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# Wintering areas on the move in the face of warmer winters

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For several decades, there have been changes in the distance of bird migration. The Eurasian Reed Warbler *Acrocephalus scirpaceus* is a Trans-Saharan migratory species, which, as recent records suggest, is increasingly wintering in the Iberian Peninsula. This study investigated the strength of the influence of climate on the wintering of this insectivorous species in the Iberian Peninsula, and also used geospatial modelling to identify the most favourable areas. The model was constructed to identify the most relevant explanatory factors of this distribution and it was assessed by applying calibration and discrimination criteria, and the influence of each factor was analysed using variation partitioning. The minimum winter temperature is the most relevant factor affecting sites suitable for the wintering of this species in Europe. The best areas are located in the southern and eastern coasts of the Iberian Peninsula and in some locations on the northern Atlantic coast of Spain. Spatial trends analysis corroborated the orientation of the flight paths of the species from their breeding areas to their wintering areas. Topography refined the model in that it is associated with habitat selection at a fine-scale. As the case of the Eurasian Reed Warbler is not unique, the results show the role of the Iberian Peninsula as a new wintering site for species usually wintering in the Sub-Saharan region, modifying their wintering strategy from Trans-Saharan to Pre-Saharan migrants, and whether the recent increase in temperature is the main cause.

## 1. Introduction

Bird migration is an evolutionary adaption for finding sites with sufficient availability of resources during the non-breeding season to ultimately increase survival and breeding competence (Newton 2008). Besides the natural learning of juveniles from experienced individuals (Flack *et al.* 2018), the onset of migration, physiological adaptions, and the characteristics of migration (orientation, time, distance, stopovers, etc.) have a genetic basis (Berthold & Querner 1981, Berthold 1988, 1991, Berthold & Helbig 1992, Gwinner 1996). However, environmental changes can affect this genetic influence, allowing the species to modify their migratory behaviour according to the

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current conditions (Berthold & Querner 1981, Berthold 1988, Berthold *et al.* 1992, Ogonowski & Conway 2009). This flexibility imparts a variable response that ultimately benefits the persistence of the population if environmental conditions change in a brief period of time (Charmantier & Gienapp 2014). Individuals have two types of response mechanisms to the environment over the short term: the microevolutionary response to natural selection (Berthold *et al*. 1992, Berthold & Querner 1995, Pulido *et al.* 2001), and phenotypic plasticity (Charmantier *et al*. 2008, Charmantier & Gienapp 2014). The former mechanism is a "non-labile" trait that is stable during the individual's lifetime, whereas phenotypic plasticity is mainly "labile", changing repeatedly in order to fit the new environmental conditions, such as the behavioural or "individual" plasticity (Charmantier & Gienapp 2014), but that also could be estable during an individual's lifetime if conditions remain unchanged (Charmantier *et al*. 2008). These traits could influence the population distribution range or migration behaviour if individuals alter their phenology in response to environmental shifts, such as climate-driven changes (Huntley *et al.* 2006, Lehikoinen & Sparks 2010, Massimino *et al.* 2015, Potvin *et al.* 2016).

As migration is the part of the annual cycle with the highest mortality rate (Alerstam & Lindström 1990), a reduction in migration distance could provide individuals with an advantage (Sillett & Holmes 2002) by increasing the survival rate and enhancing their fitness for the following breeding season (Kokko 1999, Forstmeier 2002, Alves *et al*. 2013). Long-distance migrants could probably become short-distance migrants if they establish wintering sites closer to their breeding zones (Bermejo 2012), while maintaining the original orientation of their flight paths (Ambrosini *et al*. 2016).

The Iberian Peninsula plays an important role as a bridge between Europe and Africa for migratory (Hahn *et al.* 2009) and non-migratory species, as shown by the case of some African species which have recently colonized Europe (Ramírez 2009, Elorriaga & Muñoz 2010, Morganti & Pulido 2012, Chamorro *et al.* 2017). It has been predicted that environmental changes in the Iberian Peninsula may affect migration ecology regarding the timing of departures or arrivals, number of stopovers, wintering distribution, and survival (Gordo & Sanz 2006, Halupka *et al.* 2017, Bellisario 2018, Howard *et al*. 2018, Tomotani *et al*. 2018, Triviño *et al.* 2018). Temperatures have increased and winters have become milder in the Iberian Peninsula, as predicted by climate change models (I.P.C.C. 2014, Gonzalez-Hidalgo *et al.* 2016, Vicente-Serrano & Rodríguez-Camino 2017, Vicente-Serrano *et al.* 2017). If favourable conditions persist during autumn and winter, some Iberian birds and European migrants could delay or even forgo migration and remain in the Iberian Peninsula (Gordo & Sanz 2006, Balbontín *et al*. 2009). This situation has been recently described for the White Stork (*Ciconia ciconia*) (Gordo *et al.* 2007; Vergara *et al.* 2007), the Barn Swallow (*Hirundo rustica*) (Arizaga *et al*. 2012), and the Eurasian Reed Warbler (*Acrocephalus scirpaceus*) (Nieto *et al*. 2018).

