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

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Geographical range dynamics are driven by the joint effects of abiotic factors, human ecosystem modifications, biotic interactions and the intrinsic organismal responses to these. However, the relative contribution of each component remains largely unknown. Here, we compare the contribution of life-history attributes, broad-scale gradients in climate and geographical context of species' historical ranges, as predictors of recent changes in area of occupancy for 116 terrestrial British breeding birds (74 contractors, 42 expanders) between the early 1970s and late 1990s. Regional threat classifications demonstrated that the species of highest conservation concern showed both the largest contractions and the smallest expansions. Species responded differently to climate depending on geographical distribution—northern species changed their area of occupancy (expansion or contraction) more in warmer and drier regions, whereas southern species changed more in colder and wetter environments. Species with slow life history (larger body size) tended to have a lower probability of changing their area of occupancy than species with faster life history, whereas species with greater natal dispersal capacity resisted contraction and, counterintuitively, expansion. Higher geographical fragmentation of species' range also increased expansion probability, possibly indicating a release from a previously limiting condition, for example through agricultural abandonment since the 1970s. After accounting statistically for the complexity and nonlinearity of the data, our results demonstrate two key aspects of changing area of occupancy for British birds: (i) climate is the dominant driver of change, but direction of effect depends on geographical context, and (ii) all of our predictors generally had a similar effect regardless of the direction of the change (contraction versus expansion). Although we caution applying results from Britain's highly modified and well-studied bird community to other biogeographic regions, our results do indicate that a species' propensity to change area of occupancy over decadal scales can be explained partially by a combination of simple allometric predictors of life-history pace, average climate conditions and geographical context.

1. Introduction

Understanding the complexities of range dynamics—why (and by what amount) a species' range changes over time—is an essential component for predicting future human influences on biodiversity. Range dynamics vary across species and space owing to the joint effects of abiotic factors, biotic interactions, human ecosystem modification, and intrinsic organismal responses to these [1,2].

However, a mismatch exists between studies seeking to improve understanding of the historical and ecological determinants of range dynamics, and those predicting future range changes. With increasing emphasis in ecology to predict the future distributions of species in response to climate disruption and environmental degradation [3,4], projections are typically based on expected changes in climatic factors that correlate with species' distributions (e.g. [5], but see [6]). This contrasts starkly with historical reconstructions of species' distributions that generally infer range determinants based on species-specific demographic and life-history traits (e.g. [1,7–9]).

A vexing question therefore remains—which drivers of range dynamics, if any, are more important for predicting patterns of distributional change? While ecological and life-history traits appear to predispose certain species to range contraction or expansion as local conditions change [10–12], a species' area of occupancy and its configuration, such as the proximity to barriers, niche breadth, local climate severity and landscape or population fragmentation, can potentially override a species' susceptibility to changing its range [13–15]. The problem is that there are few sufficiently comprehensive datasets that combine distributional, extrinsic (e.g. climate, land-use change) and intrinsic (e.g. life history/ecology) attributes for enough species to lend themselves to broad-scale analyses that can tease apart the relative influence of specific drivers.

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

Given the comprehensiveness of the available data, we are able to test three hypotheses simultaneously. (i) We tested whether variation in changing area of occupancy can be explained partly by life-history attributes that are expected to reflect ecological responsiveness. Here, we consider both body mass as a correlate of the pace of life history ('fast' versus 'slow' species) and natal dispersal (capacity to recolonize). In the face of rapid, human-induced global change, we predict that species with 'slower' life histories (larger bodied, longer lived species with slower reproductive rates) will be more prone to range contraction, while species with faster life histories will have a greater ability to expand their ranges [21,22]. We predict that natal dispersal capacity will be positively related to range expansion (i.e. species with higher dispersal have a greater capacity to expand if conditions permit), and negatively related to range contraction (i.e. a low dispersal capacity increases a species' susceptibility to habitat fragmentation, and further contraction of its area of

occupancy). Likewise, a species' threat status might indicate its propensity to change its area of occupancy, with threatened species more likely to contract, and non-threatened species more likely to expand their range.

