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4 **Correlates of vulnerability to climate-induced distribution changes in
European avifauna: habitat, migration and endemism**

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Abstract

Accelerated climatic change will alter species' distributions substantially by the end of the 21st Century and studies modeling distribution change using Climatic Envelope Modeling (CEM) are increasingly crucial for understanding long-term biotic implications of climate change. However, most CEM studies generate either all-species means, which are of limited practical use, or copious species-specific predictions that make it hard to draw general conclusions about those groups most vulnerable. Intermediate analyses that are half way between these two extremes are necessary to establish the relative vulnerability of species to change based on factors that can be related directly to policy and practice, including habitat associations and ecological traits such as endemism and migration status. Here we use species-specific CEM data to analyse changes in geographical distribution, range size, and overlap between current and potential ranges, for all 431 bird species breeding regularly in Europe. Future range sizes are predicted to be 80% of current range sizes, with an average overlap of 39%. However, we show that change varies significantly according to habitat, current range size, and endemism status, with no differences according to migration status. Coastal, wetland and upland birds will be significantly worse off under CEM scenarios than birds associated with woodland, farmland and heathland, while urban birds and those using multiple habitats doing best. Birds with small ranges show more severe, and spatially more complex, distribution shifts. The identification of species groups most vulnerable to climate change means that CEM predictions can now be used to inform policy and management, especially where initiatives are based on species grouped according to such variables or where habitat-specific policies are in place.

Keywords: Climate change, Climatic Envelope Models, Distribution shifts, Global warming, Species range.

1 INTRODUCTION

4 Considerable research suggests that accelerated climatic change will alter species' distributions substantially by the
end of the 21st Century. Studies typically: (1) undertake retrospective analyses of recent data; or (2) model possible
future changes. The first approach has already shown significant cross-taxonomic changes in species' distributions
(reviews by Walther *et al.* 2002; Parmesan & Yohe 2003). The second approach typically employs Climatic
Envelope Models (CEMs), which use current range to infer climatic requirements (the 'climatic envelope'), and predict
future distribution by establishing envelope movement under climate change scenarios. As predictions using
8 historical data are necessarily based on extrapolation from existing (often short-term) trends, the CEM approach is
crucial for understanding long-term implications of climate change. Moreover a modeling approach also allows for the
fact that that using historical data to predict future climate-driven changes in species' distributions can be very difficult to
undertake with any level of useful precision, given that likely future climatic changes will likely differ substantially from
12 those witnessed in the recent past. CEM analyses have been undertaken on multiple taxa, including plants (Huntley *et al.*
1995), insects (Hill *et al.* 1999) and mammals (Levinsky *et al.* 2007), and generally predict that northern hemisphere
species' ranges will undergo northwards shift, northward expansion, or southern contraction (Berry *et al.* 2001). If
undertaken carefully, with appropriate caution and appreciation of caveats and limitations (see Discussion), CEM-
16 based studies are the best available guide for informing management and conservation of biodiversity (Hannah *et al.*
2002; Pearson & Dawson 2003). Importantly, CEM data can also be linked to analyses of population change and the
potential for no-analogue communities (Green 2008; Gregory 2009; Holt *et al.* 2011).

