

# Range compression of migratory passerines in wintering grounds of the Western Mediterranean: conservation prospects

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## Summary

Because migrant birds occur in different parts of the world in different seasons, their numbers may be limited by the size of the smallest area they inhabit during the year. In addition, restricted ranges make populations more susceptible to local perturbations such that range size is frequently considered a correlate of species vulnerability. Despite this, little is known about the balance between seasonal ranges in the migrant populations of partially migratory species. These migrants are difficult to segregate from sedentary conspecifics in winter grounds and thus the extent of their ranges is difficult to assess. Here, we studied the extent of potential breeding and wintering ranges of 10 partial migratory passerines moving to winter in the Iberian Peninsula and the Maghreb. After testing migratory connectivity of the individual species, we used niche modelling to calculate the extent of potential breeding and wintering ranges in 1,113 pairs of ring recoveries linking individuals between breeding and wintering localities. The results indicate that most species show migratory connectivity and that all of them show range compression in winter relative to the breeding range, with scores ranging between 19% and 58% (mean 37%) of breeding ranges. We discuss the importance of non-breeding grounds for conserving migratory passerines in the Western Mediterranean Basin, an area under pressure from climate change and agricultural intensification.

## Introduction

Range size is considered a main correlate of species vulnerability because restricted ranges make species more vulnerable to local perturbations (Purvis *et al.* 2000, Lee and Jetz 2009, Di Marco and Santini 2015). However, the study of ranges is usually flawed by methodological difficulties in migrant species, which, as in birds, spend different periods of the year in separate locations (Sherry and Holmes 1995, Klaassen *et al.* 2014, Runge *et al.* 2015). As many migratory birds are in decline (Sanderson *et al.* 2006, Vickery *et al.* 2014), exploring the distribution and size of seasonal ranges is key to designing conservation measures at appropriate spatial-temporal scales (Marra *et al.* 2015).

Birds express a variety of migratory movements, with populations spreading or converging in non-breeding grounds (Gilroy *et al.* 2016). In the case of partially migratory species (comprising both migratory and resident individuals; Chapman *et al.* 2011), studies on range compression (reduction of non-breeding range size relative to breeding range and vice versa) are lacking. This is concerning because partial migration occurs in many species (e.g. 40% of European birds; Gilroy *et al.* 2016) and range compression can affect the size and vulnerability of migratory populations (Newton 1995, Rappole *et al.* 2003, Mills 2006, Norris and Marra 2007, Runge *et al.* 2015). This lack of information can be explained by the difficulties in separating migratory and local individuals in sympatric non-breeding grounds (de la Hera *et al.* 2012). This complicates the mapping of non-breeding ranges if compared with long-distance migrants in which range

compression can be assessed using current distribution maps available in conventional atlases (Newton 1995, Mills 2006, Gilroy *et al.* 2016).

Here, we explore the seasonal range compression of some partial migratory passerines (Passeriformes) moving to winter in the Iberian Peninsula and the Maghreb, a region reputed as a primary wintering ground for many European birds (Busse 2001). Widely-dispersed, abundant passerines are often neglected in projects focused on locating and protecting important bird areas for conservation despite the fact that they represent the bulk of the avifauna in most regions and play a significant functional role in some ecosystems (Whelan *et al.* 2008). Thus, it is interesting to explore whether seasonal changes in the range size of migratory populations reveal the existence of small areas of particular conservation concern. It has been shown that the western Mediterranean Basin is not a homogeneous wintering ground since the best areas are mainly restricted to mild lowlands and coastal areas (Tellería *et al.* 1999, 2014a, Carrascal *et al.* 2012). However, we do not know if these geographical features reduce the wintering range of migratory populations compared to their breeding grounds in central Europe.

We use ringing records linking individuals between breeding and non-breeding localities to explore if winter ranges are smaller than summer ranges. Clusters of ringing records have proven useful in detecting the location of ranges of migratory birds (e.g. Clark *et al.* 2009, Calenge *et al.* 2010), but do not depict the spatial patterning of areas suitable for populations involved in these movements. However, a set of mathematical algorithms has been developed in the last decade to predict the potential distribution of species by combining occurrence data (latitude and longitude) with environmental variables (Peterson 2001, Elith and Leathwick 2009). We combine these methods with the use of data from ringed birds to estimate potential range sizes and to explore the environmental drivers of bird distribution (Rodríguez *et al.* 2007, Wisz *et al.* 2007, Rivera *et al.* 2011). The potential ranges resulting from these analyses are used to test whether wintering ranges of migratory populations in the Iberian Peninsula and the Maghreb are smaller than their breeding ranges in central Europe.

## Methods

### *Study area*

The wintering area covers 1,700,000 km<sup>2</sup> located between 28° and 44°N at the south-western border of the Palearctic (Figure 1). It receives many migratory birds, most of them from the western side of the migratory divide crossing Europe between 10° and 20°E (Busse 2001, Møller *et al.* 2011). The most outstanding environmental gradients of this wintering ground are the sharp changes in elevation and the concomitant variation in climatic conditions and vegetation (Figure 1). The area is dominated by cereal fields, vineyards, olive groves and Mediterranean woodlands and scrublands located between the moist broadleaved woodlands and meadows of northern Iberia and the southern expanses of the Sahara.

### *Ring recoveries*

The data used in this paper refer to all birds recovered/ringed in winter (December to February) in the Iberian Peninsula and the Maghreb that were ringed/recovered in central and northern Europe during the breeding period (April to August; Figure 1). The data, ranging from 1925 to 2011, were provided by the European Union for Bird Ringing (EURING) and the Spanish Office of Migratory Species (Spanish Ministry of Agriculture, Food and Environment). Additional data on the number of ringed birds were recorded from the official page of EURING (<http://www.euring.org>; Appendix S1 in the online supplementary material). From a previous set of 13 species, we excluded *Anthus pratensis*, *Saxicola torquata* and *Carduelis carduelis* because they had less than 50 ring recoveries, a sample size that we considered too small for a comprehensive view of their seasonal ranges. The final data set included 1,113 pairs of ringed-recovered individuals for 10 species (Figure 1; Table 1).