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

2. Material and methods

(a) Bird distribution data

We compiled the area of occupancy of British birds for two periods of time, spaced nearly three decades apart: 1968–1972 (T_1) and 1995–1999 (T_2). We accumulated a total of 116 species (representing the orders Accipitriformes ($n = 14$ species), Columbiformes ($n = 5$), Galliformes ($n = 8$), Passeriformes ($n = 83$) and Strigiformes ($n = 6$)) after excluding predominately aquatic (especially marine) birds owing to the difficulty in defining explicit areas of occupancy in these groups [25]. We denoted the area of occupancy as the number of 10 km² cells of occupied on the mainland (see Introduction) in T_1 and T_2 as R_1 and R_2 , respectively.

(b) Species threat status

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

(c) Range fragmentation ('clumpiness')

Initially, we examined a previously published [27] index of the nearest-neighbour 'contagion' (C_i) as a measure of population fragmentation, but this was highly correlated (Spearman's $\rho = 0.965$) with R_1 (see correlations and calculation of C_i in the electronic supplementary material, table S1). We therefore opted for another measure of distributional 'clumpiness' (CI), calculated using FRAGSTATS v. 4 [28]. Whereas other measures of habitat fragmentation are highly correlated with area of occupancy (e.g. contagion), CI is independent of R_1 (Spearman's $\rho = -0.020$; electronic supplementary material, table S1). Clumpiness is calculated using the proportion of occupied cells in T_1 that lie adjacent to other occupied cells in T_1 ('adjacencies'). The calculation is relative to the expected number of adjacencies given a spatially random distribution of the same number of occupied cells, which largely accounts for the positive correlation between the number of adjacencies and total area of occupancy. Larger patches with compact shapes contain a higher proportion of like

adjacencies than landscapes dominated by smaller patches with complex shapes. A highly contagious (aggregated) landscape will contain a higher percentage of like adjacencies (maximum = 1), whereas a highly fragmented (disaggregated) landscape will contain proportionately fewer like adjacencies (minimum value = -1). A landscape with $CI = 0$ indicates a spatially random distribution (see more details in [28]). There was no evidence for either a monotonic or monomodal (quadratic) relationship of the CI index with the logit-transformed (see below) proportional R_1 (i.e. expressed as a proportion of the total number of available grid cells; electronic supplementary material, table S2).

(d) Bird life-history data

We compiled life-history traits for birds using a comprehensive survey of the ornithological literature [18] that is updated regularly (e.g. [29]). A description of the online sources of the information collected is available [18,29]. To maximize sample size (the number of species for which trait data exist), we focused initially on clutch size, body mass (grams) and longevity (months) traits only, all of which are among the most robust predictors of slow to fast life-history variation in birds [30]. However, body mass, clutch size and longevity were all highly correlated (electronic supplementary material, table S1), so we present further analyses with mass alone. For each species, we used data on species-typical values of adult body mass from the literature [31,32]. We also considered mean natal dispersal estimates (D_n , in kilometres) (data from [33]) as a predictor of range shift to account for the hypothesis that D_n affects changes in range size [33–35]. Mean natal dispersal is the arithmetic mean straight-line distance (kilometres) between the location of birds ringed in their year of birth and the location of their subsequent recovery at breeding age [34], defined as the minimum age at first breeding [36]. Mean natal dispersal distance was poorly correlated with the other predictors we considered (electronic supplementary material, table S1).

(e) Environmental data

We derived mean values of three predictor climate variables from the Climate Research Unit monthly climate data [37] for the initial period (T_1) plus 6 years more before the start of the surveys (1962–1972). We considered the inclusion of these additional years desirable because distributions of birds in a particular breeding season are not independent of the climate conditions in previous years. Further, we were interested in examining the influence of *climate* and not *weather* on range dynamics, requiring a sufficient number of years over which to derive variables. It is important to note that we are not testing climate change *per se*; rather, we are interested in the spatial variation in climate among species' areas of occupancy. We calculated all means from the grid cells occupied by each species during the years indicated. Climate variables included: mean minimum temperature in February (°C), mean average temperature in July (°C), and mean total annual precipitation (millimetres). Our choice of variables reflects those known to impose constraints on bird distributions as a result of widely shared physiological limitations (e.g. [38,39]).

