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Unravelling the link between productivity and climate for two sympatric *Acrocephalus* warblers across Spain

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Abstract

Capsule: An accumulated rainfall of around 100 mm favoured the productivity of the specialist Moustached Warbler *Acrocephalus melanopogon*, but temperature had a negative effect. By contrast, temperature had a positive effect on the productivity of the generalist Reed Warbler *Acrocephalus scirpaceus*, whereas rainfall had almost no effect, although productivity also peaked when rainfall approached 100 mm.

Aims: Understanding the extent to which climate and geography are driving the negative trend of Moustached Warbler productivity, and the stable trend of Reed Warbler productivity.

Methods: Using data from a breeding bird monitoring ringing scheme in Spain (PASER; 1995 – 2021), we investigated the effects of seasonal rainfall and temperature patterns on the productivity of two sympatric warblers: the resident/short-distance migrant Moustached

Warbler (occurring at nine ringing stations from a total of 129), and the generalist long-distance migrant Reed Warbler (57 out of 129 ringing stations). Analyses were performed using multi-adaptive regression splines (MARS).

Results: Between 1995 and 2021 geographical and site-specific factors drove annual productivity for both species, combined with rainfall and temperature. For the Moustached Warbler, geographical and site-related variables, together with the temporal changes (year), were more important than rainfall and temperature. For the Reed Warbler, temperature was more important than year but less than site and longitude.

Conclusion: Warmer temperatures and a higher frequency of torrential rainfall events may compromise the conservation of the vulnerable Moustached Warbler in Spain due to the adverse effect on productivity. In contrast, increasing temperatures across Spain may benefit the widely distributed Reed Warbler. Thus, Moustached Warbler populations are likely to decrease, whereas Reed Warbler populations might increase. However, further research is needed to establish the impact of climate change on survival, and its implications for the population trends and dynamics of these two sympatric warblers.

Keywords

Bird conservation; climate change; passerines; population dynamics; population trends; wetlands.

1 Introduction

Species reproductive success and ultimate productivity (i.e. the number of juveniles per adult) is influenced by environmental factors (van Weelden *et al.* 2021), especially temperature (Boucher-Lalonde *et al.* 2014, Albouy *et al.* 2020, Kiss *et al.* 2020) and precipitation (Illán *et al.* 2014, Herrando *et al.* 2019). Changes in the patterns of temperature and precipitation interact with site characteristics to create different environmental conditions, which alter population dynamics through direct impacts on the physiology of the inhabiting individuals, or indirectly due to changes in resource availability (Thompson *et al.* 2016). Therefore, the effect of precipitation and temperature patterns, and their changes, are often reflected in species' demographic parameters, such as productivity and survival (Zuckerberg *et al.* 2018). In particular, birds are very sensitive to climate change (Northrup *et al.* 2019). Nonetheless, several studies confirm that deviations from average precipitation (Brlík *et al.* 2022) and temperature values (Chiffard *et al.* 2019) impact a variety of life stages among avian populations (Hinsley *et al.* 2003). Together, these indicate that climate change will be one of the major drivers of productivity, with contrasting effects ranging from beneficial (IPBES 2023) to causing the extinction of multiple species in coming decades (Sage 2020).

Climate change also exacerbates and increases the frequency of extreme events, such as floods and droughts, often increasing offspring mortality and reducing productivity (Franklin *et al.* 2000, Rodríguez & Bustamante 2003, Arlettaz *et al.* 2010). However, while moderate to abundant rainfall before breeding seasons can positively affect productivity in arid regions, due to the increase of prey and resource availability (Rodríguez & Bustamante 2003), droughts do not usually have this mixed effect as they reduce resource availability and, hence, productivity. Droughts may limit vegetation growth and reduce prey abundance. Consequently, some birds would not reach an adequate body condition necessary for reproduction. Moreover, droughts may force birds to quit incubation to forage when prey abundance is low (Saracco *et al.* 2018).

The effect of higher temperatures can be similar to that of higher precipitation, as there are examples of increasing productivity, but such cases are typically limited to northern latitudes (Pearce-Higgins & Green 2014, Meller *et al.* 2018). For example, increased temperatures can increase re-nesting opportunities, as documented in Poland where Reed Warblers *Acrocephalus scirpaceus* started breeding progressively earlier, lengthening the laying period and increasing their productivity (Halupka *et al.* 2008). Conversely, in warm semi-arid regions, such as several regions in Spain, the expected effects of relatively high temperatures will likely be negative (Belda *et al.* 1995, Gardner *et al.* 2022) because high temperatures reduce productivity due to mismatches between breeding phenology and food availability (e.g. Watanuki *et al.* 2009, McKinnon *et al.* 2012).

Nesting site and habitat conditions play a vital role in bird productivity because resource availability and quality within a specific area directly impact breeding success, survival rate and the overall productivity of birds (Barnes *et al.* 2023). In addition, there are species-specific differences in climatic sensitivity to precipitation and temperature at given time windows. Thus, the timing of the different climatic phenomena might have different effects among species. Consequently, depending on species and site, climate change may differently modify the environmental conditions and determine the quality of the breeding site. It is customary to use seasonal (spring, summer, etc.) or monthly (May, June, July, etc.) time windows to relate the effect of climatic variables on productivity and other phenological aspects (Meller *et al.* 2018, Saracco *et al.* 2019). However, the most relevant period driving the productivity of a species can fall between two such periods; for example, encompassing the last and first fortnights of two consecutive months (Bailey & van de Pol 2016). Therefore, to further increase our knowledge on future population dynamics, it is fundamental to refine these time frames and establish climate-sensitive periods to explain how average climatic conditions interact with breeding site characteristics and foresee future population trends (Penteriani *et al.* 2014).

Spain has experienced a mean temperature rise of 0.8°C during the last century (Olcina 2020). Moreover, a significant change in rainfall patterns has been recorded during recent decades, indicating an increase in the magnitude and frequency of torrential rain events on the Mediterranean coast and an overall decrease in rain over most of the remaining territories (Ruiz-Leo *et al.* 2013, Miró *et al.* 2021). However, the exact effects of climate on critical demographic parameters of avian populations, such as productivity and survival, are still not well understood (van de Pol *et al.* 2010).

Spain is particularly notable for hosting an important percentage of the western European populations of the Moustached Warbler *Acrocephalus melanopogon*. Meanwhile, the Spanish population of the Reed Warbler, although widespread across the country, only represents a small proportion of the European population (Molina *et al.* 2022). The western European population of the Moustached Warbler is mainly found in discontinuous and fragmented wetlands along the Mediterranean coast, from the Camargue in France to El Fondo wetland in Alicante, and inland to the wetlands of La Mancha Húmeda Biosphere Reserve. The largest Spanish population is in the S'Albufera de Majorca in the Balearic Islands, followed by the marshes of the Valencia Region (mainly in Marjal de Pego-Oliva Natural Park and Marjal de Xeresa). The Spanish population was estimated at 1,000 pairs in 2007 (López Iborra & Castany 2022). However, it experienced a significant short-term decrease (between 39 and 59%) in the subsequent census carried out in 2018 (BirdLife International 2021), which justifies the inclusion of the species as 'Vulnerable' in the Spanish Red Book (Vera 2021). The Moustached Warbler is also threatened in other western Mediterranean breeding areas, such as France and Italy, where it is catalogued as 'Endangered' (UICN 2023). By contrast, the past

population trend of the Reed Warbler has been positive in Spain (Carrascal & Palomino 2008), and has been stable during the last decade (Molina *et al.* 2022), and so it is currently catalogued as 'Least Concern' (UICN 2023).

These two sympatric *Acrocephalus* species are ideal candidates to evaluate the climatic effect on productivity using a standardised dataset collected in multiple bird-ringing stations distributed across Spain (see details in the Methods). Reed Warblers are long-distance migrants, characterised by more flexible habitat requirements compared to Moustached Warblers. By contrast, Moustached Warblers are resident/short-distance migrants with a particularly restricted distribution. As a result of these contrasting characteristics, and based on ecological theory, we expected a higher adaptative potential of the Reed Warbler to different climatic scenarios, given its wider ecological and thermal niches compared to those of the Moustached Warbler (Viana & Chase 2022b).

To understand how climate-induced changes may affect the population dynamics of both species in Spain, we investigated the influence of rainfall and temperature on their productivity. We modelled the productivity of these species employing a dataset collected during the last 25 years and spanning most of the country. Additionally, we investigated the specific period (time window) in which these climate variables have the most significant impact on this demographic parameter, to define 'climate-sensitive periods', taking into account potential spatial (site, longitude, latitude and elevation) and temporal changes (year). Finally, we investigated whether there have been trends or changes in rainfall and temperature over the study period (1995–2021) during these climate-sensitive periods.

2 Methods

2.1 Field sampling and climatic and geographic data

We considered productivity as the ratio of juvenile to adult birds caught during standardised mist-netting sessions of the PASER programme (one datum per year and site) from the period 1995 to 2021 (SEO/BirdLife 2022). The PASER programme is arguably the most extensive of the three existing breeding bird monitoring ringing schemes in Spain, although some sites were not continuously active during the entire period (**Tables S1** and **S2**). The ringing stations within this scheme follow a similar methodology to other European countries (Robinson *et al.* 2009). In this specific case, the ringing season was established from the beginning of April to mid-August, divided into 10–12 equal periods of around 10 days in duration. Mist nets were systematically set up during the ringing season, starting at sunrise and remaining operational for up to five hours per visit.