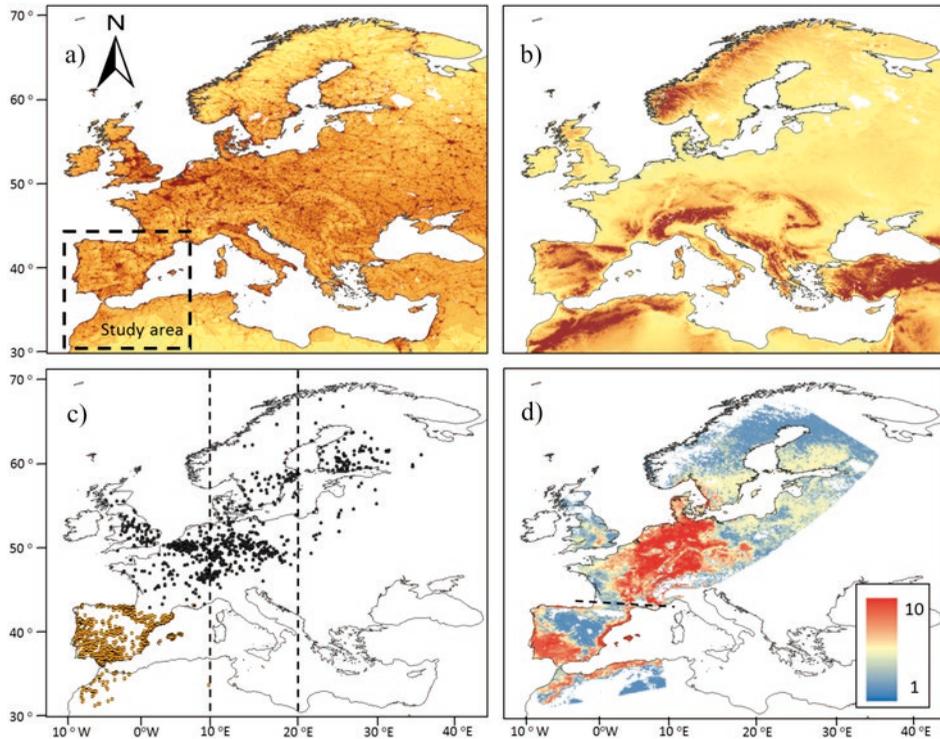


Figure 1. a) Distribution of the Human Foot Print (HFP) index in Europe. Increasing dark tones show increasingly high values of HFP. The study area is located within the striped square. b) Elevation map of the western Palearctic. Increasing dark tones show increasing elevations, with the darkest tone showing the areas over 1,000 m asl. c) Distribution in breeding and wintering areas of the 1,113 pairs of birds controlled in breeding grounds (black dots) and wintering grounds in the study area (light dots). Vertical lines show the longitudinal range within which are distributed the migratory divides of most migratory birds in Europe, according to Møller *et al.* (2011). d) Potential distribution of migratory populations as reported by the number of species (0–10) present in breeding and wintering grounds.

These data provided geo-referenced clusters of ringing records per species, which show the location of the marked individuals in breeding and wintering grounds (Figure S2-1). Finally, we explored the strength of migratory connectivity of populations (most individuals from one breeding population move to the same wintering locations; Webster *et al.* 2002) by testing if individuals that breed close to each other also winter close to each other. High connectivity will suggest that changes in particular wintering sectors of the Iberian Peninsula and the Maghreb will affect the populations of discrete breeding quarters whilst low connectivity will suggest a widespread effect of changes in breeding grounds (Finch *et al.* 2017). To test this we conducted a Mantel test (Ambrosini *et al.* 2009) with the R package 'vegan' in which the statistical significance of correlation coefficients was determined by 9,999 random permutations (Oksanen *et al.* 2015).

### Environmental predictors

The geographical location of ringing records was used to run Maxent by selecting a set of explanatory variables related to the large-scale distribution of birds in breeding and wintering areas.

Table 1. Number of pairs of ring records used to model the distribution of migratory populations in breeding and wintering grounds. R statistics and P values resulting from Mantel tests. Estimated breeding and wintering ranges of the studied passerines and range compression in wintering grounds in percentage ([wintering area/breeding area]\*100).

Species	Pairs of ring records	Mantel test (R)	Mantel test (P-value)	Breeding range (x 10 <sup>5</sup> Km <sup>2</sup> )	Wintering range (x 10 <sup>5</sup> Km <sup>2</sup> )	Range compression (%)
<i>Carduelis cannabina</i>	62	0.155	0.041	53.95	27.23	50.48
<i>Erithacus rubecula</i>	170	0.005	0.410	119.88	24.99	20.84
<i>Fringilla coelebs</i>	55	0.040	0.099	111.20	21.11	18.98
<i>Motacilla alba</i>	99	0.266	0.001	118.53	41.19	34.75
<i>Phoenicurus ochruros</i>	68	0.189	0.001	74.00	37.53	50.71
<i>Phylloscopus collybita</i>	79	0.174	0.006	111.67	26.29	23.54
<i>Sylvia atricapilla</i>	125	0.010	0.048	57.31	24.57	42.88
<i>Turdus iliacus</i>	94	-0.077	0.919	35.94	20.71	57.63
<i>Turdus merula</i>	60	0.149	0.007	68.20	13.49	19.77
<i>Turdus philomelos</i>	301	0.044	0.002	75.57	38.52	50.97
Mean				82.62	27.56	37.06

