

TESIS DOCTORAL  
POR COMPENDIO DE PUBLICACIONES

# EL CAMBIO CLIMÁTICO Y LA REDISTRIBUCIÓN ESPACIO-TEMPORAL DE LAS AVES EN EL PALEÁRTICO OCCIDENTAL

**SANDRO LÓPEZ RAMÍREZ**  
2026

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Biológica y Medio Ambiente





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DOCTORAL

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Paleártico Occidental**

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## INFORME DE AVAL DE LAS PUBLICACIONES EN COAUTORÍA

Los directores de la tesis titulada “**El cambio climático y la redistribución espacio-temporal de las aves en el Paleártico Occidental**” en la modalidad de compendio de publicaciones y presentada por el doctorando Sandro López Ramírez, del Programa de Doctorado en Diversidad Biológica y Medio Ambiente de la Universidad de Málaga, hacen constar que la tesis cumple con los requisitos de calidad del programa de doctorado. Además, los artículos publicados durante la tesis en revistas indexadas cumplen los criterios especificados por la ANECA, y no han sido utilizados en tesis anteriores.

A continuación, se indican los artículos y capítulos de libros publicados:

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Esta es la tesis doctoral nº **30** que produce el Grupo de Investigación “Biogeografía, Diversidad y Conservación” (Código RNM-262), del Departamento de Biología Animal de la Universidad de Málaga, dirigido por el Catedrático Raimundo Real Giménez.

This is the thesis number **30** produced by the Research Group “Biogeography, Diversity and Conservation” (Code RNM-262), Department of Animal Biology, University of Malaga, headed by Professor Raimundo Real Giménez.





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Doctor in Biology*

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*Las especies que sobreviven no son las más fuertes ni las más inteligentes, sino aquellas  
que se adaptan mejor al cambio*

— Charles R. Darwin

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# CAPÍTULO 0

Organización de la Tesis

Outline of the Thesis

## 0. Organización de la Tesis

---

La presente tesis doctoral está compuesta por 11 capítulos en los que se emplean modelos de distribución de especies (SDMs, por sus siglas en inglés: *Species Distribution Models*) como herramienta metodológica para estudiar y comprender las repercusiones del actual cambio climático sobre la distribución espacio-temporal de las aves en el Paleártico Occidental. Para ello se han seleccionado diferentes especies de aves que pueden considerarse representantes de grupos de especies que comparten patrones biogeográficos comunes, por lo que, al estudiar las especies seleccionadas, se estudian las características comunes para todo el grupo. Desde una perspectiva biogeográfica, se identifican los factores ambientales que condicionan las distribuciones de estas especies y se evalúa en qué medida los cambios en las condiciones climáticas están provocando cambios latitudinales y altitudinales en las distribuciones de las aves estudiadas, así como cambios en sus patrones de migración. Los resultados obtenidos contribuyen a una mejor comprensión de la dinámica de estas especies en el contexto actual de cambio climático, lo que permite predecir sus respuestas frente a estos cambios. Esta información puede ser de gran relevancia para las administraciones competentes y los gestores del medio ambiente, ya que pueden utilizarla para aumentar los esfuerzos de seguimiento y muestreo en las zonas identificadas por los modelos como altamente favorables pero que aún están desocupadas por las diferentes especies, con el objetivo de poder fundamentar efectivas estrategias de conservación.

La organización general de la tesis se explica a continuación:

En el **capítulo 1** se ofrece una introducción general a la presente tesis doctoral. En primer lugar, se presenta la enorme complejidad y variabilidad del sistema climático, describiendo los componentes internos y externos de este sistema. A continuación, se indica una definición de cambio climático y se realiza un recorrido histórico desde principios del siglo XIX sobre las primeras evidencias de un cambio climático en la Tierra, prestando especial atención al científico Milutin Milankovitch por desarrollar una teoría capaz de explicar las fluctuaciones naturales en el clima de la Tierra a largo plazo. En segundo lugar, se pone de manifiesto como la temperatura media global ha aumentado desde mediados del siglo XX, siendo los últimos diez años los más cálidos observados hasta la actualidad, encontrando el récord en 2024. También se señala como el Panel

Intergubernamental de Expertos sobre el Cambio Climático (IPCC, por sus siglas en inglés: *Intergovernmental Panel on Climate Change*) confirma en su sexto informe de evaluación que las actividades humanas, con la masiva emisión de gases con efecto invernadero a la atmósfera, son la principal causa del actual calentamiento global. Se indica que este calentamiento climático está siendo especialmente notable en el sur de Europa y norte de África, mencionando algunos de los efectos del mismo sobre el medio terrestre, entre ellos la modificación del área de distribución de las especies.

Seguidamente, se introduce la biogeografía como disciplina científica encargada de estudiar las distribuciones de las especies, tanto en el espacio como en el tiempo. También se proporciona una breve explicación de las características de las distribuciones de las especies y de sus clasificaciones según la segregación espacial de los individuos o poblaciones (distribuciones uniformes, agrupadas o aleatorias), la continuidad del área de distribución de las especies (distribuciones continuas, discontinuas o disyuntas) o su extensión mundial (distribuciones cosmopolitas, relictas y/o endémicas). A continuación, se muestra una breve introducción al dinamismo de las distribuciones de las especies, donde se explica el motivo que hace que las distribuciones sean espaciotemporalmente dinámicas, realizando una analogía con la física cuántica. Además, se muestra un breve apartado en el que se introducen los límites biogeográficos del área de distribución de las especies, donde se explica la importancia de la dinámica específica de los límites para caracterizar los cambios en las distribuciones. Posteriormente, se presenta otra breve sección sobre las regiones biogeográficas para mostrar que los organismos de las diferentes especies no suelen distribuirse independientemente unos de otros, sino que existen patrones de distribución comunes a un grupo de especies o de áreas geográficas. Esto permite contextualizar la región biogeográfica del Paleártico Occidental, donde se han llevado a cabo todos los estudios de la presente tesis doctoral.

Tras introducir el actual cambio climático y las características generales de las distribuciones de las especies, se exponen los efectos del cambio climático sobre las distribuciones de las aves. Esta sección está dividida en tres subapartados. En el primero de ellos, se explica como el calentamiento climático está impulsando las áreas de distribución de numerosas especies hacia mayores latitudes, desde el ecuador hacia los polos, centrándonos en el sur de Europa y el norte de África, donde aves típicamente africanas están comenzando a colonizar el sur del continente europeo. En el segundo, se indica como este calentamiento climático también está haciendo que las áreas de

distribución de algunas poblaciones de especies de montaña se desplacen a zonas más elevadas, con el objetivo de que estas puedan adaptarse a sus condiciones climáticas óptimas. En el último, se expone como dicho calentamiento también está modificando la fenología y los patrones de migración de numerosas especies de aves.

A continuación, se indica la importancia de los SDMs como herramienta para la conservación bajo los efectos del calentamiento climático y se explica el procedimiento general utilizado en la presente tesis para elaborar dichos modelos. De esta manera, se muestra cómo se han seleccionado los datos de distribución de las diferentes especies de aves estudiadas y las variables ambientales predictivas utilizadas, los controles previos considerados antes de realizar los modelos de distribución, el procedimiento de la regresión logística y, finalmente, el cálculo de los valores de favorabilidad. También se explica como la favorabilidad es capaz de medir el grado en el que las condiciones locales permiten una probabilidad local mayor o menor que la esperada por azar, siendo esta probabilidad esperada al azar la prevalencia de la especie en el área de estudio, principal ventaja que presenta con respecto a la regresión logística. Este procedimiento finaliza con la representación cartográfica de la distribución potencial de la especie considerada. Sin embargo, es importante tener en cuenta que los SDMs siempre presentan cierto grado de incertidumbre, la cual puede ser abordada mediante el uso de la lógica difusa. La lógica difusa presenta una serie de ventajas sobre la lógica clásica a la hora de trabajar en entornos inciertos, como es el medio natural, y para manejar conceptos vagos, como el grado en el que las condiciones son favorables para que ocurra un evento, en este caso la presencia de una especie en una zona determinada.

El primer capítulo culmina exponiendo los motivos del por qué se ha elegido concretamente a las aves para estudiar las repercusiones del cambio climático sobre las distribuciones de las especies.

Al final de la introducción se presenta el objetivo general y los diferentes objetivos específicos abordados durante el desarrollo de la presente tesis.

El **capítulo 2** se centra en comprobar si el sur del continente europeo dispone de zonas climáticamente favorables para el establecimiento de aves típicamente africanas e identificar cuáles son dichas zonas. El cambio climático actual está influyendo en las áreas de distribución de numerosas especies, observándose tanto expansiones del área de distribución como desplazamientos latitudinales. Estos cambios de distribución se están

produciendo en todo el mundo, pero cobran especial relevancia en el sur de Europa y el norte de África donde importantes barreras biogeográficas, como el mar Mediterráneo y el desierto del Sahara, delimitan la distribución septentrional de muchas especies africanas y la distribución meridional de otras muchas especies europeas. En el caso de las aves africanas, una pequeña expansión de su área de distribución hacia el norte representa un gran paso en términos biogeográficos, ya que supone la colonización de un nuevo continente. Este capítulo pretende analizar la respuesta de nueve aves típicamente africanas al cambio climático con el fin de aportar información sobre la ocupación actual y futura del continente europeo por estas aves, así como identificar áreas europeas susceptibles de recibir especies africanas. Las nueve aves estudiadas han sido observadas en España en la última década y, en algunos casos, se reproducen de forma consistente o lo han hecho esporádicamente. También se pretende evaluar y cuantificar el desequilibrio latitudinal entre las condiciones climáticas óptimas para la reproducción y las distribuciones reproductoras actuales de dos de las nueve aves estudiadas, el ratonero moro del Atlas (*Buteo rufinus cirtensis*) y el colirrojo diademado (*Phoenicurus moussieri*), así como calcular sus tasas de desplazamiento. Para ello, se modelizaron las distribuciones de las especies en sus áreas de distribución nativas, tanto en el presente como en escenarios climáticos futuros, utilizando sus áreas de reproducción actuales y un conjunto de variables topográficas y climáticas. A continuación, se combinó la favorabilidad climática de las nueve especies mediante lógica difusa. Los resultados mostraron que el sur de Europa actualmente dispone de zonas climáticamente favorables para el establecimiento del conjunto de aves africanas analizado, excepto para el buitre de Rüppell (*Gyps rueppelli*). Estas zonas se encuentran en la mitad sur de la Península Ibérica, el sur de Italia, Grecia, Turquía y en las grandes islas mediterráneas, como Baleares, Cerdeña, Sicilia, Creta y Chipre. Las previsiones futuras, considerando diferentes escenarios de cambio climático, indicaron que esta favorabilidad aumentará hacia mayores latitudes en Europa Occidental, especialmente en la mitad norte de la Península Ibérica, el centro y norte de Francia y la mitad norte de Italia, excluyendo de nuevo al buitre africano. Los resultados también mostraron que el desequilibrio latitudinal existente entre las distribuciones reproductoras del ratonero y el colirrojo y sus condiciones climáticas óptimas fue de 4 y 2.8 km al norte, a una velocidad de 1.3 y 3.4 km/año, respectivamente. Si el clima continúa calentándose, cabe esperar nuevas llegadas de individuos, aumentando la posibilidad de que se establezcan poblaciones autosuficientes en el sur de Europa. Además, nuevas especies africanas podrían empezar

a ocupar esta zona, con la probabilidad de una africanización de la fauna europea. Teniendo en cuenta el papel desempeñado por el sur de Europa como posible foco de colonización de este continente por especies africanas, es importante seguir su expansión hacia el norte y su propagación futura.

El aumento de las temperaturas por el impacto del cambio climático está haciendo que el sur de Europa adquiera unas condiciones climáticas similares a las que encontramos en el norte de África, lo que parece estar modificando los rangos de distribución de las especies. El **capítulo 3** se centra en estudiar una de las aves típicamente africanas analizadas en el capítulo anterior, el escribano sahariano (*Emberiza sahari*). En las últimas décadas, esta ave sedentaria ha aumentado su área de distribución hacia el norte en Marruecos, hasta alcanzar la costa mediterránea. Actualmente, su límite de distribución septentrional se encuentra en las mismas costas del norte de África. Sin embargo, la especie se está registrando regularmente en el sur de la Península Ibérica durante los últimos años, aún en números bajos y sin criar en Europa, en el momento de realización del estudio. Este capítulo pretendía determinar si las condiciones climáticas del sur de Europa, tanto las actuales como varias estimaciones de cambio climático basadas en diferentes escenarios de emisiones, son adecuadas para albergar a esta especie como reproductora, así como identificar dónde se dan estas condiciones. Para ello, se modelizó la distribución de la especie en su área de distribución nativa, tanto en el presente como en escenarios climáticos futuros, utilizando sus actuales áreas de distribución reproductora y un conjunto de variables ambientales. Los resultados mostraron que el cuadrante suroccidental de la Península Ibérica exhibe altos valores de favorabilidad para albergar a la especie, tanto para las condiciones climáticas actuales como para los distintos escenarios de cambio climático futuros. De hecho, las zonas más meridionales de la Península Ibérica resultaron ser tan favorable como las zonas autóctonas marroquíes y ya reciben regularmente individuos de la especie. Es muy probable que estas observaciones correspondan a aves errantes que se dispersan desde zonas de cría recientemente colonizadas en el norte de Marruecos, lo que podría indicar un proceso continuo de colonización hacia el norte, como ha ocurrido durante las últimas décadas en el norte de África. Al final del capítulo, se incluye una adenda al mismo donde se valida el modelo de distribución realizado, confirmando la reproducción de la especie en el sur de la Península Ibérica unos meses más tarde de la publicación del modelo.

En el **capítulo 4** se investigan los mecanismos que subyacen a la reciente colonización de Europa por parte de aves rapaces africanas, analizando tres especies que actualmente se están expandiendo por el sistema Afro-Paleártico: el ratonero moro del Atlas, el buitre de Rüppell y el buitre dorsiblanco africano (*Gyps africanus*). Utilizando modelos de distribución de especies basados en predictores topo-climáticos, se estima la favorabilidad ambiental para la reproducción en el Paleártico Occidental y la región Afrotropical. Los resultados revelan diferentes vías de colonización. El ratonero moro muestra una amplia favorabilidad climática en el norte de África y algunas partes del sur de Europa, lo que concuerda con la expansión de su área de distribución impulsada por el clima. Por el contrario, los buitres africanos muestran una favorabilidad climática insignificante en Europa, a pesar de que el buitre de Rüppell ya se ha reproducido en el continente, siempre en parejas híbridas con buitres leonados (*G. fulvus*), y cada vez se observan más buitres dorsiblanco africanos inmaduros. Estos patrones indican una colonización mediada por el vagabundeo asistido socialmente, con buitres inmaduros que se integran en las redes sociales y espaciales de sus congéneres europeos. Estos hallazgos demuestran que las aves rapaces africanas están traspasando las fronteras biogeográficas mediante mecanismos fundamentalmente diferentes, lo que pone de relieve la necesidad de integrar la ecología del comportamiento y las interacciones interespecíficas en las predicciones sobre la redistribución de las especies en el contexto del cambio global.

El actual calentamiento climático también está haciendo que algunas poblaciones de aves de montaña tiendan a desplazar sus áreas de distribución hacia cotas más elevadas, siguiendo sus óptimos climáticos. Sin embargo, las limitaciones de espacio a gran altitud restringen las posibilidades de las especies de montaña para hacer frente a los cambios climáticos y las hacen especialmente vulnerables. En casos extremos, el nicho climático de algunas de estas especies puede desplazarse más allá de las cumbres de las montañas, llevándolas en última instancia a la extinción. En el **capítulo 5** se estudia el caso de la collalba gris (*Oenanthe oenanthe*) en España peninsular y se compara su distribución reproductora entre 2003 y 2022. España se encuentra en el límite de distribución más meridional de la especie en Europa, donde las collalbas ocupan mayoritariamente zonas montañosas. Para determinar los factores que condicionan la presencia reproductora de la especie se construyeron modelos de favorabilidad ambiental utilizando la información de los dos últimos atlas de aves españoles y un conjunto de variables climáticas, topográficas, de actividad humana y litológicas. La influencia del clima frente al resto de

factores se obtuvo mediante un análisis de partición de la varianza. Los resultados mostraron que la especie ha sufrido una fuerte reducción (67 %) en las áreas ocupadas, así como en la favorabilidad en toda España peninsular (especialmente en la mitad sur), donde el cambio climático puede tener consecuencias de gran alcance, incluyendo extinciones locales. Además, el clima parece ser el principal factor que condiciona la distribución actual de la collalba gris en España peninsular, ya que explica > 90% de la variación en el modelo obtenido para 2022, mientras que en 2003 > 65% de la distribución se explicaba por el efecto compartido del clima junto con la topografía, la actividad humana y la litología. Curiosamente, las zonas ocupadas en 2022 se encontraban 100 metros más altas, en promedio, que en 2003. De persistir los efectos del calentamiento climático, la especie está abocada a desaparecer en su límite de distribución más meridional, siendo la población del Parque Nacional Sierra de las Nieves la más vulnerable a escala nacional. Por este motivo, es necesario poner en marcha programas de seguimiento de las poblaciones de collalbas grises, prioritariamente en los sistemas montañosos donde ya ocupan las cotas más elevadas, así como profundizar en los estudios sobre otras especies de montaña.

En el **capítulo 6** analizamos el caso de un especialista de hábitats alpinos, el gorrión alpino (*Montifringilla nivalis*). Se trata de una especie muy vulnerable al cambio climático debido a su dependencia por ambientes de gran altitud, los cuales están experimentando un calentamiento acelerado, alteraciones en la dinámica de la nieve y cambios significativos en la fenología, entre otros factores. Estos hábitats, cruciales para la reproducción y alimentación de la especie, no suelen estar suficientemente muestreados debido a su lejanía y difícil accesibilidad. Además, se están reduciendo, sobre todo en los límites del área de distribución de la especie. En este estudio se compararon los datos de distribución reproductora del gorrión alpino procedentes del II y III atlas de aves de España (1998–2002 y 2014–2018, respectivamente) y se observó un declive significativo en su área de reproducción, desapareciendo de 17 cuadrículas (11 en la Cordillera Cantábrica y 6 en los Pirineos). Sin embargo, la comparación directa entre los atlas es problemática porque 30 cuadrículas muestreadas en el II atlas no fueron muestreadas en el III, lo que podría llevar a una disminución sobreestimada. Aunque los datos de eBird de 2014–2018 mitigaron parcialmente el declive percibido, las mismas 30 cuadrículas permanecieron sin muestrear, complicando aún más una evaluación definitiva del estado actual de la especie. Los veranos con temperaturas frescas y la baja humedad, indicada

por el Índice de Humedad Topográfica (TWI, por sus siglas en inglés: *Topographic Wetness Index*), se identificaron como los factores ambientales más influyentes que afectan a la distribución reproductora de la especie, basándose en los datos de distribución tanto del III atlas como de eBird. La principal conclusión de este estudio es que la interpretación de los datos procedentes de los atlas requiere cautela, especialmente para las especies que habitan en zonas remotas o inaccesibles. Las fuentes de datos alternativas, como eBird, pueden servir de apoyo a los programas de seguimiento en curso al proporcionar información adicional sobre la distribución de las especies. Sin embargo, incluso con eBird, algunas zonas de difícil acceso siguen estando insuficientemente muestreadas, lo que hace que se siga presumiendo que están desocupadas. Aumentar los esfuerzos de seguimiento en estas regiones altamente favorables pero insuficientemente muestreadas es crucial para mejorar las estrategias de conservación de esta especie alpina en declive.

Los registros de aves migratorias europeas de larga distancia que invernan en el Paleártico Occidental están aumentando, posiblemente en respuesta a las condiciones climáticas más suaves. En el **capítulo 7** se estudia el caso concreto del papamoscas gris (*Muscicapa striata*), un migrante tradicionalmente transahariano que ha sido observado recientemente invernando al norte del desierto del Sahara. Para ello, se recopilaban registros de invernada desde 2000 hasta 2024 utilizando la plataforma de ciencia ciudadana eBird y se modeló la distribución de estos datos en Europa y Oriente Medio, utilizando un conjunto de variables topo-climáticas. Los resultados proporcionan la primera evidencia de un patrón de invernada regular de la especie en el Paleártico Occidental durante la última década, con más del 80 % de los registros localizados en la Península Ibérica y las Islas Baleares, lo que concuerda con anomalías positivas de temperatura en Europa entre 2014 y 2023. Se identificaron cuatro variables climáticas como factores significativos, siendo el rango de temperatura diario y la temperatura del trimestre más frío dentro del área de estudio los mejores predictores. Utilizando lógica difusa, se han elaborado modelos conjuntos de estas variables bajo diferentes hipótesis, las cuales se han contrastado con registros de invernada independientes en el norte de África. Las zonas de invernada más favorables se localizan en áreas costeras e insulares del Mediterráneo, aunque aún no están plenamente ocupadas. Esta especie puede servir de modelo para otras especies migratorias transaharianas que ahora invernan en el Paleártico Occidental. Si las temperaturas continúan aumentando, se espera que más

individuos cambien su estrategia de invernada de migrantes transaharianos a presaharianos, lo que provocará un aumento de las poblaciones que pasan regularmente el invierno en las costas e islas del Mediterráneo.

En el **capítulo 8** se realiza una discusión general de los temas tratados en la presente tesis, haciendo hincapié en la importancia de los modelos de distribución realizados y sugiriendo futuras líneas de investigación, partiendo del conjunto de resultados obtenidos.

En el **capítulo 9** se recogen las principales conclusiones obtenidas a partir de todos los capítulos previos.

El **capítulo 10** recopila, por orden alfabético, las referencias bibliográficas usadas en la presente tesis doctoral.

El **capítulo 11** agrupa los apéndices que pertenecen a los **capítulos 2, 4, 6 y 7**. Al final de la tesis se detalla la producción científica asociada a la misma, así como otras contribuciones y un breve *curriculum vitae* del doctorando.

## **0. Outline of the Thesis**

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The present doctoral thesis consists of 11 chapters in which species distribution models (SDMs) are used as a methodological tool to study and understand the repercussions of current climate change on the spatio-temporal distribution of birds in the Western Palaearctic. To this end, different bird species have been selected which can be considered representative of groups of species that share common biogeographical patterns, so that by studying the selected species, the characteristics common to the entire group are studied. From a biogeographical perspective, the environmental factors that condition the distributions of these species are identified and the extent to which changes in climatic conditions are causing latitudinal and altitudinal changes in the distribution of the birds studied, as well as changes in their migration patterns, is assessed. The results obtained contribute to a better understanding of the dynamics of these species in the current context of climate change, making it possible to predict their responses to these changes. This information can be of great relevance to the competent authorities and environmental managers, as they can use it to increase monitoring and sampling efforts in areas identified by the models as highly favourable but still unoccupied by the different species, with the aim of being able to base effective conservation strategies.

The general organisation of the thesis is explained below:

**Chapter 1** provides a general introduction to this doctoral thesis. First, it presents the enormous complexity and variability of the climate system, describing its internal and external components. Next, a definition of climate change is provided and a historical overview of the first evidence of climate change on Earth is given, starting in the early 19<sup>th</sup> century, with special attention paid to the scientist Milutin Milankovitch for developing a theory capable of explaining natural fluctuations in the Earth's climate over the long term. Secondly, it highlights how the global average temperature has increased since the mid-20<sup>th</sup> century, with the last ten years being the warmest on record to date, reaching a record high in 2024. It also points out how the Intergovernmental Panel on Climate Change (IPCC) confirms in its sixth assessment report that human activities, with the massive emission of greenhouse gases into the atmosphere, are the main cause of current global warming. It is noted that this climate warming is particularly noticeable in

southern Europe and northern Africa, mentioning some of its effects on the terrestrial environment, including changes in the distribution of species.

Next, biogeography is introduced as a scientific discipline responsible for studying the distribution of species, both in space and time. A brief explanation is also provided of the characteristics of species distributions and their classifications according to the spatial segregation of individuals or populations (uniform, clumped or random distributions), the continuity of the species' range (continuous, discontinuous or disjunct distributions) or their global extent (cosmopolitan, relictual and/or endemic distributions). Next, a brief introduction to the dynamics of species distributions is provided, explaining why distributions are spatiotemporally dynamic, drawing an analogy with quantum physics. In addition, there is a brief section introducing the biogeographical limits of the species' range, explaining the importance of the specific dynamics of these limits in characterising changes in distribution. Subsequently, another brief section on biogeographical regions is presented to show that organisms of different species do not usually distribute independently of each other, but rather that there are distribution patterns common to a group of species or geographical areas. This allows us to contextualise the biogeographical region of the Western Palaearctic, where all the studies in this doctoral thesis have been performed.

After introducing current climate change and the general characteristics of species distributions, the effects of climate change on bird distributions are discussed. This section is divided into three subsections. The first explains how global warming is driving the distribution areas of numerous species towards higher latitudes, from the equator towards the poles, focusing on southern Europe and northern Africa, where typically African birds are beginning to colonise the south of the European continent. The second subsection indicates how global warming is also shifting the distribution areas of some mountain species populations to higher altitudes, so that they can adapt to their optimal climatic conditions. The last subsection explains how global warming is also changing the phenology and migration patterns of numerous bird species.

Next, the importance of SDMs as a tool for conservation under the effects of global warming is indicated, and the general procedure used in this thesis to develop these models is explained. It shows how the distribution data for the different bird species studied and the predictive environmental variables used were selected, the preliminary checks performed before creating the distribution models, the logistic regression

procedure and, finally, the calculation of favourability values. It also explains how favourability can measure the degree to which local conditions allow for a local probability that is higher or lower than expected by chance, this expected probability being the prevalence of the species in the study area, which is the main advantage it has over logistic regression. This procedure ends with a cartographic representation of the potential distribution of the species under consideration. However, it is important to bear in mind that SDMs always present a certain degree of uncertainty, which can be addressed through the use of fuzzy logic. Fuzzy logic has a number of advantages over classical logic when working in uncertain environments, such as the natural environment, and for handling vague concepts, such as the degree to which conditions are favourable for an event to occur, in this case the presence of a species in a given area.

The first chapter concludes by explaining why birds were specifically chosen to study the impact of climate change on species distribution.

At the end of the introduction, the general objective and the different specific objectives addressed during the development of this thesis are presented.

**Chapter 2** focuses on verifying whether southern Europe has climatically favourable areas for the establishment of typically African birds and identifying those areas. Current climate change is influencing the range of numerous species, with both expansions in distribution area and latitudinal shifts being observed. These changes in distribution are occurring worldwide, but are particularly relevant in southern Europe and northern Africa, where important biogeographical barriers, such as the Mediterranean Sea and the Sahara Desert, delimit the northern distribution of many African species and the southern distribution of many European species. In the case of African birds, a small expansion of their range northwards represents a major step in biogeographical terms, as it involves the colonisation of a new continent. This chapter aims to analyse the response of nine typically African birds to climate change in order to provide information on the current and future occupation of the European continent by these birds, as well as to identify European areas likely to receive African species. The nine birds studied have been observed in Spain over the last decade and, in some cases, breed consistently or sporadically. It also aims to assess and quantify the latitudinal disequilibrium between optimal climatic conditions for breeding and the current breeding distributions of two of the nine birds studied, the Atlas Long-legged Buzzard (*Buteo rufinus cirtensis*) and the Moussier's Redstart (*Phoenicurus moussieri*), as well as to calculate their displacement

rates. To this end, the distributions of the species in their native ranges were modelled, both in the present and in future climate scenarios, using their current breeding areas and a set of topographical and climatic variables. The climatic favourability of the nine species was then combined using fuzzy logic. The results showed that southern Europe currently has climatically favourable areas for the establishment of the group of African birds analysed, except for Rüppell's Vulture (*Gyps rueppelli*). These areas are located in the southern half of the Iberian Peninsula, southern Italy, Greece, Turkey and the large Mediterranean islands, such as the Balearic Islands, Sardinia, Sicily, Crete and Cyprus. Future forecasts, considering different climate change scenarios, indicated that this favourability will increase towards higher latitudes in Western Europe, especially in the northern half of the Iberian Peninsula, central and northern France, and the northern half of Italy, again excluding the African vulture. The results also showed that the latitudinal disequilibrium between the breeding distributions of the Buzzard and the Redstart and their optimal climatic conditions was 4 and 2.8 km to the north, at a rate of 1.3 and 3.4 km/year, respectively. If climate continues to warm, further arrivals of individuals can be expected, increasing the possibility of self-sustaining populations becoming established in southern Europe. In addition, new African species could begin to occupy this area, with the likelihood of an Africanisation of European fauna. Given the role played by southern Europe as a possible focus for colonisation of this continent by African species, it is important to monitor their northward expansion and future spread.

The increase in temperatures due to the impact of climate change is causing southern Europe to acquire climatic conditions similar to those found in North Africa, which seems to be altering the distribution ranges of species. **Chapter 3** focuses on studying one of the typically African birds analysed in the previous chapter, the House Bunting (*Emberiza sahari*). In recent decades, this sedentary bird has increased its range northwards in Morocco, reaching the Mediterranean coast. Currently, its northern distribution limit is on the coast of North Africa. However, the species has been regularly recorded in the south of the Iberian Peninsula in recent years, albeit in low numbers and without breeding in Europe at the time of the study. This chapter aimed to determine whether the climatic conditions in southern Europe, both current conditions and various climate change estimates based on different emission scenarios, are suitable for this species to breed, as well as to identify where these conditions occur. To this end, the distribution of the species in its native range was modelled, both in the present and in future climate scenarios, using

its current breeding ranges and a set of environmental variables. The results showed that the southwestern quadrant of the Iberian Peninsula exhibits high values of favourability for hosting the species, both for current climatic conditions and for different future climate change scenarios. In fact, the southernmost areas of the Iberian Peninsula proved to be as favourable as the native Moroccan areas and already regularly receive individuals of the species. It is very likely that these observations correspond to vagrant birds dispersing from recently colonised breeding areas in northern Morocco, which could indicate a continuous process of colonisation towards the north, as has occurred in recent decades in North Africa. At the end of the chapter, an addendum validating the distribution model is included, confirming the breeding of the species in the south of the Iberian Peninsula a few months after the publication of the model.

**Chapter 4** investigates the mechanisms underlying the recent colonisation of Europe by African raptors, analysing three species that are currently expanding throughout the Afro-Palaeartic system: the Atlas Long-legged Buzzard, Rüppell's Vulture and the White-backed Vulture (*Gyps africanus*). Using species distribution models based on topoclimatic predictors, the environmental favourability for breeding in the Western Palaeartic and Afrotropical regions is estimated. The results reveal contrasting colonisation pathways. The Long-legged Buzzard shows broad climatic favourability across North Africa and parts of southern Europe, consistent with climate-driven range expansion. In contrast, African vultures exhibit negligible climatic favourability in Europe, even though Rüppell's Vulture has already bred on the continent, always in hybrid pairs with Griffon Vultures (*G. fulvus*), and White-backed Vultures are increasingly observed as immatures. These patterns indicate colonisation mediated by socially assisted vagrancy, with immature vultures integrating into the social and spatial networks of their European congeners. These findings demonstrate that African raptors are transgressing biogeographic boundaries through fundamentally different mechanisms, highlighting the need to integrate behavioural ecology and interspecific interactions into predictions of species redistribution in the context of global change.

Current global warming is also causing some mountain bird populations to shift their ranges to higher altitudes, tracking their climatic optima. However, space limitations at high altitudes constrain the ability of mountain species to cope with climate change, making them particularly vulnerable. In extreme cases, the climatic niche of some of these species may shift beyond mountaintops, ultimately leading to their extinction. **Chapter 5**

studies the case of the Northern Wheatear (*Oenanthe oenanthe*) in peninsular Spain and compares its breeding distribution between 2003 and 2022. Spain is at the southernmost limit of the species' distribution in Europe, where Wheatears mainly occupy mountainous areas. To determine the factors that condition the breeding presence of the species, environmental favourability models were built using information from the last two Spanish bird atlases and a set of climatic, topographic, human activity and lithological variables. The influence of climate compared to all other factors was obtained through a variation partitioning analysis. The results showed that the species has suffered a strong reduction (67%) in occupied areas, as well as in favourability throughout mainland Spain (especially in the southern half), where climate change may have far-reaching consequences, including local extinctions. Furthermore, climate seems to be the main factor conditioning the current distribution of the Northern Wheatear in peninsular Spain, 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. Interestingly, the occupied areas in 2022 were 100 metres higher, on average, than in 2003. If the effects of global warming persist, the species is doomed to disappear in its southernmost distribution limit, with the population of the Sierra de las Nieves National Park being the most vulnerable on a national scale. For this reason, it is necessary to implement monitoring programmes for Northern Wheatear populations, primarily in mountain systems where they already occupy the highest elevations, as well as further studies on other mountain species.

In **chapter 6**, we analyse the case of a specialist in alpine habitats, the White-winged Snowfinch (*Montifringilla nivalis*). This species is highly vulnerable to climate change due to its reliance on high-altitude environments, which are experiencing accelerated warming, alterations in snow dynamics and significant shifts in phenology, among other factors. These habitats, which are crucial for the breeding and feeding of the species, are often under-sampled due to their remoteness and difficult accessibility. Furthermore, they are shrinking, particularly at the species' range edges. This study compared breeding distribution data of the White-winged Snowfinch from the II and III Spanish bird atlases (1998–2002 and 2014–2018, respectively) and observed a significant decline in its breeding range, disappearing from 17 grid cells (11 in the Cantabrian Mountains and 6 in the Pyrenees). However, direct comparison between the atlases is problematic because 30 grid cells surveyed in the II atlas were not sampled in the III, which could lead to an

overestimated decline. Although eBird data from 2014–2018 partially mitigated the perceived decline, the same 30 grid cells remained unsampled, further complicating a definitive assessment of the species' current status. Cool summer temperatures and low humidity, as indicated by the Topographic Wetness Index (TWI), were identified as the most influential environmental factors affecting the species' breeding distribution, based on distribution data from both the III Atlas and eBird. The main conclusion of this study is that interpretation of atlas data requires caution, particularly for species inhabiting remote or inaccessible areas. Alternative data sources, such as eBird, can support ongoing monitoring programmes by providing additional insights into species distribution. However, even with eBird, certain hard-to-reach areas remain under-sampled, causing them to still be presumed unoccupied. Increasing monitoring efforts in these highly favourable but under-sampled regions is crucial to improving conservation strategies for this declining alpine species.

Records of European long-distance migrant birds wintering in the Western Palaearctic are increasing, possibly in response to milder climatic conditions. **Chapter 7** studies the specific case of the Spotted Flycatcher (*Muscicapa striata*), a traditionally trans-Saharan migrant that has recently been observed wintering north of the Sahara Desert. To this end, wintering records from 2000 to 2024 were compiled using the eBird citizen science platform, and the distribution of these data in Europe and the Middle East was modelled using a set of topo-climatic variables. The results provide the first evidence of a regular wintering pattern of the species in the Western Palaearctic during the last decade, with over 80% of the records located on the Iberian Peninsula and the Balearic Islands, which is consistent with positive temperature anomalies in Europe between 2014 and 2023. Four climatic variables were identified as significant drivers, with the diurnal temperature range and the temperature of the coldest quarter within the study area being the strongest predictors. Using fuzzy logic, ensemble models of these variables have been developed under different hypotheses, which have been tested against independent wintering records in North Africa. The most favourable wintering areas are located in coastal areas and islands of the Mediterranean, although they are not yet fully occupied. This species may serve as a model for other trans-Saharan migratory species that currently winter in the Western Palaearctic. If temperatures continue to increase, more individuals are expected to shift their wintering strategy from trans-Saharan to pre-Saharan migrants, leading to an increase in populations regularly wintering along Mediterranean coasts and islands.

**Chapter 8** provides a general discussion of the topics covered in this thesis, emphasising the importance of the distribution models performed and suggesting future lines of research based on the set of results obtained.

**Chapter 9** encompasses the main conclusions derived from all the previous chapters.

**Chapter 10** compiles, in alphabetical order, the bibliographic references used in this doctoral thesis.

**Chapter 11** compiles the appendices belonging to **chapters 2, 4, 6 and 7**. At the end of the thesis, the scientific output associated with it is detailed, along with other contributions and a brief *curriculum vitae* of the PhD student.

# CAPÍTULO 1

## Introducción General

## 1. Introducción General

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### 1.1 Primeras evidencias de un cambio climático

El clima es un sistema complejo y variable influido por múltiples factores de distinta naturaleza que interactúan entre sí a distintas escalas y generan procesos que afectan a los ecosistemas y a las especies que habitan en ellos (Lovejoy & Hannah 2005, Dessler 2021). Los factores climáticos se pueden clasificar como componentes internos y externos al propio sistema (Goosse 2015). Entre los componentes internos se incluyen la atmósfera (capa de gases que rodea la Tierra), la hidrosfera (océanos, mares, ríos, lagos y superficies de agua), la criósfera (glaciares, casquetes polares y la nieve estacional), la biosfera (todos los seres vivos que habitan en la Tierra) y la geósfera (conjunto de capas que forman la parte sólida de la Tierra). Entre los componentes externos están el Sol, la rotación de la Tierra, la geometría del Sol-Tierra y los cambios de la órbita, además de los componentes físicos del planeta (distribución de la tierra y los océanos), las características geográficas de la Tierra (topografía del fondo oceánico y configuración de las cuencas), y la masa y composición básica de la atmósfera y el océano (Goosse 2015). Además, también hay que destacar las variaciones astronómicas cíclicas: excentricidad, oblicuidad y precesión (Milankovitch 1941, Dimitrijević 2020), entre otros. A este elevado número de factores, debe añadirse la infinidad de posibles interacciones entre ellos, proporcionándonos una idea de la enorme complejidad del sistema climático y, con ello, del número de fuentes de incertidumbre que pueden asociarse a cualquier predicción sobre cambios en el clima.

Un cambio climático se define como la variación significativa en el estado del sistema climático terrestre que persiste durante largos períodos de tiempo, generalmente décadas o períodos más largos, hasta alcanzar un nuevo equilibrio (IPCC 2013). Los cambios climáticos han existido desde el inicio de la historia de la Tierra y pueden deberse a procesos internos naturales o a forzamientos externos tales como modulaciones de los ciclos solares, erupciones volcánicas o cambios antropogénicos persistentes de la composición de la atmósfera o del uso del suelo (IPCC 2022). La Convención Marco de las Naciones Unidas sobre el Cambio Climático (CMNUCC), en su artículo 1, define el actual cambio climático como “cambio de clima atribuido directa o indirectamente a la actividad humana que altera la composición de la atmósfera global y que se suma a la variabilidad natural del clima observada durante períodos de tiempo comparables”. La

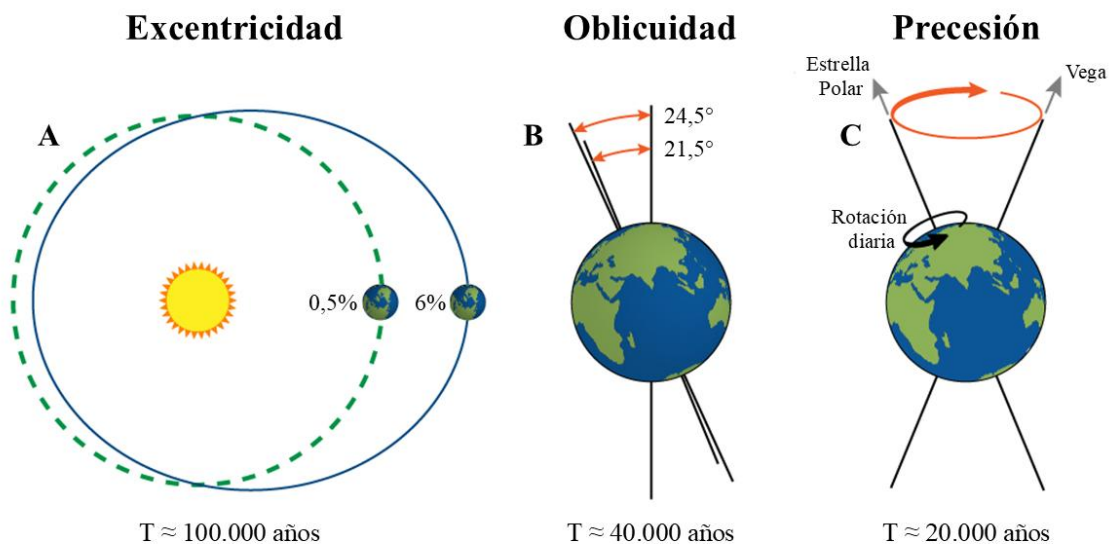
CMNUCC diferencia, pues, entre el cambio climático atribuible a las actividades humanas que alteran la composición atmosférica y la variabilidad climática atribuible a causas naturales.

Sin embargo, el hecho de que el clima sea un sistema cambiante no es algo que haya sido aceptado por la sociedad desde siempre. Las primeras evidencias de un cambio climático en la Tierra se remontan a estudios de principios del siglo XIX. En 1824, el científico francés Joseph Fourier fue el primero en proponer que la atmósfera de la Tierra podría actuar como un “invernadero”, permitiendo que la radiación solar entrara y parte de la energía quedase atrapada, manteniendo así la temperatura de la Tierra más cálida de lo que sería sin atmósfera. Fourier también observó que ciertos gases, como el dióxido de carbono ( $\text{CO}_2$ ), podían actuar como una barrera para la radiación térmica, manteniendo el calor dentro de la atmósfera terrestre (Fourier 1824). Alrededor de la década de 1830, Karl Schimper desarrolló una de las primeras teorías sobre la “Edad de Hielo” (o glaciación) (Woodward 2014). La científica estadounidense Eunice Foote realizó experimentos que demostraron que el  $\text{CO}_2$  y el vapor de agua podían retener calor, publicando sus hallazgos en 1856 (Foote 1856). Unos años más tarde, John Tyndall también confirmó el papel de los gases como el  $\text{CO}_2$  y el metano ( $\text{CH}_4$ ) en la absorción de calor y propuso que cambios en la concentración de gases en la atmósfera podían producir un “calentamiento global” (Tyndall 1861). En 1864, el británico James Croll publicó el primer estudio que relacionaba las variaciones de la órbita de la Tierra con la aparición de las eras glaciares (Croll 1864). A finales del siglo XIX, el científico sueco Svante Arrhenius fue una de las primeras personas en sugerir que la quema de combustibles fósiles podría aumentar la concentración de  $\text{CO}_2$  en la atmósfera y, con ello, la temperatura global. Arrhenius calculó que la duplicación de la concentración de  $\text{CO}_2$  en la atmósfera podría aumentar la temperatura de la Tierra y, aunque subestimó el tiempo que se tardaría en alcanzar tales niveles, su teoría fue un hito para entender la relación entre la actividad humana y el cambio climático (Arrhenius 1896).

En la primera mitad del siglo XX, el científico serbio Milutin Milankovitch complementó los estudios de Croll y desarrolló la teoría de los ciclos de Milankovitch, la cual ayudó a explicar las fluctuaciones naturales en el clima de la Tierra a largo plazo. Esta teoría describe cómo los cambios rítmicos en el ángulo de orientación de la Tierra respecto al Sol influyen en el clima global, especialmente en la aparición de las eras glaciares e interglaciares (Milankovitch 1941, Hays *et al.* 1976, Dimitrijević 2020).

Milankovitch identificó tres tipos de variaciones astronómicas que afectan la cantidad de radiación solar que llega a la Tierra en distintas épocas y latitudes (**Figura 1.1.1**). Estos tres ciclos son:

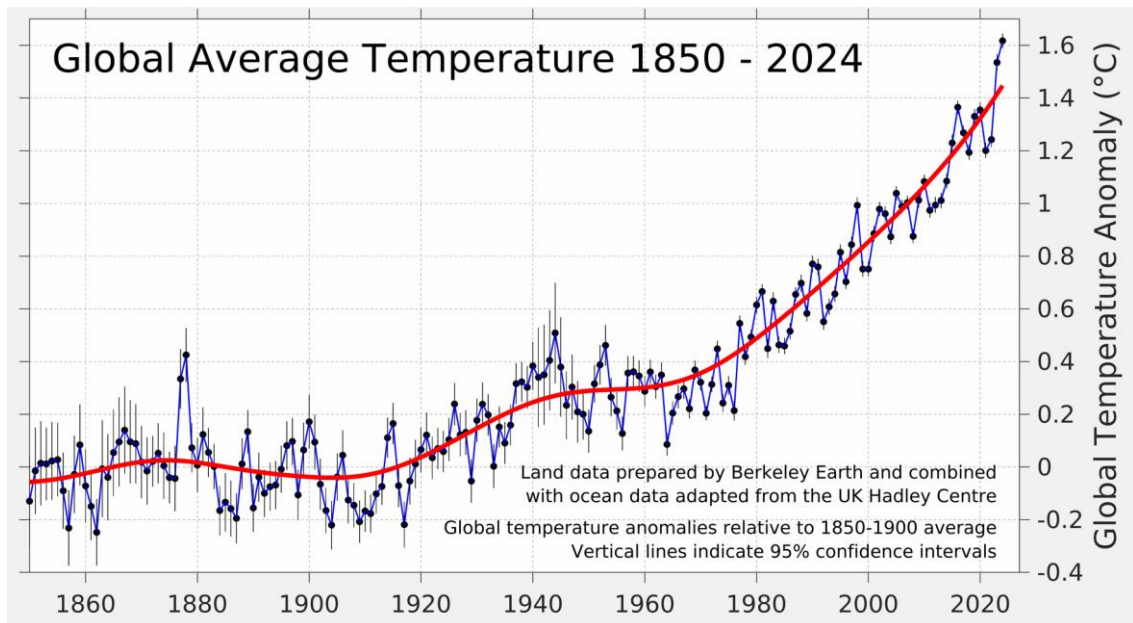
- *Excentricidad*: Describe las variaciones en la forma de la órbita terrestre alrededor del Sol, que va de casi circular (0,5%) a elíptica (6%). Este ciclo dura aproximadamente 100.000 años.
- *Oblicuidad*: Se refiere al ángulo de inclinación que presenta el eje de rotación de la Tierra con respecto a su plano orbital. Este ángulo varía entre aproximadamente  $21,5^\circ$  y  $24,5^\circ$  en un ciclo de unos 40.000 años. Actualmente, el eje de rotación de la Tierra está desviado unos  $23,4^\circ$  con respecto a la vertical.
- *Precesión*: Describe el “bamboleo” de la Tierra sobre su eje de rotación, lo que implica un cambio en la orientación de su inclinación respecto al Sol en un ciclo de aproximadamente 20.000 años.



**Figura 1.1.1.** Los ciclos de Milankovitch: excentricidad (A), oblicuidad (B) y precesión (C).

En 1930, Milankovitch consiguió que la comunidad científica aceptara por primera vez que el clima ha experimentado cambios significativos a lo largo de la historia de la Tierra con la publicación de “La climatología matemática y la teoría astronómica de los

cambios climáticos”. A lo largo de los últimos 2,5 millones de años se han producido 17 periodos glaciares, cada uno de ellos de 100.000 años aproximadamente. Los periodos glaciares han estado separados entre sí por otros más cortos denominados interglaciares, con una duración de unos 8.000 años. Actualmente nos encontramos en un periodo interglaciar llamado *Holoceno* (época más reciente del Cuaternario), el cual ya ha superado los 11.000 años. A pesar de que a lo largo de la historia de la Tierra se han producido diferentes fenómenos naturales que culminaron en cambios en las condiciones climáticas, siendo los más recientes los periodos glaciares e interglaciares que se produjeron durante el Cuaternario (Oliva *et al.* 2019, Jary & Marks 2024), la temperatura ha permanecido bastante estable (con pequeñas fluctuaciones de menos de 1°C por siglo) durante los últimos ocho milenios (Duarte *et al.* 2006, Pachauri & Meyer 2014). Sin embargo, desde mediados del siglo XX ha habido un aumento de la temperatura media global, siendo los últimos diez años los más cálidos que se han observado hasta el momento (**Figura 1.1.2**).



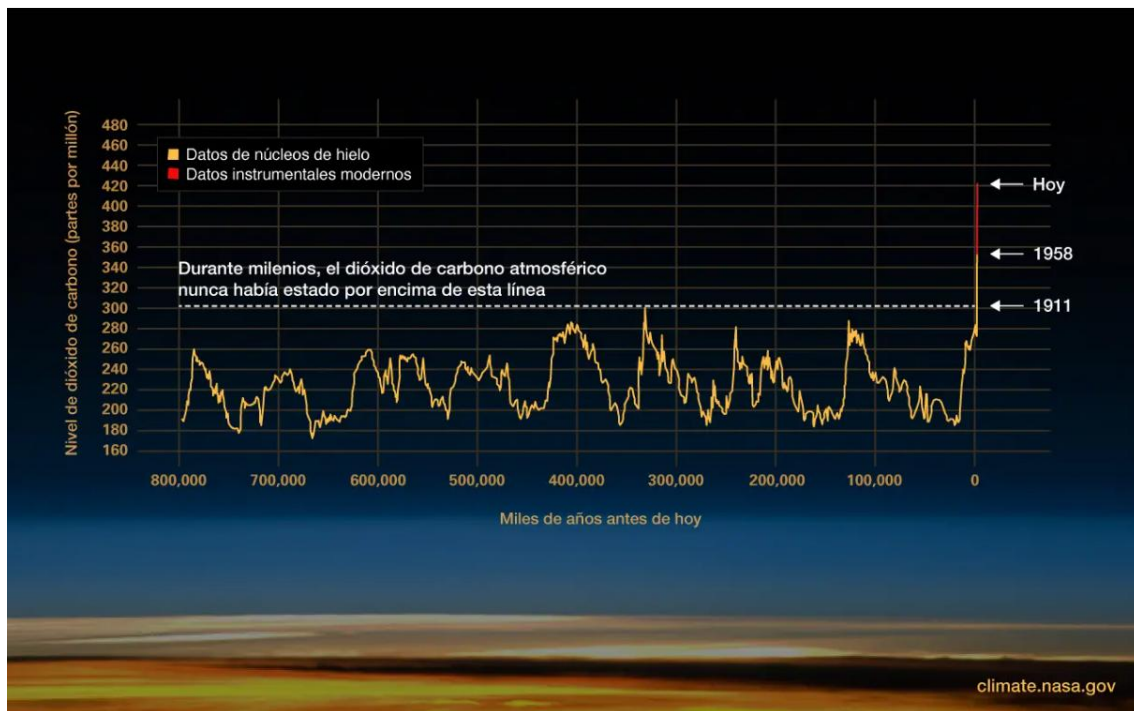
**Figura 1.1.2.** Anomalías medias globales de temperatura (°C) desde 1850 hasta 2024 relativas a la temperatura promedio del periodo 1850-1900. Este periodo suele utilizarse como referencia preindustrial para los objetivos de temperatura mundial. Fuente: © Berkeley Earth (2025).

El récord lo encontramos en 2024, el cual muestra un calentamiento de 1,62°C con respecto a la temperatura media del periodo 1850-1900 (Berkeley Earth 2025). Este es el segundo año consecutivo que la temperatura media anual supera en más de 1,5 °C la del periodo de referencia preindustrial (Berkeley Earth 2025). El Panel Intergubernamental de Expertos sobre el Cambio Climático (IPCC, por sus siglas en inglés: *Intergovernmental Panel on Climate Change*), fundado en 1988 por la Organización Meteorológica Mundial (OMM) y el Programa de las Naciones Unidas para el Medio Ambiente (PNUMA), confirma en su sexto informe de evaluación que las actividades humanas son la principal causa del actual calentamiento global, con impactos observados en todos los continentes y océanos (IPCC 2022).

## 1.2 Efecto de la actividad humana sobre el clima

Los seres vivos, al ser uno de los componentes internos del sistema climático, también ejercen una influencia sobre el clima y el ser humano, como una especie más, la ha ejercido desde su origen, aunque se ha tornado más acusada tras la revolución industrial (1780-1850) debido al rápido crecimiento de la población, al desarrollo de nuevas tecnologías y al incremento en el consumo de recursos (Duarte *et al.* 2006). El cambio climático actual presenta dos características que hacen que los cambios asociados sean únicos en la historia del planeta: en primer lugar, la rapidez con la que están sucediendo estos cambios, los cuales se están produciendo en espacios de tiempo tan cortos como décadas; y, en segundo lugar, el hecho de que una única especie, el *Homo sapiens*, es el motor principal de los mismos (Duarte *et al.* 2006, Barnett *et al.* 2015). En la actualidad, ya se ha puesto de manifiesto que el ser humano tiene capacidad para afectar directamente el clima del planeta, con la masiva emisión de gases con efecto invernadero (GEI) a la atmósfera (IPCC 2022). Las emisiones de GEI como el dióxido de carbono (CO<sub>2</sub>), el metano (CH<sub>4</sub>), el óxido nitroso (N<sub>2</sub>O), los clorofluorocarbonos (CFC<sub>s</sub>), el ozono (O<sub>3</sub>), los derivados del azufre, etc. procedentes de la quema de combustibles fósiles (carbón, petróleo y gas natural), la actividad industrial, los incendios forestales, la agricultura, la ganadería, la deforestación y los cambios en el uso del suelo interfieren en la dinámica atmosférica, alterando el clima y contribuyendo al aumento de la temperatura global (Duarte *et al.* 2006, IPCC 2022). La concentración media de CO<sub>2</sub> en la atmósfera antes de la revolución industrial era de unas 280 partes por millón (ppm), elevándose hasta 350 ppm en 1958, y en la actualidad ya supera los 420 ppm (**Figura 1.2**; Climate Change -

NASA Science 2024). Las concentraciones medias de CH<sub>4</sub> y N<sub>2</sub>O también han aumentado desde la era preindustrial hasta la actualidad de 0,71 a 1,92 ppm y de 0,275 a 0,336 ppm, respectivamente (Duarte *et al.* 2006, Climate Change - NASA Science 2024). Estos valores siguen marcando máximos históricos (son los más altos desde que se están realizando mediciones directas) y cuyas tendencias siguen en aumento, por lo que es muy probable que la temperatura media global supere regularmente los 1,5 °C con relación a los niveles de la era preindustrial en las próximas décadas (IPCC 2022).



**Figura 1.2.** Concentración media de dióxido de carbono (CO<sub>2</sub>) en la atmósfera (partes por millón, ppm) a lo largo de los últimos 800.000 años. Gráfica basada en la comparación de muestras atmosféricas contenidas en núcleos de hielo (línea naranja) y mediciones directas más recientes (línea roja). Fuente: © Climate Change - NASA Science (2024).

El calentamiento climático también puede estar aumentando la frecuencia e intensidad de los fenómenos climáticos extremos (sequías, olas de calor, tempestades, inundaciones, ciclones tropicales que alcanzan la categoría de huracán), así como acelerando el retroceso de los glaciares en las montañas y disminuyendo la extensión del hielo en los polos (Welbergen *et al.* 2008, Marx *et al.* 2021, McKechnie *et al.* 2021, Al-Yaari *et al.* 2023, Ficetola *et al.* 2024, Jaafar & Sujud 2024, Kleespies *et al.* 2024). Algunos ejemplos

de ello pueden ser las dos últimas DANAs (*Depresión Aislada en Niveles Altos*) ocurridas en las provincias de Valencia y Málaga el pasado 29 de octubre y 13 de noviembre de 2024, respectivamente; o el ciclón “Daniel” ocurrido en septiembre de 2023 y considerado el ciclón de tipo tropical mediterráneo más mortífero jamás registrado. El régimen de precipitación, más impredecible, también está mostrando cambios a niveles más regionales: en Europa central y septentrional se han registrado mayores cantidades de lluvia, mientras que en Europa meridional éstas han disminuido (EEA 2012, Coll *et al.* 2017, Drobinski *et al.* 2020). La mitad sur de la península Ibérica se ha vuelto más cálida y seca en las últimas décadas, adquiriendo unas condiciones climáticas similares a las que encontramos en el norte de África (Coll *et al.* 2017, Paniagua *et al.* 2019, Drobinski *et al.* 2020). Estos efectos del cambio climático ejercen una presión negativa sobre la disponibilidad de agua, el potencial hidroeléctrico, la productividad de los cultivos y la biodiversidad, entre otros (Harley 2011, Mekonnen & Hoekstra 2016, de Jong *et al.* 2018, Ortiz-Bobea *et al.* 2021). También pueden alterar los ciclos biológicos, modificar la estructura y composición de los ecosistemas, así como condicionar la distribución geográfica de las especies, tanto en el espacio como en el tiempo (Gordo & Sanz 2006, Lenoir *et al.* 2008, Chamorro *et al.* 2020, Du *et al.* 2021, Ficetola *et al.* 2024, López-Ramírez *et al.* 2024a).

