

1 **The relative importance of climate and habitat in determining the distributions**
2 **of species at different spatial scales: a case study with ground beetles in Great**
3 **Britain**

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16

17 **Abstract**

18

19 Experimental studies have shown that many species show preferences for different climatic
20 conditions, or may die in unsuitable conditions. Climate envelope models have been used frequently
21 in recent years to predict the presence and absence of species at large spatial scales. However, many
22 authors have postulated that the distributions of species at smaller spatial scales are determined by
23 factors such as habitat availability and biotic interactions. Climatic effects are often assumed by
24 modellers to be unimportant at fine resolutions, but few studies have actually tested this.

25

26 We sampled the distributions of 20 beetle species of the family Carabidae across three study sites by
27 pitfall trapping, and at the national scale from monitoring data. Statistical models were constructed
28 to determine which of two sets of environmental variables (temperature or broad habitat type) best
29 accounted for the observed data at the three sites and at the national (Great Britain) scale.

30

31 High-resolution temperature variables frequently produced better models (as determined by AIC)
32 than habitat features when modelling the distributions of species at a local scale, within the three
33 study sites. Conversely, habitat was always a better predictor than temperature when describing
34 species' distributions at a coarse scale within Great Britain. Northerly species were most likely to
35 occur in cool micro-sites within the study sites, whereas southerly species were most likely to occur
36 in warm micro-sites. Effects of microclimate were not limited to species at the edges of their
37 distribution, and fine-resolution temperature surfaces should therefore ideally be utilised when
38 undertaking climate-envelope modelling.

39

40 **Keywords**

41 Species distribution, spatial, temperature, climate, land cover, carabid.

42

43 **Introduction**

44

45 Climatic variables are widely used in models to predict species' distributions at relatively coarse
46 resolutions and over large spatial extents, but no consensus yet exists about the role of climate in
47 determining finer-resolution distributions approaching the scales that individuals actually
48 experience (e.g. Pearson and Dawson 2003, Elith and Leathwick 2009). This uncertainty arises, in
49 part, because there is a large difference between the spatial resolutions at which individuals
50 experience the environment and those at which distributions and climate are usually represented and
51 modelled. Most terrestrial invertebrates spend the majority of the non-dispersing phases of their
52 lives in areas of less than a square metre to a square kilometre (see Brouwers and Newton 2009 for
53 example dispersal rates). Even the most mobile species usually experience a potentially selective
54 series of local environments, rather than the “average” conditions of a much larger area. In contrast,
55 the geographic ranges of species are typically represented on distribution maps at resolutions that
56 are three to fourteen orders of magnitude coarser than this. For example, grid resolutions of 10 km x
57 10 km to 100 km x 100 km are commonly used for the production of distribution atlases (e.g. Luff
58 1998), to help quantify recent distribution changes in response to climate change (e.g. Hickling et
59 al. 2006), and for the purposes of modelling species' distributions and projecting the responses of
60 species to climate change (e.g. Huntley et al. 2007, McKenney et al. 2007). Different resolution
61 bioclimatic models give rise to quite different expectations of species' distributions and abilities to
62 survive climatic change (e.g. Randin et al. 2009). Given this mismatch, it is unclear whether coarse-
63 resolution analyses are sufficient to understand current distributions, or to project future potential
64 changes and conservation priorities.

65

66 Within a particular landscape, the background climate may be similar from place to place, and fine-
67 resolution spatial variation in the distributions of species could be determined predominantly by
68 non-climatic factors. These could include differences in vegetation cover and management (e.g.

69 Eyre et al. 2003, 2005a), or the geological substrate and soil type (e.g. Blake et al. 2003). In reality,
70 climatic and non-climatic factors are likely to combine to determine fine-resolution distributions.
71 However, the relative importance of climate and vegetation is difficult to deduce, partly because the
72 vegetation is itself often related to climate and partly because species can become restricted to
73 favoured locations or habitats in regions where the background climate is marginal (Lennon et al.
74 2002). Species may select local conditions (e.g. sparse vegetation on south-facing slopes at northern
75 range boundaries) that provide suitable microclimates for population growth (Thomas et al. 1999),
76 or they may thermoregulate, enabling species to inhabit regions far outside the geographical limits
77 that might otherwise be expected (Bryant et al. 2002). These behaviours can give rise to
78 temperature-related geographic gradients of habitat associations (e.g. Oliver et al. 2009), and
79 underlie shifts in the habitat affiliations of species following climatic warming (Thomas et al. 2001,
80 Davies et al. 2006). Hence, even when non-climatic factors appear to be the most important
81 determinants of the local distributions of species, it is difficult to evaluate whether it is the
82 microclimatic conditions that these locations provide that are important, or whether other non-
83 climatic differences are more important (Gottfried 1999, Gutiérrez Illán et al. 2010).

84

85 Assessment of the relative importance of climatic vs non-climatic factors at different spatial scales
86 requires the availability of both distributional and environmental data at equivalent resolutions.
87 However, fine-resolution temperature surfaces have yet to be combined in the same analyses as land
88 cover or habitat variables. This may in part be due to a lack of availability of fine-resolution
89 climatic data for use in local scale studies, but the recent publication of a microclimate model
90 (Bennie et al. 2008, 2010) enables us to investigate the relative importance of climatic and habitat
91 variables at a finer resolution than has previously been explored.

92

93 We utilise this microclimate model in relation to the distributions of a group of mainly predatory
94 ground beetles (Carabidae) that should not be intrinsically limited to a particular type of vegetation.

95 Habitat may still be limiting in the prey it provides and the manner in which its structure modifies
96 the microclimate experienced (Cernusca and Seeber 1981). Carabids have previously been shown to
97 have preferences for particular temperatures, both at a national scale (Eyre 2006) and within regions
98 (Martinez et al. 2009). Other important determinants of their distributions will vary depending on
99 species, but may include light levels, humidity, substrate types and possibly pH and salt levels
100 (Thiele 1977), as well as soil moisture (Gardner et al. 1997, Eyre 2006). 350 species have been
101 recorded from Britain and Ireland, with several species having Biodiversity Action Plans in Britain,
102 and many more appearing on Red Data Book lists (Luff 1998).

103

104 Here, we examine microclimatic variation and land cover type and their relationships with the
105 distributions of twenty carabid species at 25 m² spatial resolution, in three areas of the British
106 uplands (from here on local scale analyses). We compare these results with deductions based on
107 coarse-resolution (100 km² resolution) distribution models for the same species across the whole of
108 Great Britain (from here on national scale analyses). We hypothesise that climate will be the most
109 important determinant of species' distributions at the national scale, but that land cover will be
110 important at the local scale. We also hypothesise that temperature will be more important to species
111 at the edges of their range, where the background climate is likely to be marginal (e.g. Jump et al.
112 2010).