The aim was to obtain useful models and to use the response curves provided by Maxent to explore the relationships between the species occurrence probabilities and the involved variables. We used variance inflation (VIF) analysis to avoid highly correlated variables (Marquardt 1970). From a set of 11 variables (seasonal maximum, minimum and mean temperature, temperature seasonality, seasonal precipitation, precipitation seasonality, sun radiation, NDVI, bare ground, herbaceous cover and tree cover) we selected five environmental predictors per season (VIF scores under 5, range: 1.15–4.56). Mean temperatures in breeding (April to August) and wintering (December to February) ranges were selected because small birds avoid cold areas to limit excessive thermoregulatory costs (Calder and King 1974). We also included mean precipitation in breeding and wintering grounds. Precipitation improves primary productivity in wintering grounds after the Mediterranean summer (Nahal 1981), thus increasing the carrying capacity for wintering birds (Carrascal and Palomino 2012, Tellería *et al.* 2014b). However, in temperate areas higher precipitation has been related with poor breeding success. Thus, it can be suggested that the moistest sectors will be suboptimal areas for breeding (e.g. Öberg *et al.* 2015). We also included the annual Normalized Difference Vegetation Index (NDVI) as a surrogate of primary productivity from MODIS satellite-based sensor (30" resolution, or ~1 km; Carroll *et al.* 2004, Pettorelli *et al.* 2011) and, according to the strong effect of vegetation cover on passerine distribution (Wiens 1989), we included woody cover from Vegetation Continuous Fields MOD44B (Di Miceli *et al.* 2011). Finally, we considered the effect of two different variables related to the seasonal pulses of productivity tracked by migratory birds in breeding and wintering grounds (Wisz *et al.* 2007, Engler *et al.* 2014). We used precipitation seasonality (standard deviation of monthly means x 100) as a surrogate for the rain-mediated productive pulses in Mediterranean wintering grounds, and temperature seasonality as a surrogate of the productive output in central and northern European summer grounds. Climate data were recorded from Worldclim 1.4 (Hijmans *et al.* 2005) and prepared as ASCII raster maps with a resolution of 5x5 km with the raster package in R (Hijmans and Van Etten 2013, R Development Core Team 2015).

### Species distribution models

We used Maxent, a machine-learning technique based on the principle of maximum entropy (Phillips *et al.* 2006), to predict the habitat suitability of marked populations from presence data (ring records) within breeding and wintering ranges. This program has been designed to minimise the relative entropy between two probability densities (one estimated from the presence data and

one from automatically generated presences) defined in covariate space (Elith *et al.* 2011). In this way, it is possible to model the probability of the occurrence of species over a given study area. To select the area with which to calibrate the models in breeding and wintering grounds, we used the minimum convex polygon (convex hull) produced by the full set of ringing records. This is the smallest polygon in which no internal angle exceeds 180° and contains the records of all species. In both seasons and for all species, we ran Maxent (log output; regularisation multiplier  $b = 1$ ; autofeatures; convergence threshold = 0.00001) in 10 replicates with 70% of the presences as training data and the rest as test data for internal verification. Duplicate records in the same localities (e.g. ringing stations) were removed in each replicate and spatial autocorrelation was minimised by randomly removing occurrences within 5 km of each other. In addition, and since the distribution of ring recoveries can be affected by human presence (e.g. more records will be gathered in the most populated areas; Busse 2001), we used the layer of human footprint (HFP), an index of population density, land transformation and road density (Sanderson *et al.* 2002), as a bias grid (10,000 background points with a likelihood of presence proportional to HFP; Dudík *et al.* 2005). We used mean human footprint per country because it is positively related to the density of all ringing recoveries reported per country ( $r = 0.53$ ,  $P = 0.036$ ,  $n = 16$ ), a plain index of the effort applied to control ringed birds (Appendix S1). To explore the importance of each predictor (see below), we carried out jackknife analyses of the regularised gain with training data. The models were evaluated using 10-fold cross-validations measuring the accuracy by means of the area under the receiver operating characteristics curve (AUC; Fielding and Bell 1997) to assess the congruence between observed and detected records in the test data reserved for verification in Maxent (Phillips *et al.* 2006). Finally, we obtained a map by averaging the suitability models of individual species. With this map, we try to establish a comprehensive view of the main areas used by partial migratory passerines during the breeding and wintering periods. We used the 'dismo' package (Hijmans and Van Etten 2013) in R (R Development Core Team 2015) to perform all analyses.

### Potential range maps

Geographic ranges can be derived from species distribution models by applying a cut-off threshold value to distinguish suitable from unsuitable areas. The resulting maps from the previous niche modelling process were converted into binary 'presence-absence' maps using the threshold selection method based on maximising the sum of sensitivity and specificity (Manel *et al.* 2001). This threshold is recommended for conservation purposes as omission errors are avoided and sensitivity favoured (Jiménez-Valverde and Lobo 2007, Liu *et al.* 2013). We considered areas with a habitat suitability above the threshold as 'presence' and those below as 'absence'. The geographic area occupied by species in each season were calculated by converting the 'presence' raster to a polygon shape file and calculated polygon areas using the WGS 84 / UTM zone 30N (32630) projection. Finally, we measured winter range compression dividing potential winter range by breeding range (Table 1). We used the raster and 'dismo' packages (Hijmans and Van Etten 2013) in R (R Development Core Team, 2015) to calculate the potential range map of the species in both seasons.

## Results

Mantel test correlations between the geographical location of breeding and wintering sites in most species (all but Robin *Erithacus rubecula* and Redwing *Turdus iliacus*; Table 1) support the maintenance of spatial structuring in populations between breeding and wintering ranges. The AUC values resulting from niche modelling suggest a good performance of models according to current standards (AUC >0.7; Elith 2002) and the response curves provide some additional information on the way birds are distributed within breeding and wintering ranges (Table 2). For instance, the habitat suitability of species in breeding grounds was positively related to temperature and strongly affected by temperature seasonality (Table 2). In wintering grounds, most species were related to temperature and woodland cover (Table 2).