### 1.3 Las distribuciones de las especies

La distribución de una especie se define como el espacio geográfico en el que un conjunto de individuos pertenecientes al mismo taxón biológico consigue asentarse o establecerse, de manera que pueden interactuar tanto con el ambiente como con otros seres vivos (Maciel-Mata *et al.* 2015). La disciplina científica encargada de documentar y comprender los patrones de distribución de las especies en el espacio y en el tiempo, respondiendo a la pregunta de cómo varía la biodiversidad a lo largo de la superficie terrestre es la biogeografía (Lomolino *et al.* 2006a). Se trata de una ciencia interdisciplinar, ya que se nutre de otras ramas de la biología y ciencias de la Tierra, como son la ecología, la biología evolutiva, la sistemática, la geología y la genética, entre otras (Brown & Gibson 1983). Sin embargo, a diferencia de estas disciplinas, la biogeografía siempre debe tener una visión holística de los patrones que estudia, incluyendo el contexto espacio-temporal en el que se desarrollan como parte imprescindible del estudio

(Lomolino *et al.* 2006b). Por ello, también recoge características propias de la geografía y la cartografía.

Una reciente rama de la biogeografía enfoca su interés en la aplicación de los principios, teorías y análisis biogeográficos relacionados con la dinámica de las distribuciones de las especies a problemas relativos a la conservación de la biodiversidad (Whittaker *et al.* 2005). Se trata de la biogeografía de la conservación, que tiene como parte de sus objetivos proporcionar herramientas para la elección de zonas prioritarias a proteger, así como conocer en detalle los factores que condicionan las distribuciones de las especies (Ladle & Whittaker 2011). En la presente tesis doctoral, el análisis de las distribuciones de las diferentes especies estudiadas aporta resultados que pueden apoyar a las acciones de conservación y gestión eficaz de dichas especies, bajo el contexto actual de cambio climático.

### 1.3.1 Características y tipos de distribuciones

Las distribuciones de las especies están determinadas por una combinación de factores abióticos, bióticos, históricos y antropogénicos (Real *et al.* 2003, Lomolino *et al.* 2006c, Di Marco & Santini 2015, Meza Mori *et al.* 2023, Benedetti & Morelli 2024). Los factores abióticos hacen referencia a las condiciones físicas y químicas del ambiente (temperatura, precipitación, luz solar, disponibilidad de agua...), los bióticos a las propias limitaciones de las especies (fisiológicas, morfológicas, ciclos de vida...) y a las interacciones con otros organismos (competencia, depredación, mutualismo, enfermedades, parásitos...), los históricos a eventos geológicos y evolutivos que han tenido lugar a lo largo de la historia de nuestro planeta (tectónica de placas, historia evolutiva de la especie, extinciones masivas...) y los antropogénicos al impacto de la actividad humana sobre los ecosistemas (cambio climático, fragmentación del hábitat, contaminación, sobreexplotación, introducción de especies invasoras...). Los diferentes factores interaccionan entre sí, afectando positiva o negativamente a la supervivencia, reproducción, dispersión, etc. de las especies y condicionando sus distribuciones (Antúnez & Mendoza 1992, Chamorro *et al.* 2017, 2021, Rocha-Méndez *et al.* 2024). Además, también existen barreras geográficas (cadenas montañosas, mares, océanos, desiertos...) que pueden limitar la distribución de las especies (Gantenbein & Largiadèr 2003, Joger *et al.* 2007, Oppel *et al.* 2015, Efrat *et al.* 2019). La existencia de estas

barreras y factores condicionantes normalmente impiden a los individuos y poblaciones distribirse de manera uniforme en el medio, dando como resultado patrones complejos de distribución (Chamorro *et al.* 2021). La comprensión de estos factores y barreras es esencial para promover una conservación eficaz de la biodiversidad y favorecer una gestión informada de los ecosistemas.

Las distribuciones se pueden clasificar atendiendo a diferentes criterios (Espinosa *et al.* 2001, Molles 2008, Maciel-Mata *et al.* 2015). Según la manera en la que los individuos o poblaciones de una especie se segregan en el espacio, la distribución puede clasificarse como:

- *Uniforme*: cuando se maximiza la separación entre los individuos/poblaciones.
- *Agrupada*: cuando la distancia entre individuos o poblaciones vecinas es baja.
- *Aleatoria*: cuando la distancia no sigue un patrón claro.

Según la continuidad de la distribución se clasifican en:

- *Continua*: cuando las poblaciones no presentan interrupciones, posibilitando el intercambio genético entre todos los individuos.
- *Discontinua*: cuando presenta poblaciones fragmentadas debido a extinciones locales de algunas de sus poblaciones, pero las distancias entre estas permiten el intercambio genético entre los individuos.
- *Disyunta*: cuando aparecen poblaciones separadas por alguna barrera geográfica o ambiental difícil de superar de manera natural. En este caso, el intercambio genético entre los individuos es limitado o nulo.

Según la extensión global de la distribución se clasifican en:

- *Cosmopolita*: cuando hay individuos/poblaciones de la especie presentes en todos los continentes del planeta, a excepción de la Antártida.

- *Relicta*: cuando hay individuos/poblaciones de la especie que en el pasado ocupaban grandes áreas geográficas, pero actualmente están confinados en espacios de menor tamaño.
- *Endémica*: los individuos/poblaciones de la especie sólo están presentes en cierta región o zona del planeta.

### 1.3.2 Dinamismo en las áreas de distribución

Los diferentes tipos de distribuciones presentan la característica común de ser dinámicas. Esto se debe a que los individuos realizan desplazamientos diarios, estacionales, anuales, dispersiones, migraciones locales, etc. (Müller 1979). Estos continuos cambios en la localización de los organismos dificultan considerablemente conocer a priori la localización exacta de todos los individuos de la especie (Real *et al.* 2017). En los últimos años, se ha incrementado el uso de sistemas de seguimiento a distancia para monitorizar detalladamente los movimientos de ejemplares concretos (Flack *et al.* 2018, Iverson *et al.* 2023, Kunasranta *et al.* 2024, McGinness *et al.* 2024). Sin embargo, hasta la fecha es muy difícil monitorizar a todos los individuos de una especie debido a las limitaciones y dificultades que presenta dicha tecnología (Recio *et al.* 2011, Weidensaul 2012, Iverson *et al.* 2023), por lo que su uso para determinar la distribución completa de una especie es todavía escaso. Actualmente se están produciendo importantes avances en esta línea (Iverson *et al.* 2023) y es posible que en un futuro la tecnología contribuya a conocer en mayor profundidad las distribuciones de poblaciones, e incluso especies, a tiempo real.

Las distribuciones de las especies suelen estar representadas por registros de su presencia observada a una escala espacial y temporal determinada (Pleguezuelos *et al.* 2004, Palomo *et al.* 2007, Molina *et al.* 2022). Estos registros son inevitablemente incompletos y dependen de las circunstancias espacio-temporales en las que se realizaron las observaciones (Barbosa *et al.* 2013a). Además, los organismos pueden responder de forma diferente a condiciones ambientales similares en distintos lugares o momentos, por lo que su distribución no es, en principio, completamente predecible (Hengeveld 1992). La existencia de esta incertidumbre nos lleva a considerar las especies análogas a los objetos cuánticos, cuyas distribuciones se describen mejor mediante una función de onda que mediante un conjunto de localizaciones (Real *et al.* 2017). En mecánica cuántica,

hasta que un objeto (por ejemplo, una partícula) no se observa directamente (es decir, se mide), no se puede conocer su localización exacta. Lo que sí se puede saber es la probabilidad que tiene ese objeto de estar en una localidad concreta, gracias a la función de onda que describe las probabilidades de existir en cada uno de los lugares del espacio-tiempo (Zurek 1991). En ese tiempo, el objeto está parcialmente presente (y ausente) en todas las localidades, siendo mayor el “grado de presencia” en aquellas localidades cuya función de onda de probabilidad es mayor. Sólo en el momento en el que se mide la localización del objeto –lo que se conoce como el colapso de la función de onda– es cuando éste se encuentra temporalmente en esa localización medida (Zurek 1991, Real *et al.* 2017). Las especies, al ser seres físicos y, por lo tanto, tener propiedades de las leyes físicas, comparten características comunes con los objetos cuánticos como es el caso de sus distribuciones (Real *et al.* 2017). De esta manera, una especie no está ni presente ni ausente en su área de distribución, sino que está presente en cierto grado en cada una de las localidades, y la observación reiterada en esas localidades es la única forma de constatar la presencia o ausencia de la especie en una zona concreta (Gouveia *et al.* 2020). Por lo tanto, las distribuciones de las especies son dinámicas, es decir, cambian constantemente a lo largo de diferentes escalas espacio-temporales y esto se debe tener en cuenta en sus representaciones cartográficas, sobre todo a la hora de tomar decisiones que afecten a la gestión y conservación de las propias especies.

### 1.3.3 Los límites biogeográficos de las distribuciones

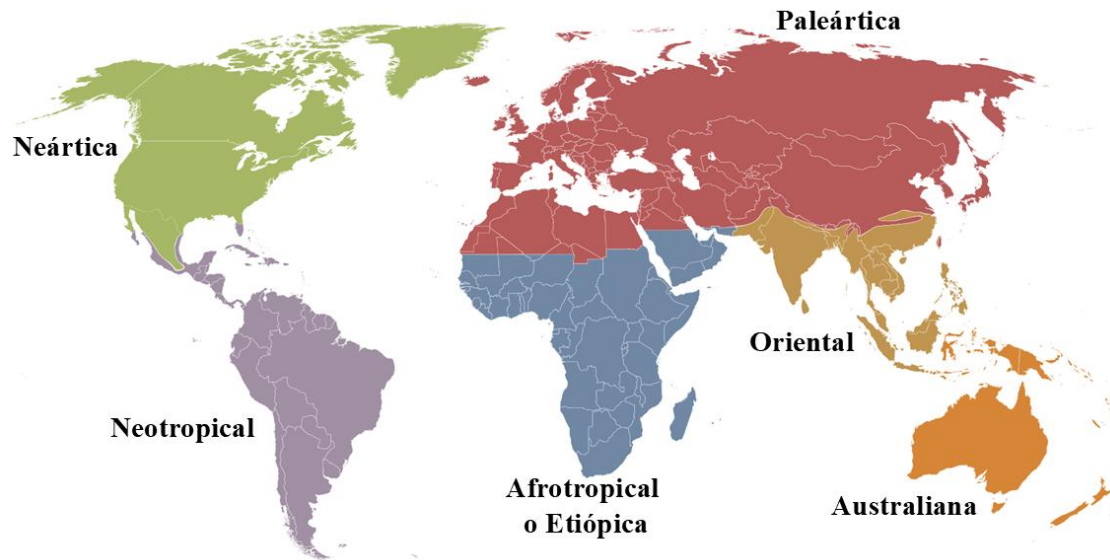
Las fronteras naturales o artificiales que determinan la distribución geográfica de una especie se conocen como límites biogeográficos (Cox *et al.* 2016). En ausencia de barreras geográficas, la distribución de una especie finaliza cuando los factores bióticos y/o abióticos limitan la supervivencia, reproducción y aptitud de los individuos (Hoffmann & Blows 1994). Esto se debe a que las condiciones ambientales para las poblaciones marginales o periféricas, aquellas que se encuentran en el límite del área de distribución, suelen ser más desfavorables que para las poblaciones centrales, haciendo que la densidad de individuos decrezca a medida que nos acercamos a los límites del área de distribución de la especie (Brown 1984, Brown *et al.* 1995, Martínez-Meyer *et al.* 2013). Las causas de este decrecimiento pueden ser diversas: los individuos de las poblaciones periféricas están próximos a sus límites de tolerancia ambiental (Mac Arthur 1972, Wiens & Graham 2005); las interacciones bióticas negativas, como la competencia

por los recursos o la depredación, pueden hacer disminuir el número de individuos (Darwin 1859); el mayor aislamiento geográfico de las poblaciones periféricas puede reducir el flujo de genes procedentes de las poblaciones del centro de la distribución, resultando en una menor capacidad de respuesta adaptativa a las condiciones de los márgenes (Kirkpatrick & Barton 1997); o, simplemente, la especie carece de la variabilidad genética que le permite adaptarse a las condiciones del otro lado del margen (Case & Taper 2000).

Los límites biogeográficos, siempre que no estén delimitados por barreras geográficas importantes que impidan su dispersión, deben ser considerados como límites difusos y dinámicos, nunca como algo estático (Müller 1979). Esto se debe, por un lado, al propio dinamismo de las áreas de distribución de las especies: los movimientos de los individuos y sus dinámicas poblacionales modifican constantemente la forma de las distribuciones y, por tanto, de sus límites (Holt & Keitt 2000). Por otro lado, las condiciones ambientales son menos favorables para la tolerancia de las especies en estas zonas, dando lugar a mayores presiones bióticas (Kirkpatrick & Barton 1997, Holt & Keitt 2005). Eventualmente, las poblaciones periféricas pueden debilitarse o desaparecer dando lugar a extinciones locales en los márgenes del área de distribución, o pueden ser repobladas con individuos procedentes de otras poblaciones (Holt 2003). Estas extinciones y recolonizaciones locales se traducen en reducciones e incrementos del área de distribución de las especies, generando una dinámica específica en los límites biogeográficos que modifica constantemente su forma (Eldredge 1995). Por este motivo, es importante conocer esta dinámica a la hora de caracterizar las distribuciones y observar la respuesta biogeográfica de las especies ante nuevos panoramas, como puede ser el incremento de las temperaturas causado por el cambio climático. La respuesta de las especies a tales cambios estará determinada, al menos en parte, por la respuesta de las poblaciones existentes en los márgenes de su área de distribución, de modo que entender cómo estas responden a las nuevas condiciones climáticas, pudiendo encontrar o no nuevos hábitats favorables, será fundamental para tomar las medidas adecuadas que ayuden a conservar la biodiversidad (Hannah *et al.* 2002, Ladle & Whittaker 2011). Además, nos permite conocer los factores que subyacen a la propia dinámica del área de distribución (Muñoz *et al.* 2025).

### 1.3.4 Regiones biogeográficas

Los organismos de las diferentes especies no suelen distribuirse independientemente unos de otros, sino que existen patrones de distribución comunes a un grupo de especies o de áreas geográficas (Lomolino *et al.* 2006c). La existencia de estos patrones de distribución ha permitido sectorizar grandes áreas del planeta en diferentes regiones biogeográficas (Wallace 1876, Holt *et al.* 2013), las cuales se diferencian y delimitan entre sí por la flora y fauna que albergan, como consecuencia de su historia evolutiva, geológica y climática (Llorente-Bousquets *et al.* 2001). El ornitólogo Sclater fue pionero en proponer un sistema de regionalización zoogeográfica mundial para las aves, reconociendo cuatro regiones para la avifauna del Viejo Mundo (Paleártica, Afrotropical o Etiópica, Índica y Australiana) y dos para la del Nuevo Mundo (Neártica y Neotropical; Sclater 1858). Este sistema regional se hizo muy popular y fue ampliamente aceptado por los naturalistas de su época, probablemente porque la mayoría de las separaciones intercontinentales coinciden con grandes barreras geográficas que, durante un tiempo geológico prolongado, han favorecido el aislamiento de la avifauna propia de cada continente (Udvardy 1969). Las diferentes regiones propuestas por Sclater también fueron asumidas para los anfibios y los reptiles por Günther (1858) y para los mamíferos por Wallace (1876), quién sustituyó el nombre de la región Índica por el de Oriental (**Figura 1.3.4**). Esta regionalización zoogeográfica de Sclater-Wallace se sigue utilizando en la actualidad o ha servido de base para crear otras nuevas (Darlington 1957, Udvardy 1975) y es susceptible de ser subdividida en unidades territoriales más pequeñas (Holt *et al.* 2013). Todos los estudios realizados en la presente tesis doctoral se han llevado a cabo en la región biogeográfica del Paleártico Occidental. Además, el **capítulo 4** también abarca la región Afrotropical.



**Figura 1.3.4.** Mapa mundial con las seis principales regiones zoogeográficas según Wallace (1876).

#### 1.4 Efectos del cambio climático sobre la distribución de las aves

Actualmente ya existe una extensa lista de trabajos que ponen de manifiesto que el cambio climático está afectando el comportamiento y la distribución de numerosas especies, tanto animales (Parmesan 1996, Thomas & Lennon 1999, Both & Visser 2001, Gordo & Sanz 2006, Sinervo *et al.* 2010, Reif & Flousek 2012, Chamorro *et al.* 2017, Borzée *et al.* 2019, Wallingford *et al.* 2020, Lazo-Cancino *et al.* 2020, Hallman *et al.* 2022) como vegetales (Lenoir *et al.* 2008, Chuine *et al.* 2010, Yu *et al.* 2010, Asse *et al.* 2018). Las distintas especies pueden responder a estos cambios de tres formas diferentes, aunque no excluyentes: desplazarse en el espacio a zonas con un clima adecuado, modificando sus áreas de distribución; cambiar los rasgos del ciclo vital en el tiempo, incluida la fenología y los ritmos diurnos, ajustándolos a las nuevas condiciones climáticas; o cambiar los rasgos del ciclo vital en su fisiología (Bellard *et al.* 2012). Aquellas con una capacidad de movimiento y/o dispersión limitada, al presentar más dificultad para modificar sus distribuciones, suelen responder alterando su comportamiento (actividad fisiológica o fenología) o adaptándose a las nuevas condiciones climáticas de acuerdo con su plasticidad genética (Beebee 1995, Myneni *et al.* 1997). Estas especies son las más vulnerables, ya que el actual cambio climático está ocurriendo a un ritmo muy rápido y, en muchos casos, no disponen del tiempo suficiente para adaptarse (Janzen 1994, Pounds & Crump 1994). Sin embargo, las especies con una

capacidad de movimiento y/o dispersión potencialmente elevada, como es el caso de las aves, buscan nuevos hábitats con condiciones climáticas favorables para su desarrollo, modificando sus distribuciones (Thomas & Lennon 1999, Maggini *et al.* 2011, Chamorro *et al.* 2017, Hallman *et al.* 2022). De esta manera, las aves pueden realizar tanto desplazamientos latitudinales (Maclean *et al.* 2008, Massimino *et al.* 2015, Chamorro *et al.* 2020, Stiels *et al.* 2021) como altitudinales (Popy *et al.* 2010, Maggini *et al.* 2011, Freeman *et al.* 2018) para encontrar nuevos territorios favorables fuera de su área de distribución habitual, así como modificaciones en su fenología y patrones de migración, en el caso de especies migratorias (Both & Visser 2001, Gordo & Sanz 2006, Horton *et al.* 2023).

#### 1.4.1 Cambios latitudinales en la distribución

El calentamiento climático está impulsando el desplazamiento de las áreas de distribución de numerosas especies hacia mayores latitudes (desde el ecuador hacia los polos), donde las nuevas condiciones climáticas también pueden ser adecuadas para su supervivencia y reproducción (Chamorro *et al.* 2020, Stafford *et al.* 2022, López-Ramírez *et al.* 2024a). Estos cambios se están produciendo a nivel mundial, tanto en el hemisferio norte como en el hemisferio sur (Hitch & Leberg 2007, Crawford *et al.* 2008, Hockey *et al.* 2011, Massimino *et al.* 2015, Stiels *et al.* 2021, Souldan *et al.* 2022). Sin embargo, cobran especial relevancia en el sur de Europa y el norte de África donde importantes barreras biogeográficas, como el mar Mediterráneo y el desierto del Sahara, delimitan la distribución septentrional de muchas especies africanas y la distribución meridional de otras muchas especies europeas (Carranza *et al.* 2006, Correia *et al.* 2015). En el caso de las aves africanas, una pequeña expansión de su área de distribución hacia el norte representa un gran paso en términos biogeográficos, ya que supone la colonización de un nuevo continente. En las últimas décadas, se han establecido y reproducido en el sur de Europa, concretamente en la mitad sur de la Península Ibérica, diferentes especies de aves africanas como el elanio azul (*Elanus caeruleus*) (England 1963), el vencejo cafre (*Apus caffer*) (Del Junco & González 1969), el vencejo moro (*A. affinis*) (Ramírez *et al.* 2002, Prieta 2022), el camachuelo trompetero (*Bucanetes githagineus*) (Barrientos, 2022), el ratonero moro del Atlas (*Buteo rufinus cirtensis*) (Elorriaga & Muñoz 2010) y, más recientemente, el bulbul naranjero (*Pycnonotus barbatus*) (Navarrete 2022), el corredor sahariano (*Cursorius cursor*) (Cabrera 2022), el buitre de Rüppell (*Gyps rueppelli*)

(Muñoz *et al.* 2024a) y el escribano sahariano (*Emberiza sahari*) (Sepúlveda & Ortega 2023, Muñoz *et al.* 2025). Además, hay otras especies de aves africanas que, aunque aún no se han establecido como reproductoras, se observan con cierta regularidad. Algunos ejemplos son el colirrojo diademado (*Phoenicurus moussieri*), la tórtola senegalesa (*Spilopelia senegalensis*), el buitre dorsiblanco africano (*G. africanus*) y el halcón borní (*Falco biarmicus*) (Chamorro *et al.* 2016, Rouco *et al.* 2022). Un patrón similar está ocurriendo actualmente con algunas aves típicamente mediterráneas, las cuales también se están desplazando hacia el norte y llegando a Europa central, donde se reproducen por primera vez. Algunos ejemplos pueden ser el abejaruco europeo (*Merops apiaster*), que ya ha aumentado el número de parejas reproductoras y ha fundado nuevas colonias en Alemania y Suiza (Knaus *et al.* 2018, Stiels *et al.* 2021), el vencejo pálido (*Apus pallidus*) o el águila culebrera (*Circaetus gallicus*), que se han asentado recientemente y también han experimentado un crecimiento poblacional en Suiza (Knaus *et al.* 2018).

#### 1.4.2 Cambios altitudinales en la distribución

Las especies de montaña están adaptadas a las fluctuantes condiciones ambientales que suelen darse a gran altitud, ya que las regiones montañosas son intrínsecamente estocásticas (Cheviron & Brumfield 2012, Bastianelli *et al.* 2017, Scridel *et al.* 2018, Bettega *et al.* 2020, Aligaz *et al.* 2024). Debido a sus estrechas adaptaciones a condiciones como temperaturas extremas, limitaciones de recursos, fenómenos meteorológicos extremos o hipoxia, estas especies son particularmente vulnerables a los cambios en el hábitat y en el clima, pudiendo afectar drásticamente sus poblaciones (Martin & Wiebe 2004, Tayleur *et al.* 2016, Brambilla *et al.* 2018), especialmente en sus márgenes de distribución de baja latitud (Engler *et al.* 2011, de Gabriel Hernando *et al.* 2021). En los dos últimos siglos, el calentamiento climático ha sido especialmente pronunciado en las zonas más elevadas en comparación con la media mundial, y se prevé que esta tendencia continúe (Brunetti *et al.* 2009, Pepin *et al.* 2015, IPCC 2022). Dicho calentamiento está haciendo que las áreas de distribución de algunas poblaciones de especies de montaña se desplacen a zonas más elevadas, con el objetivo de que estas puedan adaptarse a sus condiciones climáticas óptimas. Estos desplazamientos altitudinales inducidos por el clima se han observado en especies de montaña de todo el mundo (Lenoir *et al.* 2008, Chen *et al.* 2009, Popy *et al.* 2010, Maggini *et al.* 2011, Reif & Flousek 2012, Auer & King 2014, Freeman *et al.* 2018, Hallman *et al.* 2022) y pueden provocar una contracción

de su área de distribución debido a las limitaciones de espacio a gran altitud (La Sorte & Jetz 2010, Elsen & Tingley 2015, Flousek *et al.* 2015, Pernollet *et al.* 2015). En las zonas montañosas donde las poblaciones de aves alpinas ya ocupan las cotas más altas, su nicho climático puede desplazarse más allá de las cimas de las montañas, llevando en última instancia a la extinción local de estas poblaciones (Huntley *et al.* 2007, Sekercioglu *et al.* 2008). En las últimas décadas, varias especies de aves de montaña han mostrado tendencias poblacionales negativas en Europa como es el caso de la perdiz nival (*Lagopus muta*), el roquero rojo (*Monticola saxatilis*) o la chova piquigualda (*Pyrrhocorax graculus*) (Lehikoinen *et al.* 2019). También se han producido reducciones del área de distribución de otras poblaciones como es el caso del bisbita alpino (*Anthus spinoletta*) (Flousek *et al.* 2015), la collalba gris (*Oenanthe oenanthe*) o el gorrión alpino (*Montifringilla nivalis*), siendo las dos últimas especies objeto de estudio de la presente tesis doctoral. Además, las predicciones futuras indican que especialistas alpinos como el acentor alpino (*Prunella collaris*) o el treparriscos (*Tichodroma muraria*) también sufrirán una contracción de su área de distribución hacia mayores altitudes en el Paleártico sudoccidental como consecuencia del calentamiento climático (de Gabriel Hernando *et al.* 2021, Brambilla *et al.* 2022). Simultáneamente, algunas especies de aves típicamente mediterráneas también se están desplazando hacia cotas más altas, como es el caso de la cogujada montesina (*Galerida theklae*), la tarabilla común (*Saxicola rubicola*) o la curruca tomillera (*Curruca conspicillata*) (Zamora & Barea-Azcón 2015).

### 1.4.3 Cambios en la fenología y los patrones de migración

El calentamiento climático también está modificando la fenología y los patrones de migración de numerosas especies de aves. Desde la década de 1970, cada vez son más frecuentes los casos de especies de aves migrantes prenupciales que llegan antes a sus zonas de reproducción, probablemente como consecuencia de las temperaturas más cálidas en primavera (Gordo 2007, Chu *et al.* 2022, Askeyev *et al.* 2023). Algunos ejemplos son la cigüeña blanca (*Ciconia cinocia*), el cuco común (*Cuculus canorus*), el vencejo común (*Apus apus*), la golondrina común (*Hirundo rustica*) y el ruiseñor común (*Luscinia megarhynchos*) (Gordo & Sanz 2006). También existen casos de aves migrantes postnupciales que parten más tarde hacia sus zonas de invernada (Jenni & Kéry 2003, Lehikoinen & Jaatinen 2012, Benjumea *et al.* 2024). Sin embargo, a diferencia de las fechas de llegada en primavera, las tendencias temporales de las fechas de migración de

otoño son muy específicas de cada especie y no muestran un patrón tan claro, existiendo también casos de especies que adelantan o no modifican su fenología de migración otoñal (Sparks & Braslavská 2001, Cotton 2003, Tøttrup *et al.* 2006, Filippi-Codaccioni *et al.* 2011, Kortessalmi *et al.* 2023, Dale *et al.* 2024).

En las últimas décadas, el aumento de las temperaturas también ha hecho que los inviernos sean cada vez menos duraderos y con condiciones menos adversas en Europa y África (IPCC 2022). Si las condiciones favorables para las aves migratorias europeas de larga distancia persisten durante el otoño y el invierno, algunas especies podrían retrasar o incluso renunciar a la migración y permanecer en el Paleártico Occidental (Gordo & Sanz 2006, Martín *et al.* 2019). Un número creciente de registros muestra que aves migratorias europeas de larga distancia han invernado en la Península Ibérica durante las últimas décadas (Morganti & Pulido 2012), como la cigüeña blanca (Marchamalo 2002), la golondrina común (SEO/BirdLife 2012) o el carricero común (*Acrocephalus scirpaceus*) (Nieto *et al.* 2018, Chamorro *et al.* 2019). Otros ejemplos podrían ser la abubilla común (*Upupa epops*), el torcecuello euroasiático (*Jynx torquilla*), la lavandera boyera (*Motacilla flava*) (SEO/BirdLife 2012) o el papamoscas gris (*Muscicapa striata*), otra de las especies objeto de estudio de la presente tesis doctoral. Estas observaciones indican que el sur de Europa y, en particular, la costa de la Península Ibérica (principalmente su mitad meridional) ha ofrecido en las últimas décadas nuevas condiciones climáticas y zonas de invernada suficientemente adecuadas para promover una reducción de la distancia de migración (Rotics *et al.* 2017). Una distancia migratoria más corta podría brindar beneficios a los individuos, como una mayor supervivencia al evitar los riesgos asociados a la migración (Silllett & Holmes 2002); una llegada más temprana a sus zonas de reproducción, lo que les permitiría adquirir los mejores territorios de reproducción, así como aprovechar al máximo los recursos alimentarios disponibles (Kokko 1999, Coppack *et al.* 2003, Podhrázký *et al.* 2017); y una mejor condición física para la siguiente temporada de reproducción (Alves *et al.* 2013). De esta manera, si los migrantes de larga distancia establecen sitios de invernada más cerca de sus zonas de reproducción, podrían convertirse en migrantes de corta distancia en el futuro, o incluso comenzar a contar con individuos sedentarios.

## 1.5 Los modelos de distribución como herramienta para la conservación bajo los efectos del calentamiento climático

Los modelos de distribución de especies (SDMs, por sus siglas en inglés: *Species Distribution Models*) facilitan la comprensión de las relaciones entre las especies y su entorno (Elith & Leathwick 2009). En las últimas décadas, se han convertido en una de las herramientas más importantes en estudios sobre biogeografía, ecología, evolución, biología de la conservación y cambio climático, principalmente debido a la enorme cantidad de información ambiental que hay disponible y a la gran capacidad de gestión y análisis de dicha información (Guisan & Zimmermann 2000, Chamorro *et al.* 2020, Barras *et al.* 2021, Ahmadi *et al.* 2024). Estos modelos son capaces de estimar los requerimientos ecológicos de una especie en un área determinada asociando un conjunto de variables ambientales predictoras a su distribución geográfica (Muñoz *et al.* 2005, Muñoz & Real 2006, Castro *et al.* 2008, Aliaga-Samanez *et al.* 2020, Sun *et al.* 2020). Para ello buscan patrones biogeográficos que identifiquen y caractericen zonas donde es más “probable” que la especie se encuentre, entendiendo así cómo funciona el complejo sistema ‘especie-ambiente’ y prediciendo su comportamiento (Real *et al.* 2017). Cada vez existe un mayor número de estudios que utilizan los SDMs para comprender el efecto del cambio climático sobre las distribuciones de las especies con el fin de anticipar su respuesta a este fenómeno (Pearson & Dawson 2003, Hijmans & Graham 2006, Muñoz *et al.* 2013, 2015a, Chamorro *et al.* 2020, Barras *et al.* 2021, Ahmadi *et al.* 2024). Predecir estas respuestas en el contexto actual de calentamiento global es esencial para formular efectivas estrategias de gestión y conservación y, de esta manera, poder proteger a las especies y los ecosistemas (Huntley *et al.* 2008).

### 1.5.1 Procedimiento general utilizado para elaborar los modelos de distribución

A la hora de realizar un modelo biogeográfico de distribución realmente no existe una “receta” establecida ya que, en la mayoría de los casos, se realizan análisis específicos en función de los objetivos del estudio. Sin embargo, sí que existen una serie de fases generales por las que es necesario pasar para su elaboración (Sillero *et al.* 2021). Cada una de estas fases se describen a continuación.

### 1.5.1.1 Selección de los datos de distribución y las unidades geográficas operativas

En primer lugar, es necesario obtener las distribuciones de las especies que se van a estudiar. Esta información puede obtenerse de diferentes fuentes, siendo los atlas de distribución de especies y, más recientemente, las plataformas de ciencia ciudadana algunas de las más comunes para el caso de las aves (Keller *et al.* 2020, Johnston *et al.* 2021, Molina *et al.* 2022). En la presente tesis doctoral, los datos de distribución de las especies de aves analizadas en los **capítulos 2, 3, 4 y 7** se han obtenido de eBird (<https://ebird.org/home>), la plataforma internacional de ciencia ciudadana especializada en aves más importante que existe actualmente. En estos momentos, es la base de datos de biodiversidad más importante a nivel mundial y no para de crecer cada día, contando ya con cerca de un millón de usuarios. Sin embargo, en los **capítulos 5 y 6** los datos de distribución se obtuvieron del II y III atlas de aves de España (Martí & Del Moral 2003, Molina *et al.* 2022), ya que el objetivo de estos capítulos era comparar las distribuciones reproductoras de las aves examinadas en España peninsular desde principios de siglo (1998–2002) hasta casi entrada la tercera década del siglo XXI (2014–2018).

Por otro lado, un estudio biogeográfico debe establecer unas unidades geográficas operativas (UGOs) sobre las que estudiar el fenómeno de interés (en este caso, el efecto del cambio climático) dentro de un área geográfica determinada. Esto es así porque los fenómenos biogeográficos no ocurren en puntos adimensionales, sino en el seno de unidades geográficas que los condicionan (Lomolino *et al.* 2006b). Estas UGOs pueden ser de diversa índole: cuadrículas UTM (Muñoz *et al.* 2005, Estrada *et al.* 2008, Real *et al.* 2008, López-Ramírez *et al.* 2024b), hexágonos (Aliaga-Samanez *et al.* 2021, García-Carrasco *et al.* 2022, López-Ramírez *et al.* 2025) o cualquier segmentación del área de estudio en diferentes unidades que recojan información del entorno (García-Carrasco *et al.* 2021, 2023a, López-Ramírez *et al.* 2023), el cuál puede influir en la distribución de la especie por sus características climáticas, topográficas, antrópicas o litológicas, entre otras. Uno de los problemas que pueden aparecer es que existan unidades para las que se reporte un mayor número de registros de la especie que en otras. Esto puede deberse a diferencias en los esfuerzos de muestreo, en la experiencia de los observadores para detectar a la especie o en la facilidad para acceder a la zona de interés. Este problema puede ser especialmente relevante al utilizar plataformas de ciencia ciudadana. Por ejemplo, aunque el número de observadores de ciencia ciudadana esté aumentando en los países africanos, el número total de participantes sigue siendo significativamente mayor

en Europa o América. Esto supone un sesgo espacial que puede confundir subsiguientes análisis. Por este motivo, en los diferentes capítulos de la presente tesis, se ha elaborado una matriz para cada una de las especies estudiadas a partir de sus datos de distribución con valores de 1 en las UGOs donde se ha detectado a la especie (independientemente del número de registros) y 0 en las UGOs donde no se ha detectado.

### 1.5.1.2 Selección de las variables ambientales

En segundo lugar, es necesario plantear hipótesis sobre las características del ambiente o de la especie que creamos que pueden afectar su distribución. En base a esas hipótesis se implorarán una serie de factores causales, que deberán ser medidos por medio de variables. De esta manera, se selecciona un conjunto de variables predictivas, en base al criterio de expertos y estudios previos, las cuales permiten poner a prueba cada hipótesis sobre la relación del factor causal con la distribución de la especie. Las variables empleadas en los modelos de distribución de los distintos capítulos se eligieron en base a su potencial poder predictivo y explicativo, asumiendo su correlación con los posibles factores causales (Muñoz & Real 2006). Éstas se obtuvieron de diferentes fuentes de información en función del área de estudio a analizar (información detallada en las **Tablas 2.2, 3.1, 4.1, 5.1, 6.1 y 7.1** de los respectivos capítulos) y se descargaron en formato ráster, una representación de datos espaciales que se organiza en una cuadrícula de píxeles. Cada píxel contiene un valor que representa una medida en una ubicación geográfica concreta. Las diferentes variables descargadas se trataron mediante el sistema de información geográfica ArcGIS ([www.desktop.arcgis.com](http://www.desktop.arcgis.com)), recortándolas al área de estudio mediante la herramienta “Clip”. La información de los datos en formato ráster para cada variable se pasó a cada UGO mediante la herramienta “Zonal Statistics as Table”, la cual calcula el valor promedio de los valores del ráster en cada polígono UGO intersectado.

En la presente tesis doctoral se ha prestado especial atención al factor climático, ya que el objetivo general de la misma ha sido estudiar las repercusiones del cambio climático en la distribución reciente de las aves (ver **punto 1.7**). Sin embargo, como ya se ha indicado en el **punto 1.3.1**, las distribuciones de las especies están determinadas por una combinación de factores como el clima, la topografía, la actividad humana, la litología, la historia, las interacciones bióticas (competición, depredación, simbiosis), y las dinámicas poblacionales, entre otros (Real *et al.* 2003, Lomolino *et al.* 2006c, Acevedo *et al.* 2012, Di Marco & Santini 2015, Meza Mori *et al.* 2023, Benedetti & Morelli 2024).

De hecho, los cambios en el clima pueden influir sobre otros factores, alterando el efecto que éstos ya pueden tener sobre las distribuciones de las especies (Sander *et al.* 2023). Por ejemplo, un clima más cálido puede aumentar la competencia sobre las aves de montaña, debido a la ocupación de nuevas áreas a mayores altitudes por parte de especies de menor altitud, poniendo en peligro la viabilidad de sus poblaciones al restringir sus distribuciones a las cotas más altas (Jankowski *et al.* 2010). Esta competencia podría estar ocurriendo actualmente en la Sierra de las Nieves entre las tarabillas comunes y las collalbas grises, las cuales comparten ambiente en la actualidad, si bien presentan diferentes fenologías reproductoras, lo que plantea nuevas cuestiones. De este modo, el efecto del cambio climático sobre las especies puede deberse a la sinergia entre el clima y otros factores. Por este motivo, en los diferentes capítulos hemos combinado variables climáticas con otros factores en el proceso de modelación (ver **Tablas 2.2, 3.1, 4.1, 5.1, 6.1 y 7.1** de los respectivos capítulos), tal y como también han señalado otros autores (Márquez *et al.* 2011, Acevedo *et al.* 2012, Beans *et al.* 2012, Muñoz *et al.* 2013).

### 1.5.1.3 Controles previos

Antes de proceder a realizar un modelo de distribución es recomendable realizar unos controles previos. De esta manera, se ha controlado la multicolinealidad y el incremento en el error de tipo I en los modelos realizados en la presente tesis (Benjamini & Hochberg 1995, Zanolla *et al.* 2018). La multicolinealidad se ha controlado con el objetivo de evitar la entrada de variables redundantes en el modelo por estar altamente correlacionadas entre sí ( $r > 0,8$ ) (Zanolla *et al.* 2018). Para ello, se calcularon los coeficientes de correlación de Spearman entre las variables predictoras propuestas. Cuando la correlación entre dos variables fue superior a 0,8, sólo se retuvo aquella que tenía una relación más significativa con la distribución de la especie, de acuerdo con el estadístico de puntuación de Rao (Radhakrishna Rao 1948, Zanolla *et al.* 2018, García-Carrasco *et al.* 2021).

En los modelos de distribución en los que se emplea un elevado número de variables para predecir la presencia o ausencia de una especie, algunas de éstas pueden incorporarse por puro azar (García 2003). Este error (conocido como error de tipo I) consiste en admitir una hipótesis como verdadera siendo falsa y, en este caso concreto, aceptar que una variable tiene poder explicativo sobre la distribución de la especie cuando su relación con ella podría ser fruto del azar. Por este motivo, también se ha controlado el error de tipo I utilizando la tasa de descubrimientos falsos (FDR, por sus siglas en inglés: *False*

*Discovery Rate*) propuesta por Benjamini & Hochberg (1995), que corresponde con la proporción esperada de hipótesis falsas aceptadas. Para ello, se ha obtenido el grado de significación entre la distribución de la especie y cada una de las variables predictoras de acuerdo con el estadístico de puntuación de Rao utilizando el software RStudio. El procedimiento de Benjamini & Hochberg (1995) señala la significación mínima requerida a una variable para garantizar que su inclusión en el modelo no venga determinada por el error de tipo I. De esta manera, y basándose en el conjunto de variables preseleccionadas en el paso anterior, sólo aquellas variables cuya significación en la prueba de puntuación era inferior a un valor FDR de 0,05 fueron aceptadas para construir el modelo de distribución (Benjamini & Yekutieli 2001).

#### 1.5.1.4 La regresión logística

Tras obtener la matriz de presencias (1) / ausencias (0) de la especie en el área de estudio y seleccionar las variables ambientales significativas que no están altamente correlacionadas entre sí, se ponen a prueba hipótesis que relacionen los factores causales con la distribución de la especie, mediante el empleo de determinados análisis matemáticos. Uno de los algoritmos más utilizados en modelación es la regresión logística binaria (Teixeira *et al.* 2001, Muñoz *et al.* 2005, Castro *et al.* 2008, Márquez *et al.* 2011, Chamorro *et al.* 2017, Aliaga-Samanez *et al.* 2020, García-Carrasco *et al.* 2021), la cual se encuadra dentro de los modelos lineales generalizados (GLM, por sus siglas en inglés: *Generalized Linear Model*). Este algoritmo relaciona una variable dependiente binaria (presencia/ausencia de la especie) con un conjunto de variables independientes (variables ambientales predictoras) a través de la siguiente ecuación:

$$y = a + b_1x_1 + b_2x_2 + \dots + b_nx_n$$

donde  $a$  es la constante de la función, y  $b_1$  hasta  $b_n$  son los coeficientes que multiplican a las diferentes variables ( $x_1$  hasta  $x_n$ ) que integran el modelo. De esta manera, el resultado de la regresión logística es una combinación de variables, denominada  $y$  o *logit*, que sirve para calcular la probabilidad de presencia de la especie ( $P$ ) mediante la siguiente función:

$$P = \frac{e^y}{1 + e^y}$$

El empleo de la regresión logística en los modelos de distribución de especies presenta una serie de ventajas. La primera de ellas es que permite asociar la distribución de la especie con las variables ambientales predictoras mediante una función matemática. También permite calcular la significación de las relaciones de las variables independientes con la dependiente, por lo que es susceptible de análisis estadístico. Además, estima los coeficientes ( $a$  y  $b_1$  hasta  $b_n$ ) de la ecuación matemática y utilizando un algoritmo de aprendizaje automático basado en un gradiente ascendente de verosimilitud (Glasmachers & Igel 2010, Basha *et al.* 2018), motivo por el que la regresión logística también se define como un método de aprendizaje automático supervisado (Kebede Kassaw *et al.* 2023, Qi & Wang 2024). Sin embargo, este algoritmo también presenta algunos inconvenientes. Uno de los más destacados es que su resultado es sensible a la prevalencia de la especie en el área de estudio, es decir, la proporción de presencias con respecto al total de casos (Hosmer & Lemeshow 1989). Esto hace que, cuando las proporciones de presencias y ausencias de la especie no son iguales (que es lo que normalmente ocurre), el resultado se desvíe hacia el extremo que presenta un mayor número de casos. En estos casos, la función no refleja únicamente las condiciones ambientales óptimas para la especie según los predictores y los resultados del modelo dejan de ser comparables con los de especies con prevalencias diferentes (Real *et al.* 2006, Acevedo & Real 2012).

#### 1.5.1.5 La función de favorabilidad

Para solucionar el inconveniente más destacado de la regresión logística, asociado a que su resultado es sensible a la prevalencia de la especie en el área de estudio (Hosmer & Lemeshow 1989), Real *et al.* (2006) desarrollaron la función de favorabilidad (FF). La principal ventaja que presenta la FF con respecto a la regresión logística es que su resultado es independiente de la probabilidad estocástica de encontrar una especie en una localidad, la cual viene condicionada por el tamaño relativo de su distribución en el área de estudio, es decir, por la prevalencia (Acevedo & Real 2012). De esta manera, los valores de probabilidad obtenidos en la regresión logística son convertidos en valores de favorabilidad mediante dicha función (Real *et al.* 2006). La FF es un algoritmo matemático capaz de calcular el grado en que un determinado ambiente proporciona condiciones favorables para la presencia de una especie, cuyos valores oscilan entre 0 (favorabilidad mínima) y 1 (favorabilidad máxima). Si la regresión logística proporciona la probabilidad (relación entre el número de casos favorables y el número de casos

posibles) de que una especie se encuentre en un lugar, la favorabilidad mide el grado en el que las condiciones locales permiten una probabilidad local mayor o menor que la esperada por azar, siendo esta probabilidad esperada al azar la prevalencia de la especie en el área de estudio (Acevedo & Real 2012). Por lo tanto, la favorabilidad ( $F$ ) se puede obtener a partir de la probabilidad y de la proporción de presencias y ausencias mediante la siguiente ecuación (Real *et al.* 2006):

$$F = \frac{\frac{P}{(1-P)}}{\frac{n_1}{n_0} + \frac{P}{(1-P)}} = \frac{e^y}{\frac{n_1}{n_0} + e^y}$$

donde  $P$  es la probabilidad de que la especie analizada esté presente,  $n_1$  el número de presencias observadas,  $n_0$  el número de ausencias,  $e$  es la base de los logaritmos neperianos e  $y$  la ecuación de regresión obtenida. Como se puede observar en la ecuación anterior, la FF incorpora a la función de regresión logística la proporción de presencias y ausencias en la muestra analizada, produciendo así valores de favorabilidad que dependen únicamente del conjunto de variables ambientales utilizado para realizar el modelo (Real *et al.* 2006, Acevedo & Real 2012). De esta manera, un valor de  $F = 0,5$  en un área determinada indica que la probabilidad local de que la especie estudiada esté presente es la misma que la que se esperaría por azar dada la prevalencia de tal especie en toda el área de estudio, es decir, la probabilidad esperada por un modelo que no estuviese afectado por predictores ambientales (modelo nulo), en el que la presencia de la especie no se vería favorecida ni desfavorecida por el entorno. Si el valor de  $F > 0,5$  entonces las condiciones ambientales favorecen la presencia de la especie por encima de lo esperado al azar y, por el contrario, si el valor de  $F < 0,5$  las condiciones ambientales desfavorecen su presencia. Sin embargo, la favorabilidad es un concepto continuo y difuso (Acevedo & Real 2012), por lo que resulta poco realista utilizar un valor de  $F = 0,5$  como punto de corte para distinguir claramente las zonas favorables de las desfavorables. Por este motivo, aunque en los mapas de los diferentes capítulos de la presente tesis mostramos los valores de favorabilidad de cada UGO en 10 clases (de 0 a 1), también hemos clasificados dichos valores en tres categorías: zonas de “alta favorabilidad” ( $F \geq 0,8$ ), zonas de “favorabilidad intermedia” ( $0,8 > F > 0,2$ ) y zonas de “baja favorabilidad” ( $F \leq 0,2$ ) con el objetivo de distinguir claramente las zonas favorables de las desfavorables (Muñoz *et al.* 2005, Chamorro *et al.* 2017, 2021).

Los modelos de distribución basados en la función de favorabilidad, al ser independientes de la prevalencia y depender exclusivamente del grado en que las condiciones ambientales de un lugar son favorables para la presencia de la especie analizada (Acevedo & Real 2012), pueden compararse (Estrada *et al.* 2008, Barbosa *et al.* 2010) y combinarse mediante la aplicación de herramientas derivadas de la teoría de conjuntos difusos (Zadeh 1965, Barbosa & Real 2012). Esto es posible gracias a que los valores de favorabilidad son conmensurables, es decir, un mismo valor de favorabilidad tiene el mismo significado en los diferentes modelos que se pretenden comparar o combinar. Otros métodos de modelación ampliamente utilizados y de calidad reconocida, como por ejemplo los modelos de máxima entropía (MaxEnt, Phillips *et al.* 2006), ofrecen como resultado de sus análisis valores de idoneidad (en inglés, *suitability*). Sin embargo, hasta el momento no se ha demostrado que los valores de idoneidad obtenidos en diferentes modelos sean conmensurables (Acevedo & Real 2012).

### 1.5.2 Aplicación de la lógica difusa a los modelos de distribución de especies

En la lógica difusa los elementos se organizan en conjuntos borrosos (Zadeh 1965). Un conjunto borroso se trata de un grupo de elementos que no presentan un criterio de pertenencia definido, sino que cada elemento tiene un grado de pertenencia a dicho conjunto (Zadeh 1965). De esta manera, el conjunto no posee un límite definido, sino gradual, por lo que refleja mucho mejor el carácter continuo de la naturaleza (Salski 2006). A diferencia de la lógica clásica, en la que sólo existe la posibilidad de que los elementos pertenezcan o no al conjunto, en la lógica difusa se contempla la pertenencia parcial de los elementos al conjunto borroso. Esto quiere decir que el conjunto borroso está caracterizado por una función de pertenencia que le asigna a cada elemento su grado de pertenencia al conjunto, siendo éste un valor comprendido entre 0 (pertenencia mínima) y 1 (pertenencia máxima) (Zadeh 1965). El grado de pertenencia describe así el grado en que el elemento cumple las condiciones para pertenecer al conjunto borroso. Si aplicamos estos conceptos a la favorabilidad, la cual procede de la lógica difusa, ésta indica en qué grado las condiciones ambientales son propicias para la presencia de una especie, siendo favorables y desfavorables al mismo tiempo, y en diferentes grados. De esta manera, cada UGO del área de estudio pertenece en cierto grado, dentro del rango de valores [0, 1], al conjunto de UGOs favorables para la presencia de la especie (Real *et al.* 2006).

A modo de ejemplo, si utilizamos el concepto de “*persona alta*” como conjunto para agrupar a las personas, podríamos establecer el límite en 1,90 metros. De esta manera, únicamente aquellas personas con una altura igual o superior a 1,90 m pertenecerían al conjunto de “*persona alta*”, mientras que una persona con 1,86 m no pertenecería a este conjunto, de la misma forma e intensidad que tampoco pertenecería una persona de 1,80 m. Esto sería así aplicando la lógica clásica, la cual establece un umbral para el criterio “*alto*” que va a estar influido, en mayor o menor medida, por la percepción del observador. Sin embargo, si aplicamos la lógica difusa las tres personas tienen un grado de pertenencia al conjunto borroso “*persona alta*”, que será mayor en el caso de la persona de que mide 1,90 m y menor en la que mide 1,80 m.

### 1.5.3 Incertidumbre en los modelos de distribución

Los modelos de distribución, al tratarse de predicciones probabilísticas sobre las distribuciones de las especies, ya llevan asociados una incertidumbre intrínseca en sus resultados provocada por el propio modelo (Dormann *et al.* 2008, La Marca *et al.* 2019). Además de ésta, existen otras fuentes de incertidumbre que también afectan a los resultados de los mismos. Una de ellas es la inducida por la calidad de los datos de distribución de las especies que, en la mayoría de los casos, suelen estar incompletos (Molina *et al.* 2022), haciendo que partamos de un conjunto de datos sesgados. Otra es la relacionada con las variables ambientales predictoras. A pesar de la enorme cantidad de información ambiental que actualmente hay disponible, siempre existen variables que no se pueden medir o que, aun estando disponibles, no se consideran que influyen en el fenómeno estudiado. Sin embargo, incluso considerando todas las variables que afectan a la distribución de la especie, no es fácil conocer las distribuciones de sus individuos. Esto se debe a que la respuesta de los seres vivos al medio ambiente no es completamente determinista (Real *et al.* 2017). Las especies, al igual que ocurre con las partículas cuánticas, muestran un grado de imprevisibilidad intrínseca que hace que sus distribuciones momentáneas no sean, en principio, completamente predecibles (Gouveia *et al.* 2020). Con objetos macroscópicos inertes como cohetes o balas, si se conocen las posiciones iniciales y las fuerzas involucradas, podemos determinar con certeza dónde estarán en un punto dado en el tiempo. Con partículas cuánticas, conocer sus posiciones exactas es físicamente imposible. Esto mismo ocurre con los organismos vivos: podemos determinar los impulsores de sus distribuciones y predecir sus ubicaciones más probables,

pero no exactas, ya que tienen cierto grado de libertad de fuerzas externas y pueden responder a las mismas condiciones de diferentes maneras (Real *et al.* 2017). De esta forma, las distribuciones de las especies responden a una serie de factores que las condicionan, que los SDMs son capaces de identificar, siempre bajo un umbral de incertidumbre derivado de las fuentes explicadas anteriormente. Dada esta incertidumbre y el hecho de que las distribuciones de las especies son espaciotemporalmente dinámicas, lo que generan los SDMs son “probabilidades” de que una zona determinada pueda tener individuos de la especie que estemos analizando.

Además, si los modelos de distribución se proyectan al futuro para estimar el efecto del cambio climático sobre las distribuciones de las especies, aparecen otras fuentes de incertidumbre adicionales asociadas principalmente con los escenarios climáticos futuros (Beaumont *et al.* 2008, Diniz-Filho *et al.* 2009, Real *et al.* 2010). Actualmente existen múltiples modelos de circulación global (GCMs, por sus siglas en inglés: *Global Circulation Models*) para explicar el funcionamiento de la dinámica atmosférica y de los océanos, así como diferentes escenarios de emisiones de CO<sub>2</sub> (denominados RCPs y SSPs en el quinto y sexto informe de evaluación del IPCC por sus siglas en inglés: *Representative Concentration Pathways* y *Shared Socioeconomic Pathways*, respectivamente), los cuales reflejan la enorme incertidumbre asociada a la predicción del efecto del cambio climático futuro sobre las distribuciones de las especies (Real *et al.* 2010, Carvalho *et al.* 2011, IPCC 2022). Existen escenarios de emisiones de CO<sub>2</sub> más optimistas y otros más pesimistas, así como escenarios intermedios a dichos extremos, por lo que también existen diferentes maneras de representar las proyecciones futuras de los modelos para contemplar esta incertidumbre (Chamorro *et al.* 2020, López-Ramírez *et al.* 2023, 2024a). En la presente tesis, los modelos futuros se han representado de dos formas diferentes. Por un lado, en el **capítulo 2** sólo se representó el modelo futuro que resultó tener menos incertidumbre entre los diferentes modelos futuros individuales obtenidos según cada GCM y RCP. Para ello, se calcularon las consistencias entre las predicciones futuras para diferentes GCM asumiendo el mismo RCP y las coincidencias entre las predicciones para diferentes pares de RCP utilizando el mismo GCM (Real *et al.* 2010), con el objetivo de seleccionar los valores futuros de favorabilidad del GCM que mostrase mayor coincidencia para cada par de RCP y el RCP que mostrase la mayor consistencia para ambos GCM (López-Ramírez *et al.* 2024a). Por otro lado, en el **capítulo 3** se obtuvo una predicción de conjunto de los diferentes modelos futuros individuales

según cada GCM y RCP, calculando los valores medios de favorabilidad futura en cada UGO. También se representó la incertidumbre asociada a la predicción de conjunto calculando la diferencia entre la unión y la intersección difusas de las diferentes predicciones (Zadeh 1965, Chamorro *et al.* 2020, López-Ramírez *et al.* 2023).

Por todo lo anteriormente expuesto, identificar y cuantificar la incertidumbre en los modelos de distribución es esencial para dotar a los resultados de confianza (Beaumont *et al.* 2008, Real *et al.* 2010, Romero *et al.* 2019, Chamorro *et al.* 2020, Estrada & Real 2021). Esta práctica es fundamental si se pretende usar los pronósticos derivados de los modelos para una gestión eficaz, tanto presente como futura, de las especies y los ecosistemas. Una forma de tener en cuenta esa incertidumbre intrínseca de los seres vivos y de los modelos de distribución es mediante el empleo de los conjuntos borrosos y su consiguiente lógica difusa (Real *et al.* 2006, Estrada *et al.* 2008, Barbosa & Real 2012, Jones & Cheung 2018, Chamorro *et al.* 2020).

## **1.6 ¿Por qué elegir a las aves para estudiar las repercusiones del cambio climático sobre las distribuciones de las especies?**

A continuación, se exponen los motivos del por qué se ha elegido concretamente a este grupo animal para estudiar las repercusiones del cambio climático sobre las distribuciones de las especies:

1. Las aves, además de tener una elevada capacidad de movimiento, tienen una tasa de renovación generacional relativamente rápida y suelen depender de fuentes de alimento sensibles al entorno, lo que hace que respondan rápidamente a los cambios ambientales (Mekonen 2017). Esto las convierte en excelentes bioindicadores para estudiar los efectos del cambio climático sobre las distribuciones de las especies (Jørgensen *et al.* 2016, Anderle *et al.* 2024).