Although birds are particularly well-studied with regard to climate change, and there are several studies on
20 climate-induced investigated change in distribution, these are perhaps less well studied than climate-induced
phenological or migratory trends, despite their high ecological importance (Parmesan 2006). In retrospective analyses
Thomas & Lennon (1999) showed a northwards shift for >100 species breeding in the UK; this has subsequently been
found for North American birds (Hitch & Leberg 2007) and Finnish birds (Brommer 2004), but future predictions are
24 surprisingly sparse. In one of the most comprehensive CEM analyses for birds to date, Huntley *et al.* (2007) provided
detailed CEM analyses predicting late 21st century distributions for 431 European breeding species. However, it is hard
to draw general conclusions about factors that are important in determining species' susceptibility to climate change
from detailed species-specific information, and thus identifying species groups that require enhanced monitoring and
28 management is challenging (Miller-Rushing *et al.* 2010). So far, synthesis has been restricted to describing the
magnitude of range changes for birds in different biogeographic sub-regions (Huntley *et al.* 2007) and calculation of
all-species averages in range extent, shift, and overlap (Huntley *et al.* 2008). An intermediate analysis – half way
between the detail of individual species accounts and calculation of all-species averages that enables the vulnerability of
32 different groups of birds to be better understood – is required if climate change predictions are to usefully inform policy
and practice (Brommer, 2008; Huntley *et al.* 2008; Brommer & Møller 2010). This is akin to a guild-based approach
and is of urgent importance to conservationists (Foden *et al.* 2008; Miller-Rushing *et al.* 2010).

Here, we use species-specific CEM data from Huntley *et al.* (2007) to analyse the type of distribution shift,
36 changes in range size, and the amount of overlap between current and potential ranges for all 431 bird species
breeding regularly in Europe with regard to: (1) habitat; (2) current range size; (3) endemism; and (4) migration

status. By indentifying correlates of climate-induced distribution changes, relative vulnerability can be understood (Brommer & Møller, 2010; Miller-Rushing *et al.* 2010). This is addressing similar issues to those considered in a review of likely distribution shifts for tropical birds (Şekercioğlu *et al.* 2012) but within a meta-analysis framework. We link our findings to policy and management (where species are often grouped according to broad environmentally-relevant variables such as habitat type: Gregory *et al.* 2005), by offering recommendations for climate-informed conservation policies.

8

2. METHODS

We used current distribution data and future distribution predictions from Huntley *et al.* (2007). These data showed, for each of 431 species, the presence of breeding in 2618 terrestrial 50x50 km squares of a Universal Transverse Mercator (UTM) grid from Svalbard (North), Crete (South), the Azores (West) and Kazakhstan (East) using records from the European Bird Census Council published previously by Hagemeyer and Blair (1997). Using climate envelope modeling based on the HadCM3 climate change scenario, Huntley *et al.* (2007) predicted the distribution of each of these species, across the same spatial area, for the late 21st century. It should be noted that there are multiple General Circulation Models (GCMs) that can underpin CEM modeling and the results of any individual CEM might differ depending on which GCM is selected (Hawkins & Sutton 2009; Sykes & Osbourne 2011). Huntley *et al.* (2007) used HadCM3, after initial analysis using comparing it with two other scenarios (ECHAM4 and GFDL), given its widespread use and the fact that it is a ‘middle of the road’ model that is close to the average for the overall group of nine GCMs used by the Intergovernmental Panel for Climate Change (IPCC) (Cubasch *et al.*, 2001). We obtained, from Huntley *et al.* (2007), the following for each species: (1) Change in range size (R): the extent of a species’ simulated future range expressed as a proportion of present range (1 = no change, >1 increase, <1 decrease); (2) Overlap between a species’ present range and simulated future range (O): overlap expressed as a proportion (0 = no overlap, 1 = total overlap); (3) Type of change: the spatial difference between current distribution and simulated future distribution established by comparing distribution maps, with 1 = no change, 2 = northern expansion, 3 = southern contraction, 4 = northern shift, 5 = other change, 6 = extirpated (changes in single outlying points were ignored to avoid spurious results); and (4) Goodness-of-fit of the CEM using Cohen’s kappa (K): an index from 0 to 1 (higher values indicative of better fit) derived by comparing model-derived (simulated) present range and actual observed range of each species. R, O and K metrics were given directly by Huntley *et al.* (2007), while the type of change was determined from maps therein. K has previously been used in verification of climatic envelopes (Berry *et al.* 2001).

