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1 **Habitat availability explains variation in climate-driven range shifts across**  
2 **multiple taxonomic groups**

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5

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12

13 **Range shifting is vital for species persistence, but there is little consensus on why**  
14 **individual species vary so greatly in the rates at which their ranges have shifted in**  
15 **response to recent climate warming. Here, using 40 years of distribution data for 291**  
16 **species from 13 invertebrate taxa in Britain, we show that interactions between habitat**  
17 **availability and exposure to climate change at the range margins explain up to half of**  
18 **the variation in rates of range shift. Habitat generalists expanded faster than more**  
19 **specialised species, but this intrinsic trait explains less of the variation in range shifts**  
20 **than habitat availability, which additionally depends on extrinsic factors that may be**  
21 **rare or widespread at the range margin. Similarly, while climate change likely underlies**  
22 **polewards expansions, we find that more of the between-species variation is explained**  
23 **by differences in habitat availability than by changes in climatic suitability. A model**  
24 **that includes both habitat and climate, and their statistical interaction, explains the**  
25 **most variation in range shifts. We conclude that climate-change vulnerability**

26 **assessments should focus as much on future habitat availability as on climate sensitivity**  
27 **and exposure, with the expectation that habitat restoration and protection will**  
28 **substantially improve species' abilities to respond to uncertain future climates.**

29

## 30 **Introduction**

31 Many species are shifting their distributions polewards and to higher elevations in response to  
32 climate warming<sup>1-3</sup>, but there is extremely large variation in the rates at which the range  
33 boundaries of individual species are moving<sup>4-8</sup>. This variation could arise from differences in  
34 climate sensitivity, resource requirements, reproductive rates, phenotypic plasticity, dispersal  
35 ability or biotic interactions<sup>9-15</sup>. Meta-analyses show that species' traits related to habitat  
36 specialisation are the most consistent predictors of variation in range shift<sup>5,7</sup>. However, no  
37 combination of intrinsic traits can explain a large proportion of the variation across multiple  
38 taxonomic groups – likely due to trait interactions with extrinsic factors in range-margin  
39 landscapes<sup>5</sup>. For example, the role of habitat specialisation in facilitating or inhibiting range  
40 shifts is contingent on whether a species is specialised on habitats that are common or rare at  
41 the range margin, and on the abundance of required resources within those habitat classes.  
42 Given that landscape conditions vary, both geographically and from the perspectives of  
43 species with different resource requirements, the extent to which habitat associations underlie  
44 the observed variation in recent range shifts, relative to species- and group-level differences  
45 in climate sensitivity and exposure, remains unknown.

46

47 The 'habitat' of any species depends on many interacting factors, including physical aspects  
48 of the environment (such as geology), the nature of the vegetation (e.g., influencing  
49 microclimates), directly used resources (including host-plant densities for herbivorous  
50 insects), and sufficient capacity to escape from predators, diseases and other natural enemies.

51 Thus, the capacity of a species to utilise any particular land cover (a.k.a. ecosystem or  
52 vegetation type) could be limited by multiple factors, and different limitations may occur in  
53 different vegetation types, and in different locations within a given type. Nonetheless, it  
54 remains useful to compare the habitat breadth (specialisation to generalisation) of a set of  
55 species across a range of recognised vegetation types, and thus compare habitat availability at  
56 species' range margins with observed rates of range shift. This approach allows a wide range  
57 of species to be considered, particularly in Britain which has some of the largest datasets of  
58 species occurrence records in the world.

59

60 Here, using 25 million hectare-resolution occurrence records for invertebrate species in  
61 mainland Britain, we show that habitat-climate interactions in species' range margins explain  
62 up to half of the observed variation in rates of range shift across 291 species in 13 taxonomic  
63 groups (aquatic bugs, bees, butterflies, dragonflies and damselflies, grasshoppers and allies,  
64 ground beetles, hoverflies, macromoths, non-marine molluscs, shieldbugs and allies,  
65 soldierflies and allies, spiders, and wasps; Table S1).

66

## 67 **Results**

### 68 **Range shifts**

69 Each species considered here reaches its northern (poleward) range margin in Britain and  
70 might, therefore, be expected to expand northward during a period of sustained regional  
71 warming. We measured range shifts (latitudinal changes in the ten-northernmost occupied 10  
72 km × 10 km grid squares) between 1976-1990 and 2001-2015, during which time the mean  
73 annual temperature of the study region warmed by 0.8 °C (Fig. S1). The mean observed  
74 range shift was 51 km northwards at a rate of 2 km y<sup>-1</sup> (95% CI: [1.4, 3.8]). This is similar to  
75 rates of range shift reported previously for British fauna<sup>16,17</sup>, and is similar to or faster than

76 rates reported globally<sup>1,16</sup>. We found considerable variation among species (Fig. 1 and Table  
77 S2), with nearly all of this variation occurring within, rather than among, taxonomic groups  
78 ( $R^2 = 2\%$  in a random intercept model of range shift vs. group). Thus, major trait differences  
79 among groups cannot be responsible for the large variation in range shifts. In contrast,  
80 individualistic attributes of species and/or location-specific constraints, such as habitat, could  
81 still make strong contributions.

82

### 83 **Habitat associations**

84 For each of the 291 species we quantified habitat availability in their 1976-1990 range-  
85 margin landscapes, and a related measure of habitat specialisation<sup>18</sup> – defined as the  
86 coefficient of variation (SD/mean) in the probability of occurrence across 18 satellite-derived  
87 vegetation or habitat classes<sup>19</sup> (mapped at 1-ha resolution). While habitat specialisation and  
88 habitat availability are clearly related to one another, they are not interchangeable (Fig. 2). As  
89 for range shifts, variation in habitat specialisation and habitat availability are mainly features  
90 of differences between individual species, rather than between taxonomic groups (Fig. 1 and  
91 Tables S3-S5).