The winter survival of insectivorous species depends on the abundance of flying insects during the whole season, which is associated with mild temperatures (Lewington 2006). The Eurasian Reed Warbler, therefore, must have sufficient resources in some areas of the Iberian Peninsula to survive during winter, which would increase the wintering population size if these conditions persist. Based on this idea, and having demonstrated that the Eurasian Reed Warbler has become a regular wintering species in the Iberian Peninsula (Nieto *et al*. 2018), we hypothesise that these birds have more suitable areas for their wintering in the Iberian Peninsula than they actually occupy and therefore, an increment in wintering populations is possible. To demonstrate this, we characterized the areas in which this trans-Saharan migrant currently winters, and identified areas with similar environmental conditions which could be wintering sites in the near future, as the modelling methodology could predict occupancy in a short-term future (Muñoz, A.-R., Carrasco, E. & Real, R. unpublished data). Bearing in mind that these environmental conditions could directionally shift due to climate change, we also assessed the relevance of climate on the selection of the wintering sites. This study provides information on the future of the European populations of this species, which is an example of all Trans-Saharan migrants which are currently changing their phenology and wintering areas.

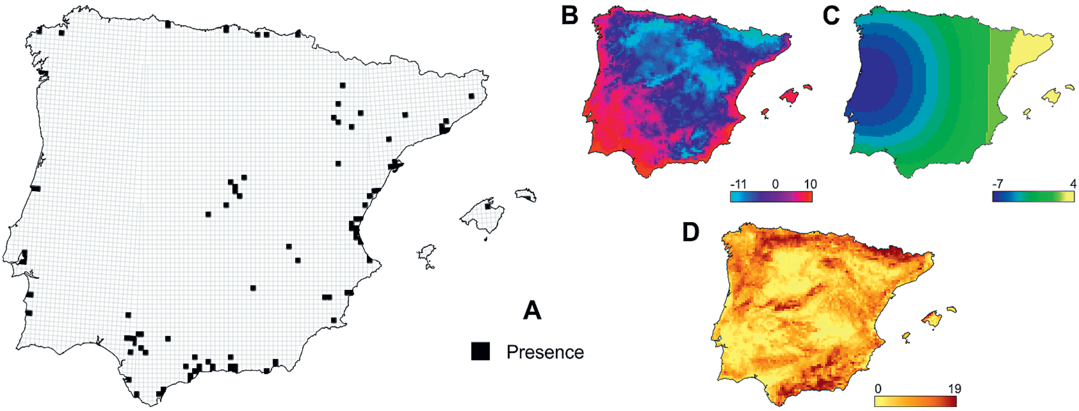

Fig. 1. Distribution of Eurasian Reed Warbler ringing data presences (black squares) in the 10 × 10 km UTM grid cells in Spain and Portugal (A), and the distributions of the mean winter minimum temperatures (B), spatial trend-surface analysis (C), and slope (D) in the Iberian Peninsula and Balearic Islands.

## 2. Methods

### 2.1. Study area

The study area was the Iberian Peninsula and the Balearic Islands (SW Europe). The Iberian Peninsula is a region with heterogeneous physiography and climate and covers nearly 600,000 km$^2$. The Balearic archipelago covers almost 5,000 km$^2$ and is located in the western Mediterranean Sea.

According to Font (2000), the study area can be divided into three climatic regions: Mediterranean, Atlantic, and Interior. The Mediterranean region includes the Balearic Islands and the southern and eastern strips of mainland Spain and is characterised by its hot and dry summers and mild winters. Mediterranean coasts have mild temperatures due to their regulation by the Mediterranean Sea. Winter temperatures range from 6°C to 10°C and barely reach an absolute minimum temperature of –7°C in the North and –2°C in the South. Some of these coasts, especially those in the provinces of Malaga and Granada, have special frost-free micro-climates that can support tropical fruit-tree crops such as avocados, papayas, mangos, and custard apples (Botas 2017).

The Atlantic region includes northern and western Spain and Portugal and has mild-cold winters, cool summers, and abundant regular precipitation. Between Lisbon in Portugal and Galicia in Spain, the mean minimum temperature on the coast ranges between 5°C to 11°C, although the absolute minimum temperature can reach –7°C. On the Spanish North Atlantic coast, the mean minimum temperature is around 6°C, although oscillations are narrower because of the influence of the warmer water of the Bay of Biscay (Anadón *et al.* 2009). The interior region includes central mainland Spain, which has high temperatures in summer but low ones in winter because of irregular and scarce precipitation and the absence of sea influences. The absolute winter temperature can reach –15°C in some regions and average minimum temperatures ranges between –2°C to 8°C. Topography has a marked influence on reducing the severe temperatures in the largest river valleys.