113

114 **Methods and analysis**

115

116 **Field Sampling**

117

118 Invertebrates were collected by pitfall trapping between the beginning of May and the end of
119 August 2008 at three sites: Lake Vyrnwy Royal Society for the Protection of Birds (RSPB) reserve
120 in Wales; Glen Finglas Woodland Trust reserve in Scotland; and the High Peak region in the Peak

121 District National Park in England (Fig. 1).

122

123 Lake Vyrnwy is adjacent to Snowdonia National Park ($52^{\circ} 47' 09''$ N, $03^{\circ} 30' 49''$ W), covers *ca.*
124 9,700 hectares, lies between *ca.* 350 and 620 m a.s.l. and contains several different vegetation types.
125 Trapping was undertaken in heathland dominated by *Calluna vulgaris* (heather). This habitat is
126 actively managed for wildlife using a combination of mowing, burning and grazing to maintain a
127 mosaic of heather and graminoids over a mainly peat soil base. This site is at the southern range
128 margin of many species with northerly distributions within the UK (Fig. 2).

129

130 Glen Finglas is situated within the Loch Lomond and the Trossachs National Park, ($56^{\circ} 16' 01''$ N,
131 $4^{\circ} 23' 20''$ W). The whole site covers *ca.* 4,100 hectares and lies between *ca.* 150 and 821 m a.s.l. It
132 contains several different habitats, and open areas are maintained by a combination of sheep and
133 cattle grazing. Trapping was undertaken in heathland dominated by *C. vulgaris* and upland
134 unimproved grassland.

135

136 The High Peak site is in the Peak District National Park, Derbyshire ($53^{\circ} 31' 25''$ N, $01^{\circ} 52' 50''$ W)
137 and lies between *ca.* 250 and 580 m a.s.l.. The site is partially grazed by sheep, with areas managed
138 for grouse shooting utilising a burning regime to maintain a mosaic of different age classes of *C.*
139 *vulgaris*. Trapping took place in dwarf-shrub heathland, upland unimproved grassland and on bare
140 peat.

141

142 Forty locations were sampled at Lake Vyrnwy and the Peak District, using a stratified random
143 sampling strategy based on sixteen categories defined on the basis of slope (shallow $0-10^{\circ}$, steep $>$
144 10°), aspect (North $315-45^{\circ}$, East $45-135^{\circ}$, South $135-225^{\circ}$, West $225-315^{\circ}$) and elevation (low $<$
145 475m , high $> 475\text{m}$). The sixteen categories were reduced to twelve by combining those that
146 covered a very small amount of the site. These twelve categories were equally represented, with the

147 addition of four sites in the lowest elevation areas. This strategy gave a comprehensive
148 representation of the range of microclimates present at each site. Forty-eight locations were sampled
149 at Glen Finglas, selected in the same way, the additional locations allowing better representation of
150 the more topographically diverse terrain present. Sample locations were georeferenced in the field
151 using a handheld Global Positioning System (Garmin GPS 60), and were at least 50 m apart to
152 reduce spatial autocorrelation.

153

154 At each sample location, five pitfall traps were deployed in a circle of 2 m diameter. Traps consisted
155 of two standard plastic vending cups nested together and sunk into the soil so that the rim of the
156 inner cup was flush with the soil surface. Each trap was filled to a 2.5 cm depth with ethylene
157 glycol antifreeze. Traps were covered with a terracotta coloured plastic saucer suspended 11cm
158 above the trap using galvanised wire. This served the dual purpose of limiting liquid loss by
159 evaporation and limiting flooding from rainfall. A surround of chicken wire (mesh diameter 20 mm)
160 aimed to exclude small mammals and livestock. Traps were emptied on a monthly basis, and the
161 antifreeze solution was replaced as necessary. Invertebrates from all five pitfalls at each sample
162 location were pooled then transferred to 100% ethanol for transport back to the lab. Carabids were
163 sorted from other invertebrates and identified to species. The entire season's catch for each trapping
164 location was then pooled for analysis to give a measure of the relative population density present at
165 any one location; pooling data in this way should average out the effects of sample error and of
166 extreme weather events on activity of individuals during different months of trapping (Baars 1979).

167

168 **Microclimatic Modelling**

169

170 A recently published microclimatic model (Bennie et al. 2008) was used to predict the microclimate
171 across the three sites¹. Hourly radiation, wind speed and air temperature data were obtained for the

¹ recoded from a Bash script running under the open source GIS program GRASS to a standalone C++ program.

172 meteorological stations recording radiation data that were closest to each of the study sites (Lake
173 Vyrnwy, 52° 45' 25" N, 03° 38' 45" W, Manchester Hulme Library, 53° 28' 01" N, 02° 15' 00" W
174 and Strathallan Airfield, 56° 19' 33" N, 3° 43' 44" W). Choice of meteorological stations was
175 limited by the requirement for radiation data, such that no other stations were close to the study
176 sites. Digital Elevation Models (DEMs) with 25 m² horizontal resolution and 1 m vertical accuracy
177 (from NERC's Earth Observation Data Centre, www.neodc.rl.ac.uk) for the three sites were used to
178 calculate slope and aspect values for each 5 m x 5 m cell using the "Slope" and "Aspect" functions
179 in the Spatial Analyst package in ArcMap v 9.2 (ESRI 2008). The microclimate model adjusted the
180 temperature values from the meteorological stations to take account of the elevation difference
181 between the meteorological station and each 25 m² grid cell in the landscape, as well as differences
182 in direct and indirect radiation associated with different slopes and aspects at different times of the
183 day and year (including the effect of hill-shading by the surrounding landscape). Hourly predicted
184 temperatures were generated for the top of the vegetation from the start of September 2007 until the
185 end of August 2008. For the purposes of this study, we assume that these vegetation surfaces are
186 correlated with the conditions experienced beneath the vegetation layer.

187

188 From these hourly predictions, annual mean (ANMEAN), mean over the sampling period (May to
189 August, MAMEAN), annual maximum (ANMAX) and annual minimum (ANMIN) temperatures
190 were calculated for each trapping location. These variables were selected as they should represent
191 the temperatures likely to be of importance in determining the distributions of a variety of species.
192 Some might respond to average temperatures, such that a certain number of days above a certain
193 temperature might be necessary for growth or development (Leirikh et al. 2009), and this might be
194 especially important during the breeding (sampling) season. Others might be killed by extremes of
195 temperature, such that very high maxima or very low minima in an area would preclude their
196 presence (Bayram and Luff 1993, Somero 2010). Different temperature variables have been found

197 to affect different aspects of carabid life histories (Althoff et al. 1994), and genders may also have
198 different temperature preferences (Atienza et al. 1996) due to physiological differences inherent in
199 the breeding period. The resolution corresponds to the scale at which ground beetles might
200 realistically be able to disperse to more favourable locations before suffering damage (see Brouwers
201 and Newton 2009).

