has been proposed that macroclimate data may overestimate
48 the thermal tolerances of species, and hence under-estimate the loss of suitable climate by
49 failing to capture warm microclimates in which species are driven to extinction¹³. Conversely,
50 it has also been suggested that cool microclimates may buffer species against climate change
51 by providing suitable microrefugia^{6,14,15}

52 Understanding of the importance of microclimate on projected range shifts has been
53 hampered by an inability to quantify microclimate over extents and durations relevant to
54 species range shifts. Here we exploit recent advances in microclimate modelling^{9,11,16} to test
55 whether macroclimate data over-estimate range shifts in comparison to microclimate. We

56 define macroclimate as conditions interpolated from weather stations at 1.5 – 2 m above-
57 ground and at grid resolutions of 1 km or more. We define microclimate as the climatic
58 conditions that organisms experience at finer resolution, often closer to the ground.

59

60 **Why range shifts may be overestimated**

61 To illustrate the mechanism by which ranges may or may not be over-estimated by
62 macroclimate data, we first consider two hypothetical examples (Fig. 1). Firstly, we imagine a
63 situation in which the geographic range of a species with a true thermal tolerance of 8 - 12°C
64 is assessed at coarse resolution. We assume that each grid cell has $\pm 5^\circ\text{C}$ of microclimatic
65 heterogeneity and any coarse grid cells with at least some suitable microclimate is occupied.
66 Consequently the thermal tolerance of the species, estimated from macroclimate data, is over-
67 estimated. When warming of 2°C is applied, under the assumption of perfect coupling, grid
68 cells predicted by macroclimate data to become climatically unsuitable are also those that lose
69 all suitable microclimate. Predictions based on microclimate and macroclimate are thus
70 identical (Fig. 1a).

71

72 Alternatively, we consider a species with the same geographic distribution as in the first
73 example and hence the same apparent thermal tolerance estimated by macroclimate data.
74 However, here we assume that near-ground temperatures are decoupled from macroclimate
75 across latitudes: at the species' warmer range margins ground temperatures are hotter than
76 air temperatures. This phenomenon is widely observed, and arises because the ground
77 absorbs more solar radiation at lower latitudes (though the degree of decoupling is also
78 affected by snow and vegetation cover, and may not be so pronounced under forest
79 canopies)⁹. Thus a species living in the same fine-scale grid-cells must have a broader thermal
80 tolerance than in example 1a, in our case 8.6-16.4°C. Since solar radiation does not increase
81 in line with climate change, the broader thermal tolerance means that species may remain in
82 coarse grid cells that macroclimate predicts to become unsuitable (Fig. 1b).

83

84 Our illustration shows that the major flaw in using macroclimate is not necessarily the climate
85 grid size *per se*. Rather, across the distribution of a species associated with open habitats,
86 there is a greater range of near-ground than macroclimate temperatures and the space-for-
87 time substitution used to estimate range-shifts thus breaks down under future climates. Given
88 that the greater spatial heterogeneity in near-ground temperature, means that range shifts
89 may not follow smooth latitudinal gradients, the resulting effects on projected range shifts
90 could be profound. Here we test whether this is the case.

91

92 **Tests of how microclimate affects range shifts**

93 We modelled associations between multiple climate variables and the distributions of 244
94 higher plant taxa (Table S1). For each taxon, species distribution models (SDMs) were
95 constructed and projected at three grid resolutions: across Europe at 0.5° (~50 km), Great
96 Britain at 5 km, and the Lizard Peninsula, in the southwest of Great Britain at 100 m. For
97 the 100 m resolution analyses, variables were derived from estimates of temperature at 5
98 cm above ground using a recently developed microclimate model¹⁶. For the other two sets
99 of analyses, existing climate products were used^{17,18}, representative of measurements
100 obtained by standard weather stations. Plant distribution records were sourced from
101 GBIF¹⁹, the Botanical Society of the British Isles²⁰ and the Environmental Records in
102 Cornwall Automated database²¹. Because our hypothesis may not apply to forest species,
103 we restrict our analyses to smaller plants and shrubs associated with open habitats. We
104 thus assigned grid cells with >50% forested cover as being unsuitable when projecting
105 distributions, though results without forest masking are presented in supporting information
106 (Extended Data Fig. 1; Tables S1-2). To allow independent validation of which climate data
107 best predicted observed range shifts, we modelled associations between historic species
108 distributions and climate (1977-1995), projected distributions to the present day (2003-
109 2021), and compared projected climate suitability at each spatial resolution to current
110 distributions.

111

112 At each spatial resolution, we quantified range shifts in three different ways. First, as a
113 measure of the shift required to track climate change, for each taxon we calculated the mean
114 of the distances between each grid cell predicted to be occupied historically and the nearest
115 climatically suitable grid cell under recent conditions (setting this to zero if a grid cell was
116 suitable in both periods). Second, for comparison, we also calculated the converse
117 measure: the distance between each grid cell predicted to be occupied currently and the
118 nearest location with suitable climate historically. Lastly, to enable calculation of the direction
119 of shift, we computed the suitability-weighted centroid of each species' range in the two
120 periods and calculated the magnitude and direction of the centroid shift.