Table 2. Estimates of relative contributions of the environmental variables in models predicting habitat suitability of species in breeding and wintering grounds. AUC scores show the fitting of models (max values = 1) and the two following values represent the percent contribution/permutation importance of each variable in the model. Percent contribution indicates the change in regularized gain by adding the corresponding variable. Permutation importance represents, for each environmental variable in turn, the resulting drop in training AUC when the values of that variable on training presence and background data are randomly permuted, normalized to show percentages. Values are averages over 10 replicate runs. Symbols in parentheses show the trend of the response curves for the quantitative variables: +, increase; -, decrease; Ω, hump-shaped = no trend).

	Breeding grounds					
	AUC max-min	Temperature seasonality (43.5-99.1)	Temperature (5.1-17.3° C)	Precipitation (45.4-126.2 mm)	NDVI (0.1-0.8)	Woodland (4.2-66.3 %)
		Contr./perm.(curve)	Contr./perm.(curve)	Contr./perm.(curve)	Contr./perm.(curve)	Contr./perm.(curve)
<i>Carduelis cannabina</i>	0.93	59.8/66.7 (Ω)	21.4/21.5 (+)	1.5/2.5 (-)	3.0/3.0 (+)	14.2/6.4 (-)
<i>Erithacus rubecula</i>	0.81	50.3/55.5 (Ω)	23.6/25.7 (+)	2.4/2.4 (=)	11.6/7.0 (=)	12.1/9.4 (Ω)
<i>Fringilla coelebs</i>	0.86	39.0/36.5 (Ω)	22.3/35.0 (+)	3.7/4.4 (-)	16.5/10.7 (=)	18.5/13.4 (Ω)
<i>Motacilla alba</i>	0.91	50.0/46.8 (-)	20.1/28.8 (+)	14.7/13.5 (-)	4.7/6.6 (+)	10.5/4.2 (-)
<i>Phoenicurus ochruros</i>	0.93	72.6/67.7 (Ω)	9.9/19.6 (+)	12.5/8.3 (-)	1.7/1.8 (+)	3.3/2.6 (Ω)
<i>Phylloscopus collybita</i>	0.91	63.9/58.2 (Ω)	21.2/26.9 (+)	9.8/10.1 (-)	2.1/2.8 (+)	3.0/2.0 (-)
<i>Sylvia atricapilla</i>	0.94	51.1/51.7 (Ω)	34.7/32.4 (+)	8.4/7.7 (Ω)	1.5/1.9 (+)	4.3/6.3 (-)
<i>Turdus iliacus</i>	0.90	37.9/25.6 (+)	17/43.7 (Ω)	3.6/7.7 (-)	25.9/17.8 (=)	15.6/5.2 (Ω)
<i>Turdus merula</i>	0.93	46.2/49.6 (Ω)	22.2/32.3 (+)	14.8/9.1 (-)	3.0/2.6 (+)	13.8/6.4 (Ω)
<i>Turdus philomelos</i>	0.87	35.9/28.8 (Ω)	36.6/48.0 (+)	10.0/7.6 (-)	5.0/4.3 (Ω)	12.5/11.3 (Ω)
mean	0.90	50.7/48.7	22.9/31.4	8.14/7.3	8.0/5.9	10.8/6.7

Table 2. Continued.

	Wintering grounds					
	AUC max-min	Precipitation seasonality (14.0-74.0)	Temperature (0.9-12.3° C)	Precipitation (8.4-157.5 mm)	NDVI (0.06-0.7)	Woodland (0.0-51.8 %)
		Contr./perm.(curve)	Contr./perm.(curve)	Contr./perm.(curve)	Contr./perm.(curve)	Contr./perm.(curve)
<i>Carduelis cannabina</i>	0.88	23.7/25.1 (-)	15.1/23.5 (+)	18.7/7.6 (-)	2.0/2.4 (Ω)	40.5/41.3 (-)
<i>Erithacus rubecula</i>	0.89	10.2/5.5 (Ω)	45.4/56.2 (+)	7.1/10.8 (Ω)	4.6/11.6 (+)	32.8/16.0 (-)
<i>Fringilla coelebs</i>	0.90	9.1/9.3 (Ω)	24.8/21.4 (+)	3.7/5.2 (+)	4.2/16.6 (+)	58.3/47. (-)
<i>Motacilla alba</i>	0.86	38.3/6.2 (+)	36.5/45.9 (+)	2.2/4.8 (+)	4.3/4.1 (Ω)	18.6/39.0 (-)
<i>Phoenicurus ochruros</i>	0.85	13.2/9.0 (+)	27.4/26.5 (+)	15.2/17.2 (Ω)	9.8/25.4 (Ω)	34.4/21.9 (-)
<i>Phylloscopus collybita</i>	0.90	9.4/5.8 (+)	41.4/41.2 (+)	7.4/7.9 (Ω)	2.4/3.1 (Ω)	39.4/42.0 (-)
<i>Sylvia atricapilla</i>	0.92	34.0/16.1 (+)	33.7/47.5 (+)	5.3/8.2 (Ω)	2.6/6.3 (Ω)	24.5/21.9 (-)
<i>Turdus iliacus</i>	0.89	12.6/7.1 (Ω)	19.1/30.3 (+)	37.9/27.6 (+)	1.3/3.2 (+)	29.1/31.9 (+)
<i>Turdus merula</i>	0.90	31.1/37.1 (-)	22.0/25.2 (+)	2.3/7.9 (+)	3.1/3.3 (+)	41.5/26.4 (+)
<i>Turdus philomelos</i>	0.89	9.7/14.2 (Ω)	39.1/30.7 (+)	7/13.5 (+)	17.6/11.4 (+)	26.7/30.2 (+)
mean	0.89	19.3/13.5	30.5/34.8	10.7/11.1	5.2/8.7	34.6/31.8

Potential range maps suggest that most of the migratory populations wintering in the western Mediterranean Basin extend their breeding grounds in central Europe west to Poland and in southern Scandinavia (Figure S2-2). These maps show that the wintering grounds occupied by migratory populations were smaller (mean 37%) than breeding grounds in all species (t-test for paired samples  $t = 5.92$ ,  $P < 0.001$ ,  $n = 10$ ; Table 1). More explicitly, potential winter ranges covered a mean area of 275,600 km<sup>2</sup> (min-max 134,900–411,190 km<sup>2</sup>, Table 1) accounting for 16% (7.9–24.2%) of the Iberian Peninsula and the Maghreb (Figure 1).

