UNIVERSIDAD COMPLUTENSE DE MADRID
FACULTAD DE CIENCIAS BIOLÓGICAS

TESIS DOCTORAL

Distribución invernal y dinámica de nicho en paseriformes migratorios

Winter distribution and niche dynamics in migratory passeriformes

MEMORIA PARA OPTAR AL GRADO DE DOCTOR

PRESENTADA POR

Guillermo Fandos Guzmán

Director

José Luis Tellería

Madrid, 2017

DISTRIBUCIÓN INVERNAL Y DINÁMICA DE NICHO EN PASERIFORMES MIGRATORIOS

WINTER DISTRIBUTION AND NICHE DYNAMICS IN MIGRATORY PASSERINES

GUILLERMO FANDOS GUZMÁN

TESIS DOCTORAL 2017

DIRECTOR:
JOSE LUIS TELLERÍA

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Winter distribution and niche dynamics in migratory passerines

Memoria presentada por Guillermo Fandos Guzmán para optar al grado de Doctor en Ciencias Biológicas, bajo la dirección del doctor José Luis Tellería, de la Universidad Complutense de Madrid.

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Dedicatoria

"I learned this, at least, by my experiment: that if one advances confidently in the direction of his dreams, and endeavors to live the life which he has imagined, he will meet with a success unexpected in common hours."

HENRY DAVID THOREAU, WALDEN: OR, LIFE IN THE WOODS

ACKNOWLEDGMENTS

Contents

CHAPTER 1 -
GENERAL INTRODUCTION

"Birds were flying from continent to continent long before we were. They reached the coldest place on Earth, Antarctica, long before we did. They can survive in the hottest of deserts. Some can remain on the wing for years at a time. They can girdle the globe. Now, we have taken over the earth and the sea and the sky, but with skill and care and knowledge, we can ensure that there is still a place on Earth for birds in all their beauty and variety — if we want to… And surely, we should"

- DAVID ATTENBOROUGH

INTRODUCTION

Animal migration consists of the relocation of individuals on large spatial scales, which habitually implies seasonal journeys from one range to another (Dingle, 2014). Compared to other animal groups, birds are well adapted for migration because, in addition to their ability to fly, they display efficient behaviour and extraordinary physiological and morphological adaptability (Newton, 2010). This combination of features produces some of the most incredible migrations in the animal world. This is the case, for instance, of the endurance flights exceeding 10,000 km carried out by bar-tailed godwits (*Limosa lapponica*) or the non-stop flight of common swifts (*Apus apus*), which complete the equivalent of up to seven round-trips to the moon during their lifetimes (Gill et al., 2009; Hedenström et al., 2016). Overall, 10,000 or so bird species are known to be migratory and move distances ranging from short hops to extraordinarily long journeys across continents (Greenberg & Marra, 2005; Newton, 2008). All these characteristics make bird migration a fascinating natural phenomenon.

Migratory movements enable birds to take advantage, for example, of seasonal highs in food abundance and better weather conditions. However, these benefits are offset by the challenges associated with migration, a very energy-demanding activity that obliges birds to cope with new environmental conditions, predators and parasites on their journeys (Alerstam et al., 2003; Pulido, 2007; Ramenofsky & Wingfield, 2007). Analyses of bird population trends across Europe (Sanderson et al., 2006) and North America (Robbins & Sauer, 1989) have found, for instance, that migrant birds are currently suffering more severe and more sustained declines than non-migrants. This general trend is associated with the accumulative impact of certain human activities (habitat loss, hunting, climate change, etc.) on the areas used by birds in their migratory circuits (Crick 2004). Thus, knowledge of the relationships between migratory species and the environments present on migratory circuits is a core requirement in any conservation strategy aimed at protecting these species (i.e. Rushton *et al.* 2004; Guisan & Thuiller 2005).

The study of range dynamics in migratory birds is a challenge given that these birds are present in areas separated by large geographical and temporal distances. As a result, migratory birds are vulnerable to habitat degradation or loss anywhere on their migratory circuit (Sherry & Holmes, 1995; Marra, 1998; Norris et al., 2004). Winter is a critical period for birds in many temperate areas since they have to cope with low temperatures and a scarcity of food (Carrascal et al., 2012). Unfortunately, a lack of data on birds' movements throughout the year has hampered to date the study of migratory birds in winter in comparison with studies conducted in the breeding season (Marra et al., 2015; Somveille et al., 2015).

The conservation of migratory birds relies on implementing appropriate conservation plans in all their seasonal habitats (Brochet et al., 2016). This is a difficult issue and, despite knowledge of certain aspects of bird winter ecology (Newton, 2010), conservation strategies for migratory birds have often failed to consider how populations are geographically linked between seasons (i.e. migratory connectivity; Webster et al., 2002). This has reduced our ability to detect where precisely migratory birds are affected by change. Fortunately, researchers today have unprecedented access to standardized high-quality methodologies that can follow migratory birds (Table 1; Robinson *et al.* 2010). The results of such studies, with support from citizen-science projects, are often stored in public databanks where it is possible to access information provided by satellite tracking devices (e.g. Movebank; www.movebank.org), ring-recoveries (e.g. EURING; www.euring.org) and geo-localized occurrences (eBird, www.ebird.org; Sullivan *et al.* 2016). These data, processed with ever-more powerful sets of statistical analyses (Hochachka et al., 2012), provide novel opportunities for advancing knowledge of migratory bird ecology throughout the year.

In this thesis, we combine ring-recovery data from Euring and species-distribution modelling techniques (Elith & Leathwick, 2009; Broennimann et al., 2012) to investigate how different migratory passerines (O. Passeriformes, C. Aves) respond to variations in environmental conditions during their annual cycles. Specifically, we study the distribution patterns and the related environmental traits of these birds on their wintering grounds in the Western Palearctic, an important area for European birds (Busse, 2001). This area in the western Mediterranean Basin is used by millions of migratory birds coming from breeding areas in central and north Europe and so any effort to protect these wintering quarters will have a huge impact on the overall conservation of European avifauna.

Table 1 Techniques used to study animal movement. Modified from Robinson *et al.* (2010)

Technique	Distances tracked (short, medium, long)	Uses	Limitations
Chemicals (isotopes) in tissues	Short–long	Assign approximate locations where individual birds molted feathers	Coarse spatial resolution. In North America, north–south resolution better than east–west. Also tends to vary with altitude and elevation, and may vary considerably within single site. Maps for other locations are less "finished" than the North America map. Maps may also vary from year to year.
Genetic markers	Short–long	Assign individuals to populations based on different genetic markers	Limited genetic differentiation in many species reduces ability to establish locations.
PTT tags (RFID; Radio Frequency Identification) High Frequency) telemetry	Short	Identify a marked individual with a reader placed at a strategic location (feeding or nesting site)	Readers are expensive and must be placed within a few meters of a nest or feeding site.
Radio (VHF; Very	Short–medium (long in rare situations with certain landscape and extraordinary effort)	Provide an individual animal's location, relay physiological data gathered from sensors	Transmission distance relatively short to ground-based receivers. Battery life of small transmitters a few weeks. Transmitter may also influence animal behavior.
Geolocators	Medium–long	Use day length to estimate latitude and longitude; primarily used on seabirds, but now small enough for medium-sized passerines	Spatial resolution varies seasonally across globe. Must recapture smaller animals to retrieve data.
Satellite telemetry	Short-long	Track larger animals across globe	Unless combined with GPS, accuracy can be low. Expensive to access data. Minimum size (about 8 g, 22 g with GPS) still too large for many species.
Radar	Short	Track intensity, speed, and direction of migration; track short flights of individuals	For most systems, there is no individual- or species-specific information. Low flying birds may be missed.

RING-RECOVERY DATA AND SPECIES DISTRIBUTION MODELLING

This thesis uses ring-recovery datasets to explore migratory bird distributions during the whole year and to understand how birds respond to environmental changes. Given that a lack of funding sometimes makes it difficult to carry out large-scale studies of species distribution using the most sophisticated methods (Table 1), data collected by citizen scientists represent a suitable alternative for use in this type of research (Du Feu et al., 2016; Sullivan et al., 2016).

The ring-recovery data used in this thesis have potential biases (Busse, 2001; Korner-Nievergelt et al., 2010) but also certain advantages if compared to other citizen-science databanks (i.e. eBird or GBIF): they provided the exact geographical origin and destination of individuals on migratory circuits (Figure 1). More explicitly, they can be used to link individuals between their breeding and wintering grounds, or between breeding/wintering grounds and stopover sites. As a result, the vast number of ringing recoveries stored in the main European database (EURING, http://www.euring.org/) can be used to improve the knowledge of population dynamics and movements that is required for addressing large-scale conservation projects (Tellería et al., 2012). About 115 million birds have been ringed in Europe and have generated around two million recoveries in Eurasia and Africa. Similar figures are reported from North America, with 63 million ringed birds and 3.5 million recoveries (Tautin 2005; Baillie *et al.* 2007). Thus, it is important to emphasize the potential of this extensive network of ringers, composed of a community of skilful and rigorous citizen scientists, as well as its suitability for use in coordinated projects (Du Feu et al., 2016).

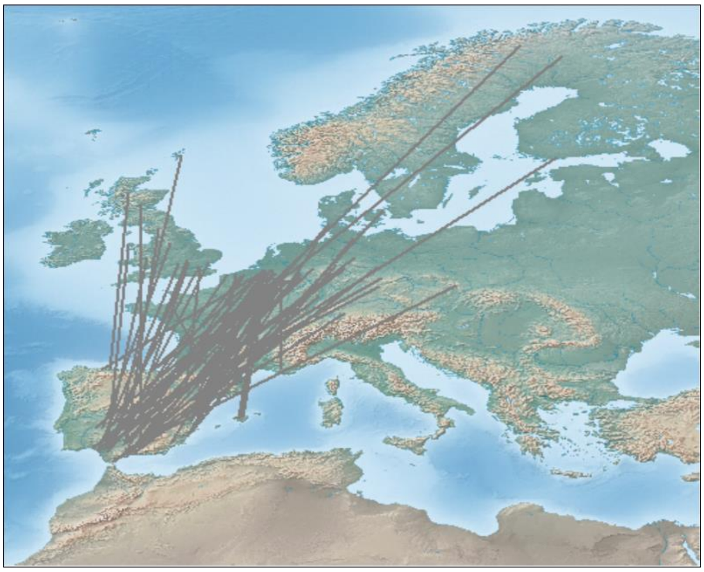

Figure 1 Lines connecting the ringing and recovery locations of 1103 migratory birds of 13 species showing the links between breeding ranges in northern and central Europe and wintering grounds in the Iberian Peninsula.

The development of new species-distribution modelling techniques has been accompanied by a growth in the accessibility to this huge amount of data. These techniques – known as Species Distribution Models (SDMs; Elith et al., 2006) – attempt to provide detailed predictions of bird distributions by relating the occurrence of species to a number of environmental predictors. In the past decade, this methodology was widely applied in different fields of ecology and evolution (Franklin, 2009; Peterson, 2011). However, little attention has been devoted to exploring the usefulness of bird ring-recovery data in modelling species distribution (Tellería et al., 2012). This approach provides an excellent opportunity for researching the main environmental features affecting the seasonal distribution of migratory birds and for understanding how changes in these factors contribute to shaping bird distribution along the migratory circuit (Webster et al., 2002; Boucher-Lalonde et al., 2014).

Nevertheless, despite the vast ring-recovery databases with information on the spatial distribution of migratory birds, ringing recoveries could provide a skewed view of the actual distribution of species due to the effects of human activity (Busse, 2001). Indeed, there are more recoveries near cities where people live than in uplands and mountain ranges (Reddy & Dávalos, 2003; Korner-Nievergelt et al., 2010). To tackle spatial variation in ringing recoveries, researchers have to take into account this geographical bias (Korner-Nievergelt et al., 2014) by, for example, examining the spatial distribution of the human footprint (HFP), a global index of population density, land transformation, accessibility and other infrastructures (Sanderson et al., 2002). This spatial index of human activity indicates the probability of detecting ringed birds (Figure 2) and, combined with environmental and ring- recovery data, can be used to predict bird distribution. After validation, the resulting SDM can be used to tackle questions about migratory bird ecology and distribution (Tellería et al., 2013b).

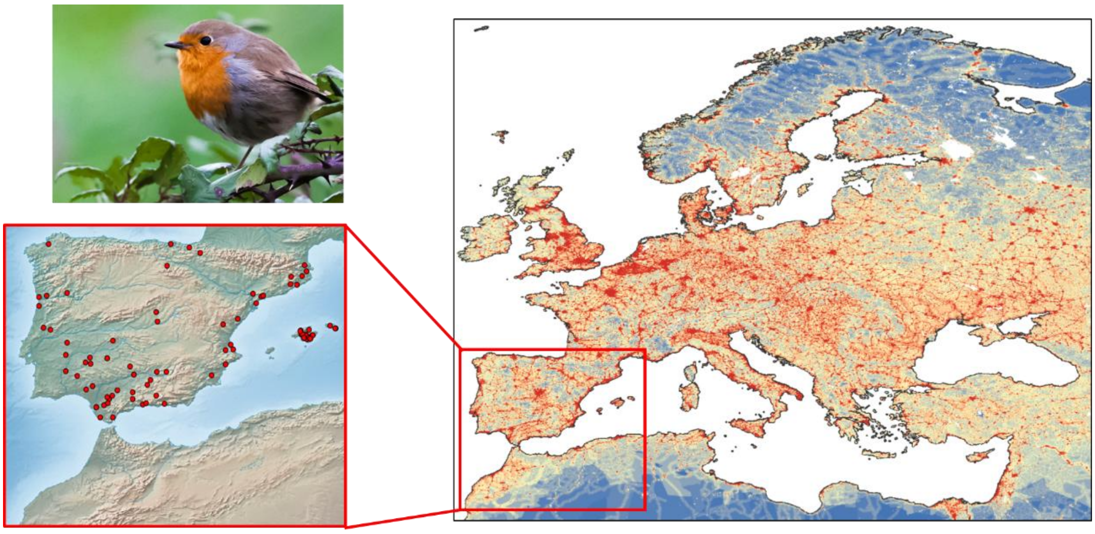

Figure 2 Left: a sample of winter ringing recoveries in the Iberian Peninsula and Maghreb of European robins (Erithacus rubecula). Right: the Human Foot Print (HFP) in Europe. It is clear that ringing recoveries are spatially correlated with high HFP values. Photograph: Elena Tena

STRUCTURE AND AIMS OF THE THESIS

In this thesis, we study the drivers of migratory bird distribution throughout the year by combining ring-recovery data with present and future environmental variables. The main goal is to update our knowledge of the mechanisms that determine the size, location and spatial dynamics of migratory species wintering in the Western Palearctic for application in conservation and spatial ecology. We have organised this thesis into three main parts.

Part A: Validation of SDM derived from ring-recovery data

This first part of the thesis evaluates the ability of SDM derived from ringing records to predict migratory birds' winter distribution. Despite the potential importance of using ringing records to describe the range of migratory birds, few studies have ever been performed that validate this methodological approach (Tellería et al., 2012; Cano et al., 2014). This validation is essential owing to the potential bias effects of inaccurate spatial locations of ringing recoveries (many of which were made before the use of GPS technology became widespread) and of the uneven spatial distribution of people reporting the presence of ringed birds (Busse, 2001). The aim of this part is to determine using field surveys whether or not the occurrence probabilities provided by the SDM do in fact predict the actual winter distribution of a migratory bird (Chapter 2) and if, as predicted, they are good predictors, this validation will demonstrate the usefulness of ringing records in the study of the dynamic nature of ranges in migratory birds (Part B). They will also be useful for detecting important conservation areas and forecasting the effects of environmental change in the winter distribution of migratory birds (Part C).

Part B: Understanding seasonal niche dynamics in migratory birds

Despite moving across different landscapes with varying environmental conditions, species-environmental relationships in migratory birds have often been regarded as static (Laube et al., 2015). However, environmental conditions in breeding and wintering sites may differ and so migratory birds have been classified as either 'niche-trackers' (i.e. they move in search of similar environmental conditions throughout the whole year; Nakazawa *et al.* 2004) or 'niche-switchers' (i.e. they change their environmental preferences between seasons; Laube et al., 2015; Gomez et al., 2016). In this second part of the thesis (Chapter 3), we use ringing recoveries to explore how migratory birds track spatio-temporal dynamics in the environmental conditions they encounter along their migratory circuit. The aim is to test the prediction that migratory behaviour should make birds use similar niche dimensions that are dynamic throughout the year (i.e. temperature or precipitation) more so than their sedentary counterparts.

Part C: Applications for Conservation

The decline of migratory species is a pressing concern worldwide and to protect them it is essential to know their distribution and environmental correlates. Chapter 2 opens up the possibility of using SDM derived from ring-recovery data to predict the range of migratory birds throughout the year and to forecast the distribution of these species under climate change scenarios. Thus, in chapter 4, we explore the distribution and size of seasonal ranges of some migratory passerines wintering in the Iberian Peninsula and Maghreb to test whether or not there is a reduction of non-breeding range size in relation to the breeding range. This imbalance between seasonal ranges has been shown to be one of the main correlates of species' vulnerability to global change (Gilroy et al., 2016). In chapter 5, we use climate projections to study the effect of climate change on the winter distribution of two migratory birds as a means of understanding the consequences of forecasted environmental changes for these model species.

The three sections of this thesis are covered by a number of chapters, some of which have been published, accepted or submitted to different international journals:

CHAPTER	PAPERS	STATUS
2	Tellería, J. L., Fernández-López, J., & **Fandos, G.** (2014). Using ring records and field surveys to predict the winter distribution of a migratory passerine. Bird Study, 61(4), 527-536.	Published
3	**Fandos, G.** and Tellería, J. L. Seasonal niche tracking in migratory populations of two partial migratory passerines	Submitted
4	**Fandos, G.** and Tellería, J. L. (2017). Range compression of migratory passerines in wintering grounds of the Western Mediterranean: conservation prospects. Bird Conservation International.	Accepted
5	Tellería, J. L., Fernández-López, J., & **Fandos, G.** (2016). Effect of climate change on Mediterranean winter ranges of two migratory passerines. PloS one, 11(1), e0146958.	Published

GENERAL METHODS

MODEL SPECIES

This thesis was conducted using a group of small migratory passerines wintering in the Iberian Peninsula and Maghreb, most of which breed on the western side of the migratory divide crossing Europe between 10–20ºE (Busse, 2001; Møller et al., 2011; Figure 1).

We selected passerines as model species for three reasons. Firstly, they are small abundant birds that occur in a broad range of habitats (Cramp & Simmons, 1988; Cramp, 1992; Cramp & Perrins, 1993, 1994; Tellería et al., 1999), which enables them to track environmental changes throughout the year; this makes them good models for exploring the environmental drivers of seasonal bird distribution. Secondly, small passerine species represent the bulk of the migratory avifauna in most regions and so play a significant functional role in certain ecosystems (Whelan et al., 2008). Finally, they are conspicuous animals that are easy to count in field sampling and so can be used to validate the species distribution models.

SPECIES DISTRIBUTION MODELS

Species distribution models (SDMs) employ statistical models to combine information on the presence (or absence) of a species with environmental patterns as a means of predicting the probability of occurrence of species. The environmental conditions of presences are compared with the environmental conditions defined in a set of randomly selected locations (i.e. the background or pseudo-absence dataset); if the environmental variables are spatially explicit, it is thus possible to assess the probability of occurrence (or suitability index) of sites in a given area by projecting the SDM predictions (Figure 3; Guisan & Zimmermann 2000). In addition, we can use the model and occurrence and environmental data from the environmental space to describe and compare niches (Broennimann et al., 2012). This framework allows us to measure differences in environmental availability and performs a principal components analysis (PCA) that relates environmental values to species-occurrence densities. For instance, this multidimensional environmental space allows us to measure the niche differences between seasons in migratory birds – independently of the number of occurrences – with an arbitrary choice of spatial resolution (Figure 3; Broennimann et al., 2012).

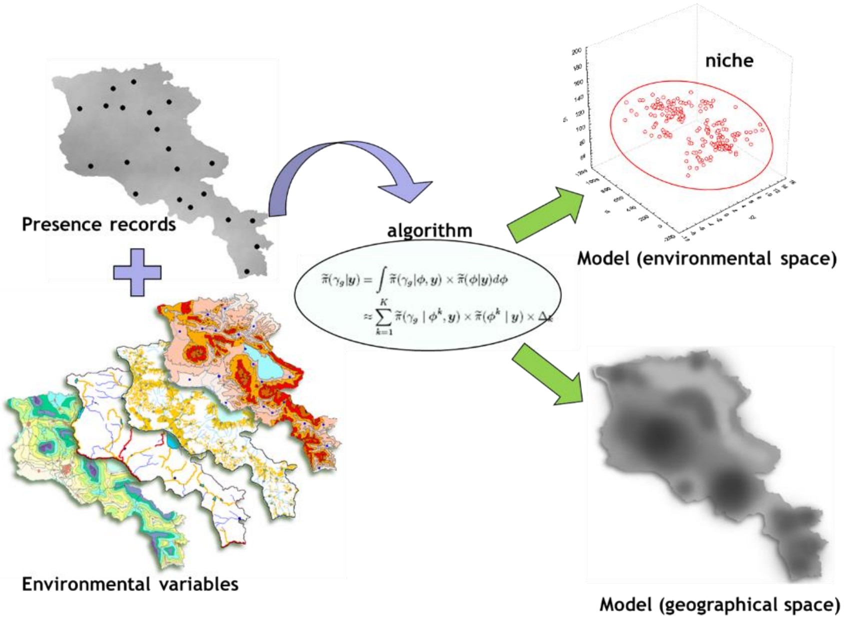

Figure 3 Main steps in SDM approaches. The presence records are linked to environmental variables to estimate the niche within an environmental space and to predict the geographical distribution of the species.

Occurrence data

The data used for the computation of the SDM refer to all birds recovered or ringed in winter (December–February) in the Iberian Peninsula or the Maghreb that, respectively, had been ringed or were subsequently recovered in central and northern Europe (for migratory populations) or in the Iberian Peninsula and Maghreb (for sedentary populations) during the breeding period (April–August). The data dates from 1925–2011 and 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 taken from the official page of EURING (http://www.euring.org). These data provide geo-referenced clusters of ringing records per species and show the location of marked individuals on breeding and wintering grounds.

Environmental variables

Fitting SDM relies on the existence of explanatory variables that define suitable environmental conditions for the species (Guisan & Zimmermann, 2000). Today, thanks to massive research in climate and the use of satellite remote-sensing techniques that explore the Earth's surface, we now have access to a massive amount of data from which we can select the variables most likely to have the greatest impact on the biology and distribution of study species. Due to their overall importance in species biology, we used climate data, cover topography and land use to approach the seasonal distribution of these migratory birds.

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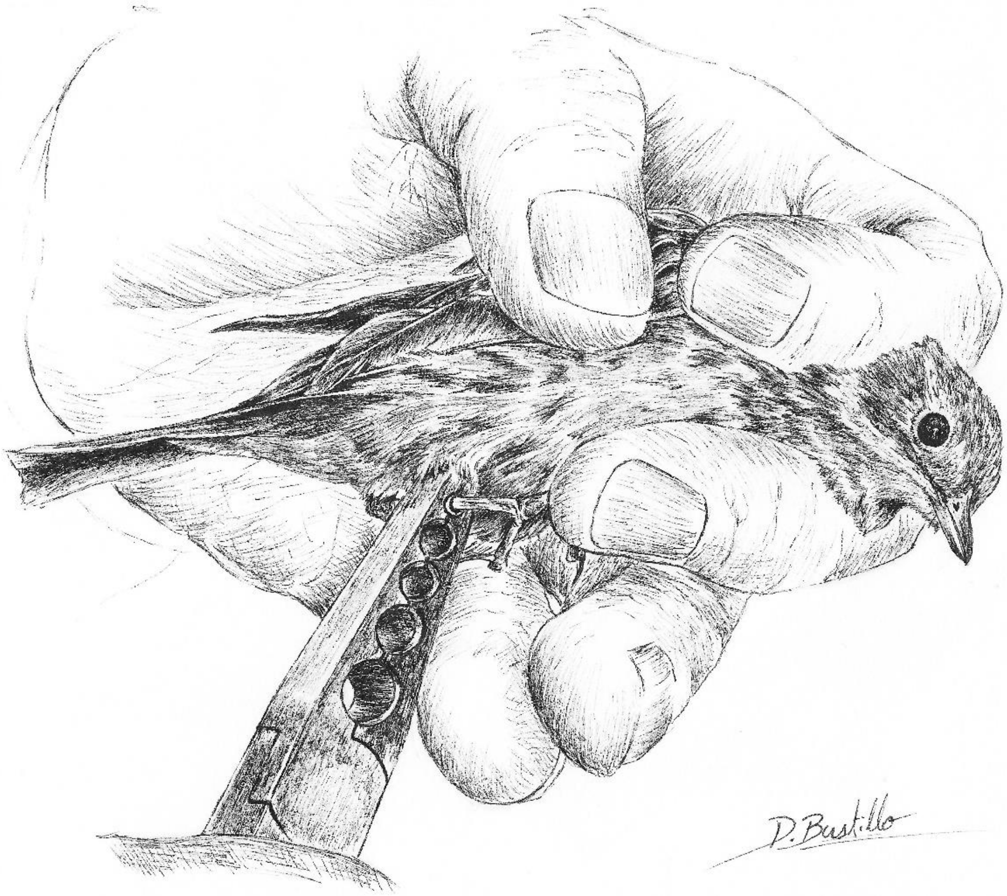

PART A -
Validation of ring-recovery models

CHAPTER 2 -

USING RING RECORDS AND FIELD SURVEYS TO PREDICT THE WINTER DISTRIBUTION OF A MIGRATORY PASSERINE

"All models are wrong, but some are useful"

- GEORGE E. P. BOX

This chapter is based on the manuscript: Tellería, J. L., Fernández-López, J., & Fandos, G. (2014). Using ring records and field surveys to predict the winter distribution of a migratory passerine. *Bird Study*, *61*(4), 527-536.

ABSTRACT

Ring records can be used to predict spatial changes in habitat suitability in wintering grounds of migratory birds as shown by a case study with the Meadow Pipit (Anthus pratensis). To forecast the winter distribution of the Meadow Pipit in the Iberian Peninsula and the Maghreb (1700000 km2) by combining ring records and fields surveys. We processed winter ring records with Maxent, a popular machine-learning technique used to predict the occurrence probability of species. We then tested whether the occurrence probabilities predicted by the model were significantly positively related to the actual abundance of the Pipit in Spain and Morocco. Occurrence probabilities provided by Maxent explained 6% of Pipit abundance distribution in partial least squares regression analyses. There was, in addition, a weak effect of geographical location (1.5%) and a strong effect of local vegetation (17.6%) on Pipit distribution. The occurrence probabilities were used to classify the winter range of the Meadow Pipit in sectors of high, medium and low suitability. The most suitable sector occupied 9% of the region (153000 km2) and was restricted to warm and moist lowlands where Pipits gather in grasslands. These results support the potential usefulness of cartographic models derived from ring records to describe the wintering range of migratory birds.

INTRODUCTION

Migratory birds spend a significant part of the year in wintering grounds where they occur in the most suitable habitats (Kelly, 1999). As a result, the extent and quality of wintering areas can restrict population sizes (Mills, 2006) or affect the subsequent reproductive success of migratory species (Webster et al., 2002; Norris et al., 2004). Consequently, the state of wintering grounds is a key issue in the conservation of migratory birds (Kirby et al., 2008).

The extent and quality of wintering grounds can be difficult to assess if it requires the use of extensive surveys in areas where skilled researchers or resources are scarce (Gillings, 2008). In such circumstances, it can be useful to explore alternative, cost effective approaches to the evaluation of the wintering grounds of bird populations (Wisz et al., 2007b). Clusters of ring records across a map have proven useful in detecting the location of wintering grounds, relating them to environmental traits or describing the seasonal displacement of migratory populations (e.g. Clark *et al.* 2009; Calenge *et al.* 2010). However, clusters of ring records do not show within range distribution of most suitable habitats despite this information being key to detecting the sectors where most individuals remain in the winter.

In the last decade, a set of mathematical algorithms has been developed to predict species distribution by combining occurrence data (latitude and longitude) with environmental variables provided by cartographic data banks (Elith & Leathwick, 2009). These methods map the occurrence probabilities of species, which can be used to predict species distribution (Franklin, 2009). In this context, occurrences provided by ringing schemes could be useful for predicting bird distributions in wintering grounds. However, predictions resulting from ring recoveries can give a skewed view of the actual distribution of birds (Busse, 2001) so that the models must be validated through the use of independent data (Araujo & Guisan, 2006). Despite the potential interest of such approaches to broaden the use of ring data banks, few studies have been carried out to validate this methodological approach (Tellería et al., 2012; Cano et al., 2014).

In this paper we use Maxent, a popular machine learning technique based on the principle of maximum entropy (Phillips et al., 2006), to predict the distribution of the Meadow Pipit *Anthus pratensis* (F. Motacillidae, O. Passeriformes) wintering in the Iberian Peninsula and Western Maghreb. This program has been designed to minimize 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). The study area (1700000 km2) is located at the southern border of the Palaearctic, a region that may act as the main wintering ground for many European birds (Busse 2001;Figure 4). Our aim is to: (1) model with Maxent the potential distribution of wintering Pipits using the information provided by the spatial distribution of ring records; (2) validate with field surveys whether the occurrence probabilities provided by the model predict the actual distribution of the species; (3) use the results to identify areas of different suitability for wintering Pipits and (4) identify the best habitats for Pipits within these areas.