2. Las aves también son uno de los grupos más conocidos y estudiados, posiblemente debido a su amplia presencia y su relativa conspicuidad (Shi *et al.* 2006, Gregory & van Strien 2010). Dada la atención que se presta a las aves desde hace varias décadas (o incluso siglos) y el elevado número de ornitólogos y personas aficionadas que hay en todo el mundo, posibilita la existencia de series largas de información y a gran escala de sus poblaciones (Shi *et al.* 2006, Bowler *et al.* 2019). El cambio climático también está

modificando las distribuciones de otros taxones con elevada capacidad de movimiento, como es el caso de murciélagos (Ke *et al.* 2024, Russo *et al.* 2024), mariposas (Goded *et al.* 2024, Hällfors *et al.* 2024), libélulas (O'Neill *et al.* 2024) o incluso peces (Janc *et al.* 2024). Sin embargo, el número de personas que observan, estudian y siguen los movimientos de estos grupos animales es menor en comparación con las aves y, consecuentemente, la información que actualmente hay disponible sobre ellos no es tan abundante (Hickling *et al.* 2006, Feldman *et al.* 2021).

3. El crecimiento en popularidad y escala de iniciativas como las plataformas de ciencia ciudadana, su aceptación por parte de la comunidad científica y el desarrollo de las nuevas tecnologías han hecho que los datos de observación estén más accesibles y rápidamente disponibles para los investigadores (Sullivan *et al.* 2014, Parris *et al.* 2023). Para el caso de las aves, al ser uno de los grupos más conocidos y estudiados como hemos comentado anteriormente, existen plataformas de ciencia ciudadana internacionales exclusivas para este grupo, como es el caso de eBird. Esta plataforma recopila información sobre la distribución y abundancia de especies de aves en todo el mundo, aprovechando la enorme popularidad en la observación de este grupo animal.

4. Las aves son la clase de vertebrados tetrápodos más diversa que existe, contando actualmente con más de 11.000 especies descritas.

5. La regionalización biogeográfica en la que nos basamos (ver **punto 1.3.4**) se realizó precisamente para las aves (Sclater 1858).

## **1.7 Objetivos de la tesis doctoral**

El objetivo general de la presente tesis doctoral es estudiar las repercusiones del cambio climático en la distribución espacio-temporal reciente de las aves en el Paleártico Occidental, evaluando en qué medida los cambios en las condiciones climáticas están provocando tanto cambios latitudinales como altitudinales en la distribución de las aves, así como cambios en sus patrones de migración.

Como objetivos específicos, esta tesis plantea los siguientes:

1. Desarrollar modelos de distribución de especies que sean herramientas biogeográficas eficaces para predecir los cambios en las áreas de distribución de las aves estudiadas, tanto en el espacio como en el tiempo (**capítulos 2, 3, 4, 5, 6 y 7**).
2. Comprobar si el sur del continente europeo dispone de zonas climáticamente favorables para el establecimiento de aves típicamente africanas e identificar cuáles son dichas zonas (**capítulos 2 y 3**).
3. Cuantificar el desequilibrio latitudinal entre las condiciones climáticas óptimas para la reproducción de aves africanas y sus distribuciones reproductoras actuales, así como calcular sus tasas de desplazamiento (**capítulo 2**).
4. Comparar el grado en que el sur de Europa está volviéndose climáticamente favorable para la reproducción de rapaces típicamente africanas de la región Afrotropical y del Paleártico Occidental (**capítulo 4**).
5. Evaluar la dinámica espacio-temporal de especies de aves de montaña en España peninsular durante el siglo XXI y estudiar el modo en el que el actual cambio climático podría estar influyendo en ella (**capítulos 5 y 6**).
6. Estudiar el cambio reciente de estatus de un migrante insectívoro típicamente transahariano, el papamoscas gris, en el Paleártico Occidental e identificar zonas de invernada climáticamente favorables para la especie que aún permanecen desocupadas durante el invierno en esta región (**capítulo 7**).



Las nueve especies de aves africanas objeto de estudio del capítulo 2 de la presente tesis. De arriba hacia abajo y de izquierda a derecha: buitres de Rüppell (*Gyps rueppelli*), bulbul naranjero (*Pycnonotus barbatus*), vencejo moro (*Apus affinis*), corredor sahariano (*Cursorius cursor*), tórtola senegalesa (*Spilopelia senegalensis*), ratonero moro del Atlas (*Buteo rufinus cirtensis*), escribano sahariano (*Emberiza sahari*), colirrojo diademado (*Phoenicurus moussieri*) y chagra de Senegal (*Tchagra senegalus*).

# CAPÍTULO 2

Evaluating the expansion of African species  
into Europe driven by climate change

Evaluación de la expansión de especies  
africanas en Europa impulsada por el  
cambio climático

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Este capítulo se basa en: / This chapter is based on:

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**López-Ramírez, S., Chamorro, D., Real, R. & Muñoz, A.-R.** (2022). Cuantificando el desequilibrio latitudinal de las áreas de distribución de las especies como consecuencia del cambio climático. En *La naturaleza atlántica: hábitats, patrimonio y vulnerabilidad. II Congreso Iberoamericano y XII Congreso Español de Biogeografía* (Beato Bergua, S., Poblete Piedrabuena, M.A. & Rodríguez Pérez, C., Eds.). Delallama Editorial, Ribadesella (Asturias), pp. 127–136.

## 2. Evaluating the expansion of African species into Europe driven by climate change

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### 2.0 Abstract

**Aim:** Ongoing climate change is presently influencing the distribution ranges of numerous species, with both range expansions and latitudinal shifts being widely observed. In southern Europe, a biogeographical border that separates African and European biota, while at the same time acting as a migratory bridge for many species, these changes are of particular relevance. This study aimed to analyse the responses of nine typically African birds to climate change to provide insights on the ongoing and potential occupation of Europe. It also aimed to assess and quantify the latitudinal disequilibrium between optimal climatic conditions for breeding and the current breeding distributions of two of these species, the Atlas Long-legged Buzzard (*Buteo rufinus cirtensis*) and the Moussier's Redstart (*Phoenicurus moussieri*), as well as to calculate their displacement rates.

**Location:** Western Palearctic and surrounding areas.

**Methods:** To this end, the distributions of the species in their native ranges were modelled, both in the present and in future climate scenarios, using their current breeding ranges and a set of topographic and climatic variables. The climatic favourability for the nine species was then combined using fuzzy logic.

**Results:** The results showed that southern Europe is highly favourable for our set of African birds, except for Rüppell's Vulture, and future forecasts indicated that this favourability would increase further north, again excluding the African Vulture.

**Main conclusions:** If the climate continues to warm, further arrivals of individuals are to be expected, increasing the possibility that self-sustaining populations may become established in southern Europe. Furthermore, new African species may start to occupy this area, with the likelihood of an Africanisation of the European fauna. Considering the role played by southern Europe as a potential focal point for the colonisation of this continent by African species, it is important to track their northward expansion and future spread.

## **2.1 Introduction**

In recent decades, the global climate has become warmer (Rohde & Hausfather 2020), with widespread effects on biological systems (Walther *et al.* 2002, Karl & Trenberth 2003, Root *et al.* 2003, DeMars *et al.* 2021). Several studies have shown how species have responded to this recent climate change through shifts that ultimately transform their ranges (Chamorro *et al.* 2017, Borzée *et al.* 2019, Lazo-Cancino *et al.* 2020, Wallingford *et al.* 2020, Soultan *et al.* 2022). For species with potentially high dispersal abilities, such as birds, movements tend to translate into altitudinal or latitudinal ascents (Huntley *et al.* 2006, Maclean *et al.* 2008, Massimino *et al.* 2015, Freeman *et al.* 2018, Stiels *et al.* 2021, López-Ramírez *et al.* 2024b) in response to the warming trend in climate (IPCC 2022). While this contributes to migratory species finding wintering quarters closer to their breeding areas (Gordo 2007), it can also conversely result in non-migratory species finding new favourable territories in areas outside their normal distribution range (Crawford *et al.* 2008, Chamorro *et al.* 2020). Predicting these range shifts is a current challenge for biogeography because they are relevant both for the species that undergo the changes and for the other species that reside in the same areas, as community compositions are ultimately altered (Wallingford *et al.* 2020). This adds uncertainty to the future status of natural populations and communities and forces conservation programmes to be adapted to new species distributions (Root & Schneider 2006, Real *et al.* 2010).

In the context of ongoing climate change, distribution changes are occurring worldwide (Stiels *et al.* 2021, Soultan *et al.* 2022, Zhu *et al.* 2022). This topic is of particular relevance in southern Europe and northern Africa, where an important biogeographical barrier separates their flora and fauna. The Strait of Gibraltar, only 14 km across at its narrowest point, is a migratory bridge for many species (Evans & Lathbury 1973, Hahn *et al.* 2009) while at the same time acting, together with the Mediterranean sea, as an effective biogeographical barrier (Gantenbein & Largiadèr 2003, Carranza *et al.* 2006, Gil-López *et al.* 2022). This area delimits the northern distribution for many African species and the southern distribution for a number of European species. In the case of birds, a short-distance expansion of African species' range towards the north represents a major step in biogeographical terms, as a new continent would be reached and colonised. In recent years, the south of the Iberian Peninsula has been acting as a focal point in the process of African birds colonising

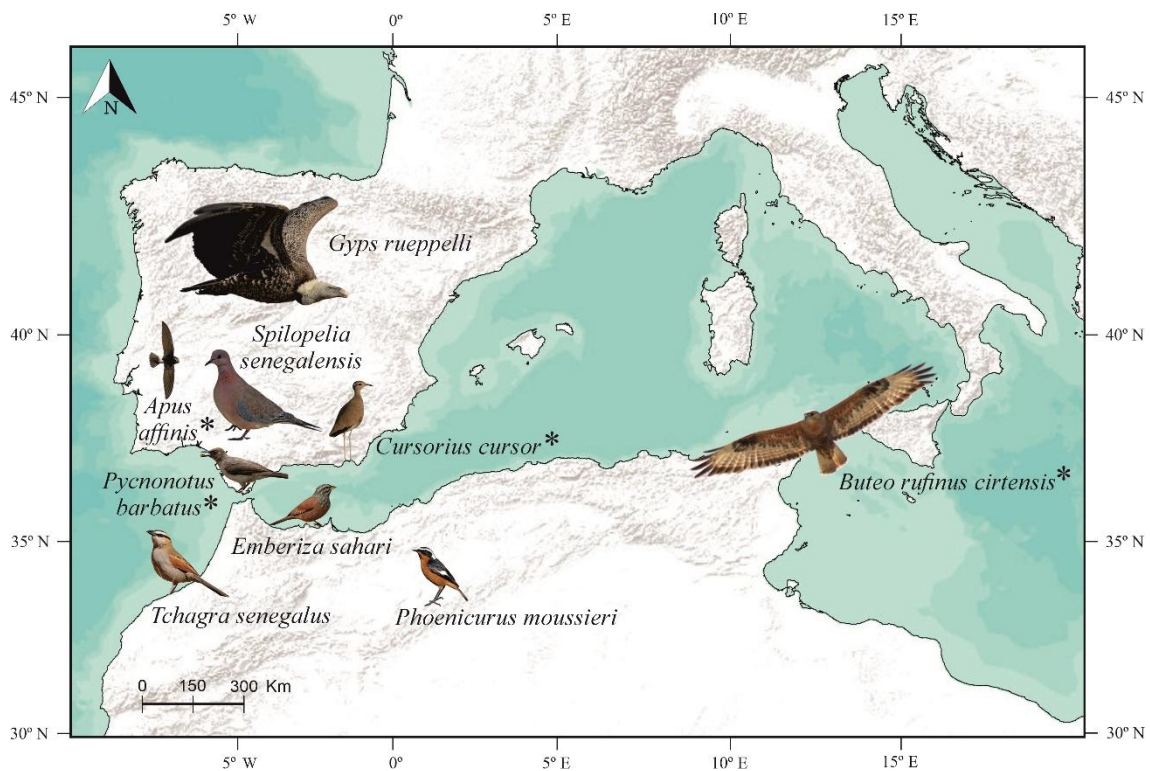
Europe (Elorriaga & Muñoz 2010, Ramírez *et al.* 2011, Chamorro *et al.* 2017), which makes it an area of great value for studying the effect of climate change on species distribution (López-Ramírez *et al.* 2023). This is not exclusive to the Mediterranean basin, as a number of species typically distributed in southern Europe have also been expanding their distribution ranges towards the north (Knaus *et al.* 2018, Stiels *et al.* 2021).

The number of records of African species in southern Europe has been increasing, aided by a growing number of observers sharing their reports through citizen science platforms. The growth in popularity and scale of these initiatives and their acceptance by the scientific community have made observational data more readily and quickly available to researchers (Sullivan *et al.* 2014, Feldman *et al.* 2021). eBird is the most important bird-related platform that collects information about the distribution and abundance of species worldwide, taking advantage of the enormous popularity of birdwatching to create a global network of volunteers who submit their observations to a central data repository via the Internet. Through a combination of broad-based community engagement and global partnerships, the volume of data being submitted to eBird has increased exponentially (Johnston *et al.* 2021).

Climate change could further increase the number of African species in Europe, increasing the possibility that self-sustaining populations may become established in southern Europe, as has already occurred with the Little Swift (*Apus affinis*) (Ramírez *et al.* 2002, Prieta 2022), and the Atlas Long-legged Buzzard (*Buteo rufinus cirtensis*) (Elorriaga & Muñoz 2010) in the last decade. Other species that are relatively regularly observed and have already been confirmed to breed in southern Spain include the Common Bulbul (*Pycnonotus barbatus*) (Navarrete 2022), the Cream-coloured Courser (*Cursorius cursor*) (Cabrera 2022) and more recently the Rüppell's Vulture (*Gyps rueppelli*) (Muñoz *et al.* 2024a), as well as others remaining in northern Africa that have not yet breed (**Figure 2.1**).

In the present study, we have selected nine typically African bird species from five different orders: two species from Accipitriformes, one from Apodiformes, one from Charadriiformes, one from Columbiformes and four from Passeriformes. All nine have been observed in Spain within the last decade and, in some cases, are consistently breeding or have sporadically bred. We aimed to analyse the response to climate change of this set of African species in order to provide information on the ongoing and future

occupation of the European continent by these birds, as well as to identify European areas susceptible to receiving African species. We also aimed to assess and quantify the latitudinal disequilibrium between optimal climatic conditions for breeding and the current breeding distributions of two of the nine birds studied, the Atlas Long-legged Buzzard and the Moussier's Redstart (*Phoenicurus moussieri*), and to estimate their displacement rates. This information will be of interest in the monitoring of the expansion of African species into Europe as a result of climate change and should also facilitate the environmental management of potentially affected areas and species.



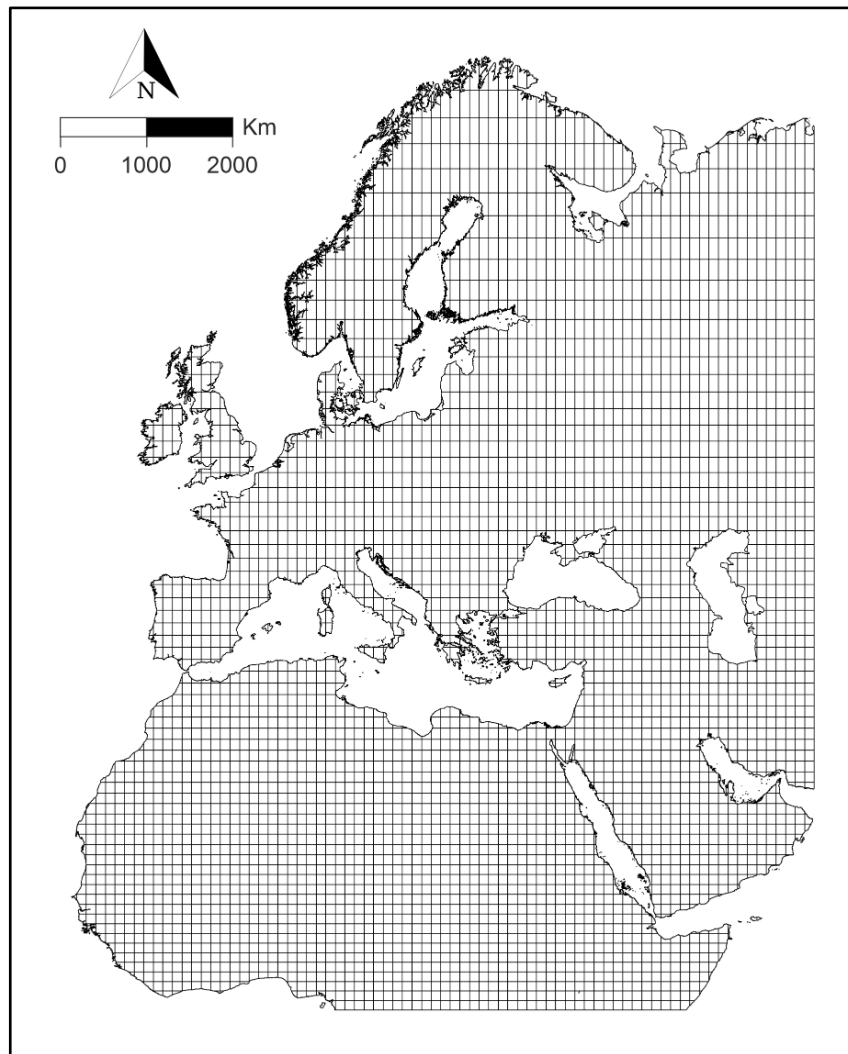
**Figure 2.1.** A representation of the current ranges of the nine African birds used in this study, showing the species that have already bred in southern Europe (indicated with an asterisk). Map projection: WGS\_1984\_World\_Mercator (ArcGIS 10.4.1).

## 2.2 Methods

### 2.2.1 Study area

The study area comprised the land region between 20°00' W to 60°00' E and 09°30' N to 70° 00' N, thus covering the Western Palearctic and surrounding areas (**Figure 2.2**). We considered the entire Western Palearctic because it is a relevant biogeographical unit

for studying the northward movement of different bird species as a consequence of a warmer climate. This area fully covers the current breeding territories of the nine species studied and has a high climatic heterogeneity, involving sub-tropical, desert, Mediterranean, Atlantic, tundra and boreal climates (Udvardy 1975, Font 2000). The study area was divided using a cell grid of 1-degree latitude  $\times$  1-degree longitude to obtain operational geographic units (OGUs,  $n = 4177$ ), using the *Create Fishnet* and *Intersect* tools from ArcGIS 10.4.1 software (ESRI 2016).



**Figure 2.2.** Study area divided into operational geographic units of 1-degree latitude  $\times$  1-degree longitude. Map projection: WGS\_1984\_World\_Mercator (ArcGIS 10.4.1).

### 2.2.2 Selected species and species distribution data

In the last decade, citizen science platforms have become key sources of global biodiversity data for certain taxa, including birds (Feldman *et al.* 2021). For this study, distribution data for determining the breeding areas of the nine selected species were obtained from eBird (<https://ebird.org/home>), an international citizen science platform specialising in birds, with nearly one million users around the world. The nine African bird species selected for this study, the number of records and the number of breeding OGUs in Africa and Europe of each of them are shown in **Table 2.1**.

We identified the OGUs where each of the selected species had been reported to breed until the end of 2020 and then used only these breeding presences to model the distribution of the species in the study area (see **Appendixes 1–9**).

**Table 2.1.** African species selected in this study with their respective number of breeding operational geographic units (OGUs) within and outside Western Europe.

Common name	Scientific name	Number of records	Breeding OGUs in Western Europe	Breeding OGUs in Africa and Eastern Europe
House Bunting	<i>Emberiza sahari</i>	5454	0	104
Common Bulbul	<i>Pycnonotus barbatus</i>	3746	1	72
Moussier's Redstart	<i>Phoenicurus moussieri</i>	3292	0	93
Laughing Dove	<i>Spilopelia senegalensis</i>	29586	0	677
Black-crowned Tchagra	<i>Tchagra senegalus</i>	1009	0	26
Rüppell's Vulture	<i>Gyps rueppelli</i>	2159	0	126
Little Swift	<i>Apus affinis</i>	1333	14	44
Cream-colored Courser	<i>Cursorius cursor</i>	5151	1	218
Atlas Long-legged Buzzard	<i>Buteo rufinus cirtensis</i>	3187	1	120

*Note:* The number of records from eBird throughout this century until the end of 2020 for each of them is also shown.

### 2.2.3 Predictor variables and future scenarios

We used a set of 21 environmental variables in the biogeographical modelling procedure, two of them related to topography and the remaining 19 related to climate between 1950 and 2000 (**Table 2.2**). We included topography together with climate in the modelling approach because otherwise their differentiated influences may be confounded and mistakenly attributed only to climate (Márquez *et al.* 2011). These variables were downloaded in raster format at a resolution of 1-km<sup>2</sup> pixels. Values of

these variables at each OGU were obtained by averaging the values of the 1-km<sup>2</sup> pixels within them using the ZONAL function of ArcGIS 10.4.1 software.

Expected future values of the climatic variables were obtained for the period 2041 to 2060 (<https://worldclim.org/>). Following the method of Chamorro *et al.* (2020), four different Representative Concentration Pathways (RCPs) were used to project future CO<sub>2</sub> emissions: 2.6, 4.5, 6.0 and 8.5 (Pachauri & Meyer 2014). To consider other sources of uncertainty in relation to the future climate of the study area, two different Global Circulation Models (GCMs) were also used: HadGEM2-ES and NorESM1-M (Real *et al.* 2010, Collins *et al.* 2011). We chose these two GCMs because they are good predictors of future climate in both Europe and Africa (McSweeney *et al.* 2015). This process resulted in eight sets of expected values of the climatic variables. We assessed whether the future values for the period 2041–2060 of the climatic variables that entered the models of the nine studied species were within the range of values that these variables had for the present.

**Table 2.2.** Variables selected to model the distribution of the nine species studied, grouped by environmental factor.

Code	Variable	Units	Source
<b>Topography</b>			
Alti	Altitude	m	(1)
Slope	Slope	Degrees	(2)
<b>Climate</b>			
Tmean	Annual mean temperature	°C	(3)
Rtday	Mean diurnal temperature range	°C	(3)
Isot	Isothermally	%	(3)
Season	Temperature seasonality	Standard deviation	(3)
Tmax	Maximum temperature of warmest month	°C	(3)
Tmin	Minimum temperature of coldest month	°C	(3)
Rtan	Temperature annual range	°C	(3)
Twet	Mean temperature of wettest quarter	°C	(3)
Tdry	Mean temperature of driest quarter	°C	(3)
Twarm	Mean temperature of warmest quarter	°C	(3)
Tcold	Mean temperature of coldest quarter	°C	(3)
Prec	Annual precipitation	mm	(3)
Pmax	Precipitation of wettest month	mm	(3)
Pmin	Precipitation of driest month	mm	(3)
Cvp	Precipitation seasonality	Coefficient of variation	(3)
Pwet	Precipitation of wettest quarter	mm	(3)
Pdry	Precipitation of driest quarter	mm	(3)
Pwarm	Precipitation of warmest quarter	mm	(3)
Pcold	Precipitation of coldest quarter	mm	(3)

*Data sources:* (1) US Geological Survey (1996); (2) calculated from *Alti* with ArcGIS software; and (3) Hijmans *et al.* (2005).

#### **2.2.4 Models for the present**

To model the distributions of the different species, we first tested the response of each species to each explanatory variable (see **Appendix 10**). This response can be linear or unimodal. A linear response implies that as the environmental gradient for an explanatory variable increases, the relationship with the presence of the species can be positive or negative. In contrast, a unimodal response implies that when a limiting value in the environmental gradient for an explanatory variable is reached, the linear positive relationship becomes negative. To this end, binary stepwise logistic regression models were performed for each of the explanatory variables separately, using their original ( $x$ ) and quadratic ( $x^2$ ) forms. A response was considered to be unimodal when the best logistic regression model included the original form in positive and the quadratic form in negative ( $x - x^2$ ), as this was the only biologically plausible unimodal response. For all variables that showed this type of unimodal response by each species individually, the result of the unimodal model ( $y$  or *logit* function) was used as an explanatory variable in the final modelling process. In all other cases, the original form of the variable was used.

To avoid problems related to multicollinearity, whenever two variables were highly correlated within a model ( $r > 0.8$ ), the one with the lower contribution was excluded (Zanolla *et al.* 2018). Based on the set of pre-selected variables in the previous step, the *false discovery rate* (FDR; Benjamini & Hochberg 1995) was evaluated to control the increase in type I errors and thereby the likelihood of obtaining false significant results when a large number of variables are used in the modelling process (García 2003). Following the procedure of Benjamini & Yekutieli (2001), only the variables whose significance in the score test was less than an FDR value of 0.05 were accepted in subsequent modelling procedures.

We performed a multivariate forward–backward stepwise logistic regression of the distributions of the species in the study area on the remaining subset of variables to obtain a comprehensive model for the current probability of breeding at every OGU, according to its climatic conditions. This procedure started with a null model that had no explanatory variables included. A multivariate model was built by adding a variable at each step if the

resulting new regression was significantly improved by the new variable, until the step in which any variable significantly increased the predictive capacity of the model was reached (Legendre & Legendre 1998). 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 of the variables introduced in the previous step. Finally, a significant combination of predictors was obtained ( $y$  or *logit*), where the coefficients of the predictor variables were estimated using a machine learning algorithm based on a likelihood ascent gradient. The relative weight of each variable in the final model was assessed using the Wald test (Wald 1943). The variance inflation factor (VIF) of each variable was used to quantify collinearity between them in the models. VIFs were calculated for each variable as the inverse of the coefficient of non-determination for a regression of that variable on all others. VIF is a positive value representing the overall correlation of each variable with all others in a model (Zuur *et al.* 2010, Muñoz *et al.* 2015b).

The result of the multivariate logistic regression was a probability of breeding based on the set of environmental variables, which was affected by the prevalence of the species that was modelled in the dataset. In this study, we combined different species' distributions, so it was mandatory to use commensurate methods unaffected by different prevalences. The effect of prevalence on the probability values was therefore removed, thus obtaining favourability values by applying the favourability function (Real *et al.* 2006). More detailed discussions of the procedure have been published previously (Chamorro *et al.* 2020, García-Carrasco *et al.* 2021, López-Ramírez *et al.* 2023). All modelling processes were run with the IBM SPSS Statistics 25 software package and our modelling approach conforms to modelling protocols proposed by Zurell *et al.* (2020) and Sillero *et al.* (2021). Maps were created using ArcMap software (ArcGIS 10.4.1; <https://desktop.arcgis.com/es/arcmap/>).

The term ‘favourability’ refers to the degree, ranging from 0 (minimum favourability) to 1 (maximum favourability), to which the environmental conditions are propitious for a species to breed (Acevedo & Real 2012, Muñoz *et al.* 2015b), with  $F = 0.5$  being the threshold separating favourable from unfavourable areas. A local favourability value of 0.5 indicates that the local probability of a species breeding is the same as its prevalence in the study area—in other words, the probability expected by a null model unaffected by environmental predictors, where breeding is neither favoured nor unfavoured by the

environment (Real *et al.* 2006). Those areas with  $F > 0.5$  therefore favour the species breeding, whereas  $F < 0.5$  indicates areas with conditions that disfavour breeding. Nevertheless, favourability is a continuous and fuzzy concept (Acevedo & Real 2012), making it unrealistic to use a favourability value of 0.5 as a cut-off to neatly distinguish favourable from unfavourable areas (Hosmer & Lemeshow 2005). Thus, although in the maps we showed the favourability values of each OGU in 10 classes, from 0 to 1, we classified them into three categories: areas of ‘high favourability’ ( $F \geq 0.8$ ), areas of ‘intermediate favourability’ ( $0.8 > F > 0.2$ ) and areas of ‘low favourability’ ( $F \leq 0.2$ ) (Chamorro *et al.* 2017).

The favourability models conducted in this study were topo-climatic as we included topography together with climate in the modelling approach. Nevertheless, we did not distinguish the effect of climate and topography on species distributions since we considered topography as an inherent part of climate. Thus, we assumed that topography would remain constant in our future projections and studied how climate changes. For this reason, hereafter we will only refer to climatic favourability instead of topo-climatic.

### **2.2.5 Model assessment**

The resulting nine climatic favourability models were assessed according to their discrimination and classification capacities. 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 classification threshold, was assessed through the following classification measures: sensitivity (the conditional probability of OGUs with reported breeding being classified as favourable), specificity (the conditional probability of OGUs with no reported breeding being classified as unfavourable), correct classification rate (CCR: the conditional probability of correctly classified OGUs), the over-prediction rate (OPR: the proportion of OGUs with no reported breeding in the area with favourability higher than 0.5) and the under-prediction rate (UPR: the proportion of OGUs with reported breeding in the area with favourability lower than 0.5). All these measures are widely used, with values ranging from 0 to 1 (Fielding & Bell 1997, Muñoz & Real 2006, Barbosa *et al.* 2013b). 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 the OGUs with reported breeding or no reported breeding in the dataset was higher or lower than 0.5, respectively.

### **2.2.6 Projection to future climatic scenarios**

Future climatic favourability values ( $F_f$ ) were obtained by replacing the present values of the climatic variables in the *logit* ( $y$ ) of the favourability function's equation with the expected future values according to each RCP and GCM for the period 2041–2060 (Real *et al.* 2010, Muñoz *et al.* 2013, Romo *et al.* 2014). This process resulted in eight expected climatic favourability models for each of the nine studied species.

### **2.2.7 Fuzzy logic**

We used fuzzy sets to represent our results because they have no clearly defined limits and therefore better reflect the continuous character of nature (Salski 2006). A fuzzy set is a class of objects with a continuum of degrees of membership, such that the set is defined by a membership function that assigns to each object a value ranging from zero to one (Zadeh 1965). The size of a fuzzy set is the sum of the degrees of membership of all the objects, which is called the cardinality of the fuzzy set. The height of a fuzzy set is defined as the largest membership value of the elements contained in that set. We defined for each species the fuzzy set of OGUs that are climatically favourable for it, where the degree of membership is the climatic favourability of the OGU for the species. We determined the fuzzy union of these fuzzy sets for the nine birds studied, both for the present and for the period 2041–2060, to obtain a joint vision of the trend that these species are expected to follow. The degree of membership of each OGU to the fuzzy union is here defined as the maximum value of favourability of the nine species in each OGU (Estrada & Real 2021), that is the degree to which each OGU is favourable for any of the species.

We also defined for each OGU the fuzzy set of species for which the OGU is climatically favourable. Then, we determined the cardinality and the height of these fuzzy sets in each OGU, both for the present and for the period 2041–2060. Cardinality is here defined as the sum of the climatic favourability values of the nine species in each OGU, and height is the maximum value of favourability of any of the nine species in each OGU

(Real *et al.* 2010). The term ‘cardinality’ used in this study is similar to the term ‘accumulated favourability’ used by Fa *et al.* (2014) and Estrada *et al.* (2008) to detect diversity hot spots. The height of the fuzzy set of species for which the OGU is climatically favourable coincides with the degree of membership of the OGU to the fuzzy union of OGUs favourable for any species. We calculated the increment ( $I$ ) in the degree of membership to the fuzzy union and cardinality of each OGU by subtracting present favourability values from future favourability values. Positive values of  $I$  indicate a gain in favourability in that OGU, whereas negative values of  $I$  mean a loss in favourability (Real *et al.* 2010).

### **2.2.8 Uncertainty assessment using fuzzy logic**

The predicted impact of climate change on species favourability would be informative for policy planning if the coincidence between predictions for different RCPs using the same GCM was lower than the consistence between predictions for the same RCP when applying different GCMs (Real *et al.* 2010). Coincidence is here defined as the concurrence between predictions according to two RCPs for a given GCM and the period 2041–2060. In equation 1 below, two RCPs (2.6 and 4.5) have been used as an example, although all six possible pairwise RCP combinations were performed.

Coincidence was computed as follows:

$$Coincidence = \frac{c(F_{2.6} \cap F_{4.5})}{c(F_{2.6} \cup F_{4.5})}, \quad (1)$$

where  $c(X)$  is the cardinality of the  $X$  fuzzy set—that is the sum of all cells' degrees of membership in the fuzzy set  $X$ .  $F_{2.6}$  is the predicted future favourability according to the GCM and the scenario 2.6, and  $F_{4.5}$  is the predicted future favourability according to the GCM and the scenario 4.5.  $F_{2.6} \cap F_{4.5}$  is the intersection between the favourabilities of scenario 2.6 and scenario 4.5, and the degree of membership of each cell to  $F_{2.6} \cap F_{4.5}$  is defined by the minimum of the two favourability values for the species in the cell.  $F_{2.6} \cup F_{4.5}$  is the union between the favourabilities for scenario 2.6 and scenario 4.5, and the degree of membership of each cell to  $F_{2.6} \cup F_{4.5}$  is defined by the maximum of the two favourability values for the species in the cell.

Consistence is defined here as the agreement between predictions for a given RCP applying different GCMs and is computed as follows:

$$Consistence = \frac{c(F_{he} \cap F_{no})}{c(F_{he} \cup F_{no})}, \quad (2)$$

where  $F_{he}$  is the predicted future favourability according to the circulation model HadGEM2-ES and  $F_{no}$  is the predicted future favourability according to the circulation model NorESM1-M.

A Wilcoxon test was used to compare the mean values of coincidence and consistence. The significance ( $p$ ) threshold that indicated if there were significant differences between the compared means was 0.05.

The GCM that showed the highest coincidence for each pair of RCPs and the RCP that showed the highest consistence for both GCMs were selected to represent the results for the period 2041–2060.

### 2.2.9 Assessment of latitudinal variation

The latitudinal disequilibrium between optimal climatic conditions for breeding and the current breeding distributions of two of the nine typically African birds studied, the Atlas Long-legged Buzzard and the Moussier's Redstart, was assessed and quantified. Their displacement rates were also estimated.

In biogeography, the barycenter ( $B$ ) of a variable in the range of a species is the centre of gravity of a species distribution along the gradient of that variable (Gauch 1982, Real *et al.* 2001). Applied to geographic coordinates, the barycenter indicates the geographic centre of the distribution range (Antúnez & Mendoza 1992). The latitudinal barycenter of the OGU with reported breeding of the two species mentioned above ( $B_{bre}$ ) was obtained as the arithmetic mean of the latitudinal values at the centre of the OGUs for each species. For present and future models, the latitudinal barycenters of climatic favourability ( $B_F$ ) were obtained by weighting latitude with favourability using the following equation (Chamorro *et al.* 2020):

$$B_F = \frac{\sum(La \times F)}{\sum F} \quad (3)$$

where  $La$  and  $F$  are the latitude (in decimal degrees) and climatic favourability values, respectively, at each OGU. For the present model, the climatic favourability barycenter was applied to the following OGUs: 1) those with reported breeding of each species ( $B_{FB}$ ), and 2) all those with reported breeding or otherwise within the longitudinal range where such species were reported to breed ( $B_{FLo}$ ). The climatic favourability barycenter was also calculated using the future ensemble forecasting models for 2041 to 2060 ( $B_{F60}$ ) and 2061 to 2080 ( $B_{F80}$ ).

Similarly to Chamorro *et al.* (2020), two indices were obtained: the latitudinal disequilibrium (Ldis) and the average rate of latitudinal climatic Favourability Displacement (FD). The latitudinal disequilibrium between the current climatic favourability for breeding and the actual breeding areas ( $Ldis = B_{FB} - B_{bre}$ ) was calculated as the difference between the geographic and climatic latitudinal barycenters in the OGUs where these species were reported to breed ( $B_{bre}$  and  $B_{FB}$ , respectively). The difference between the latitudinal climatic favourability barycenter currently within the longitudinal breeding range and that forecast for the period 2041 to 2060 ( $B_{F60} - B_{FLo}$ ) was calculated to determine the latitudinal distance that the climatic favourability was predicted to shift between the two periods. This shift is predicted to be northward if the barycenter for the future has a higher value than the current one. Likewise, we computed the difference between the latitudinal climatic favourability barycenters for the periods 2041 to 2060 and 2061 to 2080 ( $B_{F80} - B_{F60}$ ). Dividing these distances by the number of years elapsed between the periods compared, we obtained two average rates of latitudinal climatic Favourability Displacement ( $FD_{20-60}$  and  $FD_{60-80}$ , respectively). These rates represent the distance that the climatic favourability is expected to shift latitudinally every year between each period of time, assuming gradual and constant shifts over time. Ldis and FD values were calculated in latitudinal degrees and then converted into kilometres considering the equivalence of the latitudinal degree at the equator (111.12 km).

### 2.3 Results

The mathematical models and the current climatic favourability models for each of the species as well as their assessment according to their discrimination and classification capacities are shown in the appendixes (mathematical models: **Appendixes 11–19**;

current climatic favourability models: **Appendixes 20–28**; and model assessment: **Appendix 29**). All variables included in the models have a VIF lower than 6. The eight expected climatic favourability models for each of the nine studied species according to each RCP and GCM for the period 2041–2060 are also shown in the appendixes (**Appendixes 30–38**). The future values for the period 2041–2060 of the climatic variables that entered the models of the nine studied species are within the range of values for the present in more than 95.5% of grid cells.

### **2.3.1 Selecting the expected climatic favourability for the period 2041–2060**

The coincidences between predictions for different pairs of RCPs using the same GCM and the consistencies of results derived from different GCMs assuming the same RCP are shown in **Table 2.3**. Coincidences (mean = 0.888,  $n = 108$ ) are higher than consistencies (mean = 0.843,  $n = 36$ ), differing statistically significant ( $Z = -2.666$ ,  $p = 0.008$ ). Coincidence values are statistically significantly higher ( $Z = -3.758$ ,  $p = 0.0002$ ) when using the Global Circulation Model HadGEM2-ES (mean = 0.895,  $n = 54$ ) than when using NorESM1-M (mean = 0.881,  $n = 54$ ). Furthermore, when comparing between GCMs for each pair of RCPs, coincidence values are higher in all cases when using HadGEM2-ES, with the exception of pair 2.6–8.5 (see **Appendix 39**). These differences are statistically significant for two pairs of RCPs: 2.6–6.0 ( $Z = -2.666$ ,  $p = 0.008$ ) and 4.5–6.0 ( $Z = -2.310$ ,  $p = 0.021$ ). Consistence values do not differ significantly when using RCPs of 2.6, 4.5 and 6.0, although there is a nonsignificant trend towards being higher when using RCP 2.6. Consistence values are significantly lower when using an RCP of 8.5, in comparison with using RCPs of 2.6 ( $Z = -2.666$ ,  $p = 0.008$ ), 4.5 ( $Z = -2.666$ ,  $p = 0.008$ ) or 6.0 ( $Z = -2.310$ ,  $p = 0.021$ ) (see **Appendix 40**).

Based on these results, only the favourability values from the Global Circulation Model HadGEM2-ES and an RCP of 2.6 are used to update our results for the period 2041–2060 because it is the future model with the least uncertainty. The HadGEM2-ES Global Circulation Model's values are used because it is the GCM that shows the highest coincidence for each pair of RCPs, and 2.6 is used because it is the RCP that shows the highest consistence for both GCMs.

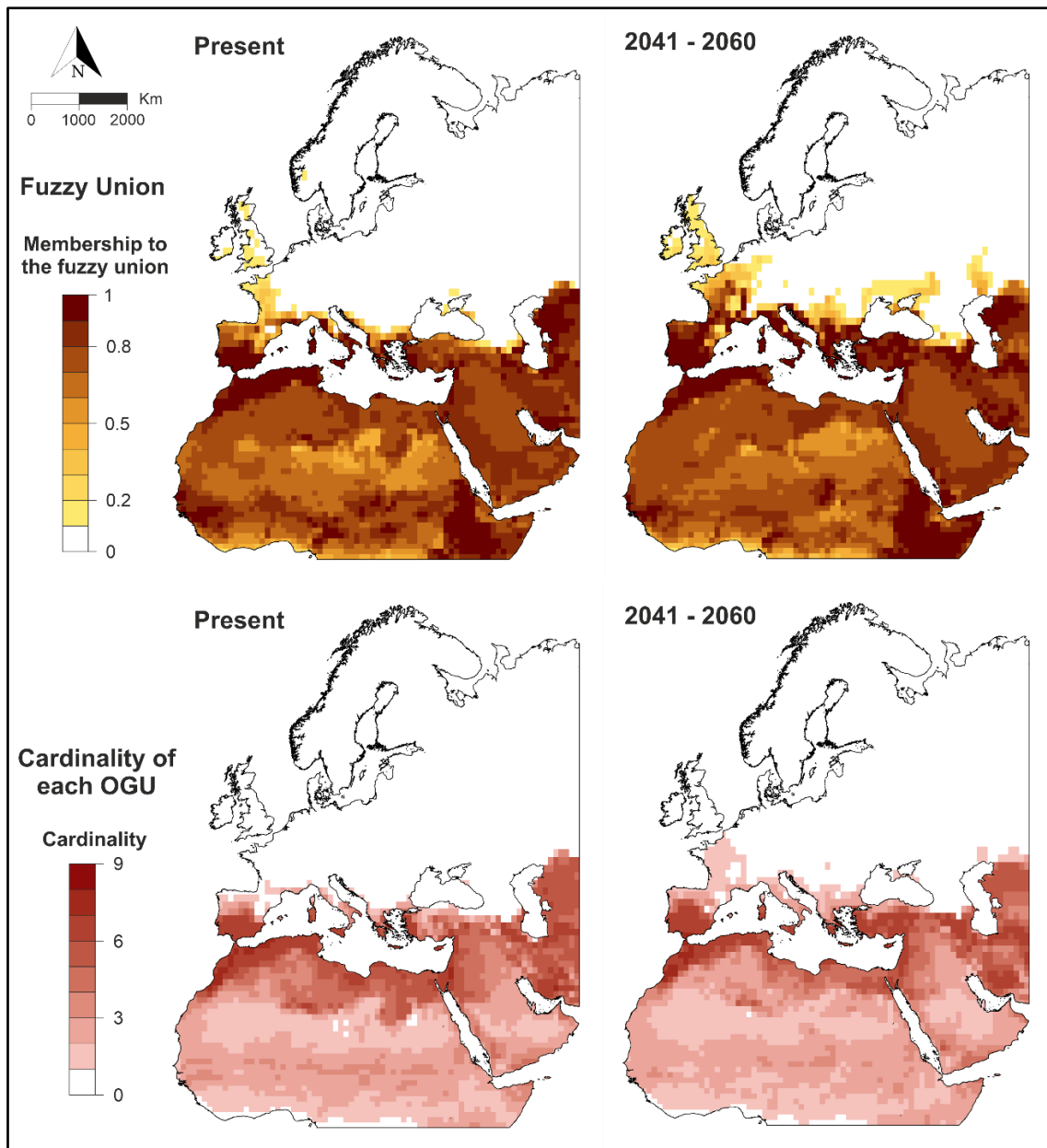
**Table 2.3.** Coincidence values between predictions using different pairs of Representative Concentration Pathways (RCPs) for each Global Circulation Model (GCM), as well as consistency values between predictions for each RCP using different GCMs.

Species	Coincidences												Consistencies			
	HadGEM2-ES						NorESM1-M						2.6	4.5	6.0	8.5
	2.6 – 4.5	2.6 – 6.0	2.6 – 8.5	4.5 – 6.0	4.5 – 8.5	6.0 – 8.5	2.6 – 4.5	2.6 – 6.0	2.6 – 8.5	4.5 – 6.0	4.5 – 8.5	6.0 – 8.5				
<i>E. sahari</i>	0.945	0.960	0.893	0.947	0.925	0.903	0.945	0.946	0.910	0.943	0.930	0.914	0.905	0.892	0.898	0.864
<i>P. barbatus</i>	0.905	0.929	0.841	0.904	0.862	0.841	0.867	0.855	0.809	0.870	0.837	0.814	0.825	0.845	0.824	0.818
<i>P. moussieri</i>	0.923	0.945	0.855	0.926	0.886	0.863	0.898	0.879	0.843	0.887	0.863	0.834	0.850	0.861	0.835	0.836
<i>S. senegalensis</i>	0.951	0.960	0.930	0.951	0.955	0.939	0.943	0.947	0.943	0.935	0.942	0.933	0.931	0.906	0.917	0.901
<i>T. senegalus</i>	0.789	0.878	0.634	0.814	0.761	0.664	0.815	0.863	0.720	0.826	0.792	0.730	0.734	0.657	0.709	0.585
<i>G. rueppelli</i>	0.938	0.918	0.923	0.935	0.929	0.934	0.883	0.889	0.894	0.908	0.936	0.902	0.887	0.883	0.881	0.882
<i>A. affinis</i>	0.891	0.918	0.820	0.892	0.843	0.820	0.844	0.836	0.780	0.852	0.813	0.788	0.797	0.822	0.805	0.796
<i>C. cursor</i>	0.965	0.972	0.946	0.966	0.967	0.951	0.965	0.965	0.948	0.966	0.958	0.955	0.944	0.929	0.944	0.924
<i>B. r. cirtensis</i>	0.914	0.936	0.829	0.922	0.873	0.853	0.907	0.899	0.841	0.904	0.875	0.849	0.828	0.828	0.819	0.779
<b>Mean</b>	0.914	0.935	0.852	0.917	0.889	0.863	0.896	0.898	0.854	0.899	0.883	0.858	0.856	0.847	0.848	0.821
<b>Mean</b>	0.895						0.881									
<b>Total mean</b>	0.888												0.843			

### **2.3.2 Combining the climatic favourability for the nine species**

Under current climatic conditions, there are already areas in the southern half of the Iberian Peninsula that are favourable for our set of African birds, with values as high as those found in Northern Africa for the same set of species (**Figure 2.3**, first row). There are also favourable areas in southern Italy, Greece, Turkey and in the large Mediterranean islands, such as the Balearics, Sardinia, Sicily, Crete and Cyprus. In the rest of Western Europe, favourability is low and concentrated mainly in southern France, northern Italy and some areas in the United Kingdom, where favourability values do not exceed 0.5. Based on climate change predictions, favourability will increase in Western Europe, especially in the northern half of the Iberian Peninsula, making the whole peninsula highly favourable for our set of African birds. It is also worth noting the increase in favourability in the northern half of Italy, as well as in central and northern France, with some areas reaching high values of favourability. Favourability is also projected to increase in Great Britain, although it will continue to be an unfavourable area for the establishment of our set of species in the near future as values remain below 0.2 (**Figure 2.3**, first row). The only exception among the species studied is Rüppell's Vulture, which exhibits low favourability values for both present and future conditions (see **Appendixes 25** and **35**, respectively).

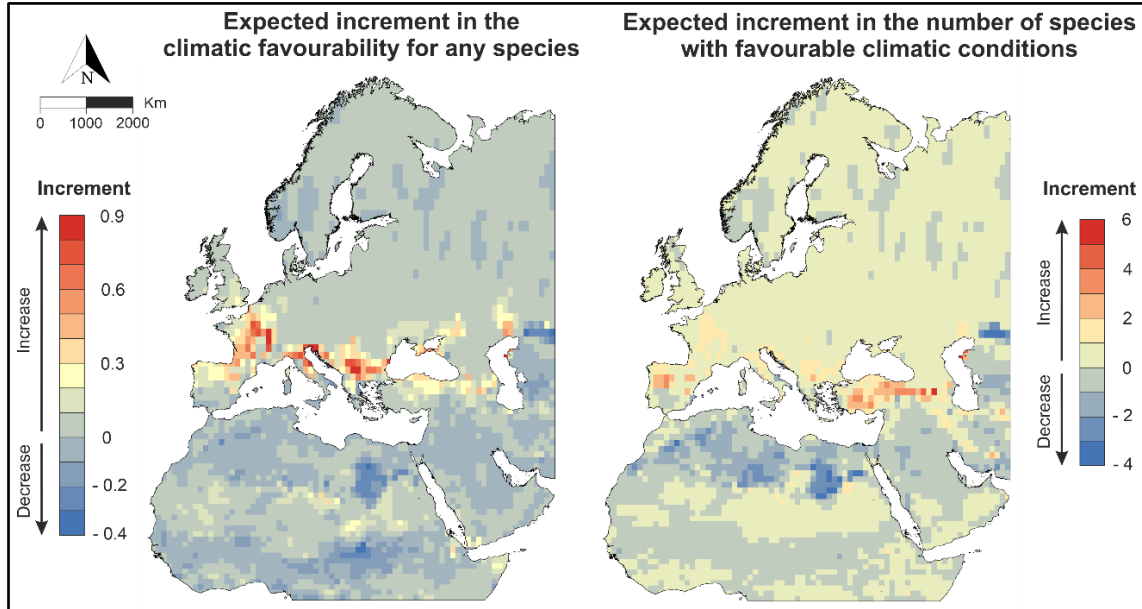
According to cardinality, the southern half of the Iberian Peninsula and the islands of Sardinia, Sicily, Crete and Cyprus, as well as southern Greece and Western Turkey, are currently the climatically favourable areas in Europe for the establishment of the largest number of our set of African birds (**Figure 2.3**, second row). In line with future forecasts, the number of African species is expected to increase in the northern half of the Iberian Peninsula and throughout Turkey. The fuzzy union and cardinality maps of the remaining seven projected models for the period 2041–2060 can be found in the appendixes (**Appendixes 41** and **42**).



**Figure 2.3.** First row: Degree of membership of each Operational Geographic Unit (OGU) to the union of the fuzzy sets of OGUs that are climatically favourable for each species (meaning the degree to which the OGU is, or is expected to be, climatically favourable for any of them). Second row: cardinality of the fuzzy sets of species for which each OGU is climatically favourable (meaning the number of species for which the OGU is, or is expected to be, climatically favourable). For the period 2041–2060 only the results of the Global Circulation Model HadGEM2-ES and the Representative Concentration Pathway 2.6 are shown.

A gain in climatic favourability for the nine African birds is expected for the period 2041–2060 in southern Europe, especially in France, northern Italy and Greece, while a

loss in climatic favourability is expected in Africa (**Figure 2.4**, left). Furthermore, the number of African species with favourable climatic conditions is expected to increase in southern Europe, especially in the northern half of the Iberian Peninsula and throughout Turkey, while it is expected to decrease in North Africa (**Figure 2.4**, right).



**Figure 2.4.** Left: Increment (I) in the degree of membership of each Operational Geographic Unit (OGU) to the union of the fuzzy sets of OGUs that are climatically favourable for each species (meaning the degree to which the OGU is expected to increase or decrease in climatic favourability for any of them between the present and the period 2041–2060). Right: Increment in the cardinality of the fuzzy sets of species for which each OGU is climatically favourable (meaning the increase or decrease in the number of species for which the OGU is expected to be climatically favourable between the present and the period 2041–2060). Warm colours indicate positive values of I, which means a gain in favourability in that OGU, whereas cold colours indicate negative values of I, which means a loss in favourability.

### 2.3.3 Results of latitudinal variation assessment

A northward disequilibrium of 0.039 and 0.025 degrees of latitude was detected between the latitudinal barycenter and the climatic favourability barycenter of the OGUs with reported breeding of the Atlas Long-legged Buzzard and the Moussier's Redstart, respectively (**Table 2.4**). A latitudinal degree is roughly equivalent to 111.12 km and therefore these disequilibriums are equivalent to 4.3 km and 2.8 km, respectively.

Applying the same equivalence, the  $FD_{20-60}$  rate value was 1.3 km/year for the Atlas Long-legged Buzzard and 3.4 km/year for the Moussier's Redstart. Assuming these rates to be similar to the current ones, the latitudinal disequilibriums of 4.3 km and 2.8 km between distribution and climatic favourability equate to a temporal disequilibrium of just over 3 years for the Buzzard and less than 1 year for the Redstart. In both species, the  $FD_{60-80}$  rate value was lower: 0.6 km/year for the Buzzard and 1.6 km/year for the Redstart.

**Table 2.4.** Results of the latitudinal variation assessment in decimal degrees for the Atlas Long-legged Buzzard (*B. r. cirtensis*) and the Moussier's Redstart (*P. moussieri*).

Measure	<i>B. r. cirtensis</i>	<i>P. moussieri</i>
$B_{bre}$	29.706	32.829
$B_{FB}$	29.745	32.855
$B_{FLo}$	25.388	29.337
$B_{F60}$	25.868	30.560
$B_{F80}$	25.971	30.850
Ldis	0.039	0.025
$FD_{20-60}$	0.012	0.031
$FD_{60-80}$	0.0051	0.015

*Note:* Latitudinal barycenter of the current breeding area ( $B_{bre}$ ). Latitudinal climatic favourability barycenters of the OGUs with reported breeding of the species ( $B_{FB}$ ), latitudinal climatic favourability barycenters of the OGUs inside the longitudinal range, where the species was reported to breed, for the current model ( $B_{FLo}$ ), and the future ensemble forecasting models for the periods 2041–2060 ( $B_{F60}$ ) and 2061–2080 ( $B_{F80}$ ). Latitudinal disequilibrium between current climatic favourability for breeding and actual breeding (Ldis) and average rates of latitudinal climatic Favourability Displacement in decimal degrees per year for the 2041–2060 ( $FD_{20-60}$ ) and the 2061–2080 ( $FD_{60-80}$ ) future periods.

## 2.4 Discussion

Over the last few decades, the number of typically African bird species observed in Europe has sharply increased. Climate change appears to be one of the main causes promoting the northward expansion of these species' ranges, a hypothesis that is reinforced by several studies conducted in Europe and Africa (Thomas & Lennon 1999, Huntley *et al.* 2006, Maclean *et al.* 2008, Real *et al.* 2013, Massimino *et al.* 2015, Chamorro *et al.* 2017, Stiels *et al.* 2021). Although the number of observers and new technologies has also increased, the recent settlement of some of these African species,

and the sporadic breeding events of some others in southern Europe, confirm the regular arrival of individuals. Recent occurrences of arrival and breeding in Europe include the Little Swift (Prieta 2022), the Atlas Long-legged Buzzard (Elorriaga & Muñoz 2010), the Common Bulbul (Navarrete 2022) and the Cream-coloured Courser (Cabrera 2022). Additionally, certain species, such as the House Bunting (*Emberiza sahari*; Sepúlveda & Ortega 2023) and the Rüppell's Vulture (Muñoz *et al.* 2024a), initiated breeding in 2023, with other species expected to start breeding soon. Climate change is expected to increase both temperature and the frequency and duration of heat waves, as well as reduce the number of cold nights and the annual mean precipitation in many mid-latitude regions (IPCC 2022). This should result in a warmer and drier environment in southern Europe, increasing its suitability for African species. These climatic alterations make the south of Europe a gateway for African species, allowing them to settle and reproduce in favourable areas and facilitating their subsequent expansion northwards.

Favourability models have proven to be useful tools for identifying new potential areas for the arrival and establishment of new individuals in the near future (Muñoz & Real 2006, Pulido-Pastor *et al.* 2018, López-Ramírez *et al.* 2023). In the present study, we constructed climatic favourability models to analyse the responses of species to climate change by identifying potentially favourable breeding areas in the European continent for nine species of African birds that are moving northwards. Our results showed that the environmental requirements of these African species fit with current climatic conditions in southern Europe, as shown by the concentration of highly favourable areas for breeding in the Mediterranean basin, including the European shore, and the generally low climatic favourability values in the rest of Europe. It is noteworthy that, among the nine species under examination, Rüppell's Vulture does not inhabit climatically favourable regions within Europe, either at present and in projected future scenarios. Nevertheless, this species is frequently sighted, with documented breeding evidence, albeit consistently in mixed pairs with Griffon Vulture (*Gyps fulvus*) (Muñoz *et al.* 2024a). This unique pattern may warrant specific research. Furthermore, our models predicted a large availability of highly favourable areas in the southern half of the Iberian Peninsula, southern Italy, Greece and Turkey, together with large Mediterranean islands such as the Balearics, Sardinia, Sicily, Crete and Cyprus. Most of these highly favourable areas remain unoccupied by African birds, indicating that their distributions are not in equilibrium with the favourable environment north of their current ranges (Chamorro *et*

*al.* 2020). Our results support the hypothesis that climate change is favouring the northward expansion of African birds and if climate warming continues, further arrivals of individuals of these species, and probably others, are to be expected in southern Europe, increasing the possibility that self-sustaining populations may become established in this area. It is necessary to consider that these species face a biogeographical barrier, the Mediterranean, which may slow the process of colonisation. Regardless, several African species have recently started to breed in southern Europe (Elorriaga & Muñoz 2010, Cabrera 2022, Navarrete 2022, Prieta 2022), and there has been an increasing and regular number of observations of other species that may become established soon (López-Ramírez *et al.* 2023). The results for the period 2041–2060 are based on the future model with the lowest uncertainty and this future projection turns out to be one of the most optimistic, as it is based on the results of the Representative Concentration Pathway 2.6. If another less optimistic future model was to be fulfilled, the climatic favourability for African birds in southern Europe would be even higher than expected from the results of this study (see **Appendixes 41 and 42**).