## Discussion

### *Distribution of potential breeding and wintering ranges*

The potential breeding ranges of individual species depicted a patchy distribution, with migratory populations reporting the highest occurrence probabilities in different inland or coastal areas of central Europe west of the migratory divide (Figure S2-2). This suggests a diverse geographical origin of populations moving to winter in the western Mediterranean. When the mean potential distribution of these species is represented (Figure 1), the emerging map reveals that the most probable source area of migratory birds is located in a region that extends from the Alps to the North and Baltic seas, and from the French Massif Central to the Slovakian Tatra Mountains, constrained to the east by the migratory divide of European bird populations (Figure 1). This seems to be the core range of the bulk of migratory passerines moving to winter in the Iberian Peninsula and the Maghreb.

The response curves provided by Maxent indicated that in breeding and wintering areas, the potential distributions of migratory populations tend to avoid the colder areas and are sited in most seasonal areas under a given threshold of summer (dryness) and winter (cold) conditions (Table 2). The importance of temperature in shaping migratory bird distribution is widely recognised, and is the result of the high thermoregulation costs of living in areas under bird thermo-neutral ranges (Swanson and Garland 2008, Carrascal *et al.* 2012, Khaliq *et al.* 2014). This could explain the avoidance by birds of elevated areas in breeding and wintering ranges (Figure 1). The potential wintering range of migratory passerines depicted a homogeneous pattern, with most birds constrained to similar lowlands and coastal sectors of the Iberian Peninsula and the Maghreb (Figure S2-2, Figure 1), where wood cover was positively (thrushes) or negatively (the rest of species) correlated, supporting the effect of specific habitat preferences on bird distribution (see Tellería *et al.* 1999, del Moral *et al.* 2012). These patterns are similar to the wintering maps reported by ring modelling of Meadow Pipit *Anthus pratensis*, Chiffchaffs *Phylloscopus collybita*, Blackcaps *Sylvia atricapilla* and Robin *Erithacus rubecula*, validated by field sampling of abundances (Tellería *et al.* 2012, 2014a, 2016).

### *Range compression in wintering grounds*

Compression of winter ranges reported by common distribution maps of species seems to occur in half of the Western Palaearctic migratory birds (Gilroy *et al.* 2016). This reveals the importance of a phenomenon that varies between species (and populations) according to the idiosyncratic features of the species and regions involved in this process. Because of this potential variability, range contraction is a context-dependent process whose effect on the conservation of migratory populations must be addressed in particular migratory populations within their geographical ranges (Gilroy *et al.* 2016).

This study, which has focused on migratory passerines wintering in the Iberian Peninsula and the Maghreb, supports a sharp reduction of potentially suitable areas in winter ranges affecting all the study species, with compression scores ranging from 19% to 58% (mean 37%) of breeding ranges (Table 1). This effect of range compression affecting all species is higher than that reported in Palearctic land birds moving to winter south of the Sahara, where 69% of species ( $n = 62$ )

experienced a reduction of ranges in non-breeding grounds (Newton 1995). In fact, our results are more similar to those reported in North American land birds moving to winter in Mesoamerica, where most birds (94%,  $n = 89$ ) showed a reduction of non-breeding range (Mills 2006). In this case, range contraction was explained by the sharp reduction of emerged lands available to birds in the Mesoamerican corridor (Mills 2006). We suspect a similar effect in the south-western border of the Palearctic, where migratory populations are restricted to a minor part of emerged lands (mean range covers 16% of the Iberian Peninsula and the Maghreb) because suitable areas are constrained by coastlines, cold highlands and the dry expanses of the Sahara (Tellería *et al.* 2014a,b).

### *Conservation prospects*

The results in this study suggest that, because of small range size, the wintering grounds in the Iberian Peninsula and the Maghreb may act as 'bottlenecks' of passerine populations involved in these migratory movements (Weber *et al.* 1999, Gilroy *et al.* 2016). This will likely occur in species tied to scarcer habitats, or limited by food availability. However, evidence available in the study area does not clearly show such limitations in the case of common passerines. Most migratory passerines arrive at this area in October, when autumn rains begin a period of primary productivity, invertebrate activity and fruit abundance (Nahal 1981, Guo *et al.* 2012). Common passerines rely on seeds, invertebrates and fruit available in extensive human-modified landscapes (e.g. cereal fields, olive groves, etc.) and Mediterranean scrublands and woodlands (Rey 2011, Del Moral *et al.* 2012, Tellería *et al.* 2014b) where field studies do not support food restriction (Díaz y Tellería 1994, Hampe 2008, Tellería *et al.* 2013). We acknowledge that this balance will be disrupted in winters of food scarcity, a situation that many birds cope with by food-tracking (Rey 2011, Tellería *et al.* 2014c). However, movement among suitable areas will not be enough if changes affect simultaneously the carrying capacity of the whole range. The south-western border of the Palearctic is expected to suffer the strong effects of climate change, with increasing temperature and decreasing rainfall (Giorgi and Lionello 2008, Schilling *et al.* 2012). In this context, the depletion or altitudinal shifts of lowland habitats suitable for wintering birds have been predicted (Ruiz-Labourdette *et al.* 2012, Ponti *et al.* 2014, Tellería *et al.* 2016).