Birds were allocated to one of eight different main habitats using classification data in Gibbons *et al.* (1993) where possible ($n = 202$ species), complemented by habitat information in Hume (2003). Current range size was estimated from Huntley *et al.* (2007) using a six category scale using the number of 50km² grid squares ($n = 2618$) with breeding populations (very restricted = 0-49 squares, restricted = 50-149, fairly restricted = 150-499, fairly widespread = 300-999, widespread = 1000-1499, ubiquitous >1500) to allow them to be entered in ANOVA analyses. Endemism status was classified as: (1) endemic – entire world breeding population in Europe ($n = 10$); (2) near-endemic – more than 90% of world breeding population in Europe ($n = 30$); or (3) cosmopolitan ($n = 391$) (Huntley *et*

al. 2007). Because endemism refers to species status in Europe relative to global occurrence, current range size and endemism were not associated (chi-square: $\chi^2 = 10.4$, d.f. = 10, $P = 0.405$), so using both variables was appropriate and did not result in multicollinearity. Finally, birds were also classified as resident, partial (usually short-distance) migrants and full (usually long-distance) migrants ($n = 76, 181, \text{ and } 174$ respectively). Partial migrants were species with seasonal movements within Europe or seasonal movements in <10% of the species' European range to external locations (typically Northern Africa).

Arcsine square-root transformation was undertaken for the proportional R and O variables, to achieve normality (one-sample Kolmogorov-Smirnov test with Lilliefors correction: $P = 0.184$ and $P = 0.182$, respectively). To identify factors influencing R and O, separate multi-way fully-factorial ANOVAs were used. Habitat, current range size, migration status, and endemism were included as fixed factors. Model goodness-of-fit estimates for each species (K) were used to weight analysis using a Weighted Least Squared approach to allow for differing robustness. This ensured that any differences in dependent variables were not simply artifacts of systematic differences in these parameters between different bird categories – for example, there was generally poor model fit for coastal and wetland birds (Huntley *et al.* 2007), possibly because the narrow linear nature of distributions was not ideally suited to a CEM/GCM approach (Hawkins & Sutton 2009). This weighting factor would have allowed for this and other instances where small range sizes might have reduce the accuracy of the CEM generated. To establish whether the type of range change differed according to habitat, current range size, endemism or migration status, Multinomial Logistic Regression (MNL) was used. The full model included all independent variables. Reduced models ($n = 14$) were created for all variable combinations and examined using Akaike's information criterion (AIC). This post-hoc model selection process combines model fit (based on log-likelihood) and parsimony, and is superior to stepwise procedures (Whittingham *et al.* 2006). Delta AICs were calculated for each model ($\Delta_i = \text{AIC}_i - \text{AIC}_{\text{min}}$) and compared using relative scoring (0-2 = excellent support, 4-7 considerably less support, ≥ 10 = essentially no support (Burnham & Anderson 2002)). Classification accuracy was also examined.

3. RESULTS

3.1 Change in range size (R)

On average, future ranges were predicted to be 80% of their current size, with increases for 23.3% species, decreases for 73.3%, and no change for 1.1% species. The remaining 2.3% (10 species) were projected to become extirpated (Barbary partridge, Berthelot's pipit, Dupont's lark, Pallas's reed bunting, trumpeter finch, white-headed duck) or almost so ($R \leq 0.06$; black-throated accentor, lesser white-fronted goose, pallid harrier, pintail snipe). The biggest increases were predicted for the chukar (345%), masked shrike (304%) and olive-tree warbler (296%).

A multiway ANOVA model (adjusted $R^2 = 0.454$) revealed significant differences for habitat, current range size and endemism, and no differences according to migration status (Table 1). There were no significant interactions. Differences in habitat were due to coastal, wetland, and upland birds undergoing more substantial range size decreases than farmland, woodland, urban, and multi-habitat birds (Fig. 1a). There was a decrease in future range size (expressed as a proportion of current range size) as current range size decreased (Fig. 1b), while near-endemic species suffered less of a decrease in range size than cosmopolitan species (Fig. 1c).

