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Research article

The northern wheatear is reducing its distribution in its southernmost European range and moving to higher altitudes

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Under the current pattern of climate change, mountain bird populations are generally shifting their ranges to higher elevations, tracking their climatic optima. Nevertheless, space limitations at high altitudes constrain mountain species' resilience to climatic change, making them particularly vulnerable. In extreme cases, the climatic niche of some species can move beyond mountaintops, ultimately driving such species to extinction. This study presents the case of the northern wheatear *Oenanthe oenanthe* in mainland Spain and compares its breeding distribution from 2003 to 2022. Spain, where the species mostly occupies mountain areas, represents its southernmost distribution limit in Europe. We built environmental favourability models using information from the two most recent Spanish bird atlases and a set of climatic, topographic, human activity and lithological variables to determine the factors affecting the occurrence of the species. The influence of climate compared to all other factors was obtained using variation partitioning analysis. The northern wheatear has suffered a strong reduction (67%) in occupied areas and also in favourability throughout mainland Spain (especially in the south) where climate change may have far-reaching consequences, including local extinctions. Climate explained more than 90% of the variation in the model obtained for 2022. Interestingly, the occupied areas were, on average, 100 m higher in 2022 than in 2003. If the effects of climate warming persist, the northern wheatear will likely disappear in its southernmost distribution limit, being the Sierra de las Nieves National Park population the most vulnerable in mainland Spain. For this reason, it is necessary to implement monitoring programmes for northern wheatear populations, with priority for mountain systems wherein they already occupy higher elevations, as well as further studies on other mountain species.

Keywords: climate change, elevation, favourability, mainland Spain, mountain birds, *Oenanthe oenanthe*, species distribution models (SDMs)

Introduction

Species ranges are dynamic as individuals make daily, seasonal and annual movements (Müller 1979). Changes in distribution are accentuated at the boundaries of



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a given species' range because environmental conditions are generally less favourable at the edge than in the centre of their distributions, normally decreasing the density of individuals (Brown et al. 1995, Lomolino and Channell 1995, Castro et al. 2008). Eventually, populations at the margins of the range weaken or disappear (local marginal extinction) or are repopulated with individuals from other populations (colonisation), generating a specific dynamic of the distributional edges that constantly modify their shape (Eldredge 1995). It is important to identify the abiotic (temperature, precipitation, humidity, etc.), biotic (natural history of the species or individual mobility), as well as anthropogenic factors that underly these changes to approach the biogeographical response of species to new scenarios, such as rising temperatures caused by climate change.

Mountain areas host unique biodiversity, and mountain species show specific ecological adaptations that enable survival in extreme climatic conditions (Körner 2007, Bastianelli et al. 2017). These mountain species' characteristics make such ecosystems particularly vulnerable to anthropogenic threats, such as climate or land use changes (Jetz et al. 2007, Scridel et al. 2018, Harrison 2020). In the context of climate change, mountain bird populations are generally shifting their ranges to higher elevations in order to track their climatic optima (Maggini et al. 2011, Reif and Flousek 2012, Auer and King 2014, Hallman et al. 2022). This shift is usually consistent with global warming temperatures and a gradient of decreasing temperature with altitude (Pautasso 2012). Nevertheless, space limitations at high altitudes constrain mountain species' resilience to climatic changes and make them particularly vulnerable. In extreme cases, the climatic niche of certain species can move beyond mountaintops, ultimately driving such species to extinction (Sekercioglu et al. 2008). Although various studies have modelled and predicted such threats in the future (La Sorte and Jetz 2010, Chamberlain et al. 2013, Harris et al. 2014), relatively little is known about the population trends of species in mountain areas due to the limited accessibility of their breeding sites and difficult working conditions (Flousek et al. 2015). Long-term datasets on mountain birds are therefore rare and provide a unique opportunity to test the environmental impacts of these specific conditions (Chamberlain et al. 2012).

Species distribution models (SDMs) have become an important tool in studies on biogeography, ecology, evolution, conservation biology and climate change, mainly due to the enormous amount of environmental information available and the high capacity to manage and analyse this information (Guisan and Zimmermann 2000, Muñoz and Real 2006, Chamorro et al. 2020, 2021, Barras et al. 2021, Pulido-Pastor et al. 2021). These models can be used to estimate the ecological requirements of a species by associating their geographical distributions with a set of predictor variables, thus allowing ecological processes to be simulated and various responses predicted. A growing variety of modelling methods are currently available (Guisan and Zimmermann 2000, Austin 2002, Gahegan 2003, Guisan and Thuiller

2005, Real et al. 2006, Elith et al. 2008, Zurell et al. 2020, Sillero et al. 2021). Several studies have used SDMs to understand the effect of climate change on species and ecosystems in order to anticipate their response to this phenomenon (Real et al. 2013, Muñoz et al. 2013, 2015a, Chamorro et al. 2020, Barras et al. 2021, López-Ramírez et al. 2023). Predicting these responses is currently a priority for alpine species and environments in order to formulate future conservation strategies and contribute to policy-making.

In this paper, we examine the case of the northern wheat-ear *Oenanthe oenanthe* in mainland Spain, which is its southernmost distribution limit in Europe, wherein the species mostly occupy high-mountain areas (Tellería et al. 1999, Keller et al. 2020), an environment recognised as highly sensitive to climate change (La Sorte and Jetz 2010, Gobiet et al. 2014, Harris et al. 2014, Flousek et al. 2015). We aim to compare the breeding distribution of this species from the beginning of the century (2003) to the present (2022) to examine potential changes in breeding distribution area and confirm whether such changes are partly related to the effects of climate change.

Material and methods

Study area

The area analysed in this study was mainland Spain, which covers nearly 85% of the Iberian Peninsula, an area of 493 518 km². Its geographical situation in south-western Europe and its location between two continents, Europe and Africa, and two large marine areas, the Mediterranean Sea and the Atlantic Ocean, define it as a biogeographical unit of great interest (Fig. 1a). Given its latitudinal position (approx. 40°N) and its topographic heterogeneity, mainland Spain has an extremely diverse climate with a mainly eastward- and southward-decreasing gradient of precipitation and a mainly northward-decreasing temperature gradient (Font 2000). In broad terms, three climatic areas can be considered: Atlantic, Mediterranean and Inland (Capel 1981). The Atlantic area includes the whole north coast and is characterized by mild winters, cool summers and abundant, regular precipitation. The Mediterranean area covers the southern and eastern coasts of Spain, with hot dry summers, mild winters and rainfall that rarely exceeds 500 mm annually. Finally, the Inland area has high temperatures in summer and low in winter, as well as irregular and scarce precipitation. Approximately three-quarters of Peninsular Spain is made up of the extensive Inner Plateau (average altitude 760 m a.s.l.), which is surrounded by major mountain ranges (Fig. 1b): the Pyrenees in the northeast (maximum altitude 3404 m a.s.l.), the Cantabrian Mountains in the northwest (maximum altitude 2648 m a.s.l.), the Iberian System in the central-eastern region (maximum altitude 2313 m a.s.l.), the Central System in the centre of the Inner Plateau (dividing it into northern and southern halves, maximum altitude 2592 m a.s.l.), Sierra Morena in the central-southern region (maximum altitude



Figure 1. Location of mainland Spain on the European continent (a) and the main mountain systems and valleys in Peninsular Spain (b).

1323 m a.s.l.) and the Baetic Mountains in the southeast, which reach the highest altitude of all peninsular Spain at 3478 m a.s.l. in Sierra Nevada (Fischer 1902).

Study species

The northern wheatear is an insectivorous, cavity-nesting passerine and is the most widely distributed species of the Muscicapidae family. Its worldwide breeding range extends throughout the Holarctic, mainly the Palearctic (Dunn et al. 2022). The wintering area for the entire global population of the species, including those breeding in the Western Hemisphere, is sub-Saharan Africa, where it occupies a wide belt from Senegal in the west to Kenya in the east (Dunn et al. 2022). In Europe, it breeds from the Mediterranean islands to Iceland and the North Cape (72°N), with the southernmost population of the continent on the Iberian Peninsula (Keller et al. 2020), where the subspecies *libanotica* is found. In our study area, the northern wheatear mainly breeds in the northern half of Spain, especially in the Duero Basin and the surrounding mountain systems. It is also established in a large part of the Pyrenean and pre-Pyrenean mountain ranges (Calleja and Pérez-Granados 2022). In the southern half of Spain, it has a preference for high mountain environments with an altitudinal gradient that increases towards the south, with breeding areas above 1550 m a.s.l. in the southernmost population, in Sierra de las Nieves National Park (Málaga) (Muñoz pers. obs.), and up to 3200 m a.s.l. in Sierra Nevada

National Park (Granada) (Tellería et al. 1999). The species preferentially selects habitats with little woody vegetation cover and with the presence of rocky substrates for nest building (Tellería et al. 1999, González-Oreja 2003).