(f) Model structure

Given the strong correlations among life-history attributes ($|\rho| = 0.377–0.595$) and among climate variables ($|\rho| = 0.599–0.788$) (electronic supplementary material, table S1), we chose to incorporate only the following plausible variables: body mass as an allometric predictor [40,41], and the minimum temperature of the coldest month (February), in various model combinations with CI (i.e. as single-term, additive and interaction models). Further, we repeated predictor combinations

in a model set where natal dispersal replaced body mass because these two variables were not strongly correlated (electronic supplementary material, table S1), and because they potentially represent different mechanisms explaining biogeographic patterns (using them in separate model sets also maximized our sample sizes). For example, body mass is strongly correlated with the pace of vital rates (e.g. reproductive output, age at primiparity), whereas natal dispersal represents a species' capacity to alter distribution in response to a changing environment. Despite these correlations, range expansion might be jointly affected by both reproductive potential (clutch size) and natal dispersal. We therefore considered two more model sets with both body mass (a proxy for clutch size) and natal dispersal (and their interaction) together. Finally, we contrasted the model set by replacing February minimum temperature with annual precipitation to account for the water-limitation aspect of climate that might influence area of occupancy. This substitution approach to define different model sets was necessary to avoid over-parametrizing models with all variables for the relatively small sample size of species considered.

Our model set expressed the change in area of occupancy (response) as a function of CI , climate and life history (predictors). We first transformed the counts of grid cells occupied at T_1 and T_2 (R_1 and R_2 , respectively) to proportions by dividing the counts by the total number of UK available grid cells (i.e. 2861). We were primarily interested in explaining variation around the $R_2 \sim R_1$ relationship given an assumption of temporal stability in area of occupancy whereby the future area occupied will be primarily a function of initial area occupied. We therefore included the logit-transformed proportional R_1 in all models as an offset (see below), using proportional R_2 as the response. This accounts for the limitation of range expansion for wide-ranging species.

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

The response R_2 is weighted by the total number of available cells in the UK and logit-transformed. We are primarily interested in the effect of the life history, climate and biogeographic fixed effects, so we set the logit-transformed proportional R_1 as an offset variable. The residuals from such a model structure represent the change in area of occupancy such that covariates can be included in the model to explain additional variation in changing area occupied. The model structure can account for the mean–variance relationship changes at the boundaries of the parameter space associated with species occupying small areas being more likely to expand, and species with a large area of occupancy more likely to contract (i.e. because they are already at or near range saturation).

We tested the null hypothesis that each potential predictor would have similar effects on the magnitude of range expanders and contractors. To test this, we included interactions between

predictor variables and a binary 'direction' factor in the model sets (0 = contraction; 1 = expansion); statistical support for an interaction effect indicates that the strength or direction (or both) of a predictor in question depends on whether species expanded or contracted in area of occupancy.

Examining the residuals of the intercept-only model relative to each predictor considered (electronic supplementary material, figure S1) demonstrated a possible nonlinear relationship for the two climate variables for both contracting and expanding species. We hypothesized that this nonlinearity could arise if more northerly, cold-adapted species responded differently to climate than southern taxa adapted to a warmer climate. Without any obvious biogeographic boundary with which to split the dataset, we elected to examine 'northern' versus 'southern' species separately based on the latitude where approximately half of the species' distributional centroids were to the north (and the other half, to the south). This latitude was 53° 41' 12" N (just south of the city of Leeds), giving 48 'northern' and 49 'southern' species. Boxplots of the predictor variables based on this split (electronic supplementary material, figure S2) confirmed that these two groups had different values for mean February minimum temperature and annual precipitation (but overlap for mass, natal dispersal and CI) for these two groups. To account for this geographical nonlinearity without imposing an arbitrary latitudinal split (and to maximize degrees of freedom), we included a quadratic term in the models for both February minimum temperature and precipitation (implemented using a second-order poly function in R).

(g) Model comparisons

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

3. Results

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

(a) Conservation concern

Nearly, all species we considered are classified globally as 'least concern' by the IUCN Red List of Threatened Species (iucnredlist.org): of the species with contracting area of occupancy, 65 (97%) were least concern, one was data deficient (*Loxia scotica*) and one was not rated (*Carduelis cabaret*); for species that expanded area of occupancy, 47 (96%) were least concern and two were near-threatened (*Milvus milvus*, *Sylvia undata*). However, many species were considered as regionally threatened [26]: for contracting species, 36.1% were 'red' (high conservation concern in the UK), 29.5% 'amber' (moderate conservation concern) and 34.4% were

