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Predictors of contraction and expansion of area of occupancy for British birds

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1 Geographical range dynamics are driven by the joint effects of abiotic factors, human
2 ecosystem modifications, biotic interactions, and the intrinsic organismal responses to
3 these. However, the relative contribution of each component remains largely unknown.
4 Here, we compare the contribution of life-history attributes, broad-scale gradients in
5 climate, and geographical context of species' historical ranges, as predictors of recent
6 changes in area of occupancy for 116 terrestrial British breeding birds (74 contractors, 42
7 expanders) between the early 1970s and late 1990s. Regional threat classifications
8 demonstrated that the species of highest conservation concern showed both the largest
9 contractions and the smallest expansions. Species responded differently to climate
10 depending on geographic distribution – northerly species changed their area of occupancy
11 (expansion or contraction) more in warmer and drier regions, whereas southerly species
12 changed more in colder and wetter environments. Species with slow life history (larger body
13 size) tended to have a lower probability of changing their area of occupancy than species
14 with faster life history, whereas species with greater natal dispersal capacity resisted
15 contraction and, counter-intuitively, expansion. Higher geographic fragmentation of species'
16 range also increased expansion probability, possibly indicating a release from a previously
17 limiting condition, for example through agricultural abandonment since the 1970s. After
18 accounting statistically for the complexity and non-linearity of the data, our results
19 demonstrate two key aspects of changing area of occupancy for British birds: (i) climate is
20 the dominant driver of change, but direction of effect depends on geographic context, and
21 (ii) all of our predictors generally had a similar effect regardless of the direction of the
22 change (contraction versus expansion). Although we caution applying results from Britain's
23 highly modified and well-studied bird community to other biogeographical regions, our
24 results do indicate that a species' propensity to change area of occupancy over decadal

25 scales can be explained partially by a combination of simple allometric predictors of life-
26 history pace, average climate conditions, and geographical context.

27

28 **Keywords:** agricultural abandonment; biogeography; body size; climate; demography;
29 dispersal; forest recovery; life history; threatened species

30

31 **1. INTRODUCTION**

32 Understanding the complexities of range dynamics — why (and by what amount) a species'
33 range changes over time — is an essential component for predicting future human
34 influences on biodiversity. Range dynamics vary across species and space owing to the joint
35 effects of abiotic factors, biotic interactions, human ecosystem modification, and intrinsic
36 organismal responses to these [1, 2]. However, a mismatch exists between studies seeking
37 to improve understanding of the historical and ecological determinants of range dynamics,
38 and those predicting future range changes. With increasing emphasis in ecology to predict
39 the future distributions of species in response to climate disruption and environmental
40 degradation [3, 4], projections are typically based on expected changes in climatic factors
41 that correlate with species' distributions (e.g., [5], but see [6]). This contrasts starkly with
42 historical reconstructions of species' distributions that generally infer range determinants
43 based on species-specific demographic and life-history traits [e.g., 1, 7, 8, 9].

44 A vexing question therefore remains – which drivers of range dynamics, if any, are
45 more important for predicting patterns of distributional change? While ecological and life-
46 history traits appear to predispose certain species to range contraction or expansion as local
47 conditions change [10-12], a species' area of occupancy and its configuration, such as the
48 proximity to barriers, niche breadth, local climate severity and landscape or population

49 fragmentation, can potentially override a species' susceptibility to changing its range [13-
50 15]. The problem is that there are few sufficiently comprehensive datasets that combine
51 distributional, extrinsic (e.g., climate, land-use change) and intrinsic (e.g., life
52 history/ecology) attributes for enough species to lend themselves to broad-scale analyses
53 that can tease apart the relative influence of specific drivers.

54 Fortunately in this regard, British breeding birds are one of the best-studied species
55 assemblages for assessing the determinants of vertebrate range dynamics, especially given
56 the breadth and relatively low bias of the sampling effort, and high proportion of the
57 species monitored [16, 17]. Since the late 1960s, there has been 98 to 100 % sampling
58 coverage of all 2861 of Britain's mainland 10-km² grid cells [16, 17], thus providing a unique
59 insight into the changing distributions of this taxon. Further, birds in general are one of the
60 best-studied taxa in terms of life-history traits, with detailed data available for many
61 European species in particular [18]. Combining this information, here we explore the joint
62 effects of potential intrinsic and extrinsic determinants of changing area of occupancy for
63 British breeding birds. Unlike most other studies that have investigated such questions using
64 predictions of future extinction risk [19, 20], we use *observed* recent patterns of changing
65 area of occupancy over approximately 30 years (between the early 1970s and late 1990s) as
66 the response variable, taking the constraints of expansion limitation into account
67 statistically for wide-ranging species.

68 Given the comprehensiveness of the available data, we are able to test three
69 hypotheses simultaneously: (i) we tested whether variation in changing area of occupancy
70 can be explained partly by life-history attributes that are expected to reflect ecological
71 responsiveness. Here we consider both body mass as a correlate of the pace of life history
72 ('fast' versus 'slow' species) and natal dispersal (capacity to recolonize). In the face of rapid,

73 human-induced global change, we predict that species with ‘slower’ life histories (larger-
74 bodied, longer-lived species with slower reproductive rates) will be more prone to range
75 contraction, while species with faster life histories will have a greater ability to expand their
76 ranges [21, 22]. We predict that natal dispersal capacity will be positively related to range
77 expansion (i.e., species with higher dispersal have a greater capacity to expand if conditions
78 permit), and negatively related to range contraction (i.e., a low dispersal capacity increases
79 a species’ susceptibility to habitat fragmentation, and further contraction of its area of
80 occupancy). Likewise, a species’ threat status might indicate its propensity to change its area
81 of occupancy, with threatened species more likely to contract, and non-threatened species
82 more likely to expand their range.