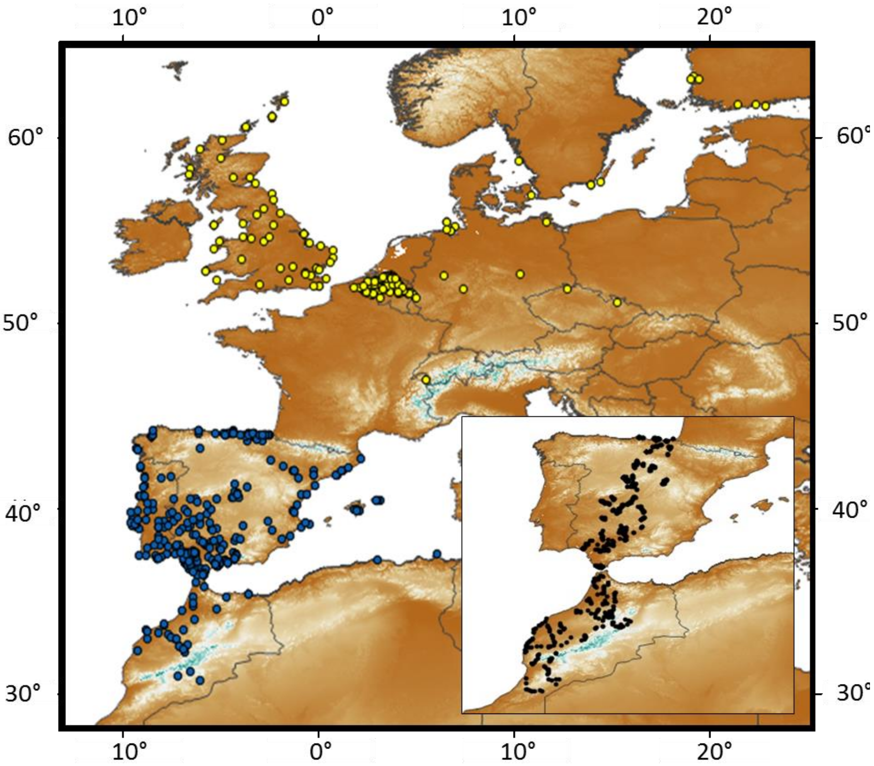

Figure 4 Distribution of winter localities in which ringed Meadow Pipits were recovered in the Iberian Peninsula and the Maghreb (yellow circles). The localities where Pipits were ringed are also recorded (blue circles). Inset: Distribution of sites where Meadow Pipit abundance was assessed.

METHODS

THE SPECIES

The Meadow Pipit is a small (14–23 g) insectivorous passerine that breeds in moorlands and pasturelands across the Palaearctic (over 42°N; Cramp 1988). The European population of the Meadow Pipit has decreased over the last few years (BirdLife International., 2014), probably due to land-use changes in breeding areas (Evans et al., 2005; Kosicki & Chylarecki, 2013). Many Pipits from the British Islands, central Europe and Scandinavia migrate to winter in the Iberian Peninsula and the Maghreb where the species occurs in meadows, fallows, irrigated fields and wooded pasturelands (Tellería et al., 1999; Thévenot et al., 2003; Vera & Giménez, 2012). Since this Pipit shows a dispersed distribution, the location and extent of the most suitable areas for wintering are not as yet known completely (see, however, Vera & Giménez 2012). This makes it difficult to detect the potential threats to the most suitable wintering areas for the species. The Meadow Pipit is, in addition, a good model to test the usefulness of ring recoveries to predict within range distribution of habitat suitability. Since the species does not breed in the Iberian Peninsula and the Maghreb, predictions based on ring recoveries in wintering grounds can be validated by the abundance distribution of the same migratory populations. This avoids the confounding effects of local birds that, in some partial migratory species, occupy different wintering habitats to migratory conspecifics (De la Hera et al., 2012).

RING RECOVERY DISTRIBUTION MODELLING

We used 318 localities where ringed Meadow Pipits were recorded at least once during December, January and February (Figure 4). Ring records were provided by the European Union for Bird Ringing (EURING) and the Spanish Office of Migratory Species (Spanish Ministry of Agriculture, Food and Environment). These records result from birds ringed in breeding grounds or migratory displacements that have been recovered during winter in the study region from 1960 to 2010 (Figure 4). The geographical location of ring records (latitude and longitude) was used to run Maxent by selecting a set of explanatory variables related to the distribution of this passerine within the Iberian Peninsula and the Maghreb. Since small birds avoid cold areas to avoid the need for excessive thermoregulatory requirements (Calder & King, 1974), and precipitation may affect the availability of moist grasslands suitable for this bird (e.g. Vanhinsberg & Chamberlain 2001; Atkinson *et al.* 2002; Kosicki & Chylarecki 2013), we selected the Mean Temperature of Coldest Quarter (bio11; TEMP) and Precipitation of Coldest Quarter of the year (bio19; RAIN) from Worldclim 1.4 for the period 1950–2000 (Hijmans et al., 2005). We also included January Normalized Difference Vegetation Index (NDVI) as a surrogate of primary productivity (Pettorelli et al., 2011). Finally, according to the landscape preferences of the Meadow Pipit (see above), we considered mean cover provided by the variable collection Vegetation Continuous Fields MOD44B for the period 2000–10 at 1 × 1 km spatial resolution (DiMiceli et al., 2011): bare ground (BARE; unsuitable), woody vegetation (WOODY; unsuitable) and herbaceous vegetation (HERBACEOUS; suitable) cover.

We ran Maxent (log output; regularization multiplier b = 1; autofeatures; convergence threshold = 0.00001) in ten replicates with 70% of the presences as training data and the rest as test data for internal verification. Duplicate records in the same localities were removed in each replicate. Since ring recovery distribution can be affected by human activity (e.g. more records are 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 in Maxent to distribute 10 000 background points with a likelihood of presence proportional to the human footprint index (Dudík et al., 2005). We used the Area Under the Curve (AUC) provided by receiver operating characteristic curves to assess the congruence between observed and detected records in the test data reserved to verification in Maxent (Phillips *et al.* 2006; see, however, Lobo *et al.* 2008). Data were managed with Quantum GIS 1.8 and GRASS GIS in 1×1 km squares (Grass Development Team, 2012).

VALIDATION OF THE MODEL

We assumed that the ability of occurrence probabilities produced by Maxent to predict Pipit abundance within the winter range of the Meadow Pipit was affected by at least two confounding effects: Geographical effects. Since Pipits move to the Iberian Peninsula and the Maghreb from the North, it is possible that the number of individuals will decrease at the southern border of the winter range producing variation in abundance that will not reflect the actual differences in carrying capacity (Sexton et al., 2009). This effect of migratory flyways on the abundance of wintering Meadow Pipits and other species has been detected elsewhere (Tellería et al., 2009; Cano et al., 2014). Habitat effects. Predictions of Pipit abundance resulting from large-scale species distribution models can be distorted at local scales by habitat preferences (Seoane et al., 2004). This means that Pipit abundance reported in line transects will be strongly affected by the local structure of habitats. Because grass and tree-covered patches represent suitable and unsuitable conditions for the Meadow Pipit (Mason & Macdonald, 1999; Vanhinsberg & Chamberlain, 2001; Atkinson et al., 2006; Suarez-Seoane et al., 2008; Kosicki & Chylarecki, 2013), we test whether the local availability of these habitat patches is able to distort the ability of occurrence probabilities to predict Pipit abundance.

FIELD WORK AND HABITAT CLASSIFICATION

We carried out field work in Morocco and Spain in December and January from 2006 to 2013. We assessed Pipit abundance in 737 localities ranging from 7 to 2057 m a.s.l along a 1500 km belt crossing the Iberian Peninsula and the Maghreb (Figure 4). We counted all Pipits seen or heard at either side of 500 m long transects irrespective of the perpendicular distance at which each individual was detected. In this way, assuming a constant inter-habitat detectability (Meadow Pipits occur in open landscapes), we obtained the number of individuals recorded per transect, a common index of bird abundance in extensive bird counts (Bibby et al., 2000). Abundance counts were checked against density estimates controlling for detectability variation using a two belt 25 m and 25+ m comparison (unpublished data): there was a strong positive correlation ($r = 0.92$, $P < 0.001$ $n = 737$), between density (no of Pipits/2.5 ha; 2.5 ha results from the sampled surface per transect 500 × 50 m) and abundance index (no Pipits/500 m). Given that the number of Pipits per transect involved more birds (1378 vs. 837) we therefore decided to use this abundance index to asses Pipit distribution. In addition, we measured vegetation traits related to the local distribution of the Meadow Pipit in 560 out of the 737 line transects used to assess abundance. Measures were taken in each transect in two 25 m radius circles separated by 200 m intervals. In each circle, we visually estimated grass layer (PASTURE), shrub (the percentage of vegetation between 0.5 and 2 m in height; SHRUB) and tree cover (the percentage of vegetation above 2 m in height, TREE). We averaged the scores of the two sampling circles to characterize each line transect. The location of each sampling point (LAT, LONG decimal degrees) was recorded with global positioning system devices.

Given the habitat preferences of the species during winter (Mason & Macdonald, 1999; Atkinson et al., 2006; Suarez-Seoane et al., 2008), we assumed that herbaceous cover was the main habitat correlated to the presence of the Pipit. Accordingly, we arranged the bird counts into three rough habitat types: arable lands (e.g. cereal fields and olive groves with some grass patches but mostly covered by bare ploughed grounds unsuitable for the species), pasturelands (meadows and tree-covered pastures – Iberian dehesas and montados – with high herbaceous cover) and woodlands (coniferous and broadleaved forests and scrublands). Bare ground unsuitable for the Meadow Pipit (e.g. rocky slopes, sandy areas, etc.) was not included in our sampling protocol.

ANALYSES

We explored the ability of occurrence probabilities to explain Pipit abundance distribution by means of partial least squares (PLS) regression, in which the effects of geographical location and habitat structure were included. This method is useful to solve the problem of lack of independence among the predictors since they are grouped in orthogonal gradients of covariation. The relative contribution of each variable to the derived factors was calculated by means of the square of predictor weights (Carrascal et al., 2009). We controlled for the effect of geographical location (including the potential effect of spatial autocorrelation) on Pipit abundance by means of the line transects' coordinates, LAT, LONG and LAT×LONG (Legendre, 1993). To explore the effect of local habitat structure we included PASTURE, SHRUB and TREE covers assessed in line transects. We repeated PLS regression analysis after splitting occurrence probabilities into three similar intervals (low, medium and high). They were used to define, respectively, wintering sectors of low, medium and high suitability within the winter range of the Meadow Pipit. Our aim was to test whether occurrence probability (OP) intervals predicted Pipit abundance distribution despite the effect of local habitat structure and geographical location. Finally, we used General Linear Models to test if Pipit abundance differed significantly among suitability sectors and habitats to identify the location of the best wintering habitats for the Meadow Pipit. We used the PLS–GLM modules of STATISTICA 7.0 (StatSoft 2004).

RESULTS

RING RECOVERY DISTRIBUTION MODELLING

TEMP was the most important variable according to Maxent and the jackknife test showed that eliminating it from the analyses dramatically lowered the predictive power of the model (Table 2). RAIN and BARE followed it in importance, and the remaining variables (HERBACEOUS, WOODY and NDVI) were only marginally important. The AUC value was 0.881 (Table 2), which suggests a good performance of the model according to current standards (Elith et al., 2002)

Table 2 Estimates of the relative contribution of the environmental variables. 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. They are normalized to show percentages. Values are averages over replicate runs. The large decrease observed in TEMP (Minimum Temperature of Coldest Month) indicates that the model depends heavily on this variable. Symbols in parentheses show the trend of the response curves for the quantitative variables +, increase; –, decrease and =, no change).

Variable	**Percent contribution**	**Permutation importance**
Temperature (TEMP)	43.8 (+)	46.4
Precipitation (RAIN)	24.1 (+)	25.0
Bare ground (BARE)	23.5 (-)	24.1
Herbaceous vegetation (HERBACEOUS)	5.8 (+)	9.4
Woody vegetation (WOODY)	1.6 (=)	2.8
Normalized Difference Vegetation Index (NDVI)	1.2 (+)	2.3
AUC±SD	0.881±0.009	

VALIDATION OF THE MODEL

Meadow Pipit abundance had a similar latitudinal trend to occurrence probabilities over the study belt crossing Spain and Morocco (Figure 5). Along the gradient there were many line transects where the species was absent. According to PLS regression, these seemed to correlate with unsuitable local conditions for the Meadow Pipit. These analyses identified one significant predictor ($P < 0.001$), among the eight variables, which explained 25% of Pipit abundance variation (Table 3). An important amount of abundance variation was attributable to the structural complexity of habitats (17.6%), with more Pipits in areas covered by pastures. Geographical location accounted for 1.5% of abundance variation suggesting a weak effect of geography. After controlling for these effects, occurrence probabilities explained 6% of abundance variation, with more Pipits in the most suitable sites according to Maxent's predictions (Table 2).

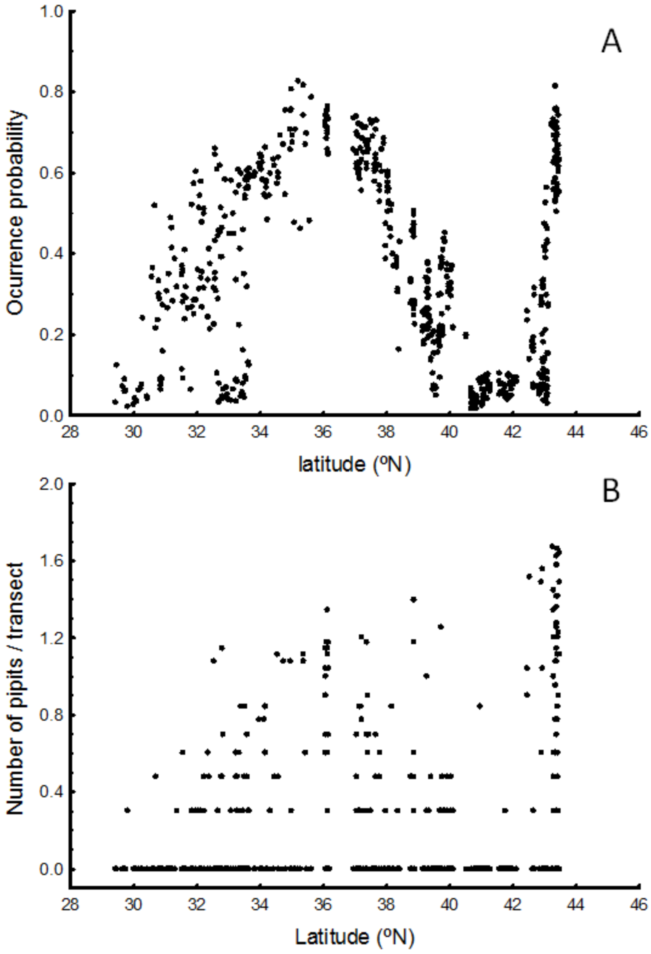

Figure 5 Latitudinal distribution of sampling sites representing the occurrence probabilities of the Meadow Pipit predicted by Maxent (a) and the actual distribution of abundances (b).

WINTERING SECTORS AND HABITATS

Since the OP produced by the model ranged from 0 to 0.825, we defined three intervals of similar OP (0–0.286, 0.287–0.555 and 0.556–0.825) to delimit wintering sectors of low, medium and high suitability for Meadow Pipits. These sectors explained 6% of Pipit abundance variation (Table 3). The suitability sectors defined by occurrence probabilities intervals showed an uneven distribution across the region (low: 75%, medium: 16% and high: 9%), with the high suitability sector covering 153 000 km2 of coastlines and lowlands (Figure 7).

Table 3 Predictor weights of PLS regression analyses and the relative contribution (%) of the variables used to explain the abundance variation of the Meadow Pipit. Only one multivariate factor was obtained per model. R2: percentages of original abundance variation. The predictor variables have been grouped into the three main categories (see text) with the whole variation (%) accounted for. OP, occurrence probability.

	Model 1 (OP scores)		**Model 2 (OP zones)**	
	weight	**R^2**	**weight**	**R^2**
LAT	-0.079	0.15	-0.07	0.13
LONG	-0.133	0.44	-0.131	0.38
LAT x LONG	-0.186	0.87	-0.183	0.74
GEOGRAPHICAL DISTRIBUTION (TOTAL)		**1.46**		**1.25**
GRASS	0.450	4.13	0.441	4.21
SHRUB	-0.484	4.77	-0.474	4.86
TREE	-0.529	5.70	-0.518	5.81
VEGETATION STRUCTURE (TOTAL)		**14.60**		**14.88**
Occurrence probability	0.494	4.97	-	-
Low occurrence probability	-	-	-0.395	3.37
Medium occurrence probability	-	-	0.111	0.27
High occurrence probability	-	-	0.325	2.29
OCCURRENCE PROBABILITY (TOTAL)		**4.97**		**5.93**
Total		**20.38**		**18.96**

Habitat (arable lands, pasturelands and woodlands) produced a strong effect on Pipit abundance distribution within suitability sectors (GLM; sector F2,711 = 58.1, P < 0.001; habitat F2,711 = 79.7, P < 0.001; sector*habitat interaction F4,711 = 25.6, P = 0.003; R2 = 0.31;Figure 6). The Meadow Pipit was more abundant in pasturelands and arable lands than in woodlands. Interestingly, pasturelands in the highly suitable sector defined by the ringing model had the highest abundances reported by transects of the entire study area (a posteriori Tukey honest significant difference tests for differences, P < 0.001 in all potential comparisons; Figure 6). This seemed to be associated with the preferences of the Meadow Pipit for grass-covered habitats because the trends in grass cover detected in line transects were also the highest in these grasslands (GLM; sector F2,552 = 13.2, P < 0.001; habitat F2,552 = 49.2, P < 0.001; sector–habitat interaction F4,552 = 5.7, P < 0.001; R2 = 0.18; Figure 6). To show the location of the most suitable habitats for the species, we mapped the distribution of herbaceous cover provided by the collection Vegetation Continuous Fields (see Methods) within the high suitability sector. Plots with increasing herbaceous cover >50%, >75% and >90% occupied, respectively, 94.5% (145000 km2), 65% (99450 km2) and 26.5% (40 545 km2) of the most suitable sectors (Figure 7).

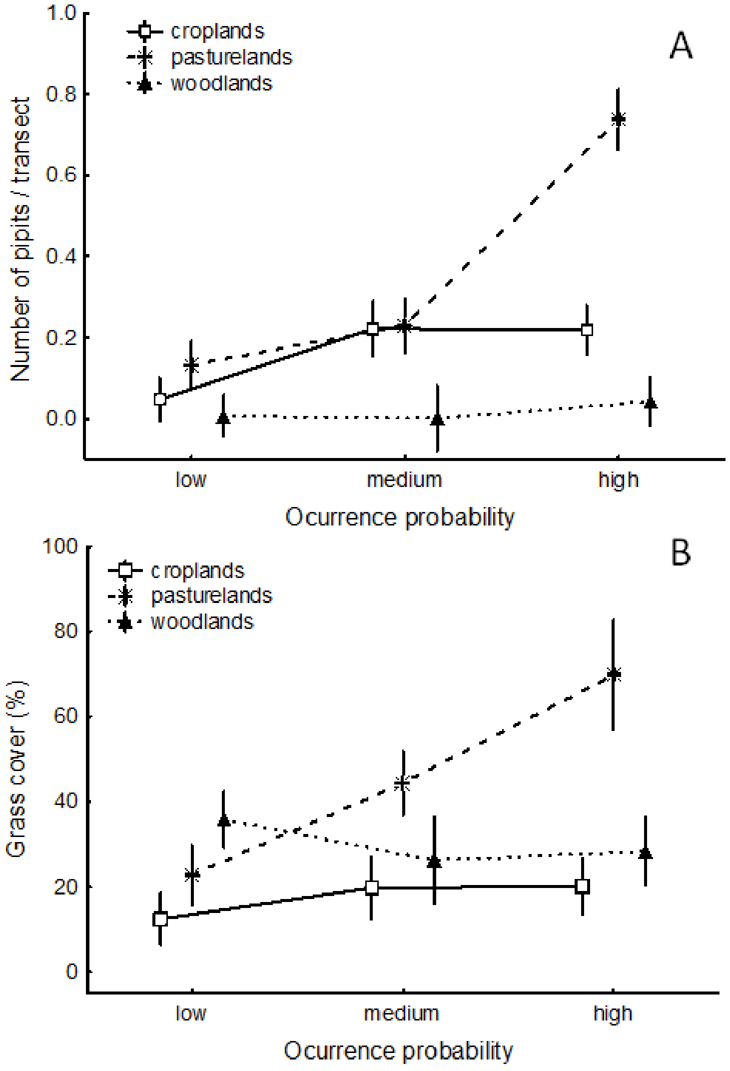

Figure 6 Distribution of the Meadow Pipit abundance (log10- transformed, a) and grass cover (b) among the three sectors of habitat suitability defined by ring recoveries and the three main habitats occupied by the species. Results show mean with 0.95 confidence intervals.

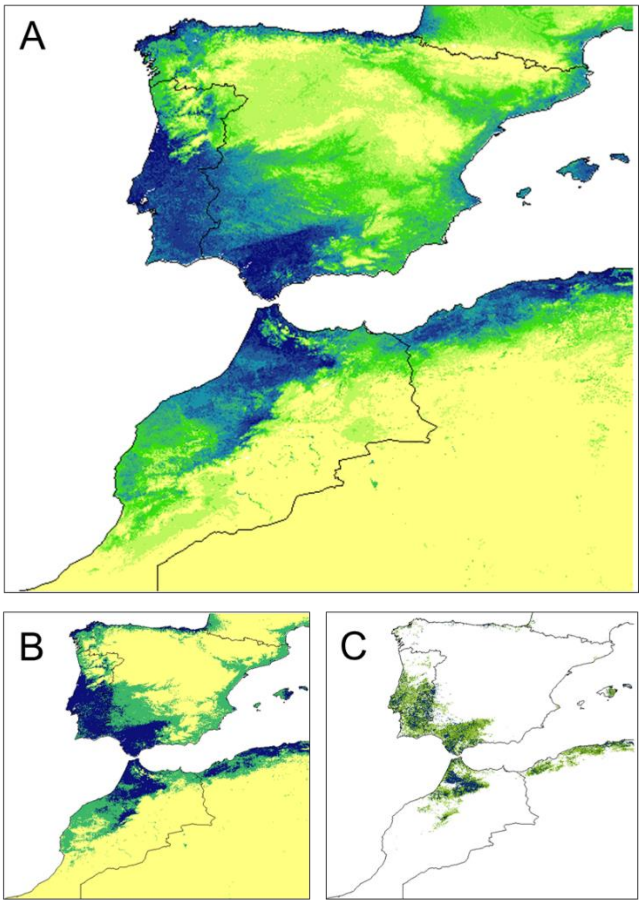

Figure 7(a) Occurrence probabilities of the Meadow Pipit in the study area. (b) Distribution of high (dark blue), medium (green) and low (yellow) suitability sectors according to similar OP intervals. (c) Distribution of herbaceous cover within the high suitability sector (green: cover > 50%, light blue: cover >75% and dark blue: cover >90%).

DISCUSSION

The relative contribution of the explanatory variables (Table 2) to the model resulting from ring recoveries, are congruent with some biological requirements of the species. For example, strong preferences for warm areas (TEMP) can be explained because low temperatures increase the risk of starvation in small birds, particularly if food availability is not sufficient to cope with energetic demands for thermoregulation (Calder & King, 1974; Canterbury, 2002). In this context, thermal constraints can play a key role in Pipit distribution in an area dominated by cold mountains and highlands where temperatures are under the suitable thermal limit for passerines (around 20°C; Calder & King 1974). Since the average mean and minimum January temperatures at our sampling points were 7.0°C (range 0.3–14.7) and 2.64°C (–5.2 to 9.6), respectively (Hijmans et al., 2005), the thermal landscape of the Iberian Peninsula and the Maghreb could explain the strong preference of Pipits for temperate sectors. This pattern has already been detected in small birds of other areas (Root, 1988; Meehan et al., 2004; Carrascal et al., 2012).

In addition to warm areas, the Meadow Pipit selected rainy sectors (RAIN). Rain is required to maintain moist grasslands suitable for this bird (Vanhinsberg & Chamberlain, 2001; Kosicki & Chylarecki, 2013). In warmer sectors of the Mediterranean region, autumn and winter rains improve winter productivity after summer drought, favouring the growth of a grass layer suitable for the species (Fernández-Ales et al., 1993). Our field surveys strongly support this interpretation because the grass layer (PASTURE) available to the Meadow Pipit at local scales was the highest in pasturelands of the high suitability sectors in the study region (Figure 6). However, NDVI, a surrogate of primary productivity (Pettorelli et al., 2011), was not a main correlate of Pipit distribution, perhaps because this index of photosynthetic activity increases in wooded areas, which are typically avoided by the Pipit. Finally, the model reflects a strong avoidance of bare ground in Pipit distribution. Therefore, according to the model, the wintering population of the Meadow Pipits excludes bare areas and includes warmer and rainier sectors.

The results of the validation model support the view that species distribution is shaped by features working at different spatial scales (McGill, 2010). In migratory birds, large-scale distribution is usually related to geographical and climate events affecting the historical configuration of migratory routes, and local distribution results from the arrangement of individuals among habitat patches according to specific preferences (Hutto, 1985; Zink, 2011). In our case, the geographical distribution of the study sites explained 1.5% of abundance variation (Table 3), indicating a weak effect of geography on the distribution of migratory Pipits. This suggests that Pipits distributed themselves across the region without constraints related to the effect of migratory flyways. Large-scale environmental variables involved in occurrence probabilities could explain 6% of the variation in the geographical distribution of the Meadow Pipit across the study area (Table 3;Figure 6) despite the fact that the final distribution of individuals was strongly affected by the local structure of habitats. In our case, the abundance of the Meadow Pipits was positively affected by pasture cover and negatively affected by shrub and tree cover, which explained most of the variation in abundance over the wintering region (15–18%; Table 3).

Sectors defined by occurrence probabilities intervals provided a clear view of the suitability of the study area for the Meadow Pipit, with the best sectors delimited by coastlines and inland highlands or deserts (Figure 7). Within this geographical arrangement of the Meadow Pipit, our study indicates a strong effect of habitats on species distribution. Sectors and habitats were able to explain more than 30% of the species' distribution over the region, with pasturelands located in high suitability sectors being key habitats for the species (Figure 6). They include coastal farmlands devoted to hay and cattle production in northern Iberia and extensive pasturelands and wooded grasslands in warmer sectors of the South (Suarez-Seoane et al., 2008; Vera & Giménez, 2012; Santos et al., 2014). This distribution is congruent with the habitat preferences of the Meadow Pipit reported in previous studies on the breeding and wintering areas of Europe (Mason & Macdonald, 1999; Vanhinsberg & Chamberlain, 2001; Atkinson et al., 2006; Kosicki & Chylarecki, 2013).

This dual approach to studying Meadow Pipit distribution (sectors vs. habitat) makes it feasible to map the location and extent of the best wintering habitats using the herbaceous cover provided by the collection Vegetation Continuous Fields (DiMiceli et al., 2011); Figure 7). This lends two additional perspectives to the distribution of Pipits in the Iberian Peninsula and the Maghreb. First, the best sectors (highest occurrence probabilities and extensive herbaceous cover) are constrained to the south-western quarter of the Iberia Peninsula (Tagus, Guadiana and Guadalquivir river basins) and the Sebou River basin in Morocco (Figure 7). These are agricultural areas situated in rainy sectors that drain the autumn–winter rains produced by low-pressure systems into the Atlantic. Moist and warm conditions support grass growth and invertebrate activity suitable for the Meadow Pipit. Second, the continuous herbaceous cover provided by Vegetation Continuous Fields allows a view of the geographical compression of the most suitable sectors for the Meadow Pipit, as has been reported for many migratory species in areas where land masses and habitats suitable for birds are restricted (Mills, 2006). For instance, the high suitability sector was distributed over only 9% of the region with the best plots (over 90% herbaceous cover) limited to 2.4% of the area (Figure 7).

The best areas for the Meadow Pipit and other species associated with warm, moist pasturelands are located in sectors of high human activity and will strongly rely on the development agenda of these regions, particularly as agricultural and urban encroachment increases. But the true consequences of these activities on Pipits are difficult to predict. In winter, Meadow Pipits select a broad set of managed habitats and seem to be quite adaptable to current changes to agro-ecosystems if moist grass and fallow patches are available (Atkinson et al., 2002; Suarez-Seoane et al., 2008; Vera & Giménez, 2012). Overgrazing and agriculture intensification are two main drivers of Meadow Pipit declines on the breeding grounds (Evans et al., 2005; Kosicki & Chylarecki, 2013). However, we do not know the impact of either process on the wintering ground studied here despite strong overgrazing in some areas of Northern Africa and the wholesale agricultural intensification of mild Mediterranean areas for fruit and vegetable growing (Mrabet & Moussadek, 2012; Schilling et al., 2012). Further investigations are also required to assess the effect of global warming at the southern border of the Palaearctic. This can affect the number of birds arriving to winter (Visser et al., 2009; Onrubia & Tellería, 2012) and may amplify the damaging effect of drought on soil water content and the extent and productivity of the grasslands used by Meadow Pipits (Falloon & Betts, 2010; García-Ruiz et al., 2011).