92

93 Habitat availability ranged from 0.5% of the range-margin landscape for the Sand Dart moth  
94 *Agrotis ripae* (restricted to coastal strandlines) to 57% for the Gatekeeper butterfly *Pyronia*  
95 *tithonus*. In a linear mixed-effects model, the marginal effect of habitat availability ( $R^2_m$ ,  
96 which controls for all other covariates in the model) explains 13% of the observed variation  
97 in species' range shifts, with an additional 8% conditional on group-level intercepts ( $R^2_c =$   
98 21%; Fig. 3a). When data are restricted to the most reliably-recorded taxonomic groups ( $n =$   
99 49 species in four groups: butterflies, dragonflies and damselflies, grasshoppers and allies,  
100 and hoverflies) the marginal  $R^2$  increases to 22%, with no effect of group (Table S6).

101

102 Habitat specialisation, independent of landscape context, explains less of the variation. Levels  
103 of specialisation ranged from 0.3 for *P. tithonus* butterfly (habitat generalist) to 1.9 for the  
104 Bog Bush Cricket *Metrioptera brachyptera* (a wetland specialist). Relatively generalist  
105 species expanded polewards faster than more specialised species (Satterthwaite's t-test:  $P =$   
106  $0.0011$ ,  $n = 291$  species), explaining  $R^2_m = 4\%$  and  $R^2_c = 6\%$  of the observed variation ( $R^2_m =$   
107  $4\%$  and  $R^2_c = 11\%$  for the most reliably-recorded groups). Thus, regardless of group-level  
108 differences in recording intensity, accounting for the differential expression of species'  
109 habitat associations in different landscapes (i.e., comparing habitat availability vs.  
110 specialisation *per se* as predictor variables) substantially increases the variation in range shift  
111 that can be explained (Table S6).

112

### 113 **Interaction with climate**

114 Some of the remaining variation between species may be due to species-specific sensitivities  
115 to different elements of the climate, and hence their exposure to climate change. In our  
116 calculations of habitat associations, we controlled for spatial differences in climate using  
117 annual 1-ha resolution maps of minimum temperature, accumulated warmth (degree-days  
118 above 5 °C), and moisture balance (ratio of rainfall to potential evapotranspiration)<sup>20,21</sup>.  
119 Hence, we defined exposure to climate change as the logged ratio of change in the climatic  
120 suitability of species' range-margin landscapes, given the change in the average climate  
121 between 1976-1990 and 2001-2015 for these three climate variables.

122

123 We found that while exposure to climate change is positively associated with rates of range  
124 shift (Satterthwaite's t-test:  $P = 0.00048$ ,  $n = 291$  species), this explains less variation than  
125 habitat availability ( $R^2_m = 4\%$  and  $R^2_c = 4\%$ , increasing to  $R^2_m = 16\%$  and  $R^2_c = 19\%$  for the

126 most reliably-recorded groups; Table S6). We found support for models including both  
127 habitat availability and exposure to climate change ( $\Delta\text{cAIC} = 2$  compared with habitat-only  
128 model<sup>122</sup>) and for their statistical interaction, especially for the most reliably-recorded groups  
129 ( $\Delta\text{cAIC} = 14$ ). Thus, species exposed to the greatest increases in climatic suitability at their  
130 range margins have expanded polewards fastest, but only to the extent that habitat was  
131 available ( $R^2_{\text{m}} = 44\%$  with no effect of group; Satterthwaite's t-test on interaction term:  $P =$   
132  $0.00069$ ,  $n = 49$  species; Fig. 3b and Table S6). Ranking groups by the geographic coverage  
133 of biological recording across both time periods, we found that the slope of the interaction  
134 term (and variation explained by the model) increases predictably with recording intensity  
135 (Pearson correlation coefficient,  $r = 0.96$ ). Extrapolating to assume universal geographic  
136 coverage of recording for all study taxa implies that habitat availability and its interaction  
137 with climate could explain over half of the observed variation in species' range shifts (Fig. 4).

138

## 139 **Discussion**

140 Our analysis confirms that range-margin dynamics vary greatly among species, and finds that  
141 up to a quarter of this variation (depending on recording effort) can be explained  
142 independently of species-level differences in exposure to climate change, by the interplay  
143 between species' habitat associations and the landscapes they encounter during range  
144 expansion. This is likely to be a minimum estimate of the effect of habitat, given that  
145 satellite-derived habitat classes do not provide a full species-eye view of environmental  
146 suitability (including available resources), land cover may change over time, and  
147 evolutionary changes in resource use can take place during range expansion<sup>20,23–28</sup>.

148

149 Around half of the variation in range shifts can be explained when also accounting for  
150 species' differential exposure to climate change (controlling for recording effort and

151 including habitat-climate interactions). On their own, species-level differences in climate  
152 sensitivity and exposure explain comparatively little of the variation in range shifts, which is  
153 perhaps surprising given the likely overall role of climate change in driving mean polewards  
154 expansions. The interaction with habitat availability, however, suggests strong climate  
155 forcing masked by habitat constraints. For example, the Emperor dragonfly *Anax imperator*  
156 has expanded polewards at 10 km y<sup>-1</sup> in response to a 43% improvement in climatic  
157 suitability, facilitated by ample range-margin habitat (22% of the landscape); conversely, the  
158 Scarce Chaser dragonfly *Libellula fulva* has been unable to respond quickly (40 m y<sup>-1</sup>) across  
159 a landscape with 4% habitat availability despite a similar improvement in range-margin  
160 climate (Table S7). The strength of the habitat-climate interaction term increases log-linearly  
161 with the quality of the species data, suggesting that shallower interaction slopes among less  
162 well-recorded taxa are a matter of reduced information rather than a reduction in actual  
163 importance.