83 We also tested whether (ii) broad-scale spatial gradients in climate (annual extremes
84 in temperature, precipitation) [23] modify a species’ likelihood of changing its area of
85 occupancy. We predict that mean minimum winter temperature mainly limits a species’
86 capacity to expand geographically, whereas species with lower drought tolerance are mainly
87 limited by annual precipitation [14]. Finally, we tested whether (iii) the geographical context
88 of a species, such as the degree of fragmentation of its subpopulations, which might reflect
89 various unmeasured constraints like species interactions and human impact, dictate its
90 propensity to change in area of occupancy. We predict that species with highly fragmented
91 populations will be more susceptible to range contraction [24].

92

93 **2. MATERIAL AND METHODS**

94 *(a) Bird distribution data*

95 We compiled the area of occupancy of British birds for two periods of time, spaced nearly
96 three decades apart: 1968-1972 (T_1) and 1995-1999 (T_2). We accumulated a total of 116

97 species (representing the orders Accipitriformes [$n = 14$ species], Columbiformes [$n = 5$],
98 Galliformes [$n = 8$], Passeriformes [$n = 83$] and Strigiformes [$n = 6$]) after excluding
99 predominately aquatic (especially marine) birds due to the difficulty in defining explicit
100 areas of occupancy in these groups [25]. We denoted the area of occupancy as the number
101 of 10-km² cells of occupied on the mainland (see Introduction) in T_1 and T_2 as R_1 and R_2 ,
102 respectively.

103

104 *(b) Species threat status*

105 We compiled the global threat status of each species based on the IUCN Red List
106 assessments (www.iucnredlist.org) to determine whether the direction and magnitude of
107 changing area of occupancy was related to the severity of threat – in our dataset, 112
108 species were ‘Least Concern’, 2 were ‘Near Threatened’, 1 was ‘Data Deficient’ and 1 was
109 unrated. We also compiled the regional (i.e., UK-specific) conservation status of each
110 species on the British birds assessment [26] where species are classified as ‘Red’ (high
111 conservation concern; $n = 24$), ‘Amber’ (moderate conservation concern; $n = 36$) or ‘Green’
112 (low conservation concern; $n = 41$; $n = 15$ species in our dataset were not assessed).

113

114 *(c) Range fragmentation ('clumpiness')*

115 Initially we examined a previously published [27] index of nearest-neighbour ‘contagion’ (C_i)
116 as a measure of population fragmentation, but this was highly correlated (Spearman’s $\rho =$
117 0.965) with R_1 (see correlations and calculation of C_i in supplementary material table S1).
118 We therefore opted for another measure of distributional ‘clumpiness’ (CI), calculated using
119 FRAGSTATS Version 4 [28]. Whereas other measures of habitat fragmentation are highly
120 correlated with area of occupancy (e.g., contagion), clumpiness is independent of R_1

121 (Spearman's $\rho = -0.020$; supplementary material table S1). Clumpiness is calculated using
122 the proportion of occupied cells in T_1 that lie adjacent to other occupied cells in T_1
123 ('adjacencies'). The calculation is relative to the expected number of adjacencies given a
124 spatially random distribution of the same number of occupied cells, which largely accounts
125 for the positive correlation between the number of adjacencies and total area of occupancy.
126 Larger patches with compact shapes contain a higher proportion of like adjacencies than
127 landscapes dominated by smaller patches with complex shapes. A highly contagious
128 (aggregated) landscape will contain a higher percentage of like adjacencies (maximum = 1),
129 whereas a highly fragmented (disaggregated) landscape will contain proportionately fewer
130 like adjacencies (minimum value = -1). A landscape with clumpiness = 0 indicates a spatially
131 random distribution [see more details in 28]. There was no evidence for either a monotonic
132 or monomodal (quadratic) relationship of the clumpiness index with the logit-transformed
133 (see below) proportional R_1 (i.e., expressed as a proportion of the total number of available
134 grid cells) (supplementary material Table S2).

135

136 *(d) Bird life-history data*

137 We compiled life-history traits for birds using a comprehensive survey of the ornithological
138 literature [18] that is updated regularly [e.g., 29]. A description of the online sources of the
139 information collected is available [18, 29]. To maximize sample size (the number of species
140 for which trait data exist), we focussed initially on clutch size, body mass (g) and longevity
141 (months) traits only, all of which are among the most robust predictors of slow to fast life-
142 history variation in birds [30]. However, body mass, clutch size and longevity were all highly
143 correlated (supplementary material table S1), so we present further analyses with mass
144 alone. For each species, we used data on species-typical values of adult body mass from the

145 literature [31, 32]. We also considered mean natal dispersal estimates (D_n , in km) [data from
146 33] as a predictor of range shift to account for the hypothesis that D_n affects changes in
147 range size [33-35]. Mean natal dispersal is the arithmetic mean straight-line distance (km) between
148 the location of birds ringed in their year of birth and the location of their subsequent recovery at
149 breeding age [34], defined as the minimum age at first breeding [36]. Mean natal dispersal
150 distance was poorly correlated with the other predictors we considered (supplementary
151 material table S1).