To conclude, the results in this paper demonstrate the usefulness of ring records to model the abundance distribution of the Meadow Pipit using Maxent, one of several methodological approaches available to model species distribution (e.g. Franklin 2009). Results agree with similar studies carried out on wintering birds in which ringing data were shown to be sound predictors of abundance distribution (Tellería et al., 2012; Cano et al., 2014) and suggest two main conclusions. First, the usefulness of the many millions of ring records stored in national and transnational data banks (Tautin, 2005; Baillie et al., 2007) to predict changes in habitat suitability in different seasons, historical periods and geographical scenarios. Second, the potential usefulness of linking the traditional use of ring records with the bourgeoning activity of new methodological approaches designed to model species distribution from occurrence data (Shirley et al., 2013).

PART B -

Understanding the seasonal niche dynamics in migratory birds

CHAPTER 3: SEASONAL NICHE TRACKING IN MIGRATORY POPULATIONS OF TWO PARTIAL MIGRATORY PASSERINES

“En la ladera de un monte, más alto que el horizonte; quiero tener buena vista; mi cuerpo será camino, le daré verde a los pinos y amarillo a la genista. Cerca del mar, porque yo nací en el Mediterráneo.”.

- JOAN MANUEL SERRAT

This chapter is based on the manuscript: Fandos, G. & Tellería, J. L. Seasonal niche tracking in migratory populations of two partial migratory passerines. *Submitted*.

ABSTRACT

Migratory birds spend periods of the year in different locations due to particular ecological circumstances. In terms of the way they track environmental conditions, migratory birds are classified as either 'niche-trackers' (i.e. they move in the search of similar conditions) or 'niche-switchers' (i.e. they change their preferences). Here we examine how migratory robins (*Erithacus rubecula*) and blackcaps (*Sylvia atricapilla*) track seasonal changes in the environment and how they differ from their sedentary counterparts. We used ringing data from breeding and non-breeding grounds to explore the conditions relating to the seasonal distribution of migratory and sedentary individuals wintering sympatrically in the Iberian Peninsula. We explored seasonal niche-tracking using multivariate analyses of increasingly more comprehensive sets of landscape and climate variables that produce different environmental scenarios. Migratory individuals tracked climatic conditions more than sedentary birds, which, on the other hand, coped with sharp changes in their permanent ranges. Migratory birds overlapped habitat structure less than sedentary individuals, which remained in the same areas throughout the year. These results suggest a trade-off between the greater ability of migratory individuals to track climatic conditions throughout the year and the capability of sedentary birds to tolerate climatic changes within their breeding ranges.

INTRODUCTION

Migration has evolved independently in numerous bird species in many parts of the world (Helbig, 2003). Indeed, an estimated 19% of the world's bird species are migratory, with the greatest rates of migratory individuals being found in highly seasonal areas of the Northern Hemisphere (Somveille et al., 2013). According to the way they respond to seasonal changes in environmental conditions, migratory birds are classified as 'niche-trackers' (i.e. they move seasonally in the search of similar conditions) or 'niche-switchers' (i.e. they change their preferences according to the period of the year; Joseph & Stockwell 2000; Martínez-Meyer et al. 2004; Nakazawa et al. 2004). However, it is not clear how migratory birds follow these strategies since it has been reported that they may display either niche-tracking or niche-switching behaviour (Joseph & Stockwell, 2000; Martínez-Meyer et al., 2004; Nakazawa et al., 2004; Laube et al., 2015; Gomez et al., 2016). These differences may be related to certain biological traits of the study species or to the effects of methodological constraints. It has been hypothesized, for instance, that niche-tracking is a plesiomorphic trait typical of sedentary birds that will develop into apomorphic niche-switching in migratory individuals (Martínez-Meyer et al., 2004; Nakazawa et al., 2004). As a result, niche-tracking and -switching will balance each other out according to the idiosyncratic evolutionary rates of migratory behaviour (Gomez et al., 2016). It has been also pointed out that early approaches to niche-tracking were probably flawed due to the inherent difficulties in working with multi-specific approaches (Peterson, 2011; Laube et al., 2015), the problems involved in comparing realized niches between areas where environmental conditions are unequally represented (Warren et al., 2008; Broennimann et al., 2012), and the use of unsuitable environmental traits to explore resource-tracking by birds (Peterson, 2011). Hence, resource-tracking should ideally be conducted using well-known model species for which the environmental variables used in the analyses are easily interpretable in terms of their biology (Tellería & Pérez-Tris, 2003).

Here we examine seasonal niche-tracking in migratory and resident European robins (*Erithacus rubecula*) and Eurasian blackcaps (*Sylvia atricapilla*), two common woodland passerines (O. Passeriformes) found in the West Palaearctic. They are both partially migratory (i.e. their populations are composed of individuals displaying different types of migratory behaviour; Chapman et al. 2011) and some individuals move from their breeding grounds in the north to wintering areas in the south (Cramp & Simmons, 1988; Cramp, 1992). On wintering grounds in the Iberian Peninsula, sedentary individuals occur sympatrically with their migratory counterparts, which carry out 'breeding partial migration' in spring (sensu Chapman et al. 2011) to breeding areas in the north (Pérez-Tris & Tellería, 2002a; Tellería & Pérez-Tris, 2003). This gives us the opportunity to explore how migratory robins and blackcaps track seasonal environmental changes operating in breeding and non-breeding periods.

It has been hypothesized that niche-tracking in birds will be affected by a trade-off between the cost for migrants of adaptations related to the tracking ability over long distances and the increased flexibility required by sedentary birds to tolerate a wider suite of conditions (Sol et al., 2005; Laube et al., 2015). This hypothesis thus predicts that migratory birds will move within a narrower range of environmental conditions than sedentary individuals, which will be obliged to cope with the changing conditions within their permanent ranges (Laube et al., 2015). However, this prediction will not apply to all niche dimensions and, for instance, migratory individuals may experience fewer seasonal changes in the dynamic niche dimensions they track (e.g. climate) than in the dimensions that are static over time (e.g. land cover; Laube et al. 2015).

To approach these issues we explore here the realized niches of robins and blackcaps that lie within an abstract hyperspace defined by different environmental variables (Hutchinson, 1957; Soberón, 2007). As we know that these passerines track food resources, thermal conditions and wooded landscapes (Telleria & Santos, 1993; Tellería & Pérez-Tris, 2003), we use several sets of variables to create different environmental hyperspaces (Gomez et al., 2016) to study seasonal niche-tracking (Warren et al., 2008; Broennimann et al., 2012). We used ringing data for individuals trapped in breeding and wintering localities (Du Feu et al., 2016) and two complementary methodological approaches to explore niche-tracking. (i) Seasonal niche overlap: we examined whether migratory individuals overlap seasonal niches more than their sedentary counterparts (Laube et al., 2015; Gomez et al., 2016). Given that birds do not maintain a perfect balance between niche-tracking and niche-switching (Laube et al., 2015; Gomez et al., 2016), we used overlap metrics to assess the strength of the differences between migratory and sedentary individuals. (ii) Seasonal niche change breadth: we took advantage of data linking individuals in breeding and non-breeding periods and an alternative method for assessing the strength of seasonal changes. To do so, we tested to see whether migratory birds have smaller Euclidean distances than sedentary birds in both breeding and non-breeding periods within the hyperspace defined for exploring niche overlap (see above).

METHODS

STUDY AREA

The Iberian Peninsula covers 580,000 km2 and is located between 36º and 44ºN on the southwestern edge of the Palearctic (Figure 8). The mountain ranges and plateaus that are the most outstanding features of this wintering area give rise to sharp changes in elevation and concomitant variation in environmental conditions (Körner, 2007). In winter, this area receives migratory blackcaps and robins from the western side of the migratory divide that crosses Europe between 10–20º E (Cantos, 1995; Bueno, 1998).

OCCURRENCE DATA

We used recoveries of robins and blackcaps trapped in the Iberian peninsula provided by the European Union for Bird Ringing (EURING) and the Spanish Office of Migratory Species (Spanish Ministry of Agriculture, Food and Environment) to classify birds according to their migratory status (Du Feu et al., 2016). We considered migratory individuals to be all those birds that were ringed/recaptured in the Iberian Peninsula in winter (December–February) and then recaptured/ringed more than 500 km away in central and northern Europe during the breeding period (April–August). We considered sedentary birds to be those that were ringed and recovered in the Iberian Peninsula in these same two periods within a distance of 50 km. These data provide two sets of geo-referenced clusters of ringing records per population (Figure 8) for which we explored seasonal niche overlap and breadth by establishing the environmental variables (see below) relating to bird occurrence (Warren et al., 2008; Broennimann et al., 2012).

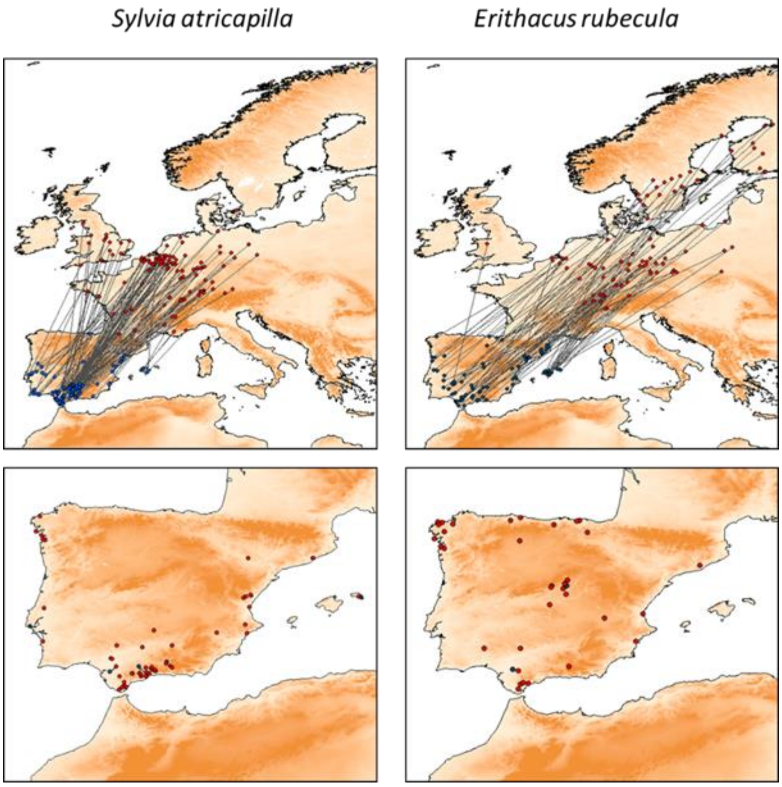

Figure 8 Distribution of individual ringing recoveries in breeding and non-breeding areas of migratory (top) and sedentary (bottom) robins (Erithacus rubecula) and blackcaps (Sylvia atricapilla).

ENVIRONMENTAL VARIABLES

The seasonal distribution of species in a given area is explained by an idiosyncratic combination of environmental traits that complicates any aprioristic selection of the variables that define bird distribution. Large-scale approaches are further hampered by the difficulties that occur when using certain key variables (Peterson, 2011) such as food availability or the accessibility of specific microhabitats that can be tracked by blackcaps and robins (Tellería & Pérez-Tris, 2003; Tellería et al., 2008). In this study, we considered a set of variables available in large-scale data sets that may affect birds direct or indirectly (Finally, due to the important effects of vegetation cover on the large-scale distribution of these birds (Telleria & Santos, 1993), we also included wood and herbaceous cover from Vegetation Continuous Fields MOD44B (DiMiceli et al., 2011). We did not include elevation in our analyses because, despite its impact as a surrogate of environmental change (Körner, 2007), most of its effects are already assessed more directly by the other previously mentioned variables. Climate data were taken from Worldclim 1.4 (Hijmans et al., 2005) and prepared as ASCII raster maps with a resolution of 1x1 km using the raster package in R (Hijmans & van Etten, 2013; R Core Team, 2015).

Table 4). For instance, we selected maximum and minimum temperatures for both periods because small birds track thermal conditions to reduce thermoregulatory costs (Joseph & Stockwell, 2000; Carrascal et al., 2012; Khaliq et al., 2014). In addition, we included mean precipitation because rainfall improves primary productivity in the warmer parts of the study area (Nahal, 1981; Chu et al., 2016). We also included the effect of temperature and precipitation seasonality (standard deviation of the monthly means x 100) to assess the seasonal pulses of productivity tracked by many migratory birds (Wisz et al., 2007a), as well as aspect as a source of microclimatic variation (Gomez et al., 2016). All these variables were combined to produce a gradient of climate and productive suitability for birds (Finally, due to the important effects of vegetation cover on the large-scale distribution of these birds (Telleria & Santos, 1993), we also included wood and herbaceous cover from Vegetation Continuous Fields MOD44B (DiMiceli et al., 2011). We did not include elevation in our analyses because, despite its impact as a surrogate of environmental change (Körner, 2007), most of its effects are already assessed more directly by the other previously mentioned variables. Climate data were taken from Worldclim 1.4 (Hijmans et al., 2005) and prepared as ASCII raster maps with a resolution of 1x1 km using the raster package in R (Hijmans & van Etten, 2013; R Core Team, 2015).

Table 4). Finally, due to the important effects of vegetation cover on the large-scale distribution of these birds (Telleria & Santos, 1993), we also included wood and herbaceous cover from Vegetation Continuous Fields MOD44B (DiMiceli et al., 2011). We did not include elevation in our analyses because, despite its impact as a surrogate of environmental change (Körner, 2007), most of its effects are already assessed more directly by the other previously mentioned variables. Climate data were taken from Worldclim 1.4 (Hijmans et al., 2005) and prepared as ASCII raster maps with a resolution of 1x1 km using the raster package in R (Hijmans & van Etten, 2013; R Core Team, 2015).

Table 4 Description and classification of variables used in the niche estimation. Abbreviations are as used in the figures

Variables	*Dimension*		*Abbreviation*	*Description*
Mean precipitation	Climate	Precipitation	prec	The mean precipitation for the breeding (April to August) and for the wintering period (December to February)
Precipitation seasonality			bio15	Precipitation Seasonality (Coefficient of Variation)

Maximum temperature		Temperature	tmax	The maximum temperature for the breeding (April to August) and for the wintering period (December to February)
Minimum temperature			tmin	The minimum temperature for the breeding (April to August) and for the wintering period (December to February)
Temperature seasonality			bio4	Temperature Seasonality (standard deviation *100)
Aspect			aspect	Aspect as a source of microclimatic variation
Bare ground	Habitat	Land Cover	bare	High values specify areas without vegetation
Wood cover			tree	High values specify high vegetation development as woodlands
Herbaceous cover			herb	High values specify open areas with vegetation

NICHE OVERLAP

We explored the environmental overlap between seasons using the multivariate approach described in Warren et al. (2008), Broennimann et al. (2012) and Cola et al. (2016). This method accounts for the seasonal differences in environmental availability between breeding and wintering grounds and performs a principal components analysis (PCA) that relates environmental values to species-occurrence densities (ringing controls) in breeding and wintering periods (Broennimann et al., 2012). Thus, it creates a multivariate environmental grid defined by PC1 and PC2 in which each cell represents a unique combination of the environmental conditions available to birds on breeding and wintering grounds. Subsequently, the method applies Gaussian kernel density functions to estimate the occupancy of each cell by the species and uses the D metric (Schoener, 1970), which ranges from 0 (completely different niches) to 1 (identical niches), to calculate the overlap between seasons. This methodological approach tests whether the environmental conditions selected by migratory and sedentary populations on breeding and non-breeding grounds are identical (niche equivalency) and whether the environmental conditions occupied in winter are more similar to conditions in breeding periods than would be expected by chance and vice-versa (niche similarity; Warren et al. 2008). We ran four PCAs to produce five PC1i and PC2i dimensions to assess seasonal overlap (D) and to apply equivalency and similarity tests: i) land cover variables (tree, plant and bare-ground cover), ii) temperatures (minimum, maximum and temperature seasonality), iii) climate (minimum, maximum and temperature seasonality, mean and precipitation seasonality, and aspect), and iv) all environmental variables (climate + land cover).

For test niche equivalency and niche similarity (Warren et al., 2008; Broennimann et al., 2012), we performed paired comparisons of the realized niches of each population between seasons. The first test evaluates if the environmental conditions that define the niches of the two populations are identical. The second test assesses the similarity in the relative distribution over the environmental conditions defining the niches of two populations, and is tested by comparing the overlap between the two realized niches to the expected distribution of overlap obtained by reallocating the density of occurrence of one entity across its range of occupancy, while the occurrence of the other remains constant. We used rand.type = 1, as both breeding and wintering niche, are randomly shifted. For both tests, expected distributions were based on 1000 iterations of the randomization procedure. All analyses were conducted in R 2.13.2 (R Core Team, 2015) using ecospat package (Cola et al., 2016).

NICHE CHANGE

We measured the Euclidean distances between the breeding and winter locations of each individual blackcap and robin in the space defined by PC1i and PC2i. This distance assesses the differences in environmental conditions experienced by individuals in breeding and non-breeding periods and is thus a synthetic approach to the seasonal niche shift of populations. We used ANOVA to test whether sedentary birds had greater Euclidean distances than migratory individuals. All analyses were conducted in R 2.13.2 (R Core Team, 2015).

RESULTS

We documented 131 sedentary blackcaps that moved 1.7 ± 0.6 km (mean ± s.e; min-max: 0.0–46.5 km) and 125 migratory blackcaps that moved 1563.4 ± 31.9 km (min-max: 509.2–2567.8 km) between their breeding and wintering sites; likewise, we logged 53 sedentary robins (1.3 ± 0.6 km; min-max: 0.0–23.4 km) and 85 migratory robins (1948.3 ± 69.7 km; min-max: 817.5–3658.9 km; Figure 8).

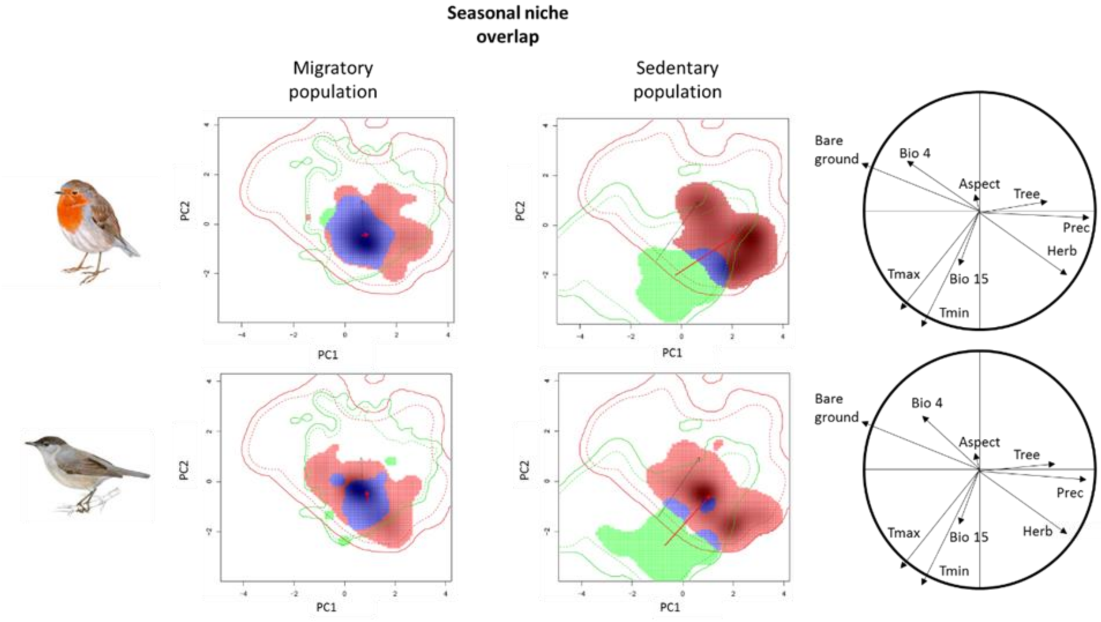

Figure 9 Representation of the environmental spaces described by the two first components of the PCA on the total set of variables. Spaces are occupied by sedentary and migratory populations of blackcaps (Sylvia atricapilla) and robins (Erithacus rubecula) in breeding (green) and wintering (red) periods. Shading represents the highest densities of occurrence; the solid and dashed contour lines illustrate, respectively, 100% and 50% of the available (background) environment. The blue colour shows seasonal overlapping. The panels on the right represent the correlation circle of the environmental variables used in the PCA

Migratory robins and blackcaps showed a greater overlap in temperature and climate than sedentary individuals (Table 5,Figure 9), a trend that was not present in land cover, which remained similar throughout the year in resident birds (Table 5; Figure 10). The Euclidean distances between the breeding and winter occurrences of individual robins and blackcaps in the space created by PC1i and PC2i (Table 5) provide support for the differences between sedentary and migratory populations reported above (Figure 11). Migratory birds experienced fewer changes in temperature and climate but greater differences in land cover than sedentary individuals. Results of ANOVA analysis were for *Erithacus rubecula:* Total variables ($F_{(1,137)}$=76.202, p<0.001); climate ($F_{(1,137)}$=137.836, p<0.001); temperature ($F_{(1,137)}$=85.354, p<0.001); land cover ($F_{(1,137)}$=4.087, p=0.045) and *Sylvia atricapilla*: Total variables ($F_{(1,255)}$=299.546, p<0.001); climate ($F_{(1,255)}$=480.914, p<0.001); temperature ($F_{(1,255)}$=247.619, p<0.001); land cover ($F_{(1,255)}$=16.533, p<0.001).

Table 5 Niche overlap, equivalency test, and similarity test between breeding and wintering grounds of migratory and sedentary blackcaps (Sylvia atricapilla) and robins (Erithacus rubecula). Tests were carried out on different multivariate environmental grids produced by PCA analyses of different sets of variables. n.s.: not significant. Niche equivalency test H_1: Is the overlap between the breeding and wintering niche higher than two random niches? Niche similarity H_1: Is the overlap between the breeding and wintering higher than when the wintering niche is randomly introduced in the breeding ground and vice versa?

	Migratory				***Residents***		
	Var. expl. PC1i + PC2i (%)	Overlap (D)	Equivalency test	Similarity test	Overlap (D)	Equivalency test	Similarity test:
Sylvia atricapilla							
Land cover	99.27	0.327	n.s.	0.029	0.896	0.039	0.009
Temperature	74.10	0.343	0.009	0.029	0.010	n.s.	n.s.
Climate	59.41	0.219	0.009	0.059	0.031	n.s.	n.s.
Total	52.81	0.250	n.s.	0.019	0.031	n.s.	n.s.
Erithacus rubecula							
Land cover	99.26	0.295	n.s.	0.108	0.910	0.009	0.009
Temperature	74.15	0.282	0.009	0.089	0.028	n.s.	0.049
Climate	59.31	0.269	0.009	0.049	0.003	n.s.	n.s.
Total	52.73	0.477	0.019	0.019	0.037	n.s.	n.s.

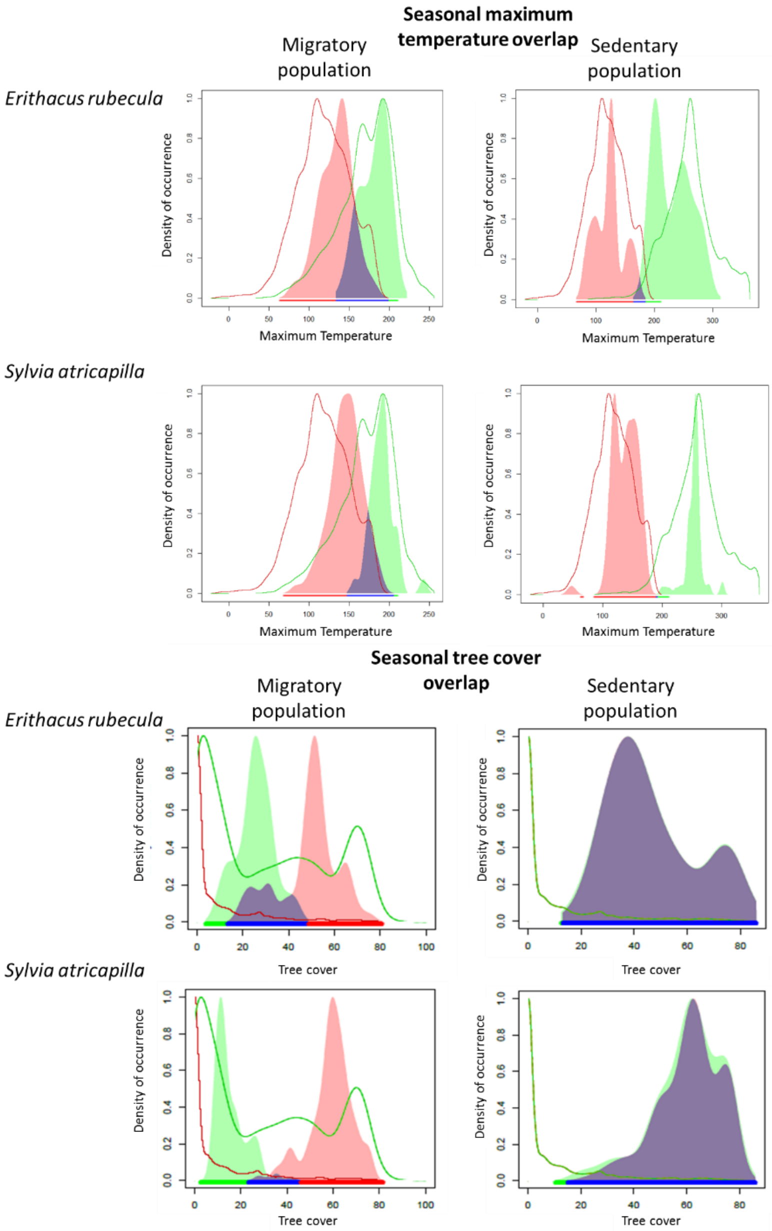

Figure 10 Seasonal overlap in maximum temperature and tree cover in sedentary and migratory populations of Erithacus rubecula and Sylvia atricapilla in breeding (green) and wintering (red) periods. The blue colour shows seasonal overlapping.

DISCUSSION

EVOLUTIONARY PROSPECTS

Variation in migratory behaviour is a widespread trait within species from the Northern Hemisphere, which shift from being essentially sedentary individuals at low latitudes to completely migratory at high latitudes (Chapman et al., 2011). These changes in migratory behaviour affect individuals, which differ in certain migration-related morphological and demographic traits (e.g. Pérez-Tris et al. 2000; Pérez-Tris & Tellería 2002b; Pérez-Tris et al. 2004a for robins and blackcaps in the study area). Although the selective pressures affecting this differentiation are far from fully known, it ioverlaps commonly agreed that adaptation for long-distance flight does not require profound changes in other biological traits (Salewski & Bruderer, 2007). In addition, it has been suggested that the ubiquity of genetic variation affecting long-distance movements in partially migratory species could produce sedentary or migratory individuals depending on prevalent conditions (Pulido, 2007). This seems to be an intrinsic trait of partially migratory birds (Salewski & Bruderer, 2007) that could explain their capability to adapt rapidly their migratory behaviour via micro-evolutionary processes to change (e.g. Bearhop et al. 2004). This suggests that the plesiomorphic state of partially migratory species is an ill-defined state from which migratory or sedentary individuals will split off according to circumstances. Thus, at the onset of migratory differentiation the partially migratory robins and blackcaps considered in this study are suitable models for exploring the way migration affects seasonal resource-tracking.