Following Eglington *et al.* (2015), only sites where juveniles and adults were simultaneously caught during at least two ringing seasons (two years) were included in the analyses. Therefore, we used the Moustached Warbler data from nine stations from a total of 129 (**Table S1**). These nine sites comprise the most important breeding sites in Spain, encompassing more than 85% of the Spanish population (Castany & López 2006). For the Reed Warbler we used data from 57 out of 129 stations (**Table S2**), encompassing all Spanish regions except Catalunya (north-east Spain), which operates its own distinct bird ringing scheme, and the Canary Islands (north-west Africa), because no data from the PASER programme were available (**Figure 1**). Captured birds were ringed and also aged and sexed whenever possible, following Svensson (1996). The collected data were used to categorise captures into juvenile

and adult groups, ensuring that individuals were not counted multiple times within the same ringing season (year).

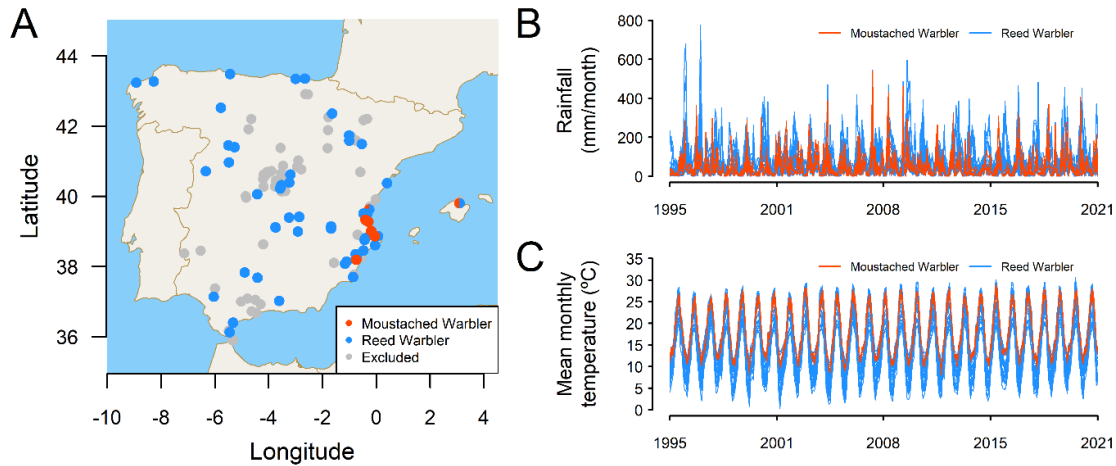


Figure 1. Location of the breeding bird monitoring ringing scheme (PASER) sites and selected sites for the Moustached Warbler and Reed Warbler across Spain (A). Rainfall (B) and mean temperature time series (C) at the monthly time scale employed for each species during the study.

In Spain, breeding Moustached Warblers are resident or migrate over short distances and begin to lay eggs in late March/early April (Ceresa *et al.* 2016). By contrast, Reed Warblers overwinter in sub-Saharan Africa and migrate to begin laying eggs in western Europe in May (Kennerley & Pearson 2010). Following Ceresa *et al.* (2020), breeding seasons were considered to last from April to June for the Moustached Warbler and from May to July for the Reed Warbler. To analyse productivity and the climate-induced changes in this demographic parameter, we included Moustached Warblers captured during an extended breeding season from April to July in order to detect juveniles from late clutches, whereas for the Reed Warbler the breeding season was restricted to the period from May to July to avoid the confounding presence of northbound migrants earlier in spring.

Climatic time series at the daily time scale for the entire study period (1995–2021) were provided by the Spanish Agency of Meteorology (AEMET) (www.aemet.es). We used Euclidean distances to assign the nearest series of the AEMET dataset to each ringing station (**Table S3**). Each series included daily rainfall (mm) and minimum and maximum temperatures (°C). An average of both temperatures was calculated to obtain the daily mean temperature (Tmean) because they presented an almost perfect correlation. In addition, we collected site codes, their longitude, latitude, elevation and the available sampling years.

2.2 Productivity modelling and climate-sensitive period assessment

We used multi-adaptive regression splines (MARS) (Friedman 1991) to model the annual productivity as the response variable. We investigated the predictive capability and effect of different climate-sensitive periods (time windows) of the accumulated rainfall (hereafter rainfall) and mean temperature (hereafter temperature) (one single value per year and site) by varying the time window (i.e. the start and end date of the period) and selecting or discarding these two variables within a variable selection scheme. Finding those different time frames or windows allowed us to determine the specific climate-sensitive period that can be considered decisive for each species (i.e. the time period or window in which the average climatic variables

have the largest impact on productivity). Among the different available modelling techniques, we selected MARS because it is a piecewise linear regression and machine learning technique, able to model nonlinearities and variable interactions that can use link functions to restrict outputs to desired distributions (e.g. between 0 and 1), like the popular generalised additive models – GAMs (Hastie & Tibshirani 1990). However, these nonlinearities and variable interactions are sought in an automated fashion, in a process driven by a series of parameters or settings, called hyperparameters, which need to be optimised. These determine the ultimate number of linear segments and interactions included in the model. This is an advantage compared with the standard implementation of a GAM that requires indicating which interactions need testing (Wood 2017).

Finding a time window in which rainfall and temperature are not drivers of the modelled productivity, but proxies (substitutes) for other important temporal trends or geographic variables (e.g. site, elevation or latitude), could be possible because these climatic variables present strong spatial and temporal correlation patterns (Martinez-Artigas *et al.* 2021). For example, at high elevations temperature tends to be lower so it could be possible to find a very short time period where temperature maximally correlates with elevation and, from a mathematical viewpoint, can substitute this geographic variable. Therefore, it is possible to identify a specific time frame where the values of rainfall and temperature accurately represent both the spatial (e.g. site) distribution and temporal (e.g. year) changes and trends of these two groups of variables and not the effect of these variables on productivity.

Such an undesired scenario could potentially mask the true influence of climate on the warblers' productivity, particularly if spatial and temporal effects on productivity hold greater significance. Accordingly, to remove the spatial and temporal variation and find the underlying effect of climate, and to minimise the possibility of finding a proxy from rainfall and temperature that substitute (i) site, (ii) longitude, (iii) latitude, (iv) elevation or (v) year (i.e. temporal changes or trend), we also included these five additional variables within the variable selection scheme (**Figure 2**). Therefore, in the case of selecting rainfall and temperature, this ensures they are drivers of productivity and not proxies of the geographic variables and/or temporal changes.

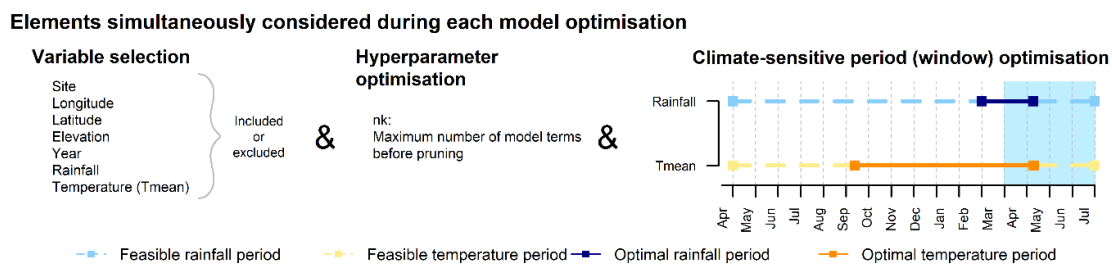


Figure 2. Elements simultaneously considered during model optimisation: (i) variable selection, including rainfall and temperature, (ii) hyperparameter optimisation, and (iii) search of the optimal climate-sensitive period (time window) for rainfall and temperature. Shaded area (in light blue) represents the breeding season and were set beforehand. The right plot shows an example of a potential solution where rainfall and temperature have been selected within the final (optimal) model. The solid line chart displays the amplitude of the determined climate-sensitive periods (time windows) for each variable and the dotted lines the studied ranges. If rainfall and/or temperature are excluded during variable selection, the associated climate-sensitive period loses significance, as the omitted variable will not be included in the training dataset.

Each tested MARS model, including different sets of variables, hyperparameters and climate-sensitivity periods, was developed in *R* (R Core Team 2021) using the *R* package *earth*

(Milborrow 2023), setting the link function to binomial to restrict the outputs between 0 and 1, as described by Zuur *et al.* (2009). We optimised the nk parameter to limit the complexity of the MARS models between 1 and 99, and restricted the maximum number of knots per predictor to three to ensure model reliability from an ecological viewpoint (Austin 2007, Muñoz-Mas *et al.* 2016b). Although in MARS the inclusion of variable interactions is internally governed by the training algorithm and the selected hyperparameters, we investigated whether the effect of site, rainfall and/or temperature varied over time by allowing them to interact with year (two-way interactions). We also allowed interactions between the geographical variables (longitude, latitude and elevation), between these variables and year (which is similar to the first set of interactions but more general), and between rainfall and temperature.