Species distribution data

The species distributions in mainland Spain were obtained from the II and III Spanish bird atlases (Martí and Del Moral 2003, Molina et al. 2022), based on fieldwork conducted in 1998–2002 and 2014–2018, respectively. Atlas data have commonly been used to model species distributions and, in both cases, we considered the standardised breeding categories normally used in ornithological atlases (Keller et al. 2020) and selected the probable-confirmed breeding categories of the northern wheatear, discarding those cases of possible breeding. We did not consider Portuguese breeding distribution data for the species in our analyses, as the latest Portuguese Breeding Bird Atlas, based on fieldwork conducted in 1999–2005, was published in 2008 (Equipa Atlas 2008) and no information comparable to that existing in Spain is currently available. We identified 2331 breeding presences in 2003 (Fig. 2a) and 844 in 2022 (Fig. 2b). Then, we used these breeding presences to model the distribution of the species in the study area for both time periods.

Northern wheatear breeding distribution data were latticed using UTM 10 × 10 km grid cells as operational geographical units (OGUs), a method used in numerous

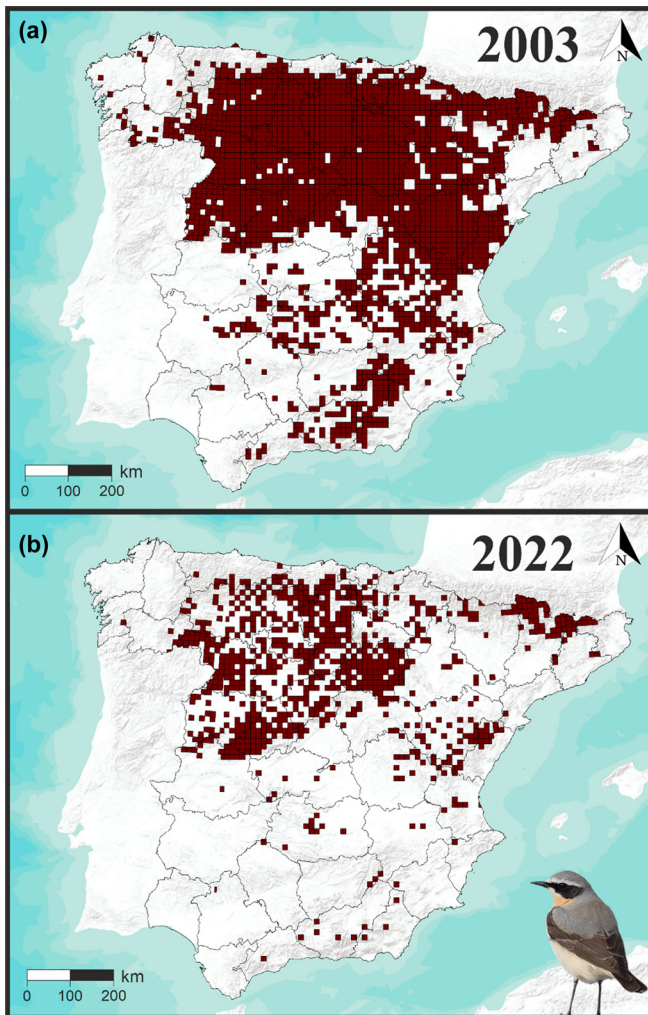


Figure 2. Northern wheatear breeding presences based on UTM 10 × 10 km grid cells of the study area in 2003 (a) and 2022 (b).

environmental modelling studies and, in addition, constitutes the cartographic basis for most species distribution atlases of Spain (Doadrio 2001, Martí and Del Moral 2003, Pleguezuelos et al. 2004, Palomo et al. 2007, Molina et al. 2022). The area of these grid cells allows the detection of macro-environmental processes occurring around sampling points that may affect species distribution patterns (Pearson and Dawson 2003); mainland Spain has a total of 5335 such grid cells.

Predictor variables

We used a set of 22 environmental variables to model the distribution of the species in mainland Spain for both time periods (Table 1). To facilitate the characterisation of the areas occupied by the species, the selected variables were grouped into the following factors: topography ($n=2$), climate ($n=9$), human activity ($n=3$) and lithology ($n=8$). These variables were chosen based on their potential predictive power, assuming their relationship to factors affecting the northern wheatear's physiology and were downloaded in

raster format at a resolution of 1 km². The values of these variables at each OGU were obtained by averaging the values within each 1 km² pixel using the *zonal* function in ArcGIS ver. 10.4.1 (ESRI 2016).

Distribution modelling

Topography, climate, human activity and lithology variables were used as predictors to produce environmental models of the northern wheatear distribution in 2003 and 2022. In order to control the noise effect of multicollinearity, pairwise Spearman correlation coefficients were calculated among all of the environmental variables. For each pair of variables with a correlation > 0.8, only the variable with the highest individual predictive power was retained (Zanolla et al. 2018, García-Carrasco et al. 2021). The false discovery rate (FDR) proposed by Benjamini and Hochberg (1995) was then used to control type I errors, which may result from the increased number of variables considered (Muñoz and Real 2013). Based on the set of pre-selected variables in the previous step, only the ones whose significance in the score test was less than an FDR value of 0.05 were used in the following steps (Benjamini and Yekutieli 2001).

To build an environmental model for each time period, we performed a multivariate forward–backward stepwise logistic regression of the species distribution on the remaining subset of variables that passed through the previous filters. This process started with a model with no variables (the null model), then a variable was added at each step only if the resulting regression was significantly improved compared to the previous step, according to the significance of the Rao's score test. Thus, the environmental variables included in the final model were a parsimonious representation of all the effects imputable to the set of variables analysed in the stepwise procedure. By using a forward–backward stepwise variable selection procedure, before adding a new variable to the model, the possibility of improving its predictive capacity was evaluated by eliminating any variable introduced in a previous step. Variables with broad-scale predictive power were added in the first steps, whereas those that added significant nuance to the previous models were added in subsequent steps. Finally, a significant combination of predictor variables was obtained (*y* or *logit*), whose coefficients were estimated using a machine learning algorithm based on a likelihood ascent gradient. The relative weight of each variable in the model was assessed using the Wald test (Wald 1943).

The logistic regression analysis produced a probability value for each OGU of breeding presence (*P*) based on environmental conditions, which was affected by the prevalence of the species modelled in the dataset. As the main aim of this study was to compare northern wheatear breeding distribution in different time periods, using commensurate methods unaffected by differing prevalence was necessary. To eliminate the effect of prevalence in the study area, *p*-values were transformed into favourability values (*F*) according to the favourability function (Real et al. 2006, Acevedo and Real 2012), using the following equation:

Table 1. Environmental variables used to model the distribution of the northern wheatear in mainland Spain in 2003 and 2022, grouped by factors.

Code	Variable and Unit	Source	
		2003	2022
Topography			
Alti	Altitude (m a.s.l.)		(1)
Slop	Slope (degrees)		(2)
Climate			
T	Mean annual temperature (°C)	(3)	(4)
TJan	Mean temperature in January (°C)	(3)	(4)
TJul	Mean temperature in July (°C)	(3)	(4)
SRad	Mean annual solar radiation (kwh m ⁻² day ⁻¹)	(3)	(4)
DFro	Mean annual number of frost days (minimum temperature ≤ 0°C)	(3)	(4)
DP01	Mean annual number of days with precipitation ≥ 0.1 mm	(3)	(4)
P	Mean annual precipitation (mm)	(3)	(4)
PET	Mean annual potential evapotranspiration (mm)	(3)	(4)
AET	Mean annual actual evapotranspiration (mm)	(= min [PET, P])	
Human activity			
DHi	Distance to the nearest highway (km)	(5)	(6)
U100	Distance to the nearest town with more than 100 000 inhabitants (km)	(5)	(6)
U500	Distance to the nearest town with more than 500 000 inhabitants (km)	(5)	(6)
Lithology			
Clay	Presence of clay		(7)
PClay	Proportion of clay		(7)
Sil	Presence of siliceous rocks		(7)
PSil	Proportion of siliceous rocks		(7)
Calc	Presence of calcareous rocks		(7)
PCalc	Proportion of calcareous rocks		(7)
Grav	Presence of gravel		(7)
PGrav	Proportion of gravel		(7)

Data sources: (1) [Farr and Kobrick \(2000\)](#); (2) calculated from Alti using the *slope* function in ArcGIS ver. 10.4.1 software; (3) [Font \(1983\)](#); (4) [AEMET and IMP \(2011\)](#); (5) [I.G.N. \(1999\)](#), data on the number of inhabitants of urban centres taken from the Instituto Nacional de Estadística (www.ine.es); (6) [DERA \(2013\)](#); (7) [IGME \(2015\)](#).