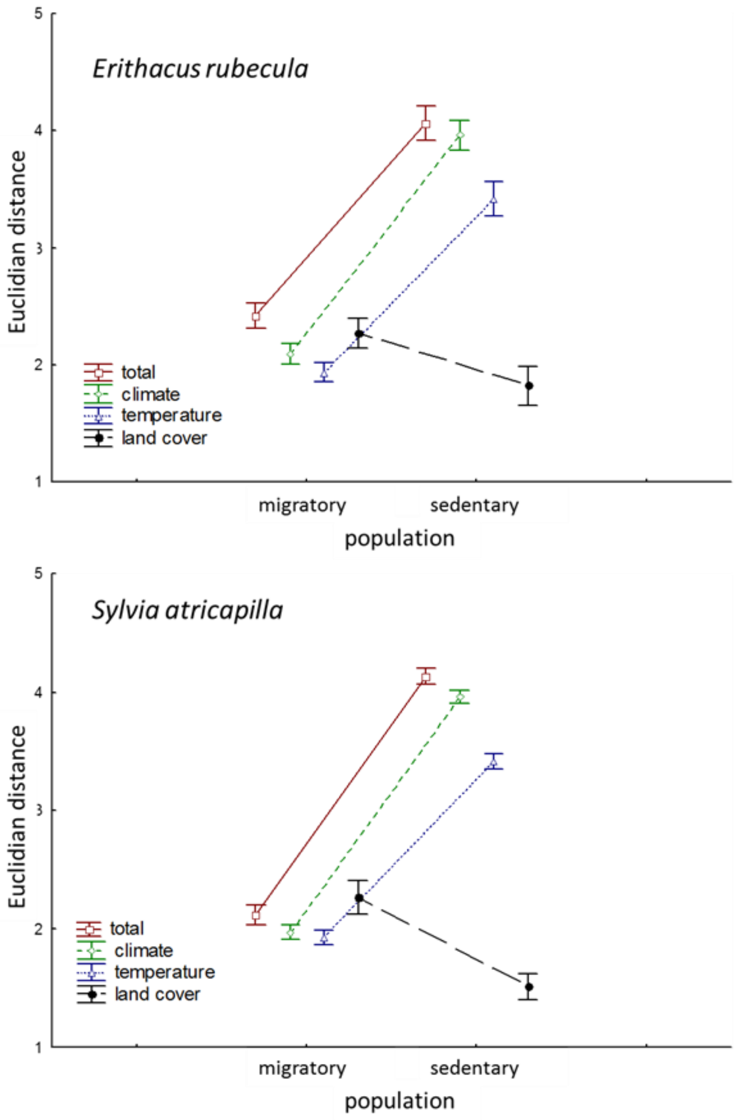

Figure 11 Mean Euclidean distances (and 95% confidence intervals) of individuals within the environmental space created by the PC1 and PC2 in blackcaps (Sylvia atricapilla) and robin (Erithacus rubecula). The results of ANOVA between migratory and sedentary populations are reported in the results section.

SEASONAL NICHE TRACKING

Migratory populations of robins and blackcaps overlapped more than their sedentary counterparts in the temporally dynamic niche dimensions considered in this study (e.g. climate variables; Finally, due to the important effects of vegetation cover on the large-scale distribution of these birds (Telleria & Santos, 1993), we also included wood and herbaceous cover from Vegetation Continuous Fields MOD44B (DiMiceli et al., 2011). We did not include elevation in our analyses because, despite its impact as a surrogate of environmental change (Körner, 2007), most of its effects are already assessed more directly by the other previously mentioned variables. Climate data were taken from Worldclim 1.4 (Hijmans et al., 2005) and prepared as ASCII raster maps with a resolution of 1x1 km using the raster package in R (Hijmans & van Etten, 2013; R Core Team, 2015).

Table 4). However, the seasonal overlap of migratory individuals was far from perfect (D=1), a pattern reported in previous work (Peterson, 2011; Laube et al., 2015). Incomplete overlapping may result from misinformation on the spatial-temporal distribution of resources, travel costs, intra- and inter-specific interactions, fidelity to sites or a lack of coincident spatial-temporal patterning of traits relevant to birds (Kennedy & Gray, 1993; Tellería & Pérez-Tris, 2003; Jiménez-valverde et al., 2009).

Overlap scores (Table 5) and reduced niche changes (Figure 11) give support for the importance of temperature in bird tracking (Joseph & Stockwell, 2000) since, when precipitation and aspect were included in a more comprehensive climate scenario, no improved patterns were found (Table 5). Thermal preferences related to the direct and/or indirect effects of temperature on birds (see Methods) are more similar in migratory than in sedentary birds since residents are compelled to face warm conditions during the breeding period (Figure 10). This suggests that sedentary individuals have to cope with the hot (and dry) summer conditions of the Mediterranean region, a constraint that is usually linked to active selection by forest birds of colder and moister woodlands for breeding in the Iberian peninsula (Telleria & Santos, 1993; Tellería & Pérez-Tris, 2003). We can speculate that the lack of these constraints in temperate and moist sectors of central Europe, where European woodland species find the most suitable habitats (Cramp & Simmons, 1988; Cramp, 1992), could explain the use of landscapes with less cover on breeding grounds (Figure 10). As a result, migratory birds overlap land cover less than residents in Iberia, which remain year-round within their permanent breeding sites (Table 5, Figure 11; see Laube *et al.* 2015). However, despite the shift from dense vegetation cover in breeding grounds to more open habitats in wintering areas that is typical of many forest birds (Zuckerberg et al., 2016), migratory individuals of both species avoided open areas, which supports the importance of specific habitat preferences in the seasonal distribution of migratory birds (Hutto, 1985).

The link between migration and small changes in the climatic niche of robins and blackcaps reported in this study is not backed up by previous work (Laube et al., 2015; Gomez et al., 2016), perhaps due to methodological differences or to the idiosyncratic traits of the study species. For instance, the analysis of niche-tracking at species level ignores within-species variation (Laube et al., 2015) and may be flawed due to the difficulties of inferring causality from multi-specific data (Garamszegi, 2014). In addition, not all individuals track the same resources under all circumstances and so an environmental trait that is closely tracked in one area may be ignored in another (Gomez et al., 2016). From this it follows that the results in this paper may also be inconsistent due to the idiosyncratic traits of the study species. For instance, our results will probably apply to other sedentary individuals in seasonal areas where residents balance out the cost of coping with abrupt environmental changes during the year with the benefits of an early occupation or defence of suitable breeding sites (Kokko, 1999).

CONCLUSIONS

The results in this paper support the hypothesis that partially migrant robins and blackcaps behave as 'niche-trackers' of certain temporally dynamic environmental traits (e.g. temperature), a behaviour pattern that agrees with the hypothetical role of niche-tracking in long-distance displacements (Levey & Stiles, 1992; Martínez-Meyer et al., 2004; Nakazawa et al., 2004; Gomez et al., 2016). Our results also suggest the potential effect of a trade-off between the cost of adaptations related to the tracking ability of migrants and the increased flexibility of sedentary individuals to tolerate a wider suite of conditions (Laube et al., 2015). Given that niche differentiation requires very long periods (Peterson, 2011), our results suggest that migratory and sedentary individuals of robins and blackcaps are good candidates for showing similar environmental preferences. More explicitly, migratory individuals appear as a specialized group occupying a restricted subset of the environmental conditions exploited by sedentary counterparts, which are able to confront all sudden seasonal changes in environmental conditions other than changes in land cover (e.g. those related to the Mediterranean summer drought). In this way, given that the sedentary populations in southern Iberian refugia seem to be linked to populations of migratory individuals that started to move northwards after the glacial withdrawal (Pérez-Tris et al., 2004), observed patterns support the view that migrants should be regarded as a stenoic fraction of southern populations that have evolved to carry out migratory movements.

PART C - Applications for conservation

CHAPTER 4 -

RANGE COMPRESSION OF MIGRATORY PASSERINES IN WINTERING GROUNDS OF THE WESTERN MEDITERRANEAN: CONSERVATION PROSPECTS

> *"In a migrant species, reproduction and the main mortality may occur in regions several hundred miles apart. This greatly complicates the study of the factors influencing numbers."*
>
> - DAVID LACK

This chapter is based on the manuscript: Fandos, G. & Tellería, J. L. (2017). Range compression of migratory passerines in wintering grounds of the Western Mediterranean: conservation prospects. Bird Conservation International. *Accepted*.

ABSTRACT

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 partial 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 to conserve migratory passerines in the Western Mediterranean Basin, an area under pressure from climate change and agricultural intensification.

Key words: Iberian Peninsula, Maghreb, migratory dispersion, niche modelling, potential distribution

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 & Jetz, 2011; Marco & 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 & Holmes, 1995; Klaassen et al., 2014; Runge et al., 2015b). 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 proper 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 partial migratory species (comprising both migratory and residents 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 et al., 2007; Runge et al., 2015b). This lack of information can be explained by the difficulties of 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 (O. 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; Carrascal & Palomino, 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 ring records linking individuals between breeding and non-breeding localities to explore if winter ranges are smaller than summer ranges. Clusters of ring 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 & Leathwick, 2009). We combine these methods with the use of ringed bird's data to estimate potential range sizes and to explore the environmental drivers of bird distribution (Rodríguez et al., 2007; Wisz et al., 2007b; 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 km2 located between 28º and 44ºN at the southwestern border of the Palearctic (Figure 12). It receives many migratory birds, most of them from the western side of the migratory divide crossing Europe between 10º-20ºE (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 climate conditions and vegetation (Figure 12). 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 12). 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; Appendices S4.1 in the supplemental materials). 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 12; Table 6). These data provided geo-referenced clusters of ring records per species, which show the location of the marked individuals in breeding and wintering grounds (Figure S 4.2-1 in the supplemental materials). 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. 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 ring 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. 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 (Marquaridt et al., 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 & 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 & Palomino, 2012; Tellería et al., 2014b). However, higher precipitation has been related in temperate areas 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 wood cover from Vegetation Continuous Fields MOD44B (DiMiceli 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., 2007b; Engler et al., 2014). We used precipitation seasonality (standard deviation of month means x 100) as a surrogate of 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 & 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 occurrence probability of marked populations from presence data (ring records) within breeding and wintering ranges. This program has been designed to minimize 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 ring records. This is the smallest polygon in which no internal angle exceeds 180º and contains the records of all species. In both seasons and for all species, we ran Maxent (log output; regularization 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 minimized 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 & Phillips 2005). We used mean human footprint per country because it is positively related to the density of all ring recoveries reported per country (r=0.53, p=0.036, n=16), a plain index of the effort applied to control ringed birds (Appendices S4.1 in the supplemental materials). To explore the importance of each predictor (see below), we carried out jackknife analyses of the regularized 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 & 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 & van Etten, 2013)in R (R 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 maximizing the sum of sensitivity and specificity (Manel et al., 2001). This threshold is recommended for conservation purposes as omission errors are avoided and sensitivity favored (Jiménez-Valverde & Lobo, 2007; Liu et al., 2013). We considered areas with an occurrence probability 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 6). We used the raster and dismo packages (Hijmans & van Etten, 2013; Hijmans et al., 2013) in R (R Core Team, 2015) to calculate the potential range map of the species in both seasons.

*Table 6 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 10^5 Km^2)	Wintering range (x 10^5 Km^2)	Range compression (%)
Carduelis cannabina	62	0,155	0,041	53.95	27.23	50.48
Erithacus rubecula	170	0,005	0,410	119.88	24.99	20.84
Fringilla coelebs	55	0,040	0,099	111.20	21.11	18.98
Motacilla alba	99	0,266	0,001	118.53	41.19	34.75
Phoenicurus ochruros	68	0,189	0,001	74.00	37.53	50.71
Phylloscopus collybita	79	0,174	0,006	111.67	26.29	23.54
Sylvia atricapilla	125	0,010	0,048	57.31	24.57	42.88
Turdus iliacus	94	-0,077	0,919	35.94	20.71	57.63
Turdus merula	60	0,149	0,007	68.20	13.49	19.77
Turdus philomelos	301	0,044	0,002	75.57	38.52	50.97
Mean				82.62	27.56	37.06

RESULTS

Strong correlation exists between breeding and wintering sites in most species (all but robins *Erithacus rubecula* and redwings *Turdus iliacus*, Table 6) supporting 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 *et al.* 2002) and the response curves provide some additional information on the way birds are distributed within breeding and wintering ranges (Table 7). For instance, the occurrence probability of species in breeding grounds was positively related to temperature and strongly affected by temperature seasonality (Table 7). In wintering grounds, most species were related to temperature and woodland cover (Table 7).

Table 7 Estimates of relative contributions of the environmental variables in models predicting occurrence probability 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	**Temperature seasonality**	**Temperature**	**Precipitation**	**NDVI**	**Woodland**
	max-min	**(43.5-99.1)** **Contr./perm.(curve)**	**(5.1-17.3º C)** **Contr./perm.(curve)**	**(45.4-126.2 mm)** **Contr./perm.(curve)**	**(0.1-0.8)** **Contr./perm.(curve)**	**(4.2-66.3 %)** **Contr./perm.(curve)**
Carduelis cannabina	0.93	59.8/66.7 (Ω)	21.4/21.5 (+)	1.5/2.5 (-)	3.0/3.0 (+)	14.2/6.4 (-)
Erithacus rubecula	0.81	50.3/55.5 (Ω)	23.6/25.7 (+)	2.4/2.4 =	11.6/7.0	12.1/9.4 (Ω)
Fringilla coelebs	0.86	39.0/36.5 (Ω)	22.3/35.0 (+)	3.7/4.4 (-)	16.5/10.7	18.5/13.4 (Ω)
Motacilla alba	0.91	50.0/46.8 (-)	20.1/28.8 (+)	14.7/13.5 (-)	4.7/6.6 (+)	10.5/4.2 (-)
Phoenicurus ochruros	0.93	72.6/67.7 (Ω)	9.9/19.6 (+)	12.5/8.3 (-)	1.7/1.8 (+)	3.3/2.6 (Ω)
Phylloscopus collybita	0.91	63.9/58.2 (Ω)	21.2/26.9 (+)	9.8/10.1 (-)	2.1/2.8 (+)	3.0/2.0 (-)
Sylvia atricapilla	0.94	51.1/51.7 (Ω)	34.7/32.4 (+)	8.4/7.7 (Ω)	1.5/1.9 (+)	4.3/6.3 (-)
Turdus iliacus	0.90	37.9/25.6 (+)	17/43.7 (Ω)	3.6/7.7 (-)	25.9/17.8	15.6/5.2 (Ω)
Turdus merula	0.93	46.2/49.6 (Ω)	22.2/32.3 (+)	14.8/9.1 (-)	3.0/2.6 (+)	13.8/6.4 (Ω)
Turdus philomelos	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**

	Wintering grounds					
	AUC	**Precipitation seasonality**	**Temperature**	**Precipitation**	**NDVI**	**Woodland**
	max-min	**(14.0-74.0)** **Contr./perm.(curve)**	**(0.9-12.3º C)** **Contr./perm.(curve)**	**(8.4-157.5 mm)** **Contr./perm.(curve)**	**(0.06-0.7)** **Contr./perm.(curve)**	**(0.0-51.8 %)** **Contr./perm.(curve)**
Carduelis cannabina	0.88	23.7/25.1 (-)	15.1/23.5 (+)	18.7/7.6 (-)	2.0/2.4 (Ω)	40.5/41.3 (-)
Erithacus rubecula	0.89	10.2/5.5 (Ω)	45.4/56.2 (+)	7.1/10.8 (Ω)	4.6/11.6 (+)	32.8/16.0 (-)
Fringilla coelebs	0.90	9.1/9.3 (Ω)	24.8/21.4 (+)	3.7/5.2 (+)	4.2/16.6 (+)	58.3/47. (-)
Motacilla alba	0.86	38.3/6.2 (+)	36.5/45.9 (+)	2.2/4.8 (+)	4.3/4.1 (Ω)	18.6/39.0 (-)
Phoenicurus ochruros	0.85	13.2/9.0 (+)	27.4/26.5 (+)	15.2/17.2 (Ω)	9.8/25.4 (Ω)	34.4/21.9 (-)
Phylloscopus collybita	0.90	9.4/5.8 (+)	41.4/41.2 (+)	7.4/7.9 (Ω)	2.4/3.1 (Ω)	39.4/42.0 (-)
Sylvia atricapilla	0.92	34.0/16.1 (+)	33.7/47.5 (+)	5.3/8.2 (Ω)	2.6/6.3 (Ω)	24.5/21.9 (-)
Turdus iliacus	0.89	12.6/7.1 (Ω)	19.1/30.3 (+)	37.9/27.6 (+)	1.3/3.2 (+)	29.1/31.9 (+)
Turdus merula	0.90	31.1/37.1 (-)	22.0/25.2 (+)	2.3/7.9 (+)	3.1/3.3 (+)	41.5/26.4 (+)
Turdus philomelos	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 S4.2-2 in the supplemental materials). 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 5). More explicitly, potential winter ranges covered a mean area of 275,600 km2 (min-max 134,900-411,190 km2,Table 6) accounting for 16% (7.9-24.2%) of the Iberian Peninsula and the Maghreb (Figure 12).

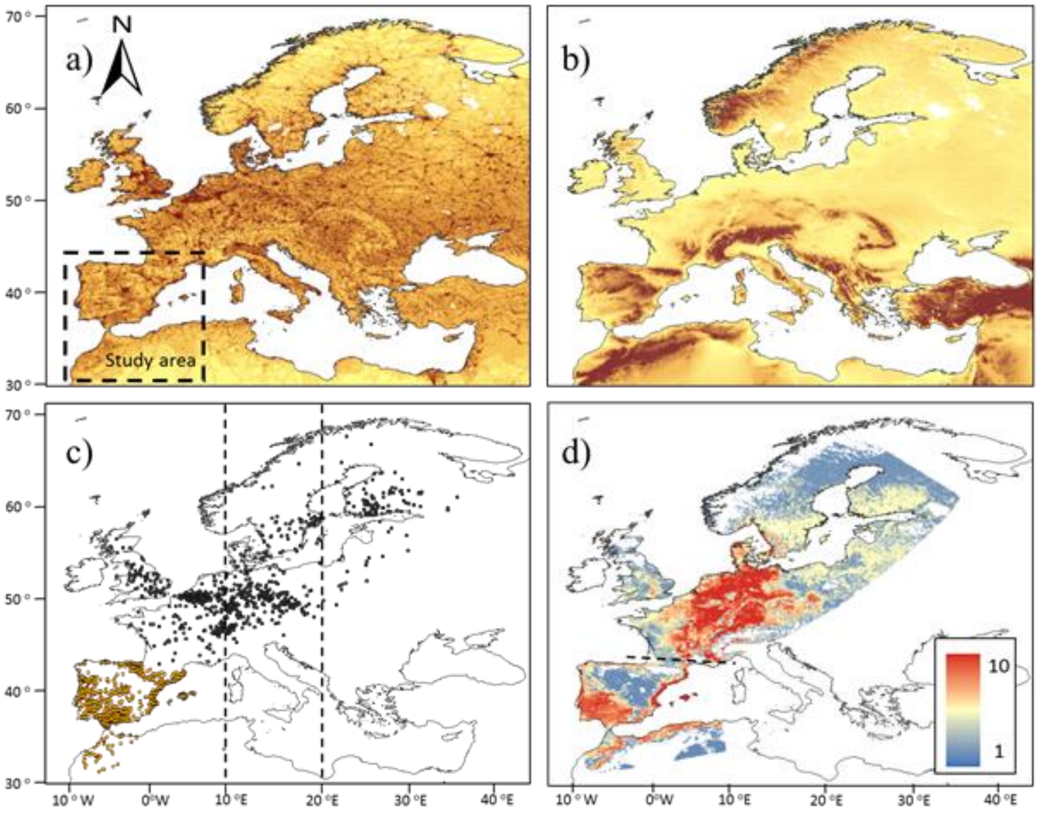

Figure 12 a) Distribution of the Human Foot Print (HFP) index in Europe. Increasing dark tones show increasingly high values of HFP. The study area is located within the striped square. b) Elevation map of the western Palearctic. Increasing dark tones show increasing elevations, with the darkest tone showing the areas over 1,000 m a.s.l. 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 (white 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)*

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 S4.2-2 in the supplemental materials). 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 12), 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 12). 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 distribution of migratory populations tends to avoid the colder areas and to distribute in most seasonal areas under a given threshold of summer (cold) and winter (dryness) conditions (Table 7). The importance of temperature in shaping migratory bird distribution is widely recognized, and is the result of the high thermoregulation costs of living in areas under bird thermo-neutral ranges (Swanson & Jr., 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 12). 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 S4.2-2 in the supplemental materials, Figure 12), where wood cover was positively (thrushes) or negatively (the rest of species) supporting the effect of specific habitat preferences on bird distribution (see Tellería *et al.* 1999; Palomino *et al.* 2012). These patterns are similar to the wintering maps reported by ring modelling of meadow pipits (*Anthus pratensis*), chiffchaffs (*Phylloscopus collybita*), blackcaps (*Sylvia atricapilla*) and robins (*Erithacus rubecula*), validated by field sampling of abundances (Tellería et al., 2012, 2014b, 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 Palearctic 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 approached on 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 6). 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 southwestern border of the Palaearctic, 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., 2014b, 2014c).

CONSERVATION PROSPECTS

Disentangling the geographic distributions of the migratory populations throughout the year may provide valuable knowledge for conservation decisions (Chen et al., 2002). Although breeding and non-breeding conditions have been studied independently, the study of migratory connectivity is essential for understanding the effects of threats along the year on migratory birds (Cresswell, 2014). Results in this paper support migratory connectivity between wintering and breeding ranges of most passerines moving to the Iberian Peninsula and the Maghreb. Lack of migratory connectivity in redwings and robins could result of within-range movements typical of some birds (Tellería et al., 2014a; Stutchbury et al., 2016) or the small scale of approach in this study (e.g. Ambrosini *et al.* 2016 report migratory connectivity of robins at continental scale). In addition, small Mantel r scores suggest that winter ranges of the species may extend outside the study area (Table 6), a pattern probably related to the high mobility of many birds in the non-breeding period (Newton, 2010). But connectivity of migratory populations seems to be a common pattern in birds (Cresswell, 2014), even at very small spatial scales of approach (Cormier et al., 2016). As a result, connectivity is expected to underpin the response of breeding populations to any local deterioration in non-breeding ranges, a main issue in migratory bird conservation (Webster et al., 2002).

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., 2014c) where field studies do not support food restriction (Díaz & Tellería, 1994; Hampe, 2008; Tellería et al., 2013a). We acknowledge that this balance will be disrupted in winters of food scarcity, a situation that many birds cope by food-tracking (Rey, 2011; Tellería et al., 2014a). However, movement among suitable areas will not be enough if changes affect simultaneously the carrying capacity of the whole range. The southwestern border of the Palearctic is expected to suffer the strong effects of climate change, with increasing temperature and decreasing rainfall (Giorgi & Lionello, 2008; Schilling et al., 2012). In this context, it has been predicted the depletion or altitudinal shifts of lowland habitats suitable for wintering birds (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 resulting carry over effects of these environmental changes (Norris et al., 2004) will affect populations in larger breeding areas of Europe.

CHAPTER 5 -

EFFECT OF CLIMATE CHANGE ON MEDITERRANEAN WINTER RANGES OF TWO MIGRATORY PASSERINES

"Prediction is very difficult, especially if it's about the future"

- NIELS BOHR

This chapter is based on the manuscript: Tellería, J. L., Fernández-López, J., & Fandos, G. (2016). Effect of climate change on mediterranean winter ranges of two migratory passerines. PloS one, 11(1), e0146958.

ABSTRACT

We studied the effect of climate change on the distribution of two insectivorous passerines (the meadow pipit *Anthus pratensis* and the chiffchaff *Phylloscopus collybita*) in wintering grounds of the Western Mediterranean basin. In this region, precipitation and temperature can affect the distribution of these birds through direct (thermoregulation costs) or indirect effects (primary productivity). Thus, it can be postulated that projected climate changes in the region will affect the extent and suitability of their wintering grounds. We studied pipit and chiffchaff abundance in several hundred localities along a belt crossing Spain and Morocco and assessed the effects of climate and other geographical and habitat predictors on bird distribution. Multivariate analyses reported a positive effect of temperature on the present distribution of the two species, with an additional effect of precipitation on the meadow pipit. These climate variables were used with Maxent to model the occurrence probabilities of species using ring recoveries as presence data. Abundance and occupancy of the two species in the study localities adjusted to the distribution models, with more birds in sectors of high climate suitability. After validation, these models were used to forecast the distribution of climate suitability according to climate projections for 2050-2070 (temperature increase and precipitation reduction). Results show an expansion of climatically suitable sectors into the highlands by the effect of warming on the two species, and a retreat of the meadow pipit from southern sectors related to rain reduction. The predicted patterns show a mean increase in climate suitability for the two species due to the warming of the large highland expanses typical of the western Mediterranean. This suggests that highlands can serve as refuge areas for wintering birds, a trend that could be applied to other areas in the Mediterranean basin and worldwide.

INTRODUCTION

Modern climate change is a main driver of large-scale species distribution, but its actual effects on individual species will result from a variety of context-dependent processes that need to be explicitly studied at the proper scales (Stenseth et al., 2002; Walther et al., 2002; Parmesan, 2006). This involves investigating the way climate change affects the environment requirements of organisms and how they cope with the changes through relocation, phenotypic plasticity or adaptation (Heller & Zavaleta, 2009). Only in this way it is possible to understand the potential effects of changes on species and to design preventive or proactive measures to cope with them realistically (Moritz & Agudo, 2013).

Migratory birds are sensitive to climate change in the different geographical sectors along their migratory journeys (Knudsen et al., 2011). This itinerancy makes it difficult to explore the potential effect of climate change on these species (Sanderson et al., 2006). In the case of European migratory birds, it has been predicted that many trans-Saharan species will shift their wintering range due to the effect of climate change (Barbet-Massin et al., 2009), but little is known about the fate of wintering grounds in the Palaearctic. Some evidence suggests a shift northwards of wintering ranges in some European birds but few studies have investigated the impacts of climate change on wintering areas in the Mediterranean Basin (Pautasso, 2012). This is, however, a main wintering ground for the Western European avifauna (Busse, 2001) because the arrival of autumn rains mitigates the limiting effects of summer drought initiating a period of primary productivity, invertebrate activity and fruit ripening suitable for wintering birds (Nahal, 1981).

The Mediterranean basin is located at the southwestern border of the Palaeartic (Figure 13), which is expected to suffer stronger effects in terms of climate change (Giorgi & Lionello, 2008; Schilling et al., 2012). Thus, it is suspected that climate change will influence the extent and suitability of this wintering ground for birds, but no information is available on the potential strength and spatial distribution of changes. These changes have potential conservation implications because can affect the survival or the subsequent reproductive success of migratory birds and thus their populations trends (Rappole et al., 2003; Norris et al., 2004; Kirby et al., 2008). In the current work, we study the potential effect of climate change in two common passerines (the meadow pipit *Anthus pratensis* and the chiffchaff *Phylloscopus collybita*) wintering in the Iberian Peninsula and the Maghreb. More explicitly, we address the following objectives:

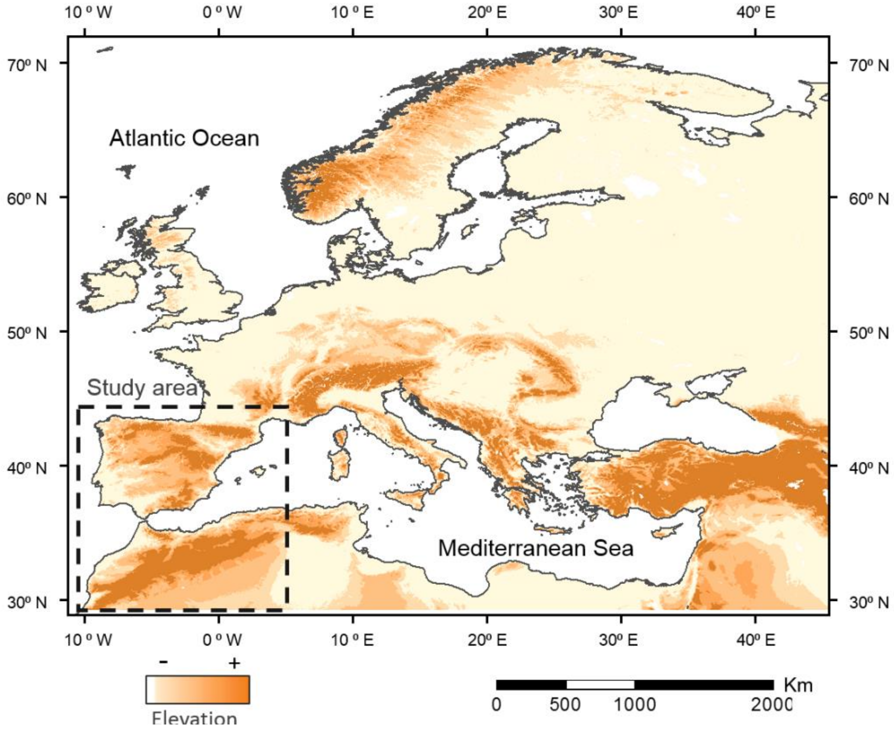

Figure 13 Elevation map of the Western Palaearctic. The study area is located within the stripped square. Increasing dark tones show increasing elevations, with the darkest tone showing the areas over 1,000 m a.s.l.

EFFECTS OF CLIMATE ON THE PRESENT DISTRIBUTION OF MIGRATORY BIRDS

We assess the effects of climate on the abundance distribution of pipits and chiffchaffs in a set of study localities along a 1500 km-long belt crossing Spain and Morocco (Figure 14). This is a preliminary step to understand the effect of climate change on birds. We assume that climate can affect the distribution of wintering passerines in two main ways. First, food availability (e.g. seeds, fruits, invertebrates) is ultimately derived from plants and the effect of climate on plant productivity (e.g. through precipitation or temperature) influences bird abundance (Lennon et al., 2000; Evans et al., 2006). Second, low temperatures increase the energy demands of these small birds, which are then forced to increase food intake to cope with thermoregulatory requirements (Calder & King, 1974; Schmidt-Nielsen, 1984). As a result, it can be postulated that the occupation of warm areas will decrease the need for thermogenesis and thus reduce individual daily energy requirements, enabling more birds to occur at a given level of productivity (Wright, 1983; Meehan et al., 2004). However, this effect of climate on bird distribution could be affected by the competing effects of other geographical and environmental features (Seoane et al., 2004; Melles et al., 2011). For instance, pipits and chiffchaffs arrive at the study area from the north. This seasonal afflux of birds could decrease the number of individuals involved in the colonization of the southern border of the winter range. This is usually related to the positive effect of migration length on mortality and energetic costs (Wikelski et al., 2003; Newton, 2010). Similar effects have already been reported in this wintering ground, where migratory fluxes affect winter distribution of birds (Tellería et al., 2009; Cano et al., 2014). In addition, birds are strongly affected by vegetation structure so that the availability of suitable sites will strongly affect their presence in a given area (Hutto, 1985). Thus, given the multiple determinants of bird distribution, we use a multivariate approach to assess the relative contribution of climate vs. other geographical and habitat predictors on the distribution of pipits and chiffchaffs.