Simultaneously searching for the best set of predictor variables, nk parameter and periods for rainfall or temperature is a complex task that requires searching strategies to tackle the impossibility of testing every potential solution. Therefore, we used Differential Evolution (Storn & Price 1997), a heuristic technique implemented in the *R* package *Deoptim* (Ardia *et al.* 2011, Mullen *et al.* 2011), to carry out this search. Differential Evolution is a population-based evolutionary algorithm loosely based on Charles Darwin's theory of natural selection. For a set of 100 solutions (population), encoded in vectors of three parts (selected variables, hyperparameters and climate-sensitivity periods) (Muñoz-Mas *et al.* 2016b, Muñoz-Mas *et al.* 2019), the Akaike Information Criterion (AIC) is calculated. Then, the search (evolution) takes place by iteratively crossing those solutions with lower AIC, and randomly altering (mutating) some of them, to find the optimal solution. The AIC for the evolved population is calculated and the evolution continues if the maximum number of generations is not achieved (500) or if the algorithm finds a better solution before 200 generations with no improvement (Muñoz-Mas *et al.* 2016a).

After identifying the best model for each species, we compared the climate-sensitive periods and assessed the variable importance. To assess the variable importance in a simple way, we used the *firm* method of the function *vi* from the *R* package *vip* 0.3.2 (Greenwell & Boehmke 2020), which computes the average change in performance after a random permutation of each variable to evaluate simultaneously the importance of the main effect of the variable and its interactions into one single index. Subsequently, we scrutinised the effect of the selected input variables with a sensitivity analysis based on partial dependence plots that are generated by permuting the values of the investigated variable across the variable range and calculating the quantiles of the resulting predictions (Friedman 2001, Muñoz-Mas *et al.* 2018).

2.3 *Time series analyses and comparison of rainfall and temperature during the climate-sensitive periods*

Rainfall and temperature could be excluded from the final models because they were part of the variable selection process. When they were selected, we further investigated the relationship between rainfall and temperature values from the climate-sensitive period with those of the breeding periods (April to June for Moustached Warbler and May to July for Reed Warbler) to check if there were differences between these two periods. We used the Kendall correlation to rate this relationship.

In addition, we explored the existence of common spatial and temporal patterns and changes in rainfall and temperature during climate-sensitive periods. To do so, we first clustered the resulting rainfall and temperature series during climate-sensitive periods (one value per site and year) employing the spin-glass algorithm (Newman & Girvan 2004, Csárdi & Nepusz 2006, Reichardt & Bornholdt 2006) over an association network based on the Kendall correlation

between pairs of rainfall or temperature series (i.e. we built two different networks). These networks were built using the functions implemented within the *R* package *igraph* (Csárdi & Nepusz 2006). We selected this approach and clustering algorithm because the former can indicate the existence of one single cluster (i.e. the changes and trends are common across Spain), and the latter because the spin-glass algorithm is able to deal with negative network weights (correlations), contrary to most of the available algorithms for clustering and community detection. Once the optimal number of clusters was determined, we graphically investigated the spatial association and temporal changes and trends of rainfall and temperature during the climate-sensitive periods. The latter were tested for each cluster using the function *mult.mk.test* implemented in the *R* package *trend* (Pohler 2015). This function allows for calculating the Kendall test simultaneously for multiple temporal series.

3 Results

3.1 Productivity modelling and climate-sensitive period assessment

For both species, the best MARS models exhibited good predictive capability ($R^2_{\text{Moustached Warbler}} = 0.90$ and $R^2_{\text{Reed Warbler}} = 0.81$). Rainfall and temperature contributed positively to model performance and were selected within the final models alongside the remaining variables, except latitude, which was excluded from the Reed Warbler's model (**Figure S1**). The optimal climate-sensitive periods (time windows), referring to the time frame during which each species displayed a greater sensitivity to climatic variables affecting productivity, were relatively similar for both species (**Figure 3**).

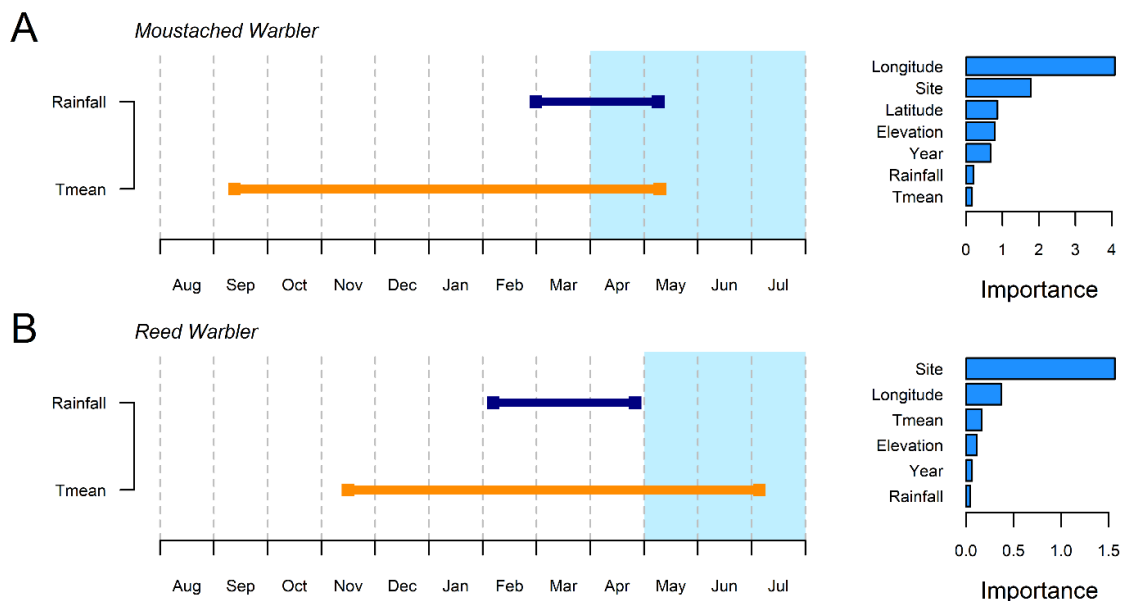


Figure 3. Relevant climate-sensitive periods of the selected rainfall and temperature (Tmean) series and variable importance in the optimal models for the Moustached Warbler (A sequence) and Reed Warbler (B sequence). The breeding season of each species is shaded in light blue.

Regarding rainfall, both periods encompassed late winter and spring. Temperature periods started in autumn and lasted until the end of spring for Moustached Warbler, and until the beginning of summer for Reed Warbler. Conversely, variable importance in both models

differed; for the Moustached Warbler the geographic variables, site and year (the temporal changes and trend) were, in that order, the most important variables, while rainfall and temperature, although included, were the least important. In contrast, for the Reed Warbler, temperature was the third most important variable, although the general relevance of the selected input variables exhibited a similar arrangement to that of the Moustached Warbler's. Longitude and site were more important than year, and the least important predictor was rainfall (**Figure 3**).

The effect of the selected variables on warbler productivity varied between the two species. For the Moustached Warbler (**Figure 4**), there was a positive effect of longitude, with the highest productivity in eastern coastal sites, which highlights the relevance of Spain's easternmost population located in S'Albufera de Majorca. This wetland holds the largest breeding population in Spain, with approximately 50% of the population (Castany & López 2006) and showed intermediate to high productivity during the study period. The spread of the percentiles in the sensitivity analyses, especially in the coastal sites located around 0° longitude, indicate strong local effects because the variable site interacted with year, rainfall and temperature (see **Figure S2**). Sites in southern latitudes exhibited higher productivity, whereas elevation indicated that lowland sites had higher productivity (**Figure 4**).

The partial dependence plot for year indicates that productivity experienced an overall decrease until 2012, and it slightly rebounded between 2013 and 2015. However, this pattern cannot be explained by the variation exhibited by rainfall and/or temperature (see subsequent analyses). Accumulated rainfall of up to 100 mm from late February to mid-May positively affected productivity, matching the nesting and chick-rearing periods. However, when rainfall exceeded this value then productivity decreased markedly. Temperatures from early September to early May, covering the breeding period and the previous winter and autumn, negatively affected productivity. Both variables interacted with site, longitude or elevation, and these effects showed a slight local variation (**Figure S2**).

For the Reed Warbler, the partial dependence plot for longitude indicated that higher values of productivity occurred proportionally more frequently in the eastern and westernmost sites and decreased on intermediate longitudes around the centre of the east – west axis of Spain (**Figure 5**). Productivity exhibited its highest median value at the lowest elevation (sea level) but had no clear overall effect on productivity, as the spread of the quantiles around 400 m indicates that the ultimate effect is mediated by the interaction with temperature (**Figure S3**). The positive effect of rainfall peaked slightly at 100 mm from early February to late April, covering the period before arrival from wintering quarters and nesting (**Figure 5**). However, its effect was less pronounced than that observed for the Moustached Warbler, and there was no effect above this value. By contrast, although temperature also interacted with site, longitude, elevation and rainfall (**Figure S3**), its overall effect from mid-November to early July on the Reed Warbler productivity was consistently positive, opposite to what was observed for the Moustached Warbler (**Figure 5**).