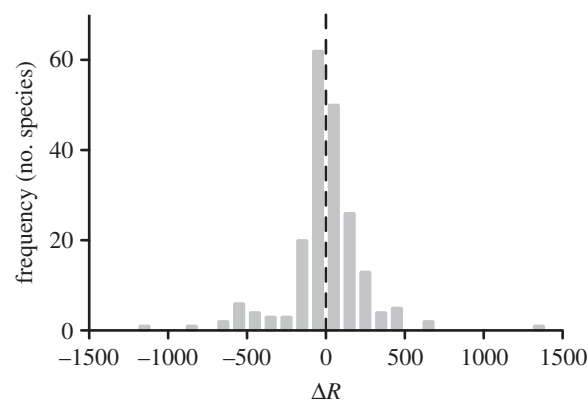


Figure 1. Histogram of the relative proportional change in area of occupancy (x-axis numbers refer to the change in number of occupied 10 × 10 km geographical cells) of 116 terrestrial bird species in the UK between 1968–1972 and 1995–1999. Negative or positive ΔR indicates species whose area of occupancy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

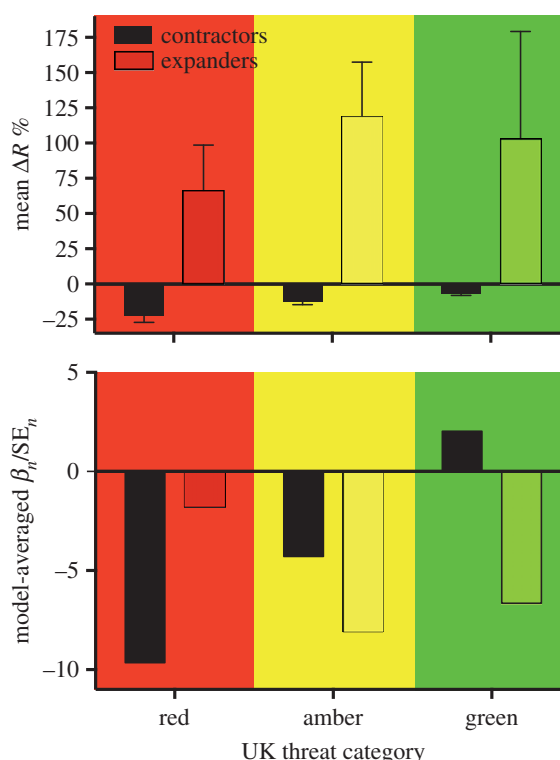


Figure 2. (top panel) Mean (\pm s.e.) percentage change in area of occupancy (ΔR) for contracting (negative ΔR , 74 species) and expanding (positive ΔR , 42 species) birds according to their UK regional threat assessment [26]: red, high conservation concern; amber, moderate concern; green, least concern. (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 T_2 (R_2) after controlling for proportional area of occupancy at T_1 (R_1)). See the electronic supplementary material, table S2 for model ranking. (Online version in colour.)

'green' (low conservation concern); for expanding species, 5.0% were red, 45.0% were amber and 50.0% were green. Thus, contracting species were, on average, of higher conservation concern than expanders based on the UK-specific threat classification criteria (full criteria given in the electronic supplementary material). This assessment also followed expectations for the relative proportional change in range (ΔR); for range-contracting species, those listed as 'red' had a more negative ΔR than amber and green species (figure 2, top panel). Likewise, expanding species in the red category

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) $M + (F + F^2) + \text{Cl}$, (ii) $M + (P + P^2) + \text{Cl}$, (iii) $D_n + (F + F^2) + \text{Cl}$ and (iv) $D_n + (P + P^2) + \text{Cl}$, with all variants testing for interactions with the direction (Dir) of change (contraction or expansion as a binary predictor). (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 finite sample size) relative to the top-ranked model (ΔAIC_c), model probabilities ($w\text{AIC}_c$) and %DE relative to the $R_2 \sim 1$ 'null' model. Analyses include 97 British birds (57 contractors and 40 expanders) for which full data (including a molecular phylogeny) were available.)

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

had the lowest mean ΔR relative to amber and green species (figure 2, top panel). The model-averaged, standardized coefficients for the British threat status by direction interaction on R_2 (the proportional area of occupancy at $T_2 = 1995-1999$) indicated that area of occupancy contracted more for red-listed species, and expanded more for amber- and green-listed species (figure 2, bottom panel; electronic supplementary material, table S3).

(b) Phylogenetic generalised least-squares models

For the 106 species for which a molecular phylogeny was available, estimated Pagel's λ was 0.29 (95% CI: 0.035–0.661) and was statistically both greater than 0 and less than 1 (mid-range phylogenetic signal). After accounting for this signal (table 1) in the phylogenetic generalized least-squares models, our predictors explained up to greater than 50% of the deviance in bird area of occupancy across model combinations (note: final sample size after accounting for missing data was 97 species, of which 57 contracted and 40 expanded; table 1).