164

165 The habitat-climate interaction emerges from multiple underlying interactions between the  
166 physical environment in each habitat class, the biological interactions found within it  
167 (including with resources and natural enemies), and microclimatic conditions generated by  
168 interactions between the vegetation and broader-scale climate<sup>29,30</sup>. More localised differences  
169 within each habitat class will also arise because of these multiple interactions, affecting  
170 spatial and temporal patterns of population growth rate (affecting the likelihood of population  
171 establishment), densities (affecting propagule numbers) and individual behavioural responses  
172 (affecting dispersal rates)<sup>31,32</sup>. Here, to include as many species and landscapes as possible,  
173 we did not attempt to isolate any particular mechanism of habitat association or climate  
174 interaction: we took a resource-based view of habitat<sup>33</sup>, recognising that a species occupies  
175 particular habitat classes because certain resources (e.g., host plants, prey, mutualists),



176 structural elements (e.g., that enable spider webs to be built), or micro-environments (e.g.,  
177 sheltered microclimates) are present somewhere within that class, and/or because negative  
178 influences (e.g., natural enemies, disruptive land management) are absent. For example,  
179 hedgerow species can be positively associated with an ‘arable’ habitat class (albeit with low  
180 habitat availability), which is a true reflection of where many of these species live, given that  
181 field boundaries are commonly demarcated by hedgerows, and that such linear features are  
182 nested within the 20-30 m grain size of satellite imagery<sup>34</sup>. Thus, the full habitat surface  
183 available to any species is finer-grained than depicted here and would likely explain an even  
184 higher percentage of the variation among species.

185

186 Our findings demonstrate the ubiquitous constraint that habitat has already imposed on  
187 climate-driven range shifts across multiple taxonomic groups. Given high uncertainty in  
188 future levels of climate warming, combined with even greater uncertainty around the impact  
189 of warming on biologically-relevant weather patterns<sup>21,35</sup>, the fact that habitat alone explains  
190 a large proportion of the variation in species’ responses is important for planning and  
191 adaptation. Global repositories of species’ distribution data and remotely-sensed habitat  
192 information make discerning habitat associations and range-margin conditions achievable for  
193 millions of species. Predictions of climate-change impact, whether based on species’ traits or  
194 their climate exposure<sup>21</sup> should, wherever possible, include this information, to better foresee  
195 and ameliorate landscape resistance to species’ movements under climate change.

196

## 197 **Methods**

### 198 **Study region**

199 The study region encompassed 2566 Ordnance Survey 10 km × 10 km grid squares (hectads)  
200 covering the British mainland plus any near-shore islands connected to the mainland by the

201 contiguous spread of hectads. During the first recording period (1976-1990), the mean annual  
202 temperature was 8.5 °C, increasing to 9.3 °C during the second recording period (2001-2015)  
203 <sup>36</sup>. The level of warming was therefore 0.8 °C (0.03 °C y<sup>-1</sup>) across the 25-year interval  
204 between the midpoints of the two recording periods. Given the latitudinal gradient in mean  
205 annual temperature, this equates to a 257-293 km northward shift in isotherms, depending on  
206 latitude (Fig. S1). At the median 1976-1990 range margin for our study species, the  
207 northward shift in isotherms was 281 km (11.2 km y<sup>-1</sup>).

208

### 209 **Species records**

210 We considered all animal groups represented in the UK Biological Records Centre (BRC,  
211 [www.brc.ac.uk](http://www.brc.ac.uk)) and included any group that contained at least five species meeting our  
212 inclusion criteria (see sections below). We identified 13 taxonomic groups, all invertebrates,  
213 with sufficient data for inclusion (Table S1), including carnivores, herbivores and omnivores,  
214 aquatic (freshwater) and terrestrial taxa, groups that disperse in the soil, by walking, by  
215 ballooning and by active flight, and spanning orders of magnitude in body mass.

216

217 Each group was covered by a formal recording scheme (Table S1). The majority of species  
218 records were collected by citizen scientist recorders, before being collated and cleaned by  
219 experts in the group/region to filter out possible errors. We retained the taxonomic  
220 distinctions and groupings used by these recording schemes (e.g., butterflies and macromoths  
221 were treated as separate groups, whereas dragonflies and damselflies were aggregated).  
222 Therefore, ‘group effects’ may reflect differences in the recording schemes as well as the  
223 effects of taxonomic group *per se*.

224

225 Each biological record represents a unique location × date observation of species presence.  
226 We removed records with ambiguous taxonomy (*sensu lato*, *sensu auct*, naming multiple  
227 species or identified only to genus). Species listed with a sub-species trinomial, with the label  
228 *sensu stricto*, with variants or different morphs were aggregated at the species level. When  
229 analysing range shifts, we used all records with at least hectad-level spatial accuracy that  
230 could be unambiguously assigned to one of the two recording periods (1976-1990 and 2001-  
231 2015). For habitat and climate associations, we used day-specific records accurate to 1-ha  
232 resolution across the period 1976-2015 (for the 291 species included in the final analysis,  
233 74% of records had this level of spatial and temporal precision, ranging from 55% in the first  
234 recording period to 80% in the second recording period).

235

#### 236 **Criteria for species inclusion**

237 We selected non-migratory species that reach their northern (cool) range boundaries in  
238 southern/lowland Britain. We defined these species as having 90% of their 1976-1990  
239 distribution in the warmest 50% of the study region<sup>36</sup> (Fig. S1), with none of these records  
240 within 100 km of the north coast. Since these species have historically been concentrated in  
241 the warmer half of Britain, it is reasonable to postulate that they might be favoured by climate  
242 warming, and that their distributions would be predicted to expand (generally polewards). As  
243 non-migrants, the range extensions we document represent the establishment of new  
244 populations over multiple generations.

245

246 We excluded species classified as non-native, alien-native hybrid, unknown origin, and those  
247 that are dependent on non-native species, as defined by the BRC and the GB Non-native  
248 Species Information Portal<sup>37</sup>. We also excluded vagrants and species thought to be extinct

249 from the study region, including species that have been reintroduced following extinction  
250 (e.g., Large Blue butterfly *Maculinea arion*).

251

252 This resulted in an eligible species set of 1570 species in 28 groups. Of these, 421 species had  
253 sufficient data to calculate range shifts, of which 305 (17 groups) also had sufficient data to  
254 calculate habitat associations (criteria detailed below). Excluding groups with fewer than five  
255 species resulted in a final dataset of 291 species in 13 groups.