Various approaches to species distribution modelling assume an equilibrium of distribution with the environment, and this may hinder their applicability for analysing the effects of climate change (Guisan & Zimmermann 2000, Guisan & Thuiller 2005). One of the main drivers of changes in species distribution is the disequilibrium between species' ranges and climatic favourability for those species. This climatic disequilibrium may attract the breeding range of the species to adjacent favourable areas, although there is also a temporal disequilibrium between the actual and the potential range of the species (Chamorro *et al.* 2020). Based on the results obtained, it was found that the mean climatically favourable condition for the Atlas Long-legged Buzzard occurs 4.3 km northwards of the mean latitudinal range of its breeding areas, while for the Moussier's Redstart it occurs 2.8 km to the north. The  $FD_{20-60}$  rate values indicate that the Buzzard and Redstart ranges are not in temporal equilibrium with the current climate by a margin of about 3 and 1 year, respectively. If climatic conditions stop changing, these results suggest that the Buzzard's range could attain equilibrium with the climate in approximately 3 years, while the Redstart would reach climate equilibrium in less than one year. Otherwise, the effect of the climatic disequilibrium will continue to attract the breeding range to the favourable adjacent areas. This latitudinal range shift is expected to decrease in the distant future (2061–2080) for both species, suggesting that the

colonization of the Western Palearctic will decelerate according to current climatic projections.

Once these species colonise the Iberian Peninsula, they may use the occupied areas as steppingstones to continue the colonisation of Western Europe. This has previously occurred with the Black-shouldered Kite (*Elanus caeruleus*), which started breeding in Extremadura and Salamanca (central west Spain) in 1975 and became established in France and Turkey in 2013 (Ferrero 1996, Balbontín *et al.* 2008, Logeais 2015, Keller *et al.* 2020). In 2014, there were 150 breeding pairs of the species in France, a number that increased to 200–250 pairs in 2017 (Keller *et al.* 2020). This example shows how a typically African species has previously become established in the same areas that our models have detected as highly favourable for the establishment of African birds. A similar pattern is now occurring with some typically Mediterranean birds that are moving northwards and reaching central Europe, where they are breeding for the first time. This is happening, for example, in Germany and Switzerland, where Mediterranean species, such as the European Bee-eater (*Merops apiaster*), have increased breeding pairs and founded new colonies (Knaus *et al.* 2018, Stiels *et al.* 2021). Another example is the Short-toed Snake-Eagle (*Circaetus gallicus*), which has recently settled and experienced population growth in Switzerland (Knaus *et al.* 2018). These observations indicate that a change in species composition is already occurring in Western Europe due to climate change, where the south is being occupied by typically African species and the centre by typically Mediterranean species.

Apart from the difficulty of crossing the Mediterranean barrier, other factors could interfere with the northward colonisation process by delaying or even stopping the spread of these African species. One of these factors is hybridisation with European species, as has already been detected between the Atlas Long-legged Buzzard and the Common Buzzard (*B. buteo buteo*) on Pantelleria Island, Italy (Corso 2009), and in the Strait of Gibraltar, Spain (Elorriaga & Muñoz 2013), as well as between the Rüppell's Vulture and the Griffon Vulture in Malaga province (southern Spain) (Muñoz *et al.* 2024a). These areas represent new contact zones where closely related African and European species currently meet. Hybridisation in these areas is favoured because African species are currently rare and, therefore, their choice of mates is restricted. If hybrids were infertile, hybridisation could slow or even constitute a barrier against the expansion of these species into the European continent (Väli *et al.* 2010, Elorriaga & Muñoz 2013, Muñoz *et al.*

2024a). Other factors could be the potential role of habitat (e.g. land use) or species' intrinsic factors (e.g. site-fidelity, conspecific attraction) and their interaction with climate distribution changes (Estrada *et al.* 2016). These could be some of the reasons why some new climatically favourable European areas could remain unoccupied by African species in the future or, conversely, why some hybrid individuals are beginning to be observed, as is happening in the Strait of Gibraltar with the Gibraltar Buzzard (*Buteo buteo* × *Buteo rufinus cirtensis*; Elorriaga & Muñoz 2013).

It is important to closely monitor the northward expansion of these and other new potentially colonising African species arriving in Europe because community compositions are being altered. Our results could be useful in direct sampling and monitoring studies of these species when planning field surveys, in such a way that top priority could be given to those areas detected as highly favourable in this study. The arrival of African species in southern Europe appears to be focused on the south of the Iberian Peninsula because yet this is the European area where confirmed new breeding records and observations are concentrated. This is likely since the climatic conditions in the south of Europe are similar to that found in North Africa. If the climate continues to warm, we can expect further arrivals of new potentially colonising African species in southern Europe, with the possibility of an Africanisation of the European fauna.



Pareja de escribanos saharianos (*Emberiza sahari*) apoyados sobre los huecos de un muro, lugar habitual de nidificación.

# CAPÍTULO 3

Southern Europe is becoming climatically favourable for African birds: anticipating the establishment of a new species

El sur de Europa se está volviendo climáticamente favorable para las aves africanas: anticipando el establecimiento de una nueva especie

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Este capítulo se basa en: / This chapter is based on:

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Muñoz, A.-R. & **López-Ramírez, S.** Africanisation of Southern Europe's avifauna is already underway (Submitted).

### **3. Southern Europe is becoming climatically favourable for African birds: anticipating the establishment of a new species**

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#### **3.0 Abstract**

**Background:** The current modification of species distribution ranges, as a response to a warmer climate, constitutes an interesting line of work and a recent challenge for biogeography. This study aimed to determine if the climatic conditions of southern Europe are adequate to host a typical African species, the House Bunting, which is registered regularly during the last years, still in low numbers. To this end, the distribution of the species in its native range was modelled, both in the present and in future climate scenarios, using its current breeding distribution areas and a set of environmental variables.

**Results:** The results showed that the southern half of the Iberian Peninsula exhibits high values of favourability to host this African species for the current climatic conditions. Furthermore, future forecasts indicated an increase in favourability for this area. The highly favourable areas we detected in the south of the Iberian Peninsula are already regularly receiving individuals of the species. These observations are very likely vagrant birds dispersing from recently colonised breeding areas in northern Morocco, which may indicate a continuous process of colonisation towards the north, as has occurred during the last decades in Northern Africa.

**Conclusions:** We cannot anticipate when the House Bunting will establish on the European continent because colonisation processes are usually slow but, according to our results, we predict its establishment in the near future. We have also identified those areas hosting favourable conditions for the species in Europe. These areas are a potential focal point for the colonisation of this and other African birds if the climate continues to warm.

### **3.1 Introduction**

The distribution of species, both in space and time, is affected by environmental, biological, historical and anthropogenic factors (Lomolino *et al.* 2006b). According to several studies, however, climate appears to be the most relevant factor for several taxa at large scales (Márquez *et al.* 2011, Chamorro *et al.* 2017, 2021, Sun *et al.* 2020). In recent decades, it has been demonstrated that the global climate is becoming warmer (Rohde & Hausfather 2020), with widespread effects on biological systems (Walther *et al.* 2002, Karl & Trenberth 2003, Root *et al.* 2003, DeMars *et al.* 2021). This recent climate change has already affected the distribution of many species (Thomas & Lennon 1999, Borzée *et al.* 2019, Lazo-Cancino *et al.* 2020, Wallingford *et al.* 2020) and is modifying the margins of their distributions over short periods of time (Thomas *et al.* 2001, Castro *et al.* 2008, Soultan *et al.* 2022). This process is more notorious in vagile species such as birds, which are frequently monitored and included in citizen science platforms (Randler 2021, Zulian *et al.* 2021).

Modifications in birds' distribution (Huntley *et al.* 2006, Maclean *et al.* 2008) and phenology (Møller *et al.* 2008, Ambrosini *et al.* 2011, Nieto *et al.* 2018), as a response to a warmer climate, constitute an interesting line of work that has begun to be addressed in recent decades. Predicting range shifts is a current challenge for biogeography because bird ranges are expected to move in response to temperature, precipitation and habitat changes (Thomas & Lennon 1999, Böhning-Gaese & Lemoine 2004, Massimino *et al.* 2015). Latitudinal and elevational movements (Huntley *et al.* 2006, Auer & King 2014, Taheri *et al.* 2016) are relevant both for the species that suffer the changes and for the other species that reside in the same areas, as community compositions are ultimately altered (Wallingford *et al.* 2020). This adds uncertainty to the future status of natural populations and communities, and forces conservation programmes to be adapted to the new species distributions (Root & Schneider 2006, Real *et al.* 2010).

This topic is of particular relevance in southern Spain and northern Morocco, where an important biogeographical barrier separates the North African and the southern European fauna and flora. The Strait of Gibraltar is a bridge for many migratory species (Evans & Lathbury 1973, Hahn *et al.* 2009) and an effective biogeographic barrier for many other taxa (Gantenbein & Largiadèr 2003, Carranza *et al.* 2006, Gil-López *et al.* 2022). This area delimits the northern distribution of some African bird species, such as the House Bunting (*Emberiza sahari*), the Moussier's Redstart (*Phoenicurus moussieri*)

or the Black-crowned Tchagra (*Tchagra senegalus*) (Billerman *et al.* 2022). If they overcome this barrier to move further north, they cross into Europe, where they come into contact with different species and, in some cases, new habitats, as is currently happening with some typically African birds (De Juana & Comité Ibérico de Rarezas de la Sociedad Española de Ornitología 1994, De Juana & Comité de Rarezas de la Sociedad Española de Ornitología 1997, Dies *et al.* 2010, Copete *et al.* 2015, Gil-Velasco *et al.* 2019). In recent decades, the Iberian Peninsula has been successfully colonised by a number of species of African birds, including the Black-shouldered Kite (*Elanus caeruleus*) (England 1963), the White-rumped Swift (*Apus caffer*) (Del Junco & González 1969), the Little Swift (*A. affinis*) (Ramírez *et al.* 2002) and, more recently, the African Long-legged Buzzard (*Buteo rufinus cirtensis*) (Elorriaga & Muñoz 2010) and the Common Bulbul (*Pycnonotus barbatus*) (Navarrete 2022). In addition, there are other species that, although not yet established as breeders, are regularly observed as a process of the unexceptional arrival of individuals. Some examples of these are Rüppell's Vulture (*Gyps rueppelli*) (Ramírez *et al.* 2011), the African White-backed Vulture (*G. africanus*) (Chamorro *et al.* 2016), the Lanner Falcon (*Falco biarmicus*) (Chamorro *et al.* 2016), the Moussier's Redstart (Gil-Velasco *et al.* 2017) and the House Bunting (Gil-Velasco *et al.* 2017). Mostly due to the relative proximity between Africa and Europe in the western Mediterranean, the southern part of the Iberian Peninsula is an adequate place for the potential establishment of these species, acting as a focal point in the colonisation process of Europe by African birds (Elorriaga & Muñoz 2010, Ramírez *et al.* 2011, Chamorro *et al.* 2017).

In recent decades, the House Bunting has increased its distribution range towards the north in Morocco until it has reached the Mediterranean coast (De Juana 2006). For this reason, we could expect it to colonise south-western Europe if the environmental conditions are adequate, reaching the Iberian Peninsula. The aim of this study is to determine if the climatic conditions of southern Europe—both current conditions and several climate change estimates based on different emission scenarios—are suitable to host the House Bunting as a breeder, and also to identify where these conditions exist. This information will be of interest in monitoring the expansion of African species as a result of climate change.

## **3.2 Methods**

### **3.2.1 Study area**

The study area comprised the land region from 20° 00' W to 60° 00' E, and from 09° 30' N to 70° 00' N, thus covering the Western Palearctic and surrounding areas (**Figure 3.1**). We considered the entire Western Palearctic because it is a relevant biogeographic unit for studying the potential expansion of the House Bunting and other bird species. This study is part of a broader project (LifeWatch ERIC, EnBiC2-Lab) that is focused on an intercontinental scale to study the effects of climate change on species distributions. This area has a high climatic heterogeneity, involving sub-tropical, desert, Mediterranean, Atlantic and tundra climates (Udvardy 1975, Font 2000), and fully covers the current breeding territories of the House Bunting.

The study area was divided using a grid cell of 1-degree latitude  $\times$  1-degree longitude to obtain operational geographic units (OGUs,  $n = 4177$ ), using the *Create Fishnet* and *Intersect* tools from ArcGIS software.

### **3.2.2 The species**

The House Bunting is closely associated with urban environments (Chedad *et al.* 2021). It ranges from the Maghreb to Chad and Mauritania in Northern Africa. Formerly, it lived only in desert or semi-desert areas, breeding in very few localities north of the Atlas Mountains before 1950. Since the mid-twentieth century, however, the species has shown a very clear tendency to increase its distribution range towards the north in Morocco, Algeria and Tunisia, occupying exclusively urban habitats. Thévenot *et al.* (2003) described in detail the House Bunting's expansion towards the north in Morocco, where it was detected in Casablanca and Guercif in the 1960s. In the 1980s, it had reached Oujda, Rabat, Fez and Meknes; by 1995 it was located in Kenitra, Sidi Slimane and Sidi Kacem, just 180 kms from the Strait of Gibraltar; and at the beginning of the twenty-first century, it had already reached Tangier. In recent years, the House Bunting has colonised large areas of northern Morocco including the Mediterranean coast (De Juana 2006). Currently, single individuals of the species are beginning to be observed regularly in the south of the Iberian Peninsula, with specific observations in the provinces of Cadiz and Malaga (see **Figure 3.4**).

### 3.2.3 Species distribution data

In the last decade, citizen science platforms have become key sources for obtaining global biodiversity data for certain taxa, such as birds (Feldman *et al.* 2021). For this study, distribution data to determine the breeding area of the House Bunting was obtained from *e-Bird* (<https://ebird.org/home>), an international citizen science platform specialising in birds, with hundreds of thousands users around the world. We used eBird records of the current century until the end of 2020 that were within the breeding season of the House Bunting (from late February to late July) (Ryan 2020). From these records, we identified the OGU where breeding of the species was assumed, and then used only these African presences to model the distribution of the species in the study area.

Recent reports of the species in Europe (**Figure 3.4**) were obtained from *e-Bird* (<https://ebird.org/home>) and the SEO/BirdLife Rarities Committee (Dies *et al.* 2011, Pardo de Santayana *et al.* 2021). All these records, which were confirmed with the help of pictures of each observation of the species, were used to validate the results provided by the distribution model.

### 3.2.4 Predictor variables and future scenarios

In the biogeographic modelling procedure, we used a set of 21 environmental variables (**Table 3.1**), two of them related to topography and the remaining 19 related to climate between 1950 and 2000. We included topography together with climate in the modelling approach because otherwise their differentiated influences may be confounded and mistakenly attributed only to climate (Márquez *et al.* 2011). Furthermore, it is important to balance the impact of climate change against the inertia promoted by other influential factors that will not change in the future, such as topography, when forecasting species distribution (Muñoz *et al.* 2013, 2015a). These variables were downloaded in raster format at a resolution of 1 km<sup>2</sup> pixels. Values of these variables at each OGU were obtained by averaging the values of the 1 km<sup>2</sup> pixels within them using the ZONAL function of ArcGIS 10.4.1 software (Chamorro *et al.* 2020).

**Table 3.1.** Variables selected to model the breeding distribution of the House Bunting, grouped by environmental factor.

Code	Variable	Units	Source
<b>Topography</b>			
Alti	Altitude	m	(1)
Slope	Slope	Degrees	(2)
<b>Climate</b>			
Tmean	Annual mean temperature	°C	(3)
Rtday	Mean diurnal temperature range	°C	(3)
Isot	Isothermally	%	(3)
Season	Temperature seasonality	Standard deviation	(3)
Tmax	Maximum temperature of warmest month	°C	(3)
Tmin	Minimum temperature of coldest month	°C	(3)
Rtan	Temperature annual range	°C	(3)
Twet	Mean temperature of wettest quarter	°C	(3)
Tdry	Mean temperature of driest quarter	°C	(3)
Twarm	Mean temperature of warmest quarter	°C	(3)
Tcold	Mean temperature of coldest quarter	°C	(3)
Prec	Annual precipitation	mm	(3)
Pmax	Precipitation of wettest month	mm	(3)
Pmin	Precipitation of driest month	mm	(3)
Cvp	Precipitation seasonality	Coefficient of variation	(3)
Pwet	Precipitation of wettest quarter	mm	(3)
Pdry	Precipitation of driest quarter	mm	(3)
Pwarm	Precipitation of warmest quarter	mm	(3)
Pcold	Precipitation of coldest quarter	mm	(3)

*Data sources:* (1) US Geological Survey (1996); (2) calculated from *Alti* with ArcGIS software; and (3) Hijmans *et al.* (2005).

Expected future values of the climatic variables were obtained for the periods 2041–2060 and 2061–2080 (<https://worldclim.org/>). In the same way as in Chamorro *et al.* (2020), four different Representative Concentration Pathways (RCPs) were used to project future CO<sub>2</sub> emissions: 2.6, 4.5, 6.0 and 8.5 (Pachauri & Meyer 2014). Two different Global Circulation Models (GCMs) were also used: HadGEM2-ES and NorESM1-M (Real *et al.* 2010, McSweeney *et al.* 2015). We used these two GCMs because they have been found to be good predictors of future climate in both Europe and Africa (McSweeney *et al.* 2015). This process resulted in eight sets of expected values of the climatic variables for each period of time. We assessed whether the climatic variables that entered the model were within the range of values that these variables had for the present.

### **3.2.5 Model for the present**

First, Spearman correlation coefficients ( $r$ ) were calculated between the selected environmental variables to reduce multicollinearity. For each pair of variables with  $r > 0.8$ , only the variable with the highest individual predictive power was retained (Fa *et al.* 2014, Aliaga-Samanez *et al.* 2020). In species distribution models in which many variables can potentially predict the presence or absence of a species, some variables may be incorporated by chance (García 2003). This type of error (type I error) can be controlled by evaluating the *False Discovery Rate* (FDR), as proposed by Benjamini & Hochberg (1995). Based on the set of pre-selected variables in the previous step, only the variables whose significance in the score test was less than an FDR value of 0.05, were accepted in subsequent modelling procedures (Benjamini & Yekutieli 2001).

Next, a comprehensive model for the current probability of breeding at every OGU according to its climatic conditions was obtained by multivariate forward–backward stepwise logistic regression. This procedure began with a null model (model with no predictor variables) that produced a constant probability of breeding at each OGU equal to the prevalence (OGUs where species have been confirmed to breed in relation to the total number of OGUs). In the first step, the procedure selected the variable with the most significant relationship to the distribution of the species, according to the Rao’s score test. In the following steps, the variable most significantly related to the residues not explained in the previous step was added to the model, until the step in which any variable significantly increased the predictive capacity of the model was reached (Legendre & Legendre 1998). 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 of the variables introduced in a previous step. Finally, a significant combination of predictors was obtained ( $y$  or *logit*), where the coefficients of the predictor variables were estimated using a machine learning algorithm based on a likelihood ascent gradient. The relative weight of each variable in the final model was assessed using the Wald test (Wald 1943).

To eliminate the effect of prevalence on the probability values obtained and to attain values that depend exclusively on the response of the species to environmental variables (Gouveia *et al.* 2020), favourability values ( $F$ ) were obtained by applying the *Favourability Function* (Real *et al.* 2006), using the following equation:

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

where  $P$  is the probability value obtained through logistic regressions,  $e$  is the Euler's number,  $\ln$  is the natural logarithm, and  $n_1$  and  $n_0$  are the number of OGU's where breeding was reported or not reported, respectively.

The favourability refers to the degree, from 0 (minimum favourability) to 1 (maximum favourability), to which the environmental conditions favour the breeding of the species (Acevedo & Real 2012, Muñoz *et al.* 2015b), with  $F = 0.5$  being the threshold separating favourable from unfavourable areas. A local favourability value of 0.5 indicates that the local probability of the species breeding is the same as its prevalence in the study area, meaning the probability expected by a null model unaffected by environmental predictors, where breeding is neither favoured nor unfavoured by the environment (Real *et al.* 2006). Those areas with  $F > 0.5$  therefore favour the species breeding, whereas  $F < 0.5$  indicates areas with conditions that disfavour breeding. Nevertheless, the use of a favourability value of 0.5 as a cut-off point for crisply distinguishing favourable from unfavourable areas is not sufficiently informative (Hosmer & Lemeshow 2005) due to the continuous and fuzzy character of favourability (Acevedo & Real 2012). For this reason, we opened a gap between the values considered as clearly favourable and clearly unfavourable. Each OGU was classified into three categories, depending on their favourability values. If the predicted favourability was higher than 0.8, which means that the odds are more than 4:1 favourable to the species, the OGU was considered as highly favourable; those areas with favourability values lower than 0.2 (odds less than 1:4) were considered unfavourable to the species; and the remaining areas were considered to be of intermediate favourability ( $0.2 \leq F \leq 0.8$ ) (Muñoz & Real 2006, Chamorro *et al.* 2020). All modelling processes were run with the IBM SPSS Statistics 25 software package.

### 3.2.6 Model assessment

The discrimination capacity of the resulting model was evaluated using the Area Under the Receiver Operating Characteristic (ROC) Curve, known as the AUC (Lobo *et al.* 2008, Romero *et al.* 2013), which has an associated significance value. As described by Fielding & Bell (1997), Muñoz & Real (2006) and Barbosa *et al.* (2013b), we applied

a set of classification measures, whose values range from 0 to 1. These measures were sensitivity (the conditional probability of OGUs with reported breeding being classified as favourable), specificity (the conditional probability of OGUs with no reported breeding being classified as unfavourable), the over-prediction rate (OPR: the proportion of OGUs with no reported breeding in the area with favourability higher than 0.5) and the under-prediction rate (UPR: the proportion of OGUs with reported breeding in the area with favourability lower than 0.5).

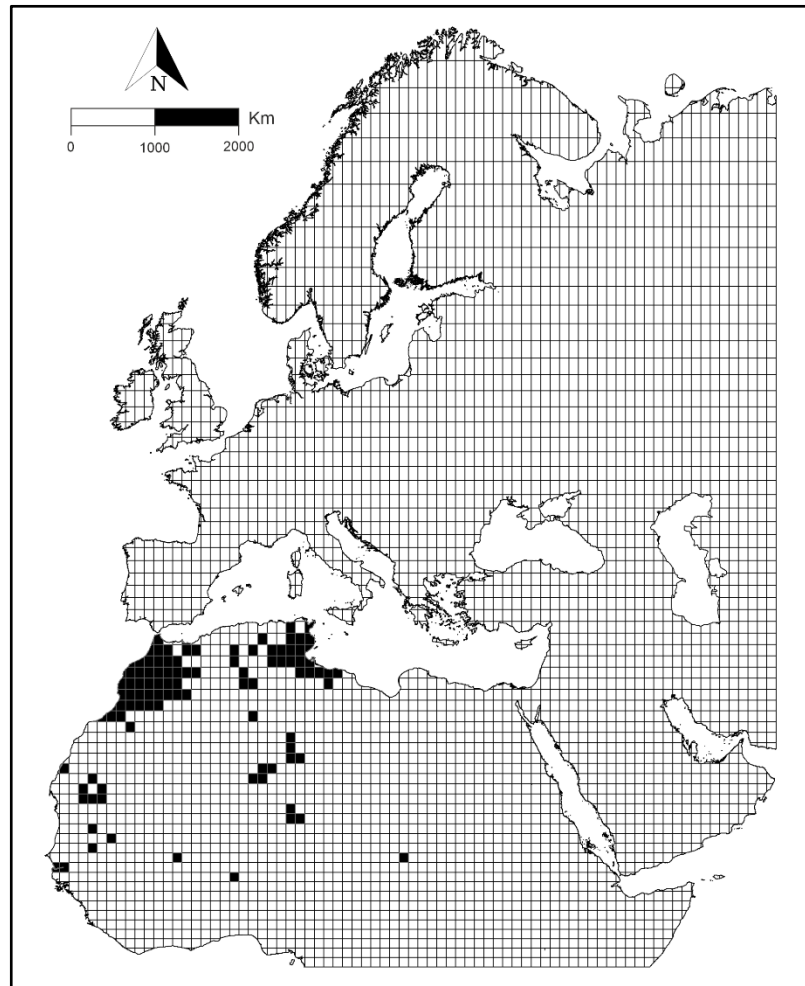
### **3.2.7 Projection to future climatic scenarios**

We obtained future climatic favourability values ( $F_f$ ) by replacing the present values of the climatic variables in the *logit* ( $y$ ) of the favourability equation (Real *et al.* 2006) with the expected future values according to each RCP and GCM, and for each future period of time (Real *et al.* 2010, Muñoz *et al.* 2013, Romo *et al.* 2014). This process resulted in eight expected climatic favourability models for each period. An ensemble forecasting of the models was obtained for each period of time by calculating the mean values of the eight future climatic favourability models at each OGU.

The uncertainty of the ensemble forecasting was computed using fuzzy set theory (Zadeh 1965), given that favourability values may be considered to be the degree of membership in the fuzzy set of areas favourable for House Bunting breeding. Thus, the favourability function is the membership function that assigns each OGU their degree of membership value (Real *et al.* 2006). The uncertainty was computed as the difference at each OGU between the fuzzy union of the eight models (the maximum value of favourability of any of them at the OGU) and their fuzzy intersection (the minimum value of favourability of any of them at the OGU) (Romero *et al.* 2019).

## **3.3 Results**

Our search for data from eBird resulted in 5520 records throughout this century, until the end of 2020. With these records we obtained a binary target variable representing breeding/not breeding at each Operational Geographic Unit (OGU) (breeding:  $n_1 = 104$ , not breeding:  $n_0 = 4073$ ). All OGUs where the species breeds were in Africa (**Figure 3.1**). The prevalence of the species in the study area was 0.025.



**Figure 3.1.** Current House Bunting breeding presences in the study area (shown in black), which was divided in grid cells of 1-degree latitude  $\times$  1-degree longitude. These presences were the only ones used in the modelling process. Map created using ArcMap software (ArcGIS 10.4.1) <https://desktop.arcgis.com/es/arcmap/>

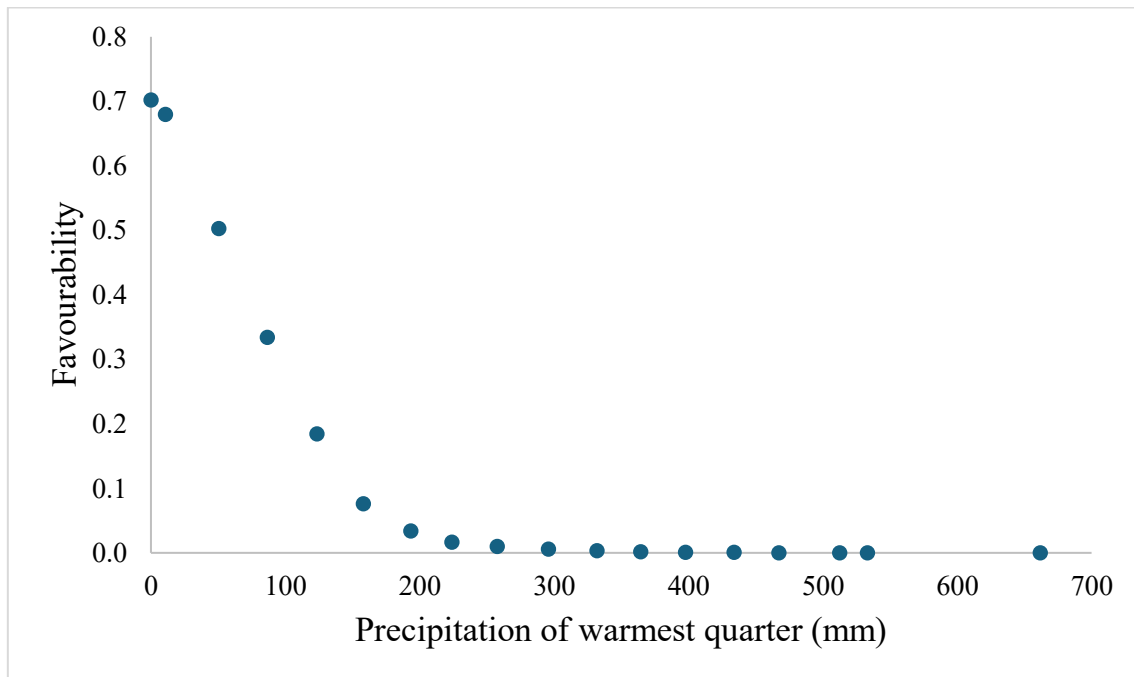
The mathematical model included three variables, two of them related to climate, whose future values were within the range of values for the present in more than 99.8% of grid cells, and altitude (**Table 3.2**). Dry weather low in precipitation in the warmest quarter was the best predictor for House Bunting breeding because this variable was the first to be entered in the stepwise procedure and, under the Wald test, this variable possessed the greatest weight in the model. According to the sign of the variables' coefficients in the logit function, precipitation in the warmest quarter had a negative effect on the species distribution while annual precipitation and altitude had a positive effect

(**Table 3.2**). The increase in precipitation of the warmest quarter in the range of 0–200 mm negatively affected the favourability for the House Bunting breeding, and precipitation values above 200 mm always resulted in negligible favourability (**Figure 3.2**).

**Table 3.2.** Variables entered into the logistic regression model via a forward–backward stepwise selection process, ranked by their order of entrance.

Variable	$\beta$	S.E.	Wald	$p$
Precipitation of warmest quarter	-0.0261	0.00406	41.345	<0.001
Annual precipitation	0.00112	0.000404	7.689	0.006
Altitude	0.000503	0.000206	5.964	0.015
Constant	-3.020	0.175	298.267	<0.001

Note:  $\beta$ s are the coefficients in the logit function, S.E. is the standard error of these coefficients, Wald is the Wald's statistics value (representing the relative importance of the variable in the model) and  $p$  is the significance of the coefficients according to the Wald test.

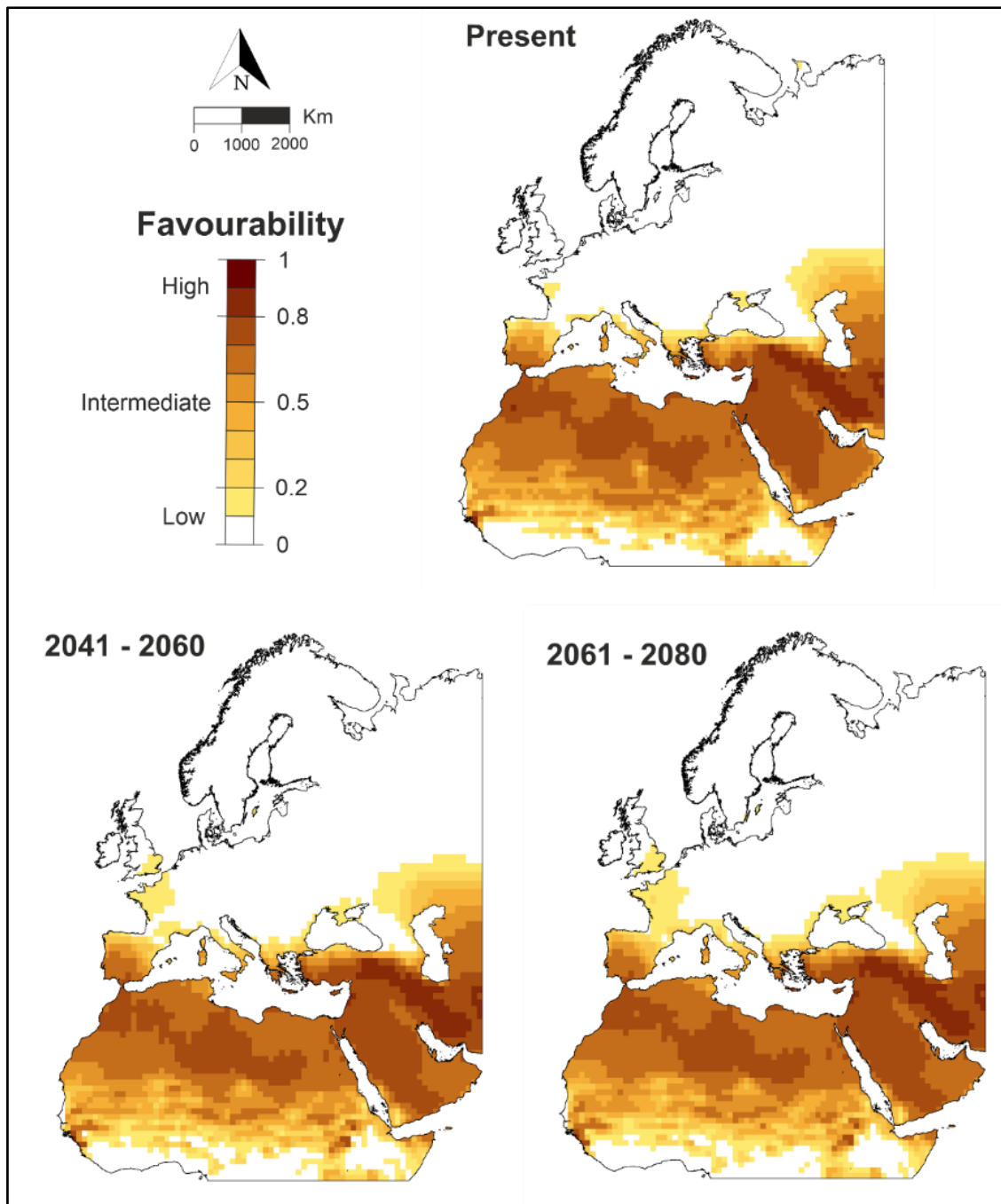


**Figure 3.2.** Sensitivity of favourability function to the variable “Precipitation of the warmest quarter”. The variable’s range values were divided into 20 points and each point represents the mean favourability value.

The southwestern quadrant of the Iberian Peninsula showed high values of favourability to host the House Bunting, both for the current climatic conditions and for the different scenarios of future climate change (**Figure 3.3**). When focusing on the southernmost areas, the Iberian Peninsula was found to be as favourable as Moroccan native areas. Considering the map for the near future (2041–2060), an increase in favourability was detected in the south of the Iberian Peninsula, especially in the area of the Strait of Gibraltar and the province of Malaga, and the favourability values increased in France and the south of the United Kingdom, although these values were always lower than 0.2. Favourability continued to increase slightly in the Iberian Peninsula, France and the south of the United Kingdom according to forecasts for the distant future (2061–2080), but no major changes were expected in relation to the near future.

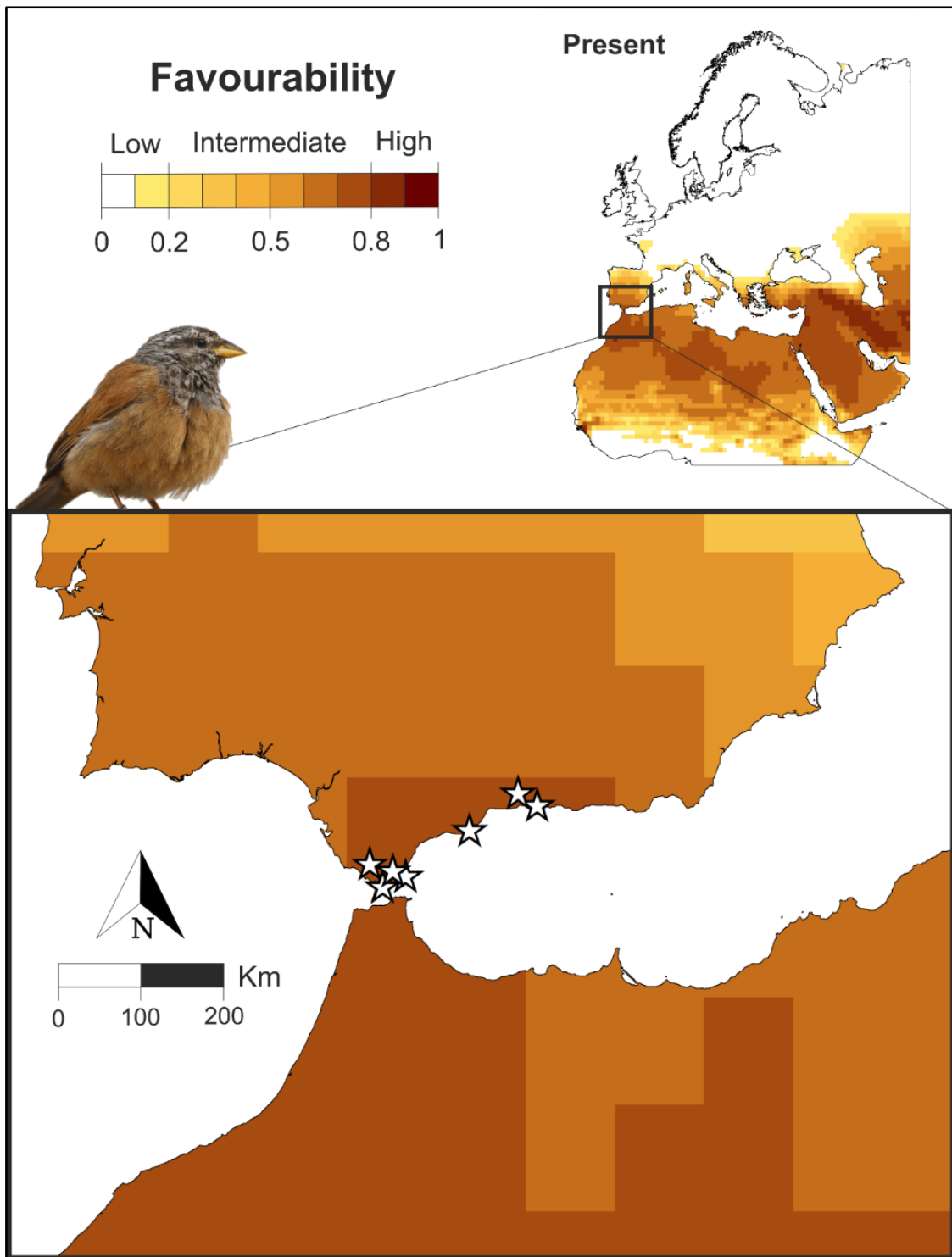
The discrimination capacity of the model was high (AUC = 0.811) and highly significant ( $p = 1.782 \times 10^{-27}$ ). According to the classification accuracy, the model showed higher sensitivity (0.923) than specificity (0.595), a low under-prediction rate (UPR = 0.003) and a high over-prediction rate (OPR = 0.945). At the time of this study, the only records of the House Bunting in Europe were found in the south of the Iberian Peninsula, in areas that our model detected as the most favourable for the species (**Figure 3.4**). The first House Bunting was observed in Europe on the 5th of August 2009, in Tarifa city (Cadiz) and the second was observed on the 13th of October of the same year in Nerja (Malaga). In recent years, regular arrivals of single individuals have been detected: in 2018 in Frigiliana (Malaga), in 2019 in Tarifa (Cadiz), in 2020 in Puertollano (Cadiz), in 2021 in both Gibraltar and Algeciras (Cadiz), and in 2022 in Fuengirola (Malaga). All these records of the species in the Iberian Peninsula took place during the dispersal period, just after the breeding season.

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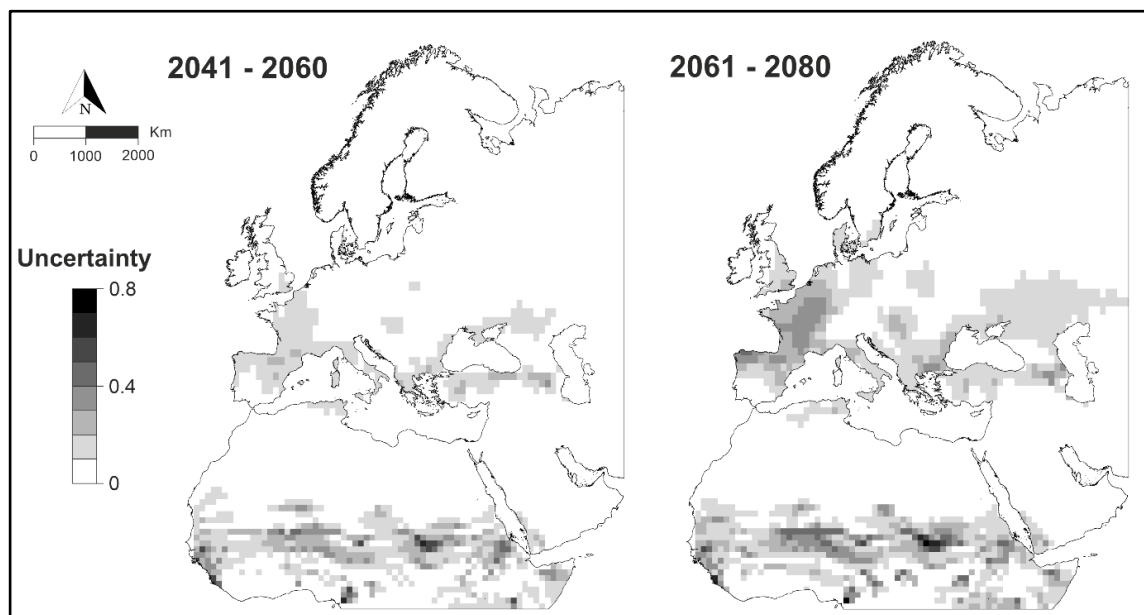
**Figure 3.3.** Cartographic representation of the current climatic favourability for House Bunting breeding in each operational geographic unit of the study area and the ensemble climatic favourability models for future periods of time. Maps created using ArcMap software (ArcGIS 10.4.1) <https://desktop.arcgis.com/es/arcmap/>

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**Figure 3.4.** Current climatic favourability for the breeding of the House Bunting in the south of the Iberian Peninsula and northern Morocco. The stars represent confirmed records of the species in Europe. Maps created using ArcMap software (ArcGIS 10.4.1) <https://desktop.arcgis.com/es/arcmap/>

There was a low mean uncertainty of less than 0.1 associated with future climate scenarios: 0.065 for the period 2041–2060 and 0.084 for the period 2061–2080 (**Figure 3.5**). For the distant future, there was an increase in uncertainty values in some European areas, including the northern half of the Iberian Peninsula, France, Belgium, the Netherlands, northern Italy, Bulgaria, Hungary and Slovakia, although in the near future the uncertainty values were much lower. The highest uncertainty values were in West Africa, Chad and Sudan, particularly for the period 2061–2080, whereas low uncertainty values were found in the south of the Iberian Peninsula and North Africa.



**Figure 3.5.** Climatic uncertainty associated with different climate change scenarios analysed for two different future time periods. Maps created using ArcMap software (ArcGIS 10.4.1) <https://desktop.arcgis.com/es/arcmap/>

### 3.4 Discussion

Over the last six decades, the House Bunting has colonised approximately 300 kms to the north in Morocco, reaching the coastal areas of North Africa (Thévenot *et al.* 2003). By the beginning of the twenty-first century, it had moved to the east, colonising as far as the frontier between Morocco and Algeria (De Juana 2006). The next step could be to colonise Western Europe due to the proximity of this area to the current populations of the species recently established in Northern Africa. Our distribution models showed that

southern Europe, specifically the southwestern quadrant of the Iberian Peninsula, hosts adequate environmental conditions for the establishment of the House Bunting, both based on the current climatic conditions and for different scenarios of future climate change.

Two of the three significant predictive variables included in the favourability model were associated with precipitation. In addition, the only non-climatic variable, altitude, was the last to be included in the model, suggesting a finer-scale effect (Muñoz & Real 2013). Consequently, the House Bunting's breeding distribution is characterised by scarce precipitation during the summer, which makes sense because it is a species that occupies arid areas. Climate change is expected to decrease the annual mean precipitation in many mid-latitude regions, especially in the Mediterranean basin (IPCC 2022). It is also expected to increase both day- and night-time temperatures and reduce the number of cold nights, as well as increasing the frequency and duration of heat waves (IPCC 2022), which will result in a warmer and drier environment in the European region, mainly in the south. Under these conditions, the possibility of African bird species becoming established in southern Europe will likely increase in coming years.

Our results showed that in Europe, the south of the Iberian Peninsula is the area with the best climatic conditions to host the House Bunting. Furthermore, it is the region closest to current and expanding populations of the species in northern Africa. The areas recently colonised in northern Morocco, where the species has occupied mostly urban areas and is already nesting (Thévenot *et al.* 2003), showed the same values of favourability as those of the southernmost tip of the Iberian Peninsula, which is as close as 14 km at the shortest distance, but does possess the natural barrier of the Strait of Gibraltar. In addition, the south of the Iberian Peninsula and North Africa had some of the lowest uncertainty values, indicating that our results were more consistent in these areas. The forecasts for the period 2061–2080 had the highest uncertainty, which is normal when the forecast time period is further away from the present (IPCC 2022). Regardless, it is expected that if the species continues its northward spread, it will establish itself in some of these favourable areas in the near future. In addition, according to our results, future forecasts indicate that the favourability will increase in these areas. Furthermore, our model showed numerous OGU's favourable for the species in southern Europe (especially in the southern half of the Iberian Peninsula) where breeding has not yet been reported. For this reason, it showed a low specificity and a high over-prediction

rate. In addition, it showed a high sensitivity and a low under-prediction rate as more than 90% of OGU's with reported breeding were classified as favourable for the species. However, apart from climate other driving factor of species distribution, such as urban expansion, may be influential in the establishment of the House Bunting in southern Europe (Rutz 2008, Márquez *et al.* 2011), given that the species prefers urban areas in Northern Africa and most of the eBird records in Spain are in towns and cities.

The favourable areas we detected in the south of the Iberian Peninsula are already regularly receiving individuals of the species. To date, these individuals have been detected in this area during the dispersal period of the species. In this way, the model can be validated because all records in Europe were included in those areas that were, previously and with independent data, predicted as highly favourable. These observations correspond very likely with vagrant birds dispersing from the recently colonised breeding areas in northern Morocco, which may indicate a continuity in the process of colonisation towards the north if they can surpass the sea barrier. There are recent cases of other African birds that have already experienced a similar expansion pattern, colonising the Iberian Peninsula, such as the Common Bulbul (Navarrete 2022) or the Cream-colored Courser (*Cursorius cursor*) (Cabrera 2022).

If the House Bunting becomes established in the south of the Iberian Peninsula, it will likely begin to colonise other areas of the European continent, as it will be much easier once the important biogeographical barrier of the Strait of Gibraltar has been overcome. These areas will likely be located in the southwestern quadrant of the Iberian Peninsula because, according to our results, they have the greatest favourability values. The species could then use these favourable areas as steppingstones to expand into the rest of Europe. This has previously occurred with the Black-shouldered Kite, which started breeding in Extremadura and Salamanca (central west Spain) in 1975, then moved northwards and became established in France in 2013 (Ferrero 1996, Balbontín *et al.* 2008, Logeais 2015). Furthermore, the establishment of the House Bunting in Europe would imply a change in communities with similar species, such as the Rock Bunting (*Emberiza cia*). Some of these changes in communities could be hybridisation, which have already occurred with other African bird species established on the European continent. Hybridisation between the African Long-legged Buzzard and the Common Buzzard (*B. buteo buteo*) has been detected in Pantelleria Island (Italy) (Corso 2009) and the Strait of Gibraltar (Elorriaga &

Muñoz 2013). Other changes could be related to competition or changes in trophic structures (Mendoza & Araujo 2022).

There are several factors that could facilitate the establishment of the House Bunting in the south of the Iberian Peninsula. The first is the short distance between the already occupied areas in northern Morocco and the favourable unoccupied areas in southern Spain, which could facilitate the natural arrival of individuals. The second is the fact that the House Bunting usually occupies urban environments (Chedad *et al.* 2021), which may imply some advantages such as greater availability of resources, less competition or protection against predators (Stofberg *et al.* 2022, Vanderwerf & Downs 2022). Thirdly, the presence of large ports and very intense maritime traffic between cities in Morocco, Spain and Gibraltar may increase the number of individuals that arrive in these areas (De Juana 2006). It should be noted, however, that individuals also arrive naturally, as there are records of House Buntings in places where there are no ports, such as Fuengirola or Frigiliana.

The possibility does exist that the House Bunting will not eventually become established on the European continent and its distribution limit will be restricted to North Africa. In this case, it is worth highlighting the important biogeographical barrier that the Strait of Gibraltar represents (Gantenbein & Largiadèr 2003, Carranza *et al.* 2006). We expect, however, that the species will eventually be able to colonise the south of the Iberian Peninsula, as has already happened with other African bird species (Del Junco & González 1969, Ramírez *et al.* 2002, Elorriaga & Muñoz 2010, Navarrete 2022). For this reason, citizen science platforms, species monitoring and follow-up programmes will play important roles in continuing to study the evolution of the species in Europe and in validating the favourability models presented in this study.

### **3.5 Conclusions**

We cannot anticipate when the House Bunting will establish on the European continent because colonisation processes are usually slow (Donahue & Lee 2008). Nevertheless, considering the fast northward expansion that the species has undergone in recent years until reaching northern Morocco, the fact that the south of the Iberian Peninsula has suitable climatic conditions for it, and the relative regularity of individuals that are already arriving in the south of the Iberian Peninsula, we predict the colonisation

of the species in the near future. In this study, we have focused on a single species but these results can be extrapolated to other African birds, with the possibility of an Africanisation of the European fauna.

### **3.6 Addendum to chapter 3**

Climate change is reshaping species distribution patterns globally, and driving an unprecedented Africanisation of southern Europe's avifauna, as species once confined to North Africa expand northward and establish breeding populations. Birds are among the most sensitive taxa to climate shifts, and species distribution models (SDMs) provide powerful tools to anticipate these changes. The House Bunting (*Emberiza sahari*), a species traditionally confined to North Africa, offers a striking example. SDMs predicted that southern Iberia, particularly Andalusia, would provide highly favourable climatic conditions both at present and under future warming scenarios (López-Ramírez *et al.* 2023). In 2023, the first documented breeding of the species in Europe occurred precisely within these high-favourability zones, validating the model's accuracy (Sepúlveda & Ortega 2023). In 2024 and 2025, additional breeding pairs were recorded in new areas, along with evidence of further arrivals and dispersal of European-born individuals (Muñoz *et al.* 2025).

The House Bunting is not an isolated case. Several other African bird species are taking advantage of increasingly suitable conditions in southern Europe. Trans-Saharan migrants such as the Spotted Flycatcher (*Muscicapa striata*) are overwintering in growing numbers (López-Ramírez *et al.* 2025), while species including the Common Bulbul (*Pycnonotus barbatus*), the Little Swift (*Apus affinis*), and the Atlas Long-legged Buzzard (*Buteo rufinus cirtensis*) have already established breeding populations or are regularly recorded in the region (López-Ramírez *et al.* 2024a). These trends highlight the Iberian Peninsula as a key gateway for African colonisation, a biogeographical frontier now shifting rapidly due to climate warming. This represents not only a redistribution of species but a fundamental reorganisation of avian communities at a continental scale.

The predictive success of SDMs underscores their value for early detection, monitoring, and adaptive conservation. Identifying climatically favourable zones allows conservationists to track new colonisers proactively and anticipate their ecological consequences (Elorriaga & Muñoz 2013, Muñoz *et al.* 2024a). The Africanisation of

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Europe's avifauna thus presents both challenges and opportunities. New arrivals may compete with native species and reshape ecological networks, but they also offer unique opportunities to study adaptation and biotic responses to climate change in real time. Similar dynamics are likely to occur in other temperate regions bordering tropical zones, making the Iberian case a sentinel for broader biogeographical transformations.

In conclusion, the expansion of the House Bunting provides compelling evidence that climate-driven range shifts are no longer hypothetical, they are happening now. African birds are moving into Europe, reshaping avifaunal assemblages and conservation priorities. As the continent continues to warm, more species are expected to follow. Monitoring and understanding these dynamics will be crucial to designing effective, forward-looking conservation strategies in a rapidly changing world.



Las tres especies de rapaces africanas objeto de estudio del capítulo 4 de la presente tesis. De arriba hacia abajo: buitre dorsiblanco africano (*Gyps africanus*), ratonero moro del Atlas (*Buteo rufinus cirtensis*) y buitre de Rüppell (*Gyps rueppelli*).

# CAPÍTULO 4

Contrasting mechanisms driving the  
northward expansion of African raptors into  
Europe

Diferentes mecanismos que impulsan la  
expansión hacia el norte de aves rapaces  
africanas hacia Europa

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Este capítulo se basa en: / This chapter is based on:

Muñoz, A.-R., **López-Ramírez, S.**, García-Carrasco, J.-M. & Real, R. Contrasting mechanisms driving the northward expansion of African raptors into Europe (under review in *Journal of Zoology*).

## **4. Contrasting mechanisms driving the northward expansion of African raptors into Europe**

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### **4.0 Abstract**

The contrasting mechanisms driving the northward expansion of African raptors into Europe provides a unique opportunity to understand how these species overcome substantial geographical barriers and a major biogeographic boundary. To explore these mechanisms, we analysed three species currently expanding across the Afro-Palaeartic system: the Atlas Long-legged Buzzard (*Buteo rufinus cirtensis*), Rüppell's Vulture (*Gyps rueppelli*), and White-backed Vulture (*Gyps africanus*). Using species distribution models based on topo-climatic predictors, we estimated environmental favourability for breeding across 6,203 operational geographic units and compared outputs with breeding records, recent sightings, ecological traits, and evidence of interspecific interactions. Our results reveal contrasting colonization pathways. The Atlas Long-legged Buzzard shows broad climatic favourability across North Africa and parts of southern Europe, consistent with climate-driven range expansion. By contrast, African vultures exhibit negligible climatic favourability in Europe. Rüppell's Vultures have bred there, always in hybrid pairs with Griffon Vultures (*Gyps fulvus*), while observations of immature White-backed Vultures remain few and anecdotal per se, yet they have been recorded increasingly and more regularly over the past few years. These patterns indicate colonization mediated by socially assisted vagrancy, with immature vultures following groups of migratory Griffon Vultures and integrating into the social and spatial networks of their European congeners. Our findings demonstrate that African raptors are transgressing current biogeographic boundaries through fundamentally different mechanisms, highlighting the need to integrate behavioural ecology and interspecific interactions into predictions of species redistribution under global change.

## 4.1 Introduction

The colonization of new territories by animal species is a complex process shaped by a combination of behavioural, ecological, physiological and environmental factors (Grinnell 1922, Simberloff & Wilson 1969, Gaggiotti *et al.* 2002, Gervais *et al.* 2021). Successful establishment typically requires overcoming biogeographical barriers (Moura *et al.* 2019), adapting to novel environmental conditions, and integrating into existing ecological communities (Elorriaga & Muñoz 2013, Muñoz *et al.* 2024a). Several mechanisms have been proposed to explain these processes, including active dispersal beyond native ranges (Simmons & Thomas 2004), passive vagrancy (Lees & Gilroy 2021), and interspecific facilitation (Svenning *et al.* 2014), which may act independently or synergistically. Dispersal entails movement beyond a species' native range, often triggered by environmental shifts or changing resource availability (Duckworth & Badyaev 2007, Chamorro *et al.* 2017). Vagrancy, defined as the occurrence of individuals outside their typical distribution range, can lead to colonization when vagrants encounter suitable conditions for survival and reproduction (Dufour *et al.* 2024). In addition, interspecific interactions, such as social guidance or shared resource use, can facilitate establishment, as seen in scenarios where closely related or socially structured species provide guidance or resources to vagrant individuals (Ramírez *et al.* 2011, Lustenhouwer & Parker 2022). These mechanisms are particularly relevant in transition zones between biogeographic regions, such as the Afro-Palaeartic, where northward range shifts are becoming increasingly frequent in response to climate change (Chen *et al.* 2011, López-Ramírez *et al.* 2023). Understanding which species can overcome such barriers, and through which mechanisms, is essential to anticipate future shifts in species distributions under ongoing global change.