### 2.2. Species and distribution data

The Eurasian Reed Warbler breeds across Europe into central Asia and North Africa (Schulze-Hagen 1997, Kennerley & Pearson 2010). It winters in Sub-Saharan Africa, although Nieto *et al.* (2018) compile some records of it wintering north of the Sahara areas, such as Morocco, the Iberian Peninsula, Sardinia and southern France (Nissardi 1998, Ramirez 1998, Bairlein 2006). Spring migration begins in late February to the beginning of June (Gainzarain Díaz 2003) and autumn migration begins in mid-July to the end of October or exceptionally early November (Schulze-Hagen 1997). In winter, the species typically inhabits reed beds, although it can also be found in bush habitats, where it feeds on medium and large insects (Cramp 1992, Kennerley & Pearson 2010).

Wintering records for the period 1990–2015 were obtained from ringing data provided by Centro de Migración de Aves (CMA) of the SEO/BirdLife, the Society of Sciences Arantzadi and the Central Nacional de Anilhagem (CEMPA) in collaboration with EURING (www.euring.org). Records between 15th November and 31st January were selected to avoid late and early migrants, respectively, and to focus on wintering individuals we selected individuals in healthy conditions and with a ±1 week of precision in recoveries at the most, following more restrictive criteria than European Bird Census Council (see Nieto *et al*. 2018 for further information).

Ringing on bad weather days is unusual, so these records cannot be attributed to aberrant individuals due to storms. Sampling effort is one of the most relevant drawbacks of this type of data. For this reason, the presence and absence of the species was mapped using 10 × 10 km UTM grid cells of the Iberian Peninsula and Balearic Islands ($n$ = 5,791) to obtain favourability models, which mitigate the effect of prevalence and the false-absences (Acevedo & Real 2012). A total of 114 presences were recorded in the study area (Fig. 1A).

## 2.3. Predictor variables

A set of 21 environmental variables related to spatial location, topography, and climate was used to identify the factors that influence the Eurasian Reed Warbler wintering in the Iberian Peninsula and Balearic Islands (Table 1). Topography and climate data were obtained by averaging the 1 $km^2$ pixel values obtained from the digitized variables in the 10 × 10 km UTM squares (i.e., Fig. 1B,D), as described in Muñoz *et al*. (2005, 2015a). Climate data has average monthly precipitation and temperature data for 1971 to 2000 (AEMET 2011) which was the source with the highest resolution and reliability for the Iberian Peninsula.

Using the spatial location variables of latitude (*La*) and longitude (*Lo*), we conducted a polynomial trend-surface analysis (Legendre & Legendre 1998), including the square and cube units and the interactions between them (i.e., $La^2$, $Lo^2$, $La^3$, $Lo^3$, $La \times Lo$, $La^2 \times Lo$, $La \times Lo^2$), that we used as a new variable (*Spat*) which describe more complex spatial patterns (Legendre 1993). Thus, we attempted to show geographical trends in species distribution associated with historical events, migration routes, or species population dynamics (Fig. 1C) by simultaneously assessing the climatic conditions in the context of spatial influences (Real *et al*. 2003, Márquez *et al.* 2004).

A large number of variables increases the likelihood of type I errors (i.e., familywise error rate, FWER), and therefore the likelihood of false results. We evaluated the False Discovery Rate (FDR; Benjamini & Hochberg 1995) to control the FWER (García 2003) using the Benjamini and Yekutieli (2001) procedure for all forms of dependency among test statistics, and accepted only those variables significantly associated with the distribution of the species with $\alpha < 0.05$ under an FDR value of 0.05.

Multicollinearity between variables was reduced by first calculating the Spearman correlation coefficients between them. We then pre-selected the candidate variables retaining only one out of any set of variables with $r > 0.8$ according to their individual predictive power (Fa *et al*. 2014). The variance inflation factor (VIF) of each predictor was used to quantify collinearity between predictors in the models. The VIFs were calculated for every predictor which fulfils the FDR and Spearman correlation criteria as the inverse of the coefficient of non-determination for a regression of that predictor on all others (Muñoz *et al*. 2015a). Values between 1 and 3 show very low multicollinearity between predictors.

Land-uses variables were not taken into account because the Eurasian Reed Warbler, despite being a habitat specialist, occurs in any reeds or marsh related vegetation, independently of their dimensions. Land-uses GIS layers do not consider small vegetation points suitable for the species wintering presence, such as vegetation in the edge of irrigation canals, so many of the 10 × 10 km UTM squares have favourable areas for the species which are not represented in the land-uses layers.