121

122 Overall, while macroclimate models predicted major range shifts, the predicted shift required
123 to track microclimatic changes was low and likely within the dispersal capability of the
124 majority of species. To track climate change at 0.5° resolution across Europe, species
125 would have had to shift on average between 3.7 and 62.4 km, with a median of 14.0 km
126 (Fig. 2a; Tables 1 and S1). At 5 km resolution across Great Britain, species would have had
127 to shift between 28.6 m and 52.1 km, with a median of 5.2 km (Fig. 2b; Tables 1 and S1).
128 At 100 m resolution across the Lizard Peninsula, however, species would have had to have
129 shifted between just 0 m and 8.1 km, with a median of just 114 m, equating to just 4.4 m
130 per year (Fig. 2c; Table S1). The distance between each grid cell predicted to be suitable
131 currently and the nearest location with suitable climate historically was similarly affected by
132 resolution (Extended Data Fig. 2; Table S1). There were similar discrepancies in the
133 predicted centroid shifts. Determined from 0.5° resolution models, shifts ranged from 2.9 to
134 163.9 km with a median of 46.5 km and in a predominantly northerly direction (Fig. 2d;
135 Tables 1 and S2). Determined from 5 km resolution models, shifts ranged from 850 m to
136 80.1 km with a median of 15.7 km, again in a predominately northerly direction (Fig. 2e;
137 Tables 1 and S2). By contrast, shifts determined using 100 m microclimate data, ranged
138 from 36.3 to 2,580 m with a median of 679 m, equating to just 25 m per year and shift

139 direction was inconsistent, reflecting the lack of strong latitudinal gradients in climate (Fig.
140 2f; Tables 1 and S2).

141

142 To ensure our results were not biased by restricting our fine-scale model calibration to a
143 small geographic area, meaning that taxa's full climate tolerances may not have been
144 adequately captured, we also constructed models using historic records and near-ground
145 temperature from across Europe at 0.5° grid resolution. We then projected the present day
146 distributions of these taxa across the Lizard Peninsula at 100 m resolution. These models
147 resulted in even more pronounced discrepancies with the macroclimate models. The
148 median distance required to track climate was just 24 m (Extended Data Fig. 3c; Tables 1
149 and S1) and the median centroid shift was just 65 m (Extended Data Fig. 3g; Tables 1 and
150 S2).

151

152 To ensure our results were not biased by peculiarities of the climate of the Lizard Peninsula,
153 we modelled, at 100 m resolution, the historic and current distributions of *Erica tetralix*
154 (Cross-leaved Heath), at 73 geographically and climatically disparate localities across
155 Europe, each 40 x 40 km in size. This species was selected as it is a keystone species of
156 European heathland, its range is almost entirely confined to Europe and adequate data
157 were available for model validation at each of the selected sites. Again shifts predicted by
158 microclimate models were lower than those predicted by macroclimate models. Whereas
159 macroclimate models predicted shifts of 16.2 km (at 0.5° resolution) and 2.0 km (at 5 km
160 resolution), the median shift predicted by microclimate models was 244 m. Similarly, while
161 the centroid shift predicted by macroclimate models was 33.7 km (at 0.5° resolution) and
162 5.2 km (at 5 km resolution), the median shift predicted using microclimate data was just 818
163 m (Tables 1 and S3).

164

165 **Why microclimate affects range shifts**

166 To investigate why the use of microclimate data might affect range shifts, particular in relation
167 to the climate niche of species, we evaluated how the three sets of models affected the
168 predicted probability of species persisting across the Lizard Peninsula. To ensure model
169 outputs were comparable at all three resolutions, we resampled (effectively smoothing) the
170 coarse-resolution model outputs to 100 m and quantified the maximum projected suitability in
171 any given 100 m grid cell.

172

173 At all three resolutions, the maximum projected suitability across the Lizard Peninsula in the
174 historic and current periods were closely correlated such that when recent climate was
175 predicted to be more suitable for a taxon, the historic climate was also more suitable (Fig. 3;
176 Extended Data Fig. 4). Macroclimate suitability was in general lower than microclimate
177 suitability in the recent period implying that, when modelled using microclimate data, species
178 have a higher predicted probability of persistence (medians: 0.5° 0.639, 5 km 0.717, 100 m
179 0.870). Additionally, the slope of the relationship between recent and historic microclimate
180 suitability was shallower than that for macroclimate suitability such that the discrepancy was
181 most marked for those species for which macroclimate suitability was low (0.5°: $F_{1,242} =$
182 572.4 , $P < 0.0001$, slope = 0.775; 5 km: $F_{1,237} = 907.8$, $P < 0.0001$, slope = 0.997; 100 m:
183 $F_{1,243} = 71.9$, $P < 0.0001$, slope = 0.624), implying that for those species with low predicted
184 probability of occurrence the likelihood of persisting was predicted to be much lower when
185 predicted using macroclimate data. Resultantly, models constructed using 0.5° resolution
186 data predicted the extirpation of six species from the Lizard Peninsula, including two
187 keystone heathland species, *Calluna vulgaris* and *Erica vagans*, for which the Lizard
188 Peninsula received its Natura 2000 designation and which certainly persist currently (Fig.
189 4). Models constructed using 5 km resolution data predicted the extirpation of one species:
190 *Viola lactea*. By contrast, models constructed using 100 m resolution near-ground data
191 predicted that all 244 taxa would remain extant. As recent distribution records²¹ suggest
192 that all taxa remain relatively common, there is strong evidence that the use of
193 macroclimate data over-estimates the risk of extirpation.

194 The smaller range shifts and retention of species predicted by microclimate models also
195 appear to be more accurate than predictions of macroclimate models. Despite high turnover
196 in occurrence records between the two periods, extirpations were predicted with far greater
197 accuracy by microclimate models, performing significantly ($P < 0.05$) better than would be
198 expected by chance for all except two taxa. By contrast, extirpations predicted by 5 km data
199 were predicted with greater accuracy than a random model for only 52% of taxa, and
200 extirpations predicted by 0.5° models, performed worse than a random model (Table S5).
201 Scale-discrepancies in the ability of the models to accurately predict establishments were
202 less pronounced, but nevertheless microclimate models still performed better (Table S5).