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

where n_1 and n_0 are the numbers of OGU with northern wheatear breeding presences and absences, respectively, for each time period within the study area.

Favourability values range from 0 (null favourability) to 1 (maximum favourability). A favourability value of 0.5 indicates that northern wheatear breeding is as probable as its prevalence in the study area ([Real et al. 2006](#)). Therefore, favourability represents the degree to which environmental conditions are propitious for breeding ([Acevedo and Real 2012](#), [Muñoz et al. 2015b](#)); a favourability value of 0.5 represents the limit separating favourable from unfavourable areas. However, given the continuous and fuzzy nature of favourability ([Acevedo and Real 2012](#)), this limit for neatly distinguishing favourable from unfavourable areas is unreliable ([Hosmer and Lemeshow 2005](#)). Consequently, we reclassified each OGU into three categories, depending on their favourability values: 'high favourability', $F \geq 0.8$; 'intermediate favourability', $0.8 > F > 0.2$; and 'low favourability', $F \leq 0.2$ ([Muñoz et al. 2005](#), [Chamorro et al. 2021](#)). All

modelling processes were run with the IBM SPSS Statistics 25 software package and maps were created using ArcMap software (ArcGIS ver. 10.4.1; <https://desktop.arcgis.com/es/arcmap/>).

According to [Legendre \(1993\)](#), interactions between factors often result in an overlaid spatial effect due to collinearity. To demonstrate this effect, we grouped the variables included in both models into two main environmental factors (climate and non-climate), then applied a variation partitioning procedure (for more detailed process see [Muñoz et al. 2005](#) and [Chamorro et al. 2019](#)) to specify how much of the variation in favourability explained by each model was attributable to the pure effect of each factor (i.e. not affected by collinearity among factors; [Borcard et al. 1992](#)) and which proportion was accounted for by more than one factor ([Legendre and Legendre 1998](#)). A negative value in the proportion explained by more than one factor suggests that the effect of one factor was obscured by another (i.e. one factor adds favourability, while the other reduces it; [Chamorro et al. 2019](#)).

Modelling assessment

The resulting favourability models were assessed and compared according to their discrimination and classification capacity. The discrimination capacity was evaluated using the

area under the receiver operating characteristic (ROC) curve, known as the AUC (Lobo et al. 2008, Romero et al. 2013). The classification capacity, using the value of $F=0.5$ as the classification threshold, was assessed through the following measures: sensitivity, the conditional probability of OGU's with reported breeding classified as favourable; specificity, the conditional probability of OGU's with no reported breeding classified as unfavourable; correct classification rate (CCR), the conditional probability of correctly classified OGU's; the over-prediction rate (OPR), the proportion of OGU's with no reported breeding in an area with favourability > 0.5 ; and the under-prediction rate (UPR), the proportion of OGU's with reported breeding in an area with favourability < 0.5 . Each of these measures is widely used, with values ranging from 0 to 1 (Fielding and Bell 1997, Barbosa et al. 2013). We also used Cohen's Kappa index (Cohen 1960), whose values range from -1 to $+1$, to measure the degree to which the favourability of OGU's with reported breeding or no reported breeding in the dataset was greater or less than 0.5, respectively.

Comparison of reported breeding OGU's between 2003 and 2022

To compare OGU's between 2003 and 2022, each of them was classified according to the following categories: OGU's with reported breeding of the northern wheatear in both time periods (maintained breeding areas), OGU's with reported breeding in 2003 but not in 2022 (extinct or unsampled breeding areas), OGU's with reported breeding in 2022 but not in 2003 (new breeding areas) and OGU's with no reported breeding in either time period (non-breeding areas). We also calculated the mean altitude of the OGU's with reported breeding in 2003 and 2022.

Results

We produced models for the two time periods of study. The model for 2003 included twelve variables: two related to topography, three to climate, one to human activity and six to lithology (Table 2). Altitude was the first variable added in the stepwise procedure and the best predictor for northern wheatear breeding in 2003, because it had the greatest weight in the model, according to the Wald test. Altitude, distance to the nearest highway, presence of gravel, presence of clay and proportion of gravel had a positive effect on species distribution. Mean annual potential evapotranspiration, proportion of siliceous rocks, mean annual actual evapotranspiration, proportion of clay, mean annual solar radiation, slope and presence of siliceous rocks had a negative effect (Table 2).

The model for 2022 included seven variables: one related to topography, four to climate, one to human activity and one to lithology (Table 3). Mean temperature in January and mean annual potential evapotranspiration were the first variables added to the stepwise procedure and were the best predictors for northern wheatear breeding in 2022 because they

Table 2. Variables added to the 2003 logistic regression model via a forward-backward stepwise selection process, ranked by order of addition. β s, coefficients in the *logit* function; SE, standard error of the coefficients; Wald, Wald's statistics value representing the relative importance of the variable in the model; p, significance of the coefficients according to the Wald test. Variable codes are shown in Table 1.

Variable	β	SE	Wald	p
Alti	0.00419	0.000242	298.356	< 0.001
PET	-0.00544	0.000963	31.911	< 0.001
PSil	-0.942	0.176	28.580	< 0.001
AET	-0.00294	0.000409	51.513	< 0.001
PCLay	-1.113	0.197	32.048	< 0.001
DHi	0.0143	0.00207	48.061	< 0.001
Grav	0.462	0.109	17.878	< 0.001
SRad	-0.0138	0.00167	68.758	< 0.001
Slop	-0.104	0.0202	26.815	< 0.001
Sil	-0.400	0.119	11.365	< 0.001
Clay	0.333	0.108	9.531	0.002
PGrav	0.724	0.259	7.782	0.005
Constant	9.063	0.649	194.839	< 0.001

had the greatest weight in the model, according to the Wald test. Mean temperature in January, mean annual potential evapotranspiration, slope, distance to the nearest highway, presence of siliceous rocks and mean annual number of days with precipitation ≥ 0.1 mm negatively affected species distribution, while mean annual actual evapotranspiration had a positive effect (Table 3).

The environmental model for 2003 showed high favourability values ($F > 0.8$) for the northern wheatear mainly in the northern half of mainland Spain, highlighting areas such as the Pyrenees, the Duero Basin and the surrounding mountain systems (Cantabrian Mountains, Iberian and Central Systems; Fig. 3a). In the southern half of peninsular Spain, this model showed high favourability values in Sierra Nevada and Sierra de Cazorla. However, the model for 2022 showed a strong reduction in favourability throughout the whole study area (mean favourability in 2003 = 0.477 versus mean favourability in 2022 = 0.368), especially in the southern half of mainland Spain. In the southernmost population in Europe, located in Sierra de las Nieves National Park, conditions are currently less favourable than 20 years ago, with favourability values < 0.5 (Fig. 3b).

Table 3. Variables added to the 2022 logistic regression model via a forward-backward stepwise selection process, ranked by order of addition. β s, coefficients in the *logit* function; SE, standard error of coefficients; Wald, Wald's statistics value representing the relative importance of the variable in the model; p, significance of the coefficients according to the Wald test. Variable codes are shown in Table 1.