## 2.4. Statistical analysis

Logistic regression analysis was used to model the winter occurrence data based on presences-absences in the 10 × 10 km UTM grid cells. Logistic

Table 1. Environmental variables used to model the distribution of Eurasian Reed Warblers grouped by their environmental factor. Data sources: 1 US Geological Survey (1996), 2 based on the DEM in Farr and Kobrick (2000), 3 IGN (1999), 4 trend-surface analysis (see Methods), 5 AEMET (2011). Variables marked with (*) had fulfilled the FDR and Spearman correlation criteria; VIF values are showed for these variables.

| Code | Variable | VIF | Source |
|---|---|---|---|
| **Topography** | | | |
| *Alti* | Mean altitude (m) | | 1 |
| *Slop* * | Slope (degrees; calculated from *Alti*) | 1.765 | 1 |
| *AltiR* | Altitudinal range (m) | | 1 |
| *SE* | Southward exposure degree | | 2 |
| *WE* | Westward exposure degree | | 2 |
| **Spatial situation** | | | |
| *La* | Latitude (degrees N) | | 3 |
| *Lo* | Longitude (degrees E) | | 3 |
| *Spat* * | Trend-surface analysis (see Methods) | 2.229 | |
| **Climate** | | | |
| *Prec* * | Mean winter precipitation (mm) | 22.411 | 4 |
| *Tm* | Mean winter temperature (ºC) | | 4 |
| *Tn* * | Mean winter minimum temperatures (ºC) | 2.187 | 4 |
| *Tx* | Mean winter maximum temperatures (ºC) | | 4 |
| *DP01* * | Days with precipitation ≥ 0.1 mm in winter | 7.682 | 4 |
| *DP1* | Days with precipitation ≥ 1 mm in winter | | 4 |
| *DP10* | Days with precipitation ≥ 10 mm in winter | | 4 |
| *DP30* * | Days with precipitation ≥ 10 mm in winter | 12.156 | 4 |
| *D0T* | Days with minimum temperature ≤ 0 ºC in winter | | 4 |
| *DIS* * | Direct irradiance at surface (Kwhm$^{-2}$day$^{-1}$) in winter | 3.451 | 4 |
| *SIR* | Surface incoming radiation (Kwhm$^{-2}$day$^{-1}$) in winter | | 4 |
| *PET* | Mean annual potential evapotranspiration (mm) | | 4 |
| *AET* | Mean annual actual evapotranspiration (mm) | | 4 |

regression analysis yields a probabilistic output (*P*) predicting a dichotomous dependent variable (presence-absence in the present case) from the set of independent variables (Hosmer & Lemeshow 1989). To eliminate the effect of prevalence, probability models were converted using the favourability function of Real *et al.* (2006):

$$F = \frac{P}{1-P} \bigg/ \left( \frac{n_1}{n_0} + \frac{P}{1-P} \right) \qquad (1)$$

where *n1* and *n0* are the number of presences and absences in the study area, respectively. Favourability values range from 0 (null favourability) to 1 (high favourability), and a favourability value of 0.5 indicates that the presence of the species is as probable as its prevalence in the corresponding study area. Hence, favourability refers to the environmental conditions that favour the presence of the species (Acevedo & Real 2012, Muñoz *et al.* 2015a). The use of a favourability value of 0.5 as a cut-off for the presence/absence of the species is unreliable when attempting to establish clearly demarcated favourable areas (Hosmer & Lemeshow 1989). Thus, we reclassified the areas into “clearly favourable” (F > 0.8), “clearly unfavourable” (F < 0.2), and areas of “intermediate favourability” (see Muñoz *et al.* 2005).

According to Legendre (1993), interactions between factors often result in an overlaid effect in space due to collinearity between them (Borcard *et al.* 1992). To demonstrate this effect, we used the variation partitioning procedure (for more detailed process see Muñoz *et al.* 2005) to specify how much of the variation of the final model was explained by the pure effect of each explanatory variable and their interactions (Legendre 1993, Legendre & Legendre 1998), and by the non-climatic variables entered into the model as a group compared to the factor climate. If interactions between variables have negative values, then there is an overlap effect between these variables (one

Table 2. Variables included in the modelling process and their coefficients (β), Wald test values, and significance (*P*) in each step. The variables are ranked according to their order of entrance. Codes are the same as in Table 1.

| | β | Wald | *P* |
|---|---|---|---|
| **Step 1** | | | |
| *Tn* | 0.405 | 103.972 | $2.052 \times 10^{-24}$ |
| Constant | –5.292 | 635.533 | $3.130 \times 10^{-140}$ |
| **Step 2** | | | |
| *Tn* | 0.311 | 57.529 | $3.330 \times 10^{-14}$ |
| *Spat* | 0.454 | 26.926 | $2.114 \times 10^{-7}$ |
| Constant | –3.088 | 47.684 | $5.008 \times 10^{-12}$ |
| **Final Step** | | | |
| *Tn* | 0.285 | 45.706 | $1.374 \times 10^{-11}$ |
| *Spat* | 0.561 | 35.332 | $2.780 \times 10^{-9}$ |
| *Slop* | –0.173 | 11.398 | $7.352 \times 10^{-4}$ |
| Constant | –2.090 | 15.860 | $6.819 \times 10^{-5}$ |

variable adds favourability, whereas the other reduces it).