203

204 **Relative importance of scale and near-ground temperature**

205 In our hypothetical example we proposed that the major flaw when using macroclimate data
206 was not necessarily resolution *per se*, but rather the discrepancy between near-ground and
207 ambient air temperature, which may be exacerbated by data resolution. To test this further,
208 we carried-out two additional sets of analyses. First, we constructed 0.5° resolution SDMs
209 for Europe using estimates of temperature 5 cm above ground. Both the distance needed
210 to track climate across Europe and the shift in the centroid of the potential distribution were
211 predicted to be moderately but significantly lower when using near-ground coarse
212 temperature than above-ground coarse (macroclimate) temperatures (suitable cell shift:
213 12% lower, paired $t_{1,242} = 2.37$, $P < 0.05$; centroid shift: 37% lower, paired $t_{1,242} = 10.98$, $P <$
214 0.0001 , Tables 1 and S1-4). Second, we constructed 100 m resolution SDMs for the Lizard
215 Peninsula using temperatures representative of those obtained by weather stations, 1.5 - 2
216 m above ground. 97 (39%) of the taxa were predicted to be extirpated from the Lizard
217 Peninsula using these high-resolution, above-ground temperatures. For the remaining taxa,
218 however, the predicted range shifts was lower than predicted using near-ground
219 microclimate data (suitable cell shift: paired $t_{1,148} = 2.42$, $P < 0.05$; centroid shift paired $t_{1,148}$
220 $= 2.23$, $P < 0.05$; Table 1). These analyses suggest that height above ground is a major flaw

221 of macroclimate models, but that height is not particularly important once temperature is
222 measured at a biologically-relevant resolution.

223

224 It is possible that we found such a striking difference between macro- and microclimate
225 projections because we selected species associated with open habitats, for which the
226 greater effects of solar irradiance on near-ground temperatures are particularly
227 pronounced. In forests, the canopy functions as a thermal insulator and buffers sub-canopy
228 microclimatic conditions²², even though forest understories also have high microclimate
229 heterogeneity^{23,24}. Nevertheless, for the taxa studied, our hypothesis was supported.
230 Projections of species range shifts made using macroclimate data systematically over-
231 estimate range shifts, partially because spatial gradients in temperature were
232 underestimated and hence thermal tolerances over-estimated. Coupled with the existence
233 of fine-resolution heterogeneity in climate, the resulting effects on projected range shifts is
234 substantial. This raises the question of why it is still commonly perceived that large range
235 shifts are necessary, to which there are several possible answers.

236

237 First, observed range shifts are generally assessed using coarse-resolution data^{4,25} such that
238 all populations must go extinct from a region for that grid cell to become newly unoccupied,
239 whereas the occurrence of just one new individual is enough to ensure that it would be
240 considered as newly occupied. In consequence, range expansion at coarse resolutions would
241 appear to be much faster than range contraction, and long-distance movement will appear to
242 be a common response to climate change. Given the disproportionate number of studies that
243 document range expansions relative to range retractions⁴, the magnitude and scale-
244 dependency of observed range shifts is rather uncertain^{5,6}. Second, the perception of a need
245 for large range shifts may be disproportionately influenced by early studies on animals in which
246 large range shifts were documented²⁶. More recent and comprehensive assessments of
247 climate-induced species redistributions⁵, point to more idiosyncratic responses, particularly
248 among plant species. Comparing our modelled projections to observed shifts for the same

249 taxa (Table S6) would seem to support this contention. Our predicted magnitudes of range
250 shifts, when modelled using microclimate, are much closer to the magnitude of observed shifts
251 than our predictions based on macroclimate data. Likewise, as with our range shifts modelled
252 using microclimate data, there is very little consistency in direction. Third, where observed
253 range shifts and extirpations have not matched the predictions of macroclimatic changes,
254 this is often attributed to a lagged-response²⁷, and thus potentially an extinction debt that
255 has yet to be paid²⁸. Fourth, the majority of projected shifts to date have used climatic and
256 biological data with grid cell sizes much larger than those used in this study¹². It is only
257 recently that methods for generating fine-resolution climate datasets have been
258 developed²⁹, and very rarely have these been used to project species range shifts^{15,25,30}.
259 Last, where projections have been made they are often poorly tested, inevitably because the
260 intention is often to predict future changes. Thus, the most common way to test the
261 performance of SDMs is to use cross-validation techniques within species current, observed
262 distributions. Such approaches suffer from the problems associated with autocorrelation,
263 thereby potentially overestimating model performance³¹. This issue is illustrated well with our
264 own coarse-scale models. Despite an inability to accurately predict extirpations, standard
265 cross-validation metrics suggested good performance (Table S7).

266

267 **Conclusions**

268 Our findings do not suggest that climate does not pose a threat to species. Despite marked
269 differences in predicted range shift distances, turnover in microclimate suitability was higher
270 than macroclimate suitability and approximately half of taxa were predicted to lose suitable
271 climate space irrespective of the resolution of climate data used. Rather our results suggest
272 that many species distribution changes in responses to climate are likely to be localised and
273 difficult to infer using coarse-resolution data. These localised shifts could fragment
274 populations, alter demography and affect community composition and ecosystem function.
275 We caution against assuming long-distance range shifts will occur as an immediate response
276 to climate, and hence that the redesign of protected area networks³² and assisted

277 colonisations⁷ are the most pressing conservation priorities. Finite conservation resources and
278 competing land-uses in many instances render such approaches impractical, emphasising the
279 need for robust measures for carrying-out conservation *in situ*³³. Rather, we emphasise the
280 need to implement measures that sustain viable populations of species within their current
281 geographic range. Conservation of areas that retain suitable microclimate could provide a
282 practical and cost-effective means of reducing extinction threat because this can be targeted
283 at specific locations.

284
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288

289 **Author contributions**

290 I.M.D.M. and E.R. conceived and designed the study. I.M.D.M performed the numerical
291 analysis and wrote the paper with contributions from E.R. Both authors discussed and
292 interpreted results.

293

294 **Competing interests**

295 The authors declare no competing interests.

296

297

298 **Tables**

299 **Table 1. Range shifts predicted by each of the models** between the two study periods: 1977-1995 and 2003-
 300 2021. Suitable cell shifts refer to the mean distances between each grid cell predicted to be occupied historically
 301 and the nearest climatically suitable grid cell under recent conditions (and vis-versa). Centroid shifts refer to
 302 the magnitude and direction of the shift in the suitability-weighted centroid of predicted. For the first six models,
 303 the median values across taxa are shown. For models 7-9 the estimated values for *Erica tetralix* are shown.
 304 For the 10th model, median values across 73 sites are shown. For model 6, the 73 taxa predicted to be
 305 extirpated are excluded in the calculation of median suitable cell shifts. Values for individual taxa are shown in
 306 Tables S1-4.