256

### 257 **Range-shift calculations**

258 To calculate range shifts, we first controlled for changes in recorder effort over time (1976-  
259 1990 to 2001-2015). We restricted distribution data to ‘well-recorded’ hectads, for which at  
260 least 10% of the regional species pool for a group was recorded present in both recording  
261 periods<sup>38</sup> (Fig. S2). For each group × hectad, we defined the regional species pool as the total  
262 number of species recorded in the nearest 100 hectads<sup>17</sup>, using all species in the database for  
263 a given taxonomic group (i.e., regardless of the above inclusion criteria).

264

265 For all species occupying at least 20 such hectads in both recording periods, we calculated  
266 northern (cool) range margins as the mean latitude of the ten-northernmost occupied hectads.  
267 We checked that species had sufficient area to expand or retreat from their 1976-1990 range  
268 margins. Hence, we excluded any species with fewer than ten recorded (as above) hectads  
269 within 100 km to the north of the range margin, and ten such hectads within 100 km to the  
270 south of the range margin<sup>17</sup>. For the remaining species, we defined range shifts as the  
271 latitudinal change (km) in range margins between 1976-1990 and 2001-2015. We converted  
272 latitudinal changes to annual rates (km y<sup>-1</sup>) by sampling random dates (10,000 times) from  
273 within each of the two 15-year recording periods, dividing latitudinal shifts by each sampled

274 interval, and recording the median rate for each species. When calculating summary rates of  
275 range shift across multiple species (e.g., Fig. 1 and Table S2), we did this separately for each  
276 sampled time interval and report the 95% confidence interval around the sample median.

277

### 278 **Habitat classification**

279 To identify habitat classes, we used a 25 m × 25 m land-cover map for Britain (LCM2007).  
280 This map was created by the NERC Centre for Ecology and Hydrology<sup>19</sup>, using combined  
281 summer and winter satellite data (Landsat-TM5, IRS-LISS3, SPOT-4 and SPOT-5 sensors,  
282 pixel size of 20-30 m) enhanced with cartographical information (e.g., Ordnance Survey data,  
283 soil types, agricultural census boundaries and urban extents). The classification was trained  
284 and validated using a large network of habitat surveys and ground reference points, producing  
285 an overall accuracy of 83%. Out of 23 habitat classes identified in LCM2007, we discarded  
286 one (saltwater), retained 14 as originally mapped, and created four aggregate classes from the  
287 remaining eight: ‘heather’ and ‘heather grassland’ became ‘dwarf shrub heath’; ‘supra-littoral  
288 rock’ and ‘littoral rock’ became ‘coastal rock’; ‘supra-littoral sediment’ and ‘littoral  
289 sediment’ became ‘coastal sediment’; ‘suburban’ and ‘urban’ became ‘built-up and gardens’.

290

### 291 **Climate estimates**

292 We estimated climatic conditions corresponding to each 1-ha species record, and the wider  
293 range-margin landscape, by spatially downscaling 5 km × 5 km resolution UKCP09 climate  
294 grids provided by the UK Met Office<sup>36</sup>. For each month of the study period (1976-2015), we  
295 used universal kriging with linear dependence on elevation to spatially interpolate mean daily  
296 minimum ( $T_{\text{Min}}$ ) and mean daily maximum ( $T_{\text{Max}}$ ) air temperatures to 1-ha resolution (Fig.  
297 S3). Elevation data were from the Ordnance Survey Terrain 50 product, resampled to the 1-ha  
298 grid. For each month and climate variable, we constructed spherical and exponential

299 variograms with distance cut-offs of 100 km and retained whichever had the lowest sum of  
300 squared errors. Kriging was implemented using the nearest 30 points. Using the same  
301 procedure, but with no dependence on elevation, we kriged UKCP09 monthly rainfall and  
302 sunshine-hours grids. Sunshine hours were then converted to sunshine fraction (dividing by  
303 day length) to estimate the proportion of the day was typically cloud-free in a given month.

304

305 Using sunshine fraction and information on topographic position, we adjusted maximum  
306 temperatures for solar radiation. First, we used the Solar Area Radiation tool in ESRI  
307 ArcMap to calculate solar radiation at 1-ha resolution, once assuming a 'flat' surface ( $SR_{Flat}$ )  
308 and then again accounting for the influence of slope, aspect and hill shading ( $SR_{Topo}$ ). In each  
309 case, sky conditions were weighted linearly towards clear skies (transmissivity = 0.7, diffuse  
310 fraction = 0.2) or overcast conditions (transmissivity = 0.2, diffuse fraction = 0.7) depending  
311 on the sunshine fraction for the corresponding month. We then used the ratio of  $SR_{Topo}$  and  
312  $SR_{Flat}$  to scale each grid cell's diurnal temperature range<sup>39</sup>, as follows:

$$313 \quad T_{MaxSR} = T_{Min} + SR_{Topo}/SR_{Flat} \times (T_{Max} - T_{Min}).$$

314 Mean daily temperatures were calculated as the mean of daily minima and daily maxima.

315 Finally, we derived three biologically-relevant annual climate variables<sup>21</sup>: minimum winter  
316 temperature, degree-days above 5 °C, and the ratio of annual rainfall to potential

317 evapotranspiration<sup>40</sup>. We defined annual variables over 12-month periods beginning 1

318 September, because this represents a more biologically-relevant annual cycle in Britain than a  
319 calendar year (which begins part-way through winter)<sup>35</sup>.

320

### 321 **Habitat and climate associations**

322 We identified habitat and climate associations using quasibinomial regression of species  
323 presence or absence overlaid on the 18 habitat classes (categorical predictor) and the three

324 annual climate variables (continuous predictors)<sup>20</sup>. The regression equation for each species  
325 was used to estimate its probability of occurrence in each habitat class, under the assumption  
326 of equal availability of all habitat classes (i.e., as close as is possible to a ‘species  
327 characteristic’) and with climate fixed at mean (centred) values. We defined levels of habitat  
328 specialisation to be the coefficient of variation across these 18 probabilities<sup>18</sup>, producing a  
329 species’ specialisation score which, for our dataset, ranged from 0.3 (generalist) to 1.9  
330 (specialist). Results are summarised by taxonomic group in Table S3 and reported for  
331 individual species in Table S7.