Variable	β	SE	Wald	p
TJan	-0.404	0.0370	119.429	< 0.001
PET	-0.0101	0.00117	73.510	< 0.001
Slop	-0.0644	0.0184	12.234	< 0.001
DHi	-0.0000148	0.00000354	17.529	< 0.001
Sil	-0.318	0.0995	10.219	0.0014
AET	0.00157	0.000494	10.050	0.002
DP01	-0.00728	0.00251	8.371	0.004
Constant	7.862	0.909	74.762	< 0.001

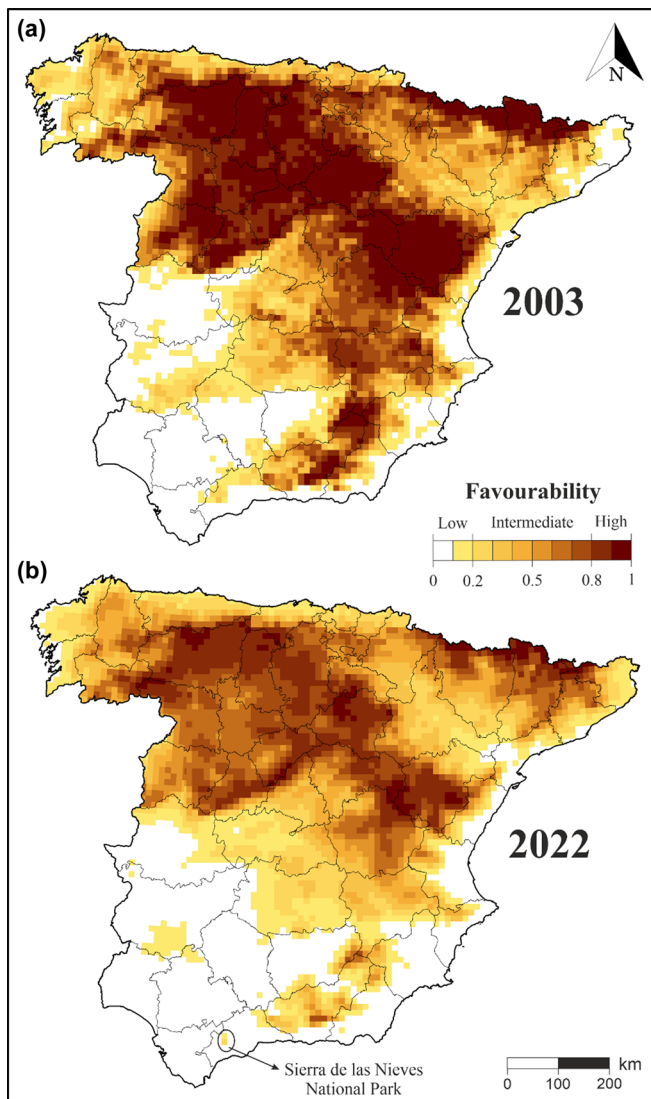


Figure 3. Favourability values for the northern wheatear in each UTM 10×10 km grid cell of mainland Spain, according to models for 2003 (a) and 2022 (b).

Both models had high discrimination ($AUC > 0.85$) and classification capacities (sensitivity, specificity and $CCR > 0.73$ and a positive Cohen's kappa value; Table 4). The 2003 favourability model, however, showed higher AUC, specificity, CCR and Cohen's kappa values compared with the 2022 favourability model, whereas the 2022 model showed higher sensitivity. Although the UPR was low in both models ($UPR < 0.17$), this was higher in 2003, whereas the OPR was substantial for the 2022 model with $> 60\%$ of the predicted favourable breeding OGUs unoccupied.

The proportion of variation explained by climate in the environmental model for 2003 was 0.144 and the proportion of variation explained by non-climatic variables was 0.203 (Fig. 4). The proportion of the shared effect between both climate and non-climate factors was 0.653. However, the proportion of variation explained by climate in the environmental

Table 4. Comparative assessment of the discrimination and classification capacities of the favourability models. Assessment indices: area under the curve, sensitivity, specificity, correct classification rate, over-prediction rate, under-prediction rate and Cohen's Kappa index.

Measure	Favourability model	
	2003	2022
Area under the curve (AUC)	0.896	0.858
Sensitivity	0.809	0.847
Specificity	0.805	0.738
Correct classification rate (CCR)	0.806	0.756
Over-prediction rate (OPR)	0.227	0.618
Under-prediction rate (UPR)	0.164	0.038
Cohen's Kappa index	0.611	0.392

model for 2022 was 0.914, showing that climate has the most significant influence on the breeding distribution of northern wheatear in mainland Spain at present. The proportion of variation explained by non-climatic variables was 0.028 and the proportion of the shared effect between both climate and non-climate factors was 0.058 (Fig. 4).

The number of OGUs with reported breeding for the northern wheatear declined sharply between 2003 and 2022 across the study area, with 1561 UTM grid cells (67%) where the species has ceased to be reported (Fig. 5). The maintained breeding areas of the species remained mainly in the northern half of mainland Spain, with a total of 770 UTM grid cells (33%). New breeding areas for the species were also scattered throughout the study area, although these only totalled 74 UTM grid cells (Fig. 5). The mean altitude of the OGUs with

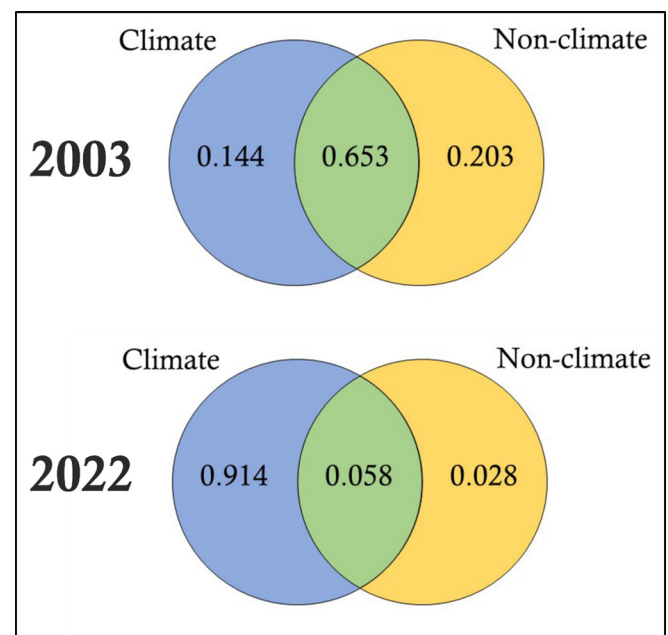


Figure 4. Variation partitioning of the 2003 and 2022 environmental models using the factor climate versus the factor combined non-climatic variables. Values within the circles represent the proportion of variation explained by the indicated factors and by their interactions.

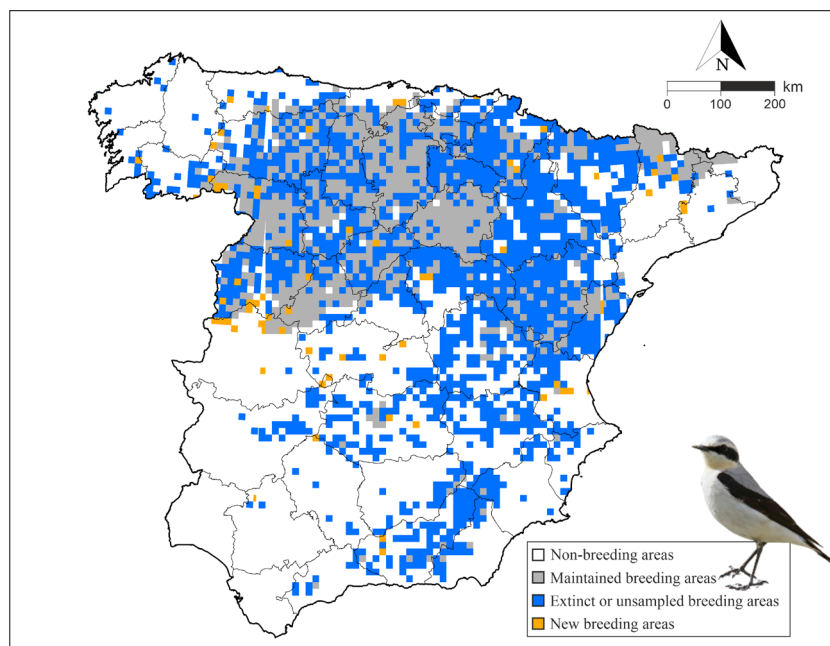


Figure 5. Comparison of reported breeding operational geographical units (OGUs) between 2003 and 2022 for the northern wheatear in mainland Spain. UTM 10×10 km grid cells were classified according to the following categories: non-breeding areas, OGUs with no reported breeding in either time period; maintained breeding areas, OGUs with reported breeding in both time periods; OGUs with reported breeding in 2003 but not in 2022; and new breeding areas, OGUs with reported breeding in 2022 but not in 2003.

reported breeding in 2003 was 913.8 m a.s.l., while in 2022 this was 1021.6 m a.s.l.