Coefficients for the saturated model of each combination are presented in the electronic supplementary material, table S4.

Overall, models including temperature explained around double the deviance in changing area of occupancy than models including precipitation (table 1). Accordingly, the quadratic term for minimum February temperature had the strongest effect on changing area of occupancy across models in a set (table 1 and figure 3), but the direction of its effect varied depending on whether the species were cold- (northern) or warm-adapted (southern). Warmer winters resulted in a greater probability of both contracting and expanding for northern species, but a lower probability of changing the area of occupancy for southern species (figure 3 and electronic supplementary material, figure S4). By contrast, greater annual precipitation resulted in less changing area of occupancy in northern species, but both greater contraction and expansion in southern species (table 1). Our prediction of changing area of occupancy being limited by temperature and precipitation appears to be upheld, but with this being conditional on whether UK bird species are cold- (northerly distributed) or warm-adapted

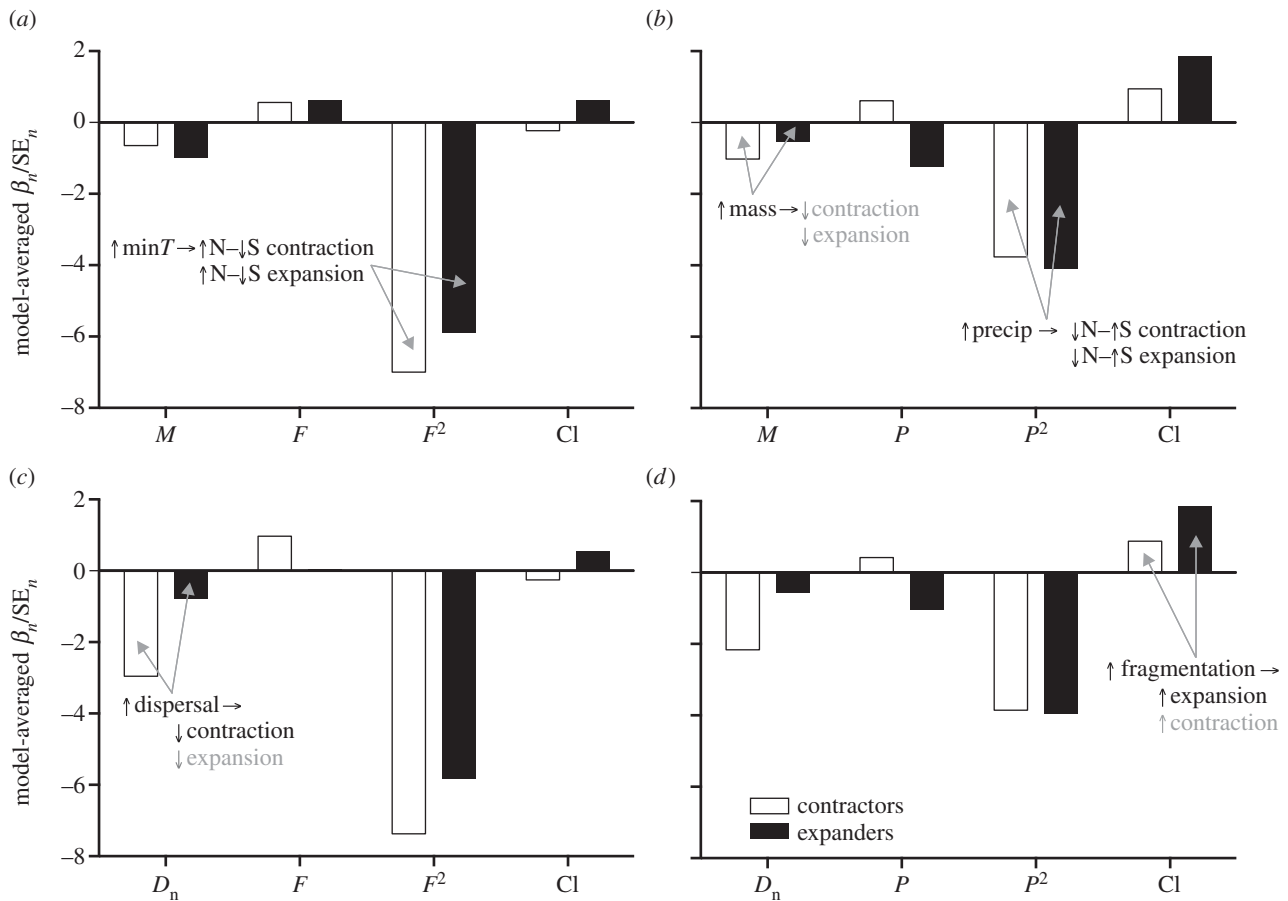


Figure 3. Model-averaged, standardized coefficients for each interaction considered in the phylogenetic generalized least-squares model sets used to model change in area of occupancy in British birds. Negative values indicate a negative relationship to proportional area of occupancy at T_2 (R_2). β_n = estimated model term (n) coefficient, SE_n = term standard error, M = body mass (grams, \log_{10} -transformed), F and F^2 = quadratic mean minimum February temperature ($^{\circ}\text{C}$), CI = dumppiness (proportion of adjacencies), P and P^2 = quadratic annual precipitation (millimetres), D_n = natal dispersal (kilometres). Analyses include 97 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. Panels (a) to (d) correspond to model contrasts (i) to (iv) in table 1, respectively.

(southerly distributed). Southern species showed reduced change in area of occupancy in drier and warmer climates, whereas northern species changed the least in colder, wetter environments.

Body mass and dispersal had comparatively weaker (but consistent) effects on change in area of occupancy; increasing body mass and natal dispersal resulted in a reduced probability of either contracting or expanding area of occupancy (figure 3). There was little evidence for an interaction between body mass and natal dispersal on change, both in terms of model ranking and deviance explained (electronic supplementary material, table S5). Finally, the degree of population fragmentation as measured by the CI index consistently demonstrated that greater fragmentation led to a higher probability of expanding area of occupancy, but the effect on contraction was weaker (figure 3). Overall, models including interactions with direction (contraction or expansion) and the fixed effects considered were poorly supported (table 1).

4. Discussion

After accounting statistically for the complexity and nonlinearity of the data, our results demonstrate two key aspects of changing area of occupancy for British birds between the 1970s and the 1990s. First, the predictors with the most