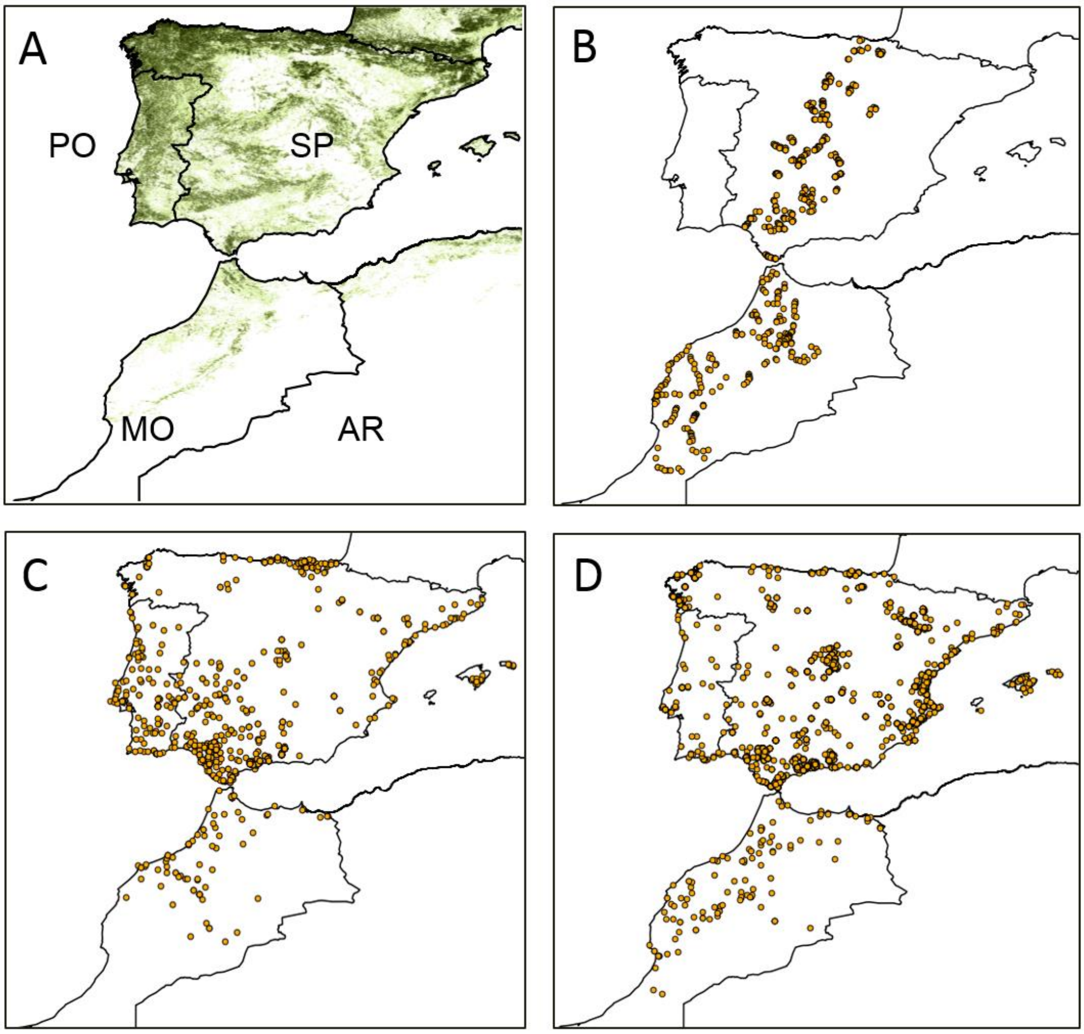

Figure 14 Study area and sampling effort distribution. A. Distribution of tree cover and political division of the study area. AR: Algeria, MO: Morocco, PO: Portugal, SP: Spain. B. Distribution of localities where the occupancy and abundance of species was sampled. C and D. Distribution of winter localities in which ringed meadow pipits and chiffchaffs were recorded.

MODELLING THE PRESENT DISTRIBUTION OF CLIMATE SUITABILITY

We use climate variables affecting pipit and chiffchaff abundance to predict the distribution of the most suitable wintering grounds. To do this, we use the spatial distribution of winter ring records provided by the European Union for Bird Ringing (Euring; http://www.euring.org/) to explore the distribution of species. As these recoveries are widely distributed throughout the study area (Figure 14) they can be used to explore the environmental preferences of birds. The models will be constructed with Maxent, a popular machine-learning technique designed to predict the occurrence probabilities of species by combining species presences (latitude and longitude) with the geographical distribution of climate variables (Phillips et al., 2006; Elith et al., 2011). The ability of these maps to identify sectors of different climatic suitability will be tested with the distribution of pipits and chiffchaffs in the study localities (Figure 14). If the actual occupancy and abundance

(Gaston et al., 2000) of birds agree with the occurrence probability maps, we will use the models to forecast the changes in the extent and suitability of wintering areas according to predictions of climate change. This approach assumes a "space-for-time" design, which attempts to predict temporal changes from present spatial correlates between species distribution and climate variables (La Sorte et al., 2009).

EFFECTS OF CLIMATE CHANGE ON THE WINTER DISTRIBUTION OF MIGRATORY BIRDS

Finally, we use the validated distribution models to forecast the suitability of wintering grounds according to climate projections. The effect of climate change on breeding bird distribution has already been studied in the western Mediterranean (Seoane & Carrascal, 2008; Triviño et al., 2013), but little is known about the way climate change will affect winter bird ranges. It has been predicted, for instance, that warming will improve the suitability of colder sectors, such as mountain and highlands (Carrascal et al., 2012). Climate predictions also suggest a reduction in precipitation in some southern areas that could reduce primary productivity (García-Ruiz et al., 2011; Guo et al., 2012) and the concomitant suitability of present wintering grounds for some species (Carrascal & Palomino, 2012; Tellería et al., 2014b). Thus, climate changes will likely be affected by latitudinal and altitudinal gradients producing a patchy distribution of the future climate trends. This study attempts to map the location and extent of these changes in climate suitability of the Iberian Peninsula and the Maghreb for the two study species.

MATERIALS AND METHODS

THE MODEL SPECIES

The meadow pipit (mean body mass 18.4 g; (Dunning, 1992)) feeds on invertebrates in meadows and grasses of open habitat patches (Cramp & Simmons, 1988). The chiffchaff (7.8 g) feeds on insects within a broader set of substrata and occurs in tree- and shrub-covered habitats (Cramp, 1992). These passerines were selected as model species for two reasons. First, they do not breed in the study area (the meadow pipit) or mainly breed in some areas of the northern Iberian Peninsula (the chiffchaff; Cuesta & Balmori 2003)). Thus, most if not all birds wintering in the study area are migratory individuals (Tellería et al., 1999; Thévenot et al., 2003; Del Moral et al., 2012). This trait is interesting from a methodological point of view because it will attenuate the confounding effects of local conspecifics on the abundance patterning of migratory individuals (De la Hera et al., 2012). In this way, predictions based on ring recoveries in wintering grounds can be validated by the abundance distribution of the same migratory populations (Tellería et al., 2014c). Second, pipits and chiffchaffs are small insectivorous passerines that occur in a broad range of habitats (Cramp, 1992). Small body size makes birds more sensitive to temperature (Schmidt-Nielsen, 1984) and a diet based on insects makes them potentially ubiquitous since these invertebrates are available in a wide range of habitats (Levey & Stiles, 1992). This implicitly assumes the potential of these species to track climate changes across the entire study area.

STUDY AREA

The study area is located between 28º and 44ºN at the southwestern border of the Palaearctic, covering an area of 1,700,000 km2 (Figure 13). It is a transitional, Mediterranean region located between the moist woodlands and meadows of the northern and western half of Iberia and the dry expanses of the Sahara (Figure 14). The area is covered by extensive bare lands, grasslands and farmlands (e.g., cereal fields, olive groves) interspersed with Mediterranean scrublands (*Pistacia lenticus, Olea europaea,* etc.) and oak (*Quercus ilex, Quercus suber*, etc.) and conifer (*Pinus halepensis, Pinus pinaster*, etc.) woodlands. The most outstanding trends along this latitudinal gradient are the sharp changes in elevation and the concomitant changes in climate conditions (Figure 15).

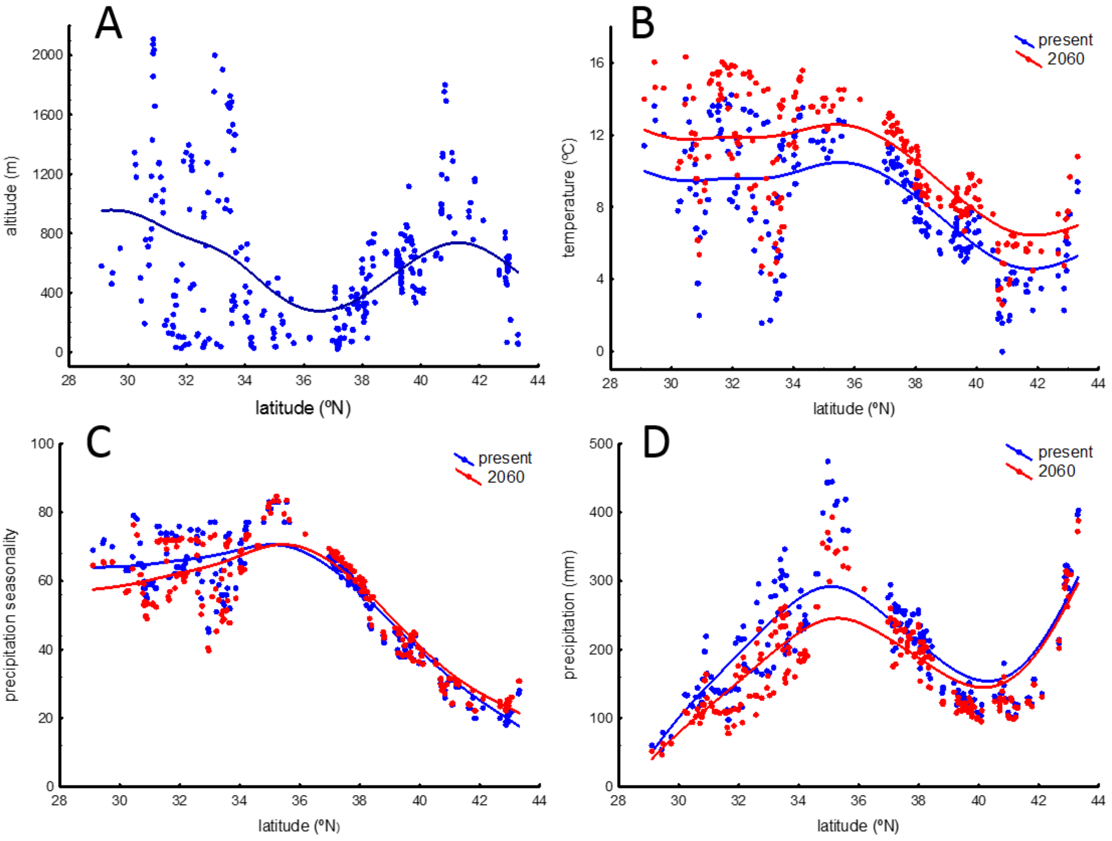

Figure 15 Elevation, climate and bird abundance distribution along the latitudinal gradient defined by the sampling localities in Figure 14B. A) Elevation, B) temperature, C) precipitation seasonality, D) precipitation. Climate variables are averages provided by the WorldClim-Global Climate Data facility (http://www.worldclim.org) for the 1950-2000 and 2050-2070 periods (see text). The abundances along the gradient of the meadow pipit (E) and the chiffchaff (F) are also reported.

EFFECTS OF CLIMATE ON THE PRESENT DISTRIBUTION OF BIRDS

Field sampling

Field work was carried out from 2006 to 2013 to assess meadow pipit and chiffchaff abundance in 556 localities ranging from 7 to 2110 m a.s.l. along a 1500 km belt crossing the Iberian Peninsula and the Maghreb (Figure 14). At these points, located in free-access sites, we recorded all individuals seen or heard at either side of 500 m-long line transects irrespective of the perpendicular distance at which each individual was detected. The number of individuals recorded per line transect is a common index of bird abundance in extensive bird counts (Bibby et al., 2000). In each transect, we measured some vegetation traits in two 25-m radius circles separated by 200-m intervals. In each circle, we visually estimated grass cover and shrub and tree layers (shrub under 0.5 m, between 0.5-2 m and >2 min height). We also recorded the number of tree and shrub species within the circles. The scores of the two sampling circles were averaged to characterize each line transect. We conducted a principal components analysis to reduce tree and shrub cover and richness to just one score. We retained a single principal component (eigenvalue: 2.80), which explained 55.94% of variance and was interpreted as a gradient of increasing vegetation cover (factor loadings for vegetation cover under 0.5m height: -0.01; cover 0.5-2 m height; 0.84; cover >2 m height: 0.77; shrub species: 0.84 and tree species: 0.90). Factor scores of each locality within the component were used as an index of shrub and tree development (woodland). The location of locality (latitude and longitude in decimal degrees) was recorded with GPS devices.

Climate

We assessed climate conditions of the study sites by using mean scores provided by Worldclim 1.4 for the 1950-2000 period (Hijmans et al., 2005). Since we propose that small birds avoid cold areas to prevent excessive thermoregulatory requirements, and precipitation may affect the productivity of Mediterranean habitats after summer drought (see Introduction), we selected Mean Temperature of Coldest Quarter (bio11) and Precipitation of Coldest Quarter of the year (bio19) as the two main climate correlates of bird distribution. In addition, we included Precipitation Seasonality (bio15) as a surrogate of the rain-mediated productive pulses typical of many dry habitats that track migratory birds (Alerstam & Enckell, 1979; Wisz et al., 2007b). Finally, to test if the present spatial patterning of climate variables is similar to that provided by Worldclim for the second half of the twentieth century, we requested from World Weather (http://en.tutiempo.net/) the available climate data (years 2012-2013) in 25 meteorological stations located along the study area (from Avilés 43.55ºN, 6.03ºW to Sidi Ifini 29.36ºN, 10.18ºW). Despite strong differences in sample size affecting the means (50 vs. 2 years), climate variables depicted similar trends (bio 11, r: 0.93; bio15:0.69 and bio19:0.70, $p<0.001$ in all cases) supporting the usefulness of climate data used in this paper to explore the features affecting the present spatial distribution of birds.

Analyses

We used meadow pipit and chiffchaff abundance distribution as response variables and climate (temperature, precipitation, precipitation seasonality) and vegetation structure (grass and woodland cover) as predictor variables. The effect of latitude (and the potential effect of spatial autocorrelation) (Legendre, 1993) on bird abundance was also included by means of the line transects' coordinates, latitude, longitude and latitude x longitude. To deal with the large number of zeros in transects (Figure 14) we used the hurdle count model approach provided by pscl-R (Jackman, 2015). These models are two-component models with a hurdle component that models the zero counts and a truncated count component for positive counts (Zuur et al., 2009). The count model is normally a truncated Poisson or negative binomial regression (with log link). The hurdle model is a bionomial logit regression or a censored count distribution model (Jackman, 2015). We used the Akaike's Information Criterion (Burnham & Anderson, 2002) to select the best model and variable combination with lmtest-R (Zeileis & Hothorn, 2002).

MODELLING THE PRESENT DISTRIBUTION OF CLIMATE SUITABILITY

Ring recovery distribution modelling

We used the localities where ringed birds were recorded in December, January and February (374 for the meadow pipit and 516 for the chiffchaff; duplicate records in the same localities were removed in each replicate) as presence data (Figure 14). These records result from birds ringed in breeding grounds or during the migratory displacements that have been recovered in the study region from 1960 to 2010. The geographical location of ring recovery localities (latitude and longitude) was used to run Maxent combined with the climate variables (temperature, precipitation, precipitation seasonality; see above). Since ring recovery distribution can be affected by human activity (e.g. more records are gathered in the most populated areas) (Busse, 2001), the layer of human footprint (an index of population density, land transformation and road density) (Sanderson et al., 2002) was used as a bias grid to distribute 10,000 background points with a likelihood of presence proportional to the human footprint index. Maxent (log output; regularization multiplier b = 1; autofeatures; convergence threshold = 0.00001) was run in 10 replicates with 75% of the presences as training data and the rest as test data for internal verification. The Area Under the Curve (AUC) provided by the receiver operating characteristic curves was used to assess the congruence between observed and detected records in the test data reserved for verification in Maxent (Phillips et al., 2006).

External validation

We used the data provided by line transects to test the ability of Maxent models to predict bird distribution. To do this, we divided the occurrence probability resulting from Maxent into three similar interval sectors between the min-max intervals. The resulting ranges were used to define maps of low, medium and high climate suitability for each species. The line transects were distributed within these sectors to test with χ2 or ANOVA analyses if the number of localities at which the species are found to occur (occupancy) (Gaston et al., 2000) and mean abundance increased from low to high climate-suitable sectors (Tellería et al., 2014c). In addition, since the distribution models were launched to predict climate suitability, the effect of habitat structure on bird distribution was controlled by selecting the habitats mainly used by pipits (grasslands, farmlands, wooded pasturelands; n=375) and chiffchaffs (wooded pasturelands, farmlands, scrublands, woodlands; n=320) according to current information on winter habitat preferences (Tellería et al., 1999; Thévenot et al., 2003; Del Moral et al., 2012). In this way, we tried to avoid the absences resulting from the unsuitability of some habitats.

EFFECTS OF CLIMATE CHANGE ON BIRD DISTRIBUTION

After validation, the Maxent models were used to project the changes in species distribution under RCP2.6 and RCP8.5 scenarios for 2050 and 2070 (AR5 report) [61] provided by the WorldClim-Global Climate Data facility (http://www.worldclim.org/). Scenario RCP2.6 is representative of mitigation policy aiming to limit the increase of global mean temperature to 2°C. Scenario RCP8.5 does not include any mitigation target (Harris et al., 2014). We used two independent global circulation models (MIROC5 and CCSM4) suitable for the study area to predict the changes. To obtain a straightforward view of the species distribution in the future, we also averaged all predicted trends for scenarios, models and time periods (2050 and 2070).

Present occurrence probabilities were subtracted from future occurrence probabilities to map the distribution of increasing and decreasing climate suitability sectors. To explore the spatial distribution of climate and climate suitability changes for pipits and chiffchaffs, we distributed 500 random points over the Iberian Peninsula and Morocco (there were actually 493 because seven points were discarded for lack of data). In each point, the reported changes in climate suitability and climate variables were used as response variables and latitude, longitude, latitude x longitude, altitude and altitude2 (to detect hump shaped distributions along the elevation gradient) were used as predictors. Present and future scores were compared by repeated measures ANOVA and the spatial trends of changes by GLM analyses. All cartographic data were managed with Quantum GIS 2.8 and GRASS GIS in 10 x 10 km squares (Grass Development Team, 2012). Statistical analyses were carried out with Statistica 8.1 (StatSoft, USA).

RESULTS

EFFECTS OF CLIMATE ON THE PRESENT DISTRIBUTION OF MIGRATORY BIRDS

A negative binomial distribution for the count model and a logistic regression for the binomial model was the best zero hurdle model for the two species (Table 8). The meadow pipit occurred more frequently in warm and rainy areas covered by grasses with low woodland cover, and the chiffchaff was more frequent in southern, warm sites covered by woodlands. The best count model was a zero altered negative binomial regression with log link (Table 8). According to this model, the meadow pipit was more abundant in northern, rainy sites covered by grasses and the chiffchaff in warm sites covered by grasses. The two methodological approaches support an effect of climate variables on the species distribution, with more frequent and abundant meadow pipits in warm and rainy sectors and more frequent and abundant chiffchaffs in warmer areas.

Table 8 Zero truncated models to explain occurrence and abundance distribution of the Meadow pipit and the Chiffchaff in wintering grounds of the Iberian peninsula and the Maghreb. Zero hurdle models show the features related to the occurrence of species and count models the features affecting abundance. These models have been selected according to AIC criterion from a broad set of alternative models and variable combinations (see text).

	Zero hurdle model				Count model			
	Meadow pipit		Chiffchaff		Meadow pipit		Chiffchaff	
	Estimate	P	Estimate	P	Estimate	P	Estimate	P
Intercept	-18.15	<0.001	7.47	0.206	16.15	0.004	-13.98	<0.001
Lat.	-		-0.49	<0.001	0.20	0.013	-	-
Long.	1.17	<0.001	2.46	0.003	0.54	0.009	-	-
Lat. x Long.	-0.04	<0.001	-0.07	0.003	-	-	-	-
Temperature	3.54	<0.001	3.95	<0.001	-	-	6.78	<0.001
Prec. season.	-	-	-	-	2.41	0.280	-	-
Precipitation	3.37	<0.001	-	-	4.25	<0.001	-	-
Grass	0.92	<0.001	-	.	0.61	0.041	0.87	<0.001
Woodland	-1.49	<0.001	0.92	<0.001	-	-	-	-

MODELLING THE PRESENT CLIMATE SUITABILITY

Winter temperatures and precipitations were the most important variables in modelling the occurrence probabilities of the meadow pipit and the chiffchaff with Maxent (Table 9). In the two species, the most suitable areas were located on coastlines and in lowlands of the study region (Figure 16). The occupancy and abundance distribution of the two species fitted well to the distribution of low, medium and high climate suitability sectors resulting from ring recovery occurrences (Table 10). As predicted, the main difference between the all habitats vs. suitable habitats approaches was related to increased occupancy and abundance scores in suitable habitats. This supports the ability of occurrence probabilities provided by Maxent to predict the distribution of pipits and chiffchaffs in the Iberian Peninsula and the Maghreb.

EFFECTS OF CLIMATE CHANGE ON BIRD DISTRIBUTION.

According to predictions for the period 2050-2070, mean temperature in winter will increase (mean ± SE, 1950-2000: 7.47 ± 0.16 ºC; 2050-2070: 9.28 ± 0.16 ºC; repeated measures ANOVA F1,492= 7,240.27, P<0.001) and mean precipitation in winter (177.732 ± 5.057 mm,161.02 ± 4.73 mm; F1,492= 518.22, P<0.001) and precipitation seasonality (48.34 ± 0.82 mm,42.73±0.64 mm; F1,492= 513.22, P<0.001) will decrease in the Iberian Peninsula and the Maghreb. These trends will be followed by a predicted increase in mean climate suitability for the meadow pipit in the winter area (mean ± SE, 1950-2000: 0.28 ± 0.01; 2050-2070: 0.33 ± 0.01; repeated measures ANOVA F1, 492= 114.21, P<0.001) and the chiffchaff (0.36 ± 0.01; 0.46±0.0.01 mm; F1, 492= 663.53, P<0.009). The changes will not be distributed evenly across the region (Figure 16). For instance, the increase in temperature and the loss of precipitation (and precipitation seasonality) will be reduced in northern sites (Table 11). Elevation will also affect climate change suggesting a hump-shaped relationship with temperature increase and precipitation reduction (the changes will be reduced at mean altitudes; Table 4). As a result, climate suitability for the meadow pipit and the chiffchaff will shift from lowlands to highlands and from southern to northern areas (Table 11; Figure 17).

Table 9 Estimates of the relative contribution of the climate variables. Percent contribution indicates the change in regularized gain by adding the corresponding variable. Permutation importance represents, for each variable in turn, the resulting drop in training AUC when the values of that variable on training presence and background data are randomly permuted. They are normalized to show percentages. Values are averages over 10 replicate runs.

Species	Variable	Percent contribution	Permutation importance
Meadow pipit	Temperature (bio11)	42.4	65.4
	Precipitation seasonality (bio15)	3.8	5.3
	Precipitation (bio19)	53.8	65.4
	AUC±SD	0.877±0.018	
Chiffchaff	Temperature (bio11)	48.2	29.1
	Precipitation seasonality (bio15)	12.2	9.6
	Precipitation (bio19)	39.6	61.3
	AUC±SD	0.836±0.017	

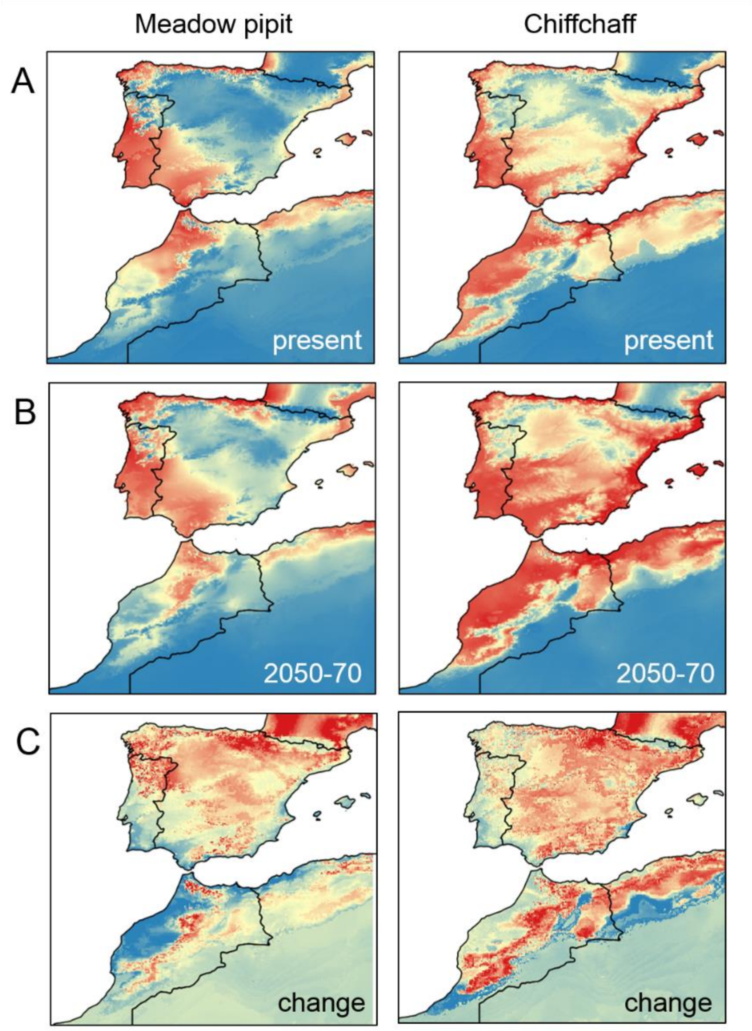

Figure 16 Trends of climate suitability. A. Distribution of high (red), medium (yellow) and low (blue) climate suitability sectors for the meadow pipit and the chiffchaff according to similar occurrence probability intervals. B. Mean predicted distributions for the period 2050-2070. C. Change in climate suitability from present to 2050-2070. Blue color represents decrease and yellow to red represent increasing rates of climate suitability.

DISCUSSION

EFFECTS OF CLIMATE ON THE PRESENT DISTRIBUTION OF MIGRATORY BIRDS

Species distribution is shaped by features acting at different scales (McGill, 2010). In the case of migratory birds, distribution results from large-scale geographical and climate processes affecting the historical configuration of migratory routes (Zink, 2011) and the local arrangement of individuals according to their particular habitat preferences (Hutto, 1985). Multi-scale approaches are thus required to detect the contribution of climate versus other features on the distribution of migratory birds (Seoane et al., 2004; Triviño et al., 2011). This has been the aim of the present study in which the distribution of wintering pipits and chiffchaffs has been related to large scale (geography and climate) and local (vegetation cover) predictor variables (Table 8).

Table 10 Distribution of the species occurrences and abundances among the three sectors of climate suitability defined by ring recoveries. The results of ANOVA and χ2 analyses to test for differences in species distribution are shown.

Species	Climate suitability	Occurrence (presences/absences)	Abundance (no birds ± SE)
Meadow pipit	Low (n=141)	0.18 (26/115)	0.62 ± 0.33
	Medium (n= 132)	0.31 (42/90)	1.31 ± 0.34
	High (n=102)	0.54 (55/47)	2.87 ± 0.38
	test	χ^2= 33.90, P<0.001	$F_{2,372}$=10.22, P<0.001
Chiffchaff	Low (n=46)	0.11 (5/41)	0.13 ± 0.20
	Medium (n= 164)	0.25 (41/123)	0.41 ± 0.11
	High (n=110)	0.70 (77/33)	1.76 ± 0.13
	test	χ^2= 73.60, P<0.001	$F_{2,317}$=53.35, P<0.001

The effect of latitude on bird distribution provided inconclusive results. The meadow pipit increased abundance in the northernmost sectors supporting the predicted effect of the distance to breeding grounds on winter distribution. However, the occupancy of the chiffchaff showed an opposite pattern, perhaps because in this species, many individuals move to wintering grounds in the Sahel (Cramp, 1992). Thus, the study area is not the actual southern border of its wintering area. After controlling for the geographical effects, the results supported habitat structure and climate as key players in bird distribution. Woodland cover was related to the occurrence of the chiffchaff (positive) and the meadow pipit (negative). In both cases, abundance was positively related to grass cover. These results are congruent with the habitat preferences of the species since the meadow pipit prefers grass patches in open habitats and the chiffchaff feeds on a broad variety of substrata (included tall grasses) in shrub- and tree-covered habitats (Cramp, 1992).