## 2.5. Model assessment

We used several indices to assess model performance. The Area Under the Receiver Operating Characteristic Curve (AUC) was used as a measure of discrimination capacity that could be a more accurate indicator when describing the distribution of the species in the different steps of the model (Hosmer & Lemeshow 1989, Romero *et al.* 2012). The weight of each added variable and the estimation of the parameter in the equation were assessed using the Wald test (Wald 1943). Classification accuracy was tested using a set of widely recognized measures, whose values range from 0 to 1 (Fielding & Bell 1997, Barbosa *et al.* 2013).

The measures used were as follows: the correct classification rate (CCR: the conditional probability of correctly classified presences and absences), sensitivity (the conditional probability of correctly classified presences), specificity (the conditional probability of correctly classified absences), the over-prediction rate (OPR: the proportion of observed and assumed absences in the predicted presence area), and the under-prediction rate (UPR: the proportion of observed presences in the predicted absence area).

We also used Cohen's Kappa (which is described as the proportion of specific agreement), whose values range from –1 to +1 (Fielding & Bell 1997). We assessed the factor predicted change in presences (Pch), where values greater than 1 predict an increase in distribution range (Muñoz & Real 2006).

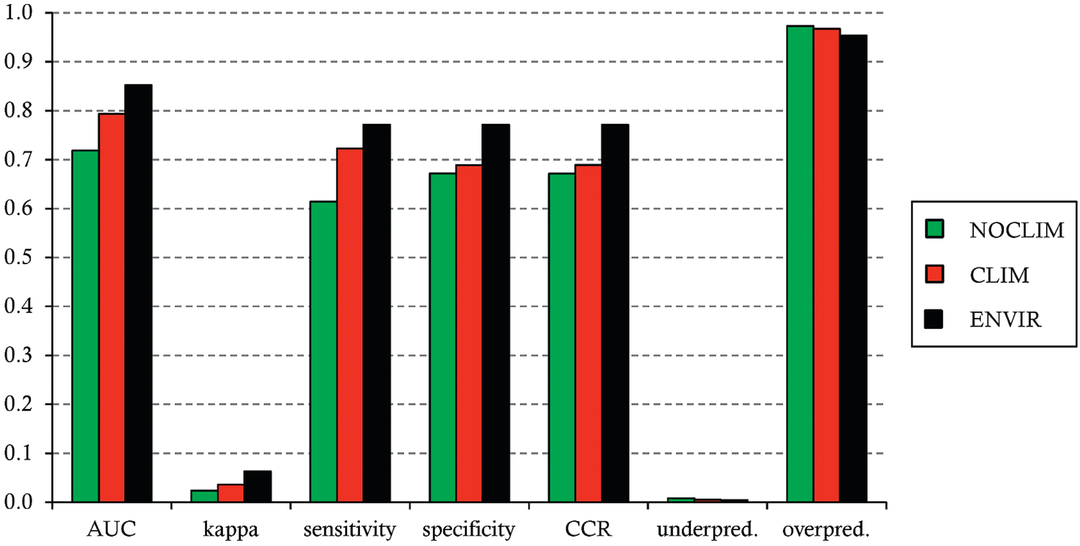

Fig. 2. Assessment scores for the Eurasian Reed Warbler distribution environmental model in the Iberian Peninsula (ENVIR, black bar), model constructed using only the climatic variable (CLIM, red bar) and the non-climatic variables (NOCLIM, green bar) entered in the environmental model. A favourability value of 0.5 was used as a cut-off for presence-absence.