Recent climate warming and associated landscape transformations are increasingly creating favourable conditions for African species to expand into southern Europe, particularly across the Moroccan–Spanish transition zone (López-Ramírez *et al.* 2024a). These changes underpin the progressive colonization of northern latitudes by species traditionally confined to North Africa or the Afrotropical region. Among the taxa currently exhibiting range shifts, African raptors stand out as a particularly illustrative case. Several species, traditionally confined to sub-Saharan or North African regions, have recently been recorded in Europe with increasing frequency. In some cases, such as the Atlas Long-legged Buzzard (*Buteo rufinus cirtensis*), successful breeding has already

been confirmed (Elorriaga & Muñoz 2010), suggesting the early stages of population establishment. The Rüppell's Vulture (*Gyps rueppelli*) has also bred in Europe, although all known breeding events have involved hybrid pairs with the Griffon Vulture (*Gyps fulvus*) (Muñoz *et al.* 2024a, Marcano-Delgado *et al.* in press). In contrast, the White-backed Vulture (*Gyps africanus*) appears to be at an earlier stage of colonization, as only juvenile or immature individuals have been observed so far (Pardo de Santayana *et al.* 2025), but its presence has become increasingly regular in recent years in both North Africa and southern Europe. These cases provide a unique opportunity to explore the contrasting mechanisms that enable colonization (López-Ramírez *et al.* 2024a).

A key aspect in the arrival of Afrotropical vultures to Europe may be the migratory behaviour of Eurasian Griffon Vultures. Each autumn, large numbers of juvenile and immature Griffons migrate from Iberia and southern France to the western Sahel, where they gather in their thousands (Bernis 1983, Griesinger 1996). These movements are highly gregarious, dominated by non-adults (Ramírez *et al.* 2019, Onrubia 2021), and involve prolonged stays in areas of West Africa where mixed-species groups are frequently formed, with Rüppell's and White-backed Vultures joining Griffon Vultures and remaining associated with them for extended periods (Muñoz *et al.* 2024b). In these mixed-species contexts, young African vultures, more prone to exploration and social association, may integrate into Griffon Vulture flocks and subsequently follow them during their northbound return to Europe in spring (Ramírez *et al.* 2011). The dramatic demographic expansion of the Iberian Griffon Vulture population in recent decades has further increased the number of individuals reaching the Sahel, thereby raising the probability of taking on African individuals into Griffon Vulture migratory groups. This socially mediated mechanism differs fundamentally from climate-driven northward expansion and provides a plausible explanation for the growing presence of Afrotropical vultures in Europe.

In this context, we hypothesize that while the Atlas Long-legged Buzzard is expanding its range through autonomous, climate-driven colonization, the movement of African vultures into Europe is facilitated by interspecific social interactions, particularly with the Griffon Vulture. This dual scenario allows us to test the relative contribution of abiotic and biotic factors to range expansion in a rapidly changing world. In this study, we analyse the breeding distributions of three African raptors that are currently expanding their ranges across the Afro-Palaeartic system. Using species distribution models, we

quantify climatic favourability for each species and interpret the resulting spatial and environmental patterns in relation to their ecological traits and behavioural strategies. Our aim is to provide a clearer understanding of the mechanisms driving recent colonization events, and to highlight their implications for the conservation of African raptor species actively establishing themselves in Europe.

## **4.2 Methods**

### **4.2.1 Study area**

The study area consisted of the Afro-Palaeartic system, comprising the Western Palaeartic (Europe, North Africa and northern-central Arabia) and the Afrotropical region (sub-Saharan Africa and southern Arabia). This area was divided using an equal-sized hexagonal grid, with each hexagon representing an operational geographic unit (OGU) spanning an area of 7,774 km<sup>2</sup> (**Figure 4.1**). The hexagonal grid was created using Discrete Global Grids for R (Barnes & Sahr 2017). In total, the study area was divided into 6,203 OGUs (2,916 in the Western Palaeartic and 3,287 in the Afrotropical region). The selected region fully covers the current breeding territories of the three African raptors studied in the Afro-Palaeartic migratory system (Moreau 1972). This region is therefore well-suited for studying the factors driving the northward colonization of African bird species in Europe.

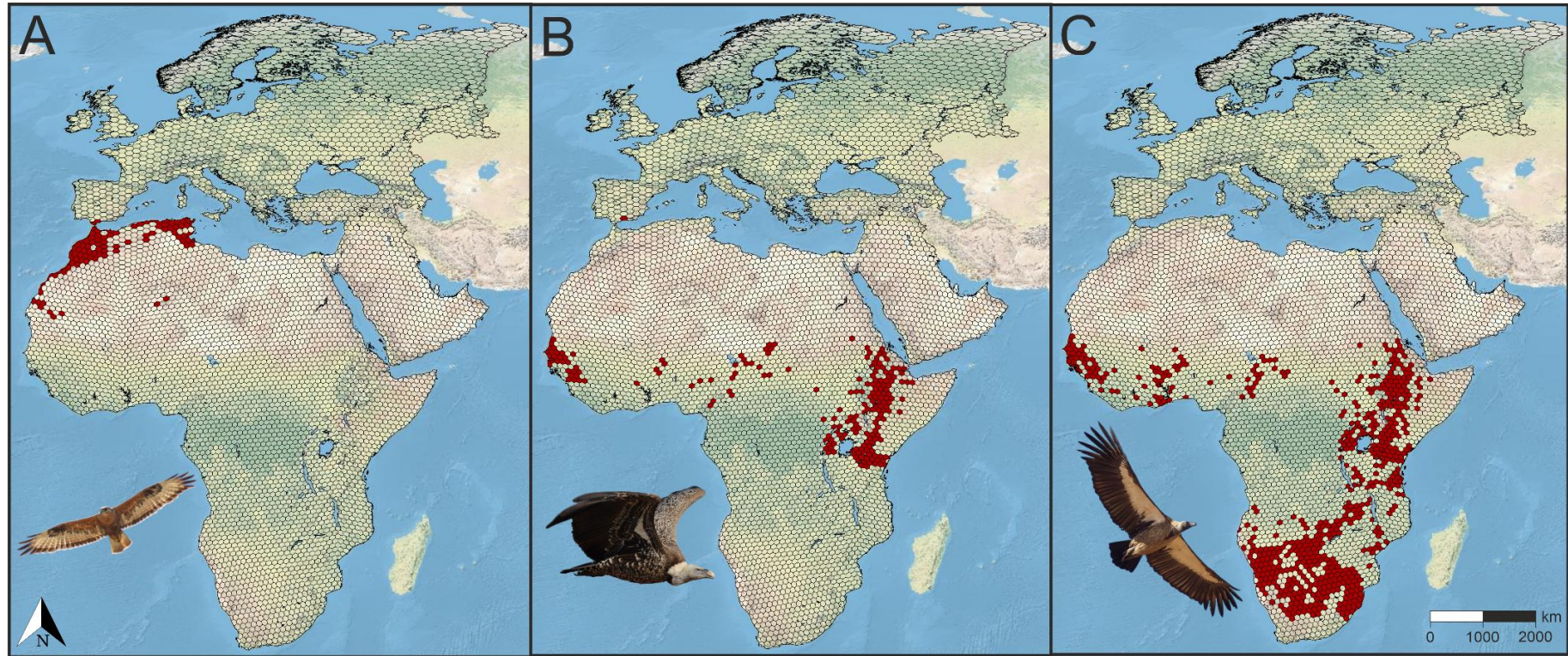
### **4.2.2 Studied species and distribution data**

The studied species included the Atlas Long-legged Buzzard (*Buteo rufinus cirtensis*), the Rüppell's Vulture (*Gyps rueppelli*) and the White-backed Vulture (*Gyps africanus*). All have been observed in southern Europe within the last years and, in some cases, are already breeding (as with the Atlas Long-legged Buzzard; Elorriaga & Muñoz 2010) or have bred only sporadically (as it is the case of the Rüppell's Vulture; Muñoz *et al.* 2024a). In the case of the White-backed Vulture, although only isolated records of juvenile or immature individuals have been documented so far, its presence in Europe has been confirmed. All three species have close congeners in Europe with which they can hybridise, a phenomenon already documented between the Atlas Long-legged Buzzard and the Common Buzzard (*B. buteo buteo*) on Pantelleria Island, Italy (Corso 2009), and

in the Strait of Gibraltar, Spain (Elorriaga & Muñoz 2013), as well as between the Rüppell's Vulture and the Griffon Vulture (*G. fulvus*) in Malaga province (southern Spain) (Muñoz *et al.* 2024a).

In terms of native distribution, the Atlas Long-legged Buzzard occurs in the African portion of the Western Palaearctic, ranging from north-west Mauritania to Egypt (**Figure 4.1A**; Orta *et al.* 2020), while the Rüppell's and White-backed Vultures are distributed in the Afrotropical region (**Figure 4.1B, C**). The Rüppell's Vulture ranges from south-west Mauritania and Senegambia eastward to Somalia, and southward into Kenya and northern Tanzania (**Figure 4.1B**; Kemp *et al.* 2020a). The White-backed Vulture is distributed from the southernmost tip of Mauritania and Senegambia through southern and eastern Sudan, Eritrea and Ethiopia, extending further south across East Africa to Namibia and north-eastern South Africa (**Figure 4.1C**; Kemp *et al.* 2020b).

To delineate the breeding areas of each species, we used occurrence records from the international citizen science platform eBird (<https://ebird.org/home>), including data from the 21<sup>st</sup> century up to the end of September 2024. Records were filtered to retain only confirmed breeding locations according to the information provided by Birds of the World (Kemp *et al.* 2020a, b; Orta *et al.* 2020). For the Atlas Long-legged Buzzard, we excluded the confirmed breeding record from Pantelleria Island, as the only record corresponds to a single hybridization event. In the case of Rüppell's Vulture, we retained the records from southern Spain in the modelling framework because they represent confirmed and continuous breeding events within the Afro-Palaearctic system, regardless of whether they are part of the colonization process or involve hybridization. Using this approach, we identified 104 breeding OGU's for the Atlas Long-legged Buzzard (**Figure 4.1A**), 197 for the Rüppell's Vulture (**Figure 4.1B**), and 584 for the White-backed Vulture (**Figure 4.1C**). For all three species, we defined the modelling area using their full biogeographic ranges to ensure a common environmental framework and avoid introducing species-specific biases. Although the Atlas Long-legged Buzzard currently breeds mostly in north-western Africa, restricting the study area to this region would artificially narrow the climatic space available for calibration and create an inconsistent modelling domain relative to the two vulture species. Using the full range for all three species therefore provides a comparable and biologically meaningful geographic context for favourability estimation, allowing the model to capture the full breadth of environmental conditions associated with the species' potential for expansion.



**Figure 4.1.** The study area (Afro-Palaeartic region), divided into a hexagonal grid, showing the current breeding occurrences of the Atlas Long-legged Buzzard (A), the Rüppell's Vulture (B), and the White-backed Vulture (C) used to build the distribution models.

### 4.2.3 Predictor variables used for distribution modelling

A set of 21 environmental variables related to topography ( $n = 2$ ) and climate ( $n = 19$ ), spanning the period 1981-2010, was used to model the breeding distribution of the three African raptors in the Afro-Palaeartic (**Table 4.1**). Topographic variables were included alongside climatic ones to avoid conflating their distinct effects and mistakenly attributing all influence to climate alone (Márquez *et al.* 2011, Muñoz *et al.* 2013).

These variables were downloaded in raster format with an approximate spatial resolution of 1 km<sup>2</sup>. For each operational geographic unit (OGU), variable values were calculated as the mean of all 1 km<sup>2</sup> raster cells contained within it, using the "zonal statistics as table" function in ArcGIS version 10.4.1 (ESRI 2016). This approach provided representative average values of the environmental conditions at each location where breeding was recorded, or not.

**Table 4.1.** Environmental variables used to model the breeding distribution of the three African raptors in the Afro-Palaeartic, grouped by factor type.

Code	Variable and units
<b>Topography</b>	
Alti	Altitude (m) <sup>1</sup>
Slope	Slope (degrees) <sup>2</sup>
<b>Climate<sup>3</sup></b>	
Tmean	Mean annual air temperature (0.1·°C-273.15)
Rtday	Mean diurnal air temperature range (0.1·°C)
Isot	Isothermality (0.1·°C)
Season	Temperature seasonality (0.1·°C/100)
Tmax	Mean daily maximum air temperature of the warmest month (0.1·°C-273.15)
Tmin	Mean daily minimum air temperature of the coldest month (0.1·°C-273.15)
Rtan	Annual range of air temperature (0.1·°C)
Twet	Mean daily air temperatures of the wettest quarter (0.1·°C-273.15)
Tdry	Mean daily air temperatures of the driest quarter (0.1·°C-273.15)
Twarm	Mean daily air temperatures of the warmest quarter (0.1·°C-273.15)
Tcold	Mean daily air temperatures of the coldest quarter (0.1·°C-273.15)
Prec	Annual precipitation amount (0.1·mm·year <sup>-1</sup> )
Pmax	Precipitation amount of the wettest month (0.1·mm·month <sup>-1</sup> )
Pmin	Precipitation amount of the driest month (0.1·mm·month <sup>-1</sup> )
Cvp	Precipitation seasonality (0.1·mm·month <sup>-1</sup> )
Pwet	Mean monthly precipitation amount of the wettest quarter (0.1·mm·month <sup>-1</sup> )
Pdry	Mean monthly precipitation amount of the driest quarter (0.1·mm·month <sup>-1</sup> )
Pwarm	Mean monthly precipitation amount of the warmest quarter (0.1·mm·month <sup>-1</sup> )
Pcold	Mean monthly precipitation amount of the coldest quarter (0.1·mm·month <sup>-1</sup> )

*Data sources:* 1. US Geological Survey (1996); 2. Elaborated from the digital elevation model using the altitude variable (US Geological Survey 1996) with the geographic information system ArcGIS Desktop 10.4.1; 3. Chelsa Climate (<http://chelsa-climate.org>).

#### **4.2.4 Distribution models**

To model the breeding distribution of each bird species in the study area, we first tested their response to each explanatory variable used in this study. This response can be monotonic, unimodal or bimodal (see **Appendix 43**). A monotonic response implies that the relationship with the breeding presence of the species is either positive or negative. A unimodal response occurs when, after reaching an optimum value along the environmental gradient, the initially positive relationship becomes negative. In contrast, a bimodal response occurs when the initially negative relationship becomes positive beyond a certain threshold along the environmental gradient. To include these types of responses in the modelling process, univariate binary stepwise logistic regression models were performed separately for each explanatory variable, using their original ( $x$ ) and quadratic ( $x^2$ ) forms. We considered a response to be unimodal when the best-fitting logistic regression model included the original form as positive and the quadratic form as negative ( $x, -x^2$ ). For all variables that showed this type of response, the result of the unimodal model ( $y$  or *logit* function) was used as an explanatory variable in the modelling process (García-Carrasco *et al.* 2024, López-Ramírez *et al.* 2024a). In all other cases, we used the original form of the variable.

We then calculated Spearman's correlation coefficients between variables to reduce multicollinearity among them. When two variables were highly correlated ( $r > 0.8$ ), we retained only the one that contributed most to explain the distribution of the species, based on their Rao's score tests (Zanolla *et al.* 2018). From the set of pre-selected variables obtained in this phase of the analysis, we calculated the false discovery rate (FDR; Benjamini & Hochberg 1995) to control for type I error inflation and reduce the likelihood of false-positive results when a large number of variables are included in the modelling process (García 2003). Following the procedure of Benjamini & Yekutieli (2001), only those variables with a Rao's score test significance below the FDR threshold of 0.05 were retained for subsequent modelling procedures.

On the remaining subset of variables that passed the above filters, we performed a multivariate stepwise logistic regression using a forward-backward stepwise selection procedure, relating species distribution to environmental predictors in the study area. In this way, we obtained an environmental model for the current probability of breeding in each OGU, according to its topo-climatic conditions. At each step, a new variable was added or an existing one removed depending on whether it significantly improved model

fit, as determined by Rao's score test, until no additional variable significantly increased the predictive capacity of the model (Legendre & Legendre 1998). This approach allowed us to identify a parsimonious subset of variables capturing the main effects from the full pool of variables considered. Once the final combination of predictors ( $y$  or *logit*) was obtained, their coefficients were estimated using a machine learning algorithm based on gradient ascent of likelihood (Glasmachers & Igel 2010, Basha *et al.* 2018). The relative contribution of each variable to the model was assessed using the Wald test (Wald 1943), and remaining multicollinearity between variables in the final model was quantified using the variance inflation factor (VIF). The VIF measures the overall correlation of each variable with the others in the model and helps identify potential collinearity issues (Zuur *et al.* 2010, Muñoz *et al.* 2015b).

The result of the multivariate logistic regression was a predicted probability ( $P$ ) of breeding for each OGU, based on the set of environmental variables. These probability values are influenced by the prevalence of the species in the study area, i.e. the proportion of OGUs where the species has been reported to breed relative to the total number of OGUs. Since the prevalence of records may be underestimated, particularly in regions with lower citizen science activity, and because we aimed to compare the spatial distributions of different species, it is essential to account for this bias. To this end, we removed the effect of prevalence by applying the favourability function (Real *et al.* 2006):

$$F = \frac{\frac{P}{1-P}}{\frac{n_1}{n_0} + \frac{P}{1-P}}$$

where  $n_1$  and  $n_0$  represent the number of OGUs where the species was reported to breed and the number of OGUs where it was not reported to breed, respectively. Favourability ( $F$ ) indicates the extent to which environmental conditions are suitable for the species to breed, ranging from 0 (minimum favourability) to 1 (maximum favourability) (Acevedo & Real 2012), with  $F = 0.5$  as the threshold separating favourable from unfavourable areas. A local favourability value of 0.5 indicates that the local probability of a species breeding equals its overall prevalence in the study area, that is, the probability expected under a null model unaffected by environmental predictors, where breeding is neither favoured nor unfavoured by the environment (Real *et al.* 2006). Values of  $F > 0.5$  indicate environmentally favourable areas for breeding, while  $F < 0.5$  correspond to unfavourable conditions. However, using a favourability value of 0.5 as a strict cut-off point to

distinguish between favourable and unfavourable areas is not sufficiently informative (Hosmer & Lemeshow 2005), due to the continuous and fuzzy nature of favourability (Acevedo & Real 2012).

To improve interpretability, the favourability values for each OGU were displayed on maps using 10 equal-width classes (ranging from 0 to 1), and additionally grouped them into four categories based on their  $F$  values: ‘high favourability’ ( $F \geq 0.8$ ), ‘intermediate-high favourability’ ( $0.8 > F > 0.5$ ), ‘intermediate-low favourability’ ( $0.5 > F > 0.2$ ), and ‘low favourability’ ( $F \leq 0.2$ ) to clearly distinguish between favourable from unfavourable areas (García-Carrasco *et al.* 2021). All modelling procedures were carried out using IBM SPSS Statistics 25, and maps were generated with ArcMap software (ArcGIS 10.4.1; [www.esri.com](http://www.esri.com)).

#### **4.2.5 Models’ assessment**

The resulting three distribution models were assessed according to their discrimination and classification capacities. Discrimination capacity was evaluated using the area under the receiver operating characteristic curve (ROC) (Lobo *et al.* 2008). Classification performance, using  $F = 0.5$  as the classification threshold, was evaluated using the following metrics: sensitivity (the conditional probability that OGUs with reported breeding are classified as favourable), specificity (the conditional probability that OGUs with no reported breeding are classified as unfavourable), correct classification rate (CCR; the overall probability of correctly classified OGUs), over-prediction rate (OPR; the proportion of OGUs with favourability higher than 0.5 without breeding records), and under-prediction rate (UPR; the proportion of OGUs with favourability lower than 0.5 with breeding records). These measures are widely used and range from 0 to 1, with higher values indicating better model performance (Fielding & Bell 1997, Barbosa *et al.* 2013b). In addition, we used Cohen's Kappa index (Cohen 1960), which ranges from  $-1$  to  $+1$ , to quantify the agreement between favourability values and breeding records, specifically whether OGUs with or without breeding were more often associated with favourability values above or below 0.5, respectively.

## 4.3 Results

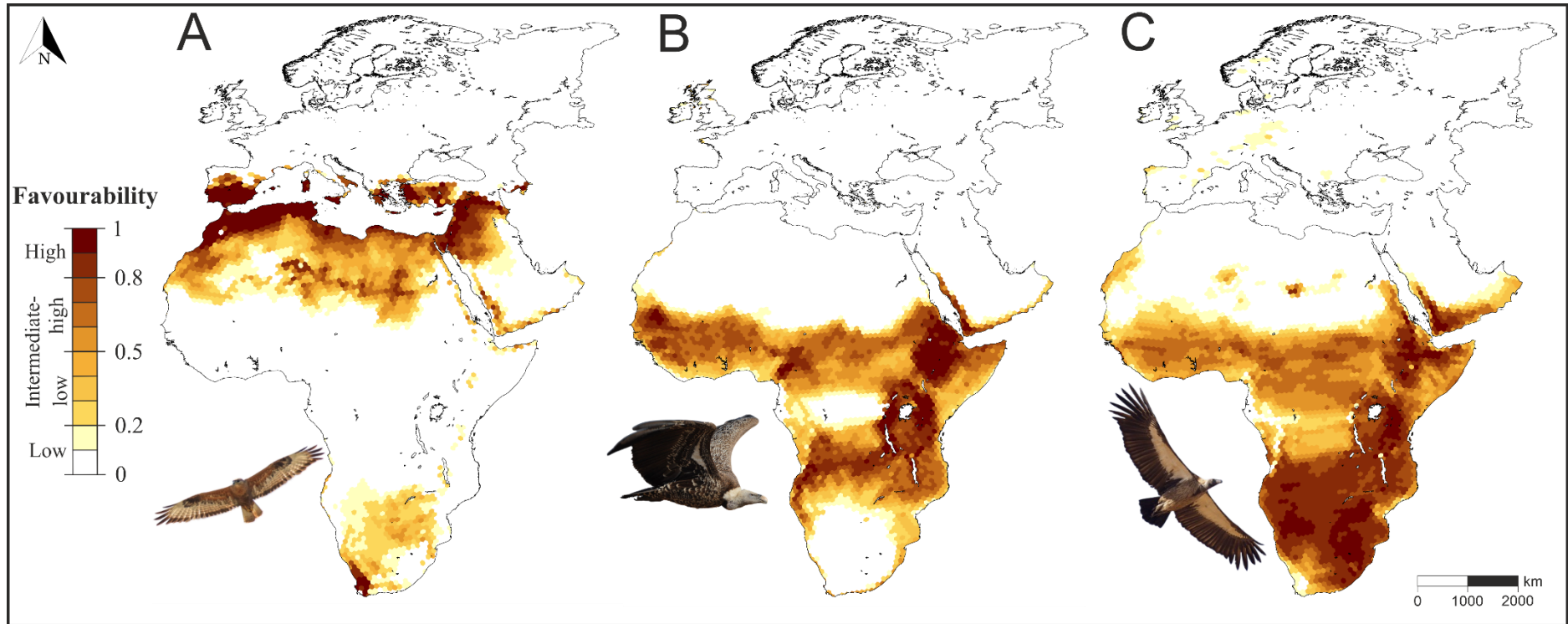
### 4.3.1 Mathematical and cartographic models

Between 8 and 11 explanatory variables were included in the biogeographical models for each species. Unimodal variables captured the distribution patterns of the three African raptors across the Afro-Palaeartic region more effectively than the linear variables. Of the 17 significant responses included in any of the models, 15 were unimodal (**Table 4.2**), indicating that the breeding distributions of the three species are primarily structured around optimal climatic ranges rather than monotonic gradients. For the Atlas Long-legged Buzzard, the most favourable breeding areas correspond to warm regions with high average temperatures and pronounced diurnal temperature variation. Northern Africa, which constitutes the species' native range, stands out as a core area of high favourability, along with southern Europe, particularly the southern half of the Iberian Peninsula and the major Mediterranean islands. The model also identifies favourable conditions in parts of the eastern Mediterranean, where its conspecific, the nominal subspecies *Buteo rufinus rufinus* occurs. South of the Sahara, the model detects areas of intermediate favourability in South Africa, likely reflecting climatic similarities with northern Africa (**Figure 4.2A**). In the case of the Rüppell's Vulture, the most favourable breeding areas are those with sufficient rainfall during the driest and hottest periods, as well as elevated temperatures during the coldest season. This combination suggests a preference for tropical habitats, extending southward primarily along coastal regions (**Figure 4.2B**). Outside these core tropical areas, favourability declines sharply, with Europe and North Africa consistently characterised by very low favourability values, indicating that climatic conditions associated with breeding suitability are largely absent at higher latitudes. By contrast, the optimal areas for the breeding of the White-backed Vulture are those experiencing consistently high temperatures throughout the year combined with low mean annual temperatures. These areas are primarily located south of the Sahel and across the southern and eastern regions of Africa (**Figure 4.2C**). For both vulture species, the distribution models show very low favourability across Europe and North Africa. Importantly, these results indicate that the climatic conditions prevailing in the Western Palaeartic do not resemble those characterising the core breeding ranges of either species. In the case of the White-backed Vulture the species-level favourability model does not capture some favourable areas in Western Africa (e.g., Senegal), where the species is known to breed.

**Table 4.2.** Variables included in the logistic regression models for the Atlas Long-legged Buzzard, Rüppell’s Vulture and White-backed Vulture via a forward–backward stepwise procedure. The prefix “U\_” indicates that the variable was included in the model in its unimodal form. Variable codes correspond to those listed in **Table 4.1**.

Variable	Atlas Long-legged Buzzard			Rüppell’s Vulture			White-backed Vulture		
	$\beta$	Wald	VIF	$\beta$	Wald	VIF	$\beta$	Wald	VIF
Alti	-	-	-	0.00137	40.794	1.288	-	-	-
U_Alti	-	-	-	-	-	-	0.524	54.603	1.467
U_Slope	0.508	10.683	1.138	0.711	22.841	1.240	-	-	-
U_Tmean	0.855	27.480	5.339	-	-	-	-0.660	19.396	5.545
U_Isot	0.456	16.015	1.497	-	-	-	0.230	6.494	4.525
U_Season	-	-	-	1.198	29.079	3.998	0.463	17.476	4.226
U_Tmin	-	-	-	1.235	37.368	16.258	-	-	-
U_Twet	-0.348	4.712	2.000	-1.075	8.992	2.407	0.468	26.423	1.833
U_Tdry	0.972	14.545	3.852	-0.815	7.226	13.452	0.630	25.063	5.193
U_Twarm	-0.537	3.940	3.495	-1.815	16.307	2.242	-	-	-
U_Prec	0.652	14.162	1.753	-	-	-	0.544	10.483	3.116
U_Pmax	-	-	-	-	-	-	-0.869	35.994	3.446
Pmin	-	-	-	-	-	-	0.00314	28.985	3.074
U_Pmin	-	-	-	0.896	5.054	1.226	-	-	-
U_Cvp	-	-	-	-	-	-	0.843	35.696	2.775
U_Pdry	0.355	6.491	1.681	-	-	-	-	-	-
U_Pwarm	-	-	-	0.649	7.381	1.507	0.788	47.296	2.323
Constant	8.011	50.397	-	-1.308	0.669	-	4.113	162.728	-

Note:  $\beta$ s are the coefficients in the logit function, Wald is the Wald’s statistics value (representing the relative importance of the variable in the model), and VIF is the variance inflation factor (used to quantify collinearity between variables in the model).



**Figure 4.2.** Topo-climatic favourability values for the breeding of the Atlas Long-legged Buzzard (A), the Rüppell's Vulture (B) and the White-backed Vulture (C) across each operational geographic unit within the Afro-Palaearctic region.

#### 4.3.2 Models' assessment

The resulting distribution models for the Atlas Long-legged Buzzard, Rüppell's Vulture, and White-backed Vulture in the Afro-Palaeartic were assessed and compared based on their discrimination and classification capacity. The AUC yielded values of 0.957, 0.927, and 0.898 for the three species, respectively (**Table 4.3**). These results indicate outstanding discrimination performance for the Atlas Long-legged Buzzard and Rüppell's Vulture, and excellent performance for the White-backed Vulture. According to the classification capacity, the Atlas Long-legged Buzzard showed the highest specificity (0.876), CCR (0.876), and over-prediction rate (0.892), while the White-backed Vulture presented the highest under-prediction rate (0.0133). The Kappa index was relatively low for the Atlas Long-legged Buzzard (0.168) and Rüppell's Vulture (0.165), but slightly higher for the White-backed Vulture (0.307), potentially indicating differences in the models' ability to delineate favourable breeding areas. Overall, the distribution models demonstrated strong discrimination ability for the three species, but their classification capacities varied, indicating potential limitations when predicting favourable areas for each of them.

**Table 4.3.** Assessment of the distribution models for the three African raptors according to their discrimination and classification capacities. Assessment indices include: Area Under the Curve (AUC), sensitivity, specificity, correct classification rate (CCR), over-prediction rate (OPR), under-prediction rate (UPR) and Cohen's Kappa index (Kappa).

Measure	Atlas Long-legged Buzzard	Rüppell's Vulture	White-backed Vulture
AUC	0.957	0.927	0.898
Sensitivity	0.885	0.904	0.904
Specificity	0.876	0.782	0.737
CCR	0.876	0.786	0.753
OPR	0.892	0.880	0.737
UPR	0.0022	0.0040	0.0133
Kappa	0.168	0.165	0.307

#### **4.4 Discussion**

The distribution models revealed currently favourable conditions for the Atlas Long-legged Buzzard in several regions of Europe, particularly across the western Mediterranean. This matches current records of this and other African species that are increasingly recorded on a regular basis in southern Europe (Elorriaga & Muñoz 2013, López-Ramírez *et al.* 2024a). In contrast, climate-based models predicted a general lack of favourable climatic conditions for the two African vulture species in Europe, despite multiple field observations documenting their presence, and even breeding attempts in the case of Rüppell's Vulture (Muñoz *et al.* 2024a). This apparent mismatch underscores the importance of incorporating behavioural mechanisms, particularly social interactions and vagrancy, into our understanding of colonization processes.

The contrasting colonization patterns observed among the studied raptors reflect the interplay between intrinsic ecological traits and external environmental or biotic drivers (Chen *et al.* 2011), and exemplify two distinct pathways through which species can overcome major biogeographic barriers, including the transition between the Afrotropical and Palaearctic realms. The Atlas Long-legged Buzzard appears to be expanding through autonomous, climate-driven range shifts, favoured by environmental continuity between North Africa and parts of southern Europe, particularly in open habitats with thermal conditions resembling those of the species' native range, which supports independent establishment without evident reliance on resident species. These findings are consistent with other climate-mediated expansions of African species into newly favourable regions of Europe, such as the Little Swift (*Apus affinis*), the Common Bulbul (*Pycnonotus barbatus*), the Cream-coloured Courser (*Cursorius cursor*) and, more recently, the House Bunting (*Emberiza sahari*) (Chamorro *et al.* 2017, López-Ramírez *et al.* 2024a, Muñoz *et al.* 2025). In contrast, the presence of Rüppell's and White-backed Vultures in Europe, despite low climatic favourability, seems to rely more heavily on other factors, such as dispersal dynamics and interspecific interactions, between others. Vagrancy, once considered a marginal process (Grinnell 1922), is now recognised as a key mechanism enabling range shifts, particularly when environmental changes create new opportunities and behavioural traits favour exploration (Lees & Gilroy 2021, Dufour *et al.* 2024). Such complexity may mirror what has been proposed for long-distance vagrant passerines, where climatic favourability alone cannot account for the observed patterns of colonization (Bozó & Csörgő 2024).

In the case of the vultures, a plausible explanation for this pattern involves socially assisted dispersal, mediated by interactions with Griffon Vultures. Species of the genus *Gyps* are highly gregarious, with strong social structure and fission–fusion dynamics (Sassi *et al.* 2024), and they frequently form large mixed-species aggregations at communal roosts and feeding sites (Donázar 1993, Cortés-Avizanda *et al.* 2012, Muñoz *et al.* 2024b). During the non-breeding season, wintering European Griffon Vultures often interact with resident African vultures at shared roosts and feeding sites in West Africa (Muñoz *et al.* 2024b). These prolonged interactions may foster strong social bonds, especially among immature individuals. Such associations likely explain how young African vultures, lacking prior experience of long-distance movements or sea crossings, can accompany Griffon Vultures back to Europe after winter (Ramírez *et al.* 2011, El Khamlichi *et al.* 2022). This hypothesis is consistent with studies showing that *Gyps* vultures rely heavily on social information to make flight and foraging decisions (Jackson *et al.* 2008, Cortés-Avizanda *et al.* 2014). As obligate scavengers, they depend on unpredictable carrion availability, which promotes close social cohesion and coordinated movements to maximize foraging success (Arrondo *et al.* 2023). Young and immature vultures are gregarious and often follow more informed individuals during soaring and displacement flights, increasing the likelihood of coordinated movements such as those of African vultures reaching Europe. This may be particularly relevant in the case of those individuals reaching the Strait of Gibraltar, an ecological barrier for soaring birds, which rely on thermal updrafts and are unable to sustain flapping flight over large bodies of water (Mellone 2020, Santos *et al.* 2020). However, young African vultures may follow Griffon Vultures that have already crossed this barrier during the previous autumn and gained experience flying over the sea. This would represent the first exposure of these African individuals to extended flights over water surfaces, which do not generate thermals and thus do not support their typical flight mode (Newton 2023). Such movements underline the importance of socially mediated dispersal in overcoming geographical and ecological barriers, and highlight the role of informed individuals in enabling range shifts for less experienced conspecifics or heterospecifics.

Once in Europe, particularly in Spain, these African vultures' benefit from favourable anthropogenic conditions, including high food availability, through both natural carcasses and supplementary feeding stations, reduced persecution or poisoning pressure, compared to many African regions (Donázar & Fernández 1990, Green *et al.* 2016, Campbell &

Botha 2018), and strong social compatibility with local vultures (Marcano-Delgado *et al.* in press). In the case of the Rüppell's Vultures, although some African individuals return to Africa after spending a few months in Europe (Ramírez 2012), others stay on the northern continent until they reach sexual maturity. These are the individuals that are now beginning to breed in Europe, so far exclusively in hybrid pairs (Muñoz *et al.* 2024a). These dynamics help explain the apparent mismatch between observed records and the predictions of our climate-based models, and underline the role of behavioural ecology in shaping unexpected colonization pathways. For the White-backed Vulture, the apparent mismatch between predicted climatic favourability and the species' known breeding areas in West Africa highlights the limitations of species-level models. This discrepancy may be of interest because the rare individuals observed in Europe may originate from marginal western populations that may be ecologically distinct from the species' core in southern Africa. Models averaging conditions across the entire range can obscure such local adaptations. These observations likely reflect dispersal from peripheral populations rather than an inability to tolerate European climates, emphasizing the importance of considering subpopulation-level variation when interpreting model predictions.

These differing mechanisms of range expansion and colonization carry important conservation implications. For the Atlas Long-legged Buzzard, which may succeed independently, maintaining suitable open habitats under favourable climatic conditions may be sufficient. However, this taxon is also susceptible to introgressive hybridisation processes with the Common Buzzard (*Buteo buteo*), especially in contact zones such as the Strait of Gibraltar (Elorriaga & Muñoz 2013). Given the close phylogenetic relationship and weak genetic differentiation between both species, this hybridisation could compromise the genetic identity of the North African taxon. In contrast, the establishment of African vultures depends not only on suitable environmental conditions, but also the continued presence of a functional ecological network anchored by Griffon Vultures. Protecting these networks, including feeding stations, roosting sites, and migratory connectivity, becomes essential. In the case of Rüppell's Vulture, hybridisation with Griffon Vultures raises significant concerns about genetic integrity, requiring close monitoring of reproductive outcomes and long-term population dynamics and consequences. For the White-backed Vulture, observations in Europe are still limited to juvenile and immature individuals. Nevertheless, the increasing frequency of records suggests that this species may also be at the early stages of a socially mediated

*Contrasting mechanisms driving the northward expansion of African raptors into Europe*

colonization process. Systematic monitoring of individuals will be crucial to determine whether these visitors eventually reach breeding age and attempt to establish in Europe.



Ejemplar macho de collalba gris (*Oenanthe Oenanthe*), en plumaje adulto

# CAPÍTULO 5

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

La collalba gris está reduciendo su distribución en su rango más meridional de Europa y desplazándose a altitudes más elevadas

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Este capítulo se basa en: / This chapter is based on:

**López-Ramírez, S., Real, R. & Muñoz, A.-R.** (2024). The northern wheatear is reducing its distribution in its southernmost European range and moving to higher altitudes. *Journal of Avian Biology*, 2024(5-6): e03217. <https://doi.org/10.1111/jav.03217> (Q1)

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

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### **5.0 Abstract**

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.

## 5.1 Introduction

Species ranges are dynamic as individuals make daily, seasonal and annual movements (Müller 1979). Changes in distribution are accentuated at the boundaries of 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 & 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 & Flousek 2012, Auer & 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 & 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 & Zimmermann 2000, Muñoz & 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 & Zimmermann 2000, Austin 2002, Gahegan 2003, Guisan & 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 (Muñoz *et al.* 2013, 2015a, Real *et al.* 2013, 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 wheatear *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 & 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.

## **5.2 Material and methods**

### **5.2.1 Study area**

The area analysed in this study was mainland Spain, which covers nearly 85% of the Iberian Peninsula, an area of 493 518 km<sup>2</sup>. 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 (**Figure 5.1A**). Given its latitudinal position (approx. 40°N) and its

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

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 (**Figure 5.1B**): 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 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).



**Figure 5.1.** Location of mainland Spain on the European continent (A) and the main mountain systems and valleys in Peninsular Spain (B).

### 5.2.2 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 & 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).

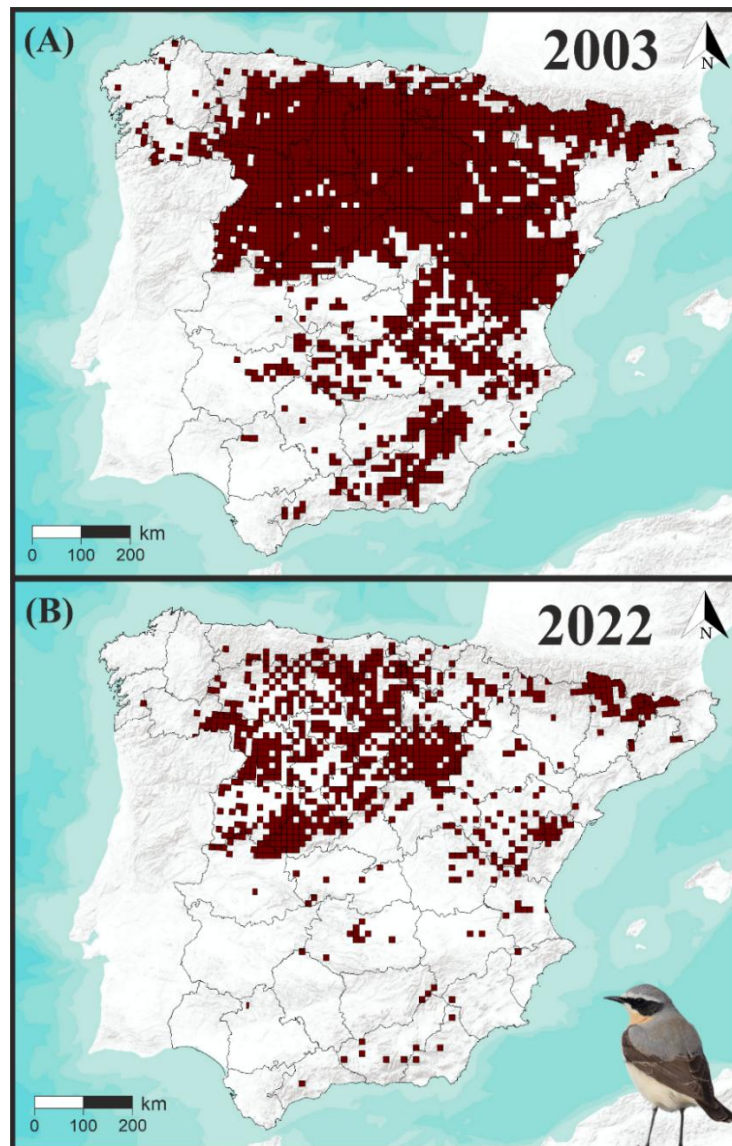
### 5.2.3 Species distribution data

The species distributions in mainland Spain were obtained from the II and III Spanish bird atlases (Martí & 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 (**Figure 5.2A**) and 844 in 2022 (**Figure 5.2B**). Then, we used these

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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  $10 \times 10$  km grid cells as operational geographical units (OGUs), a method used in numerous environmental modelling studies and, in addition, constitutes the cartographic basis for most species' distribution atlases of Spain (Doadrio 2001, Martí & 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 & Dawson 2003); mainland Spain has a total of 5335 such grid cells.



**Figure 5.2.** Northern wheatear breeding presences based on UTM  $10 \times 10$  km grid cells of the study area in 2003 (A) and 2022 (B).

#### 5.2.4 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 5.1**). 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 km<sup>2</sup>. The values of these variables at each OGU were obtained by averaging the values within each 1 km<sup>2</sup> pixel using the *zonal* function in ArcGIS ver. 10.4.1 (ESRI 2016).

**Table 5.1.** 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
<b>Topography</b>			
Alti	Altitude (m)		(1)
Slop	Slope (degrees)		(2)
<b>Climate</b>			
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 <sup>-2</sup> day <sup>-1</sup> )	(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])	
<b>Human activity</b>			
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)
<b>Lithology</b>			
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)

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*Data sources:* (1) Farr & Kobrick (2000); (2) calculated from Alti using the *slope* function in ArcGIS ver. 10.4.1 software; (3) Font (1983); (4) AEMET & 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](http://www.ine.es)); (6) DERA (2013); (7) IGME (2015).

### 5.2.5 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 & Hochberg (1995) was then used to control type I errors, which may result from the increased number of variables considered (Muñoz & 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 & 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).

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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 & Real 2012), using the following equation:

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

where  $n_1$  and  $n_0$  are the numbers of OGUs 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 & 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 & Real 2012), this limit for neatly distinguishing favourable from unfavourable areas is unreliable (Hosmer & 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 & 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).

### **5.2.6 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 OGUs with reported breeding classified as favourable; specificity, the conditional probability of OGUs with no reported breeding classified as unfavourable; correct classification rate (CCR), the conditional probability of correctly classified OGUs; the over-prediction rate (OPR), the proportion of OGUs with no reported breeding in an area with favourability  $> 0.5$ ; and the under-prediction rate (UPR), the proportion of OGUs 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 & Bell 1997, Barbosa *et al.* 2013b). 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 OGUs with reported breeding or no reported breeding in the dataset was greater or less than 0.5, respectively.

### **5.2.7 Comparison of reported breeding OGUs between 2003 and 2022**

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

### 5.3 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 5.2**). 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 5.2**).

**Table 5.2.** Variables added to the 2003 logistic regression model via a forward–backward stepwise selection process, ranked by order of addition. Variable codes are shown in **Table 5.1**.

Variable	$\beta$	S.E.	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

Note:  $\beta$ 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.

The model for 2022 included seven variables: one related to topography, four to climate, one to human activity and one to lithology (**Table 5.3**). 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 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

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precipitation  $\geq 0.1$  mm negatively affected species distribution, while mean annual actual evapotranspiration had a positive effect (**Table 5.3**).

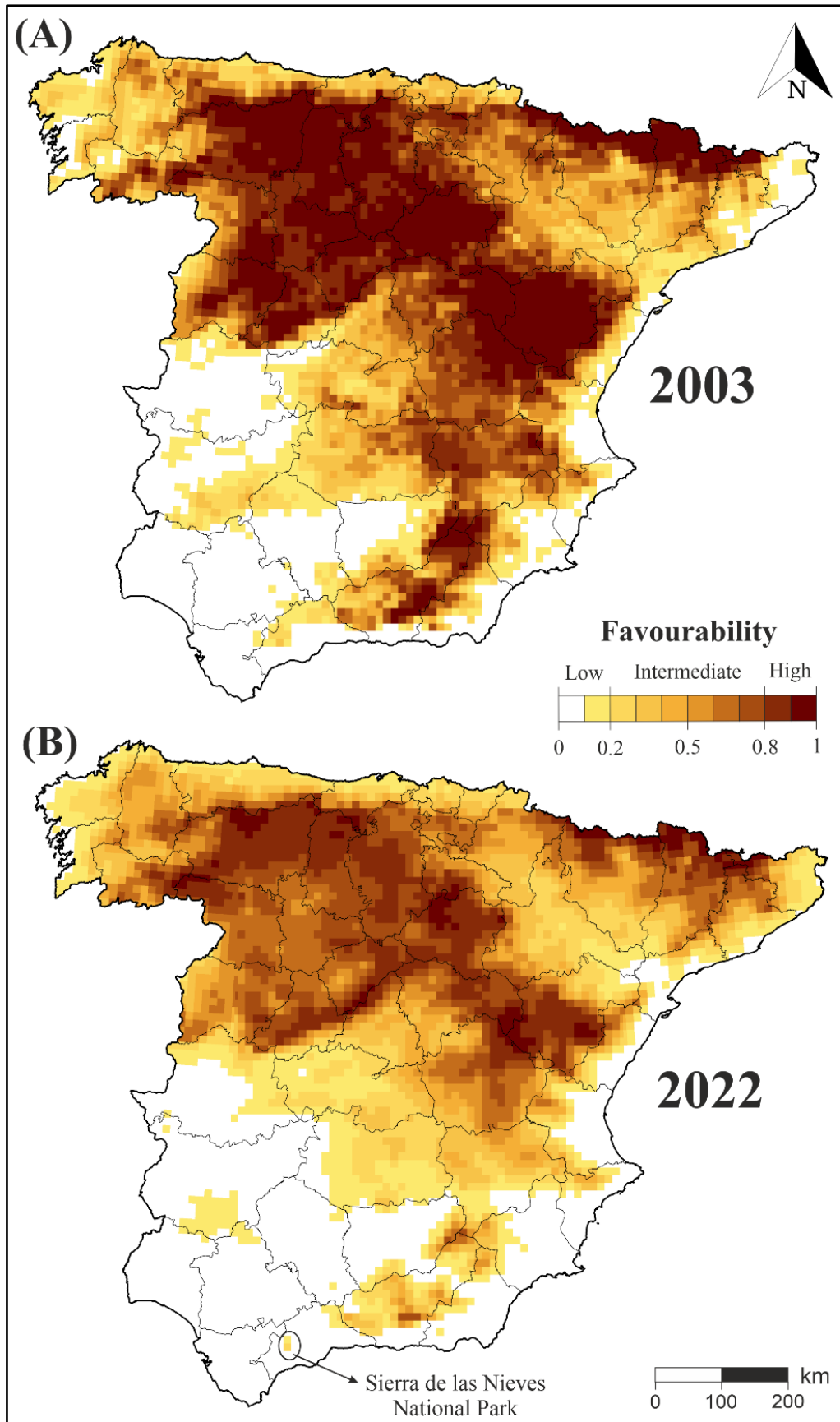
**Table 5.3.** Variables added to the 2022 logistic regression model via a forward–backward stepwise selection process, ranked by order of addition. Variable codes are shown in **Table 5.1**.

Variable	$\beta$	S.E.	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

*Note:*  $\beta$ 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.

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; **Figure 5.3A**). 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  $< 0.5$  (**Figure 5.3B**).

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**Figure 5.3.** Favourability values for the northern wheatear in each UTM  $10 \times 10$  km grid cell of mainland Spain, according to models for 2003 (A) and 2022 (B).

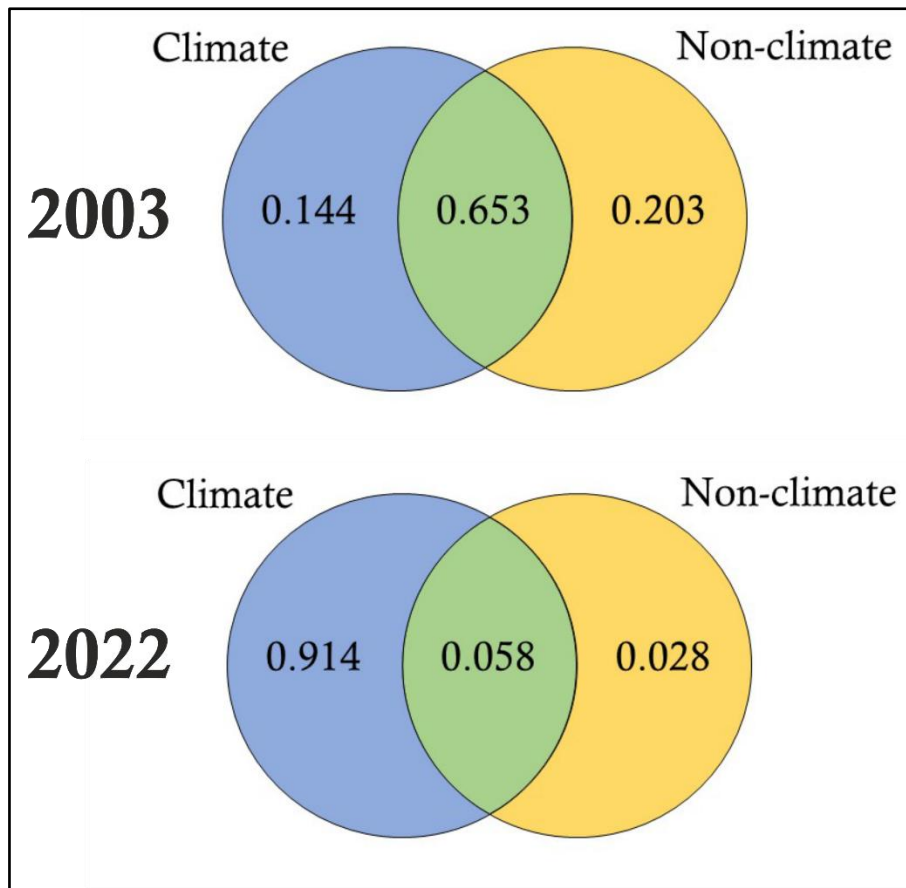
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Both models had high discrimination ( $AUC > 0.85$ ) and classification capacities (sensitivity, specificity and  $CCR > 0.73$  and a positive Cohen's kappa value; **Table 5.4**). The 2003 favourability model, however, showed higher AUC, specificity, 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 OGU's unoccupied.

**Table 5.4.** 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.

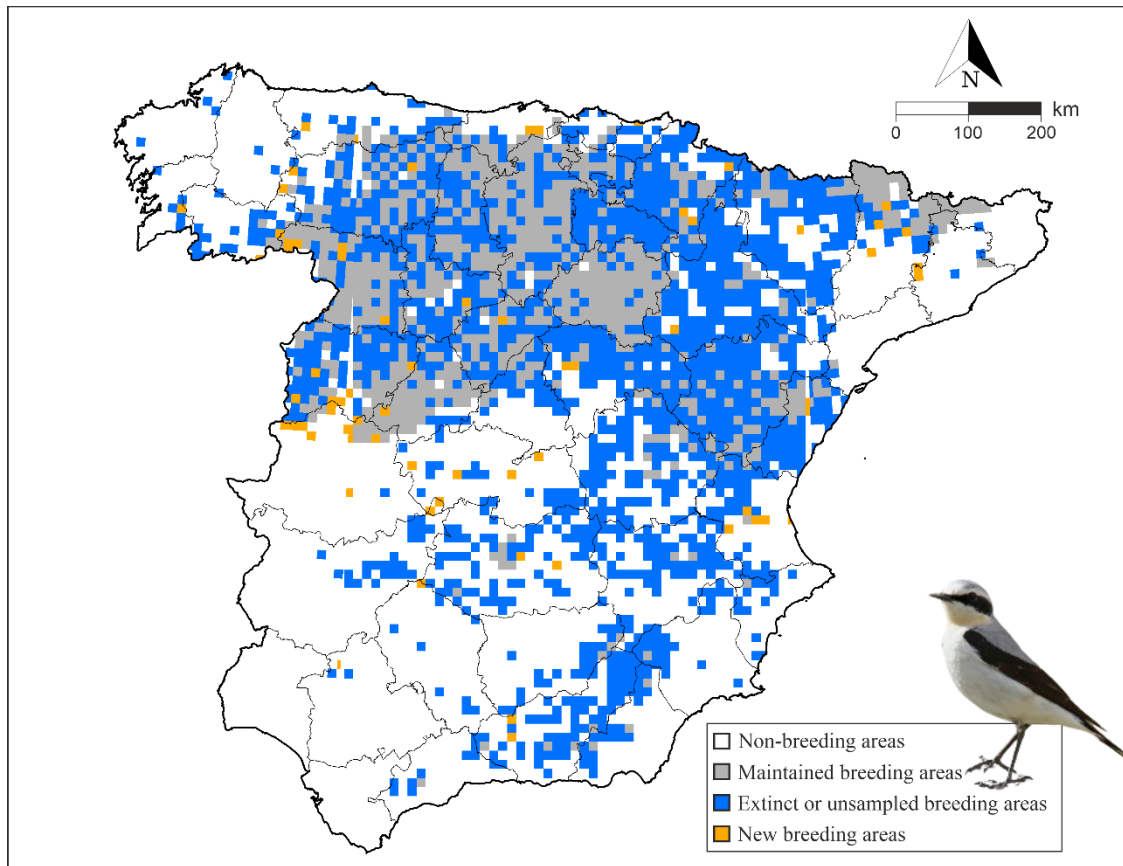
Measure	Favourability model	
	2003	2022
Area under the curve (AUC)	0.896	0.858
Sensitivity	0.809	0.847
Specificity	0.805	0.738
Correct classification rate (CCR)	0.806	0.756
Over-prediction rate (OPR)	0.227	0.618
Under-prediction rate (UPR)	0.164	0.038
Cohen's Kappa index	0.611	0.392

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 (**Figure 5.4**). 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 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 (**Figure 5.4**).



**Figure 5.4.** 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.

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 (**Figure 5.5**). 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 (**Figure 5.5**). The mean altitude of the OGUs with reported breeding in 2003 was  $913.8 \pm 371.9$  m a.s.l., while in 2022 this was  $1021.6 \pm 370.9$  m a.s.l.



**Figure 5.5.** 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.

## 5.4 Discussion

Alpine bird species are predicted to undergo serious climatically induced range contractions in the future due to climate change (La Sorte & 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 & 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 & 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 &

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 *Circaetus 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.* 2020a). 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 & Flousek 2012, Auer & 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 & 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 & 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 & 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

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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.



Gorrión alpino (*Montifringilla nivalis*) en plumaje nupcial

# CAPÍTULO 6

Climate change drives range contraction and shapes species distribution in an alpine passerine: Caution required when comparing atlas data

El cambio climático provoca la contracción del área de distribución y moldea la distribución de las especies en un paseriforme alpino: Precaución al comparar datos de atlas

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Este capítulo se basa en: / This chapter is based on:

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## **6. Climate change drives range contraction and shapes species distribution in an alpine passerine: Caution required when comparing atlas data**

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### **6.0 Abstract**

The White-winged Snowfinch (*Montifringilla nivalis*), a specialist in alpine habitats, is highly vulnerable to climate change due to its reliance on high-elevation environments, which are experiencing accelerated warming, alterations in snow dynamics, and significant shifts in phenology, among other factors. These habitats, crucial for breeding and feeding, are often undersampled due to their remoteness and difficult accessibility. Furthermore, they are shrinking, particularly at the species' range edges. Comparing data from the II and III Spanish bird atlases (1998–2002 and 2014–2018), we observed a significant decline in its breeding range, with the species disappearing from 17 grid cells (11 in the Cantabrian Mountains and 6 in the Pyrenees). However, direct comparison between the atlases is problematic because 30 grid cells surveyed in the II atlas were not sampled in the III, potentially leading to an overestimated decline. While eBird data from 2014–2018 partially mitigated the perceived decline, the same 30 grid cells have remained unsampled, further complicating a definitive assessment of the species' status. Cool summer temperatures and low humidity, as indicated by the Topographic Wetness Index (TWI), were identified as the most influential environmental factors affecting the species' breeding distribution, based on distribution data from both the III atlas and eBird, analyzed through a presence-absence distribution model. Interpreting atlas data requires caution, particularly for species inhabiting remote or inaccessible areas. Alternative data sources, such as eBird, can support ongoing monitoring programs by providing additional insights into species distribution. However, even with eBird, certain hard-to-reach areas remain under-sampled, causing them to still be presumed unoccupied. Increasing monitoring efforts in these highly favourable but undersampled regions is crucial to enhance conservation strategies for this declining alpine species.