Table 11 Mean changes of climate and climate suitability (c.s) for birds between 1950-2000 and 2050-2070 in 493 random selected sampling points distributed over the study area. The results of GLM analyses on the effects of geographical location and elevation on changes are shown. Beta (ß) figures inform about the magnitude and sign of the partial relationships of predictor variables. They have not showed in the case of non-significant effect.

	Change		ß figures							Model
	mean ± SE	Min / max	Lat.	Long.	Lat x Long	Elevation	Elevation^2	$F_{5,486}$	P	R^2
Temperature (ºC)	+2.02 ± 0.02	-33.38 / +5.50	-0.21	-	0.73	0.45	-0.30	27.84	<0.001	0.22
Precipitation seasonality	-5.61 ± 0.25	-12.00 / +52.00	0.42	1.56	-1.39	-	-	351.10	<0.001	0.78
Precipitation (mm)	-1.67 ± 0.07	-10.98 / +2.60	0.75	-2.12	2.13	0.48	-0.53	24.22	<0.001	0.20
Meadow Pipit (c.s.)	+0.05 ± 0.01	-0.27 / +0.49	0.89	-1.37	1.14	1.04	-0.57	85.03	<0.001	0.47
Chiffchaff (c.s.)	+0.10 ± 0.01	-0.23 / +0.39	0.42	-	0.66	0.66	-0.37	23.07	<0.001	0.19

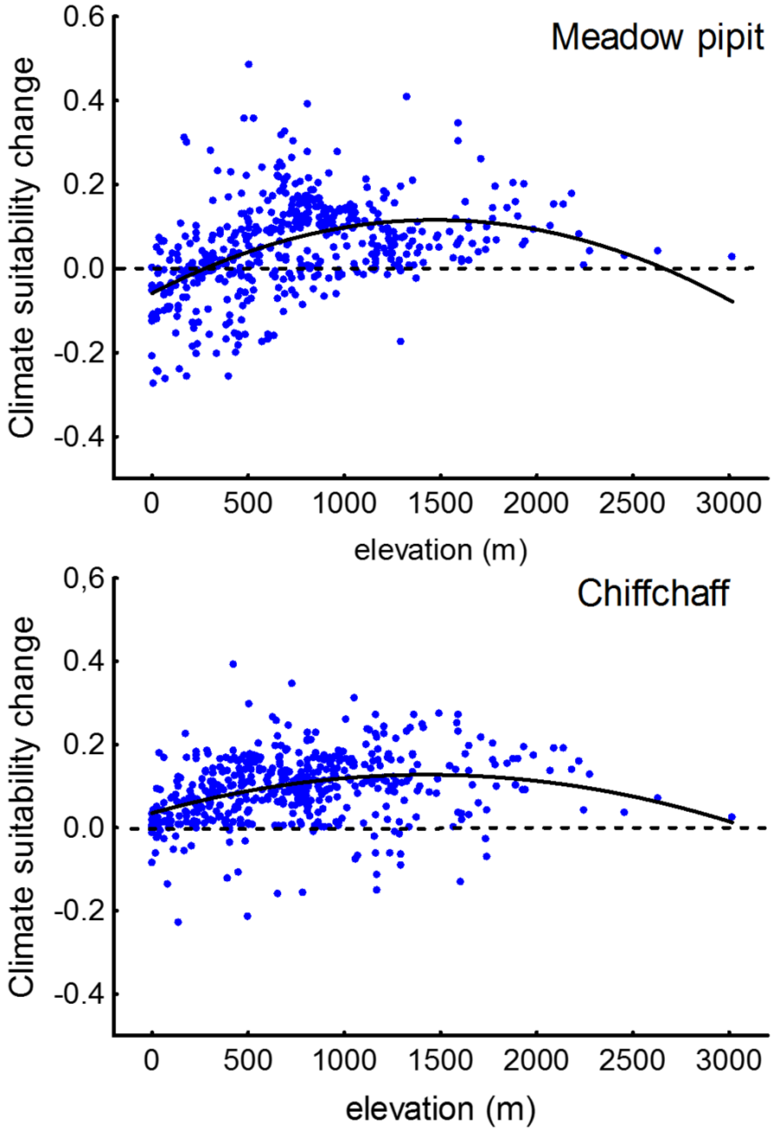

Figure 17 Latitudinal and altitudinal change in the climate suitability for wintering meadow pipits and chiffchaffs across the study region. These results have been reported by 493 random distributed sampling points across the Iberian Peninsula and Morocco (see text).

Climate variables were related to bird distribution supporting the presence of more pipits and chiffchaffs in warmer sectors (Table 8). Preferences for warmer areas could be explained by the predicted direct effect of low temperatures on thermoregulation costs (see Introduction). In an area dominated by cold mountains and highlands (Figure 13), where most sectors show mean winter temperatures (mean ± SE: 9.36ºC ± 0.18; min-max: -2.2 to 16.7ºC; n=493; see methods) under the usual thermoneutral zone of passerines (Khaliq et al., 2014), birds may be forced to increase metabolism (Swanson & Jr., 2008) or to leave colder sectors (Root, 1988; Carrascal et al., 2012). In addition to this effect of thermal landscape on bird distribution, meadow pipits were positively related to precipitation. This is probably related to their use of ground as a feeding substratum (Cramp, 1992). In the Mediterranean region, grass growth and the superficial activity of ground invertebrates are strongly related to the moisture produced by autumn and winter rains on dry ground layers resulting from summer drought (Fernández-Ales et al., 1993; Doblas-Miranda et al., 2009; Guo et al., 2012). In this way, more precipitation will result in more suitable food patches for this species (De la Hera et al., 2012). Thus, it can be concluded that rain-mediated productivity and thermal landscapes can provide a causal explanation of climate features affecting the distribution of these small passerines in the study area.

MODELLING THE DISTRIBUTION OF CLIMATE SUITABILITY

Temperature and precipitation were the best contributors to the models such that the resulting maps depicted similar distribution patterns in both species (Fig 4). The sectors with high occurrence probabilities were distributed in lowlands and low occurrence areas were restricted to highlands and inland deserts. There were, however, some differences. While the meadow pipit was mostly related to western lowlands where Atlantic rains drain, the chiffchaff showed a broader distribution. Interestingly, the models fitted well to the present distribution of the species, with higher occupancy and abundance in sectors where the Maxent models suggest high climate suitability (Table 10). This supports the usefulness of models resulting from ring recoveries and suitable climate variables to predict the geographical distribution of wintering in these birds (Wisz et al., 2007b).

EFFECTS OF CLIMATE CHANGE ON BIRD DISTRIBUTION

According to IPCC predictions (IPCC, 2014), mean temperature will increase and precipitation will decrease in the study area over the next few decades. These changes will not be spatially homogeneous in the study area. Some southern sectors will be more affected by changes (Figure 15) and, within this latitudinal trend, temperature increases will grow and precipitation loss will decline in the highlands (Table 11). This change has been reported in other studies of the effect of elevation on climate change (Kotlarski et al., 2012; Rangwala & Miller, 2012). As a result, and according to the reported effects of temperature and precipitation on the meadow pipit and chiffchaff, the models predict two main trends in climate suitability. First, mean climate suitability will improve for the two species in the Iberian Peninsula and the western Maghreb. This change seems to be related to the warming of a region where 80% of the land is over 300 m and 60% over 600 m a.s.l. (Figure 13). In this way, the improvement of winter conditions produced by warming, similar to that reported in northern areas, will provide small birds the possibility to cope with winter conditions more successfully (Carrascal et al., 2012). Second, despite the overall improvement of winter conditions, some sectors will be more vulnerable to the damaging effects of climate change in some species. This is true for the warmer lowlands of the south where the predicted decrease in precipitation will reduce the climate suitability for the meadow pipit, a species linked to moist areas (see above). The fate of water resources is a key concern in the drier sectors of the Iberian Peninsula and the Maghreb (Giorgi & Lionello, 2008; García-Ruiz et al., 2011; Schilling et al., 2012).

PROSPECTS

This study suggests five main aspects for consideration in the assessment of the weaknesses and strengths of the resulting patterns. First, it is important to consider the representativeness of the two model species. They are insectivorous and ubiquitous birds similar to many other European partial-migratory passerines (Busse, 2001). However, the alleged ability of pipits and chiffchaffs to track climate change over the study region may not apply to stenotopic species or birds forced to track resources with patchy distribution (e.g. water birds, frugivorous species). Second, it is important to state that these results refer to a scenario in which other features (e.g. vegetation cover and composition, agricultural practices, etc.) will also vary as a response to climate change (Clavero et al., 2011). As a result, climate change could promote synergetic interactions within and among species, evolutionary and ecological processes and human activity that are difficult to predict (La Sorte et al., 2009; Moritz & Agudo, 2013). Third, temperature and precipitation appear to be two main drivers of bird distribution because changes in these parameters affect the energy available for birds (see Introduction). Since energy availability has been reported to be a global driver of bird distribution, changes in these variables are probably suitable indicators of changes in other species and regions (Hawkins et al., 2003; Pearce-Higgins et al., 2015). Finally, the results highlight the main role of elevation in shaping the retreat of low latitudinal margins of Mediterranean winter ranges of birds reported in this paper. This role of elevation will probably apply in other highlands of the Mediterranean basin (Figure 13) and the planet where winter conditions for birds can benefit from warming (Fernández-Ales et al., 1993; Khaliq et al., 2014). This main role of highlands in reshuffling the wintering ranges of migratory birds in the Mediterranean basin suggests two additional observations: a) Mediterranean highlands are usually reported as refuges for species retreating northwards due to the effect of postglacial warming (Hampe & Petit, 2005). The results in this paper suggest a similar buffer effect on wintering ranges of migratory birds. The huge expanses of Mediterranean highlands (Figure 13), usually avoided by many birds in winter (Dunning, 1992; Carrascal & Palomino, 2012; Tellería et al., 2014b), would progressively increase climate suitability as warming progresses. b) However, this projected climate improvement of highlands will not be sufficient to predict an increase in migratory populations in this wintering region since warming in northern areas may reduce migratory journeys to the south (Walther et al., 2002). Alternatively, it has been postulated that warming of Mediterranean highlands could exert a positive influence on the size of local bird populations favouring winter residency and enhancing winter survival (Cano et al., 2014).

CHAPTER 6 -
SYNTHESIS AND PERSPECTIVES

"The important thing is not to stop questioning. Curiosity has its own reason for existing."

- ALBERT EINSTEIN

In this thesis, we attempt to advance our understanding of the factors influencing the distribution of migratory birds given that it is crucial to study these species throughout the whole of their annual cycles (Somveille *et al.* 2015). We used species distribution models (SDM) and other multivariate statistics to explore the potential value of ringing recoveries for investigating the seasonal distribution of passerines. However, it must be stressed that it is essential that models are validated (Tellería et al., 2012). Overall, the results of this thesis show that the information provided by the ring-recovery dataset is useful for unravelling range-wide distributional patterns in small migratory birds throughout their annual cycle. Thus, given open access and the large scale of the data used (Sullivan et al., 2014; Du Feu et al., 2016), the methodological approach developed in this thesis will be useful for improving our knowledge of migratory birds and thus will help conservation efforts in light of rapid anthropogenic change.

Global change significantly threatens migratory birds. To cope with shifts in prevalent environmental conditions, it is vital to understand the processes affecting migratory species at different scales (Runge et al., 2015a). Migratory populations seem to be distributed within more restricted environmental ranges than sedentary populations in dynamic niche dimensions (climate). This probably makes sedentary populations more resilient to climate variability within their ranges. However, sedentary populations demonstrate poor plasticity in their seasonal vegetation cover selection (Pérez-Tris et al., 2015). Thus, the results presented in this thesis suggest that niche-tracking migrants and resident individuals require different analytical and conceptual approaches when exploring the emerging threats related to global change.

Finally, it is important to realize that species are not uniform entities but, rather, are composed of individuals whose relationships with the environment differ. This view is usually lacking from most approaches to the effect of global change (Valladares et al., 2014; Pacifici et al., 2015; Kawecki & Ebert 2004). Therefore, integrating information about ecological and genetic differences within populations will constitute an effective approach for identifying how adaption plays a role in the effects of global change on biodiversity (Manel et al., 2003). It is interesting to note the potential of partially migratory species (composed of individuals and populations that differ in migratory behaviour) for exploring birds' reactions to environmental changes. We believe that resident and migratory populations of European forest passerines in the Mediterranean Basin are good models for examine these issues (Pérez-Tris et al., 2004, 2015; Hampe & Petit, 2005).

CONCLUSIONS

"I'd should think you Jedi would have more respect for the difference between knowledge and wisdom."

- DEXTER JETTSTER

I. Large-scale surveys of migratory birds can be both logistically and financially unviable. However, here we show the potential of a citizen-science database (ringing recoveries) for studying the spatio-temporal distribution of migratory birds with species distribution models (SDM).

II. Using the meadow pipit as a case study, we show that species abundance is positively correlated with the habitat suitability reported by SDM. This result supports the use of these models to track the spatio-temporal location of the best sectors for wintering birds. In addition, these models can be used to understand the consequences of current and future environmental changes for species.

III. Ringing data were also used to examine how resident and migrant European robins and blackcaps cope with seasonal changes in environmental conditions. Using multivariate approaches we showed the existence of a trade-off between the costs of adaptations relating to the tracking ability of migrants over long distances and the increased ability of sedentary individuals to tolerate a wider suite of conditions within their permanent ranges.

IV. Migratory populations wintering in the western Mediterranean Basin show a geographical ‘bottleneck’ effect since their non-breeding ranges are smaller than their breeding grounds. Thus, it is essential that these wintering areas are properly managed to conserve migratory birds breeding in large areas of northern and central Europe.

V. Temperature and precipitation seem to be the two main drivers of chiffchaff and meadow pipit distribution on their wintering grounds in the western Mediterranean Basin. Future predictions of SDM suggest an expansion of climatically suitable sectors into upland areas due to the effect of warming and a retreat from lowlands as a result of decreasing rainfall. Hence, the huge expanses of mountains in the Iberian Peninsula and Maghreb will probably act as buffer areas that will help mitigate the effects of climate change on the winter distribution of the study species.

VI. Finally, the results presented in this thesis highlight the potential of the new methodological approaches that use data provided by ringing schemes for improving our knowledge of migratory birds, a key issue in their conservation.

REFERENCES

Alerstam T. & Enckell P.H. (1979) Unpredictable Habitats and Evolution of Bird Migration. *Oikos*, **33**, 228.

Alerstam T., Hedenström A., & Åkesson S. (2003) Long-distance migration: evolution and determinants. *Oikos*, **103**, 247–260.

Ambrosini R., Cuervo J.J.J., Feu C. du, Fiedler W., Musitelli F., Rubolini D., Sicurella B., Spina F., Saino N., & Møller A.P. (2016) Migratory connectivity and effects of winter temperatures on migratory behaviour of the European robin Erithacus rubecula: a continent-wide analysis. *Journal of Animal Ecology*, **85**, 749–760.

Ambrosini R., Møller A.P., & Saino N. (2009) *A quantitative measure of migratory connectivity.*

Araujo M. & Guisan A. (2006) Five (or so) challenges for species distribution modelling. *Journal of biogeography*, **33**, 1677–1688.

Atkinson P., Fuller R., Gillings S., & Vickery J. (2006) Counting birds on farmland habitats in winter. *Bird Study*, **53**, 303–309.

Atkinson P., Fuller R., & Vickery J. (2002) Large-scale patterns of summer and winter bird distribution in relation to farmland type in England and Wales. *Ecography*, **25**, 466–480.

Baillie S., Bairlein F., Clark J., du Feu C., Fiedler W., Fransson T., Hegelbach J., Julliard R., Karcza Z., Keller L.F., Kestenholz M., Schaub M., & Spina F. (2007) Bird ringing for science and conservation. *EURING*, 1–33.

Barbet-Massin M., Walther B.A., Thuiller W., Rahbek C., & Jiguet F. (2009) Potential impacts of climate change on the winter distribution of Afro-Palaearctic migrant passerines. *Biol. Lett.*, **5**, 248–251.

Bearhop S., Hilton G.M., Votier S.C., & Waldron S. (2004) Stable isotope ratios indicate that body condition in migrating passerines is influenced by winter habitat. *Proceedings. Biological sciences / The Royal Society*, **271 Suppl**, S215-8.

Bibby C.J., Burgess N.D., Hill D.A., & Mustoe S.H. (2000) *Bird census techniques.* Elsevier, London.

BirdLife International. (2014) Available at: http://www.birdlife.org.

Boucher-Lalonde V., Kerr J.T.J., & Currie D.J. (2014) Does climate limit species richness by limiting individual species' ranges? *Proceedings. Biological sciences / The Royal Society*, **281**, 20132695.

Brochet A.-L., Van den Bosschen W., Jbour S., Ndang'ang'a P.K., Jones V.R., Abdou W.A.L.I., Al-Hmoud A.R., Asswad N.G., Atienza J.C., Atrash I., Barbara N., Bensusan K., Bino T., Celada C., Cherkaoui S.I., Costa J., Deceuninck B., Etayeb K.S., Feltrup-Azafzaf C., Figelj J., Gustin M., Kmecl P., Kocevski V., Korbetti M., Kotrosan D., Mula Laguna J., Lattuada M., Leitão D., Lopes P., López-Jiménez N., Lucić V., Micol T., Moali A., Perlman Y., Piludu N., Portolou D., Putilin K., Quaintenne G., Ramadan-Jaradi G., Ružić M., Sandor A., Sarajli N., Saveljic D., Sheldon R.D., Shialis T., Tsiopelas N., Vargas F., Thompson C., Brunner A., Grimmett R., & Butchart S.H.M. (2016) Preliminary assessment of the scope and scale of illegal killing and taking of birds in the Mediterranean. *Bird Conservation International*, **26**, 1–28.

Broennimann O., Fitzpatrick M.C., Pearman P.B., Petitpierre B., Pellissier L., Yoccoz N.G., Thuiller W., Fortin M.J., Randin C., Zimmermann N.E., Graham C.H., & Guisan A. (2012) Measuring ecological niche overlap from occurrence and spatial environmental data. *Global Ecology and Biogeography*, **21**, 481–497.

Bueno J.M. (1998) Migración e invernada de pequeños turdinos en la península ibérica. I. Pechiazul (Luscinia svecica) y Ruiseñor común (Luscinia megarhynchos). *Ardeola*, **37**, 67–73.

Burnham K. & Anderson D. (2002) *Model selection and multimodel inference: a practical information–theoretic approach.* New York.

Busse P. (2001) European passerine migration system–what is known and what is lacking. *Ring*, **23**, 3–36.

Calder W.A. & King J.R. (1974) *Thermal and caloric relations of birds.* Academic Press,

Calenge C., Guillemain M., Gauthier-Clerc M., & 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. *Journal of Ornithology*, **151**, 945–950.

Cano L.L.S., Pacheco C., Refoyo P., & Tellería J.L. (2014) Geographical and environmental factors affecting the distribution of wintering black storks Ciconia nigra in the Iberian Peninsula. **45**, 514–521.

Canterbury G. (2002) Metabolic adaptation and climatic constraints on winter bird distribution. *Ecology*, **83**, 946–957.

Cantos F.J. (1995) Migración e invernada de la curruca capirotada (*Sylvia atricapilla*). *Ecología*, **9**, 425–433.

Carrascal L.M. & Palomino D. (2012) Variación geográfica de la riqueza de especies invernantes en la península Ibérica. Estacionalidad y determinismo ambiental. *Atlas de las Aves en Invierno en España 2007-2010.* (ed. by del M. J.C., M. B., B. A., and D. Palomino), Ministerio de Agricultura, Alimentación y Medio Ambiente-SEO/BirdLife, Madrid.

Carrascal L.M., Villén-Pérez S., & Seoane J. (2012) Thermal, food and vegetation effects on winter bird species richness of Mediterranean oakwoods. *Ecological research*, **27**, 293–302.

Carrascal L.M.L., Galván I., & Gordo O. (2009) Partial least squares regression as an alternative to current regression methods used in ecology. *Oikos*, **118**, 681–690.

Carroll M.L., DiMiceli C.M., Sohlberg R.A., & Townshend J.R.G. (2004) 250m MODIS normalized difference vegetation index. .

Chapman B.B.B., Brönmark C., Nilsson J.-Å.J.J.-Å., & Hansson L.-A. (2011) The ecology and evolution of partial migration. *Oikos*, **120**, 1764–1775.

Chen G., Townsend Peterson a., & Peterson A.T. (2002) Prioritization of areas in China for the conservation of endangered birds using modelled geographical distributions. *Bird Conservation International*, **12**, 197–209.

Chu C., Bartlett M., Wang Y., He F., Weiner J., Chave J., & Sack L. (2016) Does climate directly influence NPP globally? *Global Change Biology*, **22**, 12–24.

Clark J. a., Thorup K., Stroud D. a., Nunnery T., & Museum Z. (2009) Quantifying the movement patterns of birds from ring recoveries. *Ringing & Migration*, **24**, 180–188.

Clavero M., Villero D., Brotons L., Root T., Price J., Hal K., Schneider S., Rosenzweig C., Parmesan C., Brook B., Sodhi N., Bradshaw C., Sala O., III F.C., Armesto J., Berlow E., Bloomfield J., Jetz W., Wilcove D., Dobson A., Mace G., Baillie J., Gregory R., Willis S., Jiguet F., Voříšek P., Klvaňová A., Devictor V., Julliard R., Couvet D., Jiguet F., Prodon R., Suárez-Seoane S., Osborne P., Baudry J., Clavero M., Brotons L., Estrada J., Pedrocchi V., Brotons L., Herrando S., Hagemeijer W., Blair M., Swaay C. van, Strien A. Van, Julliard R., Schweiger O., Brereton T., Vallecillo S., Brotons L., Thuiller W., Mazzoleni S., Pasquale G. di, Mulligan M., Martino P. di, Rego F., Falcucci A., Maiorano L., Boitani L., Pausas J., Llovet J., Rodrigo A., Vallejo R., Tabachnick B., Fidell L., Debussche M., Lepart J., Dervieux A., Gil-Tena A., Brotons L., Saura S., Thomas R., Coomes O., Moran E., Achard F., Angelsen A., Pausas J., Popy S., Bordignon L., Prodon R., Gregory R., Strien A. van, Voříšek P., Meyling A.G., Noble D., Opdam P., Wascher D., Pimm S., Covas R., Blondel J., Sorte F. La, & III T.F. (2011) Climate Change or Land Use Dynamics: Do We Know What Climate Change Indicators Indicate? *PLoS ONE*, **6**, e18581.

Cola V. Di, Broennimann O., Petitpierre B., Breiner F.T., D'Amen M., Randin C., Engler R., Pottier

J., Pio D., Dubuis A., Pellissier L., Mateo R.G., Hordijk W., Salamin N., & Guisan A. (2016) ecospat: an R package to support spatial analyses and modeling of species niches and distributions. *Ecography*, in press.

Cormier R.L., Humple D.L., Gardali T., & Seavy N.E. (2016) Migratory connectivity of Golden-crowned Sparrows from two wintering regions in California. *Animal Migration*, **3**, 48–56.

Cramp S. (1992) *Handbook of the Birds of Europe, the Middle East and North Africa: The Birds of the Western Palearctic: Warblers Vol 6.* Oxford University Press, Oxford.

Cramp S. & Perrins C.. (1994) *Handbook of the Birds of Europe, the Middle East and North Africa: The Birds of the Western Palearctic: Crows to Finches Vol 8.* Oxford University Press, Oxford.

Cramp S. & Perrins C. (1993) *Handbook of the Birds of Europe, the Middle East and North Africa: The Birds of the Western Palearctic: Flycatchers to Shrikes Vol 7.* Oxford University Press, Oxford.

Cramp S. & Simmons K. (1988) *Handbook of the Birds of Europe, the Middle East and North Africa: The Birds of the Western Palearctic: Tyrant Flycatchers to Thrushes Vol 5.* Oxford University Press, Oxford., Oxford.

Cresswell W. (2014) Migratory connectivity of Palaearctic-African migratory birds and their responses to environmental change: the serial residency hypothesis. *Ibis*, **156**, 493–510.

Crick H. (2004) The impact of climate change on birds. *Ibis*, .

Cuesta M. & Balmori A. (2003) Mosquitero Común y Mosquitero Ibérico. *Atlas de las aves reproductoras de España. Madrid: Dirección General de Conservación de la Naturaleza-SEO.* (ed. by R. Martí and J. del Moral), pp. 489–491.

Díaz M. & Tellería J. (1994) Predicting the effects of agricultural changes in central Spanish croplands on seed-eating overwintering birds. *Agriculture, Ecosystems & Environment*, **49**, 289–298.

DiMiceli C.M.M., Carroll M.L.L., Sohlberg R.A.A., Huang C., Hansen M.C., Townshend J.R.G.R.G., M.C. H., & Townshend J.R.G.R.G. (2011) Annual global automated MODIS vegetation continuous fields (MOD44B) at 250 m spatial resolution for data years beginning day 65, 2000–2010. .

Dingle H. (2014) *Migration: The Biology of Life on the Move. Second Edition.* Oxford University Press, USA.

Doblas-Miranda E., Sánchez-Piñero F., & González-Megías A. (2009) Vertical distribution of soil macrofauna in an arid ecosystem: Are litter and belowground compartmentalized habitats? *Pedobiologia*, **52**, 361–373.

Dudík M., Phillips S.J.S., & Schapire R.E. (2005) Correcting sample selection bias in maximum entropy density estimation. *Advances in neural information processing systems* pp. 323–330.

Dunning J.B. (1992) *CRC handbook of avian body masses.* CRC press, Boca Raton, FL.

Elith J., Burgman M.A., & Regan H.M.H. (2002) Mapping epistemic uncertainties and vague concepts in predictions of species distribution. **157**, 313–329.

Elith J., H Graham C., P Anderson R., Dudík M., Ferrier S., Guisan A., J Hijmans R., Huettmann F., R Leathwick J., Lehmann A., Li J., G Lohmann L., A Loiselle B., Manion G., Moritz C., Nakamura M., Nakazawa Y., McC M Overton J., Townsend Peterson a, J Phillips S., Richardson K., Scachetti-Pereira R., E Schapire R., Soberón J., Williams S., S Wisz M., & E Zimmermann N. (2006) Novel methods improve prediction of species' distributions from occurrence data. *Ecography*, **29**, 129–151.

Elith J. & Leathwick J. (2009) Species distribution models: ecological explanation and prediction across space and time. *Annual Review of Ecology, Evolution, and Systematics*,

40, 677–697.

Elith J., Phillips S.J., Hastie T., Dudík M., Chee Y.E., & Yates C.J. (2011) A statistical explanation of MaxEnt for ecologists. *Diversity and Distributions*, **17**, 43–57.

Engler J.O., Rödder D., Stiels D., & Förschler M.I. (2014) Suitable, reachable but not colonised: Seasonal niche duality in an endemic mountainous songbird. *Journal of Ornithology*, **155**, 657–669.

Evans D.M., Redpath S.M., Evans S.A., Elston D.A., & Dennis P. (2005) Livestock grazing affects the egg size of an insectivorous passerine. *Biology Letters*, **1**, 322–325.

Evans K.L., James N.A., & Gaston K.J. (2006) Abundance, species richness and energy availability in the North American avifauna. *Global Ecology and Biogeography*, **15**, 372–385.

Falloon P. & Betts R. (2010) Climate impacts on European agriculture and water management in the context of adaptation and mitigation—The importance of an integrated approach. *Science of The Total Environment*, **408**, 5667–5687.

Fernández-Ales R., Laffarga J.M.J., Ortega F., Alés R.F., & Laffarga J.M.J. (1993) Strategies in Mediterranean grassland annuals in relation to stress and disturbance. *Journal of Vegetation Science*, **4**, 313–322.

Du Feu C.R., Clark J.A., Schaub M., Fiedler W., & Baillie S.R. (2016) The EURING Data Bank–a critical tool for continental-scale studies of marked birds. *Ringing & Migration*, **31**, 1–18.

Fielding A.H. & Bell J.F. (1997) A review of methods for the assessment of prediction errors in conservation presence/absence models. *Environmental Conservation*, **24**, 38–49.

Franklin J. (2009) *Mapping species distributions: spatial inference and prediction.* Cambridge University Press., Cambridge.

Garamszegi L.Z. (2014) *Modern Phylogenetic Comparative Methods and Their Application in Evolutionary Biology.* Springer Berlin Heidelberg, Berlin, Heidelberg.

García-Ruiz J.J.M., López-Moreno J.I.J., Vicente-Serrano S.M., Lasanta–Martínez T., & Beguería S. (2011) Mediterranean water resources in a global change scenario. *Earth-Science Reviews*, **105**, 121–139.