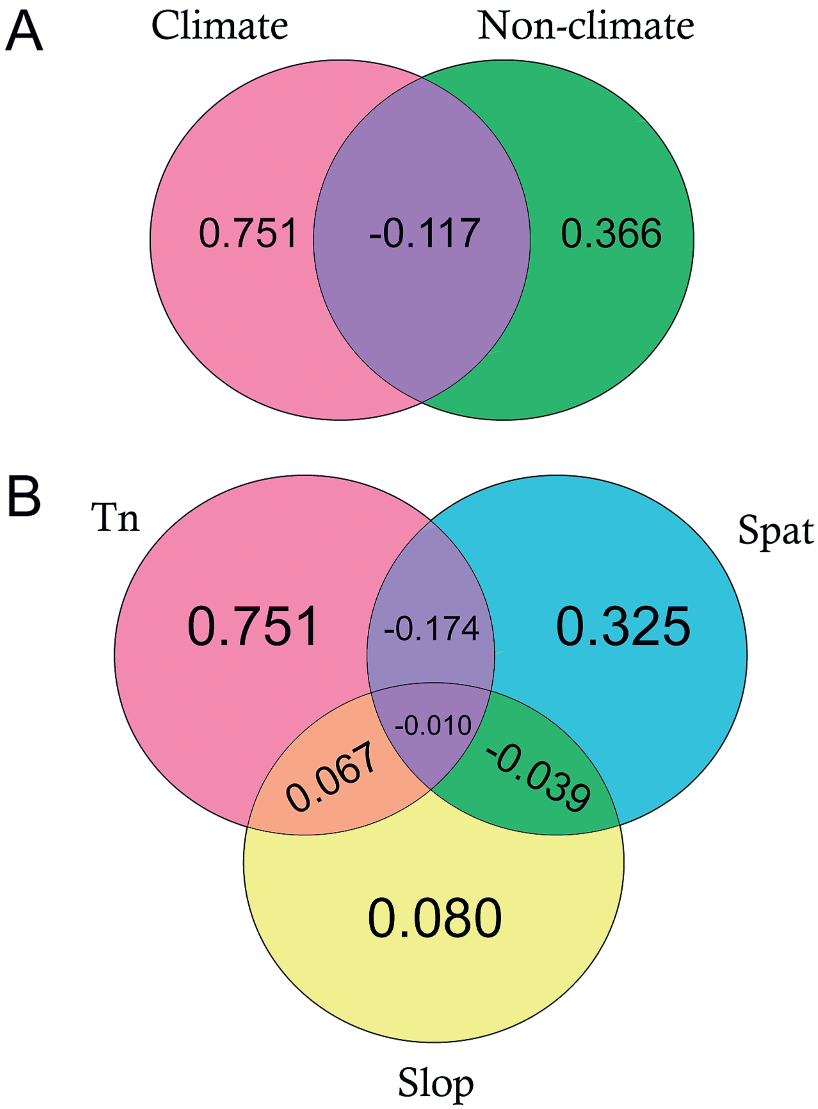

Fig. 3. Results of variation partitioning of the environmental model using the factor climate *vs* the factor combined non-climatic variables (A) and the individually considered explanatory variables (B; see codes in Table 1). Values within the circles represent the proportion of variation explained by the indicated factors and by their interactions.

## 3. Results

The predictive model of the wintering pattern of the Eurasian Reed Warbler in the study area included variables associated with climate, spatial location, and topography (Table 2; ranked by the relevance of their values on the Wald Test). The model had high discriminative capacity (AUC > 0.8) and classification capacity (CCR, sensitivity, and specificity > 0.7) and a positive kappa value. We also observed a high proportion of predicted presences in the study area in which the species was assumed to be absent (OPR > 0.9). However, the UPR had lower values (see Fig. 2). The spatial variable was calculated from the spatial trend-surface analysis (see Methods):

$$Spat = 743.2 - 37.1La - 81.9Lo + 0.5La^2 + 0.2Lo^2 + 4.01La \times Lo - 0.01Lo^3 - 0.05La^2 \times Lo \qquad (2)$$

The proportion of the variation explained by climate (mean minimum temperature) was 0.751, showing that climate had the most significant influence on the wintering of the species in the Iberian Peninsula, whereas the proportion of the vari-

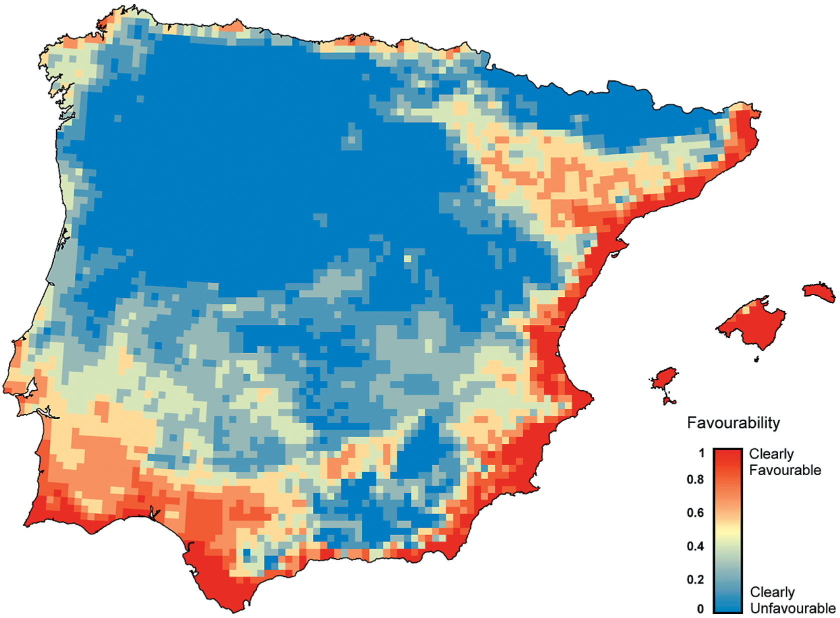

Fig. 4. Distribution of favourable sites for the Eurasian Reed Warbler in the Iberian Peninsula and Balearic Islands.

ation explained by non-climatic variables was 0.366 (Fig. 3A). The proportion of the shared effect between both climate and non-climate factors was –0.117. Spatial location and slope explained 0.325 and 0.080 of the variation of the model, respectively (Fig. 3B).