Discussion

Alpine bird species are predicted to undergo serious climatically induced range contractions in the future due to climate change (La Sorte and Jetz 2010, Chamberlain et al. 2013, Barras et al. 2021), and the northern wheatear appears to be following this pattern in its southernmost distribution limit in Europe. The results of the present study show a clear reduction in the breeding distribution of the species in many areas of Peninsular Spain between 2003 and 2022, both in the number of occupied OGUs and in terms of favourability. The high over-prediction rate in the 2022 model could be another finding of this reduction, as more than 60% of the favourable areas for the species are already unoccupied. This result may indicate that there are no longer enough individuals to occupy even the highly favourable areas. Climate seems to be the main factor conditioning the current distribution of the northern wheatear as it explains $> 90\%$ of the variation in the model obtained for 2022, whereas in 2003 $> 65\%$ of the distribution was explained by the shared effect of climate together with topography, human activity and lithological factors. The new spatial structure of the species' distribution in 2022 (more reduced and associated with mountain environments) and the use of a more updated set of climatic variables compared to that used in 2003 are probably the reasons

why the importance of climatic variables varies between models, indicating that climate has a greater weight in the current model (2022) than in the model at the beginning of the century (2003). Furthermore, the two variables with the greatest weight in the 2022 model were related to climate: mean temperature in January and mean annual potential evapotranspiration. Lower mean temperature in January as well as lower mean annual potential evapotranspiration have a positive effect on the species' breeding distribution, indicating that wet areas with colder winters favour the presence of the species during the breeding period. Some studies have demonstrated that spring phenological events are well correlated with temperature of the previous weeks/months (Walther et al. 2002, Defila and Clot 2005) and, although wheatears are found in Africa during the winter, colder winters may have an impact on the environmental conditions for the species in spring (Asse et al. 2018), making those areas more favourable. Warmer winters delay budburst and flowering of trees (Asse et al. 2018), as cold temperatures are required to break bud dormancy (Chuine et al. 2010, Yu et al. 2010), which may reduce the availability of insects for the species during the breeding period (Fletcher et al. 2013).

The reduction in the breeding distribution of the species is particularly noticeable in the southern half of Spain, where the effects of climate warming are more pronounced (IPCC 2022). Precisely in this area, research points to a northward expansion of African species which are beginning to colonise Europe (López-Ramírez et al. 2023), such as the little swift *Apus affinis* (Ramírez et al. 2002, Prieta 2022), the

Atlas long-legged buzzard *Buteo rufinus cirtensis* (Elorriaga and Muñoz 2010), the common bulbul *Pycnonotus barbatus* (Navarrete 2022), the cream-colored courser *Cursorius cursor* (Cabrera 2022) and, more recently, the house bunting *Emberiza sahari* (López-Ramírez et al. 2023, Muñoz pers. obs.). Simultaneously, some typically Mediterranean species are moving into higher elevations, as is the case of the Thekla's lark *Galerida theklae*, the European stonechat *Saxicola rubicola* or the spectacled warbler *Curruca conspicillata* (Zamora and Barea-Azcón 2015). In addition, some species are moving northwards in the European context to become established in central Europe, such as the European bee-eater *Merops apiaster* (Stiels et al. 2021) and the short-toed snake-eagle *Circetus gallicus* (Knaus et al. 2018). Overall, species are shifting their distributions northwards, while mountain birds are moving to higher elevations (Freeman et al. 2018).

In addition to the effects of global warming, there may well be other threats to the northern wheatear in Peninsular Spain, such as land abandonment or anthropogenic habitat alterations, which are threatening a wide range of species, especially those linked to mountain pastures and grasslands (Chamberlain et al. 2016, Brambilla et al. 2020). However, these threats tend to influence species distributions at a more regional or local scale and the reduction in the breeding distribution of the species has occurred across the whole of Peninsular Spain in a generalised way so, at the scale we are considering, it seems more plausible that the factor causing this reduction must be one that acts on a broad scale, such as climate (Márquez et al. 2011, Chamorro et al. 2017, 2020, 2021, Sun et al. 2020, López-Ramírez et al. 2023). We also showed that the northern wheatear in Spain currently occupies areas approximately 100 m higher in altitude compared to 2003. Such climate-induced altitudinal range shifts have been observed in mountain species globally, reaching their climatic optimum and escaping the negative population consequences of a warming climate (Lenoir et al. 2008, Chen et al. 2009, Popy et al. 2010, Maggini et al. 2011, Reif and Flousek 2012, Auer and King 2014, Grytnes et al. 2014, Freeman et al. 2018). Such upward shifts will result in range contractions or local extinctions, especially in mountain ranges where northern wheatears already occupy the highest mountaintop areas. This phenomenon is already taking place in the mountain ranges of southern Spain, particularly in Sierra de las Nieves National Park, an area with a maximum altitude of 1919 m a.s.l., where northern wheatears are already breeding at 1550–1800 m a.s.l. In this area, our current model only detected two grid cells with intermediate-low favourability for the northern wheatear and the species is only present in one of them, where they are already breeding in the mountaintops. For this reason, the northern wheatear may soon run out of space and we predict that their populations could suffer local extinctions in its southernmost distribution limit if climate continues to change in the same way; the Sierra de las Nieves population is likely the most vulnerable in our study area. The northern wheatear in southern Spain could follow in the footsteps of the water pipit *Anthus*

spinoletta in northern Spain (Melendez and Laiolo 2014), an alpine grassland specialist which is at the highest risk of extinction due to climatic warming in alpine environments (Chamberlain et al. 2013). However, these local extinctions may take time to occur because other southern mountain systems, such as Sierra Nevada (with a maximum altitude of 3478 m a.s.l.), may be acting as a source of individuals for these sink populations (Bonnot et al. 2013, Weston et al. 2016, Podolsky 2018).

A warmer climate may have adverse impacts on northern wheatear populations, directly or indirectly. Examples could include a reduction in prey abundance for breeding individuals of the species, as observed in the Scottish Highlands with the red grouse *Lagopus lagopus scotica* (Fletcher et al. 2013); changes in species interactions, such as an increased predation risk on their nests due to the earlier termination of hibernation in garden dormice *Eliomys quercinus*, as was the case in eastern Czechia with the edible dormouse *Glis glis* (Adamík and Král 2008); or more intense competition from lower-altitude species that occupy new higher-altitude areas (Jankowski et al. 2010). Other factors might include the direct detrimental effects of more frequent weather anomalies caused by higher temperatures, such as strong storms (Robinson et al. 2007), physiological stress (Barbosa et al. 2007) or complex interactions between climate and local habitat conditions (Mantyka-Pringle et al. 2012). For example, particularly high temperatures at the start of spring, a phenomenon in Spain since the end of the 20th century (Morán-Tejeda et al. 2013), can cause rapid snow melting followed by drought in late spring and early summer, which can constrain food supplies while rearing chicks. Furthermore, the nest survival probability of high mountain species decreases in years with an early onset of spring conditions, as observed in the western Italian Alps with the northern wheatear (Sander et al. 2023).

Our study provides evidence for the reduction in the breeding distribution area of the northern wheatear in mainland Spain and the occupation of higher-altitude areas, which is in line with the ongoing effects of climate change in mountain birds. This species, with one of the largest distributions of all songbirds in the world, can be used as a model for effects on other mountain birds in southern mountain systems. Recent modelling work predicts more intensive warming in mountains in the future, with potentially detrimental impacts on species adapted to living on mountaintops (La Sorte and Jetz 2010, Chamberlain et al. 2013, Barras et al. 2021); the negative population trends already observed in recent decades for the northern wheatear, and other species, are alarming. For this reason, it is necessary to implement direct sampling and monitoring programmes for northern wheatear populations, with priority for mountain systems wherein mountain birds already occupy higher elevations. This will increase our knowledge of the causal mechanisms and impacts of climate warming on these populations, which will be crucial for the formulation of future conservation strategies for mountain birds.

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Author contributions

Sandro López-Ramírez: Data curation (equal); Formal analysis (equal); Writing – original draft (equal); Writing – review and editing (equal). **Raimundo Real:** Funding acquisition (equal); Project administration (equal); Validation (equal). **Antonio-Román Muñoz:** Conceptualization (equal); Funding acquisition (equal); Project administration (equal); Supervision (equal); Validation (equal); Writing – original draft (equal); Writing – review and editing (equal).

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Data availability statement

Data are available from figshare: <https://doi.org/10.6084/m9.figshare.24099831.v2> (López-Ramírez 2023).