Gaston K.J., Blackburn T.M., Greenwood J.J.D., Gregory R.D., Quinn R.M., & Lawton J.H. (2000) Abundance-occupancy relationships. *Journal of Applied Ecology*, **37**, 39–59.

Gill R.E., Tibbitts T.L., Douglas D.C., Handel C.M., Mulcahy D.M., Gottschalck J.C., Warnock N., McCaffery B.J., Battley P.F., & Piersma T. (2009) Extreme endurance flights by landbirds crossing the Pacific Ocean: ecological corridor rather than barrier? *Proceedings of the Royal Society of London B: Biological Sciences*, **276**, .

Gillings S. (2008) Designing a winter bird atlas field methodology: issues of time and space in sampling and interactions with habitat. *Journal of Ornithology*, **149**, 345–355.

Gilroy J.J., Gill J.A., Butchart S.H.M., Jones V.R., & Franco A.M.A. (2016) Migratory diversity predicts population declines in birds. *Ecology Letters*, **19**, 308–317.

Giorgi F. & Lionello P. (2008) Climate change projections for the Mediterranean region. *Global and Planetary Change*, **63**, 90–104.

Gomez C., Tenorio E.A., Montoya P., & Cadena C.D. (2016) Niche-tracking migrants and niche-switching residents : evolution of climatic niches in New World warblers (Parulidae). *Proceedings of the Royal Society B: Biological Sciences*, **283**, 20152458.

Grass Development Team (2012) Geographic Resources Analysis Support System (GRASS) Software. Version 6.4.2. .

Greenberg R. & Marra P. (2005) The renaissance of migratory bird biology. *The birds of two worlds: the ecology and evolution of migration* pp. 437–443.

Guisan A. & Thuiller W. (2005) Predicting species distribution: offering more than simple habitat models. *Ecology Letters*, **8**, 993–1009.

Guisan A. & Zimmermann N.E. (2000) Predictive habitat distribution models in ecology. *Ecological Modelling*, **135**, 147–186.

Guo Q., Hu Z., Li S., Li X., Sun X., & Yu G. (2012) Spatial variations in aboveground net primary productivity along a climate gradient in Eurasian temperate grassland: effects of mean annual precipitation and its seasonal distribution. *Global Change Biology*, **18**, 3624–3631.

Hampe A. (2008) Fruit tracking, frugivore satiation, and their consequences for seed dispersal. *Oecologia*, **156**, 137–145.

Hampe A. & Petit R.J. (2005) Conserving biodiversity under climate change: the rear edge matters. *Ecology Letters*, **8**, 461–467.

Harris R.M.B., Grose M.R., Lee G., Bindoff N.L., Porfirio L.L., & Fox-Hughes P. (2014) Climate projections for ecologists. *Wiley Interdisciplinary Reviews: Climate Change*, **5**, 621–637.

Hawkins B.A., Porter E.E., & Felizola Diniz-Filho J.A. (2003) Productivity and history as predictors of the latitudinal diversity gradient of terrestial birds. *Ecology*, **84**, 1608–1623.

Hedenström A., Norevik G., Warfvinge K., Andersson A., Bäckman J., & Åkesson S. (2016) Annual 10-Month Aerial Life Phase in the Common Swift Apus apus. *Current Biology*, **26**, .

Helbig A.J. (2003) Evolution of Bird Migration: A Phylogenetic and Biogeographic Perspective. *Avian Migration* pp. 3–20. Springer Berlin Heidelberg, Berlin, Heidelberg.

Heller N.E. & Zavaleta E.S. (2009) Biodiversity management in the face of climate change: A review of 22 years of recommendations. *Biological Conservation*, **142**, 14–32.

Hijmans R., Phillips S., & Leathwick J. (2013) dismo: Species distribution modeling. *R package version 0.8-17*, .

Hijmans R.J. & van Etten J. (2013) raster: Geographic Data Analysis and Modeling. 4–18.

Hijmans R.R.J., Cameron S.E.S., Parra J.J.L., Jones P.G., & Jarvis A. (2005) Very high resolution interpolated climate surfaces for global land areas. *International Journal of Climatology*, **25**, 1965–1978.

Hochachka W.M., Fink D., Hutchinson R.A., Sheldon D., Wong W.K., & Kelling S. (2012) Data-intensive science applied to broad-scale citizen science. *Trends in Ecology and Evolution*, **27**, 130–137.

Hutchinson G. (1957) concluding remarks. *Cold Spring Harb. Symp. Quant. Biol*, 415–427.

Hutto R.R.L. (1985) *Habitat selection by nonbreeding, migratory land.*

IPCC (2014) Synthesis Report. Core Writing Team, Pachauri RK, Meyer LA, Contribution of Working Groups I. II and III to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change. .

Jackman S. (2015) pscl: classes and methods for R developed in the political science computational laboratory. .

Jiménez-Valverde A. & Lobo J.M. (2007) Threshold criteria for conversion of probability of species presence to either-or presence-absence. *Acta Oecologica*, **31**, 361–369.

Jiménez-valverde A., Nakazawa Y., Lira-noriega A., & Peterson A.T. (2009) Environmental Correlation Structure and Ecological Niche Model Projections. *Biodiversity Informatics*, **6**, 28–35.

Joseph L. & Stockwell D. (2000) Temperature-based models of the migration of Swainson's Flycatcher (Myiarchus swainsoni) across South America: A new use for museum specimens of migratory birds. *Proceedings of the Academy of Natural Sciences of Philadelphia*, **150**, 293–300.

Kelly J.F. (1999) Population Limitation in Birds. *The Auk*, **116**, 866–868.

Kennedy M. & Gray R.D. (1993) Can Ecological Theory Predict the Distribution of Foraging Animals? A Critical Analysis of Experiments on the Ideal Free Distribution. *Oikos*, **68**, 158.

Khaliq I., Hof C., Prinzinger R., Böhning-Gaese K., & Pfenninger M. (2014) Global variation in thermal tolerances and vulnerability of endotherms to climate change. *Proceedings of the Royal Society of London B: Biological Sciences*, **281**, .

Kirby J.J.S., Stattersfield A.A.J., Butchart S.H.S.H.M., Evans M.I.M.I.M.I., Grimmett R.F.R.F.A.R.F., Jones V.R.V.R., O'Sullivan J., Tucker G.M.G.M., Newton I., O'Sullivan J., Tucker G.M.G.M., & Newton I. (2008) Key conservation issues for migratory land- and waterbird species on the world's major flyways. *Bird Conservation International*, **18**, S49–S73.

Klaassen R.H.G.R., Hake M., Strandberg R., Koks B.J., Trierweiler C., Exo K.-M., Bairlein F., & Alerstam T. (2014) When and where does mortality occur in migratory birds? Direct evidence from long-term satellite tracking of raptors. *Journal of Animal Ecology*, **83**, 176–184.

Knudsen E., Lindén A., Both C., Jonzén N., Pulido F., Saino N., Sutherland W.J., Bach L.A., Coppack T., Ergon T., Gienapp P., Gill J.A., Gordo O., Hedenström A., Lehikoinen E., Marra P.P., Møller A.P., Nilsson A.L.K., Péron G., Ranta E., Rubolini D., Sparks T.H., Spina F., Studds C.E., Sæther S.A., Tryjanowski P., & Stenseth N.C. (2011) Challenging claims in the study of migratory birds and climate change. *Biological Reviews*, **86**, 928–946.

Kokko H. (1999) Competition for early arrival in migratory birds. *Journal of Animal Ecology*, **68**, 940–950.

Korner-Nievergelt F., Liechti F., & Thorup K. (2014) A bird distribution model for ring recovery data: Where do the European robins go? *Ecology and Evolution*, **4**, 720–731.

Korner-Nievergelt F., Sauter A., Atkinson P.W., Guélat J., Kania W., Kéry M., Köppen U., Robinson R. a., Schaub M., Thorup K., van der Jeugd H., van Noordwijk A.J., Korner-Nievergelt F., & Sauter A. (2010) Improving the analysis of movement data from marked individuals through explicit estimation of observer heterogeneity. *Journal of Avian Biology*, **41**, 8–17.

Körner C. (2007) The use of "altitude" in ecological research. *Trends in Ecology & Evolution*, **22**, 569–574.

Kosicki J.Z.J. & Chylarecki P. (2013) Predictive mapping of Meadow Pipit density using integrated remote sensing data and an atlas of vascular plants dataset. *Bird Study*, **60**, 500–508.

Kotlarski S., Bosshard T., Lüthi D., Pall P., & Schär C. (2012) Elevation gradients of European climate change in the regional climate model COSMO-CLM. *Climatic Change*, **112**, 189–215.

De la Hera I., Pérez-Tris J., Tellería J.L.J., Hera I. de la, Pérez-Tris J., & Tellería J.L.J. (2012) Habitat distribution of migratory and sedentary blackcaps Sylvia atricapilla wintering in southern Iberia: a morphological and biogeochemical approach. *Journal of avian biology*, **43**, 333–340.

Laube I., Graham C.H., & Böhning-Gaese K. (2015) Niche availability in space and time: Migration in Sylvia warblers. *Journal of Biogeography*, **42**, 1896–1906.

Lee T.T.M. & Jetz W. (2011) Unravelling the structure of species extinction risk for predictive conservation science. *Proceedings of the Royal Society of London B: Biological Sciences*, **278**, 1329–1338.

Legendre P. (1993) Spatial autocorrelation: trouble or new paradigm? *Ecology*, **74**, 1659–1673.

Lennon J.J., Greenwood J.J.D., & Turner J.R.G. (2000) Bird diversity and environmental gradients in Britain: a test of the species-energy hypothesis. *Journal of Animal Ecology*, **69**, 581–598.

Levey D.J. & Stiles F.G. (1992) Evolutionary precursors of long-distance migration: resource availability and movement patterns in neotropical landbirds. *The American Naturalist*, **140**, 447.

Liu C., White M., & Newell G. (2013) Selecting thresholds for the prediction of species occurrence with presence-only data. *Journal of Biogeography*, **40**, 778–789.

Lobo J.M.J., Jiménez-Valverde A., Jiménez-valverde A., & Real R. (2008) AUC: A misleading measure of the performance of predictive distribution models. *Global Ecology and Biogeography*, **17**, 145–151.

Manel S., Schwartz M.K., Luikart G., & Taberlet P. (2003) Landscape genetics: Combining landscape ecology and population genetics. *Trends in Ecology and Evolution*, **18**, 189–197.

Manel S., Williams H.C., & Ormerod S.J. (2001) Evaluating presence-absence models in ecology: the need to account for prevalence. *Journal of Applied Ecology*, **38**, 921–931.

Marco M. Di & Santini L. (2015) Human pressures predict species' geographic range size better than biological traits. *Global change biology*, .

Marquaridt D.W., Inverses G., Regression R., Estimation B.L., Estimation N., & Marquardt D.W. (1970) Generalized Inverses, Ridge Regression, Biased Linear Estimation, and Nonlinear Estimation. *Technometrics*, **12**, .

Marra P.P. (1998) Linking Winter and Summer Events in a Migratory Bird by Using Stable-Carbon Isotopes. *Science*, **282**, 1884–1886.

Marra P.P.P., Cohen E.B.E., Loss S.R.S.S.R., Rutter J.E., Tonra C.M., & Eb C. (2015) A call for full annual cycle research in animal ecology. *Biology*, **11**, .

Martínez-Meyer E., Peterson a T., & Navarro-Sigüenza A.G. (2004) Evolution of seasonal ecological niches in the Passerina buntings (Aves: Cardinalidae). *Proceedings of the Royal Society B Biological Sciences*, **271**, 1151–1157.

Mason C.C.F. & Macdonald S.S.M. (1999) Winter bird numbers and land-use preferences in an arable landscape in eastern England. *Bird Conservation International*, **9**, 119–127.

McGill B.B.J. (2010) Matters of Scale. *Science*, **328**, 575–576.

Meehan T.D.T., Jetz W., & Brown J.J.H.J. (2004) Energetic determinants of abundance in winter landbird communities. *Ecology Letters*, **7**, 532–537.

Melles S.J., Fortin M.J., Lindsay K., & Badzinski D. (2011) Expanding northward: influence of climate change, forest connectivity, and population processes on a threatened species' range shift. *Global Change Biology*, **17**, 17–31.

Mills A.M. (2006) Winter range compression of migrants in Central America. *Journal of Avian Biology*, **37**, 41–51.

Møller A., Garamszegi L., Peralta-Sánchez J.M., & Soler J.J. (2011) Migratory divides and their consequences for dispersal, population size and parasite–host interactions. **24**, 1744–1755.

Del Moral J.C., Molina B., Bermejo A., & PalominoD (2012) Atlas de las aves en invierno en España 2007-2010. *Ministerio de Agricultura, Alimentación y Medio Ambiente SEO/BirdLife*, .

Moritz C. & Agudo R. (2013) The future of species under climate change: resilience or decline? *Science (New York, N.Y.)*, **341**, 504–8.

Mrabet R. & Moussadek R. (2012) Conservation Agriculture in Dry Areas of Morocco : Rational for Agricultural Sustainability under Climate and Socio-Economic Change. *Field Crops Research*, **132**, 84–94.

Nahal I. (1981) The Mediterranean climate from a biological viewpoint. *Ecosystems of the world 11: Mediterranean-type shrublands.* (ed. by S.R. Di Castri F, Goodall DW), pp. 63–86. Elsevier, Amsterdam.

Nakazawa Y., Peterson A., Martinez-Meyer E., & Navarro-Sigüenza A.G. (2004) Seasonal niches of Nearctic-Neotropical migratory birds: implications for the evolution of migration. *The Auk*, **121**, 610–618.

Newton I. (1995) Relationship between breeding and wintering ranges in Palaearctic-African migrants. *Ibis*, 241–249.

Newton I. (2008) The Nearctic-Neotropical migration system. *The Migration Ecology of Birds*, 729–750.

Newton I. (2010) *The migration ecology of birds.*

Norris D.R., Marra P., Orris D.R.Y.A.N.N., & Arra P.E.P.M. (2007) Seasonal interactions, habitat quality, and population dynamics in migratory birds. *The Condor*, 535–547.

Norris D.R., Marra P.P., Kyser T.K., Sherry T.W., & Ratcliffe L.M. (2004) Tropical winter habitat limits reproductive success on the temperate breeding grounds in a migratory bird. *Proceedings. Biological sciences / The Royal Society*, **271**, 59–64.

Öberg M., Arlt D., Pärt T., Laugen A.T., Eggers S., & Low M. (2015) Rainfall during parental care reduces reproductive and survival components of fitness in a passerine bird. *Ecology and Evolution*, **5**, 345–356.

Oksanen J., Blanchet F.G., Kindt R., Legendre P., Minchin P.R., O'Hara R.B., ..., & Wagner H. (2015) Vegan: Community Ecology Package. R package version 2.3-0. .

Onrubia A. & Tellería J.L.J. (2012) Has the number of birds wintering in the Maghreb decreased? A test in the Gibraltar Strait. *Ardeola*, **59**, 123–129.

Pacifici M., Foden W.B., Visconti P., Watson J.E.M., Butchart S.H.M., Kovacs K.M., Scheffers B.R., Hole D.G., Martin T.G., Akçakaya H.R., Corlett R.T., Huntley B., Bickford D., Carr J.A., Hoffmann A.A., Midgley G.F., Pearce-Kelly P., Pearson R.G., Williams S.E., Willis S.G., Young B., & Rondinini C. (2015) Assessing species vulnerability to climate change. *Nature Climate Change*, **5**, 215–224.

Parmesan C. (2006) Ecological and Evolutionary Responses to Recent Climate Change. *Annual Review of Ecology, Evolution, and Systematics*, **37**, 637–669.

Pautasso M. (2012) Observed impacts of climate change on terrestrial birds in Europe: an overview. *Italian Journal of Zoology*, **79**, 296–314.

Pearce-Higgins J.W., Eglington S.M., Martay B., & Chamberlain D.E. (2015) Drivers of climate change impacts on bird communities. *Journal of Animal Ecology*, **84**, 943–954.

Pérez-Tris J., Bensch S., Carbonell R., Helbig A., & Tellería J.L. (2004) Historical Diversification of Migration Patterns in a Passerine Bird. *Evolution*, **58**, 1819–1832.

Pérez-Tris J., Carbonell R., De La Hera I., Ramírez A., & Tellería J.L. (2015) Conservación de poblaciones singulares ante el cambio. *Los Bosques y la Biodiversidad frente al Cambio Climático: Impactos, Vulnerabilidad y Adaptación en España* (ed. by Herrero A and Zavala MA), pp. 163–170. Ministerio de Agricultura, Alimentación y Medio Ambiente, Madrid.

Pérez-tris J., Carbonell R., & Tellería J.L. (2000) Abundance distribution, morphological variation and juvenile condition of robins,. *Journal of Biogeography*, 879–888.

Pérez-Tris J. & Tellería J.L. (2002a) Migratory and sedentary blackcaps in sympatric non-breeding grounds: Implications for the evolution of avian migration. *Journal of Animal Ecology*, **71**, 211–224.

Pérez-Tris J. & Tellería J.L. (2002b) Regional variation in seasonality affects migratory behaviour and life-history traits of two Mediterranean passerines. *Acta Oecologica*, **23**, 13–21.

Peterson A.T. (2011) Ecological niche conservatism: A time-structured review of evidence. *Journal of Biogeography*, **38**, 817–827.

Peterson a T. (2001) Predicting Species ' Geographic Distributions Based on Ecological Niche Modeling. *The Condor*, **103**, 599–605.

Pettorelli N., Ryan S., Mueller T., Bunnefeld N., Jedrzejewska B., Lima M., & Kausrud K. (2011) The Normalized Difference Vegetation Index (NDVI): unforeseen successes in animal ecology. *Climate Research*, **46**, 15–27.

Phillips S.J., Anderson R.P., & Schapire R.E. (2006) Maximum entropy modeling of species geographic distributions. *Ecological Modelling*, **190**, 231–259.

Ponti L., Gutierrez A.P., Ruti P.M., & Dell'Aquila A. (2014) Fine-scale ecological and economic assessment of climate change on olive in the Mediterranean Basin reveals winners and losers. *Proceedings of the National Academy of Sciences of the United States of America*, **111**, 5598–603.

Pulido F. (2007) The Genetics and Evolution of Avian Migration. *Bio Science*, **57**, 165–174.

Purvis A., Gittleman J.L., Cowlishaw G., & Mace G.M. (2000) Predicting extinction risk in declining species. *Society of London …*, .

R Core Team (2015) A language and environment for statistical computing; 2013. .

Ramenofsky M. & Wingfiield J.C. (2007) Regulation of Migration. *BioScience*, **57**, 135.

Rangwala I. & Miller J.R. (2012) Climate change in mountains: a review of elevation-dependent warming and its possible causes. *Climatic Change*, **114**, 527–547.

Rappole J., Helm B., & Ramos M. (2003) An integrative framework for understanding the origin and evolution of avian migration. *Journal of Avian Biology*, **34**, 124–128.

Reddy S. & Dávalos L.M.L. (2003) Geographical sampling bias and its implications for conservation priorities in Africa. *Journal of Biogeography*, **30**, 1719–1727.

Rey P.J. (2011) Preserving frugivorous birds in agro-ecosystems: lessons from Spanish olive orchards. *Journal of Applied Ecology*, **48**, 228–237.

Rivera J.H. V., Ortega-Huerta M. a., Sarkar S., & Rappole J.H. (2011) Modelling the potential winter distribution of the endangered Black-capped Vireo (Vireo atricapilla). *Bird Conservation International*, **21**, 92–106.

Robbins C. & Sauer J. (1989) Population declines in North American birds that migrate to the Neotropics. *Proceedings of the National Academy of Sciences*, **86**, 7658–7662.

Robinson W.D., Bowlin M.M.S., Bisson I., Shamoun-Baranes J., Thorup K., Diehl R.H., Kunz T.H., Mabey S., & Winkler D.W. (2010) Integrating concepts and technologies to advance the study of bird migration. *Frontiers in Ecology and the Environment*, **8**, 354–361.

Rodríguez J.P., Brotons L., Bustamante J., & Seoane J. (2007) The application of predictive modelling of species distribution to biodiversity conservation. *Diversity and Distributions*, **13**, 243–251.

Root T. (1988) Energy constraints on avian distributions and abundances. *Ecology*, **69**, 330–339.

Ruiz-Labourdette D., Nogués-Bravo D., Ollero H.S., Schmitz M.F., & Pineda F.D. (2012) Forest composition in Mediterranean mountains is projected to shift along the entire elevational gradient under climate change. *Journal of Biogeography*, **39**, 162–176.

Runge C.A., Watson J.E.M., Butchart S.H.M., Hanson J.O., Possingham H.P., & Fuller R.A. (2015a) Protected areas and global conservation of migratory birds. *Science*, **350**, .

Runge C. a, Tulloch A., Hammill E., Possingham H.P., & Fuller R. a (2015b) Geographic range size and extinction risk assessment in nomadic species. *Conservation biology : the journal of the Society for Conservation Biology*, **29**, 865–76.

Rushton S.P., Ormerod S.J.S., & Kerby G. (2004) New paradigms for modelling species distributions? *Journal of Applied Ecology*, **41**, 193–200.

Salewski V. & Bruderer B. (2007) The evolution of bird migration - A synthesis. *Naturwissenschaften*, **94**, 268–279.

Sanderson E., Jaiteh M., Levy M., & Redford K. (2002) The Human Footprint and the Last of the Wild: The human footprint is a global map of human influence on the land surface, which suggests that human beings are. *BioScience*, **52**, 891–904.

Sanderson F.J.F., Donald P.P.F., Pain D.J.D., Burfield I.I.J., & van Bommel F.P.J. (2006) Long-term population declines in Afro-Palearctic migrant birds. *Biological Conservation*, **131**, 93–105.

Santos T.., Carbonell R.., Galarza A.., Pérez-Tris J.., Ramírez A.., & Tellería J.L.. (2014) The importance of northern Spanish farmland for wintering migratory passerines: A quantitative assessment. *Bird Conservation International*, **24**, 1–16.

Schilling J., Freier K.P., Hertig E., & Scheffran J. (2012) Climate change, vulnerability and adaptation in North Africa with focus on Morocco. *Agriculture, Ecosystems and Environment*, **156**, 12–26.

Schmidt-Nielsen K. (1984) *Scaling: why is animal size so important?* Cambridge University Press.,

Schoener T.W. (1970) Nonsynchronous Spatial Overlap of Lizards in Patchy Habitats. *Ecology*, **51**, 408–418.

Seoane J., Bustamante J., Díaz-Delgado R., & Dıaz-Delgado R. (2004) Competing roles for landscape, vegetation, topography and climate in predictive models of bird distribution. *Ecological Modelling*, **171**, 209–222.

Seoane J. & Carrascal L.M. (2008) Interspecific differences in population trends of Spanish birds are related to habitat and climatic preferences. *Global Ecology and Biogeography*, **17**, 111–121.

Sexton J.P., McIntyre P.J., Angert A.L., & Rice K.J. (2009) Evolution and Ecology of Species Range Limits. *Annual Review of Ecology, Evolution, and Systematics*, **40**, 415–436.

Sherry T. & Holmes R. (1995) *Summer versus winter limitation of populations: what are the issues and what is the evidence.* Oxford University Press, New York.

Shirley S.M., Yang Z., Hutchinson R.A., Alexander J.D., Mcgarigal K., & Betts M.G. (2013) Species distribution modelling for the people: Unclassified landsat TM imagery predicts bird occurrence at fine resolutions. *Diversity and Distributions*, **19**, 855–866.

Soberón J. (2007) Grinnellian and Eltonian niches and geographic distributions of species. *Ecology Letters*, **10**, 1115–1123.

Sol D., Lefebvre L., & Rodríguez-Teijeiro J.D. (2005) Brain size, innovative propensity and migratory behaviour in temperate Palaearctic birds. *Proceedings. Biological sciences / The Royal Society*, **272**, 1433–41.

Somveille M., Manica A., Butchart S.H.M., & Rodrigues A.S.L. (2013) Mapping global diversity patterns for migratory birds. *PloS one*, **8**, e70907.

Somveille M., Rodrigues A.S.L., & Manica A. (2015) Why do birds migrate? A macroecological perspective. *Global Ecology and Biogeography*, **24**, 664–674.

La Sorte F.A., Lee T.M., Wilman H., & Jetz W. (2009) Disparities between observed and predicted impacts of climate change on winter bird assemblages. *Proceedings of the Royal Society of London B: Biological Sciences*, .

Stenseth N.C., Mysterud A., & Ottersen G. (2002) Ecological effects of climate fluctuations. *Science*, **297**, 1292–1296.

Stutchbury B.J.M., Siddiqui R., Applegate K., Hvenegaard G.T., Mammenga P., Mickle N., Pearman M., Ray J.D., Savage A., Shaheen T., & Fraser K.C. (2016) Ecological Causes and Consequences of Intratropical Migration in Temperate-Breeding Migratory Birds. *The American naturalist*, S28-40.

Suarez-Seoane S., Morena G.D. La, Eladio L., Prieto M., Manuel B., Osborne P.E., & De Juana E. (2008) Maximum entropy niche-based modelling of seasonal changes in little bustard (Tetrax tetrax) distribution. *Ecological Modelling*, **219**, 17–29.

Sullivan B.L., Aycrigg J.L., Barry J.H., Bonney R.E., Bruns N., Cooper C.B., Damoulas T., Dhondt A.A., Dietterich T., Farnsworth A., Fink D., Fitzpatrick J.W., Fredericks T., Gerbracht J., Gomes C., Hochachka W.M., Iliff M.J., Lagoze C., La Sorte F.A., Merrifield M., Morris W., Phillips T.B., Reynolds M., Rodewald A.D., Rosenberg K. V., Trautmann N.M., Wiggins A., Winkler D.W., Wong W.K., Wood C.L., Yu J., & Kelling S. (2014) The eBird enterprise: An integrated approach to development and application of citizen science. *Biological Conservation*, **169**, 31–40.

Sullivan B.L.B., Phillips T., Dayer A.A.A., Wood C.C.L., Farnsworth A., Iliff M.J., Davies I.J., Wiggins A., Fink D., Hochachka W.M., Rodewald A.D., Rosenberg K. V., Bonney R., & Kelling S. (2016) Using open access observational data for conservation action: A case study for birds. *Biological Conservation*, .

Swanson D.L. & Jr. T.G. (2008) The evolution of high summit metabolism and cold tolerance in birds and its impact on present-day distributions. *Evolution*, **63**, 184–194.

Tautin J. (2005) One hundred years of bird banding in north America. *USDA Forest Service Gen. Tech. Rep. PSW-GTR*, **191**, 815–816.

Tellería J.L., Asensio B., & Díaz M. (1999) *Aves Ibéricas. Vol. II. Paseriformes.* J. M. Reyero Publisher, Madrid. ,

Tellería J.L., Blázquez M., De La Hera I., & Pérez-Tris J. (2013a) Migratory and resident Blackcaps Sylvia atricapilla wintering in southern Spain show no resource partitioning. *Ibis*, **155**, 750–761.

Tellería J.L., Carrascal L.M., & Santos T. (2014a) Species abundance and migratory status affects large-scale fruit tracking in thrushes (Turdus spp.). *Journal of Ornithology*, **155**, 157–164.

Tellería J.L., Fandos G., López J.F., Onrubia A., & Refoyo P. (2014b) Winter Distribution of Passerine Richness in the Maghreb (North Africa): A Conservation Assessment. *Ardeola*, **61**, 335–350.

Tellería J.L., Hera I.D. La, & Perez-Tris J. (2013b) Morphological Variation as a Tool for Monitoring Bird Populations: A Review. *Ardeola*, **60**, 191–224.

Tellería J.L. & Pérez-Tris J. (2003) Seasonal distribution of a migratory bird: effects of local and regional resource tracking. *Journal of Biogeography*, **30**, 1583–1591.

Tellería J.L., Ramírez Á., Galarza A., Carbonell R., Pérez-Tris J., & Santos T. (2009) Do migratory pathways affect the regional abundance of wintering birds? A test in northern Spain. *Journal of Biogeography*, **36**, 220–229.

Tellería J.L., Ramirez A., & Pérez-Tris J. (2008) Fruit tracking between sites and years by birds in Mediterranean wintering grounds. *Ecography*, **31**, 381–388.

Telleria J.L. & Santos T. (1993) Distributional Patterns of Insectivorous Passerines in the Iberian Forests: Does Abundance Decrease Near the Border? *Journal of Biogeography*, **20**, 235.

Tellería J.L., Santos T., Refoyo P., & Muñoz J. (2012) Use of ring recoveries to predict habitat suitability in small passerines. *Diversity and Distributions*, **18**, 1130–1138.

Tellería J.L.J.L., Fernández-López J., & Fandos G. (2014c) Using ring records and field surveys to predict the winter distribution of a migratory passerine. *Bird Study*, **61**, 527–536.

Tellería J.L.J.L., Fernández-López J., & Fandos G. (2016) Effect of climate change on Mediterranean winter ranges of two migratory passerines. *PLoS ONE*, **11**, 146958.