The favourability map (Fig. 4) showed that clearly favourable areas were on the Mediterranean coast, specific Atlantic coastal areas in the north and south of the Iberian Peninsula, and some estuaries (especially those with wide rivers), whereas clearly unfavourable areas were in northern inland regions and in mountainous areas. The intermediate favourability areas with the lowest values were located in southern inland areas of the Iberian Peninsula, whereas the values increased nearer to the coast, with the exception of some large valleys (i.e., the Guadalquivir valley in the south and the Ebro valley in the north). The Pch value for the model was 16.49.

## 4. Discussion

The effect of climate on bird distribution patterns has been strongly studied since the beginning of 21st century (Žalakevičius 2001, Péron *et al.* 2007, Muñoz *et al.* 2013, Massimino *et al.* 2015, Eyres *et al.* 2017, Bay *et al.* 2018). The influence of climate change on bird migration and its consequences is a key topic within the ornithology community (Both & Visser 2001, Gordo & Sanz 2006, Lehikoinen & Sparks 2010, La Sorte *et al.* 2017). Our model shows that almost 24% of the Iberian Peninsula is favourable for the Eurasian Reed Warbler during winter (although they only occupy 10% of that), and that more than 68% can be classified as "intermediate favourability".

These results support the idea that the Iberian Peninsula is already a new wintering area for this insectivorous long-distance migrant (as occurrence data showed) and it also corroborated our hypothesis of a potential increment in the wintering populations, possible due to the existence of unoccupied favourable areas, as recently discussed by Nieto *et al.* (2018). The obtained model is relatively specific in that it correctly classified absences (Fig. 2); however, the fact that the specificity value was less than 1 shows that the model detected clearly favourable conditions in areas in which the species had not yet been detected, while preventing possible false absences with high reliability (Olivero *et al.* 2016).

Sensitivity values (especially in the first step) and the high over-prediction rate may be explained by the detection of unoccupied favourable areas, although this possibility does not mean that the model is erroneous (Muñoz & Real 2006, Barbosa *et al.* 2013). The obtained Pch value indicates that there is more than twelve times the number of favourable areas than those with confirmed presences. According to this, we predict a potential increase in wintering areas for this species in a recent future if conditions persist (Muñoz, A.-R., Carrasco, E. & Real, R. "unpublished data"). It should be noted that the sampling methodology did not cover the whole study area, and therefore many of the unoccupied regions predicted as clearly favourable could actually be occupied by the species.

Winter temperature was the variable with the greatest explanatory power in the model, when selecting those areas with the mildest winters (Table 2, Fig. 4). Milder winters favour the prey availability for Eurasian Reed Warbler (Roiz *et al.* 2014), which finally increase their physical condition and very likely improves their breeding competence (Lewington 2006, Newton 2008). In the rest of Europe, the lack of winter prey for this species forces individuals to move southwards to find sufficient food to survive (Lewington 2006). However, Nieto *et al.* (2018) demonstrated that some individuals remain close to or in their breeding sites, in the Iberian Peninsula.

If these individuals find sufficient resources during winter, they will be able to select better breeding sites than long-distance migrants due to their proximity to the sites. Furthermore, their mortality rates during migration will be lower, which will allow them to have more offspring (Kokko 1999, Forstmeier 2002, Alves *et al.* 2013). During the last decade, the severity of winters in Europe has decreased due to the influence of current climate change. In Europe, the minimum temperatures have increased during the last 20 years and there are fewer days with temperatures less than 0°C (Brunet *et al.* 2007, I.P.C.C. 2014).

"New" warmer conditions in the Iberian Peninsula throughout the year, including winter, have led to an increase in the number of flying insects, such as mosquitoes (Roiz *et al.* 2014). That constant food availability allows the birds to maintain their body conditions during the wintering season, losing less energy when they face the environment, that is also climatically less severe. Under these conditions, the individuals remaining in Europe during winter have an increased likelihood of survival until the next breeding season, a decreased likelihood of fitness impoverishment, and an increased likelihood of producing more offspring (Alves *et al.* 2013).

Thus, there could be an increase in the number of individuals that change their phenology (Arizaga *et al.* 2012, Andueza *et al.* 2014). There has already been an increase in some populations of other migratory birds, such as the Hoopoe (*Upupa epops*) and Common Swift (*Apus apus*), which have been arriving earlier in their breeding sites during the spring migration, whereas other birds, such as the Willow Warbler (*Phylloscopus trochilus*) and the Common Redstart *(Phoenicurus phoenicurus*), have been delaying their autumn migration (Jenni & Kéry 2003, Crick 2004, Gordo & Sanz 2006). These phenological shifts could ultimately lead to a change in the species distribution range if these climatic conditions persist (Maclean *et al.* 2008). However, this phenomenon could put the European and Iberian wintering populations at risk if a sudden and severe shift in climatic conditions occurs, because such a change would lead to a rapid increase in the mortality rate, thereby seriously jeopardizing their existence (Senar & Copete 1995, Maclean *et al.*, 2008, Alves *et al.* 2013).