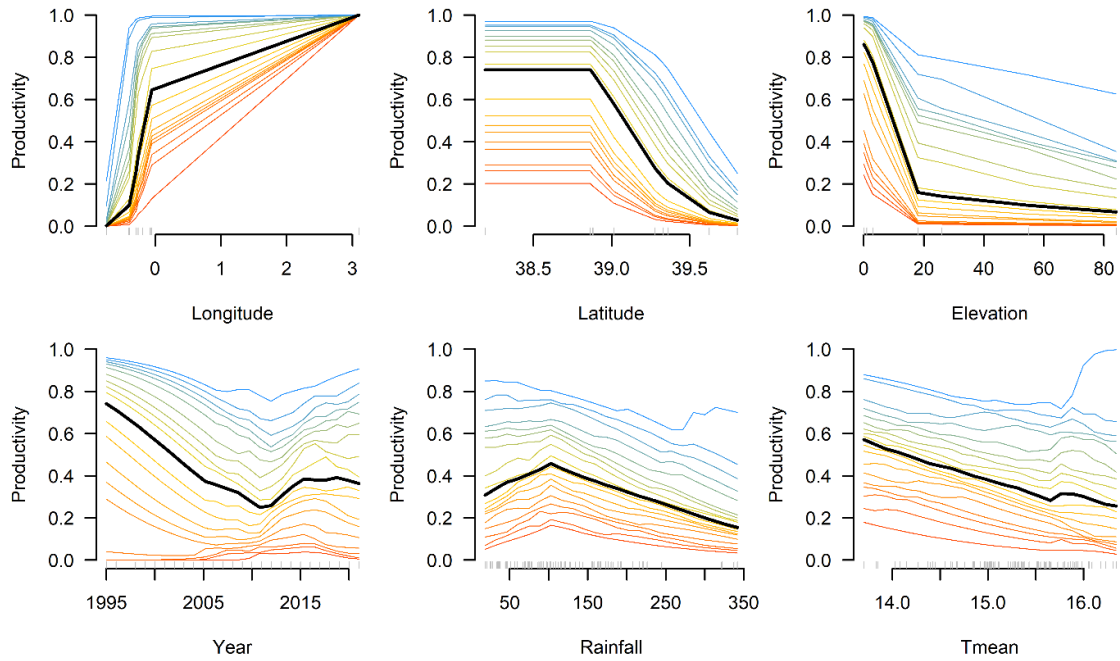


Figure 4. Sensitivity analysis (partial dependence plots) depicting the overall effect of the selected variables on Moustached Warbler productivity. The thick black central line corresponds to the 50th percentile (p50) or median. Coloured lines highlight the 5th percentiles (p5, p10, p15 ... p85, p90, p95) of the predictions along the range of the variables. Raw data points are included along the x-axis.

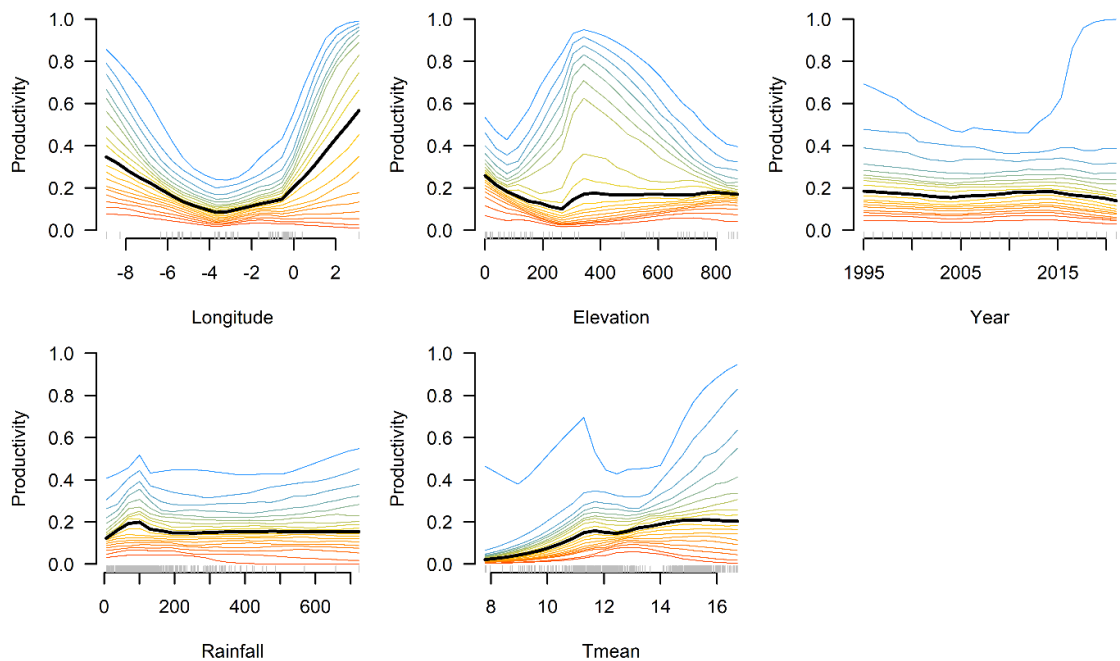


Figure 5. Sensitivity analysis (partial dependence plots) depicting the overall effect of the selected variables on Reed Warbler productivity. The thick black central line corresponds to the 50th percentile (p50) or median. Coloured lines highlight the 5th percentiles (p5, p10, p15 ... p85, p90, p95) of the predictions along the range of the variables. Raw data points are included along the x-axis.

3.2 Time series analyses and comparison of rainfall and temperature during climate-sensitive periods

Over the study period (1995–2021) rainfall and temperature values during the climate-sensitive periods correlated with those strictly covering each breeding season ($\tau = [0.13, 0.49]$; $P < 0.05$) (**Figures S4 and S5**). The lowest correlation was obtained for the Reed Warbler and rainfall, because there was no overlap between the climate-sensitive period and the breeding season, and it presented the largest number of sites and spatial extension (**Figure 1**).

The relevant climate-sensitive periods for both species showed a considerable similarity. Therefore, the cluster analysis indicated two spatial clusters for rainfall and temperature that largely coincided (**Figure 6**). The first group encompassed most of Spain and included the Moustached Warbler breeding site in the Balearic Islands, whereas the second cluster included sites located on the eastern coast of Spain where both species breed. The trend analysis indicated that over the studied period (1995–2021), rainfall during the climate-sensitive period showed a positive increase in the locations where Reed Warblers bred ($P < 0.05$). However, the variability was higher during the last decade. By contrast, the temperature and rainfall series for Moustached Warbler sites, and the temperature for Reed Warbler sites, did not exhibit any trend, although their values seem to have increased since 2015.

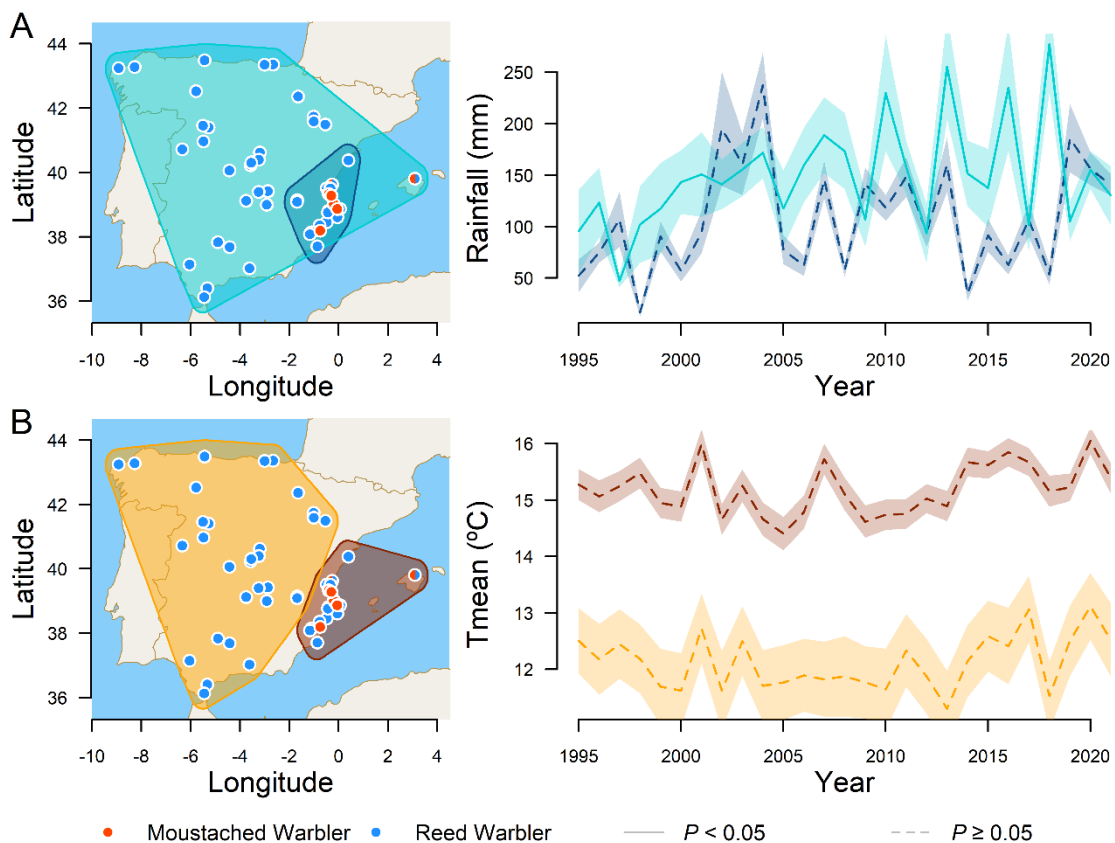


Figure 6. Spatial clusters of selected bird ringing constant-effort sites and trend analyses of the rainfall (A sequence) and temperature (B sequence) time series corresponding to the climate-sensitive periods (one value per breeding season) of each species. The depicted series represent the mean values and 0.95 confidence intervals. See Supplementary Material for a complete depiction of the clustered time series.