References

- Acevedo, P. and Real, R. 2012. Favourability: concept, distinctive characteristics and potential usefulness. – *Naturwissenschaften* 99: 515–522.
- Adamik, P. and Král, M. 2008. Climate and resource-driven long-term changes in dormice populations negatively affect hole-nesting songbirds. – *J. Zool.* 275: 209–215.
- AEMET and IMP 2011. Atlas climático ibérico: temperatura del aire y precipitación (1971–2000). – Departamento de Producción de la Agencia Estatal de Meteorología de España – Departamento de Meteorología e Clima, Instituto de Meteorología de Portugal.
- Asse, D., Chuine, I., Vitasse, Y., Yoccoz, N. G., Delpierre, N., Badeau, V., Delestrade, A. and Randin, C. F. 2018. Warmer winters reduce the advance of tree spring phenology induced by warmer springs in the Alps. – *Agric. Forest Meteorol.* 252: 220–230.
- Auer, S. K. and King, D. I. 2014. Ecological and life-history traits explain recent boundary shifts in elevation and latitude of western North American songbirds. – *Global Ecol. Biogeogr.* 23: 867–875.
- Austin, M. P. 2002. Spatial prediction of species distribution: an interface between ecological theory and statistical modelling. – *Ecol. Modell.* 157: 101–118.
- Barbosa, A., Merino, S., Benzal, J., Martínez, J. and García-Fraile, S. 2007. Population variability in heat shock proteins among three Antarctic penguin species. – *Polar Biol.* 30: 1239–1244.
- Barbosa, A. M., Real, R., Muñoz, A.-R. and Brown, J. A. 2013. New measures for assessing model equilibrium and prediction mismatch in species distribution models. – *Divers. Distrib.* 19: 1333–1338.
- Barras, A. G., Braunisch, V. and Arlettaz, R. 2021. Predictive models of distribution and abundance of a threatened mountain species show that impacts of climate change overrule those of land use change. – *Divers. Distrib.* 27: 989–1004.
- Bastianelli, G., Tavecchia, G., Meléndez, L., Seoane, J., Obeso, J. R. and Laiolo, P. 2017. Surviving at high elevations: an inter- and intra-specific analysis in a mountain bird community. – *Oecologia* 184: 293–303.
- Benjamini, Y. and Hochberg, Y. 1995. Controlling the false discovery rate: a practical and powerful approach to multiple testing. – *J. R. Stat. Soc. Ser. B* 57: 289–300.
- Benjamini, Y. and Yekutieli, D. 2001. The control of the false discovery rate in multiple testing under dependency. – *Ann. Statist.* 29: 1165–1188.
- Bonnot, T. W., Thompson, F. R., Millspaugh, J. J. and Jones-Farrand, D. T. 2013. Landscape-based population viability models demonstrate importance of strategic conservation planning for birds. – *Biol. Conserv.* 165: 104–114.
- Borcard, D., Legendre, P. and Drapeau, P. 1992. Partialling out the spatial component of ecological variation. – *Ecology* 73: 1045–1055.
- Brambilla, M., Gustin, M., Cento, M., Ilahiane, L. and Celada, C. 2020. Habitat, climate, topography and management differently affect occurrence in declining avian species: implications for conservation in changing environments. – *Sci. Total Environ.* 742: 140663.
- Brown, J. H., Mehlman, D. W. and Stevens, G. C. 1995. Spatial variation in abundance. – *Ecology* 76: 2028–2043.
- Cabrera, M. 2022. Corredor sahariano, *Cursorius cursor*. – In: Molina, B., Nebreda, A., Muñoz, A.-R., Seoane, J., Real, R., Bustamante, J. and del Moral, J. C. (eds), III Atlas de las aves en época de reproducción en España. SEO/BirdLife.
- Calleja, J. A. and Pérez-Granados, C. 2022. Collalba gris, *Oenanthe oenanthe*. – In: Molina, B., Nebreda, A., Muñoz, A.-R., Seoane, J., Real, R., Bustamante, J. and del Moral, J. C. (eds), III Atlas de las aves en época de reproducción en España. SEO/BirdLife.
- Capel, J. J. 1981. Los climas de España. – Oikos-Tau SA Ediciones.
- Castro, A., Muñoz, A.-R. and Real, R. 2008. Modelling the spatial distribution of the Tengmalm's owl *Aegolius funereus* in its Southwestern Palaearctic limit (NE Spain). – *Ardeola* 55: 71–85.
- Chamberlain, D., Arlettaz, R., Caprio, E., Maggini, R., Pedrini, P., Rolando, A. and Zbinden, N. 2012. The altitudinal frontier in avian climate impact research. – *Ibis* 154: 205–209.
- Chamberlain, D. E., Negro, M., Caprio, E. and Rolando, A. 2013. Assessing the sensitivity of alpine birds to potential future changes in habitat and climate to inform management strategies. – *Biol. Conserv.* 167: 127–135.
- Chamberlain, D. E., Pedrini, P., Brambilla, M., Rolando, A. and Girardello, M. 2016. Identifying key conservation threats to Alpine birds through expert knowledge. – *PeerJ* 4: e1723.
- Chamorro, D., Olivero, J., Real, R. and Muñoz, A.-R. 2017. Environmental factors determining the establishment of the African long-legged buzzard *Buteo rufinus cirtensis* in western Europe. – *Ibis* 159: 331–342.
- Chamorro, D., Nieto, I., Real, R. and Muñoz, A.-R. 2019. Wintering areas on the move in the face of warmer winters. – *Ornis Fenn.* 96: 41–54.
- Chamorro, D., Real, R. and Muñoz, A.-R. 2020. Fuzzy sets allow gauging the extent and rate of species range shift due to climate change. – *Sci. Rep.* 10: 16272.