## 6.1 Introduction

Biodiversity is under anthropogenic pressure worldwide at all levels, from genes to biomes (Brook *et al.* 2008, Weiskopf *et al.* 2020), and thousands of species are indeed threatened by climate and habitat changes (Parmesan & Yohe 2003, Spooner *et al.* 2018). High elevation species are particularly sensitive to climate change due to their habitation of high mountain areas, which are undergoing more extreme climate effects, such as temperature fluctuations, alterations (or loss) of snow dynamics, and vegetation encroachment, among others (Gobiet *et al.* 2014, Pepin *et al.* 2015, Algarra *et al.* 2019, Gómez-García *et al.* 2023, Aligaz *et al.* 2024). Warming has been especially pronounced at higher elevations compared to the global average over the past two centuries, a trend that is expected to continue (Brunetti *et al.* 2009, Pepin *et al.* 2015, IPCC 2022). Mountain systems harbour rich biodiversity worldwide (Körner & Ohsawa 2006, Martin *et al.* 2021) and, although they cover only ~25 % of Earth's land surface, they host nearly half of the planet's terrestrial biodiversity hotspots (Myers *et al.* 2000) and are home to a high percentage of endemic species (Essl *et al.* 2009, Dirnböck *et al.* 2011, Hof & Allen 2019).

Alpine species are adapted to the fluctuating environmental conditions typically found at high elevations, as alpine environments are inherently stochastic (Lu *et al.* 2009, Cheviron & Brumfield 2012, Bettega *et al.* 2020, de Zwaan *et al.* 2020). Due to life-histories shaped by conditions such as temperature extremes, resource limitations, extreme weather events, and hypoxia, these species are highly susceptible to long-term, sustained changes in temperature and precipitation, particularly snow, which could dramatically impact their populations (Martin & Wiebe 2004, Tingley *et al.* 2009, Tayleur *et al.* 2016), especially at the lower-latitude margins of their distribution (Engler *et al.* 2011, López-Ramírez *et al.* 2024b). In fact, many species are threatened by the frequent additive or even synergistic effects of climate change, land-abandonment, and human-induced habitat alterations (Mantyka-Pringle *et al.* 2012, Chamberlain *et al.* 2013, 2016, Barras *et al.* 2020, 2021), particularly those linked to mountain grassland and pastures (Brambilla *et al.* 2020a, García-Navas *et al.* 2020), which are likely to exert stronger pressure at lower elevations.

Birds are highly mobile, have a relatively rapid generation turnover rate, and are often dependent on environmentally sensitive food sources, meaning they respond quickly to environmental changes. They are also relatively easy to observe and census for studying long-term population changes, making them excellent bio-indicators for investigating the

impacts of climate change on mountain biodiversity (Chamberlain *et al.* 2013, Lehtikoinen *et al.* 2019). Mountain bird species are considered to be at higher risk than birds from other habitats (Chamberlain *et al.* 2016, Brambilla *et al.* 2017a, Scridel *et al.* 2017, 2018, 2021). Under global warming, these populations are generally shifting their ranges to higher elevations to track their climatic optima (Maggini *et al.* 2011, Pernollet *et al.* 2015, Barras *et al.* 2021). Consequently, such distribution shifts may result in range contraction in pyramidal mountain systems due to space limitations at high elevations (La Sorte & Jetz 2010, Elsen & Tingley 2015, Flousek *et al.* 2015), particularly at the margins of species' ranges (de Gabriel Hernando *et al.* 2021, González-Hernández *et al.* 2021, López-Ramírez *et al.* 2024b). In mountain areas where alpine birds already occupy the summits, their climatic niche may shift beyond mountaintops, ultimately driving such species to local extinctions (Huntley *et al.* 2007, Sekercioglu *et al.* 2008, López-Ramírez *et al.* 2024b). Whilst the general decline in lowland bird populations is well documented (Flousek *et al.* 2015), alpine avifauna has received comparatively little attention worldwide (Lehtikoinen *et al.* 2014, de Zwaan *et al.* 2022, Walker *et al.* 2024) due to challenging research logistics (Chamberlain *et al.* 2012). This lack of data hinders our understanding of how these species respond to climate change and habitat alterations.

The strong pressures acting on alpine bird species call for conservation strategies, which are essential to anticipate the impacts of global warming on their populations (Hannah 2011, Groves *et al.* 2012). Species distribution models (SDMs) represent one of the most common and powerful tools to explore the associations between species distributions and environmental factors in the context of climate change (López-Ramírez *et al.* 2024a), mainly due to the enormous amount of available environmental data and the high capacity to manage and analyse it (Hijmans & Graham 2006, Chamorro *et al.* 2020, Barras *et al.* 2021, Ahmadi *et al.* 2024). These models can estimate the ecological requirements of a species in a given area by associating a set of environmental predictor variables with its geographical distribution, thus allowing the simulation of ecological processes and the projection of potential distributional shifts under different climate change scenarios (Chamorro *et al.* 2017, López-Ramírez *et al.* 2023, Ahmadi *et al.* 2024). Consequently, SDMs provide insights into the potential responses of alpine birds to climate change (Moritz & Agudo 2013, Engler *et al.* 2017, Barras *et al.* 2021, Scridel *et al.* 2021) and can help identify unoccupied suitable areas for them, which may be particularly relevant for prioritizing species monitoring efforts in these areas, thus

enhancing future conservation planning. While many studies rely on the direct comparison of distribution atlases to assess these changes and discuss the effects of climate change (e.g., Marjakangas *et al.* 2023), the results of such atlases may not always be comparable, particularly for high mountain species where sampling difficulties are greater or inconsistent.

In this study, we focused on the White-winged Snowfinch (*Montifringilla nivalis*), an exemplary flagship species symbolizing high-elevation habitats that require protection due to their sensitivity to climate change (Brambilla *et al.* 2017b). This bird is highly dependent on specific environments, such as snow patches and short alpine grasslands (Brambilla *et al.* 2017a, 2018), and is therefore potentially threatened by global warming (Maggini *et al.* 2014, Brambilla *et al.* 2016, 2020b), as rising temperatures are altering or causing the loss of snow cover dynamics and reducing alpine grasslands, which are being replaced by more shrubby vegetation. By focusing on this species, we aim to bring attention to the conservation needs of alpine ecosystems, which are particularly vulnerable to climate change (de Gabriel Hernando *et al.* 2021). Although future projections indicate a reduction in the species' breeding range (Maggini *et al.* 2014, Brambilla *et al.* 2020b), the White-winged Snowfinch has been little investigated until recently and is still classified as 'Least Concern' in the last Red List of European Birds (BirdLife International 2021). However, the species has suffered range contractions and population declines in recent years (Kilzer *et al.* 2011, Issa & Muller 2015, Knaus *et al.* 2018) and there is evidence that global warming may be an important cause of these declines (Scridel *et al.* 2017, Brambilla *et al.* 2018, Strinella *et al.* 2020, Schano *et al.* 2021, de Gabriel Hernando *et al.* 2022). Due to the different sampling efforts among traditional atlases, capturing the true extent of such declines is difficult, particularly in challenging mountainous terrains. Therefore, our study aims to address this gap by integrating additional data sources and focusing on detailed modelling approaches. We focused on the Spanish population of the species, which represents the western limit of its global distribution, and aimed to compare the breeding distribution of this alpine bird from the beginning of the century (1998–2002) to the present (2014–2018) to examine potential changes and assess whether these changes are associated with changes in environmental conditions. Using a presence-absence distribution modelling approach, we also aimed to identify favourable areas for the species that currently remain unoccupied, with the goal of incorporating them into monitoring efforts and enhancing their

protection. This information is essential for better understanding the species' distribution patterns for conservation-related purposes.

## 6.2 Methods

### 6.2.1 Study area

The study area analysed in this paper is peninsular Spain, which covers an area of 493,518 km<sup>2</sup> and occupies nearly 85 % of the Iberian Peninsula. Its geographical position in southwestern Europe, between two continents, Europe and Africa, and two large marine areas, the Mediterranean Sea and the Atlantic Ocean, defines it as a biogeographic unit of great interest (**Figure 6.1a**). Given its latitudinal position (approximately 40° N) and topographic heterogeneity, mainland Spain has an extremely diverse climate. Precipitation generally decreases towards the east and south, while temperature decreases towards the north (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 characterised 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 experiences high temperatures in summer and low in winter, as well as irregular and scarce precipitation. Peninsular Spain is also one of the most mountainous regions in Europe (Font 2000). Approximately three-quarters of the study area is made up of the extensive Inner Plateau (average altitude 760 m), which is surrounded by major mountain systems (**Figure 6.1b**). These include the Pyrenees in the northeast (maximum altitude 3404 m), the Cantabrian Mountains in the northwest (maximum altitude 2648 m), the Iberian System in the central-eastern region (maximum altitude 2313 m), the Central System in the centre of the Inner Plateau (dividing it into northern and southern halves, maximum altitude 2592 m), Sierra Morena in the central-southern region (maximum altitude 1323 m) and the Baetic Mountains in the southeast, which reach the highest altitude in peninsular Spain at 3478 m in Sierra Nevada (Fischer 1902). These mountain systems exhibit significant climatic diversity, which is influenced by factors such as altitude, geographical location, and proximity to the sea. The Pyrenees, for instance, have an alpine climate in the highlands, oceanic in the west, and Mediterranean characteristics in the east, with cold winters with heavy snowfall and short,

cool summers. The Cantabrian Mountains have an oceanic mountain climate, marked by high humidity, abundant precipitation year-round, cold winters with snowfall, and cool summers. The Iberian and the Central Systems experience a continental climate, characterised by cold winters with snowfall, hot and dry summers, and irregular precipitation. Sierra Morena has a Mediterranean climate with continental influences, featuring mild winters, very hot summers, and scarce, irregular precipitation. Finally, the Baetic Mountains are dominated by a Mediterranean mountain climate, with cold winters and frequent snowfall at higher altitudes, cool summers in the highlands, and moderate precipitation. The highlands of Sierra Nevada are dominated by an alpine climate, with very cold winters, frequent snowfalls, and cool, short summers (Font 2000).



**Figure 6.1.** Location of mainland Spain on the European continent (a) and the main mountain systems in the study area (b).

### **6.2.2 The species**

The White-winged Snowfinch is one of the most characteristic passerines of alpine habitats, occupying mountain massifs from the Himalayas to western Europe within the temperate climate belt (Summers-Smith & Bonan 2020). The whole breeding range of the nominate subspecies *M.n.nivalis* is confined to Europe and restricted to higher elevations of central and southern mountain massifs, ranging from the Cantabrian Mountains in north-western Spain through the Pyrenees, the Alps, Corsica and the Apennines east to Greece (Keller *et al.* 2020). The White-winged Snowfinch is mainly a resident species, although winter movements to lower elevations and even across different mountain chains have been observed (Resano-Mayor *et al.* 2017, 2020). The Spanish population constitutes the western limit of the species' global distribution and is divided into two cores (Gil 2022). One of them is in the Pyrenees, from eastern Navarre to western Lleida (Elósegui Aldasoro 1985, Estrada *et al.* 2004, Gil & Pérez 2018) and the other is in the Cantabrian Mountains, between Somiedo Natural Park, Peña Prieta, and Curavacas (Gil 2022). Snowfinches usually breed at altitudes above 1800 m in the Iberian Peninsula (Cramp & Perrins 1994) and occupy similar breeding habitats to those described in other high mountain areas, showing a predilection for alpine grassland, rocky habitats, and snow patches (Cramp & Perrins 1994, Antor 1995, Strinella *et al.* 2007, Grangé 2008). Nests are usually located in rock crevices or human-built infrastructures such as mountain buildings or ski-lift pylons (Cramp & Perrins 1994, Grangé 2008). During the nestling rearing period, adults collect invertebrate prey around nest sites, frequently on or at the margins of melting snow patches and in short-sward alpine grasslands (Cramp & Perrins 1994, Antor 1995, Strinella *et al.* 2007, Brambilla *et al.* 2017b).

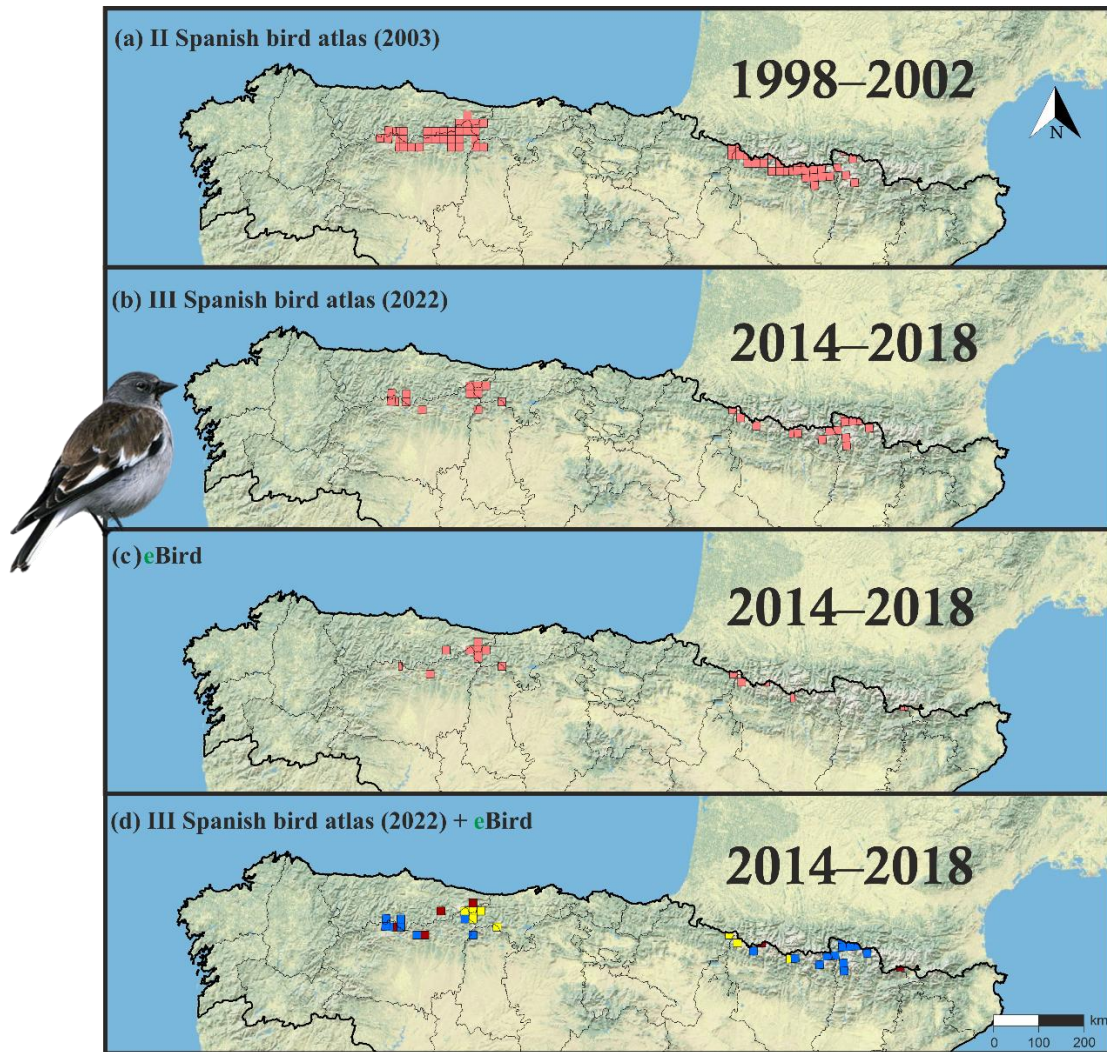
### **6.2.3 Species distribution data**

The species distributions in the study area were obtained from the II and III Spanish bird atlases (Martí & Del Moral 2003, Molina *et al.* 2022), based on fieldwork conducted in 1998–2002 and 2014–2018, respectively. In both cases, we considered the standardised breeding categories commonly used in ornithological atlases (Keller *et al.* 2020) and selected the confirmed, probable, and possible breeding categories of the White-winged Snowfinch. We used UTM 10 × 10 km grid cells as operational geographic units (OGUs) to lattice the breeding distribution data of the species. This method forms the cartographic

basis for most species distribution atlases and has been used in numerous environmental modelling studies (Pleguezuelos *et al.* 2004, Muñoz & Real 2006, Palomo *et al.* 2007, Estrada *et al.* 2008, Real *et al.* 2008, Molina *et al.* 2022, Zajac *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 & Dawson 2003, Niamir *et al.* 2019). Peninsular Spain has a total of 5335 such grid cells. Using the II Spanish bird atlas, we identified 69 breeding grid cells for the period 1998–2002, 34 of which were located in the Cantabrian Mountains and 35 in the Pyrenees (**Figure 6.2a**). Similarly, using the III Spanish bird atlas, we identified 30 breeding grid cells for the period 2014–2018, 13 of which were located in the Cantabrian Mountains and 17 in the Pyrenees (**Figure 6.2b**).

As the sampling effort in the III Spanish bird atlas was lower than in the previous atlas (which had complete coverage over the whole study area), with a total of 30 unsampled grid cells, we supplemented the White-winged Snowfinch's breeding distribution data with information from the international citizen science platform eBird (<https://ebird.org/home>). To this end, we selected eBird records from 15 April to 15 June for the period 2014–2018 to coincide with the breeding months and sampling period considered in the III Spanish bird atlas. Using this information, we identified 14 grid cells, nine of them in the Cantabrian Mountains and five in the Pyrenees (**Figure 6.2c**). Six of these grid cells were new (i.e. not considered in the III Spanish bird atlas) -four located in the Cantabrian Mountains and two in the Pyrenees- and eight grid cells were common to both sources (**Figure 6.2d**). When we added the information provided by eBird to the III Spanish bird atlas, we obtained a breeding distribution comprising 36 grid cells, 17 of them in the Cantabrian Mountains and 19 in the Pyrenees (**Figure 6.2d**).

To model the distribution of the species in the study area for the period 2014–2018, we used two datasets for all analyses: firstly, the breeding presences of the species considering only the III Spanish bird atlas (**Figure 6.2b**) and secondly the III Spanish bird atlas plus eBird data (**Figure 6.2d**).



**Figure 6.2.** White-winged Snowfinch breeding presences based on UTM  $10 \times 10$  km grid cells for the period 1998–2002 considering the II Spanish bird atlas (a) and for the period 2014–2018 considering the III Spanish bird atlas (b), eBird (c) and the III Spanish bird atlas + eBird (d). For the last case, the grid cells provided by the III Spanish bird atlas are shown in blue, those provided by eBird in red and those provided by both sources in yellow.

To geographically identify areas where the species was presumably extirpated, we compared the breeding distributions between the periods 1998–2002 and 2014–2018. We conducted this comparison in two ways: first, considering only the II and III Spanish bird atlases, respectively; and second, considering the II Spanish bird atlas for the period 1998–2002 and the III Spanish bird atlas plus eBird data for the period 2014–2018. For this purpose, each OGU was classified according to the following categories: OGUs with reported breeding of the White-winged Snowfinch in both time periods (maintained breeding areas); OGUs with reported breeding in 2014–2018 but not in 1998–2002 (new

breeding areas); OGU with reported breeding in 1998–2002 but not in 2014–2018 that were sampled during 2014–2018 (presumably extirpated breeding areas); and OGU with reported breeding in 1998–2002 that were not sampled during 2014–2018 (unsampled areas). We calculated the mean altitude of the OGU with reported breeding in 1998–2002 (II Spanish bird atlas) and 2014–2018, considering in this case the III Spanish bird atlas plus eBird data. Furthermore, we obtained the mean altitude of the new, maintained, and extirpated breeding areas using the III Spanish bird atlas plus eBird data for the period 2014–2018.

#### 6.2.4 Predictor variables

A set of 82 environmental variables was used to model the distribution of the species in mainland Spain (**Table 6.1**). To facilitate the characterisation of the areas occupied by the species, the selected variables were grouped into the following factors: topography ( $n = 4$ ), climate ( $n = 70$ ) and lithology ( $n = 8$ ). These variables were chosen based on their potential predictive power, assuming their relationship to factors affecting the breeding distribution of the White-winged Snowfinch, and were downloaded in raster format with an approximately 1 km<sup>2</sup> pixel resolution. The values of these variables at each OGU were obtained by averaging the 1 km<sup>2</sup> pixel values within each OGU using the *Zonal Statistic as Table* function in ArcGIS version 10.4.1 (ESRI 2016), providing an average value for the surrounding environment in which each presence (and absence) was recorded.

**Table 6.1.** Environmental variables used to model the breeding distribution of the White-winged Snowfinch in mainland Spain, grouped by factors.

Code	Variable and Unit	Source
<b>Topography</b>		
Alti	Altitude (m)	(1)
AR	Altitude range (m)	(1)
Slop	Slope (Degrees)	(2)
TWI	Topographic Wetness Index	(3)
<b>Climate</b>		
T	Mean annual temperature (°C)	(4)
T <sub>Spr</sub>	Mean temperature in spring (°C)	(4)
T <sub>Sum</sub>	Mean temperature in summer (°C)	(4)
T <sub>Aut</sub>	Mean temperature in autumn (°C)	(4)
T <sub>Win</sub>	Mean temperature in winter (°C)	(4)
T <sub>Jan</sub>	Mean temperature in January (°C)	(4)

*Climate change drives range contraction and shapes species distribution in an alpine passerine: Caution required when comparing atlas data*

T <sub>Jul</sub>	Mean temperature in July (°C)	(4)
T <sub>n</sub>	Minimum mean annual temperature (°C)	(4)
T <sub>nSpr</sub>	Minimum mean temperature in spring (°C)	(4)
T <sub>nSum</sub>	Minimum mean temperature in summer (°C)	(4)
T <sub>nAut</sub>	Minimum mean temperature in autumn (°C)	(4)
T <sub>nWin</sub>	Minimum mean temperature in winter (°C)	(4)
T <sub>nJan</sub>	Minimum mean temperature in January (°C)	(4)
T <sub>nJul</sub>	Minimum mean temperature in July (°C)	(4)
T <sub>x</sub>	Maximum mean annual temperature (°C)	(4)
T <sub>xSpr</sub>	Maximum mean temperature in spring (°C)	(4)
T <sub>xSum</sub>	Maximum mean temperature in summer (°C)	(4)
T <sub>xAut</sub>	Maximum mean temperature in autumn (°C)	(4)
T <sub>xWin</sub>	Maximum mean temperature in winter (°C)	(4)
T <sub>xJan</sub>	Maximum mean temperature in January (°C)	(4)
T <sub>xJul</sub>	Maximum mean temperature in July (°C)	(4)
DT <sub>n0</sub>	Mean annual number of days with minimum temperature $\leq 0$ °C	(4)
DT <sub>n0Spr</sub>	Mean number of days with minimum temperature $\leq 0$ °C in spring	(4)
DT <sub>n0Sum</sub>	Mean number of days with minimum temperature $\leq 0$ °C in summer	(4)
DT <sub>n0Aut</sub>	Mean number of days with minimum temperature $\leq 0$ °C in autumn	(4)
DT <sub>n0Win</sub>	Mean number of days with minimum temperature $\leq 0$ °C in winter	(4)
DT <sub>n20</sub>	Mean annual number of days with minimum temperature $\geq 20$ °C	(4)
DT <sub>n20Aut</sub>	Mean number of days with minimum temperature $\geq 20$ °C in autumn	(4)
DT <sub>x25</sub>	Mean annual number of days with maximum temperature $\geq 25$ °C	(4)
DT <sub>x25Spr</sub>	Mean number of days with maximum temperature $\geq 25$ °C in spring	(4)
DT <sub>x25Sum</sub>	Mean number of days with maximum temperature $\geq 25$ °C in summer	(4)
DT <sub>x25Aut</sub>	Mean number of days with maximum temperature $\geq 25$ °C in autumn	(4)
DT <sub>x25Win</sub>	Mean number of days with maximum temperature $\geq 25$ °C in winter	(4)
P	Mean annual precipitation (mm)	(4)
P <sub>Spr</sub>	Mean precipitation in spring (mm)	(4)
P <sub>Sum</sub>	Mean precipitation in summer (mm)	(4)
P <sub>Aut</sub>	Mean precipitation in autumn (mm)	(4)
P <sub>Win</sub>	Mean precipitation in winter (mm)	(4)
DP01	Mean annual number of days with precipitation $\geq 0.1$ mm	(4)
DP01 <sub>Spr</sub>	Mean number of days with precipitation $\geq 0.1$ mm in spring	(4)
DP01 <sub>Sum</sub>	Mean number of days with precipitation $\geq 0.1$ mm in summer	(4)
DP01 <sub>Aut</sub>	Mean number of days with precipitation $\geq 0.1$ mm in autumn	(4)
DP01 <sub>Win</sub>	Mean number of days with precipitation $\geq 0.1$ mm in winter	(4)
DP1	Mean annual number of days with precipitation $\geq 1$ mm	(4)
DP1 <sub>Spr</sub>	Mean number of days with precipitation $\geq 1$ mm in spring	(4)
DP1 <sub>Sum</sub>	Mean number of days with precipitation $\geq 1$ mm in summer	(4)
DP1 <sub>Aut</sub>	Mean number of days with precipitation $\geq 1$ mm in autumn	(4)



DP1 <sub>Win</sub>	Mean number of days with precipitation $\geq 1$ mm in winter	(4)
DP10	Mean annual number of days with precipitation $\geq 10$ mm	(4)
DP10 <sub>Spr</sub>	Mean number of days with precipitation $\geq 10$ mm in spring	(4)
DP10 <sub>Sum</sub>	Mean number of days with precipitation $\geq 10$ mm in summer	(4)
DP10 <sub>Aut</sub>	Mean number of days with precipitation $\geq 10$ mm in autumn	(4)
DP10 <sub>Win</sub>	Mean number of days with precipitation $\geq 10$ mm in winter	(4)
DP30	Mean annual number of days with precipitation $\geq 30$ mm	(4)
DP30 <sub>Spr</sub>	Mean number of days with precipitation $\geq 30$ mm in spring	(4)
DP30 <sub>Sum</sub>	Mean number of days with precipitation $\geq 30$ mm in summer	(4)
DP30 <sub>Aut</sub>	Mean number of days with precipitation $\geq 30$ mm in autumn	(4)
DP30 <sub>Win</sub>	Mean number of days with precipitation $\geq 30$ mm in winter	(4)
MDI	Mean direct irradiance [1983-2005] ( $\text{kwh m}^{-2} \text{ day}^{-1}$ )	(4)
MDI <sub>Spr</sub>	Mean direct irradiance in spring ( $\text{kwh m}^{-2} \text{ day}^{-1}$ )	(4)
MDI <sub>Sum</sub>	Mean direct irradiance in summer ( $\text{kwh m}^{-2} \text{ day}^{-1}$ )	(4)
MDI <sub>Aut</sub>	Mean direct irradiance in autumn ( $\text{kwh m}^{-2} \text{ day}^{-1}$ )	(4)
MDI <sub>Win</sub>	Mean direct irradiance in winter ( $\text{kwh m}^{-2} \text{ day}^{-1}$ )	(4)
MGI	Mean global irradiance [1983-2005] ( $\text{kwh m}^{-2} \text{ day}^{-1}$ )	(4)
MGI <sub>Spr</sub>	Mean global irradiance in spring ( $\text{kwh m}^{-2} \text{ day}^{-1}$ )	(4)
MGI <sub>Sum</sub>	Mean global irradiance in summer ( $\text{kwh m}^{-2} \text{ day}^{-1}$ )	(4)
MGI <sub>Aut</sub>	Mean global irradiance in autumn ( $\text{kwh m}^{-2} \text{ day}^{-1}$ )	(4)
MGI <sub>Win</sub>	Mean global irradiance in winter ( $\text{kwh m}^{-2} \text{ day}^{-1}$ )	(4)
PET	Mean annual potential evapotranspiration (mm)	(4)
AET	Mean annual actual evapotranspiration (mm)	(= min [PET, P])
<b>Lithology</b>		
Clay	Presence of clay	(5)
PClay	Proportion of clay	(5)
Sil	Presence of siliceous rocks	(5)
PSil	Proportion of siliceous rocks	(5)
Calc	Presence of calcareous rocks	(5)
PCalc	Proportion of calcareous rocks	(5)
Grav	Presence of gravel	(5)
PGrav	Proportion of gravel	(5)

*Data sources:* (1) Farr & Kobrick (2000); (2) calculated from Alti using the *slope* function in ArcGIS ver. 10.4.1 software; (3) <https://www.hydrosheds.org/products> (4) AEMET & IMP (2011); (5) IGME (2015).

### 6.2.5 Distribution modelling

Topographic, climatic, and lithological variables were used as predictors to produce environmental models of the White-winged Snowfinch's breeding distribution for the period 2014–2018. First, Spearman correlation coefficients ( $r$ ) were calculated between the selected variables to control for multicollinearity among the predictor variables within each factor. For each pair of variables with  $r > 0.8$  within each factor, only the one with the most significant relationship to the species' breeding distribution was retained, according to the significance of Rao's score test (Radhakrishna Rao 1948, Zanolla *et al.* 2018, López-Ramírez *et al.* 2023). In SDMs involving a large number of variables, some predictors may be incorporated by chance (García 2003). To control for this type I error,

we evaluated the False Discovery Rate (FDR) as proposed by Benjamini & Hochberg (1995). Based on the set of pre-selected variables from the previous step, only the ones whose significance in the score test was less than an FDR adjusted value of 0.05 were used in the following steps (Benjamini & Yekutieli 2001).

To build an environmental model for each set of distribution data, we performed a forward–backward stepwise binary logistic regression using the breeding distribution data of the species for the period 2014–2018 and the remaining subset of variables that passed the above filters, to obtain the probability of breeding in each OGU. This process started with a null model containing no predictor variables that produced a constant probability of breeding for each OGU equal to the prevalence (the proportion of OGUs where species has been confirmed to breed relative to the total number of OGUs). In the first step, the procedure selected the variable with the most significant relationship to the distribution of the species, according to the significance of the Rao’s score test (Radhakrishna Rao 1948). In the following steps, it added the variable most significantly related to the residuals not explained by the previous step, until no additional variable significantly increased the predictive capacity of the model (Legendre & Legendre 1998). Thus, the environmental variables included in the final model, an ensemble model, were a parsimonious representation of all the effects attributable 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, we evaluated the possibility of improving its predictive capacity 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, we obtained a significant combination of predictor variables ( $y$  or *logit*), whose coefficients were estimated using a machine learning algorithm based on a gradient ascent of likelihood (Glasmachers & Igel 2010, Basha *et al.* 2018). For this reason, logistic regression is also defined as a supervised machine learning method (Kebede Kassaw *et al.* 2023, Qi & Wang 2024). The relative weight of each variable in the final model was assessed using the Wald test (Wald 1943).

When building the distribution models, we excluded the 30 grid cells with reported breeding of the species in 1998–2002 that were not sampled during 2014–2018 (see **Figure 6.3: unsampled areas**) to avoid false absences. We then extrapolated the resulting

models to the entire study area, and calculated favourability values ( $F$ ) using the following equation (Real *et al.* 2006):

$$F = \frac{e^y}{\frac{n_1}{n_0} + e^y}$$

where  $n_1$  and  $n_0$  are the numbers of OGU's with breeding presences and absences of the White-winged Snowfinch for the period 2014–2018, excluding the unsampled grid cells;  $e$  is the base of the natural logarithm; and  $y$  is the linear combination of predictor variables (i.e. the *logit*) from the logistic regression defining probability values.

By obtaining favourability values rather than probability values, we eliminate the effect of prevalence in the study area and attain values that depend exclusively on the species' response to environmental variables (Real *et al.* 2006, Acevedo & Real 2012). The resulting favourability values range from 0 (minimum favourability) to 1 (maximum favourability) and refer to the degree to which environmental conditions favour the breeding of the White-winged Snowfinch, with  $F = 0.5$  representing the threshold separating favourable from unfavourable areas (Muñoz *et al.* 2005). A local favourability value of 0.5 indicates that the local probability of the species breeding is equal to its prevalence in the study area. This represents the probability expected by a null model unaffected by environmental predictors, where breeding is neither favoured nor unfavoured by the environment (Acevedo & Real 2012). Those areas with  $F > 0.5$  therefore favour the species breeding, whereas  $F < 0.5$  indicates areas with environmental conditions that disfavour breeding. However, the use of a favourability value of 0.5 as a strict cut-off point for distinguishing favourable from unfavourable areas is not sufficiently informative (Hosmer & Lemeshow 2005) due to the continuous and fuzzy nature of favourability (Acevedo & Real 2012). Consequently, we classified the areas into four categories, depending on their favourability values: 'high favourability' ( $F \geq 0.8$ ), 'intermediate-high favourability' ( $0.8 > F > 0.5$ ), 'intermediate-low favourability' ( $0.5 > F > 0.2$ ) and 'low favourability' ( $F \leq 0.2$ ) (García-Carrasco *et al.* 2021, Aliaga-Samanez *et al.* 2022). All modelling processes were run with the IBM SPSS Statistics 25 software package, and maps were created using ArcMap software (ArcGIS version 10.4.1; <https://desktop.arcgis.com/es/arcmap/>). We also calculated the mean environmental

favourability values of the OGU in each of the current cores (Cantabrian Mountains and Pyrenees) for each of the resulting models.

### **6.2.6 Models' assessment**

The resulting models were assessed and compared based on their discrimination and classification capacities. Discrimination capacity was evaluated using the area under the receiver operating characteristic (ROC) curve, known as the AUC (Lobo *et al.* 2008). Classification capacity was assessed using  $F = 0.5$  as the classification threshold, and the following measures were calculated: sensitivity (the proportion of OGUs with reported breeding correctly classified as favourable), specificity (the proportion of OGUs with no reported breeding classified as unfavourable), correct classification rate (CCR: the overall proportion of correctly classified OGUs), over-prediction rate (OPR: the proportion of OGUs with no reported breeding classified as favourable, i.e.,  $F > 0.5$ ), and under-prediction rate (UPR: the proportion of OGUs with reported breeding classified as unfavourable, i.e.,  $F < 0.5$ ). These measures are widely used and have values ranging from 0 to 1 (Fielding & Bell 1997, Barbosa *et al.* 2013b). We also used Cohen's Kappa index (Cohen 1960), which ranges from  $-1$  to  $+1$ , to measure the degree to which the favourability of OGUs with reported breeding or no reported breeding in the dataset was greater or less than 0.5, respectively.

### **6.2.7 Variation partitioning analysis**

Interactions between factors often result in an overlapping spatial effect due to collinearity between them (Borcard *et al.* 1992, Legendre 1993). To demonstrate this effect, we grouped the variables included in the models into two main environmental factors: climatic and non-climatic. Then, we performed a variation partitioning procedure (for a more detailed process see Muñoz & Real 2006 and Chamorro *et al.* 2019) to quantify how much of the variation in the favourability of the final model was explained by the pure effect of each factor (i.e. unaffected by collinearity between them; Borcard *et al.* 1992) and what proportion was attributable to their interaction (Legendre 1993, Legendre & Legendre 1998). If the interaction term between factors has negative values, then there is an overlap effect between them (one factor adds favourability, while the other reduces it).

### 6.3 Results

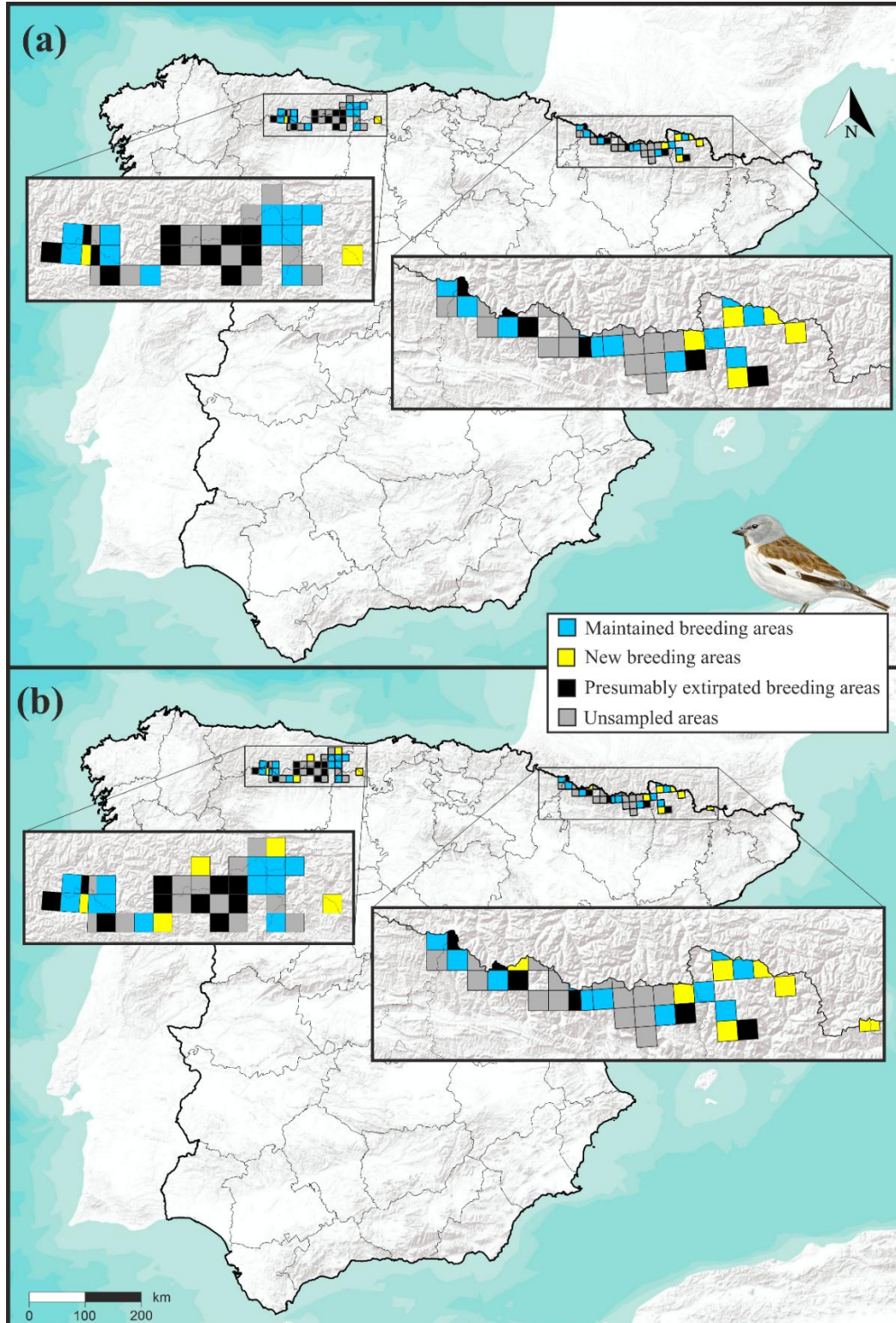
When directly comparing the two distribution atlases, we found that the III atlas did not sample 30 grid cells where the species had been recorded in the II atlas (**Figure 6.3a**). This crucial information regarding the lack of repeatability between the two sampling periods was obtained by requesting the data from the entity responsible for the atlas, the Spanish Ornithological Society (SEO/BirdLife), as this information is not available in the published atlases themselves. The absence of data in these grid cells could lead to the mistaken assumption that the species had disappeared from these areas, but that is not necessarily the case. While the White-winged Snowfinch has indeed experienced a decline over the last two decades, interpreting the extent of this decline requires careful consideration of these unsampled grid cells. Complementing the atlas data with information from eBird for the period 2014–2018 slightly reduces the perceived decline but still leaves 30 grid cells (43.5 %) unsampled in both cases (**Figure 6.3a, b**). This means that we currently lack information on whether the species is still breeding in 12 grid cells in the Cantabrian Mountains (35.3 %) and 18 grid cells in the Pyrenees (51.4 %).

Considering only the information from both atlases, the number of squares where White-winged Snowfinch were reported as breeding across mainland Spain decreased between 1998–2002 and 2014–2018. Specifically, there were 17 grid cells (24.6 %) where the species was reported breeding in the II atlas but not in the III, indicating presumed local extirpations. This includes 11 grid cells in the Cantabrian Mountains (32.4 % of its grid cells) and 6 grid cells in the Pyrenees (17.1 % of its grid cells), where the species is presumed extinct (**Figure 6.3a**). The remaining breeding areas, where the species was reported in both atlases, total 22 grid cells (31.9 %); 11 grid cells in the Cantabrian Mountains (32.4 %) and 11 in the Pyrenees (31.4 %). Additionally, new breeding areas emerged in both population cores, totalling eight grid cells: two in the Cantabrian Mountains and six in the Pyrenees (**Figure 6.3a**).

When supplementing the previous information with data from eBird, the number of grid cells with reported breeding for the White-winged Snowfinch continued to show a decline between 1998–2002 and 2014–2018 across mainland Spain. There are 16 grid cells (23.2 %) where the species has presumably disappeared during the study period, with 10 grid cells in the Cantabrian Mountains (29.4 %) and 6 grid cells in the Pyrenees (17.1 %) where the species is no longer detected (**Figure 6.3b**). The maintained breeding

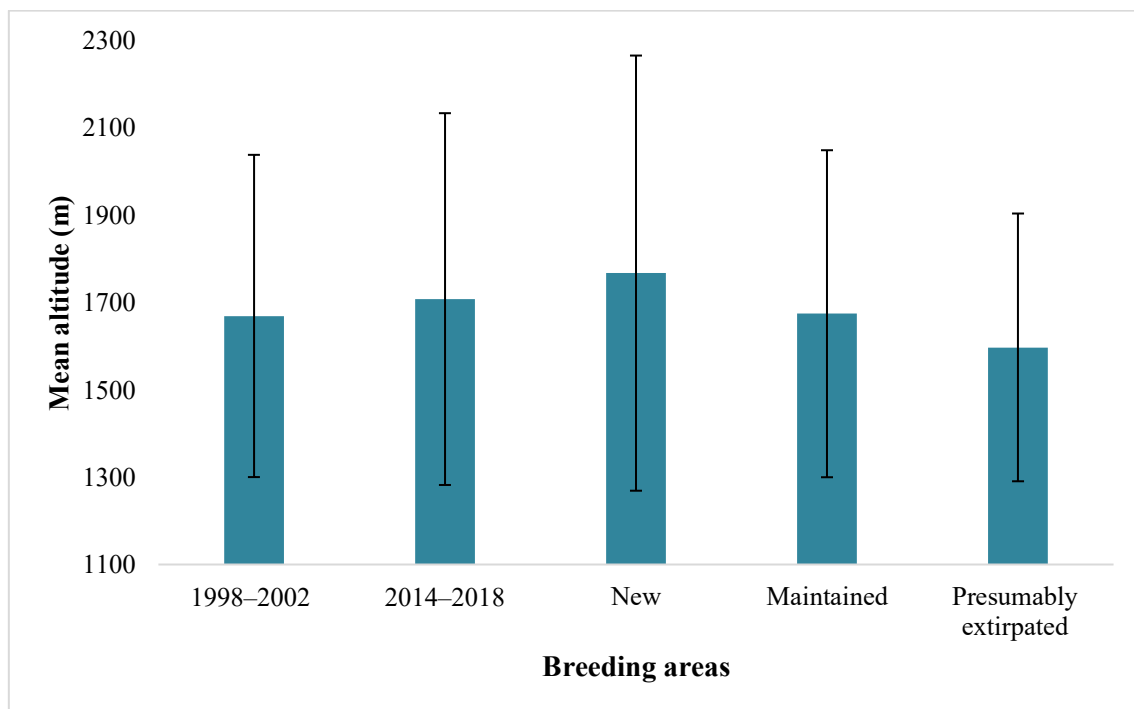
*Climate change drives range contraction and shapes species distribution in an alpine passerine: Caution required when comparing atlas data*

areas remained in both population cores, totalling 23 grid cells (33.3 %); 12 in the Cantabrian Mountains (35.3 %), and 11 grid cells in the Pyrenees (31.4 %). New breeding areas also appeared in both population cores, totalling 13 grid cells, with five in the Cantabrian Mountains and eight in the Pyrenees (**Figure 6.3b**).



**Figure 6.3.** Comparison of reported breeding operational geographical units (OGUs) for the White-winged Snowfinch in peninsular Spain between 1998–2002 (II Spanish bird atlas) and 2014–2018, considering only the III Spanish bird atlas data (a) and the III Spanish bird atlas plus eBird data (b). UTM 10 × 10 km grid cells were classified according to the following categories: maintained breeding areas (OGUs with reported breeding in both time periods), new breeding areas (OGUs with reported breeding in 2014–2018 but not in 1998–2002), presumably extirpated breeding areas (OGUs with reported breeding in 1998–2002 but not in 2014–2018 and they were sampled) and unsampled areas (OGUs with reported breeding in 1998–2002 that were not sampled during 2014–2018).

A comparison of the two periods reveals that the mean altitude of OGUs where breeding was reported increased from 1668.6 m in 1998–2002 to 1707.2 m in 2014–2018, which suggests an increase in the altitude of the species' breeding areas. Specifically, the mean altitudes were 1766.6 m for new breeding areas, 1673.7 m for maintained breeding areas, and 1596.7 m for presumably extirpated breeding areas (**Figure 6.4**).



**Figure 6.4.** Mean altitude (m) of operational geographical units (OGUs) with reported breeding for the White-winged Snowfinch in 1998–2002, 2014–2018 and considering the new, maintained and presumably extirpated breeding areas.

The resulting models for the period 2014–2018 are very similar in all aspects (mathematical models, cartographic models, model assessments and variation partitioning analysis). Therefore, we have decided to include only the results of the model that incorporates the III Spanish bird atlas plus eBird data in the manuscript, as it provides new breeding occurrences of the species not considered in the last Spanish bird atlas. The results of the model considering only the III Spanish bird atlas data are provided in the appendixes (mathematical model: **Appendix 44**; favourability model: **Appendix 45**; and variation partitioning analysis: **Appendix 46**).

The final model included two variables: one related to climate and the other to topography (**Table 6.2**). Mean temperature in July was the first variable added in the stepwise procedure and emerged as the strongest predictor of the breeding distribution of the White-winged Snowfinch in our study area, having the greatest weight in the model according to the Wald test. Both mean temperature in July and Topographic Wetness Index (TWI) negatively affected the breeding distribution of the species (**Table 6.2**), indicating that its distribution is influenced by low humidity areas with cool summers.

**Table 6.2.** Variables added to the logistic regression model considering the III Spanish bird atlas plus eBird data via a forward–backward stepwise selection process, ranked according to their order of entrance. Variable codes are shown in **Table 6.1**.

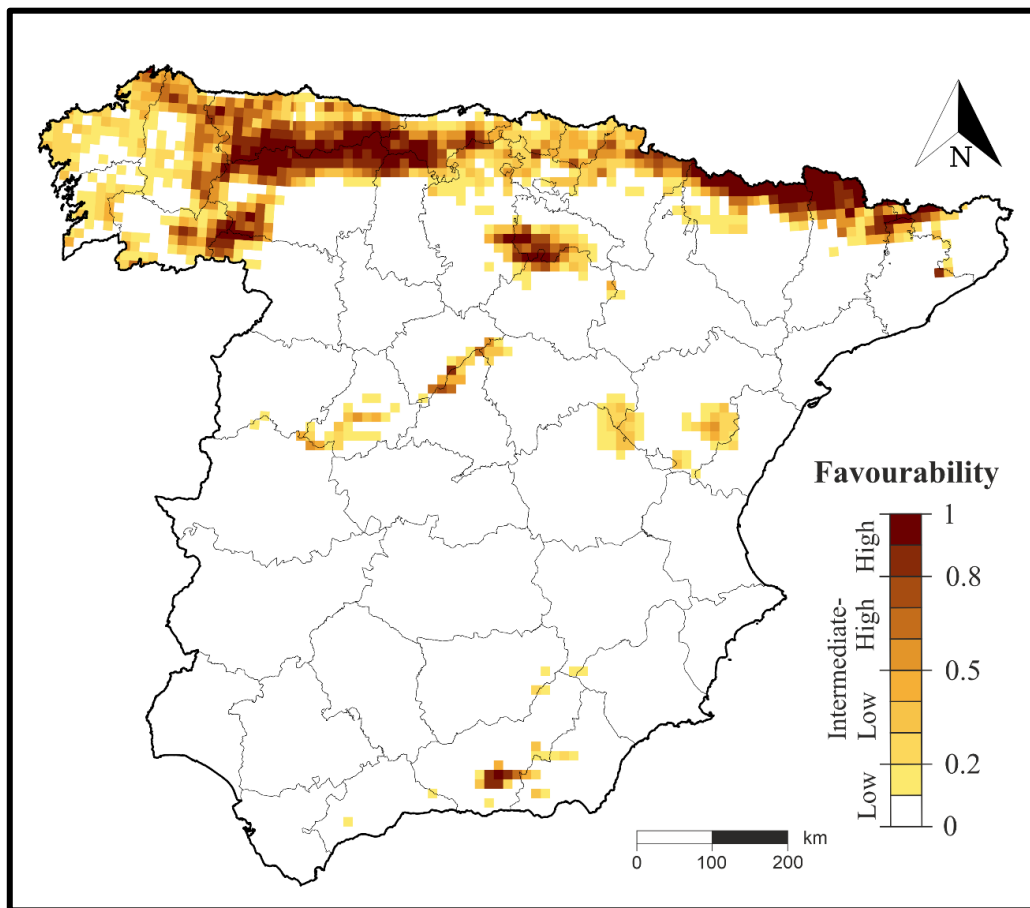
Variable	$\beta$	S.E.	Wald	<i>p</i>
T <sub>Jul</sub>	-0.796	0.145	30.218	< 0.001
TWI	-1.591	0.626	6.458	0.011
Constant	35.184	8.636	16.596	< 0.001

*Note:*  $\beta$ s are the coefficients in the *logit* function; S.E. is the standard error of these coefficients; Wald is the value of the Wald's statistic, representing the relative importance of the variable in the model; *p* is the significance of the coefficients according to the Wald test.

The environmental favourability model indicated high favourability values for the breeding of the White-winged Snowfinch both in the Pyrenees (from Navarre to western Girona) and in the Cantabrian Mountains (**Figure 6.5**). The mean environmental favourability values of the current Cantabrian and Pyrenean cores were 0.925 and 0.978, respectively. High favourability values were also found in areas where the species is currently absent, such as the Mountains of León (north-western Spain), Picos de Urbión (north of the Iberian System), the eastern part of the Central System, and Sierra Nevada

(a mountain massif that hosts the highest altitudes of the Iberian Peninsula, isolated in southern Spain). The model showed intermediate-low favourability values in the Sierras de Cuenca and Javalambre (south of the Iberian System) and in the western part of the Central System. In the rest of the study area, favourability values were low.

The discrimination capacity of both models was very high ( $AUC > 0.99$ , **Table 6.3**). Regarding classification capacity, both models showed full sensitivity (1), high specificity ( $> 0.93$ ), and a high correct classification rate ( $CCR > 0.93$ ). They also had zero underprediction rates ( $UPR = 0$ ) but exhibited very high over-prediction rates ( $OPR > 0.9$ ), with over 90 % of the predicted favourable breeding OGU's unoccupied. The over-prediction rate was slightly lower in the model that included the III Spanish bird atlas plus eBird data (**Table 6.3**). Both models had positive Cohen's kappa values, which were slightly higher in the model that incorporated the III Spanish bird atlas plus eBird data.

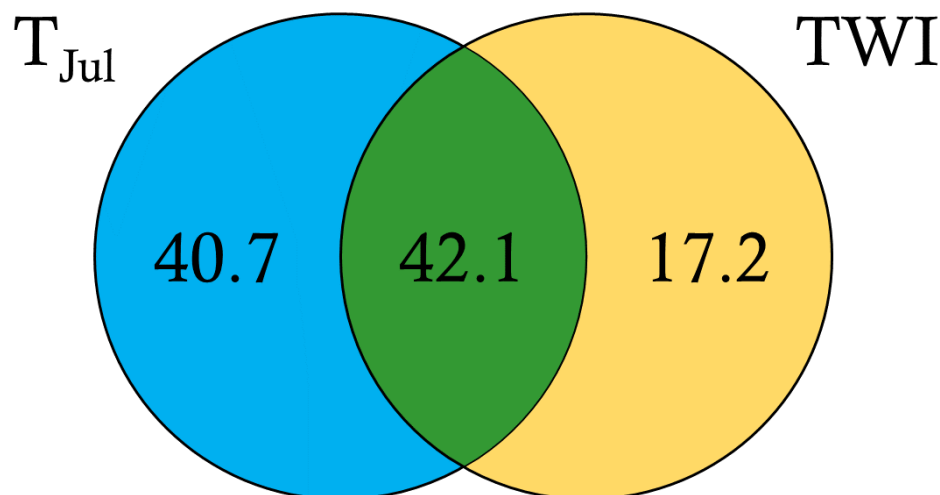


**Figure 6.5.** Favourability values for the breeding of the White-winged Snowfinch in peninsular Spain, displayed for each UTM  $10 \times 10$  km grid cell, according to the environmental model considering data from the III Spanish bird atlas plus eBird records.

**Table 6.3.** Comparative assessment of the discrimination and classification capacities of the resulting favourability models. Assessment indices include: area under the curve (AUC), sensitivity, specificity, correct classification rate (CCR), over-prediction rate (OPR), under-prediction rate (UPR) and Cohen’s Kappa index (Kappa).

Measure	Favourability model	
	III Spanish bird atlas	III Spanish bird atlas + eBird
AUC	0.993	0.992
Sensitivity	1	1
Specificity	0.937	0.935
CCR	0.937	0.935
OPR	0.918	0.906
UPR	0	0
Kappa	0.143	0.162

The pure effect of mean temperature in July in the environmental model accounted for 40.7 % of the explained variation. The pure effect of the Topographic Wetness Index (TWI) explained 17.2 %, and the shared variance between both variables was 42.1 % (Figure 6.6). These results indicate that areas with cool summers have the greatest influence on the breeding distribution of the White-winged Snowfinch in peninsular Spain.



**Figure 6.6.** Results of the variation partitioning of the environmental model considering the III Spanish bird atlas plus eBird data, using the two explanatory variables that entered the model: mean temperature in July ( $T_{Jul}$ ) and Topographic Wetness Index (TWI). Values shown in the diagram represent the percentages of variation explained exclusively by each variable and by their interaction.

## 6.4 Discussion

Mountain ranges in the south-western Palearctic have historically acted as climatic refugia for alpine specialist species during glacial contractions (Kropf *et al.* 2003, Schmitt 2009), and currently harbour rear-edge plant and animal communities that have persisted during both cold and warm periods. However, their specific biogeographical traits, such as their location in the temperate zone, limited altitudinal ranges, and dominant east–west orientation, make them particularly susceptible to biodiversity losses due to climate change (Thuiller *et al.* 2005, Benito *et al.* 2011). Our investigation reveals a decrease in the breeding distribution of the White-winged Snowfinch at its western global boundary over the past two decades. When considering only the data from the II and III Spanish bird atlases, the decline is pronounced. This reduction is slightly less severe when additional information from eBird for the period 2014–2018 is incorporated; however, it is important to note that the same 30 grid cells (43.5 %) remain unsampled in both cases. To accurately assess the species' current status and avoid overestimating the decline, it is essential to increase monitoring efforts in these unsampled, highly favourable areas. Identifying these regions, which are likely to be more difficult to access, is crucial for future sampling, as it will help gain a more comprehensive understanding of the species' current distribution and inform conservation strategies. One key application of our results is their potential use in guiding the selection of grid cells for targeted monitoring efforts. This is particularly relevant for ongoing species-specific surveys, such as the one currently being developed by the Spanish Society of Ornithology (SEO/BirdLife).