4 Discussion

Local effects, such as the availability of food resources, suitable nesting habitats, and the presence of predators and/or competitors, substantially influence bird productivity, playing a crucial role in shaping their breeding success and overall population dynamics (Tozer *et al.* 2010, Barnes *et al.* 2023). Consequently, in accordance with the results of this study, a significant portion of the variability in productivity, and their changes and trends, cannot solely be explained by climatic variables (McLean *et al.* 2022, Jensen *et al.* 2023).

During the study period (1995–2021), Moustached Warblers exhibited a clear decrease in productivity, while Reed Warblers did not exhibit any general trend, although the year variable was selected, indicating that additional factors are governing the productivity of both species. Nevertheless, although less relevant than the site-specific and geographic effects, the optimal models included rainfall and temperature as predictors, and the climate-sensitive period exhibited great similarities between both species.

Accumulated rainfall during the climate-sensitive period showed a positive effect on Moustached Warbler productivity from late February to mid-May (including nesting and chick-rearing) until it exceeded 100 mm, when the effect became negative. In contrast, there was no apparent association between Reed Warbler productivity and accumulated rainfall above this 100 mm threshold. Still, the effect was slightly positive when accumulated rainfall approximated 100 mm from early February to late April, which included the period before the birds' arrival from the wintering quarters and subsequent nesting.

Moustached Warblers in Spain start nesting in mid-March, and Reed Warblers in May (Ceresa *et al.* 2020). Therefore, our results suggest that persistent rain during the breeding season can have marked adverse effects on the productivity of Moustached Warblers. However, the later arrival and nesting of Reed Warblers, after the rainfall-sensitive period selected by the models, may represent an ecological advantage for the species, as heavy rainfall is uncommon in Spain from May onwards (Senent-Aparicio *et al.* 2023). In addition, food abundance is one of the most relevant factors triggering breeding at any given time (Dunn & Winkler 2010). Insectivorous birds are particularly affected by adverse weather during the breeding season because it reduces food availability, as prey becomes less active (Avery & Krebs 1984), having deleterious effects on both the offspring and their parents (Öberg *et al.* 2015) and ultimately inducing chick mortality. Thus, in agreement with previous studies, it can be concluded that for the Moustached Warbler persistent rainfall most probably affects reproduction by requiring a higher energy investment for body maintenance, at the expense of egg production and/or the accumulation of fat reserves before nesting (Sarà *et al.* 2022).

The decreased productivity we observed for the Moustached Warbler between 1995 and 2012, despite the rebound after that year, was very likely involved in determining the population decline of this species in Spain during the last decades (BirdLife International 2021). Our results suggest that site-specific factors are involved in decreased productivity (local changes in habitat structure or predation rates), which may indicate habitat degradation in the relatively few marshlands currently hosting this species. Moreover, even though the multivariate Kendall indicated no trend in accumulated rainfall during the climate-sensitive period in the easternmost cluster between 1995 and 2021, flood and drought intensity is expected to increase on the Mediterranean coast (Frauenfeld & Davis 2003), which could further impact Moustached Warbler productivity. In particular, in the Gulf of Valencia, where the most significant populations of the Moustached Warbler are located, the occurrence of extreme weather phenomena seems to be increasingly common (Sánchez-Almodóvar *et al.* 2022), with climate predictions for the 2040 horizon suggesting an increase in rainfall and torrential events

(Miró *et al.* 2021, Ripple *et al.* 2023). In this sense, an increased temperature in the Mediterranean Sea has been identified as one of the main factors extending the period of increased risk of torrential events (Pastor *et al.* 2020), which might coincide with the breeding season for Moustached Warbler. Therefore, although the ultimate effect strongly depends on site-specific characteristics, the increase in rainfall and torrential events during late winter/early spring could negatively affect productivity, one of the fundamental rates that determine population trends.

For both species the most relevant climate-sensitive period for temperature extended from the breeding season to the previous autumn and winter, indicating a year-round effect. However, despite similarities observed in their climate-sensitive periods, the two species exhibited opposite responses. This discrepancy could arise from a phenological mismatch with site conditions and differences in specialisation, which may have disfavoured Moustached Warblers while favouring Reed Warblers. A feeding experiment on Reed Warblers suggested that advancing spring phenology increases food availability early in the breeding season, leading to higher productivity (Vafidis *et al.* 2016). This finding aligns with our results and is consistent with previous studies that have found a positive link between average temperature and Reed Warbler productivity (Schaefer *et al.* 2006, Halupka *et al.* 2008). Temperature-related changes in vegetation and arthropod abundance, and their effect on productivity, have also been observed in other passerines (Pipoly *et al.* 2013).

In contrast, for the Moustached Warbler, a resident/short-distance migrant, the negative relationship between mean temperature and productivity might be related to the shifts in peak insect abundance and mismatches between the chick-rearing period and the emergence of critical resources. Moreover, the Moustached Warbler is one of the Iberian marsh passerines with more stringent habitat requirements, particularly during the breeding season (Poulin *et al.* 2002, Vera *et al.* 2016, Alambiaga *et al.* 2021), as it avoids homogeneous large reedbeds in favour of habitats where the bulrush *Thypha domingensis* and Saw Sedge *Cladium mariscus* are present. Conversely, the Reed Warbler is more flexible in habitat selection and is commonly found not only within homogeneous reedbeds but also in a variety of other habitats, such as riversides. Thus, the negative effect of temperature on Moustached Warbler productivity could be linked to its restricted range and even more so by its high degree of specialisation, which agrees with the reduced adaptability of specialists to climate change suggested by Viana & Chase (2022a). Our results are also consistent with previous work demonstrating a negative impact of warming on habitat specialists that have a narrow niche breadth (Davey *et al.* 2012, Pearce-Higgins *et al.* 2015).

In conclusion, this study provides new insights into the response of Moustached and Reed Warblers to climatic conditions across Spain. On the one hand, high habitat specialisation and the limited distribution of the Moustached Warbler might compromise the population's ability to match a suitable climatic space (Platts *et al.* 2019). On the other hand, the forecasted climate change-induced rise in temperature might benefit the more generalist Reed Warbler, whose productivity exhibited a positive relationship with temperature. Our results provide a basis for understanding the extent to which both species' abundance and distribution might be affected by climatic conditions. These findings should encourage management and monitoring efforts to sustain populations and enhance our knowledge of warbler population dynamics. The most relevant variables that were selected indicated prominent site-specific effects on productivity, rather than climatic ones. Therefore, prioritising habitat management and preventing habitat degradation should be of utmost importance for the conservation of both species, particularly in the context of ongoing global change.

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Supplementary electronic material

Table S1. Bird ringing stations of the PASER programme (codes and names), coordinates, periods and total number of years used for the Moustached Warbler analysis.

| Site code | Station | Latitude (deg north) | Longitude (deg east) | Available data period | Total |
|-----------|---|----------------------|----------------------|----------------------------------|-------|
| ES41469 | El Fondo d'Elx Natural Park | 38.19 | -0.74 | 1995-1996; 2003-2007; 2009-2011 | 10 |
| ES41620 | Marjal de Pegó-Oliva Natural Park | 38.88 | 0.07 | 2011-2015; 2019 | 6 |
| ES41666 | Junqueres (Marjal de Pegó-Oliva Natural Park) | 38.86 | -0.05 | 2004-2021 | 18 |
| ES44347 | Marjal del Moro | 39.62 | -0.25 | 1996; 1998-2003; 2005-2007; 2009 | 11 |
| ES444 | Marjal de Xeresa | 39.01 | -0.18 | 2013-2021 | 9 |
| ES444108 | Tancat de la Ratlla | 39.32 | -0.39 | 2011-2016; 2018-2019 | 8 |
| ES444380 | Tancat de la Pipa | 39.36 | -0.39 | 2010-2016; 2018-2020 | 10 |
| ES444416 | Tancat de l'Illa | 39.27 | -0.29 | 2014-2015; 2017-2021 | 7 |
| ES71287 | S'Albufera de Majorca | 39.80 | 3.09 | 2006-2009 | 4 |

Table S2. Bird ringing stations of the PASER programme (codes and names), coordinates, periods and total number of years used for the Reed Warbler analysis.