Model description	Suitable cell shift (km)		Centroid shift	
	Historic to recent	Historic to recent	Magnitude (km)	Direction (°)
1. Europe (constructed and projected at 0.5° grid resolution using temperatures 1.5-2m above ground)	14.0	7.2	46.5	347
2. Great Britain (constructed and projected at 5 km grid resolution using temperatures 1.5-2m above ground)	5.2	2.1	15.7	.343
3. Lizard Peninsula (constructed and projected at 100m grid resolution using temperatures 5 cm above ground)	0.1	0.1	0.6	145
4. Europe (constructed and projected at 0.5° grid resolution using temperatures 5 cm above ground)	6.1	0.4	29.3	96
5. Lizard Peninsula (constructed using 5 cm above ground temperatures across Europe at 0.5° grid resolution and projected at 100 m resolution)	0.0	0.0	0.1	20
6. Lizard Peninsula (constructed and projected at 100m grid resolution using temperatures 1.5 m above ground)	0.0	0.0	0.8	138
7. <i>Erica tetralix</i> Europe (constructed and projected at 0.5° grid resolution using temperatures 1.5-2m above ground)	16.2	11.7	33.7	324
8. <i>Erica tetralix</i> Great Britain (constructed and projected at 5 km grid resolution using temperatures 1.5-2m above ground)	2.0	1.2	5.2	2
9. <i>Erica tetralix</i> Lizard Peninsula (constructed and projected at 100m grid resolution using temperatures 5 cm above ground)	0.0	0.3	1.8	334
10. <i>Erica tetralix</i> 73 sites across Europe (constructed and projected at 100 m grid resolution using temperatures 5 cm above ground)	0.3	0.2	0.8	67

307
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387

388 **Methods**

389 *Climate data*

390 Monthly global gridded 0.5 degree climate data for the period 1979-2021 were obtained from
391 the Climatic Research Unit¹⁷ and the data for Europe and surrounding nearby land areas
392 (32°W - 50°E, 27°N - 83°N) extracted from this. Monthly 1 km gridded climate data for Great
393 Britain were obtained from the Met Office¹⁸ and coarsened to a grid resolution of 5 km to match
394 the resolution of plant distribution data. Monthly 100 m gridded temperature data for the Lizard
395 Peninsula were obtained by aggregating the hourly outputs from a microclimate model,
396 microclima, previously developed for the study region¹⁶. Using this approach, mesoclimatic
397 effects (cold-air drainage, coastal exposure and elevation) are determined from the coarse-
398 resolution climate surfaces using thin-plate spline models, with coastal exposure and elevation

399 included as predictors. Differences between mesoclimate (T_{meso}) microclimate temperatures
400 (T_{micro}), in this case for 5 cm above ground, are then determined from terrain, vegetation and
401 ground properties using energy balance equations such that

402

$$403 \quad T_{micro} - T_{meso} = \frac{r_{HR}}{\rho c_p} (R_{net} - L - G)$$

404 Where R_{net} is the net radiation flux, L is the latent heat flux, G the ground heat flux, r_{HR}
405 resistance to heat loss, ρ the density of air and c_p the specific heat of air at constant pressure.

406 Assuming ρ and c_p to be approximately constant and L and G to be relatively small and
407 proportional to net radiation¹⁶, $T_{micro} - T_{meso}$ is thus a linear function of R_{net} , the gradient of
408 which is a measure of the thermal coupling of the surface to the atmosphere, which varies as
409 a function of both the structure of the vegetation and wind speed, and in this instances, fitted
410 using 89,250 field measurements of temperature obtained using data-loggers deployed at 35
411 locations across the study site¹¹.

412

413 To derive 100m resolution temperature data for the 73 *Erica tetralix* locations across Europe,
414 we used the R³⁴ package *microclima*^{16,35}, which automatically downscales sub-daily climate
415 data from the National Centres for Environmental prediction³⁶, using high-resolution digital
416 elevation data. Here, instead of field calibration data to determine the relationship between
417 temperature and net radiation, an entirely from first principles microclimate model,
418 NicheMapR³⁷ is used to derive the slope for a point location at the centre of each study area,
419 and the same slope then applied across the study area, but with wind speed and radiation
420 altered by terrain. The same approach was used to generate microclimate temperatures 5 cm
421 above ground across Europe at 0.5° resolution, but here mesoclimatic effects are not modelled
422 (see online code³⁸). To derive 100m resolution macroclimate temperature measurements for
423 the Lizard Peninsula, we used *microclima*¹⁶ to model the mesoclimatic effects, but omitted the
424 further step of modelling near-ground temperatures.

425

426 Monthly 100m gridded rainfall data for the Lizard Peninsula were derived by spatially
427 interpolating 5 km gridded rainfall data using a thin-plate spline, with 100m resolution elevation
428 data included as an additional covariate. Interpolation was performed using the fields
429 package³⁹ for R³⁴. The same procedure was used to downscale rainfall at 73 locations across
430 Europe, though using rainfall data the Climatic Research Unit. At all scales, monthly data
431 were used to reconstruct, for two study periods: 1977-1995 and 2003-2021, the 19 widely
432 used “Bioclim” variables presented in Hijmans *et al*⁶⁹, following the Anuclim method⁴⁰.