152

153 *(e) Environmental data*

154 We derived mean values of three predictor climate variables from the Climate Research Unit
155 (CRU) monthly climate data [37] for the initial period (T_1) plus six years more before the
156 start of the surveys (1962–1972). We considered the inclusion of these additional years
157 desirable because distributions of birds in a particular breeding season are not independent
158 of the climate conditions in the previous years. Further, we were interested in examining
159 the influence of *climate* and not *weather* on range dynamics, requiring a sufficient number
160 of years over which to derive variables. It is important to note that we are not testing
161 climate change per se; rather, we are interested in the spatial variation in climate among
162 species' areas of occupancy. We calculated all means from the grid cells occupied by each
163 species during the years indicated. Climate variables included: mean minimum temperature
164 in February (°C), mean average temperature in July (°C), and mean total annual precipitation
165 (mm). Our choice of variables reflects those known to impose constraints on bird
166 distributions as a result of widely shared physiological limitations [e.g., 38, 39].

167

168 *(f) Model structure*

169 Given the strong correlations among life history attributes ($|\rho| = 0.377$ to 0.595) and among
170 climate variables ($|\rho| = 0.599$ to 0.788) (supplementary material table S1), we chose to
171 incorporate only the following plausible variables: body mass as an allometric predictor [40,
172 41], and the minimum temperature of the coldest month (February), in various model
173 combinations with clumpiness (i.e., as single-term, additive and interaction models).
174 Further, we repeated predictor combinations in a model set where natal dispersal replaced
175 body mass because these two variables were not strongly correlated (supplementary
176 material table S1), and because they potentially represent different mechanisms explaining
177 biogeographic patterns (using them in separate model sets also maximized our sample
178 sizes). For example, body mass is strongly correlated with the pace of vital rates (e.g.,
179 reproductive output, age at primiparity), whereas natal dispersal capacity represents a
180 species' capacity to alter distribution in response to a changing environment. Despite this
181 correlation, range expansion might be jointly affected by both reproductive potential (clutch
182 size) and dispersal capacity. We therefore considered two more model sets with both body
183 mass (a proxy for clutch size) and natal dispersal (and their interaction) together. Finally, we
184 contrasted the model set by replacing February minimum temperature with annual
185 precipitation to account for the water-limitation aspect of climate that might influence area
186 of occupancy. This substitution approach to define different model sets was necessary to
187 avoid over-parameterizing models with all variables for the relatively small sample size of
188 species considered.

189 Our model set expressed the change in area of occupancy (response) as a function of
190 clumpiness, climate and life history (predictors). We first transformed the counts of grid
191 cells occupied at T_1 and T_2 (R_1 and R_2 , respectively) to proportions by dividing the counts by
192 the total number of UK available grid cells (= 2861). We were primarily interested in

193 explaining variation around the $R_2 \sim R_1$ relationship given an assumption of temporal stability
194 in area of occupancy whereby the future area occupied will be primarily a function of initial
195 area occupied. We therefore included the logit-transformed proportional R_1 in all models as
196 an offset (see below), using proportional R_2 as the response. This accounts for the limitation
197 of range expansion for wide-ranging species.

198 Species represent phylogenetic units with shared evolutionary histories and so
199 treating them as statistically independent in models can violate underlying assumptions and
200 potentially bias results [42]. This was particularly so with our dataset, with approximately
201 70% of species included in the final datasets in the order Passeriformes (see Results). There
202 are currently no maximum-likelihood methods available to incorporate a full phylogeny with
203 a binomial response variable (*cf.* binary data) [43]. We therefore constructed phylogenetic
204 generalized least-squares models implemented by the `pgls` function in the *caper* library
205 [44] in *R* [45], which included phylogenetic structure as a covariance matrix in the linear
206 models. We used a recently published molecular phylogeny for 106 British breeding bird
207 species [46] to obtain the variance-covariance matrix representation of the phylogenetic
208 tree. We assumed a model of trait evolution based on Brownian motion for which trait
209 variance accumulates linearly with time, and the expected covariances of related species are
210 proportional to the amount of shared evolutionary history (phylogenetic branch length) [47,
211 48]. From this matrix, we estimated Pagel's λ , a branch-length scaling parameter that varies
212 between 0 and 1 (low to high phylogenetic signal) [49].

213 The response R_2 is weighted by the total number of available cells in the UK and logit-
214 transformed. We are primarily interested in the effect of the life history, climate and
215 biogeographic fixed effects, so we set the logit-transformed proportional R_1 as an offset
216 variable. The residuals from such a model structure represent the change in area of

217 occupancy such that covariates can be included in the model to explain additional variation
218 in changing area occupied. The model structure can account for the mean-variance
219 relationship changes at the boundaries of the parameter space associated with species
220 occupying small areas being more likely to expand, and species with a large area of
221 occupancy more likely to contract (i.e., because they are already at or near range
222 saturation).