| Site code | Station | Latitude (deg north) | Longitude (deg east) | Available data period | Total |
|-----------|------------------------|----------------------|----------------------|---------------------------------|-------|
| ES01312 | Lestimoño | 43.27 | -8.27 | 2006-2008 | 3 |
| ES01330 | Puenteceso | 43.24 | -8.91 | 2005-2007; 2009-2016; 2019-2021 | 14 |
| ES05448 | Ría Villaviciosa | 43.48 | -5.43 | 2004-2009 | 6 |
| ES08192 | Gautéguiz de Arteaga | 43.35 | 2.65 | 2003-2005 | 3 |
| ES08195 | Bolue | 43.21 | -3.30 | 2014-2016 | 3 |
| ES12157 | Villadangos del Páramo | 42.52 | -5.77 | 1997-2005 | 9 |
| ES1553 | Huerta | 40.96 | -5.59 | 1997-2001; 2005-2006 | 7 |
| ES15656 | Castraz | 40.71 | -6.33 | 2012; 2014; 2015 | 3 |
| ES18182 | Embalse de San José | 41.39 | -5.26 | 2013-2016; 2019 | 5 |
| ES1936 | Dehesa de Castrillo | 41.45 | -5.49 | 1999-2000; 2002-2004 | 5 |
| ES2071 | Laguna de Manjavacas | 39.41 | -2.86 | 2015-2016; 2018 | 3 |
| ES2094 | Mota del Cuervo | 39.41 | -2.86 | 1997-2013 | 17 |
| ES21734 | Finca la Aceña | 40.61 | -3.18 | 2013-2016; 2019; 2021 | 6 |
| ES24596 | Traibuenas | 42.35 | -1.64 | 1999-2016; 2018-2021 | 21 |
| ES261044 | Mejana del Tambor | 41.73 | -1.00 | 2013; 2015-2016 | 3 |
| ES26139 | Juslibol | 41.58 | -1.00 | 2006; 2009; 2011-2015 | 7 |
| ES26445 | La Mechana | 41.01 | -0.49 | 1999-2001 | 3 |

| | | | | | |
|-----------|---|-------|-------|------------------------------------|----|
| ES31178 | Prat | 40.22 | 0.24 | 1999-2010 | 12 |
| ES40121 | Puente Torres | 39.11 | -1.65 | 2000-2002 | 3 |
| ES4079 | Laguna de Tinajeros | 39.08 | -1.67 | 2008-2011; 2014-2016; 2019 | 8 |
| ES41277 | Río Algar | 38.60 | -0.04 | 2009-2015; 2018 | 8 |
| ES41469 | El Fondo d'Elx Natural Park | 38.19 | -0.74 | 1995-1996; 2002-2007, 2009-2011 | 11 |
| ES41557 | Pantano de Elche | 38.30 | -0.72 | 1999-2000; 2011-2012 | 4 |
| ES41584 | Gaianes | 38.8 | -0.4 | 2009-2011 | 2 |
| ES41598 | Mutxamel | 38.45 | -0.47 | 2008-2011; 2013-2014 | 6 |
| ES41620 | Marjal de Pegó-Oliva Natural Park | 38.88 | 0.07 | 2011-2015; 2019 | 6 |
| ES41657 | Río Vinalopó | 38.35 | -0.76 | 2009-2016; 2018-2021 | 12 |
| ES41665 | Río Serpis | 38.75 | -0.43 | 2007-2008 | 2 |
| ES41666 | Junqueres (Marjal de Pegó-Oliva Natural Park) | 38.86 | -0.05 | 2004-2021 | 18 |
| ES43359 | Rambla Ajaunque | 38.13 | -1.16 | 2002-2003; 2005 | 3 |
| ES43441 | Marina del Carmolí | 37.70 | -0.85 | 2000-2002 | 3 |
| ES43649 | Río Segura | 38.08 | -1.16 | 2011-2012 | 2 |
| ES44347 | Marjal del Moro | 39.62 | -0.25 | 1996; 1998-2007; 2009 | 12 |
| ES444 | Marjal de Xeresa | 39.01 | -0.18 | 2013-2021 | 9 |
| ES444108 | Tancat de la Ratlla | 39.32 | -0.39 | 2011-2016; 2018-2019 | 8 |
| ES444368 | Paser Turia | 39.51 | -0.47 | 2008-2013 | 6 |
| ES444380 | Tancat de la Pipa | 39.36 | -0.39 | 2010-2016; 2018-2021 | 11 |
| ES444404 | Silla | 39.35 | -0.38 | 2011-2014 | 4 |
| ES444405 | Tancat de Milia | 39.3 | -0.35 | 2012-2015; 2018 | 5 |
| ES444416 | Tancat de l'Illa | 39.27 | -0.29 | 2014-2015; 2017-2021 | 7 |
| ES4489 | Barranc del Carraixet | 39.30 | 0.19 | 2010-2015; 2018-2019 | 8 |
| ES52138 | P.N. Tablas de Daimiel | 39.11 | -3.74 | 2008; 2016; 2019 | 3 |
| ES52140 | Laguna Cenagosa | 38.99 | -2.91 | 1998-2003 | 6 |
| ES52548 | Laguna de la Veguilla | 39.39 | -3.23 | 2006-2016 | 11 |
| ES5282 | La Quebrada | 39.11 | -3.74 | 1997-2005; 2007; 2009- 2015 | 17 |
| ES53390 | Las Minas | 40.22 | -3.57 | 1995-2016; 2018-2021 | 25 |
| ES534073 | Rivas-Vaciamadrid | 40.31 | -3.52 | 1999-2000 | 2 |
| ES53465 | Nuevo Baztán | 40.39 | -3.23 | 2005-2016; 2018-2021 | 16 |
| ES53470 | Presa del Rey | 40.30 | -3.54 | 1998-2006; 2008-2014 | 16 |
| ES54136 | La Higuera | 40.05 | -4.42 | 1995-2016; 2019 | 23 |
| ES6010862 | Junta de los ríos | 36.40 | -5.32 | 2009-2012; 2014-2015 | 6 |
| ES60272 | Río Palomares | 36.12 | -5.45 | 2004-2005; 2007-2008; 2011-2012 | 6 |
| ES61678 | La Veguilla | 37.83 | -4.88 | 2002-2006; 2009-2014 | 11 |
| ES61682 | Huerta Bernardo | 37.41 | -4.28 | 2015-2016; 2018-2019 | 4 |
| ES62532 | Lagunas de Padul | 37.02 | -3.60 | 2007-2009 | 3 |
| ES66532 | La Quintanilla | 37.13 | -6.04 | 2012-2016; 2018-2021 | 6 |
| ES71287 | S'Albufera de Majorca | 39.80 | 3.09 | 2006-2009 | 4 |

Table S3. Distance from PASER bird ringing stations to the nearest climatic time series provided by the Spanish Agency of Meteorology (AEMET).

| Site code | Station | Distance (m) |
|-----------|---|--------------|
| ES01312 | Lestimoño | 806.32 |
| ES01330 | Puenteceso | 3658.46 |
| ES05448 | Ría Villaviciosa | 2081.51 |
| ES08192 | Gautéguiz de Arteaga | 1386.39 |
| ES08195 | Bolue | 2418.58 |
| ES12157 | Villadangos del Páramo | 2952.18 |
| ES1553 | Huerta | 1919.73 |
| ES15656 | Castraz | 1894.08 |
| ES18182 | Embalse de San José | 220.95 |
| ES1936 | Dehesa de Castrillo | 2541.92 |
| ES2071 | Laguna de Manjavacas | 2706.61 |
| ES2094 | Mota del Cuervo | 2726.56 |
| ES21734 | Finca la Aceña | 1984.81 |
| ES24596 | Traibuenas | 2746.51 |
| ES261044 | Mejana del Tambor | 2863.14 |
| ES26139 | Juslibol | 1830.27 |
| ES26445 | La Mechana | 1848.20 |
| ES31178 | Prat | 2609.13 |
| ES40121 | Puente Torres | 2492.81 |
| ES4079 | Laguna de Tinajeros | 2030.87 |
| ES41277 | Río Algar | 4068.28 |
| ES41469 | El Fondo d'Elx Natural Park | 2718.73 |
| ES41557 | Pantano de Elche | 2715.27 |
| ES41584 | Gaianes | 1379.17 |
| ES41598 | Mutxamel | 2835.12 |
| ES41620 | Marjal de Pegó-Oliva Natural Park | 1584.22 |
| ES41657 | Río Vinalopó | 2695.32 |
| ES41665 | Río Serpis | 1196.88 |
| ES41666 | Junqueres (Marjal de Pegó-Oliva Natural Park) | 4064.72 |
| ES43359 | Rambla Ajauque | 605.29 |
| ES43441 | Marina del Carmolí | 3364.06 |
| ES43649 | Río Segura | 2110.62 |
| ES44347 | Marjal del Moro | 2954.74 |
| ES444 | Marjal de Xeresa | 2501.67 |
| ES444108 | Tancat de la Ratlla | 1634.57 |
| ES444368 | Paser Turia | 1597.93 |
| ES444380 | Tancat de la Pipa | 2068.46 |
| ES444404 | Silla | 1375.52 |
| ES444405 | Tancat de Milia | 1949.65 |
| ES444416 | Tancat de l'Illa | 3218.61 |
| ES4489 | Barranc del Carraixet | 3085.68 |

| | | |
|-----------|------------------------|---------|
| ES52138 | P.N. Tablas de Daimiel | 2028.04 |
| ES52140 | Laguna Cenagosa | 1424.80 |
| ES52548 | Laguna de la Veguilla | 3073.82 |
| ES5282 | La Quebrada | 1059.25 |
| ES53390 | Las Minas | 711.35 |
| ES534073 | Rivas-Vaciamadrid | 1385.45 |
| ES53465 | Nuevo Baztán | 2773.54 |
| ES53470 | Presa del Rey | 3731.19 |
| ES54136 | La Higuera | 2249.09 |
| ES6010862 | Junta de los ríos | 467.88 |
| ES60272 | Río Palomares | 5734.81 |
| ES61678 | La Veguilla | 2931.65 |
| ES61682 | Huerta Bernardo | 1243.84 |
| ES62532 | Lagunas de Padul | 1471.09 |
| ES66532 | La Quintanilla | 2199.41 |
| ES71287 | S'Albufera de Majorca | 3012.05 |