202

203 **Local Scale Modelling**

204

205 Species were selected for modelling at the local scale according to the following criteria: They were
206 present at five or more sampling locations in a site, with at least ten individuals across the site, and
207 were only modelled at the sites where these criteria were met. Abundance data were transformed to
208 presence/absence data to enable meaningful comparison with the national data, as the strength and
209 direction of relationships between species distribution and temperature can be affected by the type
210 of response variable (Diez & Pulliam 2007). Presence/absence was the response variable in a
211 Generalised Linear Model (GLM) with Binomial error structure and logit link function. Predictor
212 variables were split into two sets: temperature and habitat. The temperature set comprised
213 ANMEAN, MAMEAN, ANMAX and ANMIN in °C. There were several habitat variables,
214 depending on the number of habitat types present in the site (seven in Glen Finglas, five in Lake
215 Vyrnwy and six in the Peak District). Presence or absence of each habitat type at the sampled
216 locations were considered as separate factors (extracted from the Land Cover Map 2000 dataset
217 from the Centre for Ecology and Hydrology (CEH), which is based on the dominant habitat within
218 25 x 25 m polygons). In addition, the number of land-cover categories present within a 100 m
219 diameter buffer around each point (NH) was calculated. To account for damage to traps caused by
220 grazing livestock, a trapping effort variable was included as a log-offset in all models,
221 corresponding to the proportion of the trapping effort that was lost to such damage at each location
222 (e.g. loss of two of the five pitfall traps at a given location in one month). Linear and quadratic

223 relationships were explored, and best models were built using a backwards stepwise procedure
224 using the Akaike Information Criterion (AIC) as the basis for rejection or inclusion within each set
225 of variables (temperature and habitat) in the BIOMOD package for R (Thuiller 2009). Area under
226 the receiver operating characteristic curve (AUC) was calculated using a 70/30 data split, with 70%
227 being used for training and the remaining 30% being used for testing. Residuals from the best
228 models for each species were checked for spatial autocorrelation using Moran's I in ArcGIS.

229

230 **National Scale Modelling**

231

232 To compare the perceived effects of different study scales, we used distribution records from the
233 National Biodiversity Network (NBN) Gateway (<http://data.nbn.org.uk>), at 10 km x 10 km grid
234 resolution (i.e. 100 km² cells) for Great Britain. Long term average climatic variables for 1961-90
235 were obtained at 25 km² resolution from the UK Climate Impacts Programme (UKCIP
236 <http://www.metoffice.gov.uk/climatechange/science/monitoring/ukcp09/>), and summary percentage
237 cover of the broad habitat categories at 1 km² resolution from the CEH Land Cover Map 2000
238 (CEH www.ceh.ac.uk/sections/seo/lcm2000_home.html). The resolutions were harmonised by
239 summarising the climatic and land cover data to 100 km² resolution in ArcGIS, to match the
240 distributional data; the mean of four cells was used for the temperature variables, and the total area
241 covered for the habitat categories. Species' presences were taken as 100 km² grid cells where a
242 given species had been recorded, using data from the NBN gateway from 1961-2009 to reflect the
243 available climate data. Because sampling of carabid beetles in Britain is not exhaustive, a species
244 may be truly present in some cells where it has not been recorded. To reduce this concern,
245 "absences" were taken to be only those 100 km² grid cells that were known to have been sampled
246 for ground beetles (i.e., other carabid species had been recorded from them, Fig. 2). For each
247 species, we generated a response variable of presences and absences from the UK. We then used a
248 GLM with a binomial error structure and logit link function fitted to two sets of variables, habitat

249 (the percentage cover of each of fifteen habitat categories) and temperature (average mean,
250 maximum and minimum over the 1961-90 period) using the BIOMOD package for R (Thuiller
251 2009). For each variable set, a best model was produced using backwards stepwise selection based
252 on AIC. Area under the receiver operating characteristic curve (AUC) was calculated using a 70/30
253 data split, with 70% being used for training and the remaining 30% being used for testing.

254

255 **Results**

256

257 **Local scale distribution modelling**

258

259 We collected a total of 41 species of Carabidae: 35 species from Glen Finglas, 29 species from Lake
260 Vyrnwy and 19 species from the Peak District. Twenty of these fulfilled the modelling criteria at one
261 or more sites (Table 1). Across sites and species, temperature variables were the *most important*
262 (best model selected by AIC) for 22 out of 41 species/site combinations (Glen Finglas 11/18; Lake
263 Vyrnwy 8/14; Peak District 3/9; Fig. 3), whereas habitat variables produced the best model in 17 of
264 the 41 analyses (Glen Finglas 7/18; Lake Vyrnwy 5/14; Peak District 5/9; Fig. 3). For two
265 species/site combinations, distributions were explained by neither temperature nor habitat variables
266 (Supplementary material Appendix 1, Tables A1-A3). After accounting for spatial autocorrelation in
267 the predictor variables, we found only weak evidence for spatial autocorrelation in the species'
268 distributions. The residuals from the best models were significantly clumped in only three of the 41
269 analyses, and p-values for the Moran's I statistic were never less than 0.005.

270

271 The sampled species can be represented on a continuous “northerliness” scale by the mean of their
272 latitudinal records in Great Britain. The slope of the regression of each species' presence/absence at
273 each site in landscapes where the species occurred against annual mean temperature (at 25 m²
274 resolution) and its northerliness index were negatively correlated (Fig. 4; Spearman's $r = -0.48$, $n =$

275 20, $p < 0.02$). This negative correlation shows that northerly species tended to occur in cool locations
276 within landscapes (negative regression coefficients), whereas more southerly species tended to be
277 found in relatively warm places (positive regression coefficients).

278

279 **National scale distribution modelling**

280

281 Our analysis revealed that habitat models were better than temperature models at predicting the
282 presence/absence of all species modelled (Fig. 3). In general, model fit was poor (13/20 species
283 $AUC < 0.7$ for habitat models, 16/20 species $AUC < 0.7$ for temperature models). However, both
284 habitat ($AUC > 0.8$) and temperature models ($AUC > 0.7$) performed best for the four most
285 northerly-distributed species (Supplementary materials Appendix 1, Table A4), suggesting that
286 coarse resolution habitat and temperature models both perform better on species at the edges of
287 their range.

288

289 **Discussion**

290

291 By using high resolution (25 m²) surfaces that reflect local thermal environments, the local
292 distributions of species could frequently be explained in terms of climatic variables. We interpret
293 this result cautiously because of the slightly coarser resolution of the habitat data, but also the
294 higher number of habitat variables. Temperature appears to be as important as habitat as a predictor
295 of the presence of species at finer resolutions. Northerly species were most often found in cool
296 micro-sites within landscapes. Southerly species showed the reverse pattern, being found in warm
297 environments within the study sites. However, the effects of climatic variables were not restricted to
298 species at the thermal edges of their geographic distributions, and many “widespread” species were
299 statistically associated with particular thermal environments within study sites. In contrast, land
300 cover was always more important in analyses of species’ distributions at the national scale.