3.2 Range overlap between current and projected range (O)

On average, the overlap between current and future ranges was predicted to be 39%, with no overlap predicted for 6.3% species and <1% overlap for a further 10.9%. An overlap of >50% was expected for 40% of species, with most overlap for the kestrel, cuckoo and swallow (all 91%), great tit (93%), and Sardinian warbler (97%).

A multiway ANOVA model (adjusted $R^2 = 0.681$) revealed significant differences for habitat, current range size, and endemism and no differences according to migration status (Table 1). When considering the main effects, differences in habitat type were due to considerably less overlap for coastal, wetland and upland birds compared to farmland, woodland, urban and multi-habitat birds (Fig. 1d). There was more overlap for birds with larger current range sizes (Fig. 1e), while cosmopolitan species had more overlap than endemic and near-endemic species (Fig. 1f). There was also a significant interaction between habitat and current range size (Table 1). This interaction was caused by wetland birds having larger overlap values compared to coastal birds when current range sizes were large, a situation that was reversed when range sizes were small.

3.3 Type of range change

Of the 14 reduced models run (each of the four variables - habitat type, current range size, endemism, and migration status – independently and then every unique combination of these), five reduced models had an excellent level of support ($\Delta_i < 2$) (Table 2). Habitat and endemism were each entered into three of these models and range size was entered into two models; migration status was never entered. The model with the lowest AIC (and thus the best balance between model fit and parsimony) contained only habitat and endemism as predictors. This significant model classified 45.7% of cases correctly, with a slight increase in model classification to 47.3% being possible if endemism was replaced with range size ($\Delta_i = 1.02$). The full model had only slightly better accuracy (48.1%) and weak support ($\Delta_i = 6.84$) due to the large number of variables, while 44.3% accuracy was possible just using habitat ($\Delta_i = 0.02$) – these models have very similar levels of support.

When taking all 14 reduced models into account, those containing habitat and current range size were more important as regards classification accuracy than those containing endemism or migration status (Fig. 2a) while habitat, current range size and endemism generated substantially better models based on Δ_i , (lower values) than those containing migration (Fig. 2b). Exploring these patterns further revealed that, in general, more coastal, wetland and heathland species were predicted to undergo southern contraction, while species predicted to become extirpated in Europe (or nearly so) were only found in wetland, farmland and upland habitats. Species using multiple habitats were all predicted to shift or expand northwards (Table 3). The diversity of different types of range change decreased as current range size increased, with loss of species only occurring in the two smallest range size categories. Endemic species were much more likely to undergo southern contraction than near-endemics or cosmopolitan species (Table 3).

4. DISCUSSION

Conservation of birds within Europe is typically *in-situ*, often using a protected area (PA) approach. This could pose problems, especially as range change is expected to be especially large in birds (Harrison *et al.* 2006) and 35% of birds

have traits, such as specialized habitat requirements or poor dispersal ability, that make them vulnerable to climatic change (Foden *et al.* 2008). Indeed, although PAs are becoming increasingly less suited to species-specific conservation (e.g. Araujo *et al.* 2004; Hannah *et al.* 2007), current distribution “snapshots” are still used to inform avian site-based initiatives (Gaston 2006). For example, the Important Bird Areas (IBA) program designates areas based on the rarity of species currently present (with, ironically, one of the definitions for rarity being range-restriction), while areas considered crucial for survival of rare species at a European level are given Special Protection Area (SPA) status under the Conservation of Wild Birds Directive and, for wetland sites, international protection under the Ramsar convention. Despite analyses predicting substantial range movements (Huntley *et al.* 2008; this paper), allowances are not yet being made for such changes in distribution. Understanding how range change parameters are influenced by ecological variables, such as habitat, is a key first step in successful adaptation of current policy (Hole *et al.* 2009).