223 We tested the null hypothesis that each potential predictor would have similar effects
224 on the magnitude of range expanders and contractors. To test this, we included interactions
225 between predictor variables and a binary 'direction' factor in the model sets (0 = range
226 contraction; 1 = expansion); statistical support for an interaction effect indicates that the
227 strength or direction (or both) of a predictor in question depends on whether species
228 expanded or contracted in area of occupancy.

229 Examining the residuals of the intercept-only model relative to each predictor
230 considered (supplementary material figure S1) demonstrated a possible non-linear
231 relationship for the two climate variables for both contracting and expanding species. We
232 hypothesized that this non-linearity could arise if more northerly, cold-adapted species
233 responded differently to climate than southern taxa adapted to a warmer climate. Without
234 any obvious biogeographical boundary with which to split the dataset, we elected to
235 examine 'northern' versus 'southern' species separately based on the latitude where
236 approximately half of the species' distributional centroids were to the north (and the other
237 half, to the south). This latitude was 53° 41' 12" N (just south of the city of Leeds), giving 48
238 'northern' and 49 'southern' species. Boxplots of the predictor variables based on this split
239 (supplementary material figure S2) confirmed that these two groups had different values for
240 mean February minimum temperature and annual precipitation (but overlap for mass, natal

241 dispersal and clumpiness) for these two groups. To account for this geographic non-linearity
242 without imposing an arbitrary latitudinal split (and to maximise degrees of freedom), we
243 included a quadratic term in the models for both February minimum temperature and
244 precipitation (implemented using a second-order `poly` function in *R*).

245

246 *(g) Model comparisons*

247 We compared and ranked models using Akaike's information criterion corrected for finite
248 samples (AIC_c) [50]. We quantified the strength of support for each model relative to the
249 entire model set using AIC_c weights (= model probabilities, $wAIC_c$), and its structural
250 goodness-of-fit with per cent deviance explained (%DE). We then calculated standardized
251 coefficients (β_n/SE_n) for each term in each model of the set [51], and then averaged these
252 across all models based on $wAIC_c$ (re-calculating $\sum wAIC_c = 1$ over the models in which each
253 term appeared). The value of these model-averaged, standardized effect sizes provided a
254 relative rank of the importance of each predictor.

255

256 **3. RESULTS**

257 The subset of British terrestrial birds with area of occupancy information was 116 species,
258 where 74 species contracted and 42 expanded (figure 1) from 1968-1972 to 1995-1999. We
259 included all directional changes, no matter how small, because the intensive sampling effort
260 at the coarse scale of 10×10 km grid cells likely means that even small changes in area of
261 occupancy over nearly three decades are biologically meaningful.

262

263 *(a) Conservation concern*

264 Nearly all species we considered are classified globally as ‘Least Concern’ by the IUCN Red
265 List of Threatened species (iucnredlist.org): of the species with contracting area of
266 occupancy, 65 (97 %) were Least Concern, 1 was Data Deficient (*Loxia scotica*) and 1 was not
267 rated (*Carduelis cabaret*); for species that expanded area of occupancy, 47 (96 %) were
268 Least Concern, and 2 were Near-Threatened (*Milvus milvus*, *Sylvia undata*). However, many
269 species were considered as regionally threatened [26]: for contracting species, 36.1 % were
270 ‘Red’ (high conservation concern in the U.K.), 29.5 % ‘Amber’ (moderate conservation
271 concern) and 34.4 % were ‘Green’ (low conservation concern); for expanding species, 5.0 %
272 were Red, 45.0 % were Amber, and 50.0 % were Green. Thus, contracting species were, on
273 average, of higher conservation concern than expanders based on the UK-specific threat
274 classification criteria (full criteria given in supplementary material). This assessment also
275 followed expectations for the relative proportional change in range (ΔR); for range-
276 contracting species, those listed as ‘Red’ had a more negative ΔR than Amber and Green
277 species (figure 2, top panel). Likewise, expanding species in the Red category had the lowest
278 mean ΔR relative to Amber and Green species (figure 2, top panel). The model-averaged,
279 standardized coefficients for the British threat status by direction interaction on R_2 (the
280 proportional area of occupancy at Time 2 = 1995-1999) indicated that area of occupancy
281 contracted more for Red-listed species, and expanded more for Amber- and Green-listed
282 species) (figure 2, bottom panel; electronic supplementary material table S3).

283

284 (b) Phylogenetic generalised least-squares models

285 For the 106 species for which a molecular phylogeny was available, estimated Pagel’s λ was
286 0.29 (95% CI: 0.035 to 0.661) and was statistically both > 0 and < 1 (mid-range phylogenetic
287 signal). After accounting for this signal (table 1) in the phylogenetic generalised least-

288 squares models, our predictors explained up to > 50% of the deviance in bird area of
289 occupancy across model combinations (note: final sample size after accounting for missing
290 data was 97 species, of which 57 contracted and 40 expanded; table1). Coefficients for the
291 saturated model of each combination are presented in supplementary material table S4.