332

333 Given the finer grain of the land-cover map (25 m × 25 m) compared with the species data (1  
334 ha), some species records could potentially be associated with multiple habitat classes. In  
335 these cases, we assigned the majority habitat class for the 1-ha pixel, and included weights to  
336 indicate the proportion of the pixel covered by this habitat<sup>41</sup>. Climate values were specific to  
337 the year of a species observation, except where a species was observed in the same 1-ha pixel  
338 in multiple years, in which cases we assigned the mean climate values across those years.

339

340 We otherwise took all recorded presences to be ‘true’ for the purposes of modelling and  
341 included in the final analysis all species with presence records in at least 200 distinct 1-ha  
342 pixels (approximately 20 presence pixels for each parameter estimated by the model; mean  
343 records [distinct pixels] per species = 8,167 [2,238], median = 1,390 [694], range = 260-  
344 343,040 [201-104,960]). Inferring absence data from presence-only datasets is inherently  
345 more difficult. To minimise the number of false absences, we applied the following controls.  
346 First, we only included as potential absences those pixels that had been visited by recorders  
347 of the same recording scheme (as deduced from records of other species within the same  
348 recording scheme), within 50-km of a presence observation for the target species, and

349 excluding landscapes occupied during only one recording period. We did this to account for,  
350 respectively, lack of visitation by appropriate recorders, historical barriers to dispersal, and  
351 changes in land cover.

352

353 Second, we filtered absences according to time of year, given their location, for example to  
354 avoid treating late summer data as absences if the target species' flight period is in spring.  
355 We did this by fitting smooth phenology curves to the frequencies of record dates (days of the  
356 year) for the target species. To account for spatial variations in phenology, we restricted these  
357 records to within 50 km of a particular absence site. Potential absences with record dates in  
358 the tails (lower or upper 10% area under the curve) of these location- and species-specific  
359 phenology curves were excluded. In the few cases where smoothing splines could not be  
360 constructed, we defined the tails of the phenology curve directly from the raw dates (10<sup>th</sup> and  
361 90<sup>th</sup> percentiles, correcting for year-breaks where needed).

362

363 The remaining absences were from 1-ha pixels visited under the same recording scheme as  
364 the target species, in landscapes near where the target species had been recorded in both time  
365 periods, and within the appropriate phenological time windows. The absences still varied in  
366 reliability, however, because some qualifying pixels had only been visited only once, whereas  
367 others had been visited multiple times. Third, therefore, we weighted absence data by the  
368 probability of recording the target species if it was present, given the number times ( $t$ ) the  
369 absence pixel was visited:

370 
$$\frac{1}{n} \sum_{s=1..n} 1 - (1 - p_s)^t$$

371 That is, one minus the probability of failing to detect the species on every occasion, where the  
372  $p_s$  are probabilities of detection across  $n$  known presence sites for the target species  
373 (calculated as the number of times the species was recorded in site  $s$  divided by the number of



374 times  $s$  was visited). To account for spatial variations in abundance (and therefore  
375 detectability) we calculated  $p_s$  using data restricted to within 50 km of the absence site.

376

### 377 **Conditions at species' range margins**

378 We obtained spatial estimates of habitat availability by predicting each species' regression  
379 model back on the land-cover map, with climate fixed at mean (centred) values. Habitat  
380 availability at the range margin was defined as the mean value across all 25 m × 25 m land-  
381 cover pixels in a circular 50-km buffer around the ten-northernmost hectads (or >10 hectads  
382 when >1 hectad tied for having the 10<sup>th</sup> highest latitude) that were used to define the range  
383 margin in the first recording period (1976-1990); i.e., landscapes across which the species  
384 had potential to expand or retract over time. Habitat availability for individual species ranged  
385 from 0.5% (very little of the landscape could be colonised) to 57% of the landscape (ample  
386 opportunity for expansion; Tables S4 and S7). Habitat availability exhibited positive skew  
387 (Fig. 1; Shapiro-Wilk,  $W = 0.75$ ,  $P < 10^{-20}$ ,  $n = 291$  species) and so we  $\log_{10}$ -transformed  
388 these values to improve normality ( $W = 0.997$ ,  $P = 0.90$ ).

389

390 We defined exposure to climate change as the logged ratio of mean range-margin conditions  
391 in 1976-1990 versus 2001-2015. That is, we predicted each species' regression model back  
392 on the land-cover map twice, first with annual climate set to its mean condition for the period  
393 1976-1990, and second with climate set to its mean condition for 2001-2015. Since habitat  
394 data were constant in the model, the ratio of these predictions was >1 if climatic suitability  
395 improved over time, <1 if climatic suitability deteriorated, and =1 if there was no change in  
396 climatic suitability. We defined exposure using logged ratios so that there was symmetry  
397 about the no-change line; i.e., absolute exposure had the same magnitude when climate was  
398 improving as when it was deteriorating. Our usage of the term 'exposure' equates to change

399 in climatic suitability for a species and encompasses both sensitivity to climate and the extent  
400 to which relevant aspects of climate have changed (*cf.* IPCC terminology of exposure being  
401 independent of sensitivity<sup>21</sup>).

402

### 403 **Models of range shift**

404 We modelled species' observed range shifts as linear functions of habitat specialisation,  
405 log<sub>10</sub>-transformed habitat availability at the range margin, and exposure to climate change at  
406 the range margin. We constructed single-predictor models, as well as multivariate models  
407 where collinearity among predictors was low (Table S6): habitat specialisation and log<sub>10</sub>-  
408 habitat availability were highly correlated ( $r = -0.53$ ; Fig. 2) and so we did not include both in  
409 the same model, whereas exposure to climate change was uncorrelated with both of these  
410 predictors ( $r = -0.02$  and  $r = 0.07$ , respectively). To account for phylogenetic relatedness and  
411 methodological differences in recording between taxonomic groups (i.e., across recording  
412 schemes), we used linear mixed-effects models with taxonomic group as the random intercept  
413 term (Table S6).