4.1 The influence of habitat

Our analyses have shown that habitat is a key influence on range change. Coastal, wetland and upland birds show more substantial decreases in range size, and exhibit less overlap between current and future ranges, than species in other habitats. This is largely caused by: (1) the high prevalence of southern contraction rather than northern shift / expansion; and (2) most predicted extirpations occurring within wetland and upland habitats. For these birds, current site-specific initiatives might not be suitable for long-term conservation, especially given their low overlap values. Instead, creating additional PAs by integrating CEM distribution predictions and reserve selection algorithms (Araujo *et al.* 2004), is recommended, together with broader-scale management. PA supplementation already appears to be an effective strategy for plants in Europe, and a proactive approach (creating new PAs using predictions) is less costly than a reactive one, even given inherent uncertainties (Hannah *et al.* 2007). Broader-scale approaches include continued use of legislative protection for rare species, as well as non-reserve based habitat improvement. Farmland and woodland birds have average range size declines and overlap values, and are mainly undergoing northwards shift or expansion. As many such species are declining across Europe (Gregory *et al.* 2005), species- and site-specific management needs to be considered on a case-by-case basis. Broader-scale initiatives, such as agri-environment schemes and encouraging suitable management of national and community woodlands, including the provision of nest sites where these are limiting, should also be considered. Heathland birds are most variable in terms of type of range change: almost one-third are predicted to undergo “other” change. This implies that species-climate relationships are not, predominantly, latitudinal, and suggests that appropriate management is likely to be species-specific. Birds associated with urban areas, and those using multiple habitats, suffer smallest declines in range size, have above-average overlap values, and are mainly predicted to expand (rather than shift) northwards. This suggests that current distributions can be maintained and such species may not be a priority for climate-informed management.

Although creating and maintaining high levels of connectivity is a vital climate change mitigation strategy for all species undergoing distribution changes (Hannah *et al.* 2007; Hole *et al.* 2009), our study suggests that it is especially important for those species with low overlap values and that require specific habitats (viz. wetland and heathland birds and, to a lesser extent, farmland, woodland and upland birds).

4.2 The relevance of current range size and endemism

Species with small current ranges had: (1) larger proportional declines; (2) lower overlap values; and (3) a greater diversity of range change types. Thus, the implications of climate change may be more severe, and spatially more complex, for such species; and parallels the situation that might be seen for species with small population sizes (Holt et al. 2011). Prioritizing the conservation of species with small ranges is long-standing practice, but is even more important in the light of predicted climate change. For range-restricted species, designations of PAs within the predicted distribution, and the creation of stepping stones and corridors to facilitate dispersal, are critical, particularly for poor dispersers (Peterson *et al.* 2001). Endemic and near-endemic species typically have smaller reductions in range size compared to cosmopolitan species, but have lower overlap values. This is concerning given that endemics, especially range-restricted ones, are likely to have low dispersal power, such that their future range could comprise only those areas of their existing range that remain suitable (Thomas *et al.* 2004; Wormworth & Mallon 2006). Cosmopolitan species that have restricted European distributions because Europe is at the edge of their overall range (e.g. Steppe Eagle and Paddyfield Warbler) might be considered less of a priority than species that have both a restricted distribution and are endemic or near-endemic (e.g. Spanish Imperial Eagle and Azure-winged Magpie).

4.3 Migration status

Effects of climate change on migrants has been a research priority for some time (Wormworth & Mallon 2006), partly because it has been implicated in population dynamics of declining long-distance migrants (Sanderson *et al.* 2006). However, our multivariate analyses show that migrants are not differentially affected by climate change as regards distribution compared to residents. (As a cautionary point, it should be noted that migration status was a significant factor in a univariate analyses due to its collinearity with habitat and range size predictors.) Given that studies of breeding phenology have indicated migrants are affected more substantially by climate change, with concomitant influences on population size (Both *et al.* 2006), it seems that phenological impacts are likely to be more important in migratory birds' response to future climate change than potential biogeographical shifts. This finding contrasts, to some extent, with recent observed change in range margins for birds in Finland and North America (Brommer & Møller 2010), where migrant birds showed a greater distribution shift geographically than residents. However, it should be noted that our analyses examined change in range size, overlap, and type of range change, not geographical distance covered, and also that ours is an analysis of projected change, not a retrospective one.