292 Overall, models including temperature explained around double the deviance in
293 changing area of occupancy than models including precipitation (table 1). Accordingly, the
294 quadratic term for minimum February temperature had the strongest effect on changing
295 area of occupancy across models in a set (table 1 & figure 3), but the direction of its effect
296 varied depending on whether the species were cold- (northerly) or warm-adapted
297 (southerly). Warmer winters resulted in a greater probability of both contracting and
298 expanding for northerly species, but a lower probability of changing the area of occupancy
299 for southerly species (figure 3 and supplementary material figure S4). In contrast, greater
300 annual precipitation resulted in less changing area of occupancy in northerly species, but
301 both greater contraction and expansion in southerly species (table 1). Our prediction of
302 changing area of occupancy being limited by temperature and precipitation appears to be
303 upheld, but with this being conditional on whether UK bird species are cold- (northerly
304 distributed) or warm-adapted (southerly distributed). Southerly species showed reduced
305 change in area of occupancy in drier and warmer climates, whereas northerly species
306 changed the least in colder, wetter environments.

307 Body mass and dispersal had comparatively weaker (but consistent) effects on range
308 shift; increasing body mass and natal dispersal resulted in a reduced probability of both
309 contracting or expanding area of occupancy (figure 3). There was little evidence for an
310 interaction between body mass and natal dispersal on change both in terms of model
311 ranking and deviance explained (supplementary material table S5). Finally, the degree of

312 population fragmentation as measured by the clumpiness index consistently demonstrated
313 that greater fragmentation led to a higher probability of expanding area of occupancy, but
314 the effect on contraction was weaker (figure 3). Overall, models including interactions with
315 direction (contraction or expansion) and the fixed effects considered were poorly supported
316 (table 1).

317

318 **4. DISCUSSION**

319 After accounting statistically for the complexity and non-linearity of the data, our results
320 demonstrate two key aspects of changing area of occupancy for British birds between the
321 1970s and the 1990s. First, the predictors with the most influence on range shift were those
322 describing climate. This relationship depended on the distribution of the species considered,
323 and therefore likely reflects a degree of local adaptation. Northern species were more likely
324 to contract or expand their ranges when minimum winter temperatures were warmer and
325 annual precipitation lower, whereas southern species changed more under opposite
326 conditions (colder and wetter). This could suggest that warming winters [52] might be
327 leading more cold-adapted (northern) species to change their area of occupancy, such as
328 can occur when birds alter their northern and southern range margins differentially in
329 response to a warming climate [53]. The effect of precipitation also suggests that drought
330 could potentially play a similar role in changing the area of occupancy of cold- and wet-
331 adapted species.

332 The second, and somewhat surprising, main finding was that the predictors we
333 considered generally had similar effects regardless of the direction of the change
334 (contraction versus expansion). Our prediction that faster life histories should result in a
335 greater capacity for expansion was upheld (figure 3), and we found that species with slower

336 life histories resisted range contraction. The latter trend might indicate that having a slow
337 life history could buffer a species from environmental change, whereas species with more
338 rapid turn-over could be strongly forced to alter distributions [54].

339 On the other hand, a higher natal dispersal capacity appeared to limit range
340 contractions as expected, but entirely counter-intuitive to our predictions, it also correlated
341 with a lower probability of range expansion. The former result here adheres to accepted
342 conservation-biology principles [55]. In contrast, the latter result appears to contradict
343 known mechanisms of range expansion [56, 57], and supports the idea that local context is
344 more important than life-history or ecological traits *per se* in determining decadal patterns
345 of changing area of occupancy in birds. Indeed, rapid expansion can arise when a previously
346 limiting condition is removed [e.g., forest pest expansion as winter severity decreases; 58].
347 In Britain, as in many parts of Europe, large areas of former agricultural land have been
348 abandoned during the last 50 years [59, 60], leading to an increase in secondary forest and
349 shrubland cover. For some forest and shrubland bird species, this landscape change might
350 have provided increasing areas of suitable habitat and/or improved connectivity for
351 previously fragmented and isolated subpopulations. The obvious exception is farmland
352 birds, where agricultural abandonment is thought to be a substantial cause of decline [59].
353 In our sample, a similar percentage of species in both change categories were classed as
354 'forest', 'woodland' or 'shrub' species (expanders = 64.0 %; contractors = 64.1 %;
355 classifications from [18, 29]), even though contractors had a higher percentage of 'artificial'
356 (i.e., including farms, plantations, suburban, and other such modified habitats), 'grassland'
357 and 'plains' species than expanders (26.9 and 14 %, respectively). Such differences suggest
358 that 'farmland' birds might have responded negatively to agricultural abandonment,
359 whereas other habitat specialists could have benefited.

360 Contrary to expectation however, population clumpiness affected the change in area
361 of occupancy only for contracting species. Thus, species with more fragmented ranges
362 tended to have greater range expansions, even when the effects of initial area of occupancy
363 were offset. Scattered populations are often separated into isolated, small subpopulations
364 subject to high probability of extirpation as a result of localized stochastic events [61, 62]. In
365 contrast, the influence of fragmentation on expanding birds might be mechanistically
366 different. For species with highly fragmented sub-populations that become more connected
367 following some favourable environmental condition, a rapid expansion might become
368 possible as local sub-population limitations (e.g., Allee effects, inbreeding depression) [63]
369 are overcome [64].