414

### 415 **Sensitivity to recording level**

416 We ranked the 13 taxonomic groups by descending geographic coverage of citizen-science  
417 recording, defined by the number of hectads where there has been sufficient recording for at  
418 least 25% of the regional species richness (considering the nearest 100 hectads) to have been  
419 sampled in both recording periods (Table S1). In Fig. 1, we summarise between-species  
420 variation separately for: (1) four groups with the high intensity recording; (2) eight groups  
421 with lower intensity recording; and (3) macromoths. We plotted macromoths separately  
422 because, unlike other groups, moth recording uses attractant methods (light traps at night) so  
423 that the areas sampled – and thus habitat associations – are more uncertain.

424

425 The proportion of variation in range shift that could be explained was higher for taxonomic  
426 groups with higher recording intensity, but the signs of the relationships were consistent  
427 (Table S6), demonstrating that the patterns we report are qualitatively robust to recording  
428 intensity. In Fig. 4 we systematically varied the threshold of recording coverage, above which  
429 species are included in the habitat-climate interaction model. For example, when the  
430 recording threshold is low, many groups are eligible for inclusion; when the threshold is high,  
431 only the best-recorded groups are included. For consistency in statistical power across  
432 different levels of group inclusion, each point in Fig. 4 was generated by averaging over  
433 10,000 randomised draws of 30 species from three qualifying groups.

434

435 We conducted statistical and spatial analyses using R version 3.6.1, with packages lme4<sup>42</sup>,  
436 lmerTest<sup>43</sup>, MuMIn<sup>44</sup>, cAIC4<sup>22</sup>, doParallel<sup>45</sup>, raster<sup>46</sup> and rgeos<sup>47</sup>.

437

### 438 **Data availability**

439 The datasets that support this study are available from the following sources: species  
440 distribution data via the UK Biological Records Centre ([www.brc.ac.uk](http://www.brc.ac.uk)); land-cover data  
441 under licence via EDINA (<https://digimap.edina.ac.uk>); climate data from the UK Met Office  
442 (<https://catalogue.ceda.ac.uk/uuid/87f43af9d02e42f483351d79b3d6162a>). Downscaled  
443 climate grids and R-scripts for our analysis are archived online at [URL pending].

444

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449

450 **Author contributions**

451 PJP, SCM, GP, JKH, THO and CDT conceived the work and designed analyses. GDP and

452 RF generated databases; PJP carried out analyses; PJP, SCM and CDT drafted the paper. All

453 authors interpreted analyses and contributed to the final text.

454

455 **Competing interests**

456 The authors declare no competing interests.

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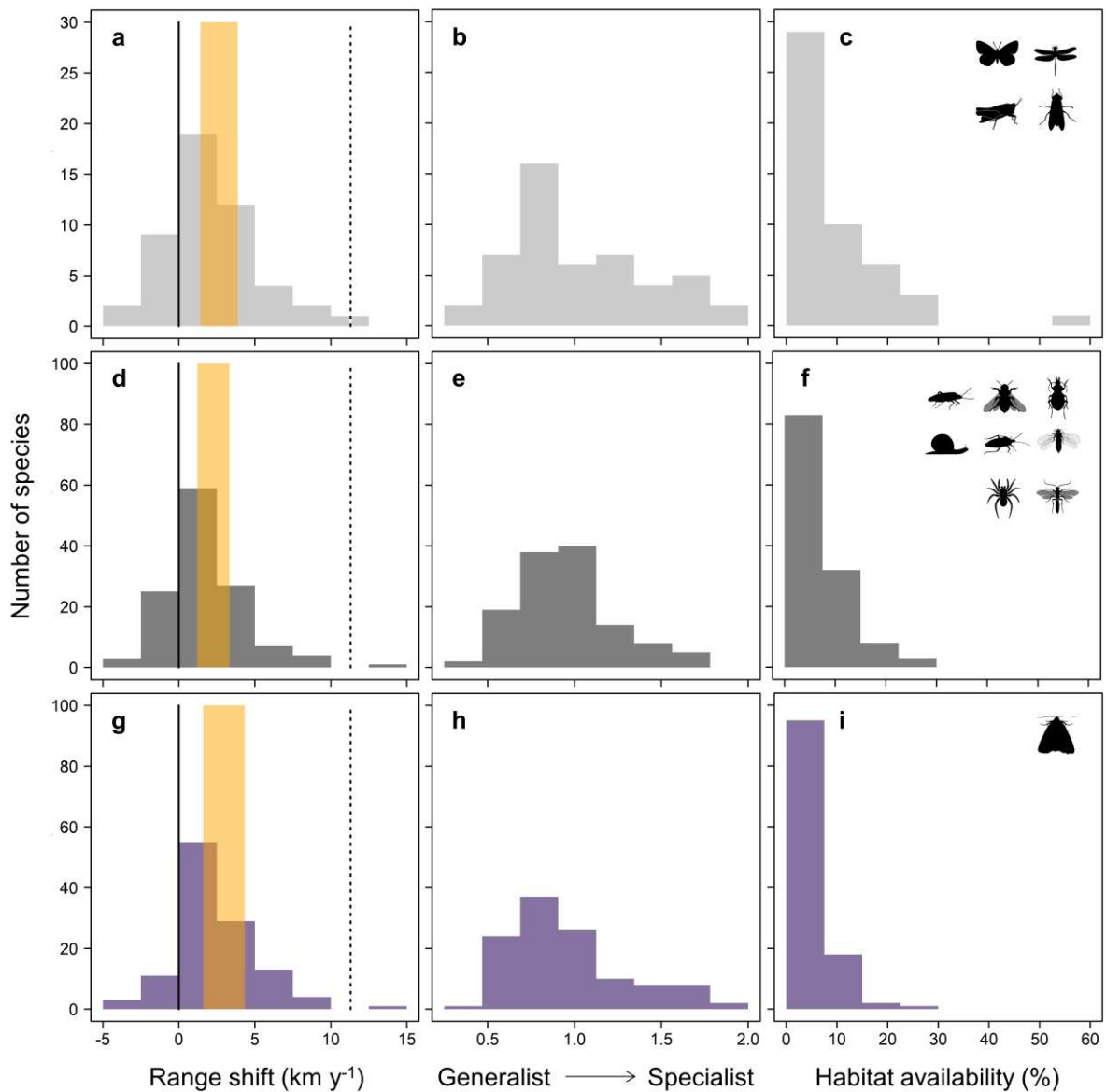
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570