433

434 *Species distribution data*

435 Records of vascular plants across the Lizard Peninsula were obtained from Environmental
436 Records in Cornwall Automated (ERICA) database, a compilation of verified local biodiversity
437 records curated by members of the Cornwall and Isles of Scilly Federation for Biological
438 Recorders²¹. Records georeferenced to a precision of >100m were removed and the
439 remaining data used to determine the presence of species within each 100m grid cell in each
440 of two study periods. The 244 taxa present in at least 20 grid cells in the historic period and
441 associated with heathland and grassland were selected for all subsequent analysis (Table
442 S1). For the same taxa, occurrence records from across Great Britain were obtained from the
443 Botanical Society of the British Isles²⁰, and their presence in 5 km grid cells determined in the
444 same two periods. Plant records from across Europe and surrounding land masses (32°W -
445 50°E, 27°N - 83°N) were downloaded from the Global Biodiversity Information Facility
446 (GBIF)¹⁹. For the fine-resolution *E. tetralix* analyses, only records georeferenced to ≤100 m
447 were used. At each of the three resolutions plant distribution records are recorded in a similar
448 way: they represent the presence of a taxa at any given location recorded by volunteer citizen
449 scientists, but absences are not recorded.

450

451 *Modelling distributions*

452 We used species distribution models⁴² to predict distribution shifts for each taxon at each of
453 the three spatial resolutions. In each instance we constructed the model using historic

454 distribution and climate data and projected distributions forward to the present day, thus
455 permitting robust empirical validation. Because the 'bioclim' variables were correlated with one
456 another, and to ensure greater transferability between regions or time periods⁴³, we performed
457 Principal Components Analyses (PCA), and used the first 7 components, which together
458 explained >99% of the variance, as climatic predictors of species distributions. To do so, the
459 bioclim variables from both periods were averaged prior to performing the PCA and then
460 predicted separately for both periods, thereby ensuring that relationships between bioclim
461 variables and principal components were identical in both periods. The relationship between
462 principal components and bioclim variables is shown in Table S8.

463

464 To account for spatial biases in recording effort^{44,45}, which is particularly pronounced in the
465 European datasets (with a paucity of records from Eastern Europe), we subsampled the data
466 in a manner proportional to the log-transformed number of visits to each square such that
467 presences were less likely to be generated from grid cells with high visit coverage, whereas
468 pseudo-absences were more likely to be generated from grid cells with high coverage. The
469 number of visits to each square was calculated as the number of unique date, species and
470 record ID combinations in each grid cell and thus represents the total observer effort of all
471 analysed taxa. For each species, pseudo-absences were generated from within the convex
472 hull of occurrences geographically, to avoid over-representing climates that fall outside a
473 species' geographic range⁴⁶.

474

475 To account for methodological uncertainties in models, we generated species distribution
476 using three varied, but widely used model classes, namely Maxent⁴⁷, General Additive
477 Models⁴⁸ and random forests⁴⁹. To account for possible spatial autocorrelation in model
478 coefficients, we spatially-kriged the residuals of each distribution model using inverse-distance
479 squared weightings and creating new distribution models with same sub-sampled distribution
480 data, but with this variable included as an autocovariate⁵⁰. The results reported are from a

481 final probabilistic weighted (by cross-validation True Skill Statistic, TSS) ensemble distribution
482 each species and period, constructed using the 'sdm' package⁵¹ for R³⁴.

483

484 We investigated whether our results could be biased because 100m resolution models, based
485 only on data from the Lizard Peninsula, might underestimate species' full climate envelope.
486 To do so, we fitted models using historic 0.5° resolution plant and climate data from the
487 European region, here using temperature estimates for 5 cm above ground. For all taxa, we
488 then projected the models in both periods at 100 m resolution across the Lizard Peninsula. To
489 compare the relative importance of resolution and the use of near-ground data, we also fitted
490 and projected species distribution models at 0.5° across Europe using near-ground estimates
491 of climate, and across the Lizard Peninsula at 100 m resolution using estimates of climate for
492 1.5-2 m above ground.

493

494 As the taxa for which analyses were performed were associated with open habitats, we
495 masked areas with 50% forest cover as unsuitable in the ensemble distribution predictions,
496 though results without masking are also presented in supporting information. Forest cover
497 data in each 0.5° grid cell across Europe were sourced from CORINE⁵² and for Great Britain
498 and the Lizard Peninsula, from the UKCEH Land Cover Map 2020⁵³.

499

500 *Model validation*

501 We independently evaluated the ensemble models within the time period for which they were
502 projected using the Boyce index using the 'ecospat' package for R⁵⁴. We also determined the
503 proportion of number that establishments and extirpations between the two time periods were
504 accurately predicted. Probabilistic ensemble projections of distributions were thus converted
505 to binary outputs using a predicted probability of occurrence threshold set separately for each
506 taxa that ensured that 90% of observed presences occurred in grid cells with suitable climate.
507 To account for incomplete observer coverage, and hence the likelihood that an apparent

508 absence in either period is a false absence, we computed the fraction of apparent
509 establishment and extinction (in both periods) that were predicted by each ensemble model.
510 For each taxa, we then generated an equivalent number of historic and more recent records
511 randomly and assessed model performance in the same way. The randomisation process was
512 repeated 1000 times, and the proportion of times the model performed better than random
513 assessed.

514

515 *Range shifts*

516 We quantified range shifts in three different ways. First, we computed the suitability-weighted
517 centroid of each species' climatically suitable range in the two periods and calculated the
518 magnitude and direction of the centroid shift. Prior to doing so, we converted the distributions
519 to a Lambert Azimuthal equal area projection (EPSG:3035) to avoid over-weighting suitability
520 at higher latitudes. The centroids were then converted to the World Mercator projection
521 (EPSG: 3395), for calculating the direction of the shift. The magnitude of the shift was then
522 calculated using the 'spDists' function associated with R package 'sp'⁵⁵, which calculates true
523 Euclidian distance irrespective of projection geometry. Second, we converted the probabilistic
524 projections of species distributions to binary output using the procedure described above.
525 Then, for each historically occupied grid cell, we calculated the centre-to-centre distance
526 between that grid cell and the nearest climatically suitable location under present day
527 conditions, setting this distance at zero if the grid cell was suitable in both periods.
528 Calculations were performed using the spDists' function to account for projection geometry.
529 Third, for comparison, we also calculated the distance between each grid cell predicted to
530 be occupied currently and the nearest location with suitable climate historically.