301

302 Our results, and those of Gutiérrez Illán et al. (2010) appear to run counter to the commonly-held
303 perception that habitat and vegetation variables will be most important at a local scale, whereas
304 climatic variables will predominate in apparent importance at more extensive scales (e.g. Pearson
305 and Dawson 2003, but see Tingley and Herman 2009). Our explanation for this apparent
306 discrepancy relates to the spatial resolutions and extents of the analyses. Fine resolution, within-
307 landscape analyses of the distributions and abundances of species rarely consider the importance of
308 microclimates on species' local distributions. Microclimates are recognised as being important
309 towards the edges of species' ranges (Thomas et al. 1999), and in determining species' survival in
310 the context of environmental stochasticity (e.g. Kindvall 1996, Oliver et al. 2010), and there is a
311 large body of evidence showing the importance of temperature to the growth and survival of species
312 (e.g. Bayram and Luff 1993, Leirikh et al. 2009, Somero 2010). In the absence of high resolution
313 microclimatic data for inclusion in distribution models, local distributions of species are typically
314 explained in terms of the variables that are commonly available at such resolution, such as resource,
315 habitat and vegetation variables. The distributions of these “habitat” variables are often correlated
316 with climatic variation within a site (different vegetation types are associated with different slopes,
317 aspects and local elevations, e.g. Lakhani and Davis 1982), so a statistical association between a
318 species and a particular habitat type cannot always be unambiguously ascribed to habitat or to
319 microclimate (but see Huntley and Baxter 2003).

320

321 This is further confounded by the fact that different habitats not only *occur* predominantly in
322 different microclimates but that they also *generate* different microclimates through variation in
323 vegetation density and height. For example, Schneider and Eugster (2005) found that converting
324 peat wetlands to productive agricultural land reduced the temperature range in the study site by 0.6
325 °C. Similarly, Suggitt et al. (2011) found that the minimum temperature in woodlands was 4-6 °C
326 warmer than in nearby heathlands and grasslands, and Thomas (1983) reported that short turf can

327 generate 8 °C higher surface temperatures than tall turf, within the same grassland. It is possible
328 that, in the absence of appropriate high-resolution microclimatic data, much of the within-landscape
329 variation in species' abundance and distribution is being mistakenly attributed to habitat-related
330 factors, thereby underestimating the role of climatic variables (and hence climatic change) in
331 affecting species' local distributions. Our analyses only considered microclimatic variation
332 associated with topography, calculated at the top of the vegetation layer. However, beetles were
333 trapped below the vegetation, so additional sources of microclimatic variation related to habitat type
334 were not included, and we may still have underestimated the role of thermal variation. The fine-
335 resolution vegetation structure data required to determine this indirect effect of land cover are not
336 yet available for most areas, although the increasing availability and use of fine resolution LiDAR
337 data may provide a solution (Müller and Brandl 2009).

338

339 For the national scale analysis, local climatic variation associated with different topographies and
340 vegetation types within 100 km² cells may be as large as, or greater than, the climatic variation
341 between cells (e.g. we observed a range of over 6 °C in monthly maximum temperatures between
342 different locations within the Peak District site). This thermal variation may partly be captured by
343 the frequencies of different land cover types; it is possible that our national scale analysis assigns
344 greatest importance to land cover type simply because vegetation types provide proxies for the
345 range of local microclimatic conditions within each 100 km² grid cell. Likewise, including
346 elevational range within coarse grid cells can improve the fit of distribution models because this
347 reflects the likelihood that suitable local climates will be found somewhere within the grid cell
348 (Luoto and Heikkinen 2008), since temperatures tend to decrease with increasing elevation. For
349 widespread species, climate may contribute to variation in presence, but such variation is only
350 weakly correlated with the smoothed 100 km² climatic surfaces that were available to use in the 100
351 km² resolution analysis of Britain.

352

353 At yet coarser resolutions, land cover may appear to be less important (Luoto et al. 2007) because
354 all grid cells contain a diversity of topographies (south- and north-facing slopes) and vegetation
355 types (which vary in shadiness, for example), providing a wide range of local climates. Such coarse-
356 resolution grids give the impression of solid distributions within the core parts of species' ranges,
357 with a relatively "sharp" climatic margin, giving rise to the conclusion that climatic variables
358 dominate distributions at very coarse resolution, particularly when analysed at continental extents.
359 We are left with the somewhat uncomfortable conclusion that the perceived relative importance of
360 climatic and non-climatic determinants of species' distributions may have as much to do with the
361 nature of the data available, and the resolution and extent of the analysis, as with the real separate
362 and combined effects of climatic versus non-climatic variables.

363

364 More positively, finer-resolution microclimatic approaches, such as those adopted here, may begin
365 to provide projections of species' responses to climatic change at a scale that is relevant to
366 conservation planning. Thermally-driven shifts in species' vegetation associations (Davies et al.
367 2006) may enable us to identify ways of adapting management regimes to maintain suitable
368 microclimates for species within sites. Microclimate models such as that used here can help identify
369 heterogeneous landscapes and climatic refugia where species may be most buffered against
370 extinction (e.g. Kindvall 1996, Oliver et al. 2010). Microclimatic modelling could also be used to
371 improve assessments of conservation status by refining estimates of the area of land occupied by
372 species, especially in mountainous regions, where many species of conservation concern occur. The
373 conservation status of species is often determined, in part, by estimates of the extent of occurrence
374 (from coarse resolution maps) or area of occupancy (the area actually occupied within the extent of
375 occurrence, from finer resolution maps) (IUCN 2010). The coarse resolution extent of occurrence
376 may include large areas that are unsuitable for a species, hence it is preferable to use area of
377 occupancy criteria. However, this more accurate measure is unknown for 98% of all birds
378 (Sekercioglu et al. 2008), which are a relatively well studied group. Fine-resolution models

379 incorporating microclimatic variation as well as other appropriate fine-resolution data could be used
380 to assess current status and project future trends more realistically than is possible with coarser-
381 resolution models (Williams et al. 2003).

382

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394

395 **REFERENCES**

396

- 397 Althoff, G. H. et al. 1994. Dependence of running activity and net reproduction in *Carabus*
398 *autonitens* on temperature. – In: Desender, K. et al. (eds), *Carabid Beetles: Ecology and Evolution*.
399 Kluwer Academic Publishers, Dordrecht, Netherlands, pp. 95-100.
- 400
- 401 Atienza, J. C. et al. 1996. Role of temperature in habitat selection and activity patterns in the ground
402 beetle *Angoleus nitidus*. - *Pedobiologia* 40: 240-250.
- 403
- 404 Baars, M. A. 1979. Catches in pitfall traps in relation to mean densities of Carabid beetles. -
405 *Oecologia* 41: 25-46.
- 406
- 407 Bayram, A. and Luff, M. L. 1993. Cold-hardiness of wolf-spiders (Lycosidae, Araneae) with

408 particular reference to *Pardosa pullata* (Clerck). - Journal of Thermal Biology 18: 263-268.