370 Although none of the species we assessed is listed as globally threatened, this region-
371 specific threat assessment showed species of highest UK conservation concern to exhibit
372 either the greatest range contractions or lowest range expansions (figure 2) compared to
373 species in low threat categories. Admittedly, this result is partially expected given that at
374 least some of the assessments are based partially on range contractions ('Red' species: at
375 least 50 % contraction of UK breeding range; 'Amber' species: 25 to 49 % contraction of UK
376 breeding range) [26]. However, UK threatened species did not always contract during the
377 interval we investigated, nor did expanding species universally belong to the lowest threat
378 categories.

379 Despite relying on data describing changing area of occupancy for one of the best-
380 studied vertebrate assemblages, there are several caveats regarding the transferability of
381 our results to other biogeographical regions. First, the more widespread a species, the lower
382 the probability that its range will expand further. As species occupy an increasing proportion
383 of their UK range, their overall susceptibility to UK range-wide depletions diminishes, thus

384 buffering them from range contraction. These same widespread species are also ultimately
385 limited by the amount of remaining suitable habitat and by decreasing habitat suitability at
386 range margins [65, 66], such that expansion becomes more and more unlikely as the
387 realized niche is gradually used up given the available landscape. While we accounted for
388 this problem partially using the logit of proportional area of occupancy, focussing strictly on
389 UK populations somewhat limits inference. Second, the large extent to which British
390 landscapes had already been modified prior to the 1970s means that British bird species'
391 distributions have already been shaped by human-dominated or managed landscapes. This
392 suggests that the area of occupancy contractions between the 1970s and 1990s might
393 represent late-stage processes for the remaining, most-resilient species that persisted
394 through the worst environmental changes of the last few centuries to millennia.
395 Distributional attributes that reflect isolation, local extinction debt [67] and Allee effects
396 [68] are probably more important once the most disturbance-sensitive species have already
397 disappeared (as they have in the UK). Third, most British bird species are migratory [31] in
398 contrast to most bird species globally that are sedentary, particularly in the tropics [69].

399 Future investigations into the processes governing the change in area of occupancy by
400 birds would be aided by data measuring contemporaneous land-use change between study
401 periods, because this would permit a further categorization of species in terms of the
402 change in relative habitat availability. In our study, detailed land-use data were unavailable
403 for the earlier period (1968-1972), so we were unable to assess this component. Further,
404 global metrics of threat (most of our study species were IUCN Least Concern) might fail to
405 encapsulate regional changes in area of occupancy, emphasizing the importance of using
406 robust regional metrics of threat [including IUCN regional categories, e.g., 70] as proxies for
407 regional range dynamics whenever they are available. Overall, our study provides a valuable

408 guide for predicting future range dynamics, and/or modifying expectations from species
409 distribution models, especially for taxa within already highly modified landscapes with few
410 associated life-history or local climate data. We have shown that a relatively simple
411 assessment of body mass, mean climate attributes, area of occupancy and distributional
412 clumpiness can explain a large component of the variation in species' range dynamics,
413 without need for recourse to difficult-to-measure traits. This potential short-cut needs
414 verification on other taxa and biogeographical regions to be helpful for resource-limited
415 conservation projects.

416

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Table 1. Five top-ranked generalized least-squares models incorporating phylogenetic non-independence to explain variation in R_2 (proportional area of occupancy at $T_2 = 1995-1999$), incorporating life history (mass [M] or natal dispersal [D_n]), climate (quadratic February minimum temperature [$F+F^2$] or precipitation [$P+P^2$] term) and clumpiness (Cl) as predictors. Main model combinations are (i) $M + (F+F^2) + Cl$, (ii) $M + (P+P^2) + Cl$, (iii) $D_n + (F+F^2) + Cl$ and (iv) $D_n + (P+P^2) + Cl$, with all variants testing for interactions with the direction (Dir) of change (contraction or expansion). All models included the logit-transformed proportional R_1 (range size at $T_1 = 1968-1972$) as an offset variable. Listed are maximum log-likelihood (LL), parameter count (k), change in Akaike's information criterion (corrected for sample size) relative to the top-ranked model (ΔAIC_c), model probabilities ($wAIC_c$) and per cent deviance explained (%DE) relative to the $R_2 \sim 1$ 'null' model. Analyses include 97 British birds (57 contractors, 40 expanders) for which full data (including a molecular phylogeny) were available.