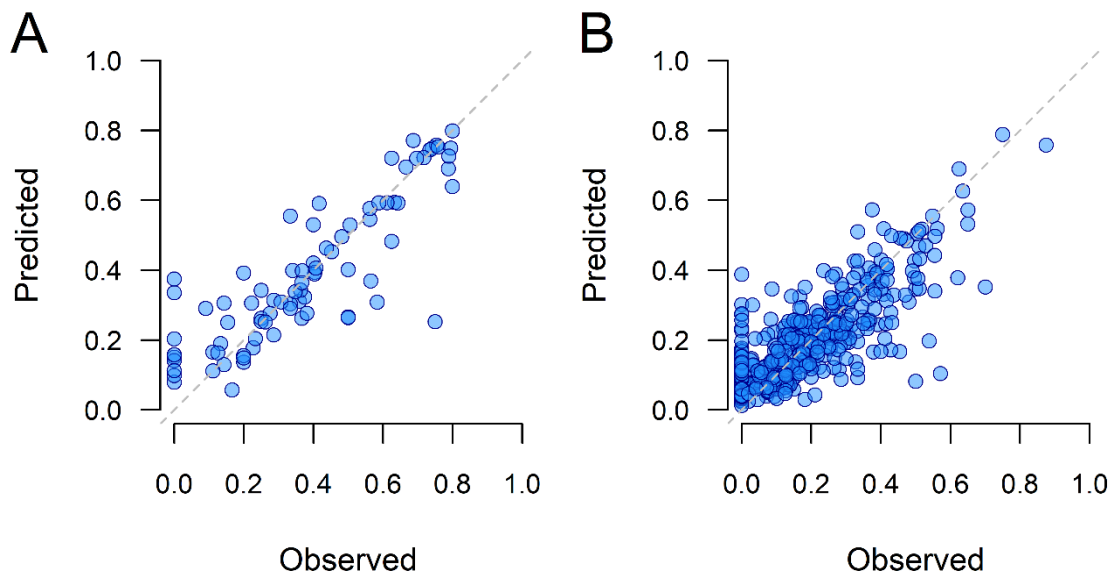


Figure S1. Models evaluation, observed vs. predicted values of Moustached Warbler (A) and Reed Warbler (B).

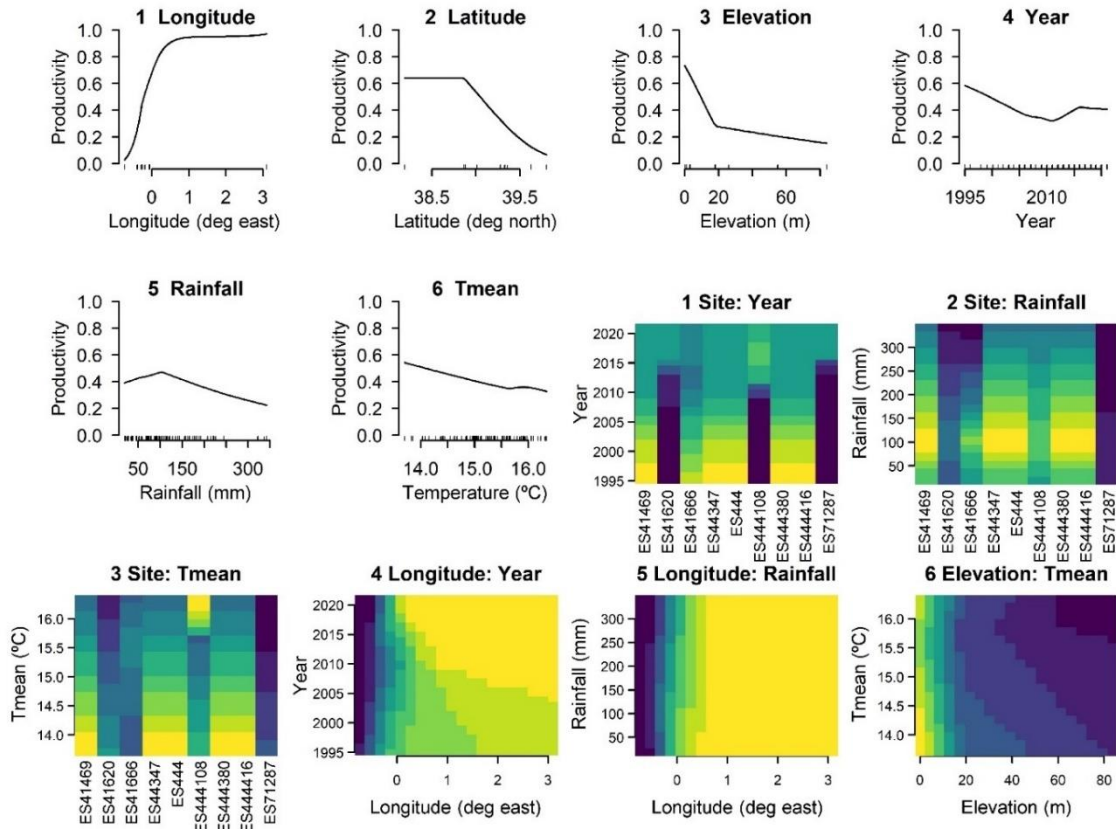


Figure S2. Sensitive analysis of the six variables selected by the model and interacting effects (coloured figures) for Moustached Warbler. Darker colours (navy blue) mean lower productivity and lighter higher productivity (yellow). Site interacted with three of the six variables (Year, Rainfall and Tmean). Particularly three sites (ES41620, ES444108, ES71287) showed a strong interaction with Year, Rainfall and Tmean.