Thévenot M., Vernon R., & Bergier P. (2003) The birds of Morocco. British Ornithologists' Union. *British Ornithologists' Club, Tring,* .

Triviño M., Cabeza M., Thuiller W., Hickler T., & Araújo M.B. (2013) Risk assessment for Iberian birds under global change. *Biological Conservation*, **168**, 192–200.

Triviño M., Thuiller W., Cabeza M., Hickler T., & Araújo M.B. (2011) The contribution of vegetation and landscape configuration for predicting environmental change impacts on iberian birds. *PLoS ONE*, **6**, .

Valladares F., Matesanz S., Guilhaumon F., Araújo M.B., Balaguer L., Benito-Garzón M., Cornwell W., Gianoli E., van Kleunen M., Naya D.E., Nicotra A.B., Poorter H., & Zavala M.A. (2014) The effects of phenotypic plasticity and local adaptation on forecasts of species range shifts under climate change. *Ecology Letters*, **17**, 1351–1364.

Vanhinsberg D. & Chamberlain D. (2001) Habitat associations of breeding Meadow Pipits Anthus pratensis in the British uplands. *Bird Study*, **48**, 159–172.

Vera P. & Giménez M. (2012) *Bisbita pratense Anthus pratensis.* Ministerio de Agricultura, Alimentacion y Medio Ambiente-SEO/BirdLife, Madrid., Madrid.

Vickery J.A., Ewing S., Smith K.W., Pain D.J., Bairlein F., Škorpilová J., & Gregory R.D. (2014) The decline of Afro-Paleartic migrants and an assessment of potential causes. *International Journal of Avian Science*, **156**, 1–22.

Visser M.E., Perdeck A.C., van Balen J.H., & Both C. (2009) Climate change leads to decreasing bird migration distances. *Global Change Biology*, **15**, 1859–1865.

Walther G.-R., Post E., Convey P., Menzel A., Parmesan C., Beebee T.J.C., Fromentin J.-M., Hoegh-Guldberg O., & Bairlein F. (2002) Ecological responses to recent climate change. *Nature*, **416**, 389–395.

Warren D.L., Glor R.E., & Turelli M. (2008) Environmental niche equivalency versus conservatism: quantitative approaches to niche evolution. *Evolution; international journal of organic evolution*, **62**, 2868–83.

Weber T.P., Houston A.I., & Ens B.J. (1999) Consequences of Habitat Loss at Migratory Stopover Sites: A Theoretical Investigation. *Journal of Avian Biology*, **30**, 416.

Webster M.S., Marra P.P., Haig S.M., Bensch S., & Holmes R.T. (2002) Links between worlds: unraveling migratory connectivity. *Trends in Ecology & Evolution*, **17**, 76–83.

Whelan C.J., Wenny D.G., & Marquis R.J. (2008) Ecosystem services provided by birds. *Annals of the New York academy of sciences*, **1134**, 25–60.

Wiens J.A. (1989) Spatial Scaling in Ecology. *Functional Ecology*, **3**, 385.

Wikelski M., Tarlow E.M., Raim A., Diehl R.H., Larkin R.P., & Visser G.H. (2003) Avian metabolism: Costs of migration in free-flying songbirds. *Nature*, **423**, 704–704.

Wisz M., Walther B., & Rahbek C. (2007a) Using potential distributions to explore determinants of Western Palaearctic migratory songbird species richness in sub-Saharan Africa. *Journal of Biogeography*, .

Wisz M.S.M., Walther B. a. B., & Rahbek C. (2007b) Using potential distributions to explore determinants of Western Palaearctic migratory songbird species richness in sub-Saharan Africa. *Journal of Biogeography*, **34**, 828–841.

Wright D.H. (1983) Species-Energy Theory: An Extension of Species-Area Theory. *Oikos*, **41**, 496.

Zeileis A. & Hothorn T. (2002) Diagnostic checking in regression relationships. *R News*, 7–10.

Zink R.R.M. (2011) The evolution of avian migration. *Biological Journal of the Linnean Society*, **104**, 237–250.

Zuckerberg B., Fink D., La Sorte F.A., Hochachka W.M., & Kelling S. (2016) Novel seasonal land cover associations for eastern North American forest birds identified through dynamic species distribution modelling. *Diversity and Distributions*, **22**, 717–730.

Zuur A.F., Ieno E.N., Walker N.J., Saveliev A.A., & Smith G.M. (2009) Mixed Effects Modelling for Nested Data. pp. 101–142. Springer New York,

RESUMEN

INTRODUCCIÓN

Muchas de las poblaciones de aves son migratorias, es decir realizan desplazamientos en respuesta a los cambios estacionales en las condiciones ambientales. Esto provoca que los individuos envueltos en estos movimientos afronten diferentes condiciones y peligros a lo largo del año. A pesar de estos retos, la migración ha evolucionado debido a que las ventajas compensan en muchas ocasiones los inconvenientes asociados a los peligros de una vida itinerante. Sin embargo, el balance entre los beneficios y costes de la migración pudieran verse descompensados por culpa del cambio global dando lugar a cambios en el patrón actual de los movimientos de muchas poblaciones de aves. Para poder realizar un diagnóstico de su situación actual y elaborar estrategias específicas para su conservación, es indispensable conocer la relación de las especies migratorias con las condiciones ambientales que les rodean.

El estudio de los factores que determinan la distribución y la abundancia de las aves migratorias es difícil de abordar ya que estos se manifiestan a lo largo del ciclo anual en diferentes áreas. En este sentido, el invierno es una época crítica para este grupo de especies al tener que afrontar bajas temperaturas y escasez de alimentos. Esto ha sido difícil de estudiar en muchos casos por la falta de datos sobre la distribución de sus poblaciones en esa época del año. Sin embargo, la creciente disponibilidad de datos procedentes de emisores satélite de seguimiento (por ejemplo, Movebank), recuperación de anillas (por ejemplo, EURING) y programas de ciencia ciudadana (por ejemplo, eBird), junto con el acceso sin precedentes a potentes análisis bioinformáticos y diferentes técnicas estadísticas, nos permite avanzar hoy en el conocimiento de la ecología de las aves a lo largo de todo el año.

Esta tesis intenta contribuir al conocimiento de los factores ambientales que afectan a la distribución de las aves migratorias combinando los datos de las recuperaciones de anillas con las técnicas de modelización de la distribución potencial de las especies. Más explícitamente, su objetivo es describir los mecanismos que determinan el tamaño, la ubicación y la dinámica de distribución de las especies migratorias en las zonas de invernada localizadas en el oeste del Paleártico para así poder desarrollar una gestión adecuada de sus poblaciones. Esta zona, situada al oeste de la cuenca del Mediterráneo, actúa como área de invernada principal para muchos individuos que crían en el centro y norte de Europa. Se trata, por ello, de una zona donde los esfuerzos dirigidos a la protección de los mejores sectores para las aves pueden tener un impacto sustancial en la conservación de las poblaciones de aves europeas.

OBJETIVOS Y RESULTADOS

Los objetivos de esta tesis están organizados en tres partes. En la primera validamos el uso de recuperaciones de anillas en la predicción de la distribución de las aves migratorias. En la segunda discutimos los diferentes aspectos relacionados con el comportamiento migratorio y la respuesta a los cambios estacionales en dos especies de aves migratorias parciales. Y, finalmente, en la última aplicamos estos conceptos en dos estudios relacionados con la conservación de las zonas de invernada de las aves migratorias en la Península Ibérica y el Magreb.

En el primer capítulo, validamos si la calidad de hábitat resultado de los modelos de distribución de especies construidos con recuperaciones de aves anilladas predice bien la distribución invernal de un ave migratoria. Esta validación es interesante pues errores de adscripción (por ejemplo con las coordenadas) o el potencial sesgo en la distribución de las recuperaciones de las anillas pudiera dar resultados equívocos. Para ello, hemos utilizado las recuperaciones en invierno de las anillas del Bisbita Pratense (*Anthus pratensis*) en la Península Ibérica y el Magreb. Los resultados muestran que la calidad de hábitat predicha por el modelo de distribución está positivamente relacionada con la abundancia de esta especie en una serie de muestreos realizados en España y Marruecos. Los resultados son utilizados para evaluar la utilidad de los modelos de distribución de especies derivados de las anillas para describir el área de invernada de las aves migratorias y poder así priorizar los esfuerzos en conservación sobre los mejores sectores de invernada.

En el siguiente capítulo se usan nuevamente las recuperaciones de aves anilladas para estudiar la respuesta de las poblaciones de aves migratorias a los cambios estacionales. Las condiciones ambientales que experimentan las aves migratorias en el área de cría y de invernada pueden diferir notablemente o ser muy similares. Testamos la hipótesis de que el comportamiento migratorio debiera distribuir a las aves entre condiciones más similares que las residentes, sobre todo en aquellas dimensiones del nicho más dinámicas (clima). Para ello, examinamos cómo responden a los cambios estacionales de las condiciones ambientales las poblaciones migratorias de petirrojos (*Erithacus rubecula*) y currucas capirotadas (*Sylvia atricapilla*) y la forma en que difieren de sus homólogos sedentarios. Los resultados muestran que las poblaciones migratorias rastrean a lo largo del año condiciones climáticas más similares que las sedentarias, las cuales experimentan drásticos cambios climáticos en sus áreas de residencia. Por el contrario, las poblaciones migratorias difirieron en mayor medida en la estructura del paisaje seleccionada a lo largo del año. Estos resultados sugieren un equilibrio entre la capacidad de los individuos migratorios para rastrear las condiciones climáticas a lo largo del año y la de las aves sedentarias para tolerar fuertes cambios climáticos dentro de sus áreas de cría.

Los capítulos anteriores brindan la posibilidad de utilizar los modelos de distribución de especies derivados de las recuperaciones de anillas para predecir el área de distribución de las aves migratorias a lo largo del año. Esto nos permite comparar el área ocupada por estas poblaciones en sus cuarteles de cría e invernada y así identificar la presencia de potenciales cuellos de botella al tamaño de sus poblaciones. Para abordar este objetivo se estudió en un tercer capítulo la distribución potencial del área de cría e invernada en 10 especies de paseriformes migratorios parciales que invernan en la Península Ibérica y el Magreb. Los resultados indican que todas las especies muestran una compresión del área de invernada en relación con el de reproducción. Dado a que se considera que este desequilibrio entre las áreas estacionales es un buen indicador de la vulnerabilidad de las especies migratorias al cambio global, los resultados resaltan la importancia conservacionista de las zonas de invernada situadas en la Cuenca del Mediterráneo Occidental, un área que se encuentra bajo la presión continua del cambio climático y la intensificación agrícola.

Finalmente, a la vista de las reducidas áreas de invernada de las poblaciones invernantes en la Península ibérica y el Magreb, cobra mayor importancia entender su potencial evolución en un escenario de cambio global. En el último capítulo, se estudia el efecto del cambio climático en la distribución invernal de dos aves mayoritariamente migratorias (el bisbita pratense, *Anthus pratensis* y el mosquitero común, *Phylloscopus collybita*) en nuestra zona de estudio. Tras comprobar que la temperatura y la precipitación determinan fuertemente su actual distribución invernal, usamos los modelos de distribución de especies generados con las anillas para pronosticar la distribución potencial de las zonas de invernada según las proyecciones climáticas para 2050-2070 (aumento de la temperatura y reducción de la precipitación). Los resultados muestran que el incremento de temperatura provoca una expansión de los sectores climáticamente adecuados hacia zonas de mayor altitud, y un retroceso de la calidad de hábitat en las zonas más meridionales debido a una reducción drástica de la precipitación. Estos resultados invitan a analizar el papel amortiguador de la altitud sobre los futuros cambios en la distribución de las aves migratorias en un área que, como la península Ibérica y el Magreb, está fuertemente dominada por montañas y mesetas.

DISCUSIÓN

Cada vez hay más evidencias de la importancia de conocer la distribución de las poblaciones migratorias a lo largo de todo el año ya que sus requerimientos de nicho pueden variar estacionalmente y los procesos que determinan el tamaño, la ubicación geográfica y la dinámica de distribución son muy complejos e involucran múltiples factores que interactúan entre sí. En esta tesis, se ha intentado avanzar en el conocimiento actual de los factores que influyen en la distribución invernal de las aves migratorias y su dinámica estacional con el fin de poder identificar los mejores sectores de invernada en donde priorizar las estrategias de conservación.

La tesis muestra el valor potencial de los datos obtenidos a partir de la recuperación de anillas para investigar los patrones de distribución invernal de los paseriformes y así poder predecir los posibles efectos de los cambios ambientales sobre su distribución. Para ello es esencial resaltar la necesidad de validar las predicciones resultantes de estos modelos con los resultados obtenidos mediante el estudio de la abundancia de las aves en las áreas de estudio. En general, las recuperaciones de anillas son útiles para esclarecer los patrones de distribución a lo largo del ciclo anual en aves migratorias de pequeño tamaño. Es previsible que el desarrollo de los dispositivos rastreadores por satélite, más precisos y cada vez más pequeños, pueda proporcionar nueva y fascinante información sobre las amenazas y los patrones migratorios de muchas aves de pequeño tamaño.

Debido al cambio global al que están sometidas las especies actualmente, es importante identificar los posibles factores que expliquen su vulnerabilidad y permitan evaluar los cambios en su distribución actual. En este sentido, y por lo comentado arriba, las poblaciones migratorias, con una estrategia más rastreadora, y las poblaciones residentes, con una estrategia opuesta, requieren diferentes enfoques a la hora de analizar sus reacciones a las cambiantes condiciones ambientales.

Por último, parece importante recordar que las especies no son entidades uniformes, sino que están compuestas por diferentes poblaciones que difieren en sus respuestas a las condiciones ambientales que les rodea. La adaptación local y la plasticidad de las poblaciones sedentarias de aves forestales podrían desempeñar un papel crucial en la persistencia de estas especies ante el cambio global.

SUMMARY

BACKGROUND

Many avian populations are migratory and make regular movements as responses to seasonal changes in environmental conditions. As a result, the individuals involved in these movements have to face up to a variety of environmental conditions and threats throughout the year. Nevertheless, the inherent advantages for migratory populations are greater than the risks associated with these movements. This trade-off may be disrupted by global change, which could affect the migratory behaviour of many birds. The understanding of the relationships between migratory birds and the environment is thus a key issue in any assessment of the impact of human change on these species and in the design of conservation measures.

The factors that determine the distribution and abundance of migratory birds are difficult to determine exactly since they usually occur throughout the whole migratory circuit. The lack of data on bird movements during the year hampers the study of migratory species; this is the case of their distributions in winter, a critical period for migratory birds in which they have to cope with low temperatures and food shortages. However, the growing wealth of data provided by tracking devices (e.g. Movebank), ringing schemes (e.g. EURING) and other citizen-science programs (e.g. eBird), along with today's unprecedented access to modelling techniques, now offer exciting opportunities for advancing knowledge of migratory bird ecology throughout the whole year

The aim of this thesis was to improve our understanding of the environmental drivers shaping migratory bird distributions throughout the year by combining ring-recovery data and species-distribution modelling techniques. More explicitly, we aim to describe the features affecting the size, location and seasonal dynamics of the birds wintering in the Western Palearctic. The western Mediterranean is used by vast amounts of migratory birds from central and northern Europe and it is thus a region where the efforts aimed at protecting wintering birds will benefit the conservation of European avifauna on a broader scale.

OBJECTIVES AND RESULTS

This thesis is arranged in three main parts. First of all, we validate the use of ringing recoveries as a means of predicting birds' winter distribution. Then, we discuss different aspects of the relationship between migratory behaviour and the responses to seasonal changes, before, finally, applying these concepts and methods to two studies related to the conservation of migratory birds wintering in the Iberian Peninsula and the Maghreb.

In the first chapter, we test whether or not the habitat suitability scores provided by the species distribution models resulting from ring-recovery data predict the actual winter distribution of migratory birds. This is essential because ring-recoveries may give a skewed view of the real distribution of migratory birds. We used recoveries of wintering meadow pipits *(Anthus pratensis*) in the Iberian Peninsula and Maghreb to show that the species distribution models do predict the true abundance of this pipit in Spain and Morocco. Finally, we discuss the usefulness of the models derived from ringing records for predicting the wintering ranges of migratory birds.

In the next chapter, we also use ring-recoveries to explore how migratory birds relate to the spatio-temporal changes occurring in environmental conditions during the year. We tested the hypothesis that migratory birds look for similar conditions throughout the whole year, above all in niche dimensions that are dynamic (climate). We studied how migratory robins (*Erithacus rubecula*) and blackcaps (*Sylvia atricapilla*) track environmental changes and how they differ from their sedentary counterparts. The results show that migratory individuals overlapped more in terms of climate conditions than sedentary birds, which had to withstand severe climate changes in their permanent ranges. These results suggest that there is a trade-off between the increased ability of migratory individuals to track climate conditions during the year and the capability of sedentary birds to tolerate abrupt climatic changes within their breeding ranges.

These first two chapters highlight how the species distribution models derived from ring-recoveries can be used to predict the breeding and non-breeding ranges of migratory birds. This allows us to compare the size of these two ranges and to identify possible geographical bottlenecks that might affect migratory bird populations. We explored the potential size of breeding and wintering grounds in 10 partially migratory passerines that winter in the Iberian Peninsula and the Maghreb. The results indicate that, unlike in their breeding areas, all the species show range compression on winter grounds. This imbalance between seasonal ranges has been proved to be a potential correlate of species' vulnerability to change. We continue by discussing the importance of the non-breeding grounds situated in the western Mediterranean Basin in the conservation of migratory passerines.

Finally, we use climate projections to study the effects of climate change on the winter distribution of two migratory passerines (meadow pipit *Anthus pratensis* and chiffchaff *Phylloscopus collybita*). Climate predictions suggest that in coming decades temperatures will increase and precipitation will fall in the study area. After showing that temperature and precipitation are the main drivers of the winter distribution of both pipits and chiffchaffs, we use the models resulting from ring-recoveries to forecast the distribution of these birds for the period 2050–2070. Our results show that the predicted changes in climate will increase climatic suitability in uplands but reduce habitat suitability in lowlands, good evidence of how upland buffer areas will mitigate the effects of climate change on wintering birds in regions where both mountains and lowlands are present.

SYNTHESIS

This thesis provides support for the value of ring-recovery data in research into migration strategies and the seasonal distribution of passerines. The testing of the models (a highly important methodological part of the process) shows that the results of ringing recoveries are useful for unravelling the features affecting the seasonal distribution of small migratory passerines. We agree, however, that the development of satellite trackers and other, increasingly smaller devices will provide fresh (and better) information about migratory patterns and threats to songbirds. Nevertheless, our approach to ringing recoveries does provide three exciting results that merit further investigation: a) migratory and sedentary birds differ in resource tracking, a trait that could affect their ability to cope with global change; b) range contraction on wintering grounds may jeopardize the migratory populations of partially migratory passerines since habitat alteration in small wintering areas will affect individuals over larger breeding areas; c) climate change will potentially modify these wintering areas and its effects, according to our predictions, will be buffered by the huge expanses of mountains in the Iberian Peninsula and the Maghreb. Thus, data resulting from the selfless work of thousands of ringers provide excellent material for studying and conserving migratory passerines.

Supplementary material

CHAPTER 4: Range compression of migratory passerines in wintering grounds of the Western Mediterranean: conservation prospects.

SUPPLEMENT-S4.1. Relationships between human foot print index and ringing activity in Europe.

Distribution modelling with Maxent provides the opportunity to cope with the effect of biased sampling effort by including any cartographical information in which the spatial distribution of sampling effort is reported (Dudík *et al*. 2005). We assumed that ringing or recovering a ringed bird is a contingent process related to the activity of ringers, hunters and people in general, something related to human density and the accessibility of habitats, as reported by the density of roads and other infrastructures. In this case, we used the Human Foot Print index (which considers a set of spatial data related to population density, land transformation, accessibility, and electrical power infrastructures; Sanderson et al. 2002) as a main predictor of the probability of capturing or recovering a ringed bird. To test this, we compared the density of living and dead ringed birds recovered by country as reported by EURING (http://www.euring.org/; Figure S 4.1-1, Table S4.1) with the mean HFP per country. Results support this relationship (Figure S 4.1-2).

Dudík M., Phillips S. J. & Schapire R.E. (2005). Correcting sample selection bias in maximum entropy density estimation. Advances in neural information processing systems 18. MIT Press, Cambridge, Massachusetts

Sanderson E.W., Jaiteh M., Levy M.A., Redford K.H., Wannebo A.V. & Woolmer G. (2002). The human footprints and the last of the wild. BioScience 52: 891–904

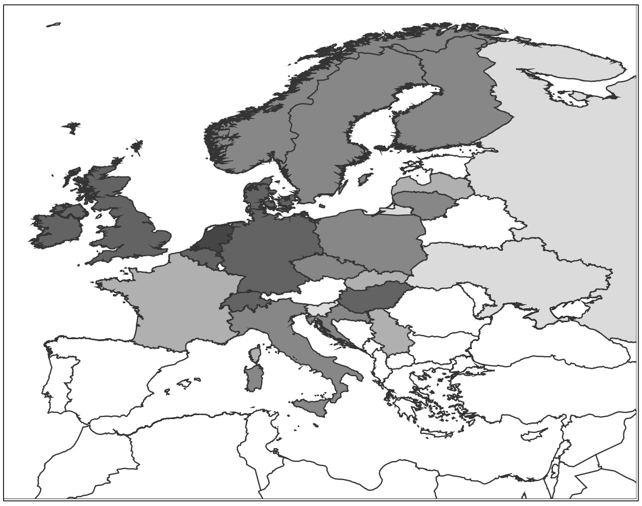

Figure S 4.1-1. Distribution of bird ringing activity as reported by the total number of living and dead birds controlled by national schemes in Europe. The number of controlled birds, reported by EURING (http://www.euring.org/) was divided by the area of the country to obtain an index of the ringing effort (see Table S4.1) Data were log-transformed to smooth inter-country differences

Table S4.1. Number of controlled ringed living and dead birds per country reported by EURING (http://www.euring.org/), mean Human Foot Print Index and land surface. Ringing effort per country was obtained by surface the number of recoveries.

Country	Land surface (Km^2)	HFP	Ring Recoveries
Belgium	30528	50,46	99747
Czech Republic	78866	43,22	52953
Denmark	43094	48,23	189287
Finland	338145	18,989	246429
France	547030	40,127	21441
Germany	357021	44,052	719996
Latvia	64589	34	859
Lithuania	65200	35,99	38065
Netherlands	41526	48,175	1191960
Norway	385156	21,147	26384
Poland	312685	39,08	175618
Slovakia	48845	39,06	4262
Slovenia	20273	32,68	29
Sweden	449964	22,222	143439
Switzerland	41285	42,112	74622
UK and Ireland	315100	44,06	689468

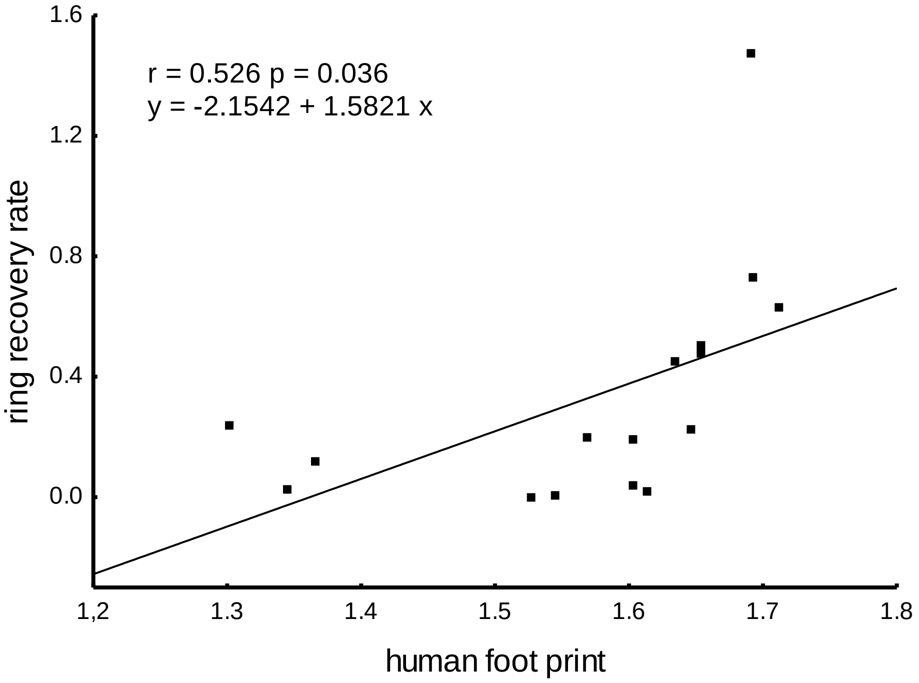

Figure S 4.1-2. Relationships between the mean human foot print and the rate of ring recoveries per country. This relationship can be improved when the highest recovery rate of the Netherlands (r=0.68, P=0.005) or the scores of the three Scandinavian (Sweden, Norway and Finland) countries in the left of the graph (r:0.83, P<0.001) are removed. Note than data were log$_{10}$ transformed.

SUPLEMENT-S 4.2

Figure S 4.2-1. Distribution of ring records in breeding and wintering populations. Last map shows the minimum convex polygons used to model distribution in the breeding and wintering grounds

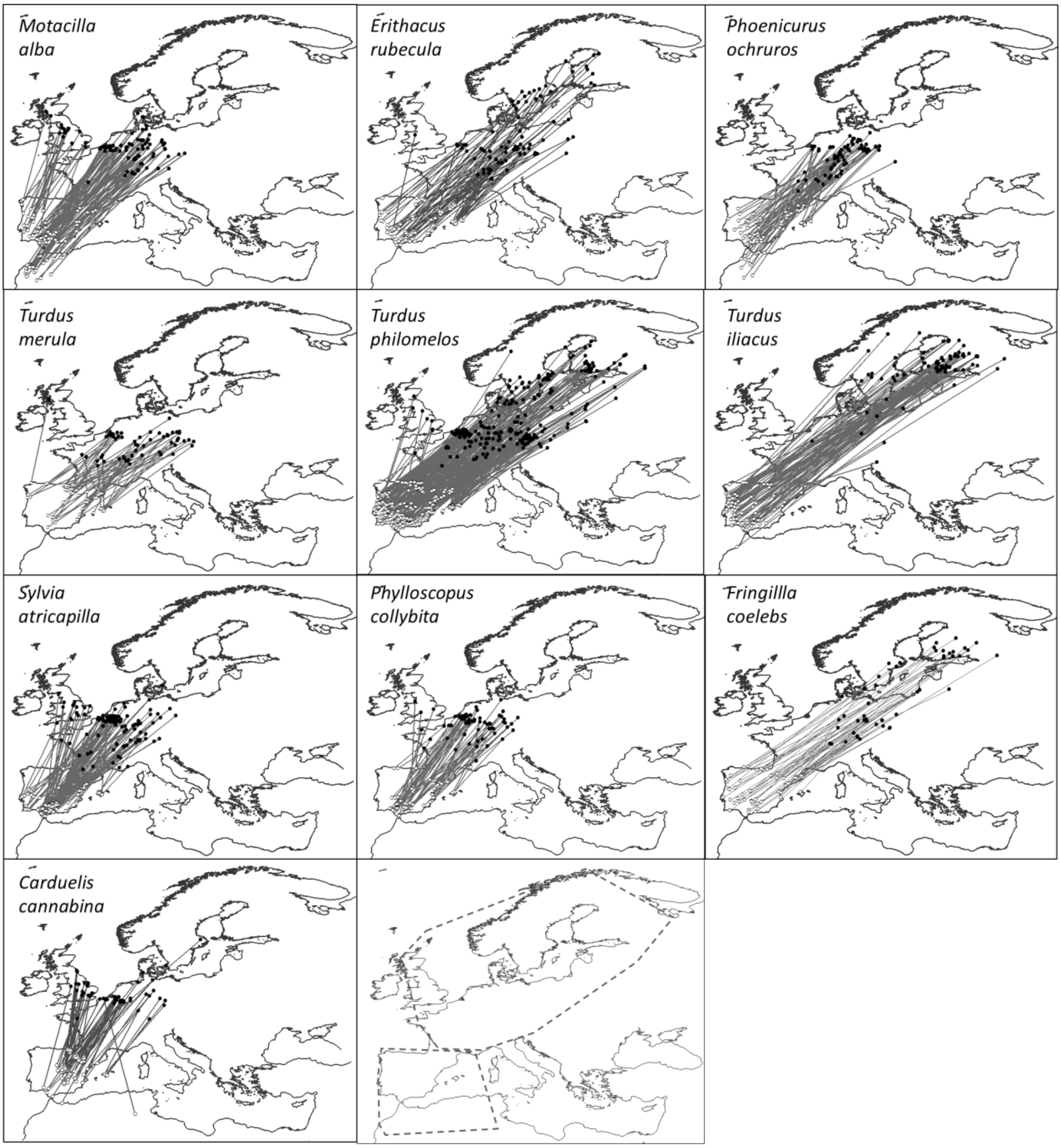

Figure S 4.2-2. Range map of migratory populations in breeding and wintering grounds as reported by applying the ´maximizing sum of sensitivity and specificity´ threshold to the occurrence probabilities map. Last map shows the minimum convex polygons used to model distribution in the breeding and wintering grounds.