4.4 Caveats and conclusions

CEM as a tool for predicting biotic change is necessarily a simplification, which has attracted criticism (e.g. Davis *et al.* 1998; Peterson *et al.* 2001; Beale *et al.* 2008; Synes & Osborne 2011). For example, whilst climate is clearly important in determining potential ranges, and CEM can provide an indication of these, there are numerous other, often biotic, factors that influence actual range (akin to fundamental and realized niches). Food sources and nest-site availability, as well as competitors, predators and parasites, are likely important factors determining range, but these may be only loosely associated with climate (Davis *et al.* 1998). CEMs also assume that species and the niches will not adapt (Holt et al. 2011) and that species can move freely to regions with favorable climatic conditions, whereas, in

reality, dispersal power might restrict movements (Peterson *et al.* 2001): for example, the Scottish crossbill is predicted to move to Iceland (Huntley *et al.* 2007), a re-location that seems unlikely. However, despite such caveats, CEM can provide valuable (and otherwise unobtainable) insights into range shifts under climate change (Hannah *et al.* 2002; Pearson & Dawson 2003).

A major challenge in creating climate-aware conservation strategies is insufficient understanding of those species (and communities) most at risk from climate change (Wormworth & Mallon 2006). Increasing this understanding requires analyses across species groupings that are biologically meaningful and informative for policy. Here, we demonstrate, for the first time, that habitat and current range size are crucial in determining likely changes, with coastal, wetland, and upland birds, and those with small range sizes, seeming especially vulnerable. This can now be used to inform monitoring, research and management initiatives for birds throughout Europe, and we suggest that holistic policy and management decisions for other taxonomic groups should be based on similar analyses.

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Table 1 – Multiway ANOVAs for change in range size (R) and overlap between current and future ranges (O).
 There were no significant interactions other than those shown ($P > 0.200$).

	Change in range size (R)					Overlap (O)				
	df	SS	MS	<i>F</i>	<i>P</i>	df	SS	MS	<i>F</i>	<i>P</i>
Corrected Model	103	15.295	0.148	3.660	<0.001	118	24.248	0.205	8.752	<0.001
Habitat	7	0.740	0.106	2.588	0.013	7	0.529	0.076	3.221	0.003
Current Range Size	5	1.948	0.390	9.606	<0.001	5	4.179	0.836	35.597	<0.001
Endemism	2	0.320	0.160	3.950	0.021	2	0.209	0.105	4.452	0.012
Migration Status	2	0.014	0.007	0.168	0.845	2	0.009	0.004	0.189	0.828
Habitat * Current Range Size	-	-	-	-	-	25	1.031	0.041	1.756	0.016
Error	326	13.500	0.041			311	7.302	0.023		
Corrected Total	429	24.463				429	31.550			

Table 2 – Full multinomial logistic regression model and the five reduced models that returned a delta AIC of <2 (designating excellent support); the nine reduced models with delta AIC >2 are excluded.

Variables	Delta AIC	P	% Correct
Habitat, Endemism	0	<0.001	45.7
Habitat	0.02	<0.001	44.3
Range size, Endemism	0.35	<0.001	42.0
Endemism	0.64	0.054	38.5
Habitat, Range size	1.02	<0.001	47.3
Full model (Habitat, Range size, Endemism, Migration status)	6.84	<0.001	48.1