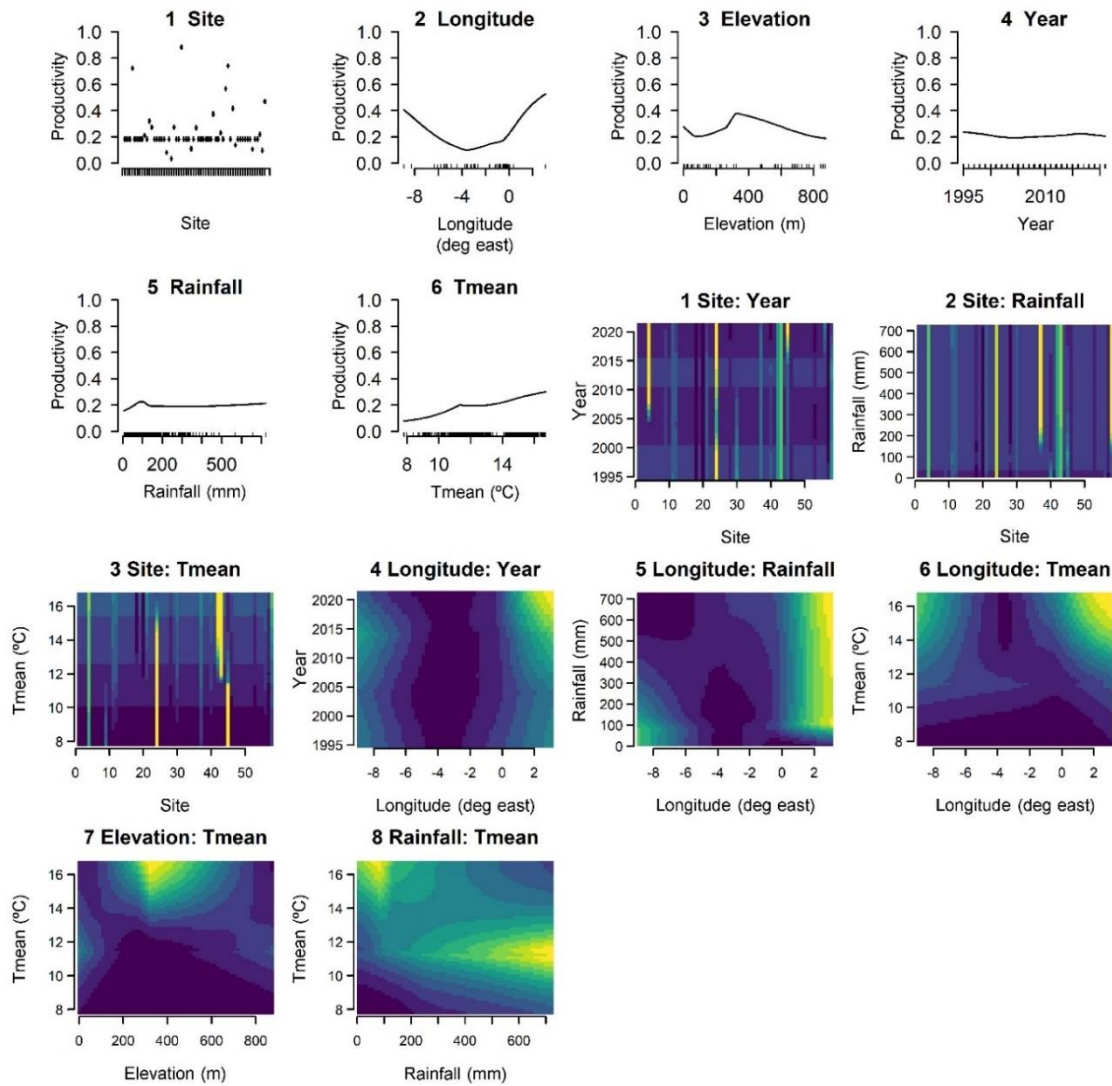


Figure S3. Sensitive analysis of the six variables selected by the model and interacting effects (coloured figures) for Reed Warbler. Darker colours (navy blue) mean lower productivity and lighter higher productivity (yellow). Site and Longitude interacted with three of the six variables (Year, Rainfall and Tmean).

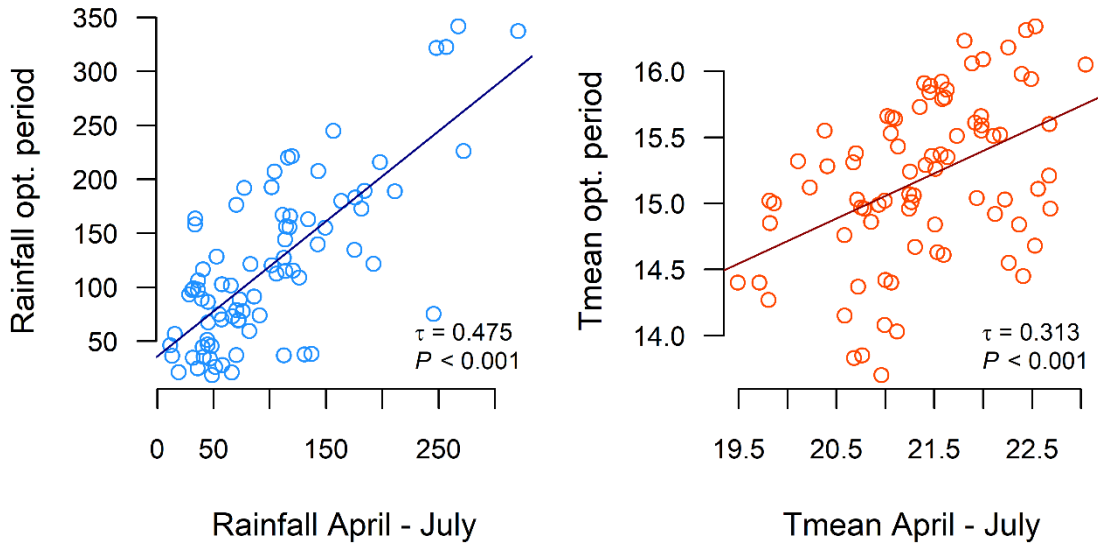


Figure S4. Correlations of rainfall and temperature from the climate-sensitive periods with the period covering each breeding season for Moustached Warbler.

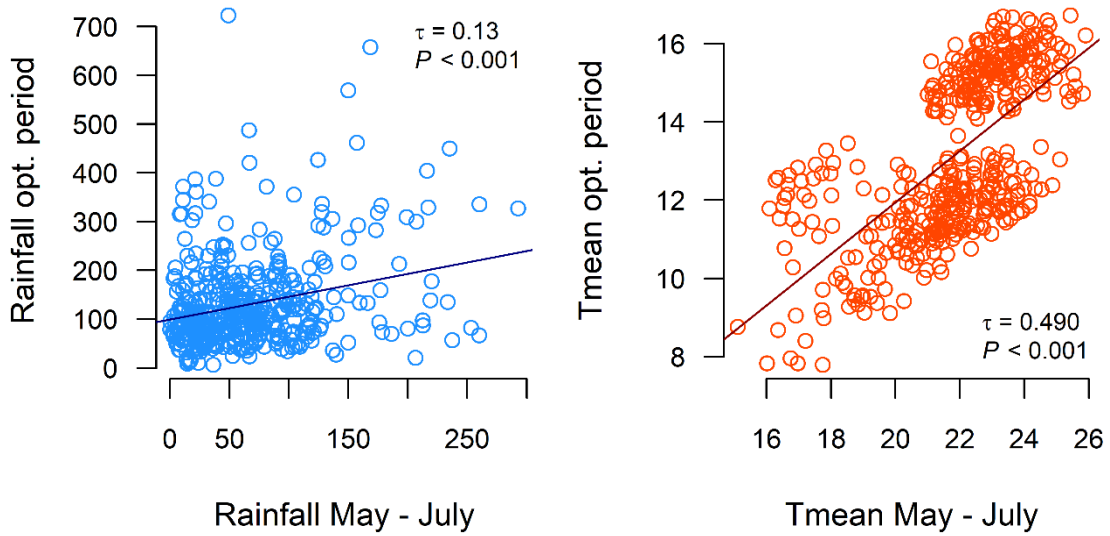


Figure S5. Correlations of rainfall and temperature from the climate-sensitive periods with the period covering each breeding season for Reed Warbler.

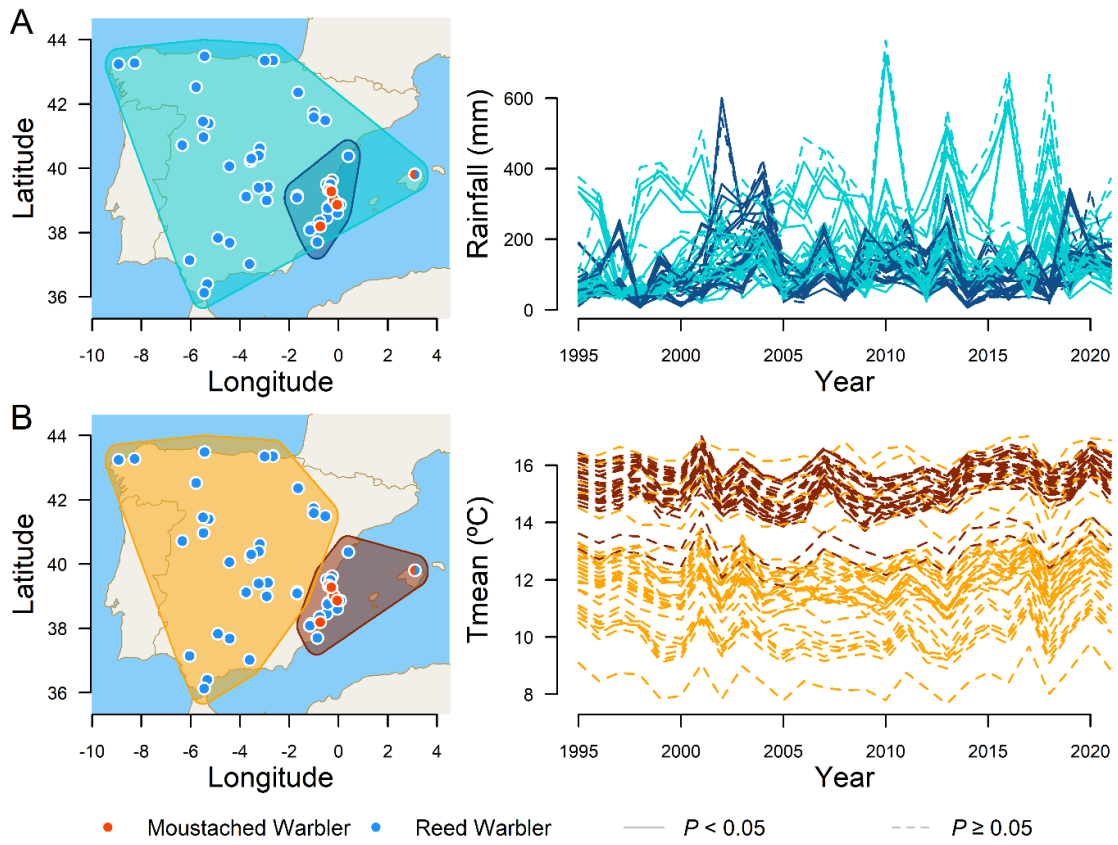


Figure S6. Temporal series and clusters of rainfall and temperatures recorded at the bird ringing stations.