409

410 Bennie, J. et al. 2008. Slope, aspect and climate: Spatially explicit and implicit models of
411 topographic microclimate in chalk grassland. - Ecological Modelling 216: 47-59.

412

413 Bennie, J. et al. 2010. Predicting spatial and temporal patterns of bud-burst and spring frost risk in
414 north-west Europe: the implications of local adaptation to climate. - Global Change Biology 16:
415 1503-1514.

416

417 Blake, S. et al. 2003. The relationship between the classification of Scottish ground beetle
418 assemblages (Coleoptera, Carabidae) and the National Vegetation Classification of British plant
419 communities. - Ecography 26: 602-616.

420

421 Brouwers, N. C. and Newton, A. C. 2009. Movement rates of woodland invertebrates: a systematic
422 review of empirical evidence. - Insect Conservation and Diversity 2: 10-22.

423

424 Bryant, S. R. et al. 2002. The influence of thermal ecology on the distribution of three nymphalid
425 butterflies. - Journal of Applied Ecology 39: 43-55.

426

427 Cernusca, A. and Seeber, M. C. 1981. Canopy Structure, microclimate and the energy budget in
428 different alpine plant communities. – In: Grace, J. et al. (eds), Plants and their Atmospheric
429 Environment. Blackwell Scientific Publications, Oxford, pp. 75-81.

430

431 Davies, Z. G. et al. 2006. Changing habitat associations of a thermally constrained species, the
432 silver-spotted skipper butterfly, in response to climate warming. - Journal of Animal Ecology 75:
433 247-256.

434

435 Diez, J.M. & Pulliam, H.R. 2007. Hierarchical analysis of species distributions and abundance
436 across environmental gradients. - *Ecology* 88: 3144-3152.

437

438 Elith, J. and Leathwick, J. R. 2009. Species distribution models: ecological explanation and
439 prediction across space and time. - *Annual Review of Ecology, Evolution and Systematics* 40: 677-
440 697.

441

442 Eyre, M. D. 2006. A strategic interpretation of beetle (Coleoptera) assemblages, biotopes, habitats
443 and distribution, and the conservation implications. - *Journal of Insect Conservation* 10: 151-160.

444

445 Eyre, M. D. et al. 2003. The relationship between British ground beetles (Coleoptera, Carabidae)
446 and land cover. - *Journal of Biogeography* 30: 719-730.

447

448 Eyre, M. D. et al. 2005a. Assessing the relationship between grassland Auchenorrhyncha
449 (Homoptera) and land cover. - *Agriculture, Ecosystems & Environment* 109: 187-191.

450

451 Eyre, M. D. et al. 2005b. Investigating the relationships between the distribution of British ground
452 beetle species (Coleoptera, Carabidae) and temperature, precipitation and altitude. - *Journal of*
453 *Biogeography* 32: 973-983.

454

455 Gardner, S. M. et al. 1997. Carabid communities on heather moorlands in North East Scotland: The
456 consequences of grazing pressure for community diversity. - *Biological Conservation* 81: 275-286.

457

458 Gottfried, M. et al. 1999. A fine-scaled predictive model for changes in species distribution patterns
459 of high mountain plants induced by climate warming. - *Diversity and Distributions* 5: 241-251.

460

461 Gutiérrez Illán, J. et al. 2010. The contributions of topoclimate and land cover to species
462 distributions and abundance: fine-resolution tests for a mountain butterfly fauna. - *Global Ecology*
463 and *Biogeography* 19: 159-173.

464

465 Hickling, R. et al. 2006. The distributions of a wide range of taxonomic groups are expanding
466 polewards. - *Global Change Biology* 12: 450-455.

467

468 Hill, J. K. et al. 1999. Climate and habitat availability determine 20th century changes in a
469 butterfly's range margin. - *Proceedings of the Royal Society B: Biological Sciences* 266: 1197-1206.

470

471 Huntley, B. and Baxter 2003. Insights on synergies: Models and methods. - In: Hannah, L and
472 Lovejoy, T. E. (eds) *Climate change and biodiversity: Synergistic impacts*. Conservation
473 International, Washington, DC. pp. 15-23.

474

475 Huntley, B. et al. 2007. *A climatic atlas of European breeding birds*. - Lynx Edicions, Barcelona.

476

477 IUCN 2010. *Guidelines for Using the IUCN Red List Categories and Criteria: Version 8.0*. Prepared
478 by the Standards and Petitions Subcommittee, March 2010.

479 <http://intranet.iucn.org/webfiles/doc/SSC/RedList/RedListGuidelines.pdf>.

480

481 Jump, A. S. et al. 2006. Rapid climate change-related growth decline at the southern range edge of
482 *Fagus sylvatica*. - *Global Change Biology* 12: 2163-2174.

483

484 Kindvall, O. 1996. Habitat heterogeneity and survival in a bush cricket metapopulation. - *Ecology*
485 77: 207-214.

486

487 Lakhani, K. H. and Davis, B. N. K. 1982. Multiple regression models of the distribution of
488 *Helianthemum chamaecistus* in relation to aspect and slope at Barnack, England. - Journal of
489 Applied Ecology 19: 621-629.

490

491 Leirikh, A. N. et al. 2009. Cold hardiness and development rate as elements of adaptive strategies of
492 phalangiid harvestmen (Opiliones, Phalangidae) in northeastern Asia. - Entomological Review 89:
493 323-331.

494

495 Lennon, J. J. et al. 2002. Are Alaskan trees found in locally more favourable sites in marginal areas?
496 - Global Ecology and Biogeography 11: 103-114.

497

498 Luff, M. L. 1998. Provisional atlas of the ground beetles (Coleoptera, Carabidae) of Britain. -
499 Biological Records Centre, Monks Wood, Cambs.

500

501 Luoto, M. and Heikkinen, R. K. 2008. Disregarding topographical heterogeneity biases species
502 turnover assessments based on bioclimatic models. - Global Change Biology 14: 483-494.

503

504 Luoto, M. et al. 2007. The role of land cover in bioclimatic models depends on spatial resolution. -
505 Global Ecology and Biogeography 16: 34-42.

506

507 Martinez, A. et al. 2009. Effects of some ecological variables on carabid communities in native and
508 non-native forests in the Ibaizabal basin (Basque country, Spain). - Annals of Forest Science, 66:
509 Art. No. 304.