Although climate models have been demonstrated to have a high explanatory power, more reliable models are obtained when climatic and non-climatic variables are used together (Márquez *et al.* 2011). Regarding the spatial factor, the trend-surface analysis showed directionality in the spatial favourability of the Iberian Peninsula for this species (Fig. 1 D). Eastern followed by northern and southern coastal areas were the most favourable areas, whereas the Portuguese and Spanish inland areas were the least favourable. Given the spatial location of the Iberian Peninsula (i.e., acting as a border between Africa and Europe), many individuals from different breeding grounds arrive there, follow the Mediterranean coast until reaching the south, and then fly on to Africa (Kennerley & Pearson 2010, BirdLife International & NatureServe 2015).

The wintering areas in the northern Iberian Peninsula coast could be explained by the arrival of British birds in these areas, given that this region is the first land they encounter in their migration across the sea and it is favourable. The results of the trend-surface analysis demonstrate the favourability of sites in the northern Iberian Peninsula, while sites in the eastern and southern Iberian Peninsula are on the main migration routes of birds from Northern and Central Europe (Moreau 1972, Åkesson *et al.* 1996, Åkesson & Walinder 2002, Procházka *et al*. 2016). These results support the relevance of the migration orientation, which has a strong genetic basis (Berthold & Helbig 1992). More specifically, the breeding origin of the individuals affects their arrival site because, as nocturnal migrants, they migrate on a broad front but maintain their orientation in order not to become lost (Bermejo 2012, Alves *et al*. 2013, Hasselquist *et al.* 2017).

This trend into maintain the orientation during their migration could explain the absences in the south-western quarter of the Iberian Peninsula, although having mild winter temperatures, but being remote from the typical migration routes of the species (Moreau 1972, Font 2000, Kennerley & Pearson 2010, Andueza *et al*. 2014). The slope of the terrain also influenced potential distribution during winter because it reduced the favourability of the mountain ranges, even when they were near to the coast, despite suitable temperatures in these areas. This type of effect also occurs in areas of the interior of the peninsula, where, despite their being flat, the altitude of the plateaus makes the temperatures unsuitable to the species. However, slope and climate both increase favourability in sites close to the coast and in wide rivers and valleys where reed-bed communities are more abundant because the climate is suitable and the low slope allows water to accumulate, thus facilitating the presence of the species (Cramp 1992, Bermejo *et al.* 2003, Kennerley & Pearson 2010, Bermejo 2012). Hence, the topography factor is associated with the selection of optimal habitats for wintering by the Eurasian Reed Warbler.

This modelling approach shows that climate is a determinant factor in the wintering strategy changes this species is experiencing in Europe, although other environmental conditions are relevant at a regional scale. The Eurasian Reed Warbler could be considered as a model of many of other Trans-Saharan migrants that have begun to winter in the Iberian Peninsula in recent years. The relationship between climate and species phenology gives rise to some hypotheses concerning the way in which species have responded to environmental variability in recent decades, and also sheds some light on the response of species distributions to climate change (Muñoz 2015b). If temperature increases continue, we could assume that more individuals would shorten their migration distance, and thus the size of populations regularly wintering in Europe would increase.

However, the future of these populations could be at risk if climatic conditions undergo sudden and severe changes, which would entail high mortality rates in the proportion of birds wintering in Europe. The results of this study could be useful when applying direct sampling methodologies by giving priority to the most favourable areas, thus facilitating the sampling and monitoring of the species during winter. Although more research is required, results also contribute to our understanding of the effect of climate, especially in relation to the uncertainty surrounding the effect of climate change on species phenology and distribution.

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## Rytikerttusen talvehtimisalueet: ilmastonmuutoksen vaikutus

Muuttomatkojen pituuksissa on tapahtunut muutoksia viime vuosikymmenten aikana. Rytikerttunen on Saharan eteläpuolelle muuttava laji, joka talvehtii enenevässä määrin Iberian niemimaalla. Tässä tutkimuksessa selvitimme ilmastonmuutoksen mahdollisia vaikutuksia rytikerttusen talvehtimisen Iberian niemimaalla, ja käytimme geospatiaalista mallinnusta sopivimpien talvehtimisalueiden tunnistamiseen. Mallin avulla selvitimme tärkeimmät tekijät jotka vaikuttavat talvehtimisalueisiin. Malli validointiin erilaisten kalibrointi- ja diskriminointimenetelmien avulla. Talven alin lämpötila selitti talvehtimisalueiden sijaintia parhaiten.

Soveltuvimmat alueet sijaitsivat Iberian niemimaan etelä- ja länsirannikolla, sekä muutamilla Atlantin puolen pohjoisen rannikoilla. Analyysin tulokset vastasivat myös todettuja lentoreittejä pesimäalueelta talvehtimisalueelle. Kun malliin lisättiin topografia, saatiin habitaatteja selvitettyä myös pienemmässä mittakaavassa. Tulokset osoittavat, että Iberian niemimaa voi olla uusi talvehtimisalue monille Saharan eteläpuolella talvehtiville lajeille, muuttaen niiden talvehtimisreittejä.

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