- Chamorro, D., Martínez-Freiría, F., Real, R. and Muñoz, A.-R. 2021. Understanding parapatry: how do environment and competitive interactions shape Iberian vipers' distributions? – *J. Biogeogr.* 48: 1322–1335.
- Chen, I. C., Shiu, H. J., Benedick, S., Holloway, J. D., Chey, V. K., Barlow, H. S., Hill, J. K. and Thomas, C. D. 2009. Elevation increases in moth assemblages over 42 years on a tropical mountain. – *Proc. Natl Acad. Sci. USA* 106: 1479–1483.
- Chuine, I., Morin, X. and Bugmann, H. 2010. Warming, photo-periods, and tree phenology. – *Science* 329: 277–278.
- Cohen, J. 1960. A coefficient of agreement for nominal scales. – *Educ. Psychol. Meas.* 20: 37–46.
- Defila, C. and Clot, B. 2005. Phytophenological trends in the Swiss Alps, 1951–2002. – *Meteorol. Z.* 14: 191–196.
- DERA 2013. Datos espaciales de referencia de Andalucía. – Instituto de Estadística y Cartografía de Andalucía, Consejería de Economía y Conocimiento.
- Doadrio, I. 2001. Atlas y Libro Rojo de los Peces Continentales de España. – Ministerio de Medio Ambiente-CSIC.
- Dunn, E. H., Hussell, D. J. T., Kren, J. and Zoerb, A. C. 2022. Northern wheatear (*Oenanthe oenanthe*). – In: Rodewald, P. G. and Keeney, B. K. (eds), *Birds of the world*. Cornell Laboratory of Ornithology. <https://doi.org/10.2173/bow.norwhe.02.1>
- Eldredge, N. 1995. Reinventing Darwin: great evolutionary debate. – Weidenfeld & Nicolson.
- Elith, J., Leathwick, J. R. and Hastie, T. 2008. A working guide to boosted regression trees. – *J. Anim. Ecol.* 77: 802–813.
- Elorriaga, J. and Muñoz, A.-R. 2010. First breeding record of North African long-legged buzzard *Buteo rufinus cirtensis* in continental Europe. – *Br. Birds* 103: 399–401.
- Equipa Atlas 2008. Atlas das Aves Nidificantes em Portugal (1999–2005). – Instituto da Conservação da Natureza e da Biodiversidade, Sociedade Portuguesa Para o Estudo das Aves, Parque Natural da Madeira e Secretaria Regional do Ambiente e do Mar.
- ESRI 2016. ArcGIS [software GIS], ver. 10.4.1. – <https://www.esri.com/en-us/arcgis/products/arcgis-desktop/resources>
- Farr, T. G. and Kobrick, M. 2000. Shuttle radar topography mission produces a wealth of data. – *Eos Trans. Am. Geophys. Union* 81: 583.
- Fielding, A. H. and Bell, J. F. 1997. A review of methods for the assessment of prediction errors in conservation presence/absence models. – *Environ. Conserv.* 24: 38–49.
- Fischer, T. 1902. The Iberian Peninsula. – In: Mill, H. R. (ed.), *The international geography*. D. Appleton and Company, pp. 368–385.
- Fletcher, K., Howarth, D., Kirby, A., Dunn, R. and Smith, A. 2013. Effect of climate change on breeding phenology, clutch size and chick survival of an upland bird. – *Ibis* 155: 456–463.
- Flousek, J., Telenský, T., Hanzelka, J. and Reif, J. 2015. Population trends of central European montane birds provide evidence for adverse impacts of climate change on high-altitude species. – *PLoS One* 10: e0139465.
- Font, I. 1983. Atlas climático de España. – Instituto Nacional de Meteorología.
- Font, I. 2000. Climatología de España y Portugal. – Universidad de Salamanca.
- Freeman, B. G., Scholer, M. N., Ruiz-Gutierrez, V. and Fitzpatrick, J. W. 2018. Climate change causes upslope shifts and mountaintop extirpations in a tropical bird community. – *Proc. Natl Acad. Sci. USA* 115: 11982–11987.
- Gahegan, M. 2003. Is inductive machine learning just another wild goose (or might it lay the golden egg)? – *Int. J. Geogr. Inf. Sci.* 17: 69–92.
- García-Carrasco, J. M., Muñoz, A.-R., Olivero, J., Segura, M. and Real, R. 2021. Predicting the spatio-temporal spread of West Nile virus in Europe. – *PLoS Negl. Trop. Dis.* 15: e0009022.
- Gobiet, A., Kotlarski, S., Beniston, M., Heinrich, G., Rajczak, J. and Stoffel, M. 2014. 21st century climate change in the European Alps—a review. – *Sci. Total Environ.* 493: 1138–1151.
- González-Oreja, J. A. 2003. Aplicación de análisis multivariantes al estudio de las relaciones entre las aves y sus hábitats: un ejemplo con passeriformes montanos no forestales. – *Ardeola* 50: 47–58.
- Grytnes, J.-A., Kapfer, J., Jurasinski, G., Birks, H. H., Henriksen, H., Klanderud, K., Odland, A., Ohlson, M., Wipf, S. and Birks, H. J. B. 2014. Identifying the driving factors behind observed elevational range shifts on European mountains. – *Global Ecol. Biogeogr.* 23: 876–884.
- Guisan, A. and Zimmermann, N. E. 2000. Predictive habitat distribution models in ecology. – *Ecol. Modell.* 135: 147–186.
- Guisan, A. and Thuiller, W. 2005. Predicting species distribution: offering more than simple habitat models. – *Ecol. Lett.* 8: 993–1009.
- Hallman, T. A., Guélat, J., Antoniazza, S., Kéry, M. and Sattler, T. 2022. Rapid elevational shifts of Switzerland's avifauna and associated species traits. – *Ecosphere* 13: e4194.
- Harris, J. B. C., Dwi Putra, D., Gregory, S. D., Brook, B. W., Prawiradilaga, D. M., Sodhi, N. S., Wei, D. and Fordham, D. A. 2014. Rapid deforestation threatens mid-elevational endemic birds but climate change is most important at higher elevations. – *Divers. Distrib.* 20: 773–785.
- Harrison, S. 2020. Plant community diversity will decline more than increase under climatic warming. – *Philos. Trans. R. Soc. B* 375: 20190106.
- Hosmer, D. W. and Lemeshow, S. 2005. Assessing the fit of the model. – In: Shewhart, W. A. and Wilks, S. S. (eds.), *Applied logistic regression*. 2nd ed. John Wiley and Sons, pp. 143–202.
- I.G.N. 1999. Mapa de carreteras. Península Ibérica, baleares y Canarias. – Instituto Geográfico Nacional/Ministerio de Fomento.
- IGME 2015. Mapa Geológico de la Península Ibérica, Baleares y Canarias a Escala 1/1.000.000. – Instituto Geológico y Minero de España (IGME), Laboratorio Nacional Portugués de Energía y Geología (LNEG)/Ministerio de Ciencia, Innovación y Universidades.
- IPCC 2022. Climate change 2022: impacts, adaptation and vulnerability. – Contribution of Working Group II to the Sixth Assessment Report of the Intergovernmental Panel on Climate Change.
- Jankowski, J. E., Robinson, S. K. and Levey, D. J. 2010. Squeezed at the top: interspecific aggression may constrain elevational ranges in tropical birds. – *Ecology* 91: 1877–1884.
- Jetz, W., Wilcove, D. S. and Dobson, A. P. 2007. Projected impacts of climate and land-use change on the global diversity of birds. – *PLoS Biol.* 5: e157.
- Keller, V., Herrando, S., Voříšek, P., Franch, M., Kipson, M., Milanesi, P., Martí, D., Anton, M., Klvaňová, A., Kalyakin, M. V., Bauer, H.-G. and Poppen, R. P. B. 2020. European breeding bird Atlas 2: distribution, abundance and change. – European Bird Census Council & Lynx Edicions.
- Knaus, P., Antoniazza, S., Wechsler, S., Guélat, J., Kéry, M., Strelbel, N. and Sattler, T. 2018. Swiss breeding bird Atlas 2013–2016. Distribution and population trends of birds in Switzerland and Liechtenstein. – Swiss Ornithological Institute.
- Körner, C. 2007. The use of “altitude” in ecological research. – *Trends Ecol. Evol.* 22: 569–574.
- La Sorte, F. A. and Jetz, W. 2010. Projected range contractions of montane biodiversity under global warming. – *Proc. R. Soc. B* 277: 3401–3410.