Distribution atlases are essential tools for species monitoring and management (Hagemeijer & Blair 1997, Keller *et al.* 2020), with many studies employing them to discuss the effects of climate change (e.g., Marjakangas *et al.* 2023). However, for species inhabiting mountainous regions, their utility may be limited due to challenging terrain and accessibility issues (Chamberlain *et al.* 2012). Our findings emphasize that direct atlas comparisons may be unreliable when atlases are based on 10 × 10 km grid cells, especially for high mountain species, where sampling difficulties are greater. Complementing atlas data with citizen science platforms like eBird can enhance the accuracy of species distribution assessments (Sullivan *et al.* 2014). Extending the sampling period by two weeks (16–30 June), as done with eBird by considering the entire month, increased the number of occupied grid cells. This adjustment, likely driven by the increased detectability of fledglings already in flight, demonstrates that a longer sampling

period improves the representation of the species' breeding distribution. Further monitoring, coupled with detailed studies on species phenology and microhabitat characteristics, will provide a more comprehensive understanding of the Snowfinch's ecological needs and its responses to environmental changes (Scridel *et al.* 2024).

Both the Pyrenean and Cantabrian populations show connections to those in the Alps, as documented by Resano-Mayor *et al.* (2020), although the Cantabrian core appears to be more isolated (Resano-Mayor *et al.* 2017). Our results indicate a greater reduction in the breeding distribution of the species in the Cantabrian core compared to the Pyrenees, both when considering only the atlas data and when including eBird data for the period 2014–2018. This higher extirpation rate in the Cantabrian core supports the notion that this population is indeed more isolated from other European populations. Additionally, although the mean environmental favourabilities in each core area are similar, the mean favourability of the Cantabrian core is slightly lower than that of the Pyrenees. Notably, the number of new grid cells is higher in the Pyrenees than in the Cantabrian Mountains. Consequently, based on our analysis of the species' current occupied range and the favourability values obtained, we support the idea that the Cantabrian core is more isolated from the broader European populations, as perceived by other authors (Resano-Mayor *et al.* 2017), although definitive confirmation awaits further investigations, including genetic and GPS tracking studies.

Our findings also indicate that, although the mean altitude of the OGU's with reported breeding in 2014–2018 was slightly higher compared to 1998–2002, the differences are minimal. This similarity may stem from the species being an obligate alpine bird, occupying the highest elevations within our study area as early as 1998–2002. Conversely, the mean altitude of newly occupied squares is approximately 170 m higher than those from which the species has disappeared. This outcome is likely influenced by the higher number of new squares located in the Pyrenees, where the altitudinal range is approximately 100 m higher than in the Cantabrian Mountains. This finding suggests that the Pyrenees offer the species a broader range of mobility for ascending in altitude compared to the Cantabrian Mountains.

At a broad-scale, the breeding distribution of the species in peninsular Spain is primarily influenced by areas with cool summers, as the *mean temperature in July* (with a negative coefficient) was the first variable added to the model and had the greatest

weight according to the Wald test. Additionally, the breeding distribution within our study area is constrained by low humidity areas, since the model incorporates the *Topographic Wetness Index* (also with a negative coefficient) as a significant variable. Summer temperatures emerge as the main factor shaping the current breeding distribution of the White-winged Snowfinch, accounting for over 40 % of the variation in the model. Climate change is contributing to higher summer temperatures, more frequent and longer heat waves, and lower average annual rainfall in many mid-latitude regions, particularly affecting the Iberian Peninsula (IPCC 2022). Consequently, this trend is leading to a warmer and drier environment in the European region, especially in southern areas, with discernible adverse effects on the White-winged Snowfinch.

The distribution model obtained delineates areas exhibiting high favourability for the species that are presently unoccupied, including the Mountains of León (northwest Spain), Picos de Urbión (north of the Iberian System), and the Central System. This aspect could contribute to the notably high over-prediction rate observed in the model. These areas, situated in close proximity to the two existing cores, hold the potential for species occupancy and merit inclusion in monitoring programs and intensified conservation efforts. Particularly noteworthy is the area of high favourability in the Picos de Urbión, which may serve as a connecting link between the two current population cores in Spain. In southern Spain, specifically in Sierra Nevada, our model also identifies areas with high favourability. Although the species is currently considered extirpated there, this region still preserves the environmental conditions necessary to support it. Its absence in the area today does not rule out the possibility of recolonization in the future, as occasional sightings of the species have been reported in southern regions, including the most recent one in Alicante in 2022. However, this scenario is highly improbable due to the significant isolation of the Sierra Nevada massif, primarily caused by its distance from the nearest core populations. The White-winged Snowfinch was present in Sierra Nevada until the late 19th century and was considered a common species (Saunders 1871). However, by the 1950s-1960s, its presence in this area was already considered unlikely, as no recent observations had been recorded and no confirmed specimens were known (Niethammer 1957). The elevated over-prediction rate in the model may represent another facet of the marked reduction, with over 94 % of the favourable areas for the species currently unoccupied. This outcome suggests a potential shortage of individuals to populate even

the highly favourable areas, as well as the presence of additional constraints, beyond environmental conditions, that may be limiting the species' occupancy.

In conclusion, our study highlights a concerning decline in the breeding distribution of the White-winged Snowfinch at its western global boundary, likely influenced by climate change and habitat alterations. The isolation of the Cantabrian core and the species' limited ability to shift altitudinally due to topographical constraints emphasize the vulnerability of this population. These findings underscore the importance of critically assessing the comparability of distribution atlases, especially for high mountain species with sampling challenges, as discrepancies may lead to misinterpretations of species' responses to climate change. There is an urgent need to increase sampling efforts, especially in unsampled and high-favourability areas, to obtain a more accurate understanding of the species' current distribution, and to integrate fine-scale behavioural and ecological data into SDMs to improve accuracy and provide a more comprehensive understanding of the species' ecological needs. Complementing traditional atlas data with citizen science platforms can enhance monitoring and conservation strategies. Further research, including genetic studies and GPS tracking, is essential to fully understand the population dynamics and connectivity of the species. Intensified conservation efforts are required to protect existing populations and facilitate the recolonization of unoccupied but suitable habitats.



Papamoscas gris (*Muscicapa striata*)

# CAPÍTULO 7

Climate-driven shifts in trans-Saharan bird migration illustrated by the spotted flycatcher (*Muscicapa striata*)

Cambios provocados por el clima en la migración de aves transaharianas, ilustrados por el papamoscas gris (*Muscicapa striata*)

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Este capítulo se basa en: / This chapter is based on:

**López-Ramírez, S.**, García-Carrasco, J.-M., Real, R. & Muñoz, A.-R. (2025). Climate-driven shifts in trans-Saharan bird migration illustrated by the spotted flycatcher (*Muscicapa striata*). *Scientific Reports*, 15(1): 35201. <https://doi.org/10.1038/s41598-025-19138-9> (Q1)

## **7. Climate-driven shifts in trans-Saharan bird migration illustrated by the spotted flycatcher (*Muscicapa striata*)**

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### **7.0 Abstract**

Records of European long-distance migrant birds wintering in the Western Palaearctic have increased recently, possibly in response to milder climatic conditions due to climate change. The spotted flycatcher (*Muscicapa striata*), traditionally a trans-Saharan migrant, has recently been observed wintering north of the Sahara Desert. This study examines the winter status of this species in the Western Palaearctic and identifies climatically favourable yet unoccupied wintering areas. We compiled wintering records from 2000 to 2024 using the citizen science platform eBird. We then modelled the distribution of these data across Europe and the Middle East using 19 climatic and two topographic variables. Our results provide the first evidence of a regular wintering pattern of the species in the Western Palaearctic over the last decade, with over 80% of the records located on the Iberian Peninsula and the Balearic Islands. This aligns with positive temperature anomalies in Europe between 2014–2023. We identified four climatic variables as significant drivers, with the diurnal temperature range and the temperature of the coldest quarter within the study area being the strongest predictors. Favourable wintering areas encompass much of the Mediterranean basin and large Mediterranean islands. Using fuzzy logic, we produced ensemble models of these variables under different hypotheses regarding their relative importance, tested against independent North African wintering records. The most supported hypothesis indicates that while favourable values in the four variables are important, they are not essential, meaning that favourable values in some variables can compensate for less favourable values in others. This species may serve as a model for other trans-Saharan migrants now wintering in the Western Palaearctic. If temperatures continue to increase, more individuals are expected to shift their wintering strategy from trans-Saharan to pre-Saharan migrants, leading to an increase in the populations regularly wintering along Mediterranean coasts and islands.

## 7.1 Introduction

Bird migration is one of the greatest wildlife spectacles, producing massive global changes in bird distributions twice yearly. It is an evolutionary adaptation to find areas with sufficient resource availability during the non-breeding season to ultimately increase survival and breeding competition (Newton 2023). Migration strategies (e.g. direction, time, distance, and stopovers), the onset of migration and physiological adaptations have a genetic basis (Berthold & Querner 1981, Berthold 1988, 1991, Berthold & Helbig 1992, Gwinner 1996), in addition to the natural learning process of juveniles from experienced individuals (Flack *et al.* 2018). However, environmental changes can affect the manifestation of this genetic base, allowing a species to modify its migratory behaviour according to the current conditions (Berthold *et al.* 1992, Ogonowski & Conway 2009). This flexibility allows a variable response that ultimately benefits the persistence of the population if environmental conditions change in a short time (Charmantier & Gienapp 2014, Horton *et al.* 2023). Individuals have two types of short-term response mechanisms to the environment: the microevolutionary response to natural selection, which is a ‘non-labile’ trait that remains stable throughout an individual’s lifetime (Berthold *et al.* 1992, Berthold & Querner 1995, Pulido *et al.* 2001, Møller *et al.* 2017, Helm *et al.* 2019), and phenotypic plasticity, which is mainly ‘labile’ and can change repeatedly to fit the new environmental conditions (Charmantier *et al.* 2008, Charmantier & Gienapp 2014, Conklin *et al.* 2021, Horton *et al.* 2023). These changes are currently influencing the distribution range of some species (Stiels *et al.* 2021, López-Ramírez *et al.* 2023, 2024a, b), as well as the migratory behaviour of others, since individuals are adapting their phenology in response to environmental shifts, such as climate-driven changes (Gordo & Sanz 2006, Bussière *et al.* 2015, Potvin *et al.* 2016, Chamorro *et al.* 2019).

Migration is the part of the annual cycle with the highest mortality rate, especially for long-distance migrants which often have to cross large ecological barriers (Sergio *et al.* 2019, Newton 2025). A shorter migration distance could provide benefits to individuals, such as higher survival (Silllett & Holmes 2002); earlier arrival at their breeding grounds, allowing them to acquire breeding territories earlier and take full advantage of the available food resources (Kokko 1999, Coppack *et al.* 2003, Podhrázský *et al.* 2017); and improved fitness for the next breeding season (Alves *et al.* 2013). Therefore, if long-distance migrants establish wintering sites closer to their breeding grounds, they could become short-distance migrants.

Over the past few decades, temperatures have increased, and winters have become milder in Europe and Africa (IPCC 2022). If favourable conditions for long-distance migratory birds persist during autumn and winter, some species could delay or even forgo migration and remain in the Western Palaearctic (Gordo & Sanz 2006, Martín *et al.* 2019). An increasing number of records show that long-distance bird migrants breeding in Europe have been wintering in the Iberian Peninsula over the last decades (Morganti & Pulido 2012), such as the white stork (*Ciconia ciconia*) (Marchamalo 2002), the barn swallow (*Hirundo rustica*) (SEO/BirdLife 2012), and the Eurasian reed warbler (*Acrocephalus scirpaceus*) (Nieto *et al.* 2018, Chamorro *et al.* 2019). Other examples include the Eurasian hoopoe (*Upupa epops*), the Eurasian wryneck (*Jynx torquilla*), and the yellow wagtail (*Motacilla flava*) (SEO/BirdLife 2012). These observations indicate that in recent decades, Southern Europe, particularly the south of the Iberian Peninsula, has offered new climatic conditions and wintering areas sufficiently suitable to promote a reduction in migration distance (Rotics *et al.* 2017). In addition, these temperature changes facilitate a northward expansion of African birds which have colonised Southern Europe during the past few decades (Ramírez *et al.* 2002, Elorriaga & Muñoz 2010, Cabrera 2022, Navarrete 2022, López-Ramírez *et al.* 2023, 2024a, Muñoz *et al.* 2024a).

In this study, we focus on the spotted flycatcher (*Muscicapa striata*), a Palaearctic long-distance migrant that breeds in Northwest Africa and across Europe into Central Asia, and winters south of the Sahara Desert (Taylor 2020). In recent years, the international citizen science platform eBird (<https://ebird.org/home>) has shown some records of the species wintering north of the Sahara, which are currently considered anecdotal cases. While the number of wintering records has been increasing, no systematic study has provided a detailed overview of the current situation of the species in the Western Palaearctic during winter, which may be relevant in the current context of climate change. Therefore, this study primarily aimed to examine the status of the spotted flycatcher during winter in the Western Palaearctic. For this purpose, we used eBird data for Europe, North Africa, and the Middle East from 2000 to 2024 to obtain information about its spatial and temporal distribution during winter. Our assumption was based on the increasing temperatures over the last two decades (IPCC 2022). We also hypothesised that this species has even more favourable wintering areas in the Western Palaearctic than it currently occupies, which could lead to an increase in wintering populations in this region if climatic conditions remain favourable. To demonstrate this, we derived the

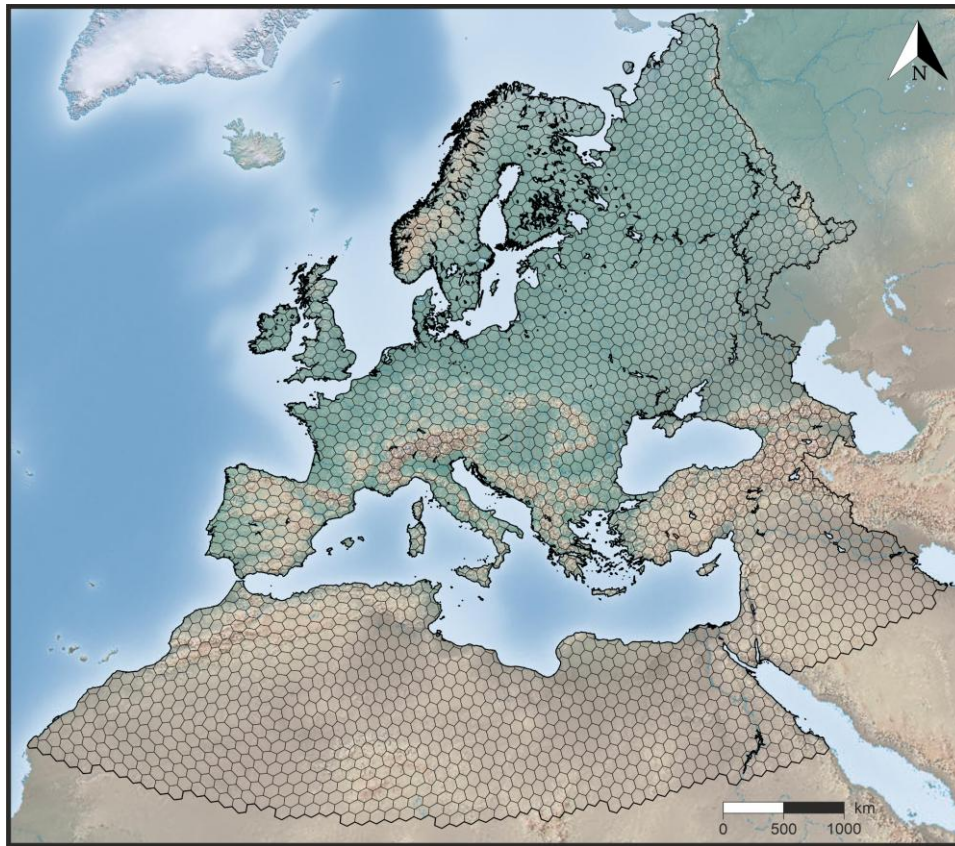
characteristics of the spotted flycatcher's current wintering areas in the Western Palaearctic and identified similar climatic regions that could become future wintering sites based on the short-term predictions from the distribution models (López-Ramírez *et al.* 2023). To this end, we formulated four hypotheses. **Hypothesis 1 (H1):** *all variables included in the model are relevant for the wintering of the species, but none are limiting;* **Hypothesis 2 (H2):** *all variables included in the model are limiting for the wintering of the species;* **Hypothesis 3 (H3):** *temperature and precipitation are generally limiting for the wintering of the species;* **Hypothesis 4 (H4):** *the winter temperature, along with the combination of the other variables included in the model, limit the wintering of the species.* Temperature conditions influence food availability for insectivorous species during winter, mainly the abundance of flying insects (Ratte 1984, Matthäus *et al.* 2023). Therefore, in H4, we have considered the temperature of the coldest quarter within the study area as one of the limiting variables. This research could be considered as an example for analogous studies of other insectivorous trans-Saharan migrants that are currently changing their phenology and wintering grounds.

## 7.2 Methods

### 7.2.1 Study area

The study area comprised the land area from 15° W to 65° E and from 20° N to 70° N, covering the Western Palaearctic and encompassing Europe, the Middle East, and North Africa. This area was divided using a hexagonal grid, with each hexagon representing an operational geographic unit (OGU) spanning an area of 7,774 km<sup>2</sup>. This biogeographical area had a total of 2,759 OGUs (**Figure 7.1**). The Western Palaearctic is a region with heterogeneous physiography and climate, including desert, Mediterranean, Atlantic, tundra, and boreal climates (Mill 1902, Udvardy 1975, Font 2000).

The selected area allows for the effects of climate change on the wintering of trans-Saharan birds, such as the spotted flycatcher, to be studied, since any record of the species during the wintering period in Europe, the Middle East or North Africa is unusual.



**Figure 7.1.** The study area divided into operational geographic units (OGUs). Map projection: GCS\_WGS\_1984 (ArcGIS 10.4.1).

### 7.2.2 The study species

The spotted flycatcher is a migratory insectivorous passerine, and is the most common and widespread flycatcher in the Western Palaearctic (Cramp & Simmons 1983). It breeds from mid-May to mid-August across Europe into Central Asia, and from April to July in Northwest Africa (Cramp & Simmons 1983). All populations traditionally winter in sub-Saharan Africa; however, over the last two decades, records from eBird have shown some individuals wintering north of the Sahara. Spring migration from the wintering grounds in sub-Saharan Africa to the Western Palaearctic begins in late February and continues until June, while autumn migration to the south starts in mid-August and ends in mid-November, with peak activity occurring in September and October (Taylor 2020). The species effectively inhabits any open woodland or timbered area with raised perches providing an open view. In breeding areas, it prefers well-spaced mature trees and has, therefore, adapted well to avenues, parks, gardens, orchards, and other artificial habitats. It also occupies many types of deciduous or coniferous woodland and is found in trees

along streams, rivers, and the edges of standing water. It occupies similar habitats in African non-breeding quarters (Taylor 2020).

### 7.2.3 Species distribution data

We obtained wintering records of the species from the eBird platform from 1 December 2000 to 31 January 2024. We considered records between 1 December and 31 January as wintering to avoid late post-breeding and early pre-breeding migrants, respectively. All records were verified using pictures of each observation. When multiple records indicated the same or very close locations on similar dates within the same wintering period, it was assumed to be the same individual, and only one record was retained.

### 7.2.4 Predictor variables used for distribution modelling and climate data

A set of 21 environmental variables related to topography ( $n = 2$ ) and climate ( $n = 19$ ) between 1981 and 2010 were used to model the wintering distribution of the species in the Western Palaearctic (**Table 7.1**). We included topography along with climate in the modelling approach to avoid conflating their distinct effects and mistakenly attributing them solely to climate (Márquez *et al.* 2011, Muñoz *et al.* 2013).

These variables were downloaded in raster format with an approximately 1 km<sup>2</sup> pixel resolution. The values of these variables at each OGU were obtained by averaging the 1 km<sup>2</sup> pixel values within each OGU using the *zonal statistic as table* function in ArcGIS version 10.4.1 (ESRI 2016), providing an average value for the surrounding environment in which each presence (and absence) was recorded.

**Table 7.1.** The variables selected to model the wintering distribution of the spotted flycatcher in the Western Palaearctic, grouped by environmental factor.

Code	Variable and units	Source
<b>Topography</b>		
Alti	Altitude (m)	1
Slope	Slope (degrees)	2
<b>Climate</b>		

Tmean	Mean annual air temperature (0.1·°C-273.15)	3
Rtday	Mean diurnal air temperature range (0.1·°C)	3
Isot	Isothermality (0.1·°C; ratio of diurnal to annual temperature variation)	3
Season	Temperature seasonality (0.1·°C/100; standard deviation of the monthly mean temperatures)	3
Tmax	Mean daily maximum air temperature of the warmest month (0.1·°C-273.15)	3
Tmin	Mean daily minimum air temperature of the coldest month (0.1·°C-273.15)	3
Rtan	Annual range of air temperature (0.1·°C)	3
Twet	Mean daily air temperatures of the wettest quarter (0.1·°C-273.15)	3
Tdry	Mean daily air temperatures of the driest quarter (0.1·°C-273.15)	3
Twarm	Mean daily air temperatures of the warmest quarter (0.1·°C-273.15)	3
Tcold	Mean daily air temperatures of the coldest quarter (0.1·°C-273.15)	3
Prec	Annual precipitation amount (0.1·mm·year <sup>-1</sup> )	3
Pmax	Precipitation amount of the wettest month (0.1·mm·month <sup>-1</sup> )	3
Pmin	Precipitation amount of the driest month (0.1·mm·month <sup>-1</sup> )	3
Cvp	Precipitation seasonality (0.1·mm·month <sup>-1</sup> ; standard deviation of the monthly precipitation estimates expressed as a percentage of the mean of those estimates, i.e. the annual mean)	3
Pwet	Mean monthly precipitation amount of the wettest quarter (0.1·mm·month <sup>-1</sup> )	3
Pdry	Mean monthly precipitation amount of the driest quarter (0.1·mm·month <sup>-1</sup> )	3
Pwarm	Mean monthly precipitation amount of the warmest quarter (0.1·mm·month <sup>-1</sup> )	3
Pcold	Mean monthly precipitation amount of the coldest quarter (0.1·mm·month <sup>-1</sup> )	3

*Data sources:* 1. US Geological Survey (1996); 2. Elaborated from the digital elevation model using the altitude variable (US Geological Survey 1996) with the geographic information system ArcGIS Desktop 10.4.1; 3. Chelsa Climate (<http://chelsa-climate.org>). The term ‘quarter’ refers to a three-month period (i.e. trimester) in this context.

The average estimated surface temperature change in Europe according to 1991–2020 reference levels (°C) for each year from 1979 to 2023 was downloaded from Copernicus Climate Change Service (C3S, <https://climate.copernicus.eu>). This estimated temperature change was then averaged for the periods 1979–2000, 2001–2013, and 2014–2023.

### 7.2.5 Modelling procedure

We used logistic regression analysis to identify potentially favourable areas where spotted flycatchers might appear during winter but are not currently detected. Logistic regression is a supervised machine learning algorithm that allows the use of environmental variables, such as topographic and climatic factors (**Table 7.1**), to explain the binary dependent variable (presence/absence) (Hosmer & Lemeshow 1980). Understanding the environmental conditions that explain the current winter distribution of the spotted flycatcher could help identify other areas with similar environmental characteristics that might also support individuals during this time of the year.

We initially calculated Spearman's correlation coefficients between variables to reduce multicollinearity among them (Zanolla *et al.* 2018, López-Ramírez & Muñoz 2025). For each pair of variables with  $r > 0.8$ , only the variable that showed the most significant relationship with the species' wintering distribution was retained, according to the statistical significance of Rao's score test (Radhakrishna Rao 1948). The type II errors for the null hypotheses were controlled using the score test ( $p < 0.05$ ), while the type I errors for the alternative hypotheses were managed using the false discovery rate ( $q < 0.05$ ) (Benjamini & Hochberg 1995, Benjamini & Yekutieli 2001, García-Carrasco *et al.* 2023b). Due to the high number of variables, we controlled for type I errors by implementing statistical corrections to minimise the likelihood of false positives, ensuring our findings are more robust and reliable. On the subset of variables that passed the two previous filters, we tested the response of the winter distribution of the species to each explanatory variable in Europe and the Middle East. This response can be monotonic or unimodal, in both cases with possible plateaus of no additional response of the species to the environment (**Appendix 47**). A monotonic response implies that the relationship of the explanatory variable with the wintering presence of the species is either positive or negative. In contrast, a unimodal response implies that after an optimum value in the environmental gradient is reached, the initially positive linear relationship becomes negative. To this end, binary stepwise logistic regression models were performed separately for each explanatory variable, using their original ( $x$ ) and quadratic ( $x^2$ ) forms. A response was considered unimodal when the best logistic regression model included the original form as positive and the quadratic form as negative ( $x, -x^2$ ), as this was the only biologically plausible unimodal response. For all variables that showed this type of unimodal response, the result of the unimodal model ( $y$  or *logit* function) was used as an explanatory variable in the final modelling process (García-Carrasco *et al.* 2024, López-Ramírez *et al.* 2024a). In all other cases, the original form of the variable was used. Then, we performed an ensemble forecasting with the remaining subset of variables that passed the above filters using a multivariate stepwise logistic regression to obtain the probability of wintering in each OGU. This process started with a null model containing no predictor variables that produced a constant probability of wintering for each OGU equal to the prevalence (the proportion of OGUs where species has been confirmed to winter relative to the total number of OGUs). In the first step, the procedure selected the variable with the most significant relationship to the winter distribution of the species, according to the significance of the Rao's score test (Radhakrishna Rao 1948). In the following steps, it

added the variable most significantly related to the residuals not explained by the previous step, until no additional variable significantly increased the predictive capacity of the model (Legendre & Legendre 1998). Thus, the environmental variables included in the multivariate model, an ensemble model, were a parsimonious representation of all the effects attributable to the set of variables analysed in the stepwise procedure. Finally, we obtained a significant combination of predictor variables ( $y$  or *logit*), whose coefficients were estimated using a machine learning algorithm based on a gradient ascent of likelihood (Glasmachers & Igel 2010, Basha *et al.* 2018). As this was unlikely for highly correlated variables, this stepwise procedure also contributed to reduce multicollinearity among explanatory variables. The relative weight of each variable in the final model was assessed using the Wald test (Wald 1943) and the remaining multicollinearity between them by calculating the Variance Inflation Factor (VIF). The different steps followed to select the predictor variables are summarised in the appendixes (see **Appendix 48**).

We identified the OGUs where the species was confirmed to winter in the Western Palearctic and then used the wintering occurrences in Europe and the Middle East to model the distribution of the species in this region, as North Africa is under-sampled and, by excluding it, we reduced the number of false absences included in the models. We also excluded Gibraltar from the modelling process, as its OGU was mostly located on the African continent. We then checked that there were no problems in extrapolating the model to North Africa by confirming that the mathematical domain of the function of the unimodal variables that entered the model was within the logical domain in the training area (i.e. Europe and the Middle East; **Appendixes 49–52**). We then extrapolated the model to North Africa. The logistic regression analysis provides a probabilistic output which details the probability of finding a spotted flycatcher in a given area based on its environmental characteristics. Since the prevalence of records may be underestimated, especially in regions with less citizen science activity or lower participation, it is essential to account for this bias. To address this, we transformed the probability outputs into favourability outputs using the favourability function (Real *et al.* 2006):

$$F = \frac{\frac{P}{1-P}}{\frac{n_1}{n_0} + \frac{P}{1-P}}$$

where  $n_1$  and  $n_0$  represent the number of wintering presences and absences in the study area, respectively. Favourability ( $F$ ) values range from 0 (unfavourable environmental

conditions) to 1 (highly favourable environmental conditions), with a value of 0.5 suggesting that the likelihood of the species' presence is equal to its prevalence in the study area. Therefore, favourability refers to the extent to which environmental conditions favour the presence of the spotted flycatcher during the winter. Our modelling approach conforms to modelling protocols proposed by Sillero *et al.* (2021). All modelling processes were run with the IBM SPSS Statistics 25 software package, and maps were created using ArcMap software (ArcGIS version 10.4.1; <https://desktop.arcgis.com/es/arcmap/>).

### 7.2.6 Hypotheses testing through models' assessment and validation

The favourability model derived from the multivariate logistic regression probability values was used to test H1. To test H2, we determined the fuzzy intersection between the favourability outputs of the univariate models of each variable included in the multivariate model. The degree of membership of each OGU to the fuzzy intersection was defined as the minimum value of favourability among the univariate models in each OGU (Estrada & Real 2021, López-Ramírez *et al.* 2024a). To test H3, we first calculated the fuzzy union of the favourability outputs from the univariate models separately for temperature-related and precipitation-related variables. The degree of membership of each OGU to the fuzzy union was defined as the maximum value of favourability among the univariate models in each OGU (Estrada & Real 2021, López-Ramírez *et al.* 2024a). We then calculated the fuzzy intersection between the favourability outputs of the temperature and precipitation models. To test H4, we initially computed the fuzzy union of the favourability outputs from the univariate models for all variables except the variable *mean daily air temperatures of the coldest quarter*. We then calculated the fuzzy intersection between the favourability of this temperature variable and the fuzzy union of all other variables. We also calculated the mean favourability in Europe and the Middle East, and separately in North Africa, from these models.

The resulting univariate and ensemble distribution models, as well as their corresponding hypotheses, were assessed and compared according to their discrimination and classification capacity in Europe and the Middle East, and when extrapolated to North Africa. The discrimination capacity was evaluated using the area under the receiver operating characteristic curve (AUC) (Lobo *et al.* 2008). The classification capacity,

using  $F = 0.5$  as the classification threshold, was assessed through the following measures: sensitivity (conditional probability of OGUUs with reported wintering presences classified as favourable), specificity (conditional probability of OGUUs with no reported wintering presences classified as unfavourable), correct classification rate (CCR; conditional probability of correctly classified OGUUs), the over-prediction rate (OPR; the proportion of OGUUs with no reported wintering presences in an area with  $F > 0.5$ ), and the under-prediction rate (UPR; the proportion of OGUUs with reported wintering presences in an area with  $F < 0.5$ ). These measures are widely used, with values ranging from 0 to 1 (Fielding & Bell 1997, Barbosa *et al.* 2013b). 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 OGUUs with reported or no reported wintering presences in the dataset was greater or less than 0.5, respectively.

The wintering occurrences in North Africa and Gibraltar, which were not included in the modelling process given that their OGUUs were mostly or entirely located on the African continent, were used to validate the results of the different distribution models and their corresponding hypotheses. To this end, the discrimination capacity of the ensemble models in North Africa was assessed using the AUC and the classification capacity using the sensitivity and specificity.

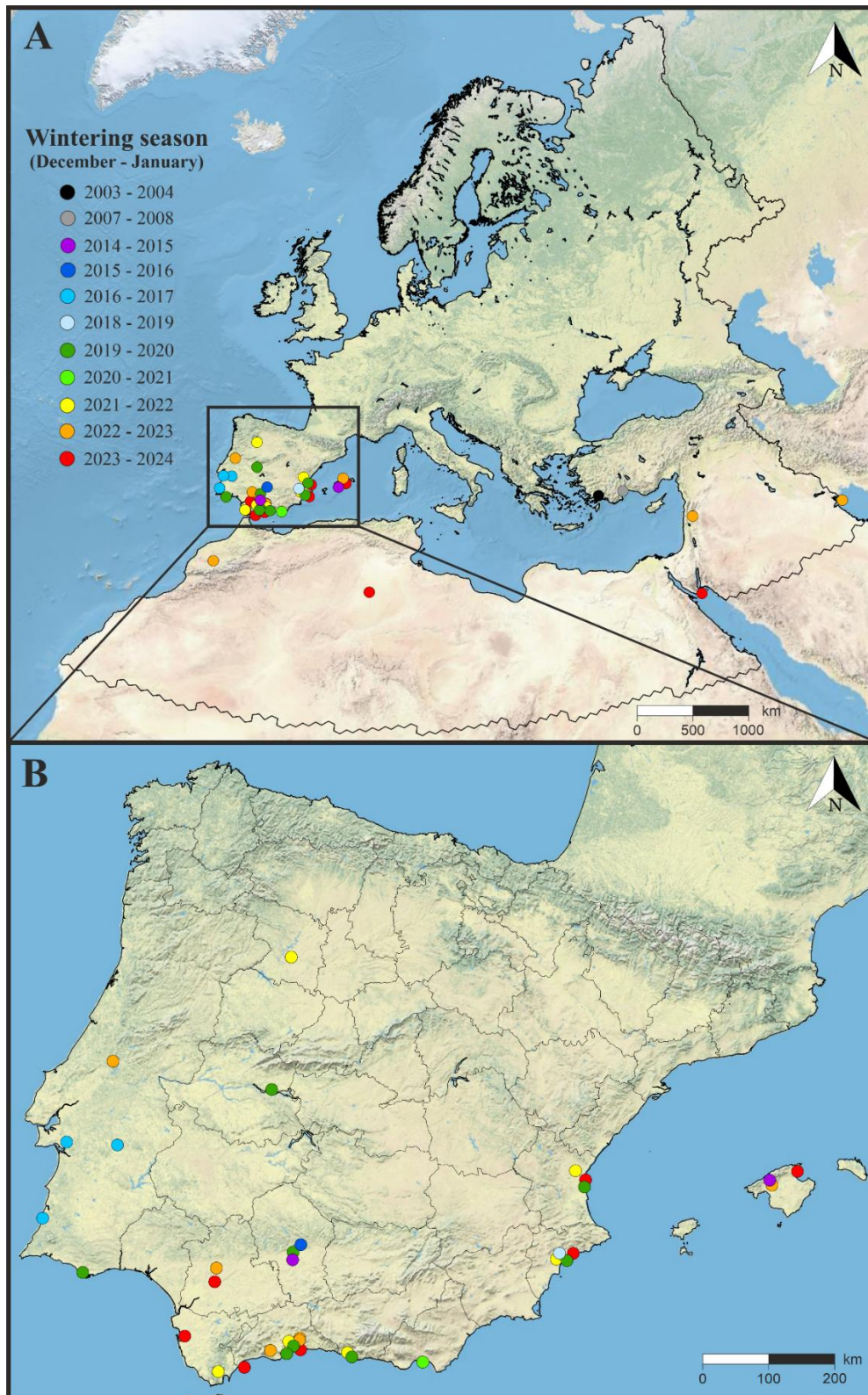
### **7.2.7 Variation partitioning analysis**

Interactions between factors often produce an overlaid spatial effect due to collinearity (Borcard *et al.* 1992, Legendre 1993). To illustrate this effect, we grouped the variables included in the distribution model according to H1 into two main factors: temperature and precipitation. We then employed a variation partitioning procedure (for a more detailed process, see Chamorro *et al.* 2019 and Muñoz *et al.* 2005) to determine the extent to which the variation in favourability of the final model was explained by the pure effects of each factor (i.e. unaffected by collinearity between them; Borcard *et al.* 1992) and the proportion attributable to their interaction (Legendre 1993, Legendre & Legendre 1998).

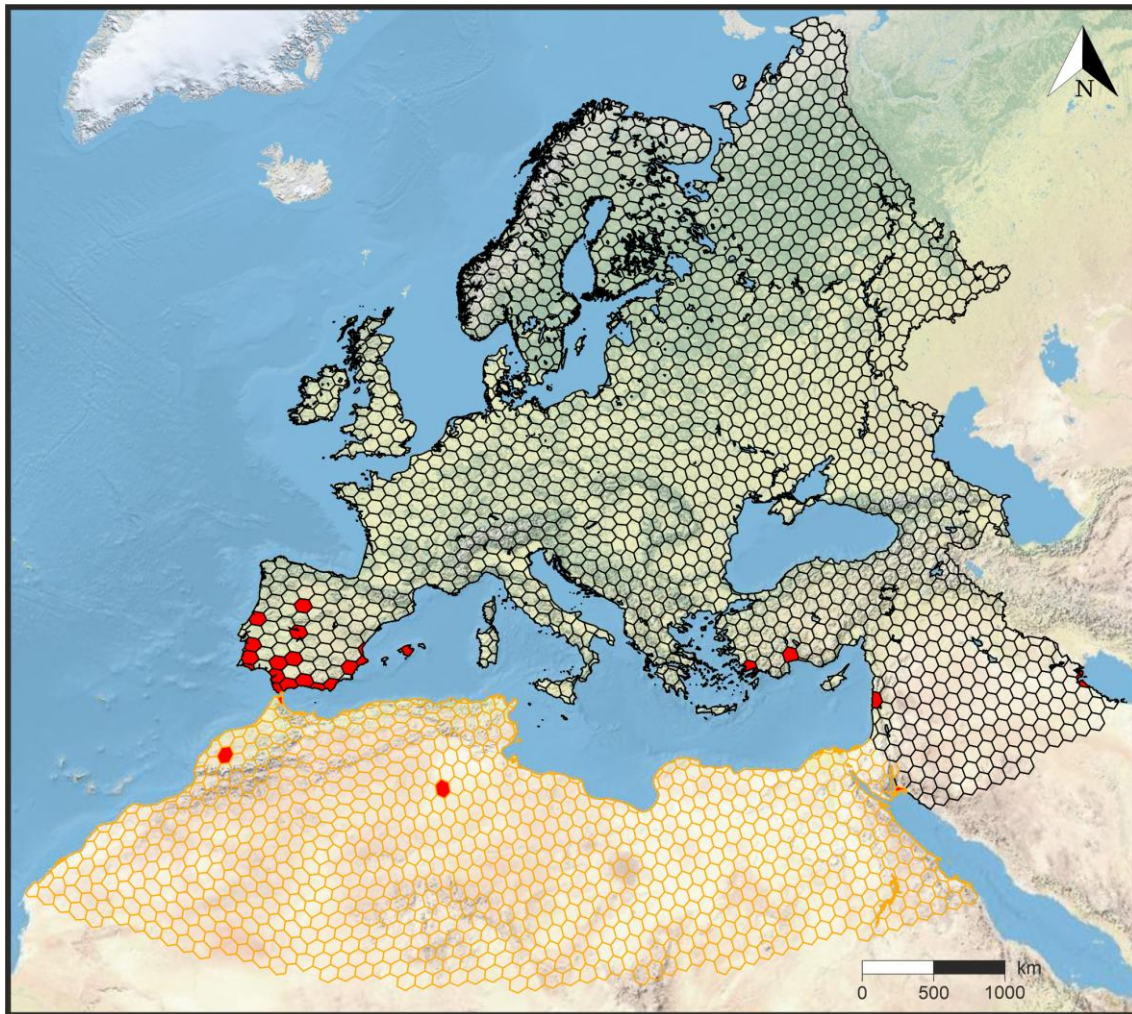
### 7.3 Results

Our eBird database search yielded 42 wintering records of the species in the Western Palaearctic from 1 December 2000 to 31 January 2024. They were located at the western and eastern extremities of the Mediterranean basin, mainly along the European shore, with some scattered records in North Africa (**Figure 7.2**). We identified wintering records of the species in Peninsular Spain ( $n = 27$ ), Portugal ( $n = 5$ ), Balearic Islands ( $n = 3$ ), Turkey ( $n = 2$ ), Morocco ( $n = 1$ ), Algeria ( $n = 1$ ), Israel ( $n = 1$ ), Egypt ( $n = 1$ ), and Kuwait ( $n = 1$ ). More than 80% of the records were detected on the Iberian Peninsula and the Balearic Islands (**Figure 7.2B**). The first wintering bird of the species in the entire Western Palaearctic was detected on 12 January 2004, and the second on 22 December 2007, both in Southwestern Turkey (**Figure 7.2A**). The species was not observed again until the winter of 2014–2015, when two individuals were detected: one in the south of the Iberian Peninsula and the other in the Balearic Islands (**Figure 7.2B**). These were the first wintering records of the spotted flycatcher in Europe. Since the winter of 2014–2015, the species has been recorded every winter in Europe, except for the winter of 2017–2018, when there were no records across the entire Western Palaearctic (**Figure 7.2A, B**). The number of records per wintering season has increased in recent years, starting from the winter of 2019–2020, primarily in the southern half of the Iberian Peninsula (**Figure 7.2B**).

From the records described above, we identified 26 OGUs in the Western Palaearctic where the species was confirmed to winter (**Figure 7.3**). We used the 22 OGUs located in Europe and the Middle East to model the distribution of the species specifically in this region (**Figure 7.3**, black outlined hexagons). Europe and the Middle East have a total of 1887 OGUs, so that the number of absences considered to perform the model was 1865.

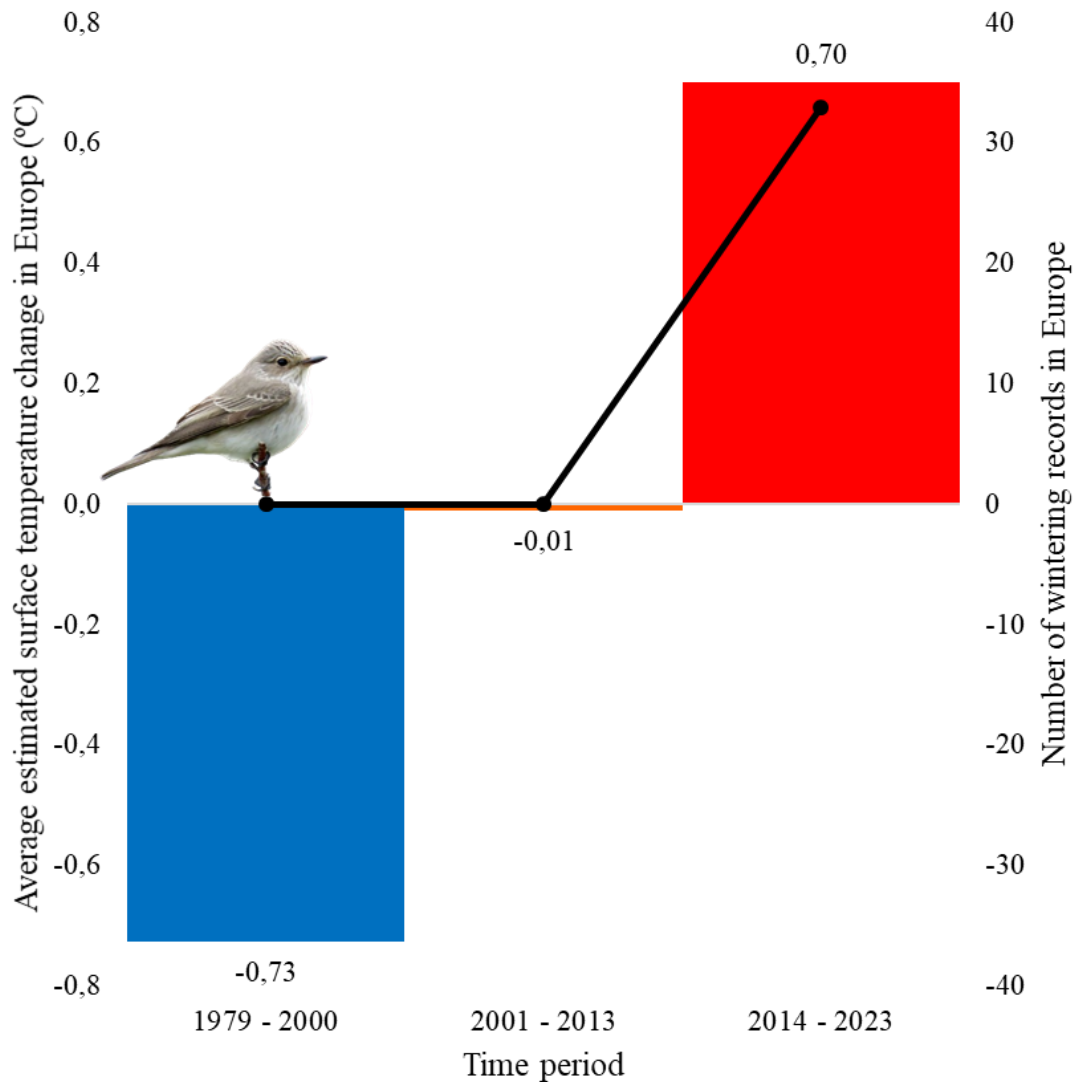


**Figure 7.2. A:** Wintering records of the spotted flycatcher in the Western Palearctic from 1 December 2000 to 31 January 2024, with each colour representing the wintering season for the record. Wintering seasons not represented indicate that there were no records of the species. **B:** Detailed view of the wintering records in the Iberian Peninsula and the Balearic Islands, where more than 80% of the records were detected. Map projection: GCS\_WGS\_1984 (ArcGIS 10.4.1).



**Figure 7.3.** Operational geographic units (OGUs) corresponding to the wintering presence of the spotted flycatcher (red hexagons) based on the records shown in **Figure 7.2A**. We used the wintering presences in Europe and the Middle East to model the distribution of the species only in this region (black outlined hexagons) and then extrapolated the model to North Africa (orange outlined hexagons). Map projection: GCS\_WGS\_1984 (ArcGIS 10.4.1).

Wintering records of the species in Europe were concentrated in the period 2014–2023, coinciding with the average surface temperature on the continent higher than 1991–2020 baseline (**Figure 7.4**). No records of the species were detected in Europe until the winter of 2014–2015, during which the average surface temperature on the continent was lower in 1979–2000 and in 2001–2013 almost equal to the reference level.



**Figure 7.4.** Average estimated surface temperature change in Europe (°C) relative to 1991–2020 reference level for three periods during 1979–2023 (bars; Copernicus Climate Change Service: <https://climate.copernicus.eu>), and the number of wintering records of the spotted flycatcher in Europe (black line). The average temperature for the period 1991–2020 was 9.2°C.

The wintering distribution model for the spotted flycatcher included four climate-related variables: three related to temperature and one to precipitation (**Table 7.2**). Precipitation and temperature seasonalities were the first and second variables added in the stepwise procedure, respectively, but they had less weight in the model according to the Wald test. The mean diurnal air temperature range and mean daily air temperatures of the coldest quarter were the third and final variables added in the stepwise procedure, respectively. They were the most significant predictors of the wintering distribution of the

species in Europe and the Middle East, as they had the greatest weight in the model according to the Wald test. All four variables included in the model exhibited a unimodal response, meaning they positively affected the wintering distribution of the species only within a specific range of values (**Appendixes 49–52**). Therefore, precipitation seasonality, temperature seasonality, mean diurnal air temperature range, and mean daily air temperatures of the coldest quarter positively affected the wintering distribution of the spotted flycatcher within the following ranges using an  $F$  threshold of 0.5: 40–95 mm/month for precipitation seasonality (**Appendix 49**), 3°C–7°C for temperature seasonality (**Appendix 50**), 7.5°C–12.5°C for mean diurnal air temperature range (**Appendix 51**), and 5°C–15°C for mean daily air temperatures of the coldest quarter (**Appendix 52**).

**Table 7.2.** The variables included in the logistic regression model for the spotted flycatcher via a forward-backward stepwise selection process, ranked by their order of inclusion. All variables are prefixed with “U\_” since they showed a unimodal response in the species’ wintering distribution and were included in the model as such. Variable codes are listed in **Table 7.1**.

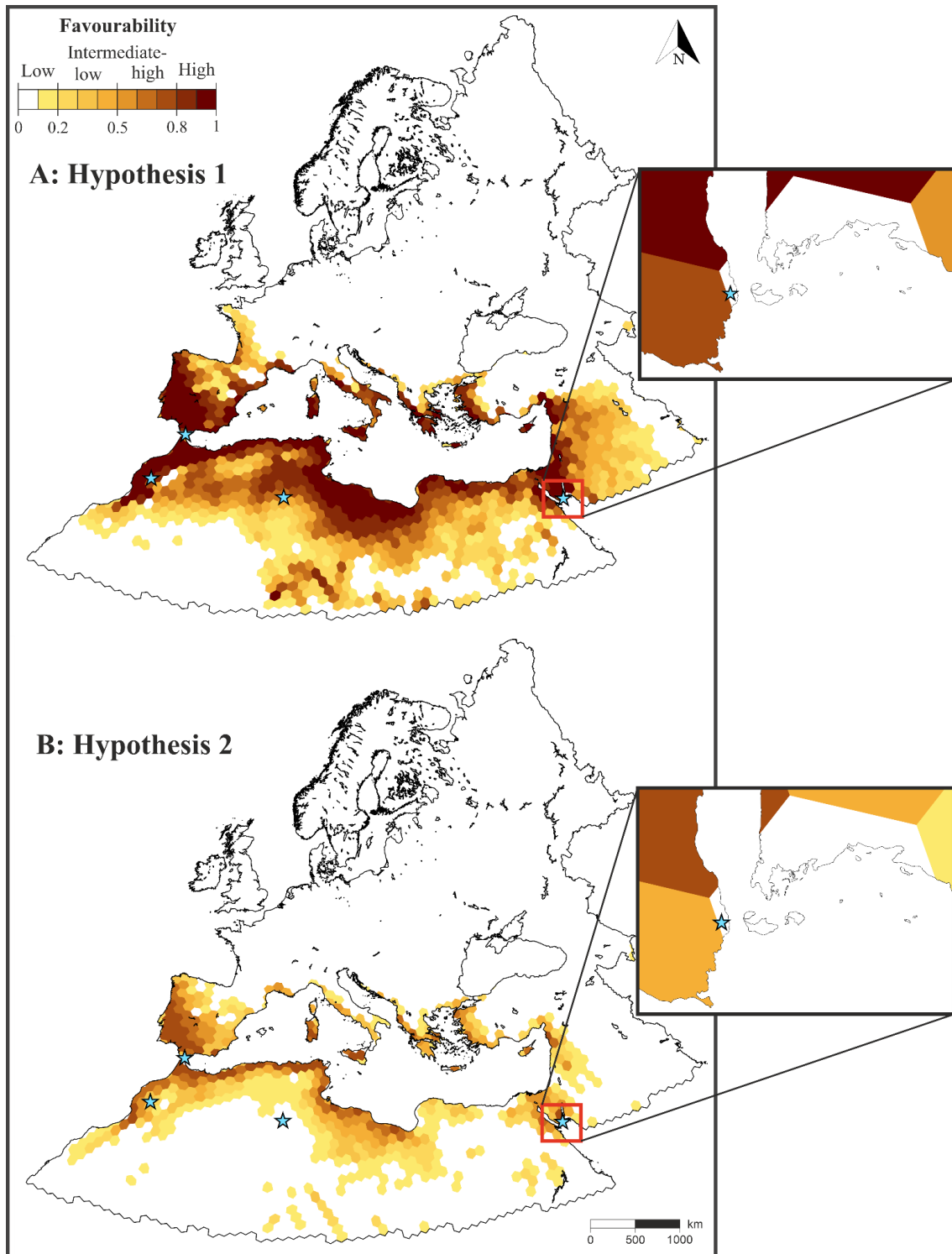
Variable	$\beta$	S.E.	Wald	$p$	VIF
U_Cvp	0.359	0.2001	3.209	0.0732	1.950
U_Season	0.538	0.239	5.071	0.0243	4.021
U_Rtday	0.801	0.239	11.204	< 0.001	2.147
U_Tcold	1.0539	0.392	7.214	0.00723	5.003
Constant	7.629	1.704	20.043	< 0.001	

*Note:*  $\beta$  is the coefficient in the logit function, S.E. is the standard error of each coefficient, Wald is the Wald statistic value (representing the relative importance of the variable in the model),  $p$  is the significance of each coefficient according to the Wald test, and VIF is the variance inflation factor (used to quantify collinearity between variables in the model).

The favourability values for the wintering of the spotted flycatcher in each OGU of the Western Palaearctic according to each unimodal variable included in the model are shown in the supplementary material (**Appendixes 53–56**), together with the assessment of these univariate models (**Appendix 57**). The favourability models according to H1 and H2 had the best assessment based on their discrimination and classification capacities, compared to those according to H3 and H4 (compare **Table 7.3 and Appendix 59**). Therefore, we decided to only present the favourability models according to H1 and H2 in the manuscript. The results of the models according to H3 and H4 are provided in the supplementary material (**Appendix 58**).

The resulting climatic favourability model according to H1 shows high favourability values for the wintering of the species over most of the Mediterranean basin, both on the European and African shores, except for Northern Italy and Greece (**Figure 7.5A**). Areas with suitable climatic conditions for wintering of the spotted flycatcher include most of the Iberian Peninsula, Southern France, the southern half of Italy, Southern Greece, the west coast of Turkey, the Mediterranean coast of the Middle East, and the entire North African coast. Large Mediterranean islands such as Sardinia, Sicily, Crete, and Cyprus also have highly favourable climatic conditions for the species to winter. While the species has not yet been recorded in most places around the Mediterranean basin, in the last two winters (2022–2023 and 2023–2024), it has been recorded in new areas (**Figure 7.2**). The climatic favourability model according to H2 is more restrictive and only shows intermediate-high favourability values in most of the Mediterranean coastal areas, especially in North Africa. It also shows intermediate-high favourability values in the southwestern quadrant of the Iberian Peninsula and the large Mediterranean islands such as Sardinia, Sicily, Crete, and Cyprus (**Figure 7.5B**). The mean favourability of the models according to H1 and H2 was 0.112 and 0.044 in Europe and the Middle East and 0.371 and 0.143 in North Africa, respectively.

To validate the resulting models, we used recently confirmed wintering records of the species not included in the modelling process (**Figure 7.5**, blue stars). According to H1, all the records were located in areas with high or intermediate-high climatic favourability ( $F_{Morocco} = 0.911$ ,  $F_{Algeria} = 0.682$ ,  $F_{Gibraltar} = 0.577$ ) except for the record located on the Sinai Peninsula (Egypt), which was in an area with low favourability ( $F_{Egypt} = 0.021$ ). However, according to H2, all records were located in areas with low climatic favourability ( $F_{Gibraltar} = 0.070$ ,  $F_{Algeria} = 0.063$ ,  $F_{Egypt} = 0.019$ ) except for the record located in Morocco, which was in an area with intermediate-low favourability ( $F_{Morocco} = 0.334$ ). An assessment of the discrimination and classification capacities of the ensemble models in North Africa to compare the different hypotheses can be found in the supplementary material, where H1 obtained the best assessment (**Appendix 60**).



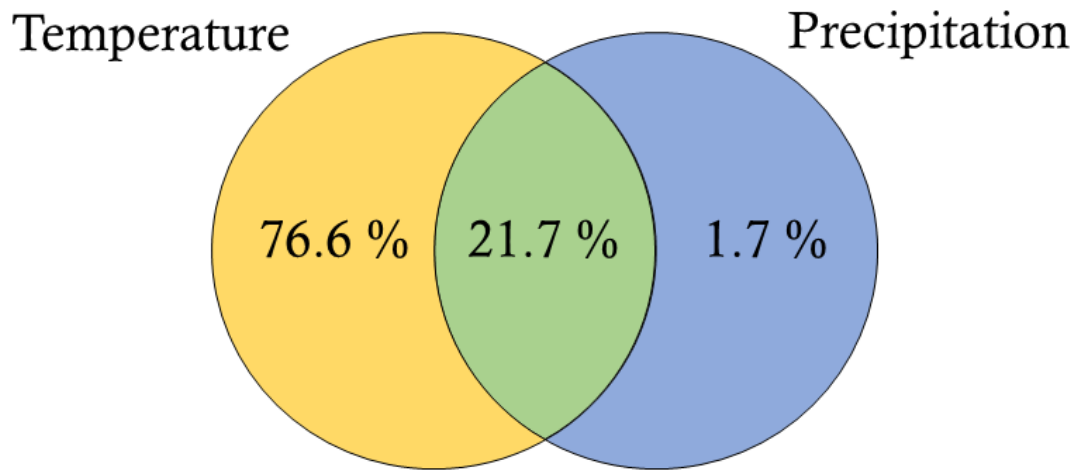
**Figure 7.5.** Climatic favourability ( $F$ ) values for the wintering of the spotted flycatcher in each operational geographic unit of the Western Palearctic according to **A:** hypothesis 1 (H1: *all variables included in the model are relevant for the wintering of the species, but none are limiting*) and **B:** hypothesis 2 (H2: *all variables included in the model are limiting for the wintering of the species*). Blue stars represent confirmed wintering records of the species not included in the modelling process. Map projection: GCS\_WGS\_1984 (ArcGIS 10.4.1).