510

511 McKenney, D. W. et al. 2007. Potential impacts of climate change on the distribution of North
512 American trees. - *Bioscience* 57: 939-948.
513

514 Müller, J. and Brandl, R. 2009. Assessing biodiversity by remote sensing in mountainous terrain:
515 the potential of LiDAR to predict forest beetle assemblages. - *Journal of Applied Ecology* 46: 897-
516 905.
517

518 Oliver, T. et al. 2010. Heterogeneous landscapes promote population stability. - *Ecology Letters* 13:
519 473-484.
520

521 Opdam, P. and Wascher, D. 2004. Climate change meets habitat fragmentation: linking landscape
522 and biogeographical scale levels in research and conservation. - *Biological Conservation* 117: 285-
523 297.
524

525 Parmesan, C. and Yohe, G. 2003. A globally coherent fingerprint of climate change impacts across
526 natural systems. - *Nature* 421: 37-42.
527

528 Pearson, R. G. and Dawson, T. P. 2003. Predicting the impacts of climate change on the distribution
529 of species: are bioclimate envelope models useful? - *Global Ecology and Biogeography* 12: 361-
530 371.
531

532 Randin, C. F. et al. 2009. Climate change and plant distribution: local models predict high-elevation
533 persistence. - *Global Change Biology* 15: 1557-1569.
534

535 Ribera, I. et al. 2001. Effect of land disturbance and stress on species traits of ground beetle
536 assemblages. - *Ecology* 82: 1112-1129.

537

538 Roy, D. B. and Thomas, J. A. 2003. Seasonal variation in the niche, habitat availability and
539 population fluctuations of a bivoltine thermophilous insect near its range margin. - *Oecologia* 134:
540 439-444.

541

542 Schneider, N. and Eugster, W. 2005. Historical land use changes and mesoscale summer climate on
543 the Swiss Plateau. - *Journal of Geophysical Research: Atmospheres* 110: ARTN D19102 2005

544

545 Sekercioglu, C. H. et al. 2008 Climate change, elevational range shifts, and bird extinctions. -
546 *Conservation Biology* 22: 140-150.

547

548 Suggitt, A. J. et al. 2011. Habitat microclimates drive fine-scale variation in extreme temperatures. -
549 *Oikos* 120: 1-8.

550

551 Somero, G. N. 2010. The physiology of climate change: how potentials for acclimatization and
552 genetic adaptation will determine 'winners' and 'losers'. - *Journal of Experimental Biology* 213: 912-
553 920.

554

555 Thiele, H. U. 1977. Carabid beetles in their environments: A study on habitat selection by
556 adaptations in physiology and behavior. – Springer-Verlag, Berlin and New York.

557

558 Thomas, C. D. et al. 2001. Ecological and evolutionary processes at expanding range margins. -
559 *Nature* 411: 577-581.

560

561 Thomas, J. A. 1983. The ecology and conservation of *Lysandra bellargus* (Lepidoptera, Lycaenidae)
562 in Britain. - *Journal of Applied Ecology* 20: 59-83.

563

564 Thomas, J. A. et al. 1999. Intraspecific variation in habitat availability among ectothermic animals
565 near their climatic limits and their centres of range. - *Functional Ecology* 13: 55-64.

566

567 Thuiller, W. et al. 2009. BIOMOD - a platform for ensemble forecasting of species distributions. -
568 *Ecography* 32: 369-373.

569

570 Tingley, R. and Herman, T. B. 2009. Land-cover data improve bioclimatic models for anurans and
571 turtles at a regional scale. - *Journal of Biogeography* 36: 1656-1672.

572

573 Williams, S. E. et al. 2003. Climate change in Australian tropical rainforests: an impending
574 environmental catastrophe. - *Proceedings of the Royal Society B: Biological Sciences* 270: 1887-
575 1892.

576

577 Supplementary material (Appendix EXXXXXX at <www.oikosoffice.lu.se/appendix>). Appendix 1

578

579 Table 1: The abundance of the twenty selected species at each field site. Species present at a site,
 580 but not fulfilling the modelling criteria, are designated by *.

581

Species	Peak	Lake Vyrnwy	Glen Finglas
<i>Abax parallelepipedus</i>	0	48	66
<i>Agonum fuliginosum</i>	15	89	38
<i>Amara lunicollis</i>	15	10	37
<i>Carabus arvensis</i>	0	53	191
<i>Carabus glabratus</i>	0	437	162
<i>Carabus problematicus</i>	126	19	159
<i>Carabus violaceus</i>	110	125	167
<i>Cychrus caraboides</i>	11	45	13
<i>Loricera pilicornis</i>	6 *	0	81
<i>Nebria brevicollis</i>	22	0	0
<i>Notiophilus biguttatus</i>	6 *	10	0
<i>Patrobus assimilis</i>	4 *	0	24
<i>Poecilus versicolor</i>	0	50	337
<i>Pterostichus adstrictus</i>	85	0	75
<i>Pterostichus aethiops</i>	0	0	12
<i>Pterostichus diligens</i>	139	240	43
<i>Pterostichus madidus</i>	2 *	123	620
<i>Pterostichus melanarius</i>	0	0	134
<i>Pterostichus niger</i>	0	76	468
<i>Pterostichus nigrata</i>	86	1752	623

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583

584 **Figure legends:**

585 Figure 1: a) Location of the three field sites (white circles) within Great Britain in relation to annual
586 mean temperature (°C) during the period 1961-90 at 5 km resolution; (b,c,d) Examples of the
587 presence (black triangles) and absence (white circles) of individual species at the three study sites in
588 relation to modelled annual mean temperature (°C) at 5 m resolution. All temperature layers are
589 shown on the same scale.

590

591 Figure 2: The distribution of *Carabus glabratus* within Great Britain. Black squares are where the
592 species has been recorded as present, white areas are where the species has not been recorded, but a
593 record of at least one other carabid exists and grey squares are where no carabids of any species
594 have been recorded. White circles show the locations of the three field sites, and distances are in
595 kilometres.

596

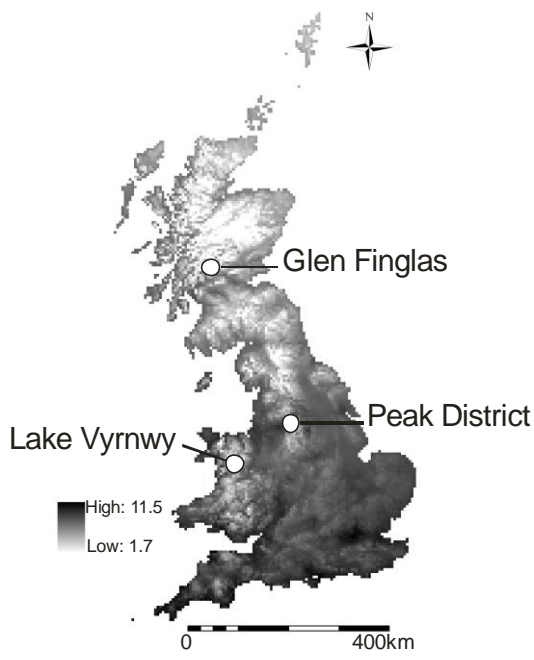
597 Figure 3: The relative importance of habitat and temperature variables to the twenty carabid species
598 at the three sites and across Great Britain.