- Legendre, P. 1993. Spatial autocorrelation: trouble or new paradigm? – *Ecology* 74: 1659–1673.
- Legendre, P. and Legendre, L. 1998. Numerical ecology. – Elsevier.
- Lenoir, J., Gégout, J. C., Marquet, P. A., de Ruffray, P. and Brisse, H. 2008. A significant upward shift in plant species optimum elevation during the 20th century. – *Science* 320: 1768–1771.
- Lobo, J. M., Jiménez-Valverde, A. and Real, R. 2008. AUC: a misleading measure of the performance of predictive distribution models. – *Global Ecol. Biogeogr.* 17: 145–151.
- Lomolino, M. V. and Channell, R. 1995. Splendid isolation: patterns of geographic range collapse in endangered mammals. – *J. Mammal.* 76: 335–347.
- López-Ramírez, S. 2023. Data from: The northern wheatear is reducing its distribution in its southernmost European range and moving to higher altitudes. – Figshare Repository, <https://doi.org/10.6084/m9.figshare.24099831.v2>
- López-Ramírez, S., Chamorro, D., Real, R. and Muñoz, A.-R. 2023. Southern Europe is becoming climatically favourable for African birds: anticipating the establishment of a new species. – *Front. Zool.* 20: 18.
- Maggini, R., Lehmann, A., Kéry, M., Schmid, H., Beniston, M., Jenni, L. and Zbinden, N. 2011. Are Swiss birds tracking climate change?. Detecting elevational shifts using response curve shapes. – *Ecol. Modell.* 222: 21–32.
- Mantyka-Pringle, C. S., Martin, T. G. and Rhodes, J. R. 2012. Interactions between climate and habitat loss effects on biodiversity: a systematic review and meta-analysis. – *Global Change Biol.* 18: 1239–1252.
- Márquez, A. L., Real, R., Olivero, J. and Estrada, A. 2011. Combining climate with other influential factors for modelling the impact of climate change on species distribution. – *Clim. Change* 108: 135–157.
- Martí, R. and Del Moral, J. C. (eds). 2003. Atlas de las Aves reproductoras de España. – Dirección General de Conservación de la Naturaleza- Sociedad Española de Ornitología.
- Melendez, L. and Laiolo, P. 2014. The role of climate in constraining the elevational range of the water pipit *Anthus spinoletta* in an alpine environment. – *Ibis* 156: 276–287.
- Molina, B., Nebreda, A., Muñoz, A.-R., Seoane, J., Real, R., Bustamante, J. and Del Moral, J. C. (eds). 2022. III. Atlas de aves en época de reproducción en España. – SEO/BirdLife.
- Morán-Tejada, E., Herrera, S., López-Moreno, J. I., Revuelto, J., Lehmann, A. and Beniston, M. 2013. Evolution and frequency (1970–2007) of combined temperature-precipitation modes in the Spanish mountains and sensitivity of snow cover. – *Reg. Environ. Change* 13: 873–885.
- Müller, P. 1979. El área de distribución y su dinámica. – Introducción a la Zoogeografía. Editorial Blume, pp. 23–52.
- Muñoz, A.-R. and Real, R. 2006. Assessing the potential range expansion of the exotic monk parakeet in Spain. – *Divers. Distrib.* 12: 656–665.
- Muñoz, A.-R. and Real, R. 2013. Distribution of Bonelli's eagle *Aquila fasciata* in southern Spain: scale may matter. – *Acta Ornithol.* 48: 93–101.
- Muñoz, A.-R., Real, R., Barbosa, A. M. and Vargas, J. M. 2005. Modelling the distribution of Bonelli's eagle in Spain: implications for conservation planning. – *Divers. Distrib.* 11: 477–486.
- Muñoz, A.-R., Márquez, A. L. and Real, R. 2013. Updating known distribution models for forecasting climate change impact on endangered species. – *PLoS One* 8: e65462.
- Muñoz, A.-R., Márquez, A. L. and Real, R. 2015a. An approach to consider behavioral plasticity as a source of uncertainty when forecasting species' response to climate change. – *Ecol. Evol.* 5: 2359–2373.
- Muñoz, A.-R., Jiménez-Valverde, A., Márquez, A. L., Moleón, M. and Real, R. 2015b. Environmental favourability as a cost-efficient tool to estimate carrying capacity. – *Divers. Distrib.* 21: 1388–1400.
- Navarrete, J. 2022. Bulbul naranjero, *Pycnonotus barbatus*. – In: Molina, B., Nebreda, A., Muñoz, A.-R., Seoane, J., Real, R., Bustamante, J. and del Moral, J. C. (eds), III Atlas de las aves en época de reproducción en España. SEO/BirdLife.
- Palomo, L. J., Gisbert, J. and Blanco, J. C. (eds). 2007. Atlas y Libro Rojo de los Mamíferos Terrestres de España. – Dirección General para la Biodiversidad-SECEM-SECEMU.
- Pautasso, M. 2012. Observed impacts of climate change on terrestrial birds in Europe: an overview. – *Ital. J. Zool.* 79: 296–314.
- Pearson, R. G. and Dawson, T. P. 2003. Predicting the impacts of climate change on the distribution of species: are bioclimate envelope models useful? – *Global Ecol. Biogeogr.* 12: 361–371.
- Pleguezuelos, J. M., Márquez, R. and Lizana, M. (eds). 2004. Atlas y Libro Rojo de los Anfibios y Reptiles de España. – Dirección General de Conservación de la Naturaleza-Asociación Herpetológica Española (3a impresión).
- Podolsky, A. L. 2018. Applying songbird population dynamics models to conservation biology needs. – *Theor. Appl. Ecol.* 2018: 99–107.
- Popy, S., Bordignon, L. and Prodon, R. 2010. A weak upward elevational shift in the distributions of breeding birds in the Italian Alps. – *J. Biogeogr.* 37: 57–67.
- Prieta, J. 2022. Vencejo moro, *Apus affinis*. – In: Molina, B., Nebreda, A., Muñoz, A.-R., Seoane, J., Real, R., Bustamante, J., del Moral, J. C. (eds), III Atlas de las aves en época de reproducción en España. SEO/BirdLife.
- Pulido-Pastor, A., Márquez, A. L., Guerrero, J. C., García-Barros, E. and Real, R. 2021. Metapopulation patterns of Iberian butterflies revealed by fuzzy logic. – *Insects* 12: 392.
- Ramírez, J., Simón, M., Solís, S., Pérez, C. and García, E. 2002. Vencejo moro *Apus affinis* Observaciones de Aves Raras en España. – *Ardeola* 49: 161.
- Real, R., Barbosa, A. M. and Vargas, J. M. 2006. Obtaining environmental favourability functions from logistic regression. – *Environ. Ecol. Stat.* 13: 237–245.
- Real, R., Romero, D., Olivero, J., Estrada, A. and Márquez, A. L. 2013. Estimating how inflated or obscured effects of climate affect forecasted species distribution. – *PLoS One* 8: e53646.
- Reif, J. and Flousek, J. 2012. The role of species' ecological traits in climatically driven altitudinal range shifts of central European birds. – *Oikos* 121: 1053–1060.
- Robinson, R. A., Baillie, S. R. and Crick, H. Q. P. 2007. Weather-dependent survival: implications of climate change for passerine population processes. – *Ibis* 149: 357–364.
- Romero, D., Olivero, J. and Real, R. 2013. Comparative assessment of different methods for using land-cover variables for distribution modelling of *Salamandra salamandra longirostris*. – *Environ. Conserv.* 40: 48–59.
- Sander, M. M., Jähnig, S., Lisovski, S., Mermillon, C., Alba, R., Rosselli, D. and Chamberlain, D. 2023. High nest failure but better nestling quality for early breeders in an alpine population of northern wheatear (*Oenanthe oenanthe*). – *Ibis* 165: 125–141.
- Scridel, D., Brambilla, M., Martin, K., Lehtikoinen, A., Lemma, A., Matteo, A., Jähnig, S., Caprio, E., Bogliani, G., Pedrini, P., Rolando, A., Arlettaz, R. and Chamberlain, D. 2018. A review and meta-analysis of the effects of climate change on Holarctic mountain and upland bird populations. – *Ibis* 160: 489–515.

- Sekercioglu, C. H., Schneider, S. H., Fay, J. P. and Loarie, S. R. 2008. Climate change, elevational range shifts, and bird extinctions. – *Conserv. Biol.* 22: 140–150.
- Sillero, N., Arenas-Castro, S., Enriquez-Urzelai, U., Vale, C. G., Sousa-Guedes, D., Martínez-Freiría, F., Real, R. and Barbosa, A. M. 2021. Want to model a species niche? A step-by-step guideline on correlative ecological niche modelling. – *Ecol. Modell.* 456: 109671.
- Stiels, D., Bastian, H. V., Bastian, A., Schidelko, K. and Engler, J. O. 2021. An iconic messenger of climate change? Predicting the range dynamics of the European bee-eater (*Merops apiaster*). – *J. Ornithol.* 162: 631–644.
- Sun, J., Qiu, H., Guo, J., Xu, X., Wu, D., Zhong, L., Jiang, B., Jiao, J., Yuan, W., Huang, Y., Shen, A. and Wang, W. 2020. Modeling the potential distribution of *Zelkova schneideriana* under different human activity intensities and climate change patterns in China. – *Global Ecol. Conserv.* 21: e00840.
- Tellería, J. L., Asensio, B. and Díaz, M. 1999. Aves Ibéricas II: passeriformes. – J. M. Reyero Editor.
- Wald, A. 1943. Tests of statistical hypotheses concerning several parameters when the number of observations is large. – *Trans. Am. Math. Soc.* 54: 426–482.
- Walther, G. R., Post, E., Convey, P., Menzel, A., Parmesan, C., Beebee, T. J. C., Fromentin, J. M., Hoegh-Guldberg, O. and Bairlein, F. 2002. Ecological responses to recent climate change. – *Nature* 416: 389–395.
- Weston, K. A., Taylor, S. S. and Robertson, B. C. 2016. Identifying populations for management: fine-scale population structure in the New Zealand alpine rock wren (*Xenicus gilviventris*). – *Conserv. Genet.* 17: 691–701.
- Yu, H., Luedeling, E. and Xu, J. 2010. Winter and spring warming result in delayed spring phenology on the Tibetan Plateau. – *Proc. Natl Acad. Sci. USA* 107: 22151–22156.
- Zamora, R. and Barea-Azcón, J. M. 2015. Long-term changes in mountain passerine bird communities in the Sierra Nevada (southern Spain): a 30-year case study. – *Ardeola* 62: 3–18.
- Zanolla, M., Altamirano, M., Carmona, R., De la Rosa, J., Souza-Egipsy, V., Sherwood, A., Tsiamis, K., Barbosa, A. M., Muñoz, A.-R. and Andreakis, N. 2018. Assessing global range expansion in a cryptic species complex: insights from the red seaweed genus *Asparagopsis* (Florideophyceae). – *J. Phycol.* 54: 12–24.
- Zurell, D., Franklin, J., König, C., Bouchet, P. J., Dormann, C. F., Elith, J., Fandos, G., Feng, X., Guillera-Arroita, G., Guisan, A., Lahoz-Monfort, J. J., Leitão, P. J., Park, D. S., Peterson, A. T., Rapacciuolo, G., Schmatz, D. R., Schröder, B., Serra-Diaz, J. M., Thuiller, W., Yates, K. L., Zimmermann, N. E. and Merow, C. 2020. A standard protocol for reporting species distribution models. – *Ecography* 43: 1261–1277.