571

572 **Figure 1 | Latitudinal range-margin shift, habitat specialisation, and habitat availability**

573 **in species' range margins. a-c,** Four taxonomic groups with high recording intensity

574 (butterflies, dragonflies and damselflies, grasshoppers and allies, and hoverflies; n = 49

575 species). **d-f,** Eight groups with lower recording intensity (n = 126 species). **g-i,** Macromoths

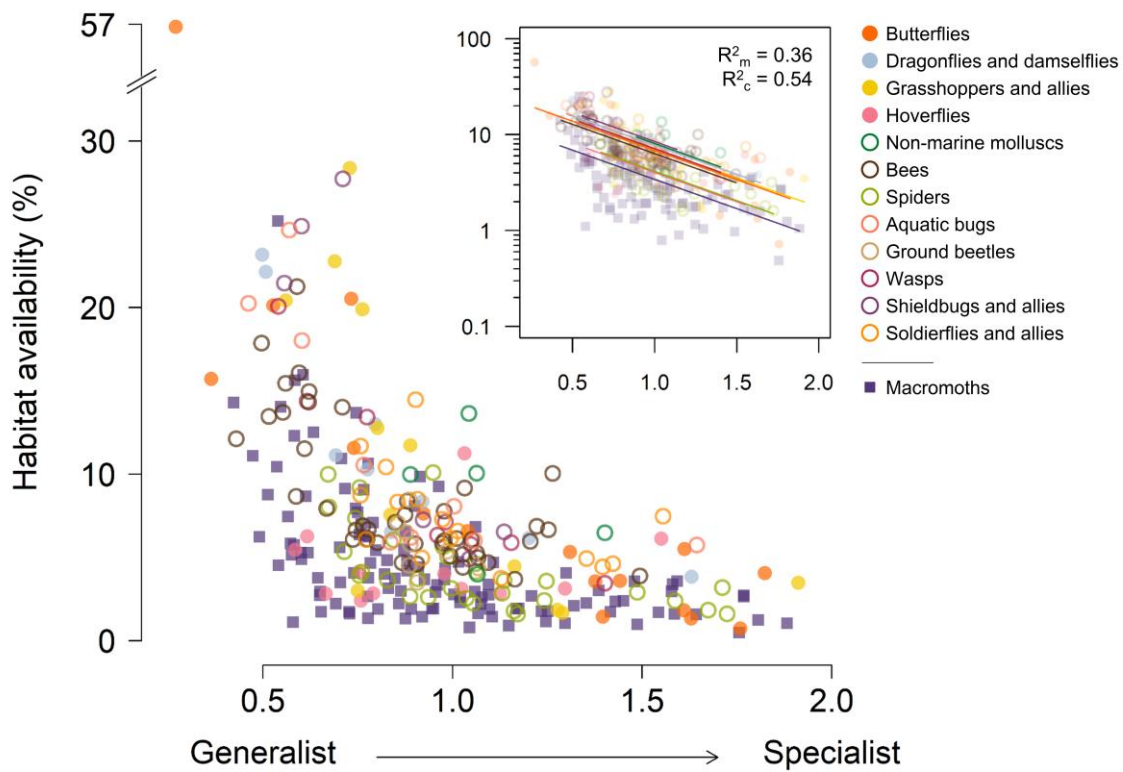
576 (different recording method, n = 116 species). In a, d and g: solid lines show zero shift,

577 orange bars show 95% CIs for mean observed shifts, and dotted lines show the shift in mean

578 annual isotherms given observed warming between the two recording periods (1976-1990

579 and 2001-2015; 11.2 km y<sup>-1</sup>, Fig. S1). Group icons are from <http://phylopic.org/>: under CC0

580 1.0 (<https://creativecommons.org/publicdomain/zero/1.0/>), except the following in which case  
581 CC BY 3.0 (<https://creativecommons.org/licenses/by/3.0/>): aquatic bugs, shieldbugs and  
582 allies (Dave Angelini); bees, wasps (Melissa Broussard); dragonflies and damselflies,  
583 hoverflies, macromoths (Gareth Monger); and ground beetles (T. Michael Keesey  
584 [vectorization], Thorsten Assmann, Jörn Buse, Claudia Drees, Ariel-Leib-Leonid Friedman,  
585 Tal Levanony, Andrea Matern, Anika Timm, and David W. Wrase [photography]).



586

587

588 **Figure 2 | Relationship between habitat specialisation and habitat availability in species'**

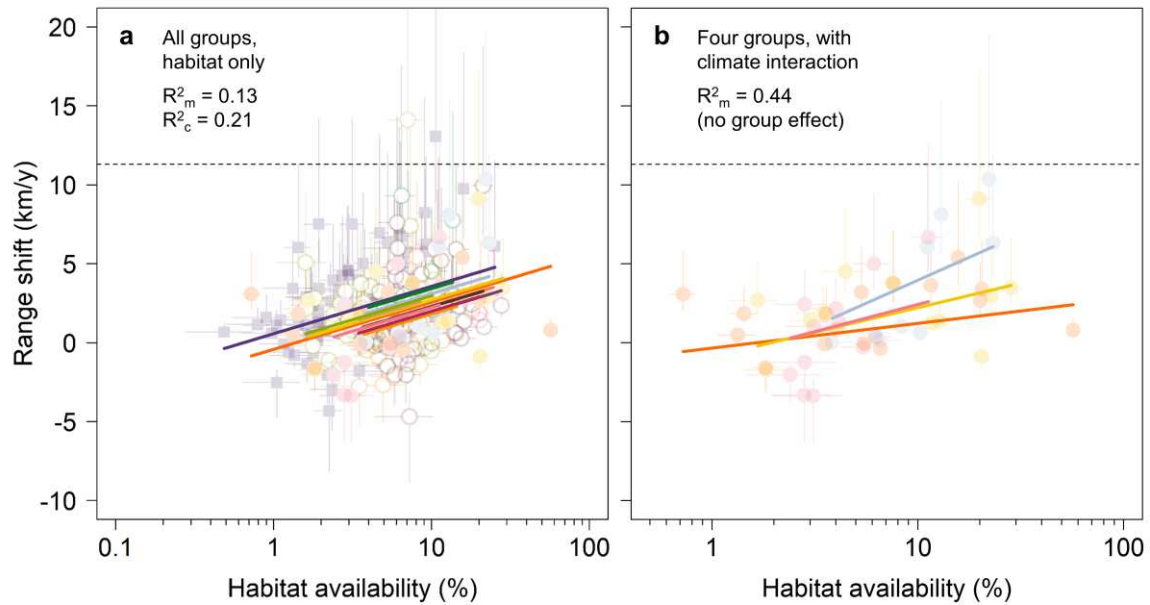
589 **range margins.** Plotted on untransformed axis and with log-linear scaling (inset, with fitted