The response of birds to these changes in wintering areas is difficult to predict (La Sorte *et al.* 2009) but the potential carry-over effects of these environmental changes (Norris *et al.* 2004) will probably affect populations in larger breeding areas of Europe. In this context, the study of migratory connectivity is essential to understanding the effects of these changes on breeding populations (Creswell 2014). Migratory connectivity may vary along a continuum, from strong to weak (Finch *et al.* 2017), and our results support this variability. Most passerines wintering in the Iberian Peninsula and the Maghreb show significant but different correlation coefficient scores in Mantel tests, and two species report lack of migratory connectivity (Table 1). This lack of connectivity in Redwing and Robin could result from within-range movements typical of some birds (Tellería *et al.* 2014c, Stutchbury *et al.* 2016) or the relatively small scale of approach in this study (Creswell 2014; e.g. Ambrosini *et al.* 2016 report migratory connectivity of Robins at continental scales). But, as a whole, the results in this paper suggest that connectivity is expected to underpin the response of breeding populations in central Europe to local changes in non-breeding grounds of the Western Mediterranean. We agree that this may affect just a part of populations on breeding grounds if some individuals spread out to alternative wintering grounds or are able to shift their ranges in response to changes (Finch *et al.* 2017).

### **Supplementary Material**

To view supplementary material for this article, please visit <https://doi.org/10.1017/S0959270917000120>

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## References

- Ambrosini, R., Møller, A. P. and Saino, N. (2009) A quantitative measure of migratory connectivity. *J. Theor. Biol.* 257: 203–211.
- Ambrosini, R., Cuervo, J. J., Feu, C., Fiedler, W., Musitelli, F., Rubolini, D., Sicurella, B., Spina, F., Saino, N. and Møller, A. P. (2016) Migratory connectivity and effects of winter temperatures on migratory behaviour of the European robin *Erithacus rubecula*: a continent-wide analysis. *J. Anim. Ecol.* 85: 749–760.
- Busse, P. (2001) European passerine migration system—what is known and what is lacking. *Ring* 23: 3–36.
- Calder, W. A. and King, J. R. (1974) Thermal and caloric relations of birds. Pp. 259–413 in D. S. Farner and J. R. King, eds. *Avian biology*. Vol. 4. London, UK: Academic Press.
- Calenge, C., Guillemain, M., Gauthier-Clerc, M. and Simon, G. (2010) A new exploratory approach to the study of the spatio-temporal distribution of ring recoveries: the example of Teal (*Anas crecca*) ringed in Camargue, Southern France. *J. Ornithol.* 151: 945–950.
- Carrascal, L. M. and Palomino, D. (2012) Variación geográfica de la riqueza de especies invernantes en la península Ibérica. Estacionalidad y determinismo ambiental. In: J. C. del Moral, B. Molina, A. Bermejo and D. Palomino, eds. *Atlas de las aves en invierno en España 2007-2010*. Madrid, Spain: Ministerio de Agricultura, Alimentación y Medio Ambiente-SEO/BirdLife.
- Carrascal, L. M., Villén-Pérez, S. and Seoane, J. (2012) Thermal, food and vegetation effects on winter bird species richness of Mediterranean oakwoods. *Ecol. Res.* 27: 293–302.
- Carroll, M. L., DiMiceli, C. M., Sohlberg, R. A. and Townshend, J. R. G. (2004) 250m MODIS Normalized Difference Vegetation Index, 250ndvi28920033435, Collection 4, Day 289, 2003. College Park, Maryland: University of Maryland.
- Chapman, B. B., Brönmark, C., Nilsson, J. A. and Hansson, L. A. (2011) The ecology and evolution of partial migration. *Oikos* 120: 1764–1775.
- Clark, J. A., Thorup, K. and Stroud, D. A. (2009) Quantifying the movement patterns of birds from ring recoveries. *Ring and Migration* 24: 180–188.
- Cresswell, W. (2014) Migratory connectivity of Palaearctic–African migratory birds and their responses to environmental change: the serial residency hypothesis. *Ibis*, 156: 493–510.
- Díaz, M. and Tellería, J. (1994) Predicting the effects of agricultural changes in central Spanish croplands on seed-eating overwintering birds. *Agricult. Ecosyst. Environ.* 49: 289–298.
- de la Hera, I., Pérez-Tris, J. and Tellería, J. L. (2012) Habitat distribution of migratory and sedentary blackcaps *Sylvia atricapilla* wintering in southern Iberia: a morphological and biogeochemical approach. *J. Avian Biol.* 43: 333–340.
- del Moral, J. C., Molina, B., Bermejo, A. and Palomino, D. (2012) *Atlas de las aves en invierno en España 2007-2010*. Madrid, Spain: Ministerio de Agricultura, Alimentación y Medio Ambiente- SEO/BirdLife.
- Di Marco, M. and Santini, L. (2015) Human pressures predict species' geographic range size better than biological traits. *Glob. Change Biol.* 21: 2169–2178.
- Di Miceli, C. M., Carroll, M. L., Sohlberg, R. A., Huang, C., Hansen, M. C. and Townshend, J. R. G. (2011) *Annual global automated MODIS vegetation continuous*