599

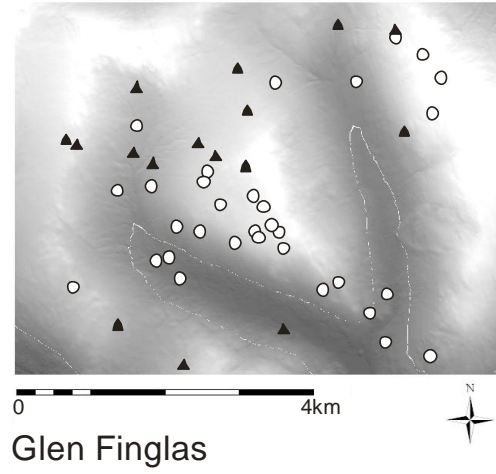
600 Figure 4: The relationship between the mean regression coefficient (from up to three sites) of
601 species presence/absence on modelled annual mean temperature (ANMEAN) and the mean latitude
602 of the GB distribution of the 20 selected Carabid species. For the purposes of illustration, all models
603 were constrained to use ANMEAN (the mean annual temperature in °C), despite other temperature
604 variables often being better predictors of the distributions of species. Labels denote codes for each
605 species; Af = *Agonum fuliginosum*, Al = *Amara lunicollis*, Ap = *Abax parallelepipedus*, Ca =
606 *Carabus arvensis*, Cg = *C. glabratus*, Cp = *C. problematicus*, Cv = *C. violaceus*, Cc = *Cychrus*
607 *caraboides*, Lp = *Loricera pilicornis*, Neb = *Nebria brevicollis*, Nob = *Notiophilus biguttatus*, Pas =
608 *Patrobis assimilis*, Pad = *Pterostichus adstrictus*, Pae = *P. aethiops*, Pd = *P. diligens*, Pma = *P.*
609 *madidus*, Pme = *P. melanarius*, Pn = *P. nigrita*, PN = *P. niger*, Pv = *Poecilus versicolor*.

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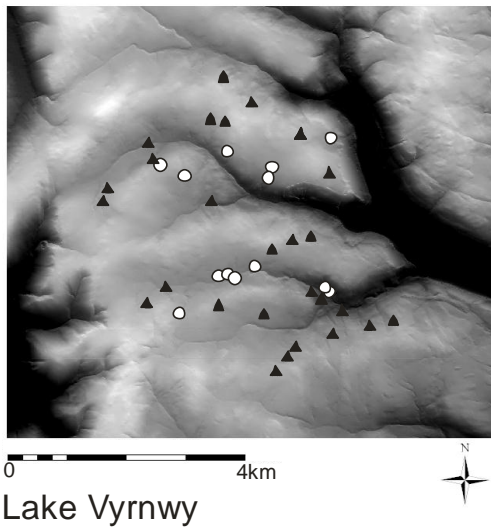
a)



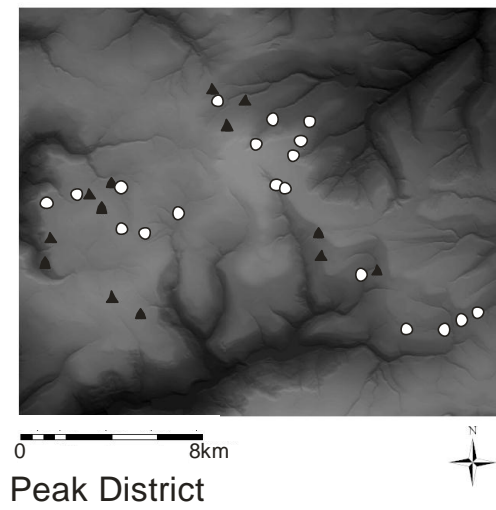
b)

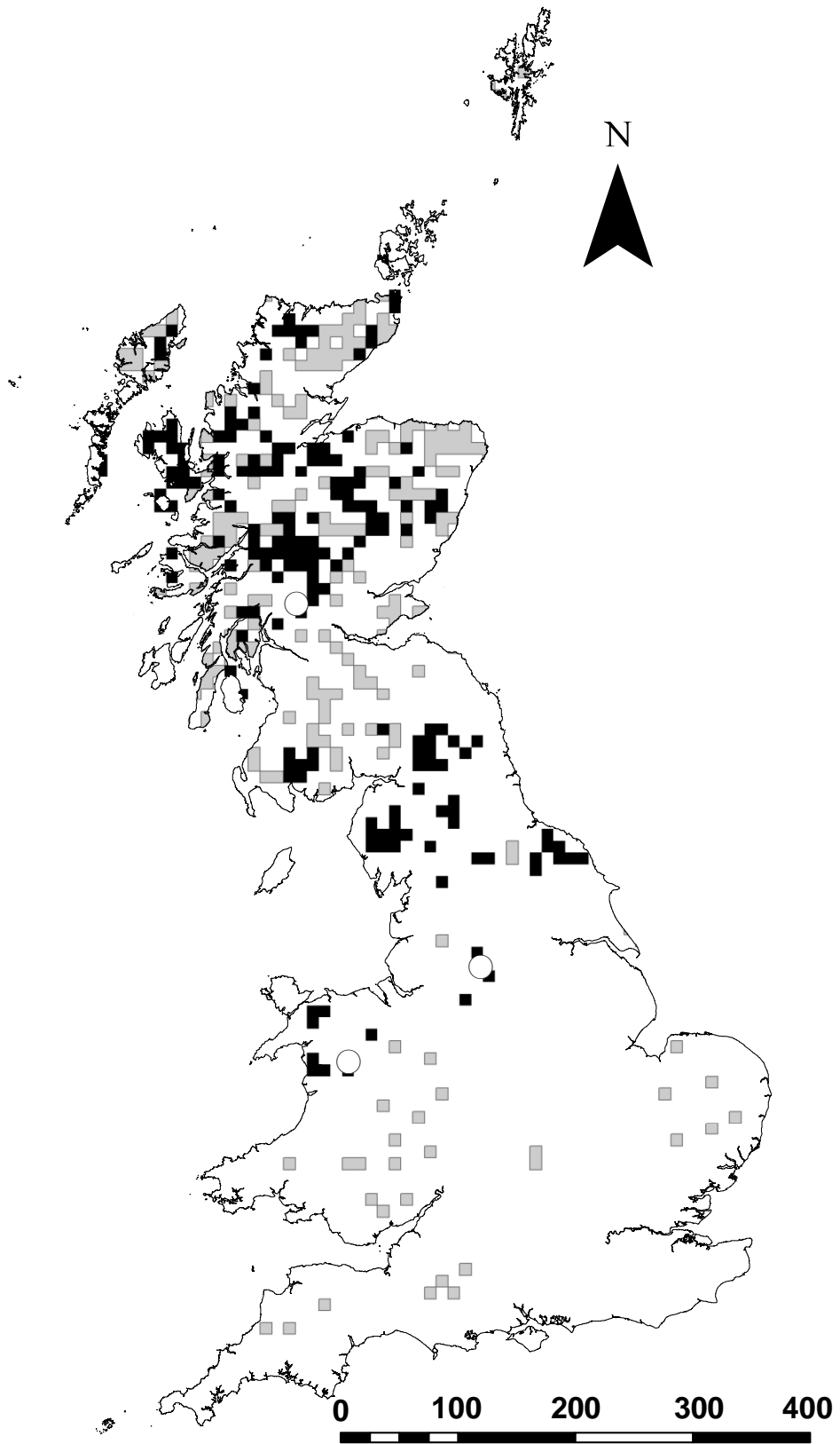


c)