531

532 **Data availability**

533 The global gridded 0.5 degree climate dataset is available from
534 <https://crudata.uea.ac.uk/cru/data/hrq/>. The UK gridded climate dataset is available from
535 <https://www.metoffice.gov.uk/research/climate/maps-and-data/data/haduk-grid/datasets>.

536 Datasets required to generate the 100m resolution gridded climate dataset for the Lizard
537 Peninsula are included with R package microclima¹⁶ available from
538 <https://github.com/ilyamaclean/microclima>. Plant distribution datasets required to run the
539 models are published online³⁸. Forest cover datasets are publically available from UKCEH⁵³
540 and <https://land.copernicus.eu/pan-european/corine-land-cover>

541

542 **Code availability**

543 All data and code used for the analysis are available on request from the corresponding
544 author and are published online³⁸. The microclima¹⁶ R package is available from
545 <https://github.com/ilyamaclean/microclima>.

546

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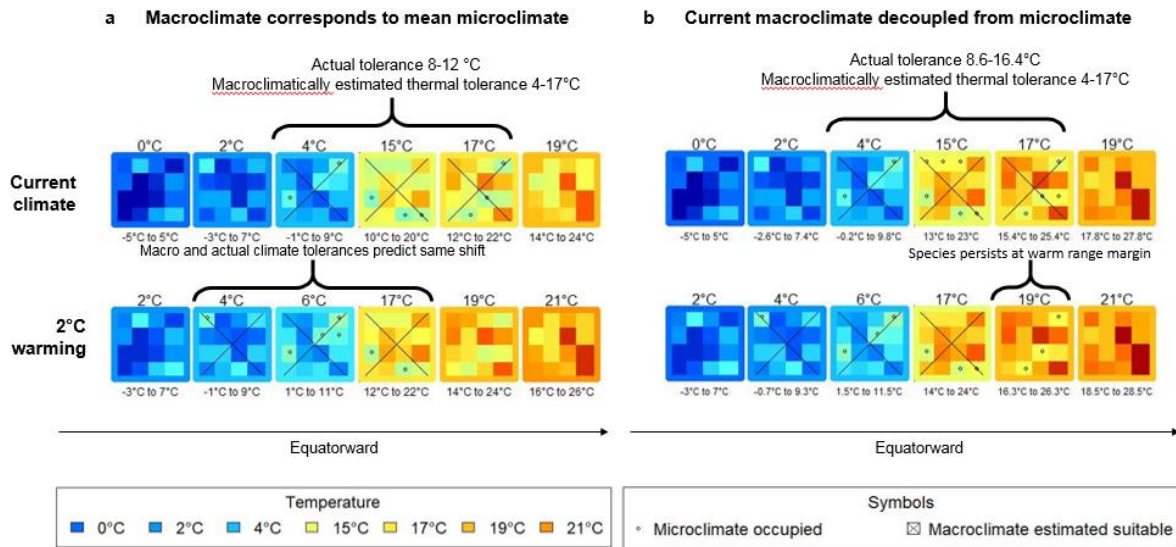
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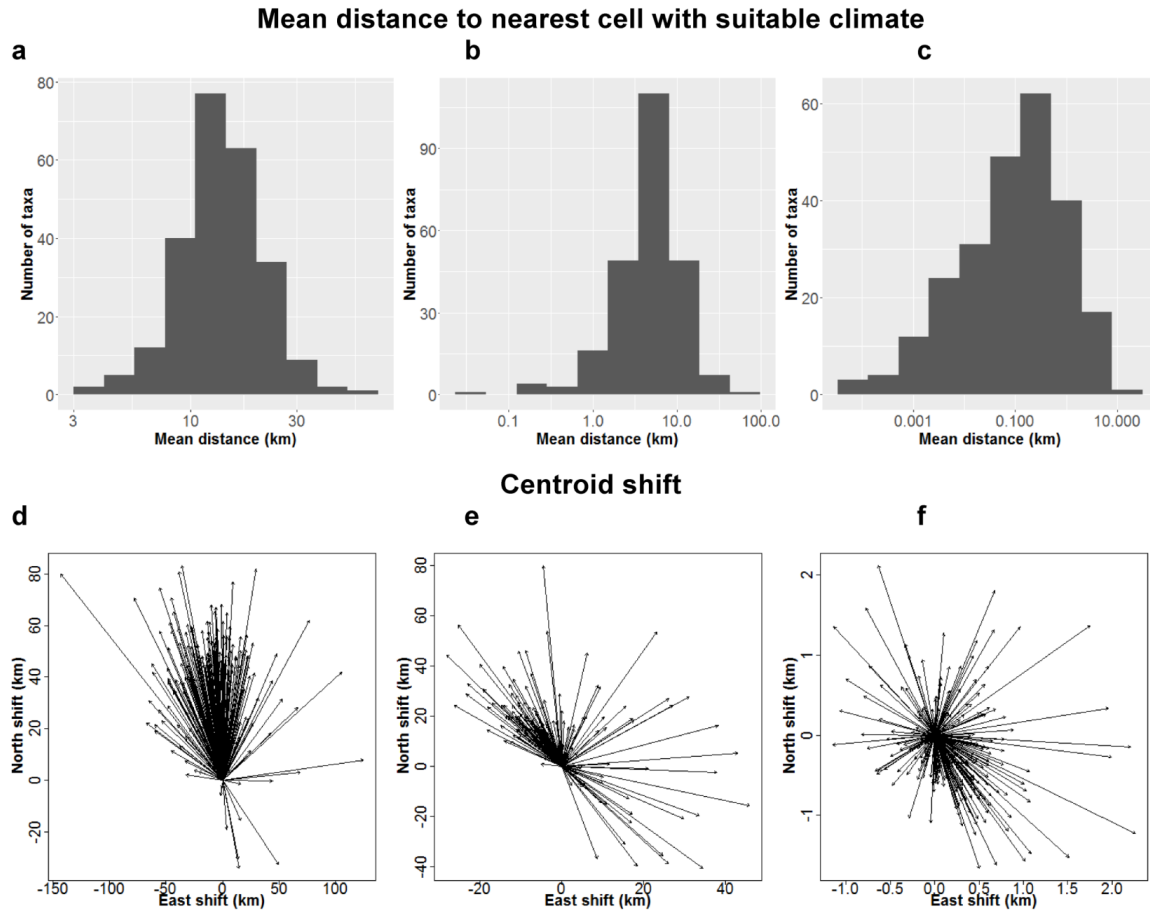
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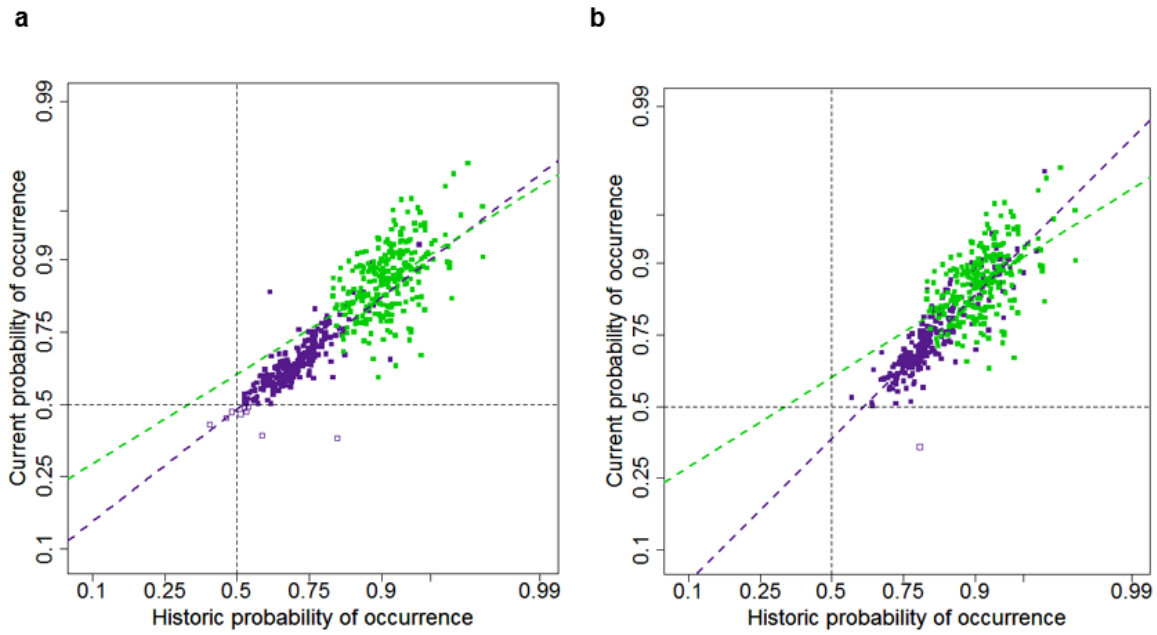
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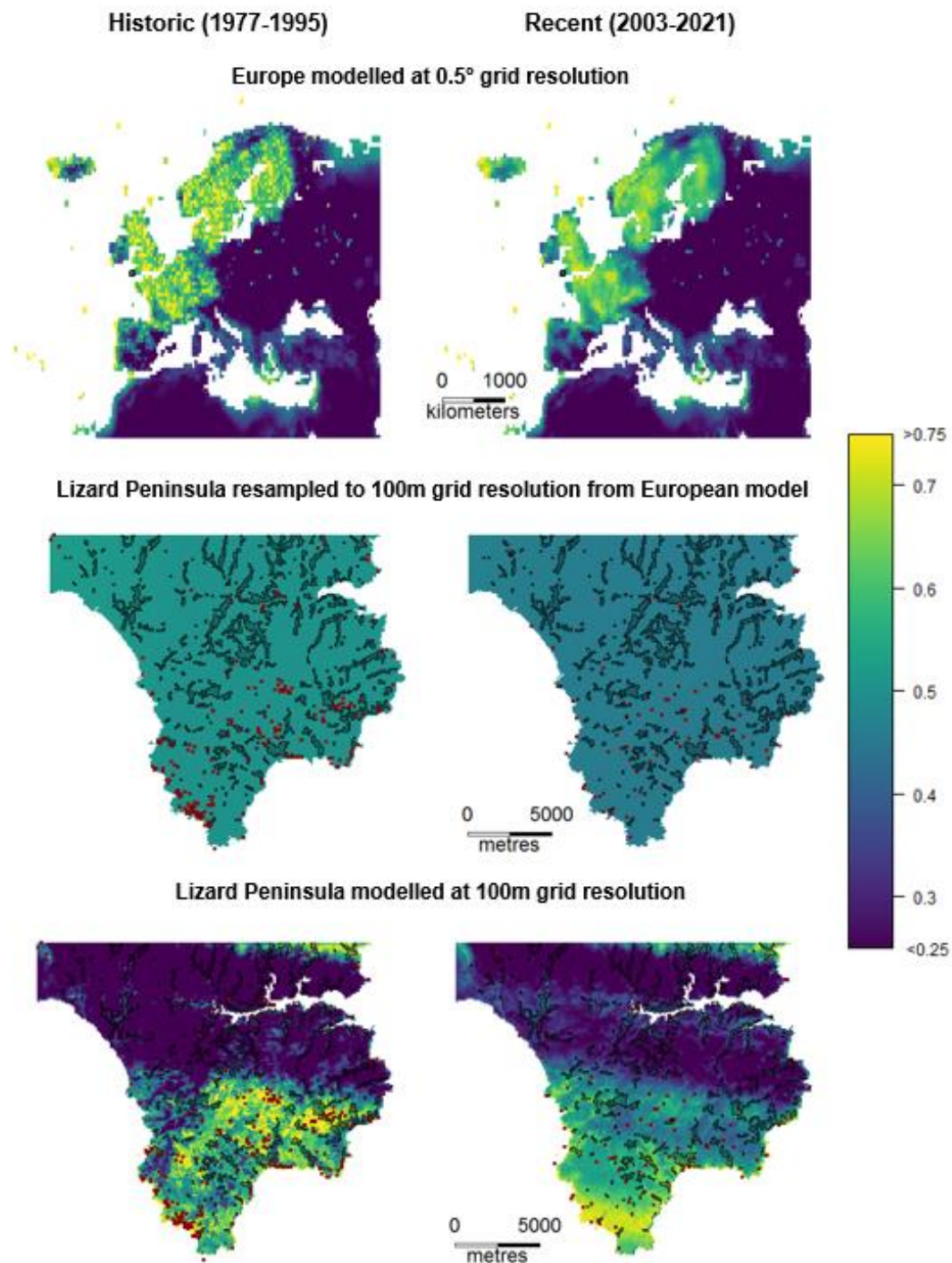
600 **Fig. 1.** Microclimate and range shifts. Latitudinal gradients in macroclimate, microclimate, species' current
 601 occupancy and predicted occupancy under projected future climate. Coarse grid cells represent macroclimate,
 602 fine grid-cells represent microclimate. The outline colour of the coarse grid-cells and the labels in large font above
 603 them give macroclimate mean annual temperature. The fill colour of the fine grid-cells indicate microclimate mean