- fields (MOD44B) at 250 m spatial resolution for data years beginning day 65, 2000–2010, Collection 5 Percent Tree Cover. College Park, MD, USA: University of Maryland.
- Dudík, M., Phillips, S. J. and Schapire, R. E. (2005) Correcting sample selection bias in maximum entropy density estimation. *Adv. Neural Inf. Process Syst.* 17: 323–330.
- Elith, J. (2002) Quantitative methods for modelling species habitat: comparative performance and an application to Australian plants. Pp. 39–58 in S. Ferson and M. Burgman, eds. *Quantitative methods for conservation biology*. New York, USA: Springer.
- Elith, J. and Leathwick, J. R. (2009) Species distribution models: ecological explanation and prediction across space and time. *Annu. Rev. Ecol. Evol. Syst.* 40: 677–697.
- Elith, J., Phillips, S. J., Hastie, T., Dudík, M., Chee, Y. E. and Yates, C. J. (2011) A statistical explanation of MaxEnt for ecologists. *Divers. Distrib.* 17: 43–57.
- Engler, J. O., Rödger, D., Stiel, D. and Förschler, M. I. (2014) Suitable, reachable but not colonised: seasonal niche duality in an endemic mountainous songbird. *J. Ornithol.* 155: 657–669.
- Fielding, A. H. and Bell, J. F. (1997) A review of methods for the assessment of prediction errors in conservation presence/absence models. *Environ. Conserv.* 24: 38–49.
- Finch, T., Butler, S., Franco, A. and Cresswell, W. (2017) Low migratory connectivity is common in long-distance migrant birds. *J. Anim. Ecol.* doi: 10.1111/1365-2656.12635.
- Gilroy, J. J., Gill, J. A., Butchart, S. H., Jones, V. R. and Franco, A. (2016) Migratory diversity predicts population declines in birds. *Ecol. Lett.* 19: 308–317.
- Giorgi, F. and Lionello, P. (2008) Climate change projections for the Mediterranean region. *Glob. Planet. Chang.* 63: 90–104.
- Guo, Q., Hu, Z., Li, S., Li, X., Sun, X. and Yu, G. (2012) Spatial variations in above-ground net primary productivity along a climate gradient in Eurasian temperate grassland: effects of mean annual precipitation and its seasonal distribution. *Glob. Chang. Biol.* 18: 3624–3631.
- Hampe, A. (2008). Fruit tracking, frugivore satiation, and their consequences for seed dispersal. *Oecologia* 156: 137–145.
- Hijmans, R. J., Cameron, S. E., Parra, J. L., Jones, P. G. and Jarvis, A. (2005) Very high resolution interpolated climate surfaces for global land areas. *Int. J. Climatol.* 25: 1965–1978.
- Hijmans, R. J. and Van Etten, J. (2013) Raster: geographic data analysis and modelling. *R package version 2.1–49*.
- Jiménez-Valverde, A. and Lobo, J. M. (2007) Threshold criteria for conversion of probability of species presence to either-or presence-absence. *Acta Oecol.* 31: 361–369.
- Khaliq, I., Hof, C., Prinzing, R., Böhning-Gaese, K. and Pfenninger, M. (2014) Global variation in thermal tolerances and vulnerability of endotherms to climate change. *Proc. Roy. Soc. B.* 281: 20141097
- Klaassen, R. H., Hake, M., Strandberg, R., Koks, B. J., Trierweiler, C., Exo, K. M. and Alerstam, T. (2014) When and where does mortality occur in migratory birds? Direct evidence from long-term satellite tracking of raptors. *J. Anim. Ecol.* 83: 176–184.
- La Sorte, F. A., Lee, T. M., Wilman, H. and Jetz, W. (2009) Disparities between observed and predicted impacts of climate change on winter bird assemblages. *Proc. Roy. Soc. B.* 276: 3167–3174.
- Lee, T. M. and Jetz, W. (2011) Unravelling the structure of species extinction risk for predictive conservation science. *Proc. Roy. Soc. B.* 278: 1329–1338.
- Liu, C., White, M. and Newell, G. (2013) Selecting thresholds for the prediction of species occurrence with presence-only data. *J. Biogeogr.* 40: 778–789.
- Manel, S., Williams, H. C. and Ormerod, S. J. (2001) Evaluating presence-absence models in ecology: the need to account for prevalence. *J. Appl. Ecol.* 38: 921–931.
- Marquardt, D. W. (1970) Generalized inverses, ridge regression, biased linear estimation, and nonlinear estimation. *Technometrics*, 12: 591–612.
- Marra, P. P., Cohen, E. B., Loss, S. R., Rutter, J. E. and Tonra, C. M. (2015) A call for full annual cycle research in animal ecology. *Biol. Lett.* 11.
- Mills, A. M. (2006) Winter range compression of migrants in Central America. *J. Avian Biol.* 37: 41–51.
- Møller, A. P., Garamszegi, L. Z., Peralta-Sánchez, J. M. and Soler, J. J. (2014) Migratory divides