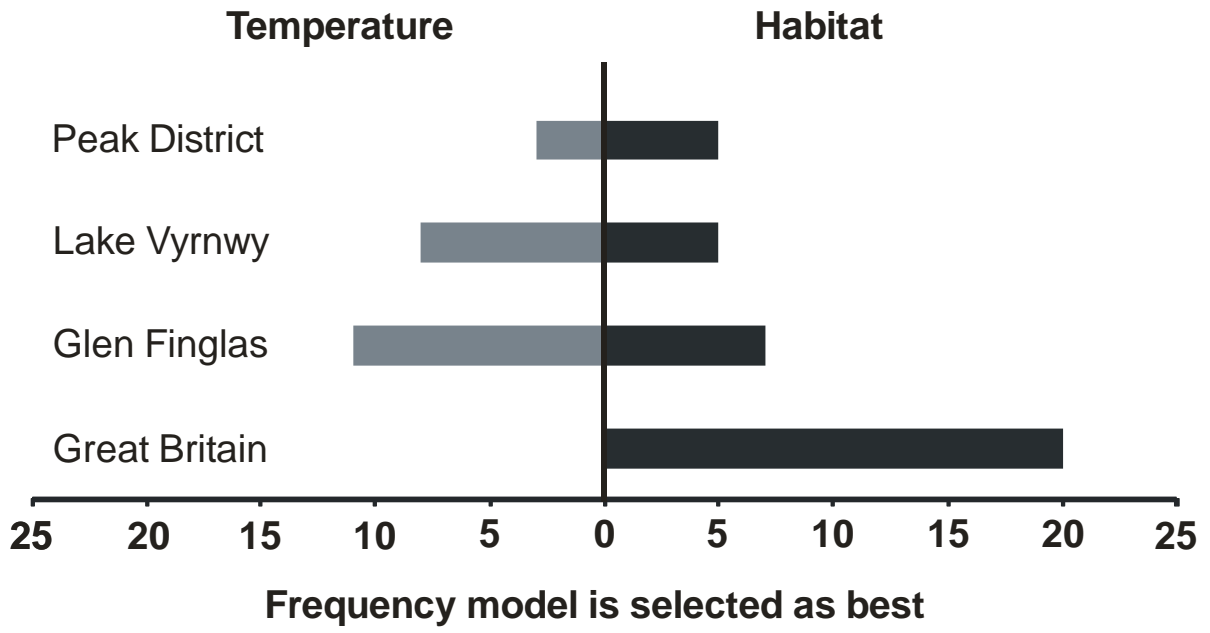


d)





616 **Figure 3:**



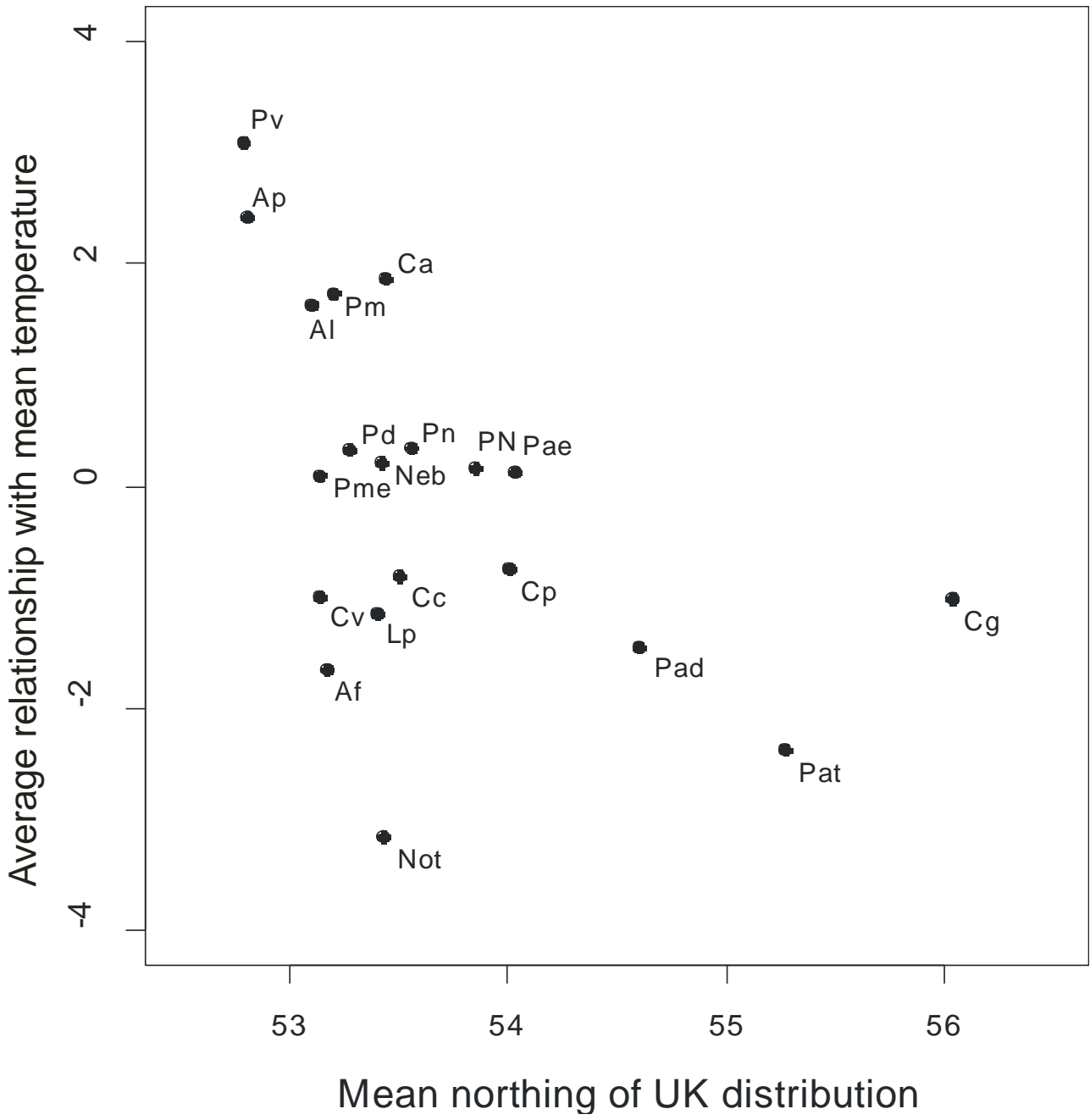
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620 **Figure 4:**

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