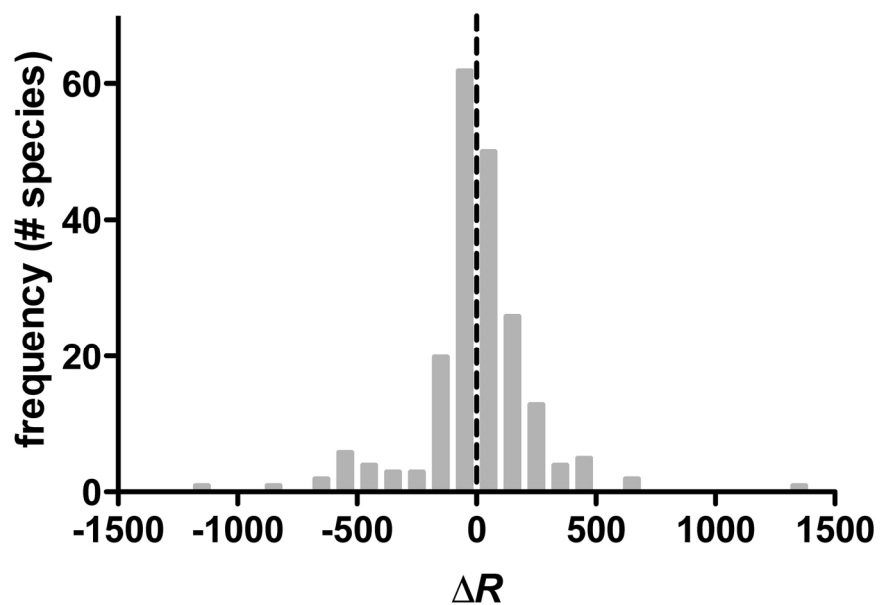
Model	LL	k	ΔAIC_c	$wAIC_c$	%DE
(i) Mass+Temp+Clumpiness					
$\sim(F+F^2)+Dir$	-168.571	4	0	0.386	48.5
$\sim M+(F+F^2)+Dir$	-167.890	5	0.863	0.251	48.6
$\sim(F+F^2)+Cl+Dir$	-168.563	5	2.208	0.128	47.9
$\sim(F+F^2)\times Dir$	-167.874	6	3.104	0.082	48.1
$\sim M+(F+F^2)+Cl+Dir$	-167.890	6	3.136	0.080	48.1
(ii) Mass+Precip+Clumpiness					
$\sim(P+P^2)+Dir$	-186.169	4	0	0.235	25.9
$\sim(P+P^2)+Cl+Dir$	-185.094	5	0.074	0.226	26.7
$\sim M+(P+P^2)+Cl+Dir$	-184.437	6	1.033	0.140	26.9
$\sim M+(P+P^2)+Dir$	-185.674	5	1.233	0.127	25.9
$\sim M+(P+P^2)+(Cl\times Dir)$	-183.399	7	1.284	0.124	27.7
(iii) Natal Disp+Temp+Clumpiness					
$\sim D_n+(F+F^2)+Dir$	-165.109	5	0	0.464	51.5
$\sim(D_n\times Dir)+(F+F^2)+Cl$	-163.749	7	1.880	0.181	51.8
$\sim D_n+(F+F^2)+Cl+Dir$	-165.106	6	2.267	0.149	51.0
$\sim D_n+((F+F^2)\times Dir)+Cl$	-163.709	8	4.176	0.058	51.3
$\sim D_n+(F+F^2)+(Cl\times Dir)$	-164.920	7	4.221	0.056	50.6
(iv) Natal Disp+Precip+Clumpiness					
$\sim D_n+(P+P^2)+Cl+Dir$	-182.970	6	0	0.219	29.1
$\sim D_n+(P+P^2)+Dir$	-184.114	5	0.014	0.218	28.2
$\sim D_n+(P+P^2)+(Cl\times Dir)$	-181.931	7	0.246	0.194	29.8
$\sim(D_n\times Dir)+(P+P^2)+Cl$	-182.325	7	1.034	0.131	29.3
$\sim(P+P^2)+Dir$	-186.169	4	1.900	0.085	25.9

Figure Captions

Figure 1. Histogram of the relative proportional change in area of occupancy (x-axis numbers refer to the change in number of occupied 10×10 km geographical cells) of 116 terrestrial bird species in the United Kingdom between 1968-1972 and 1995-1999. Negative or positive ΔR indicates species whose area of occupancy contracted or expanded between the two periods, respectively.

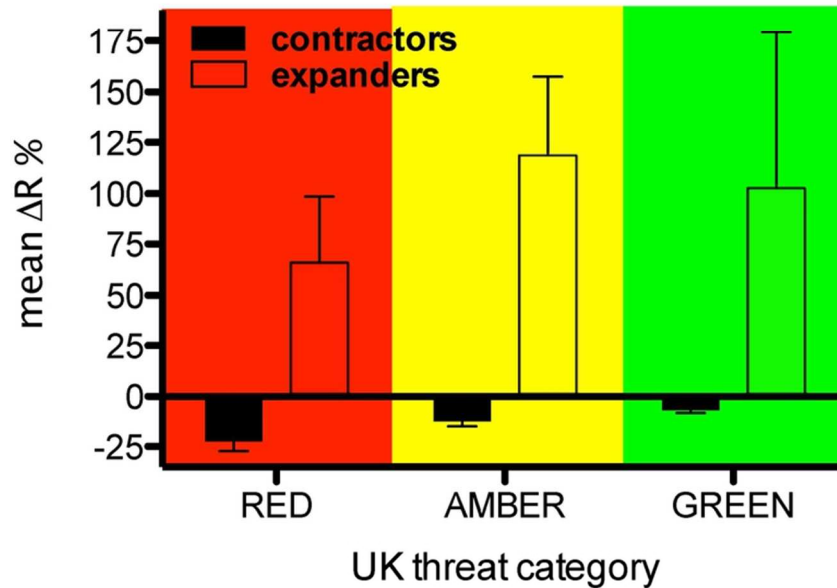
Figure 2. (top panel) Mean (\pm standard error) percentage change in area of occupancy (ΔR) for contracting (negative ΔR , 74 species) and expanding (positive ΔR , 42 species) birds according to their United Kingdom regional threat assessment [26]: Red = high conservation concern; Amber = moderate concern; Green = least concern. (bottom panel) Model-averaged, standardized effect sizes (β_n/SE_n) of threat status and direction (contraction or expansion) interactions on range shift (i.e., proportional area of occupancy at Time 2 (R_2) after controlling for proportional area of occupancy at Time 1 (R_1)). See supplementary material Table S2 for model ranking.