 604 annual temperature and the text in small font below each coarse grid-cell shows the range of microclimate
 605 temperatures within each coarse grid-cell. Microclimatic temperatures within each coarse grid cell range from -5
 606 to +5°C from the macroclimate temperature. Crosses indicate which coarse grid-cells are projected to be suitable
 607 using macroclimate. Points indicate which fine grid-cells are currently occupied or will be suitable under warming,
 608 based on the species' true thermal tolerance. In (a) a hypothetical species with a true thermal tolerance range of 8
 609 to 12°C occupies all grid coarse cells with suitable microclimate (top row). Microclimate is coupled with microclimate
 610 and increases as latitude decreases towards the equator. Although macroclimate over-estimates the species'
 611 thermal tolerances, when uniform warming of 2°C is applied to all cells (bottom row), coarse- and fine resolution
 612 data yield exactly the same predicted range shift. This is because grid-cells predicted to be climatically unsuitable
 613 by macroclimate data, are also those that lose suitable microclimatic conditions. In (b) a hypothetical species with
 614 the same current geographic distribution as in (a) is shown (top row). Here, microclimate is decoupled from
 615 microclimate and increases by a greater amount than macroclimate as latitude decreases towards the equator, as
 616 might be expected as latitudinal gradients are driven by solar radiation. Here the macroclimate thermal tolerance
 617 is again estimated as 4-17°C, but the true thermal tolerance is greater than in the first example. The decoupling
 618 between macro and microclimate decreases with climate change. Consequently, coarse- and fine resolution data
 619 yield different predicted range shifts, with fine-scale data predicting that species persists at its warm range margin.