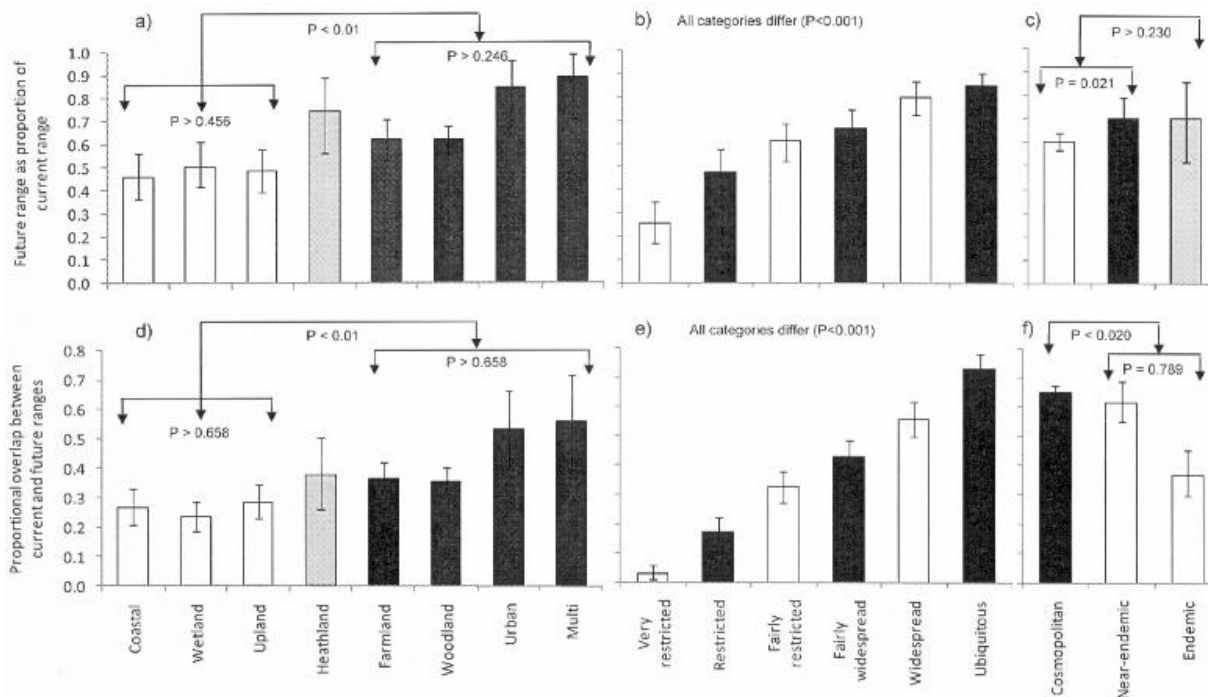
4

Table 3 - Percentage of each type of range change type for birds within key ecological groupings