Figure 3. Model-averaged, standardized coefficients for each interaction considered in the phylogenetic generalized least-squares model sets. Negative values indicate a negative relationship to proportional area of occupancy at Time 2 (R_2). β_n estimated model term (n) coefficient, SE_n = term standard error, M = body mass (g, \log_{10} -transformed), F & F^2 = quadratic mean minimum February temperature ($^{\circ}\text{C}$), Cl = clumpiness (proportion of adjacencies), P & P^2 = quadratic annual precipitation (mm), D_n = natal dispersal (km). Analyses include 116 British birds (57 contractors, 40 expanders). See modelling metrics in Table 1. Shown in text are the directions of the most influential predictors of change for contractors and expanders (for climate variables, directions shift according to the quadratic relationship, which approximates a north (N)-south (S) split). Greyed text indicates weaker influence.



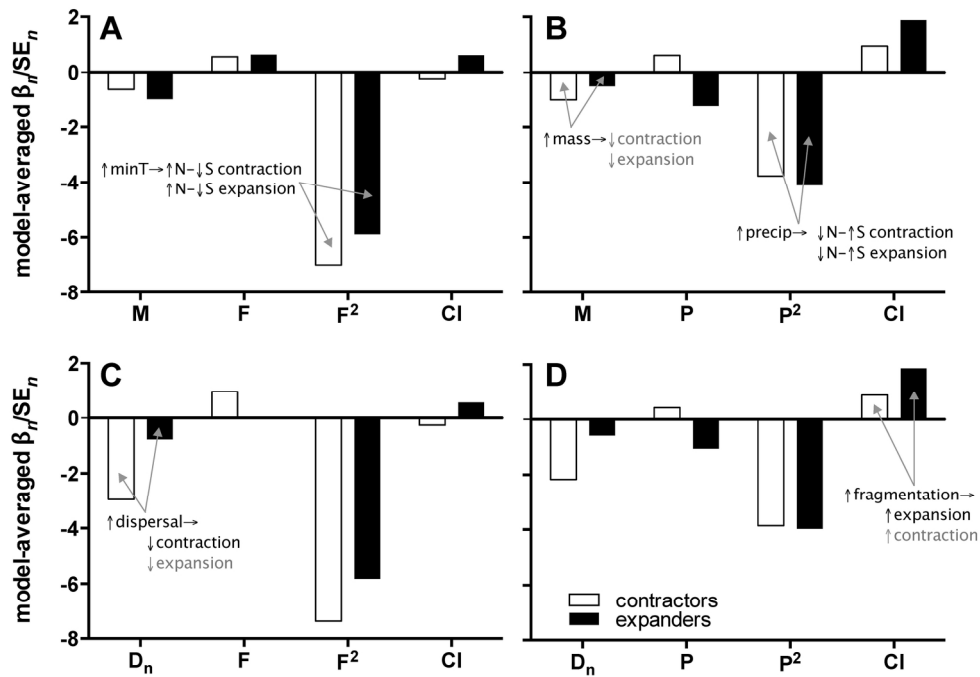
Histogram of the relative proportional change in area of occupancy (x-axis numbers refer to the change in number of occupied 10×10 km geographical cells) of 116 terrestrial bird species in the United Kingdom between 1968-1972 and 1995-1999. Negative or positive ΔR indicates species whose area of occupancy contracted or expanded between the two periods, respectively.

171x126mm (300 x 300 DPI)



(top panel) Mean (\pm standard error) percentage change in area of occupancy (ΔR) for contracting (negative ΔR , 74 species) and expanding (positive ΔR , 42 species) birds according to their United Kingdom regional threat assessment [26]: Red = high conservation concern; Amber = moderate concern; Green = least concern. (bottom panel) Model-averaged, standardized effect sizes (β_n/SE_n) of threat status and direction (contraction or expansion) interactions on range shift (i.e., proportional area of occupancy at Time 2 (R_2) after controlling for proportional area of occupancy at Time 1 (R_1)). See supplementary material Table S2 for model ranking.

77x54mm (300 x 300 DPI)



Model-averaged, standardized coefficients for each interaction considered in the phylogenetic generalized least-squares model sets. Negative values indicate a negative relationship to proportional area of occupancy at Time 2 (R2). β_n estimated model term (n) coefficient, SE_n = term standard error, M = body mass (g, log₁₀-transformed), F & F² = quadratic mean minimum February temperature (°C), CI = clumpiness (proportion of adjacencies), P & P² = quadratic annual precipitation (mm), D_n = natal dispersal (km). Analyses include 116 British birds (57 contractors, 40 expanders). See modelling metrics in Table 1. Shown in text are the directions of the most influential predictors of change for contractors and expanders (for climate variables, directions shift according to the quadratic relationship, which approximates a north (N)-south (S) split). Greyed text indicates weaker influence.

176x128mm (300 x 300 DPI)