620 **Fig. 2. Range shifts predicted using macro- and microclimate data.** Top: how far taxa would need to move
 621 in order to track climatic changes. Here the mean distances between each grid cell predicted to be occupied
 622 historically (1977-1995) and the nearest location with climatically suitable conditions under recent condition
 623 (2003-2021) is predicted using **(a)** 0.5° and **(b)** 5 km grid resolution macroclimate data and **(c)** 100 m grid
 624 resolution microclimate data for each of 244 plant taxa. Bottom: here the magnitude and direction of the shift
 625 in the suitability-weighted centroid of each taxa's distribution is shown, modelled at **(d)** 0.5°, **(e)** 5 km and **(f)**
 626 100 m resolution.
 627
 628



629 **Fig. 3. Suitability predicted using macro- and microclimate.** Here the relationship between the maximum
 630 current (2003-2021) and historic (1977-1995) predicted probability of occurrence on the Lizard Peninsula is
 631 shown for all taxa, demonstrating that when microclimate (green) data are used, the relationship is shallower
 632 than when macroclimate (purple) data are used. In consequence, when modelled using microclimate data,
 633 fewer extirpations are predicted. The green and purple dashed lines are the line-of-best fit for the modelled
 634 relationship for microclimate and macroclimate respectively. In **(a)** macroclimate occurrence is derived from
 635 0.5° grid resolution models and in **(b)** from 5 km grid resolution models.
 636
 637



641 **Shifts in climatically suitable conditions predicted using macro- and microclimate data.** In (a) the historic
 642 (1977-1995) and recent (2003-2021) probability of occurrence of *Calluna vulgaris* is modelled across Europe
 643 using 0.5° grid resolution species distribution models and in (b) outputs from this model are resampled
 644 projected to the Lizard Peninsula (50.1°N, 5.2°E) showing that mean suitability of macroclimate is reduced from
 645 0.507 to 0.461 and would therefore become extirpated from the Lizard Peninsula. In (c) the historic (1977-
 646 1995) and recent (2003-2021) probability of occurrence of *C. vulgaris* is modelled across the Lizard Peninsula
 647 at 100 m grid resolution using microclimate estimates of temperature for 5 cm above ground. The species is
 648 predicted to retain suitable microclimate and therefore persist in places that broadly match those in which it
 649 currently occurs, as shown by the red squares on the maps, which are localities from which there are historic
 650 (left) and recent (right) records. The grey shaded polygons cover grid cells with >50% woodland cover, which
 651 were masked out for analyses reported upon in the main text. Note that few data from Eastern Europe were
 652 available for training the models. It is thus possible that true range of *C. vulgaris* extends further east across
 653 Europe than is implied by our models.