- and their consequences for dispersal, population size and parasite–host interactions. *J. Evol. Biol.* 24: 1744–1755.
- Nahal, I. (1981) The Mediterranean climate from a biological viewpoint. Pp. 63–86 in F. Di Castri, D. W. Goodall and R. L. Specht, eds. *Ecosystems of the world 11: Mediterranean-type shrublands*. Amsterdam, The Netherlands: Elsevier.
- Newton, I. (1995) Relationship between breeding and wintering ranges in Palaearctic–African migrants. *Ibis* 137: 241–249.
- Norris, D. R., Marra, P. P., Kyser, T. K., Sherry, T. W. and Ratcliffe, L. M. (2004) Tropical winter habitat limits reproductive success on the temperate breeding grounds in a migratory bird. *Proc. Roy. Soc. Lond. B Biol.* 271: 59–64.
- Norris, D. and Marra, P. P. (2007) Seasonal interactions, habitat quality, and population dynamics in migratory birds. *The Condor* 109: 535–547.
- Öberg, M., Arlt, D., Pärt, T., Laugen, A. T., Eggers, S. and Low, M. (2015) Rainfall during parental care reduces reproductive and survival components of fitness in a passerine bird. *Ecol. Evol.* 5: 345–356.
- Okansen, J., Blanchet, F. G., Kindt, R. *et al.* (2015) Vegan: Community ecology package. R package version 2.3-0.
- Peterson, A. T. (2001) Predicting species geographic distributions based on ecological niche modelling. *The Condor* 103: 599–605.
- Pettorelli, N., Ryan, S., Mueller, T., Bunnefeld, N., Jedrzejewska, B., Lima, M. and Kausrud, K. (2011) The Normalized Difference Vegetation Index (NDVI): unforeseen successes in animal ecology. *Climate Res.* 46: 15–27.
- Phillips, S. J., Anderson, R. P. and Schapire, R. P. (2006) Maximum entropy modelling of species geographic distributions. *Ecol. Model.* 190: 231–259.
- Ponti, L., Gutierrez, A. P., Ruti, P. M. and Dell’Aquila, A. (2014) Fine-scale ecological and economic assessment of climate change on olive in the Mediterranean Basin reveals winners and losers. *Proc. Natl. Acad. Sci. U.S.A.* 111: 5598–5603.
- Purvis, A., Gittleman, J. L., Cowlshaw, G. and Mace, G. M. (2000) Predicting extinction risk in declining species. *Proc. Roy. Soc. B.* 267: 1947–1952.
- R Development Core Team (2015) *R: A language and environment for statistical computing*. Vienna, Austria: R Foundation for Statistical Computing. <http://www.R-project.org/>
- Rappole, J. H., Helm, B. and Ramos, M. A. (2003) An integrative framework for understanding the origin and evolution of avian migration. *J. Avian Biol.* 124–128.
- Rey, P. J. (2011) Preserving frugivorous birds in agro-ecosystems: lessons from Spanish olive orchards. *J. Appl. Ecol.* 48: 228–237.
- Rivera, J. H. V., Ortega-Huerta, M. A., Sarkar, S., and Rappole, J. H. (2011) Modelling the potential winter distribution of the endangered Black-capped Vireo (*Vireo atricapilla*). *Bird Conserv Internatn.* 21: 92–106.
- Rodríguez, J. P., Brotons, L., Bustamante, J. and Seoane, J. (2007) The application of predictive modelling of species distribution to biodiversity conservation. *Divers. Distrib.* 13: 243–251.
- Ruiz-Labourdette, D., Nogués-Bravo, D., Ollero, H. S., Schmitz, M. F. and Pineda, F. D. (2012) Forest composition in Mediterranean mountains is projected to shift along the entire elevational gradient under climate change. *J. Biogeogr.* 39: 162–176.
- Runge, C. A., Tulloch, A., Hammill, E., Possingham, H. P. and Fuller, R. A. (2015) Geographic range size and extinction risk assessment in nomadic species. *Conserv. Biol.* 29: 865–876.
- Sanderson, E. W., Jaiteh, M., Levy, M. A., Redford, K. H., Wannebo, A. V. and Woolmer, G. (2002) The human footprints and the last of the wild. *BioScience* 52: 891–904.
- Schilling, J., Freier, K. P., Hertig, E. and Scheffran, J. (2012) Climate change, vulnerability and adaptation in North Africa with focus on Morocco. *Agr. Ecosyst. Environ.* 156: 12–26.
- Sherry, T. W. and Holmes, R. T. (1995) Summer versus winter limitation of populations: what are the issues and what is the evidence. Pp. 85–120 in T. E. Martin and D. M. Finch, eds. *Ecology and management of Neotropical migratory birds* New York, USA: Oxford University Press.
- Stutchbury, B. J., Siddiqui, R., Applegate, K., Hvenegaard, G. T., Mammenga, P., Mickle, N.,

- Pearman, M., Ray, J. D., Savage, A., Shaheen, T. and Fraser, K. C. (2016) Ecological causes and consequences of intratropical migration in temperate-breeding migratory birds. *Amer. Nat.* 188: S28–S40.
- Swanson, D. L. and Garland, T. (2008) The evolution of high summit metabolism and cold tolerance in birds and its impact on present-day distributions. *Evolution* 63: 184–194.
- Tellería, J. L., Asensio, B. and Díaz, M. (1999) *Aves Ibéricas, Vol. 2. Passeriformes*. Madrid, Spain: J. M. Reyero Editor.
- Tellería, J. L., Santos, T., Refoyo, P. and Muñoz, J. (2012) Use of ring recoveries to predict habitat suitability in small passerines. *Divers. Distrib.* 18: 1130–1138.
- Tellería, J. L., Blázquez, M., De La Hera, I. and Pérez-Tris, J. (2013) Migratory and resident Blackcaps *Sylvia atricapilla* wintering in southern Spain show no resource partitioning. *Ibis* 155: 750–761.
- Tellería, J. L., Fernández-López, J. and Fandos, G. (2014a) Using ring records and field surveys to predict the winter distribution of a migratory passerine. *Bird Stud.* 61: 527–536.
- Tellería, J. L., Fandos, G., López, J. F., Onrubia, A. and Refoyo, P. (2014b) Winter distribution of passerine richness in the Maghreb (North Africa): A conservation assessment. *Ardeola* 61: 335–350.
- Tellería, J. L., Carrascal, L. M. and Santos, T. (2014c) Species abundance and migratory status affects large-scale fruit tracking in thrushes (*Turdus* spp.). *J. Ornithol.* 155: 157–164.
- Tellería, J. L., Fernández-López, J. and Fandos, G. (2016) Effect of climate change on Mediterranean winter ranges of two migratory passerines. *PLOS One* 11: 11.
- Vickery, J. A., Ewing, S. R., Smith, K. W., Pain, D. J., Bairlein, F., Škorpilová, J. and Gregory, R. D. (2014) The decline of Afro-Palaeartic migrants and an assessment of potential causes. *Ibis* 156: 1–22.
- Weber, T. P., Houston, A. I. and Ens, B. J. (1999) Consequences of habitat loss at migratory stopover sites: a theoretical investigation. *J. Avian Biol.* 30: 416–426.
- Webster, M. S., Marra, P. P., Haig, S. M., Bensch, S. and Holmes, R. T. (2002) Links between worlds: unravelling migratory connectivity. *Trends Ecol. Evol.* 17: 76–83.
- Whelan, C. J., Wenny, D. G. and Marquis, R. J. (2008) Ecosystem services provided by birds. *Ann. N. Y. Acad. Sci.* 1134: 25–60.
- Wiens, J. A. (1989) *The ecology of bird communities*. Cambridge, UK: Cambridge University Press.
- Wisz, M. S., Walther, B. A. and Rahbek, C. (2007) Using potential distributions to explore determinants of Western Palaeartic migratory songbird species richness in sub-Saharan Africa. *J. Biogeogr.* 34: 828–841.

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