590 lines from a random intercept model). In the colour key, taxonomic groups are listed in

591 descending order of geographic coverage of citizen-science recording: solid circles show four

592 groups with high recording intensity, open circles show eight groups with lower recording

593 intensity, squares show macromoths (different recording method).



594

595

596 **Figure 3 | Relationships between habitat availability and species' range shifts. a,**

597 Random intercept model (conditional on group), including all 291 species across 13

598 taxonomic groups. **b,** Habitat-climate interaction model, restricted to four groups with high

599 recording intensity (butterflies, dragonflies and damselflies, grasshoppers and allies, and

600 hoverflies;  $n = 49$  species). In a, coloured lines show the random effect of taxonomic group

601 on the fixed effect of  $\log_{10}$ -habitat availability in species' range margins. In b, group has no

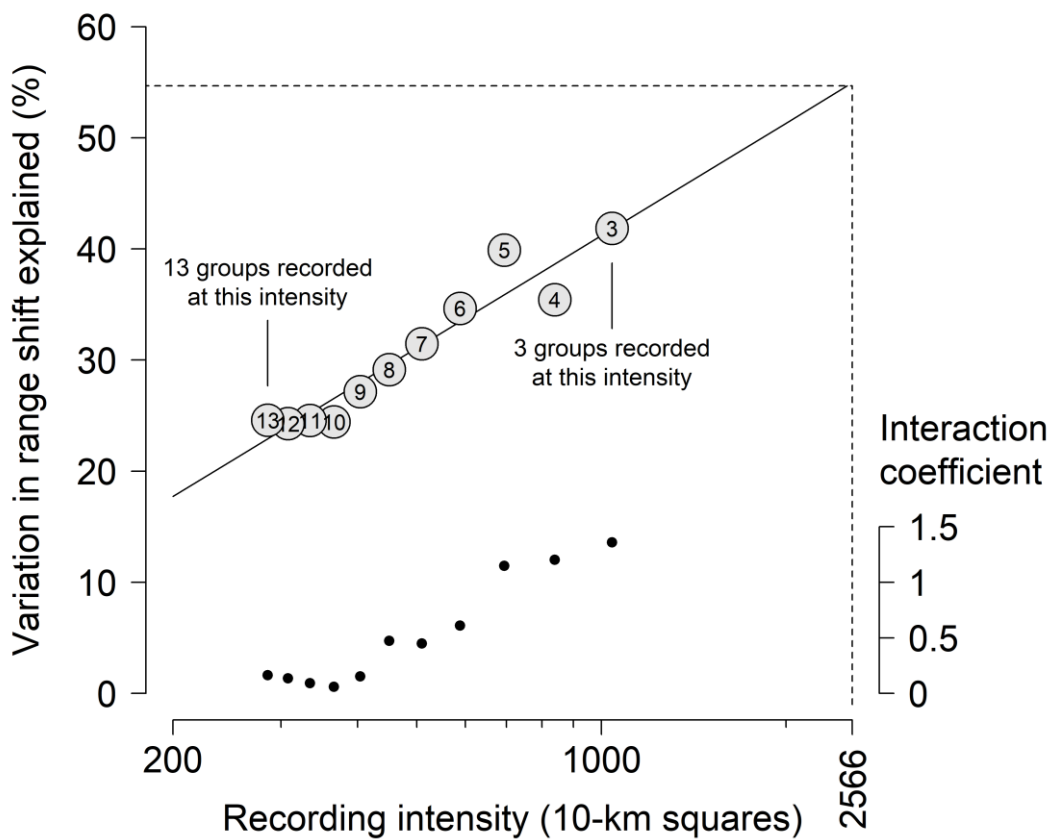
602 effect but for illustration we plot the mean exposure to climate change for species within each

603 taxonomic group. Error bars represent 95% CI around rates of range shift (given the breadth

604 of recording periods) and habitat availability (from logistic regression). Dotted lines show the

605 shift in mean annual isotherms given observed warming between the two recording periods

606 (1976-1990 and 2001-2015;  $11.2 \text{ km y}^{-1}$ , Fig. S1).



607

608

609 **Figure 4 | Relationship between recording intensity and the variation in range shift**

610 **explained by habitat availability and climate.** The fixed effects are  $\log_{10}$ -habitat

611 availability at the range margin, exposure to climate change at the range margin, and their

612 interaction. The higher the recording intensity, the steeper the interaction slope (black dots)

613 and the greater the marginal  $R^2$  of habitat and climate (grey circles), up to a theoretical

614 maximum of  $R^2_m = 55\%$  (dashed lines). Recording intensity is the number of  $10 \text{ km} \times 10 \text{ km}$

615 squares where at least 25% of the regional species richness for a taxonomic group was

616 recorded in both 1976-1990 and 2001-2015 (mean across groups, up to a maximum 2566

617 squares in Britain). The pool of groups decreases from left to right as recording intensity

618 increases (model degrees of freedom fixed by drawing 30 species from any three qualifying

619 groups, plotting mean values over 10,000 repetitions).