influence on changing area of occupancy were those describing climate. This relationship depended on the distribution of the species considered, and therefore probably reflects a degree of local adaptation. Northern species were more likely to contract or expand their area of occupancy when minimum winter temperatures were warmer and annual precipitation lower, whereas southern species changed more under opposite conditions (colder and wetter). This could suggest that warming winters [52] might be leading more cold-adapted (northern) species to change their area of occupancy, such as can occur when birds alter their northern and southern range margins differentially in response to a warming climate [53]. The effect of precipitation also suggests that drought could potentially play a similar role in changing the area of occupancy of cold- and wet-adapted species.

The second, and somewhat surprising, main finding was that the predictors we considered generally had similar effects regardless of the direction of the change (contraction versus expansion). Our prediction that faster life histories should result in a greater capacity for expansion was upheld (figure 3), and we found that species with slower life histories resisted range contraction. The latter trend might indicate that having a slow life history could buffer a species from environmental change, whereas species with more rapid turn-over could be strongly forced to alter distributions [54].

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

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

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

Despite relying on data describing changing area of occupancy for one of the best-studied vertebrate assemblages, there are several caveats regarding the transferability of our results to other biogeographic regions. First, the more widespread a species, the lower the probability that

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

Future investigations into the processes governing the change in area of occupancy by birds would be aided by data measuring contemporaneous land-use change between study periods, because this would permit a further categorization of species in terms of the change in relative habitat availability. In our study, detailed land-use data were unavailable for the earlier period (1968–1972), so we were unable to assess this component. Further, global metrics of threat (most of our study species were IUCN Least Concern) might fail to encapsulate regional changes in area of occupancy, emphasizing the importance of using robust regional metrics of threat (including IUCN regional categories, e.g. [70]) as proxies for regional range dynamics whenever they are available. Overall, our study provides a valuable guide for predicting future range dynamics, and/or modifying expectations from species distribution models, especially for taxa within already highly modified landscapes with few associated life-history or local climate data. We have shown that a relatively simple assessment of body mass, mean climate attributes, area of occupancy and distributional clumpiness can explain a large component of the variation in species' range dynamics, without need for recourse to difficult-to-measure traits. This potential short-cut needs verification on other taxa and biogeographic regions to be helpful for resource-limited conservation projects.

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