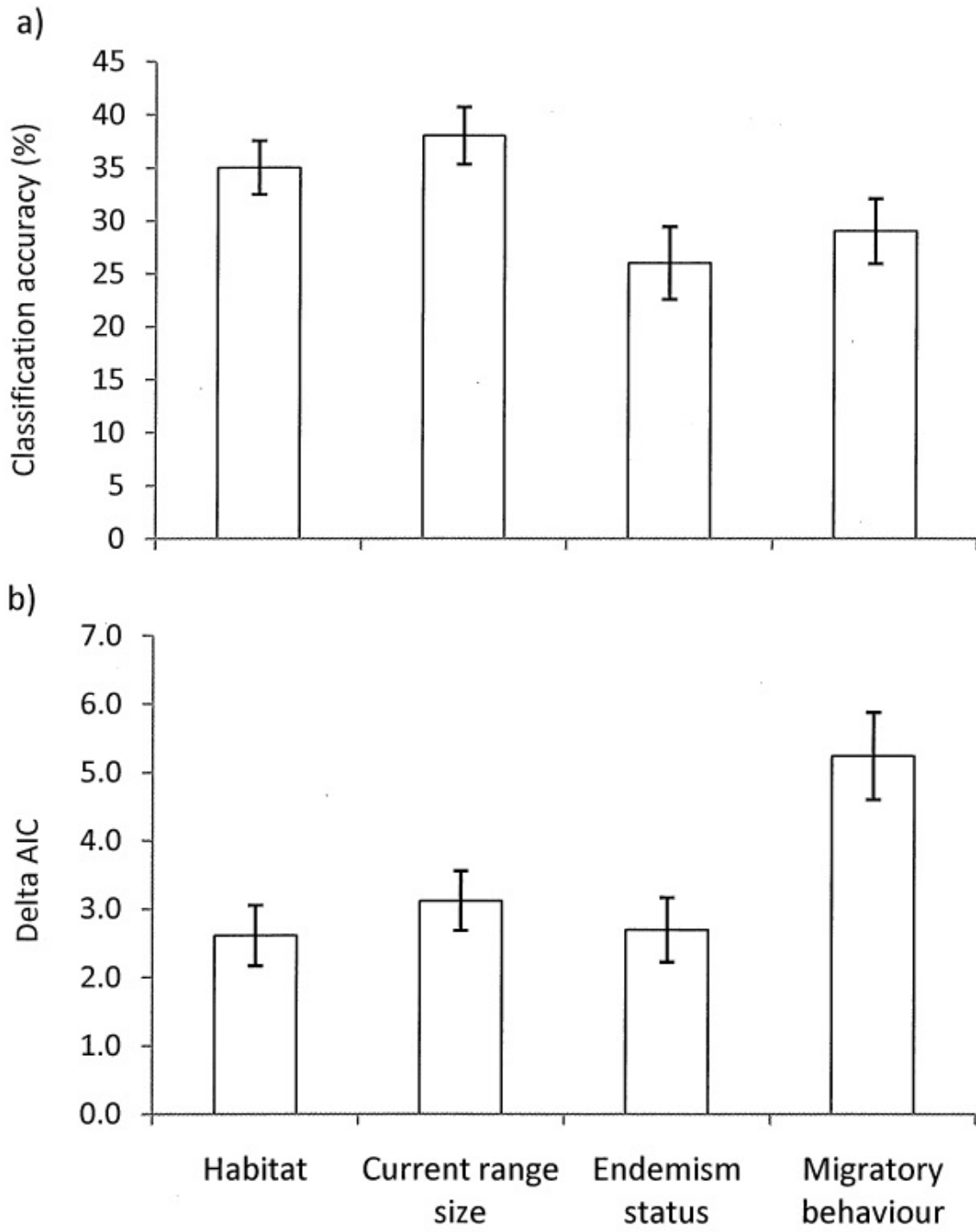
Change Type	Habitat								Current Range Size						Endemism		
	Coastal	Wetland	Farmland	Upland	Heathland	Woodland	Urban	Multi	Very restricted	Restricted	Fairly restricted	Fairly widespread	Widespread	Ubiquitous	Cosmopolitan	Near Endemic	Endemic
None	22	10	7	5	-	2	13	-	23	13	8	3	2	3	8	7	10
N Shift	22	39	26	47	20	54	13	17	21	25	43	38	53	45	37	53	30
N Expansion	27	31	49	30	40	29	50	83	2	22	33	46	42	52	35	27	10
S Contraction	17	7	-	2	10	2	-	-	15	13	2	1	3	-	6	-	-
Other	12	10	15	11	30	13	25	-	26	25	13	12	-	-	12	13	50
Extirpation	-	4	3	5	-	-	-	-	13	3	-	-	-	-	3	-	-

Figure Legends

- Figure 1 – Proportional change in range size (a-c) and amount of overlap between current and predicted future range (d-f) for European birds grouped according to habitat, absolute current range size and endemism status. Graphs use back-transformed Estimated Marginal Means (EMM) from a multi-way ANOVA, with graphs for each dependent variable accounting for co-variation in habitat, range size and endemism parameters between species. Error bars show 95% CI; overlap cannot be used reliably to infer significance in EMM data. Grey bars = categories that do not differ from other categories; white and dark grey bars = categories that differ.
- 4
- 8 Figure 2 – Comparison of all models containing each of the four independent variables (n = 14 models each) in terms of (a) classification accuracy (higher = better); and (b) Δ AIC (lower = better on the basis of model fit and parsimony). Error bars show 95% CI.



Final Fig. 1



Final Fig. 2