The resulting models according to H1 and H2 had high discrimination (AUC > 0.91) and classification (sensitivity, specificity, and CCR > 0.82 and a positive Cohen's kappa except for the model according to H2, which showed a lower sensitivity) capacities in Europe and the Middle East and when extrapolated to North Africa (**Table 7.3**). However, the model according to H1 showed higher AUC and sensitivity than the model according to H2, both in Europe and the Middle East and its extrapolation to North Africa. In contrast, the model according to H2 showed higher specificity, CCR, and Cohen's kappa than the model according to H1, both in Europe and the Middle East and its extrapolation to North Africa. The UPR were very low in all cases (<0.01), whereas the OPR was substantial in all cases, especially in the models extrapolated to North Africa, with >90% of the predicted favourable wintering OGU's unoccupied.

**Table 7.3.** Comparative assessment of the discrimination and classification capacities of the climatic favourability models according to H1 and H2 in Europe and the Middle East and their extrapolation to North Africa. Assessment indices: area under the curve (AUC), sensitivity, specificity, correct classification rate (CCR), over-prediction rate (OPR), under-prediction rate (UPR), and Cohen's kappa index (Kappa).

Measure	Europe and the Middle East		Europe, the Middle East and North Africa	
	H1	H2	H1	H2
AUC	0.976	0.968	0.932	0.913
Sensitivity	0.955	0.545	0.923	0.462
Specificity	0.907	0.976	0.825	0.956
CCR	0.907	0.971	0.825	0.952
OPR	0.893	0.789	0.952	0.908
UPR	0.000591	0.00546	0.000888	0.00533
Kappa	0.175	0.292	0.074	0.139

The pure effect of temperature in the climatic model according to H1 explained 76.6% of the variation. In contrast, the pure effect of precipitation explained only 1.7% of the variation, and the joint effect of both factors explained 21.7% of the variation (**Figure 7.6**). These results show that temperature has the greatest influence on the winter distribution of the spotted flycatcher in the Western Palaeartic.



**Figure 7.6.** Variation partitioning of the climatic favourability model according to H1 using temperature and precipitation factors. The temperature factor includes the unimodal variables temperature seasonality, mean diurnal air temperature range, and daily air temperatures of the coldest quarter. The precipitation factor includes the unimodal variable precipitation seasonality. Values within the circles represent the percentage of variation explained by the indicated factors and their interaction.

#### 7.4 Discussion

The scientific community has increasingly focused on the effects of climate change on animal distribution patterns, a subject extensively studied since the early twenty-first century (Žalakevičius 2001, Gordo & Sanz 2006, Péron *et al.* 2007, Blois *et al.* 2013, Muñoz *et al.* 2013, Massimino *et al.* 2015, Bay *et al.* 2018, López-Ramírez *et al.* 2024a). While several studies have explored the influence of climate change on bird migration—primarily examining long-term shifts in spring arrival dates, autumn departures, and duration of stays (Both & Visser 2001, Gordo & Sanz 2006, Lehikoinen & Sparks 2010, Bussière *et al.* 2015, Potvin *et al.* 2016)—there is limited information available on the responses to climate change during the winter period (Chamorro *et al.* 2019). In this study, we provide the first evidence of regular wintering of the spotted flycatcher in the Western Palaearctic. Although traditionally all populations winter in sub-Saharan Africa (Taylor 2020), our findings indicate that wintering in the Western Palaearctic has become a relatively common phenomenon, particularly in recent years. Previous explanations for trans-Saharan migrants wintering in the Western Palaearctic have often focused on less experienced or juvenile individuals and sick or disoriented individuals. However, this does not seem to apply to the spotted flycatcher. Except for the winter of 2017–2018, the

species has been regularly observed since the winter of 2014–2015, and the number of records has increased over the last two winters (2022–2023 and 2023–2024), suggesting a consistent wintering pattern.

The winter survival of insectivorous species like the spotted flycatcher is closely linked to the availability of flying insects, which is influenced by mild temperatures (Ratte 1984, Matthäus *et al.* 2023). Additionally, some insectivorous birds switch to a more frugivorous diet during winter (Arizaga *et al.* 2012). While the spotted flycatcher can consume small fruits from genera such as *Berberis*, *Rhamnus*, *Cornus*, *Sorbus*, *Lonicera*, *Prunus*, *Morus*, *Rubus*, and *Trema* (Taylor 2020), this option seems unlikely as most of these genera do not bear fruit in winter. Therefore, the growing number of records in recent years may be related to warmer temperatures in the Western Palearctic, leading to milder winters (IPCC 2022). The species primarily winters in coastal areas and large valleys in the Western Palearctic, where milder temperatures may facilitate the availability of insects and other invertebrates. If these favourable conditions persist, the wintering population size could continue to increase in the coming years. Other factors may also contribute to the wintering of the species in the Western Palearctic, such as the expansion of green spaces, including parks, urban forests, and grasslands, particularly in Europe (Leng *et al.* 2023). Conversely, the growing number of wintering records might also be linked to more observers using citizen science platforms like eBird (Sullivan *et al.* 2014, Amano *et al.* 2016, Pocock *et al.* 2017). However, it is important to note that rare bird observations were documented before these platforms existed, although the information often took longer to become publicly available (SEO/BirdLife 2012, SEO/BirdLife 2024).

As a nocturnal migrant, the spotted flycatcher follows a broad-fronted migration that covers much of the Mediterranean region (Thorup & Rabøl 2001). Nonetheless, most wintering records are concentrated on the Iberian Peninsula, which serves as a critical stopover for European spotted flycatchers during their post-breeding migration (Hernández 2009). The availability of resources (Hernández 2009), combined with mild autumns and winters (Gordo & Sanz 2006), may lead the species to stay through the winter if environmental conditions allow, primarily due to food availability. This view is supported by the significant number of records from the Iberian Peninsula, accounting for three-quarters of the records in the entire Western Palearctic. In addition to these records, our distribution models further support the idea that the Western Palearctic is emerging

as a new wintering area for this long-distance migratory insectivore. Our models identify favourable wintering areas across much of the Mediterranean basin, including both European and African shores and large Mediterranean islands such as Sardinia, Sicily, Crete, and Cyprus. While our models exhibited an OPR of >78% in Europe and the Middle East, this does not necessarily indicate that they are erroneous (Muñoz & Real 2006, Barbosa *et al.* 2013b). Instead, it suggests they have identified favourable conditions in regions where the species has not yet been detected during winter.

When extrapolating the models to North Africa, the OPR exceeded 90%, suggesting that even more favourable but unoccupied (or undetected) wintering areas exist in North Africa compared to Europe and the Middle East. Indeed, the mean favourability was higher in North Africa than in Europe and the Middle East with both models, despite the lower number of wintering records. Notably, while the number of citizen science observers in African countries is steadily increasing, the overall number of participants remains significantly higher in Europe. Therefore, many areas predicted to be favourable in North Africa could indeed be occupied by the species during winter. Consequently, further research in North Africa is necessary, along with the promotion of citizen science, to better understand the role of this region in the wintering of the species and potentially other trans-Saharan migrants.

The model according to H1 was more optimistic, whereas the model according to H2 was more restrictive, requiring high favourability across all four variables in each OGU for the overall model favourability to be high. We propose that the current wintering situation of the spotted flycatcher in the Western Palearctic likely falls somewhere between these two models. While both models exhibited high discrimination and classification capacities, the actual situation may be closer to the model according to H1, which is supported by the validation of all four wintering records. Three of these records were located in areas with high or intermediate-high climatic favourability values. While the record from the Sinai Peninsula (Egypt) was in an area with low favourability, most of the OGU in which it was located is in Saudi Arabia, and the part of the OGU in the Sinai Peninsula likely has similar favourability to the surrounding high-favourability area (**Figure 7.5**). Furthermore, H1 obtained the best assessment among the different ensemble models according to their discrimination and classification capacities in North Africa (**Appendix 60**).

Based on these considerations, we predict a potential increase in the wintering populations of the species, mainly in the coastal areas and island systems of the Mediterranean, if climatic conditions in the Western Palaearctic remain consistent over the coming winters (IPCC 2022). Precipitation and temperature seasonalities were key predictors in determining the broader winter distribution of the species, being the first and second variables included in the model, respectively. The first variable excluded Northern and Central Europe due to low precipitation seasonality and some regions of western and eastern North Africa due to high precipitation seasonality (**Appendixes 49 and 53**). The second variable excluded continental areas of the Western Palaearctic because of high temperature seasonality, focusing instead on the coastal areas within the study area (**Appendixes 50 and 54**). The mean diurnal air temperature range had the greatest explanatory power in the model (**Table 7.2**), identifying areas with a mean diurnal air temperature of between 7.5°C and 12.5°C, broadly corresponding to Mediterranean regions (**Appendixes 51 and 55**). The mean daily air temperature of the coldest quarter was the second most influential variable in the model, adding significant detail as the last variable included. This variable identified areas with mild but not excessively warm winters in the Western Palaearctic (**Appendixes 52 and 56**).

In summary, the regions characterised by favourable climatic conditions for the wintering of the spotted flycatcher are predominantly located along the coastal areas of the Mediterranean basin, where winters are typically mild. Temperature has emerged as the primary environmental factor influencing the wintering distribution of the species, as shown by the variation partitioning analysis (**Figure 7.6**), indicating that it plays a far more significant role than precipitation. The severity of winters in the Western Palaearctic has decreased in recent decades, particularly in Southern Europe and Northern Africa, due to ongoing climate change (Brunet *et al.* 2007, IPCC 2022). These newly established warmer conditions throughout the year, including winter, have led to an increase in the abundance of flying insects, such as mosquitoes (Roiz *et al.* 2014), enhancing prey availability for spotted flycatchers. With temperature being a key driver of insect abundance and activity, warmer winters directly benefit the species by providing a more consistent food supply.

The species will likely establish a stable wintering population in the Western Palaearctic if it can access sufficient resources during the winter months, potentially providing these individuals with advantages over long-distance migrant populations as

winters continue to moderate. Food availability allows the species to maintain optimal body condition throughout the winter, reducing energy expenditure in less severe climatic environments (Alves *et al.* 2013, Newton 2023). Milder temperatures also reduce the thermoregulatory demands on the species, lowering their overall energy costs. Furthermore, their proximity to breeding sites in the following spring enables them to select superior breeding locations compared to long-distance migrants (Forstmeier 2002, Podhrázký *et al.* 2017). Additionally, lower migration-related mortality is anticipated, which could result in higher reproductive success (Sillert & Holmes 2002, Alves *et al.* 2013, Lok *et al.* 2017). However, since temperature is the primary factor driving the current winter distribution, any rapid fluctuations or extreme cold events could significantly disrupt these newly established wintering populations, leading to greater mortality and posing a significant threat to their existence (Senar & Copete 1995, Maclean *et al.* 2008).

Given that the primary purpose of bird migration is to reach environments with optimal conditions at specific times (Berthold 2001), the ability to adapt migratory behaviour has likely been crucial since the onset of animal migration on a planet subjected to environmental change (Fiedler 2003). The spotted flycatcher's ability to adjust its migratory behaviour, largely in response to rising temperatures, suggests that this flexibility may be a critical factor in population regulation. Ultimately, the diversity of migratory strategies across different geographical regions, and even among species within the same area, serves as a survival strategy that may have significant implications for population regulation and viability (Lok *et al.* 2015, Rotics *et al.* 2017). Whether staying on breeding grounds throughout the winter or shortening migration distances improves winter survival or breeding success in spotted flycatchers remains unclear. Consequently, ongoing monitoring is essential to understand and track the temporal evolution of this long-distance migrant, which is now wintering north of the Sahara.

The spotted flycatcher may serve as a model for other trans-Saharan migrants that have recently begun wintering in the Western Palaearctic. If temperature increases persist, more long-distance migrants are expected to shorten their migration routes, leading to larger populations regularly wintering in the Western Palaearctic, particularly in coastal areas and island systems within the Mediterranean. This trend has already been observed in species such as the Eurasian reed warbler (Nieto *et al.* 2018, Chamorro *et al.* 2019). Our findings could guide targeted sampling and monitoring efforts by prioritising areas

*Climate-driven shifts in trans-Saharan bird migration illustrated by the spotted flycatcher  
(Muscicapa striata)*

identified as highly favourable by the distribution models, thereby improving the efficiency of winter monitoring. While further research is necessary, this study significantly advances our understanding of the impact of climate change on the phenology and winter distribution of the species.

# CAPÍTULO 8

## Discusión General

## 8. Discusión General

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El actual cambio climático está afectando de manera creciente a todo nuestro planeta (IPCC 2022). Este cambio reciente en las condiciones climáticas, acelerado por las actividades humanas (Duarte *et al.* 2006, IPCC 2022), ha generado cambios en el medio natural, alterando los ecosistemas y afectando a las especies que estos contienen (Dessler 2021). De hecho, el calentamiento global, que está siendo más acusado desde mediados del siglo XX, ya ha modificado el comportamiento y la distribución de numerosas especies tanto en el espacio como en el tiempo (Parmesan 1996, Thomas & Lennon 1999, Both & Visser 2001, Gordo & Sanz 2006, Reif & Flousek 2012, Chamorro *et al.* 2017, Hallman *et al.* 2022, López-Ramírez *et al.* 2023), afectando así a la biodiversidad global. Este es uno de los motivos principales por los que la comunidad científica se ha centrado cada vez más en los efectos del cambio climático sobre los patrones de distribución de las especies, un tema ampliamente estudiado desde principios del siglo XXI (Žalakevičius 2001, Péron *et al.* 2007, Muñoz *et al.* 2013, Massimino *et al.* 2015, Bay *et al.* 2018) y que conforma el eje central de esta tesis doctoral.

La biogeografía proporciona herramientas metodológicas eficaces, como los SDMs, para estudiar y comprender la dinámica espacio-temporal de las distribuciones, contribuyendo así a la conservación de la biodiversidad (Whittaker *et al.* 2005). Los SDMs nos permiten conocer en detalle los factores que condicionan las distribuciones de las especies, así como predecir sus respuestas frente a cambios en las condiciones climáticas. Esta información esencial debería ser considerada por las administraciones competentes y los gestores del medio ambiente para aumentar los esfuerzos de seguimiento y muestreo en las zonas identificadas por los modelos como altamente favorables pero que aún están desocupadas por las diferentes especies, con el objetivo de poder fundamentar efectivas estrategias de conservación.

Los resultados obtenidos en la presente tesis ponen de manifiesto que los cambios en el clima acontecidos a lo largo de las últimas décadas están provocando cambios en la distribución espacio-temporal reciente de las aves en el Paleártico Occidental. De esta manera, especies de aves típicamente africanas están ampliando sus áreas de distribución hacia mayores latitudes y están comenzando a colonizar el sur del continente europeo (**capítulos 2, 3 y 4**) y a modificar las comunidades. Del mismo modo, algunas especies

de aves de montaña están ascendiendo en altura y reduciendo sus áreas de distribución en España peninsular como consecuencia del calentamiento climático y las limitaciones de espacio a gran altitud (**capítulos 5 y 6**). También existen casos de especies de aves migratorias típicamente transaharianas que están comenzando a contar con individuos que permanecen durante el invierno al norte del desierto del Sahara (**capítulo 7**). La información resultante de los modelos de distribución de las diferentes especies estudiadas en la presente tesis doctoral puede ayudar a entender tales cambios, así como apoyar a las acciones de conservación y gestión eficaz de dichas especies, en el contexto actual de calentamiento climático.

### 8.1 Colonización del sur de Europa por aves típicamente africanas

Según el IPCC (2022), el cambio climático está aumentando tanto las temperaturas como la frecuencia y duración de las olas de calor, así como reduciendo la precipitación media anual en el sur de Europa, haciendo que esta región sea más cálida y seca. Esta podría ser una de las causas principales por la que especies de aves típicamente africanas están expandiendo sus áreas de distribución hacia el norte y están comenzando a colonizar el sur del continente europeo (**capítulos 2, 3 y 4**; Elorriaga & Muñoz 2010, Chamorro *et al.* 2017), ya que este se está aridificando. Esta hipótesis ha sido reforzada por varios estudios realizados tanto en Europa como en África (Thomas & Lennon 1999, Huntley *et al.* 2006, Maclean *et al.* 2008, Real *et al.* 2013, Massimino *et al.* 2015, Chamorro *et al.* 2017, Stiels *et al.* 2021). Las aves africanas observadas en Europa a lo largo de las últimas décadas se han detectado principalmente en la mitad sur de la Península Ibérica (López-Ramírez *et al.* 2024a). Por un lado, esto puede deberse a que es una de las zonas del sur de Europa con mayor favorabilidad climática para estas especies. De hecho, posee una favorabilidad climática similar a la que encontramos en el norte de África (**capítulos 2 y 3**). Por otro lado, es la región más próxima al norte de África (tan solo 14 km en su punto más estrecho) donde actualmente se encuentran las poblaciones de las diferentes especies africanas que están expandiendo sus áreas de distribución hacia mayores latitudes.

Es necesario tener en cuenta que los procesos de colonización suelen ser lentos (Donahue & Lee 2008), especialmente cuando las especies se enfrentan a barreras biogeográficas como, en este caso, el mar Mediterráneo (Correia *et al.* 2015). A pesar de ello, varias especies africanas han empezado a reproducirse recientemente en el sur de

Europa (Elorriaga & Muñoz 2010, Cabrera 2022, Navarrete 2022, Prieta 2022, Muñoz *et al.* 2025), por lo que parece que la expansión hacia el norte está ocurriendo más rápido de lo esperado. Un ejemplo de ello lo encontramos en uno de los taxones típicamente africanos estudiados en la presente tesis, el escribano sahariano (**capítulo 3**). En mayo de 2023, se predecía su reproducción en el sur de la Península Ibérica (López-Ramírez *et al.* 2023) y en agosto de ese mismo año se confirmó el primer registro de reproducción de la especie en el sur del continente europeo (Sepúlveda & Ortega 2023). Estos resultados indican que ya se está produciendo un cambio en la composición de aves en Europa sudoccidental debido al cambio climático, del mismo modo que Europa central está siendo ocupada por especies de aves típicamente mediterráneas (Knaus *et al.* 2018, Stiels *et al.* 2021). Si el clima continúa calentándose, cabe esperar que estas aves africanas sigan desplazándose hacia mayores latitudes en Europa, como así lo indican las proyecciones futuras (**capítulos 2 y 3**), y que nuevas especies africanas potencialmente colonizadoras lleguen al sur de Europa, con la posibilidad de que se produzca una *africanización* de la avifauna europea.

Al margen de los patrones generales de distribución, existen especies africanas que han comenzado a colonizar el sur de Europa, a pesar de que las condiciones climáticas de esta región no resultan favorables para su establecimiento como reproductoras, como es el caso del buitre de Rüppell o, aún más incipiente, el buitre dorsiblanco africano (**capítulo 4**). Estas dos especies pueden observarse en el sur de Europa, contando con pruebas documentadas de reproducción en el caso del buitre de Rüppell aunque, hasta el momento, siempre en parejas mixtas con el buitre leonado (Muñoz *et al.* 2024a). El creciente número de registros de estas especies en Europa meridional puede estar influido por el apoyo que supone para los individuos juveniles o inmaduros la migración hacia el norte de los buitres leonados. Estos resultados también ponen de manifiesto que no todos los casos de aves típicamente africanas que están expandiendo sus áreas de distribución hacia mayores latitudes son consecuencia del cambio climático, sino que hay otros factores que influyen en los procesos de colonización.

## 8.2 Aumento altitudinal y contracción del área de distribución en aves de montaña

Los efectos actuales del calentamiento climático también están afectando a las aves de montaña en España peninsular (**capítulos 5 y 6**). Los resultados de la presente tesis

demuestran que las poblaciones de collalba gris y gorrión alpino en esta región ocupan zonas más elevadas que a comienzos del siglo XXI. Estos desplazamientos altitudinales inducidos por el clima se han observado en especies de montaña de todo el mundo, permitiendo a las poblaciones alcanzar sus óptimos climáticos y escapar de las consecuencias negativas de un clima cada vez más cálido (Lenoir *et al.* 2008, Chen *et al.* 2009, Popy *et al.* 2010, Maggini *et al.* 2011, Reif & Flousek 2012, Auer & King 2014, Grytnes *et al.* 2014, Freeman *et al.* 2018). Tales desplazamientos inevitablemente ocasionan reducciones del área de distribución debido a las limitaciones de espacio a gran altitud (**capítulos 5 y 6**), incluso pudiéndose llegar a producir extinciones locales de algunas poblaciones en aquellos sistemas montañosos donde las especies ya están ocupando las zonas más elevadas, como anunciamos que podría ocurrir con la collalba gris en el Parque Nacional de la Sierra de las Nieves (**capítulo 5**). La reducción de la distribución reproductora de esta especie ha sido especialmente notable en la mitad sur de España (**capítulo 5**), una de las zonas del sur de Europa donde los efectos del calentamiento climático están siendo más pronunciados (IPCC 2022). Simultáneamente, algunas aves típicamente mediterráneas también se están desplazando hacia cotas más elevadas en esta zona, como es el caso de la cogujada montesina, la tarabilla común o la curruca tomillera (Zamora & Barea-Azcón 2015).

Los atlas de distribución son herramientas esenciales para el seguimiento y la gestión de las especies (Hagemeyer & Blair 1997, Martí & Del Moral 2003, Keller *et al.* 2020, Molina *et al.* 2022) y muchos estudios los emplean para analizar los efectos del cambio climático (Marjakangas *et al.* 2023), al igual que se ha hecho en los **capítulos 5 y 6** de la presente tesis. Sin embargo, los resultados del **capítulo 6** revelan que, a pesar de que el gorrión alpino ha reducido su distribución reproductora a lo largo de las dos últimas décadas en España peninsular, tal reducción está sobreestimada si se realiza una comparación directa entre los dos últimos atlas de aves de España (Martí & Del Moral 2003, Molina *et al.* 2022). Esto se debe principalmente a que las dificultades de muestreo son mayores para las especies que habitan regiones montañosas, debido a su lejanía, problemas de accesibilidad y dificultades del terreno (Chamberlain *et al.* 2012). Por este motivo, existen cuadrículas que quedan sin muestrear en la mayoría de los atlas de distribución (Molina *et al.* 2022), lo que puede dar lugar a una sobreestimación de los cambios (**capítulo 6**). Para evaluar con precisión el estado actual de estas especies y evitar sobreestimar el declive, es esencial aumentar los esfuerzos de seguimiento y muestreo en

estas zonas no muestreadas detectadas por los modelos de distribución como altamente favorables. La Sociedad Española de Ornitología (SEO/BirdLife) está desarrollando actualmente muestreos específicos para especies de alta montaña (<https://seo.org/censo-de-aves-de-alta-montana-2024/>), como es el caso del gorrión alpino, por lo que la identificación de estas regiones altamente favorables para la especie puede ayudar a orientar la selección de cuadrículas a muestrear.

### 8.3 Reducción de la distancia migratoria en aves típicamente transaharianas

El cambio climático también ha disminuido la severidad de los inviernos en las últimas décadas, haciéndolos cada vez más suaves, especialmente en el sur de Europa y el norte de África (Brunet *et al.* 2007, IPCC 2022). Este incremento de las temperaturas invernales está haciendo que algunas poblaciones de aves migradoras típicamente transaharianas reduzcan su distancia migratoria y permanezcan más próximas a sus zonas de reproducción durante el invierno (Gordo & Sanz 2006, Chamorro *et al.* 2019, Martín *et al.* 2019), convirtiendo así a parte de la población en presaharianas, como está empezando a ocurrir con el papamoscas gris en los últimos años (**capítulo 7**). Al tratarse de una especie insectívora, los inviernos más cálidos deben estar favoreciendo la abundancia y actividad de los invertebrados que componen su dieta (Ratte 1984, Roiz *et al.* 2014), proporcionando así un suministro de alimento constante a aquellos individuos de la especie que permanecen durante la época invernal al norte del desierto del Sahara. La mayor parte de los registros de invernada de la especie también se concentran en la mitad sur de la Península Ibérica, principalmente en las zonas costeras, al igual que ocurre con los registros de las aves africanas que están colonizando el continente europeo (**capítulos 2 y 3**). Esto puede deberse a que la mitad sur de la Península Ibérica, como ya se ha comentado anteriormente, es una de las zonas del sur de Europa donde los efectos del calentamiento climático están siendo más notables y, por lo tanto, una de las zonas europeas con los inviernos más suaves (IPCC 2022). También puede ser debido a que la Península Ibérica es una región de escala crucial para las poblaciones europeas de papamoscas grises durante su migración postnupcial (Hernández 2009). Si persisten las temperaturas suaves durante el invierno en los próximos años, es de esperar que un mayor número de migrantes insectívoros transaharianos acorten sus rutas migratorias, dando lugar a poblaciones más numerosas que invernen regularmente en el Paleártico Occidental, principalmente en las zonas costeras y los sistemas insulares de la Cuenca del

Mediterráneo, que son las zonas de invernada identificadas por los modelos como altamente favorables (**capítulo 7**). Esta tendencia ya se ha observado en otras especies insectívoras transaharianas como el carricero común (Nieto *et al.* 2018, Chamorro *et al.* 2019). A pesar de que la mayor parte de los registros de la especie se concentran en la Península Ibérica, es lógico pensar que este fenómeno es muy probable que también esté ocurriendo en otras zonas de Europa y norte de África donde el esfuerzo de muestreo es menor.

#### 8.4 Aspectos generales sobre los cambios en las áreas de distribución de las especies

Los desplazamientos latitudinales de aves típicamente africanas (**capítulos 2, 3 y 4**), los desplazamientos altitudinales de algunas aves de montaña (**capítulos 5 y 6**) y los cambios en los patrones de migración de aves insectívoras típicamente transaharianas (**capítulo 7**), aunque son relativamente recientes y requieren una investigación más profunda, ya están empezando a tener implicaciones ecológicas sobre los ecosistemas. Algunas de las aves africanas que han colonizado el sur de Europa se han integrado exitosamente en las comunidades locales y están produciendo cambios, aunque hasta el momento sutiles, en las mismas. Algunos de estos cambios son hibridaciones con congéneres europeos, como ya ha ocurrido entre el ratonero moro del Atlas y el ratonero común (*B. buteo buteo*) en la isla de Pantelleria, Italia (Corso 2009) y en el Estrecho de Gibraltar (Elorriaga & Muñoz 2013), así como entre el buitre de Rüppell y el buitre leonado (*G. fulvus*) en la provincia de Málaga (Muñoz *et al.* 2024a). Otros cambios podrían estar relacionados con cambios en las estructuras tróficas (Mendoza & Araujo 2022) o con la competencia (Jankowski *et al.* 2010). El reciente establecimiento del escribano sahariano en el sur de la Península Ibérica es muy probable que conlleve un reajuste y una redistribución de recursos con las especies residentes, como el gorrión común (*Passer domesticus*), al compartir el mismo entorno urbano. En este caso, seguramente no exista una fuerte competencia entre ambas especies, ya que el alimento no suele ser un factor limitante en estos ambientes (Stofberg *et al.* 2022). También podría tener otras implicaciones ecológicas, como la posible hibridación con el escribano montesino (*Emberiza cia*), aunque esto es menos probable que ocurra ya que, a pesar de ser especies taxonómicamente similares, poseen diferentes preferencias de hábitat (Muñoz *et al.* 2025). Del mismo modo, las aves de alta montaña también están sufriendo una competencia más intensa por parte de especies de menor altitud que están ocupando

nuevas zonas más elevadas (Jankowski *et al.* 2010). La competencia con las aves residentes o migradoras presaharianas también podría incrementarse en los próximos años si el número de migrantes transaharianos que permanecen durante el invierno en el Paleártico Occidental sigue aumentando.

En los diferentes capítulos de la presente tesis, se ha puesto de manifiesto que el clima es uno de los factores más importantes para explicar las distribuciones de las especies a grandes resoluciones de estudio, al igual que también lo han hecho otras investigaciones (Chamorro *et al.* 2017, Sun *et al.* 2020). Las oscilaciones e irregularidades del clima obligan a las especies a estar continuamente adaptándose o aclimatándose a las condiciones cambiantes del medio (Kirkpatrick & Barton 1997, Merilä & Hendry 2014). El actual cambio climático favorecido por la acción humana está ocurriendo a un ritmo muy rápido (Duarte *et al.* 2006, Barnett *et al.* 2015), haciendo que las especies no se encuentren en equilibrio con las nuevas condiciones climáticas que se están dando en algunas zonas de su área de distribución (Chamorro *et al.* 2020). Las especies son capaces de responder a tales cambios, pero no lo hacen de manera simultánea a los cambios climáticos, generándose así cierto desfase espacio-temporal entre sus distribuciones actuales y las zonas donde las nuevas condiciones climáticas son favorables para ellas (**capítulo 2**). De hecho, este desequilibrio climático es una de las principales fuerzas que impulsa a las especies a ocupar las zonas adyacentes favorables, promoviendo así cambios en sus distribuciones (Lomolino *et al.* 2006c, Chamorro *et al.* 2020). A diferencia de algunos métodos de modelación que asumen un equilibrio entre las distribuciones de las especies y su entorno (Guisan & Zimmermann 2000, Guisan & Thuiller 2005), lo que puede dificultar su aplicabilidad para analizar los efectos del cambio climático, los modelos de favorabilidad climática realizados en la presente tesis tienen en cuenta tal desequilibrio (**capítulos 2, 3, 4 y 7**). Estos modelos no representan necesariamente las distribuciones actuales de las especies ya que, al existir también un desequilibrio temporal entre el área de distribución real y potencial de las especies (Chamorro *et al.* 2020), son capaces de detectar las zonas climáticamente favorables para las mismas que aún permanecen desocupadas, anticipándose así a su distribución en un futuro próximo (López-Ramírez *et al.* 2023). Este es el motivo por el que la mayor parte de los modelos presentan una tasa de sobre-predicción elevada. El elevado potencial predictivo de los diferentes modelos permite crear el concepto de diversidad oscura (Pärtel *et al.* 2011), para recoger a aquellas especies que presentan áreas favorables desocupadas en una

región, bien porque aún no han alcanzado estas zonas, pero pueden hacerlo en un futuro próximo (**capítulos 2, 3, 4 y 7**) o bien porque actualmente han desaparecido (**capítulos 5 y 6**).

Las aves son uno de los grupos animales que más rápido responden a los cambios ambientales (Mekonen 2017), por lo que siempre que tengan la posibilidad se desplazarán hacia las nuevas zonas climáticamente favorables, aproximándose así al equilibrio climático comentado anteriormente y adaptándose a este planeta cambiante. Uno de los mejores ejemplos lo encontramos en las aves africanas que están colonizando Europa, las cuales son capaces de alcanzar las zonas climáticamente favorables del sur de este continente, a pesar de que tienen que superar importantes barreras geográficas como el mar Mediterráneo (**capítulos 2 y 3**) y, en algunos casos, también el desierto del Sahara (**capítulo 4**). El problema radica en aquellas especies que no disponen del margen suficiente para continuar desplazándose, como les ocurre a aquellas que habitan en latitudes elevadas próximas a los polos o en las cotas más altas de las montañas. En estos casos, las especies reducen sus áreas de distribución hasta el punto de poder llegar a producirse la extinción local de alguna de sus poblaciones (**capítulos 5 y 6**).

Los modelos de distribución realizados en la presente tesis, al estar basados en la función de favorabilidad (Real *et al.* 2006), son independientes de la prevalencia de los datos, representando así la manera en la que las especies responden únicamente a las condiciones ambientales de cada región (Acevedo & Real 2012). De esta manera, se obtienen modelos conmensurables, esenciales a la hora de realizar análisis comparativos de distribuciones (**capítulos 4, 5 y 6**) y combinar modelos aplicando operaciones derivadas de la lógica difusa (unión e intersección difusas; **capítulos 2 y 7**).

### 8.5 Futuras líneas de investigación

Los resultados proporcionados en la presente tesis doctoral nos permiten anticiparnos a los cambios espacio-temporales de distribución de las diferentes especies de aves estudiadas en el Paleártico Occidental, principalmente debidos a los efectos del calentamiento climático. Esta información proporciona una base sólida para orientar el seguimiento futuro de estas especies, dando prioridad a las zonas altamente favorables, y evaluar en qué medida se cumplen las predicciones de los modelos realizados en un contexto de cambio climático acelerado.

Aun así, tras los resultados obtenidos a partir de esta tesis, surgen nuevas oportunidades para continuar futuras investigaciones. En primer lugar, es importante continuar monitorizando la expansión hacia el norte de las especies de aves africanas estudiadas, así como de otras nuevas especies africanas potencialmente colonizadoras que lleguen al sur de Europa. Esto permitirá validar los resultados de los modelos realizados, corroborar las tendencias de estas especies frente al cambio climático y actualizar los modelos con los nuevos datos recopilados. También sería interesante estudiar el efecto del cambio climático sobre especies de aves típicamente mediterráneas que están ampliando sus áreas de distribución al norte peninsular y centro de Europa. Investigaciones más detalladas podrían implicar el uso de sistemas de seguimiento a distancia para monitorizar los movimientos de ejemplares concretos e incluso de poblaciones, si se abarata el coste de estos dispositivos. Esto permitiría desvelar ciertas incógnitas que actualmente existen con algunas de las especies estudiadas. Por ejemplo, si la población de collalbas grises de Sierra Nevada está actuando como una fuente de ejemplares para la población sumidero de Sierra de las Nieves; si la población cantábrica de gorrión alpino verdaderamente está más aislada del resto de poblaciones europeas; o si los papamoscas grises que permanecen durante el invierno en el Paleártico Occidental pasan a ser migrantes de corta distancia o sedentarios por pertenecer a poblaciones del centro o sur de Europa, respectivamente.

# CAPÍTULO 9

## Conclusiones

## 9. Conclusiones

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Las principales conclusiones obtenidas en esta tesis doctoral son las siguientes:

1. Las distribuciones en el Paleártico Occidental de las aves aquí estudiadas están sufriendo modificaciones tanto en el espacio como en el tiempo debido, en gran parte, a los efectos del actual cambio climático. El calentamiento climático está provocando cambios latitudinales y altitudinales en la distribución de estas aves, así como cambios en sus patrones de migración.
2. Todos estos cambios se detectan con especial intensidad en la mitad sur de la Península Ibérica, una de las zonas del sur de Europa donde los efectos del calentamiento climático están siendo más notables.
3. Los modelos de distribución utilizados han demostrado ser herramientas biogeográficas eficaces para describir las distribuciones de las especies, explicar sus condicionantes ambientales y predecir cambios futuros, identificando también aquellas zonas favorables actualmente desocupadas.
4. El sur de Europa dispone ya de zonas climáticamente favorables para el establecimiento de aves típicamente africanas. Estas zonas se localizan principalmente en la mitad sur de la Península Ibérica, el sur de Italia, Grecia, Turquía y grandes islas mediterráneas, como Baleares, Cerdeña, Sicilia, Creta y Chipre.
5. Las proyecciones climáticas, considerando diferentes escenarios de cambio, indican que la favorabilidad para el establecimiento de aves típicamente africanas aumentará hacia mayores latitudes en Europa Occidental, especialmente en la mitad norte de la Península Ibérica, el centro y norte de Francia y la mitad norte de Italia.
6. La proximidad geográfica y la similitud climática entre el norte de África y el sur de la Península Ibérica convierten a esta última en una puerta de entrada clave para especies africanas, como el escribano sahariano.

7. El cambio climático está favoreciendo la permeabilidad de barreras biogeográficas, como el mar Mediterráneo y el desierto del Sahara, al crear zonas climáticamente favorables en el sur de Europa que atraen a las aves africanas.
8. Los modelos de distribución basados en la función de favorabilidad combinados con análisis de baricentro permiten detectar el desequilibrio latitudinal entre las zonas actualmente ocupadas por aves africanas y las zonas climáticamente adecuadas para las mismas, cuantificando además la velocidad de estos desplazamientos, lo que supone un avance importante en el entendimiento de la respuesta de las especies al cambio climático.
9. No obstante, existen casos de rapaces africanas, como el buitre de Rüppell o el buitre dorsiblanco africano, que también están comenzando a colonizar el sur del continente europeo, a pesar de no ser regiones óptimas para su reproducción. El creciente número de registros de estas especies en Europa meridional puede estar influido por las relaciones sociales entre especies tan gregarias como los buitres.
10. Las poblaciones de dos especies de aves de montaña, la collalba gris y el gorrión alpino, han reducido sus distribuciones reproductoras y se han desplazado en altura en España peninsular desde principios del siglo XXI, especialmente en el caso de la collalba gris, que ocupa actualmente cotas unos 100 m más elevadas. La población del Parque Nacional de la Sierra de las Nieves aparece como la más vulnerable de España.
11. Las diferencias metodológicas y de esfuerzo de muestreo al comparar bases de datos de distintos periodos pueden conducir a errores en la estimación de las tendencias de distribución de una especie, como muestra el caso del gorrión alpino, donde dificultades en la realización de los muestreos pueden generar vacíos en zonas favorables. Para evaluar con mayor precisión el estado actual de estas especies y evitar sobreestimar el declive, se recomienda reforzar el seguimiento en estas zonas poco o nada muestreadas.

12. Algunas poblaciones de papamoscas gris están acortando sus migraciones e invernando regularmente en el Paleártico Occidental, favorecidas por inviernos más suaves y mayor disponibilidad de invertebrados. Las zonas más favorables para esta invernada se localizan en áreas costeras e insulares del Mediterráneo, aunque aún no están plenamente ocupadas. Por ello, se trata de zonas potenciales a ocupar por papamoscas y otros migrantes insectívoros transaharianos en los próximos inviernos si continúan los efectos del calentamiento climático.
13. La capacidad de combinar modelos mediante lógica difusa ofrece un marco comparativo robusto para analizar diferentes especies de forma integrada.
14. La información derivada de esta tesis permite anticiparse a los cambios espacio-temporales en la distribución de aves del Paleártico Occidental. Más allá de las aplicaciones directas en conservación, estos resultados proporcionan una base sólida para orientar el seguimiento futuro y evaluar la validez de las predicciones en un contexto de cambio climático acelerado.

# CAPÍTULO 10

## Referencias bibliográficas

## 10. Referencias bibliográficas

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- Acevedo, P., Jiménez-Valverde, A., Melo-Ferreira, J., Real, R. & Alves, P.C.** 2012. Parapatric species and the implications for climate change studies: A case study on hares in Europe. *Glob. Chang. Biol.* **18**: 1509–1519.
- Acevedo, P. & Real, R.** 2012. Favourability: concept, distinctive characteristics and potential usefulness. *Naturwissenschaften* **99**: 515–522.
- Adamík, P. & Král, M.** 2008. Climate and resource-driven long-term changes in dormice populations negatively affect hole-nesting songbirds. *J. Zool.* **275**: 209–215.
- AEMET & 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.
- Ahmadi, M., Nawaz, M.A., Asadi, H., Hemami, M., Naderi, M., Shafapourtehrany, M. & Shabani, F.** 2024. Protecting alpine biodiversity in the Middle East from climate change: Implications for high-elevation birds. *Divers. Distrib.* **30**: e13826.
- Al-Yaari, A., Condom, T., Junquas, C., Rabatel, A., Ramseyer, V., Sicart, J., Masiokas, M., Cauvy-Fraunié, S. & Dangles, O.** 2023. Climate variability and glacier evolution at selected sites across the world: Past trends and future projections. *Earth's Futur.* **11**: e2023EF003618.
- Algarra, J.A., Cariñanos, P., Herrero, J., Delgado-Capel, M., Ramos-Lorente, M.M. & Díaz de la Guardia, C.** 2019. Tracking Montane Mediterranean grasslands: Analysis of the effects of snow with other related hydro-meteorological variables and land-use change on pollen emissions. *Sci. Total Environ.* **649**: 889–901.
- Aliaga-Samanez, A., Real, R., Vermeer, J. & Olivero, J.** 2020. Modelling species distributions limited by geographical barriers: A case study with African and American primates. *Glob. Ecol. Biogeogr.* **29**: 444–453.
- Aliaga-Samanez, A., Cobos-Mayo, M., Real, R., Segura, M., Romero, D., Fa, J.E. & Olivero, J.** 2021. Worldwide dynamic biogeography of zoonotic and anthroponotic dengue. *PLoS Negl. Trop. Dis.* **15**: e0009496.
- Aliaga-Samanez, A., Real, R., Segura, M., Marfil-Daza, C. & Olivero, J.** 2022. Yellow fever surveillance suggests zoonotic and anthroponotic emergent potential. *Commun. Biol.* **5**: 1–12.
- Aligaz, M.A., Bekele, A. & Bogale, B.A.** 2024. Predicting climate change impact on the habitat of Ethiopia's spot-breasted lapwing using ensemble model. *Glob. Ecol. Conserv.* **54**: e03139.

- Alves, J.A., Gunnarsson, T.G., Hayhow, D.B., Appleton, G.F., Potts, P.M., Sutherland, W.J. & Gill, J.A. 2013. Costs, benefits, and fitness consequences of different migratory strategies. *Ecology* **94**: 11–17.
- Amano, T., Lamming, J.D.L. & Sutherland, W.J. 2016. Spatial gaps in global biodiversity information and the role of citizen science. *Bioscience* **66**: 393–400.
- Ambrosini, R., Rubolini, D., Møller, A.P., Bani, L., Clark, J., Karcza, Z., Vangeluwe, D., du Feu, C., Spina, F. & Saino, N. 2011. Climate change and the long-term northward shift in the African wintering range of the barn swallow *Hirundo rustica*. *Clim. Res.* **49**: 131–141.
- Anderle, M., Brambilla, M., Angelini, L., Guariento, E., Panizza, C., Plunger, J., Seeber, J., Stifter, S., Tappeiner, U., Tasser, E. & Hilpold, A. 2024. Efficiency of birds as bioindicators for other taxa in mountain farmlands. *Ecol. Indic.* **158**: 111569.
- Antor, R.J. 1995. The importance of arthropod fallout on snow patches for the foraging of high-alpine birds. *J. Avian Biol.* **26**: 81–85.
- Antúnez, A. & Mendoza, M. 1992. Factores que determinan el área de distribución geográfica de las especies: conceptos, modelos y métodos de análisis. In: *Objetivos y Métodos Biogeográficos. Aplicaciones en Herpetología. Monografías de Herpetología* (J. M. Vargas, R. Real, & A. Antúnez, eds), pp. 51–72. Asociación Herpetológica Española, Valencia.
- Arizaga, J., Díez, E., Aranguren, I., Asenjo, I., Cuadrado, J.F., Elozegi, Z., Goikoetxea, J., Herrero, A., Jauregi, J.I., Mendiburu, A. & Sánchez, J.M. 2012. Wintering survival of insect-eating passerines in southern Europe. *Bird Study* **59**: 37–42.
- Arrhenius, S. 1896. On the influence of carbonic acid in the air upon the temperature of the ground. *London, Edinburgh, Dublin Philos. Mag. J. Sci.* **41**: 237–276.
- Arrondo, E., Sebastián-González, E., Moleón, M., Morales-Reyes, Z., María Gil-Sánchez, J., Cortés-Avizanda, A., Ceballos, O., Donázar, J.A. & Sánchez-Zapata, J.A. 2023. Vulture culture: dietary specialization of an obligate scavenger. *Proc. R. Soc. B Biol. Sci.* **290**: 20221951.
- Askeyev, O., Askeyev, A., Askeyev, I. & Sparks, T. 2023. Significantly earlier spring migration in most bird species at the eastern limit of Europe. *Animals* **13**: 3031.
- Asse, D., Chuine, I., Vitasse, Y., Yoccoz, N.G., Delpierre, N., Badeau, V., Delestrade, A. & Randin, C.F. 2018. Warmer winters reduce the advance of tree spring phenology induced by warmer springs in the Alps. *Agric. For. Meteorol.* **252**: 220–230.

- Auer, S.K. & King, D.I.** 2014. Ecological and life-history traits explain recent boundary shifts in elevation and latitude of western North American songbirds. *Glob. 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.
- Balbontín, J., Negro, J.J., Sarasola, J.H., Ferrero, J.J. & Rivera, D.** 2008. Land-use changes may explain the recent range expansion of the Black-shouldered Kite *Elanus caeruleus* in southern Europe. *Ibis (Lond. 1859)*. **150**: 707–716.
- Barbosa, A., Merino, S., Benzal, J., Martínez, J. & 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. & Vargas, J.M.** 2010. Use of Coarse-resolution models of species' distributions to guide local conservation inferences. *Conserv. Biol.* **24**: 1378–1387.
- Barbosa, A.M. & Real, R.** 2012. Applying fuzzy logic to comparative distribution modelling: A case study with two sympatric amphibians. *Sci. World J.* **2012**: 428206.
- Barbosa, A.M., Pautasso, M. & Figueiredo, D.** 2013a. Species-people correlations and the need to account for survey effort in biodiversity analyses. *Divers. Distrib.* **19**: 1188–1197.
- Barbosa, A.M., Real, R., Muñoz, A.-R. & Brown, J.A.** 2013b. New measures for assessing model equilibrium and prediction mismatch in species distribution models. *Divers. Distrib.* **19**: 1333–1338.
- Barnes, R. & Sahr, K.** 2017. Discrete global grids for R. – R package ver. 2.0.4.
- Barnett, J., Evans, L.S., Gross, C., Kiem, A.S., Kingsford, R.T., Palutikof, J.P., Pickering, C.M. & Smithers, S.G.** 2015. From barriers to limits to climate change adaptation: Path dependency and the speed of change. *Ecol. Soc.* **20**: 5.
- Barras, A.G., Marti, S., Ettlin, S., Vignali, S., Resano-Mayor, J., Braunisch, V. & Arlettaz, R.** 2020. The importance of seasonal environmental factors in the foraging habitat selection of Alpine Ring Ouzels *Turdus torquatus alpestris*. *Ibis (Lond. 1859)*. **162**: 505–519.
- Barras, A.G., Braunisch, V. & 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.
- Barrientos, R.** 2022. Camachuelo trompetero, *Bucanetes githagineus*. In: *III Atlas de las aves en época de reproducción en España* (B. Molina, A. Nebreda, A. R. Muñoz, J. Seoane, R. Real, J. Bustamante, & J. C. del Moral, eds). SEO/BirdLife, Madrid. <https://atlasaves.seo.org/ave/camachuelo-trompetero/>

- Basha, S.M., Rajput, D.S. & Vandhan, V.** 2018. Impact of Gradient ascent and Boosting algorithm in classification. *Int. J. Intell. Eng. Syst.* **11**: 41–49.
- Bastianelli, G., Tavecchia, G., Meléndez, L., Seoane, J., Obeso, J.R. & Laiolo, P.** 2017. Surviving at high elevations: An inter- and intra-specific analysis in a mountain bird community. *Oecologia* **184**: 293–303.
- Bay, R.A., Harrigan, R.J., Underwood, V. Le, Gibbs, H.L., Smith, T.B. & Ruegg, K.** 2018. Genomic signals of selection predict climate-driven population declines in a migratory bird. *Science (80-. ).* **359**: 83–86.
- Beans, C.M., Kilkenny, F.F. & Galloway, L.F.** 2012. Climate suitability and human influences combined explain the range expansion of an invasive horticultural plant. *Biol. Invasions* **14**: 2067–2078.
- Beaumont, L.J., Hughes, L. & Pitman, A.J.** 2008. Why is the choice of future climate scenarios for species distribution modelling important?. *Ecol. Lett.* **11**: 1135–1146.
- Beebee, T.J.C.** 1995. Amphibian breeding and climate. *Nature* **374**: 219–220.
- Bellard, C., Bertelsmeier, C., Leadley, P., Thuiller, W. & Courchamp, F.** 2012. Impacts of climate change on the future of biodiversity. *Ecol. Lett.* **15**: 365–377.
- Benedetti, Y. & Morelli, F.** 2024. Global distribution range of birds is negatively correlated with their level of diet specialization. *J. Biogeogr.* **51**: 2062–2069.
- Benito, B., Lorite, J. & Peñas, J.** 2011. Simulating potential effects of climatic warming on altitudinal patterns of key species in Mediterranean-alpine ecosystems. *Clim. Change* **108**: 471–483.
- Benjamini, Y. & 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. & Yekutieli, D.** 2001. The control of the false discovery rate in multiple testing under dependency. *Ann. Stat.* **29**: 1165–1188.
- Benjumea, R., Astrain, C., Istúriz, A., Oria, P., Ibarrola, I. & Delgado, M.D.M.** 2024. Weather conditions at different spatial and temporal scales influence avian post-breeding migration patterns on route. *J. Zool.* **323**: 305–316.
- Berkeley Earth.** 2025. Global temperature report for 2024. <https://berkeleyearth.org/global-temperature-report-for-2024/>
- Bernis, F.** 1983. Migration of the common Griffon Vulture in the Western Palearctic. In: *Vulture biology and management* (S. R. Wilbur & J. A. Jackson, eds), pp. 185–196. Berkeley, University of California.
- Berthold, P.** 1988. Evolutionary aspects of migratory behavior in European warblers. *J. Evol. Biol.* **1**: 195–209.

- Berthold, P.** 1991. Genetic control of migratory behaviour in birds. *Trends Ecol. Evol.* **6**: 254–257.
- Berthold, P.** 2001. *Bird migration: A general survey*. Oxford University Press, Oxford.
- Berthold, P. & Querner, U.** 1981. Genetic basis of migratory behavior in European warblers. *Science (80-. )*. **212**: 77–79.
- Berthold, P. & Helbig, A.J.** 1992. The genetics of bird migration: Stimulus, timing, and direction. *Ibis (Lond. 1859)*. **134**: 35–40.
- Berthold, P. & Querner, U.** 1995. Microevolutionary aspects of bird migration based on experimental results. *Isr. J. Zool.* **41**: 377–385.
- Berthold, P., Helbig, A.J., Mohr, G. & Querner, U.** 1992. Rapid microevolution of migratory behaviour in a wild bird species. *Nature* **360**: 668–670.
- Bettega, C., Fernández-González, Á., Ramón Obeso, J. & Delgado, M.D.M.** 2020. Circannual variation in habitat use of the White-winged Snowfinch *Montifringilla nivalis nivalis*. *Ibis (Lond. 1859)*. **162**: 1251–1261.
- Billerman, S.M., Keeney, B.K., Rodewald, P.G. & Schulenberg, T.S.** 2022. *Birds of the World*. Cornell Laboratory of Ornithology, Ithaca, NY, USA.
- BirdLife International.** 2021. *European Red List of Birds*. Publications Office of the European Union, Luxembourg.
- Blois, J.L., Zarnetske, P.L., Fitzpatrick, M.C. & Finnegan, S.** 2013. Climate change and the past, present, and future of biotic interactions. *Science (80-. )*. **341**: 499–504.
- Böhning-Gaese, K. & Lemoine, N.** 2004. Importance of climate change for the ranges, communities and conservation of birds. *Adv. Ecol. Res.* **35**: 211–236.
- Bonnot, T.W., Thompson, F.R., Millspaugh, J.J. & 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. & Drapeau, P.** 1992. Partialling out the spatial component of ecological variation. *Ecology* **73**: 1045–1055.
- Borzée, A., Andersen, D., Groffen, J., Kim, H.-T., Bae, Y. & Jang, Y.** 2019. Climate change-based models predict range shifts in the distribution of the only Asian plethodontid salamander: *Karsenia koreana*. *Sci. Rep.* **9**: 11838.
- Both, C. & Visser, M.E.** 2001. Adjustment to climate change is constrained by arrival date in a long-distance migrant bird. *Nature* **411**: 296–298.
- Bowler, D.E., Heldbjerg, H., Fox, A.D., de Jong, M. & Böhning-Gaese, K.** 2019. Long-term declines of European insectivorous bird populations and potential causes. *Conserv. Biol.* **33**: 1120–1130.

- Bozó, L. & Csörgő, T.** 2024. Causes of vagrancy of North Asian passerines in western Europe. *Ibis (Lond. 1859)*. **166**: 5–22.
- Brambilla, M., Pedrini, P., Rolando, A. & Chamberlain, D.E.** 2016. Climate change will increase the potential conflict between skiing and high-elevation bird species in the Alps. *J. Biogeogr.* **43**: 2299–2309.
- Brambilla, M., Caprio, E., Assandri, G., Scridel, D., Bassi, E., Bionda, R., Celada, C., Falco, R., Bogliani, G., Pedrini, P., Rolando, A. & Chamberlain, D.** 2017a. A spatially explicit definition of conservation priorities according to population resistance and resilience, species importance and level of threat in a changing climate. *Divers. Distrib.* **23**: 727–738.
- Brambilla, M., Cortesi, M., Capelli, F., Chamberlain, D., Pedrini, P. & Rubolini, D.** 2017b. Foraging habitat selection by Alpine White-winged Snowfinches *Montifringilla nivalis* during the nestling rearing period. *J. Ornithol.* **158**: 277–286.
- Brambilla, M., Resano-Mayor, J., Scridel, D., Anderle, M., Bogliani, G., Braunisch, V., Capelli, F., Cortesi, M., Horrenberger, N., Pedrini, P., Sangalli, B., Chamberlain, D., Arlettaz, R. & Rubolini, D.** 2018. Past and future impact of climate change on foraging habitat suitability in a high-alpine bird species: Management options to buffer against global warming effects. *Biol. Conserv.* **221**: 209–218.
- Brambilla, M., Gustin, M., Cento, M., Ilahiane, L. & Celada, C.** 2020a. Habitat, climate, topography and management differently affect occurrence in declining avian species: Implications for conservation in changing environments. *Sci. Total Environ.* **742**: 140663.
- Brambilla, M., Resano-Mayor, J., Arlettaz, R., Bettega, C., Binggeli, A., Bogliani, G., Braunisch, V., Celada, C., Chamberlain, D., Carricaburu, J.C., Delgado, M.D.M., Fontanilles, P., Kmecl, P., Korner, F., Lindner, R., Pedrini, P., Pöhacker, J., Rubinič, B., Schano, C., Scridel, D., Strinella, E., Teufelbauer, N. & De Gabriel Hernando, M.** 2020b. Potential distribution of a climate sensitive species, the White-winged Snowfinch *Montifringilla nivalis* in Europe. *Bird Conserv. Int.* **30**: 522–532.
- Brambilla, M., Rubolini, D., Appukuttan, O., Calvi, G., Karger, D.N., Kmecl, P., Mihelič, T., Sattler, T., Seaman, B., Teufelbauer, N., Wahl, J. & Celada, C.** 2022. Identifying climate refugia for high-elevation Alpine birds under current climate warming predictions. *Glob. Chang. Biol.* **28**: 4276–4291.
- Brook, B.W., Sodhi, N.S. & Bradshaw, C.J.A.** 2008. Synergies among extinction drivers under global change. *Trends Ecol. Evol.* **23**: 453–460.
- Brown, J.H. & Gibson, A.C.** 1983. *Biogeography*. Mosby, St. Louis, Missouri, USA.
- Brown, J.H.** 1984. On the relationship between abundance and distribution of species. *Am. Nat.* **124**: 255–279.

- Brown, J.H., Mehlman, D.W. & Stevens, G.C.** 1995. Spatial variation in abundance. *Ecology* **76**: 2028–2043.
- Brunet, M., Jones, P.D., Sigró, J., Saladié, O., Aguilar, E., Moberg, A., Della-Marta, P.M., Lister, D., Walther, A. & López, D.** 2007. Temporal and spatial temperature variability and change over Spain during 1850–2005. *J. Geophys. Res. Atmos.* **112**: 1–28.
- Brunetti, M., Lentini, G., Maugeri, M., Nanni, T., Auer, I., Böhm, R. & Schöner, W.** 2009. Climate variability and change in the Greater Alpine Region over the last two centuries based on multi-variable analysis. *Int. J. Climatol.* **29**: 2197–2225.
- Bussière, E.M.S., Underhill, L.G. & Altwegg, R.** 2015. Patterns of bird migration phenology in South Africa suggest northern hemisphere climate as the most consistent driver of change. *Glob. Chang. Biol.* **21**: 2179–2190.
- Cabrera, M.** 2022. Corredor sahariano, *Cursorius cursor*. In: *III Atlas de las aves en época de reproducción en España* (B. Molina, A. Nebreda, A. R. Muñoz, J. Seoane, R. Real, J. Bustamante, & J. C. del Moral, eds). SEO/BirdLife, Madrid. <https://atlasaves.seo.org/ave/corredor-sahariano/>
- Calleja, J.A. & Pérez-Granados, C.** 2022. Collalba gris, *Oenanthe oenanthe*. In: *III Atlas de las aves en época de reproducción en España* (B. Molina, A. Nebreda, A. R. Muñoz, J. Seoane, R. Real, J. Bustamante, & J. C. Del Moral, eds). SEO/BirdLife, Madrid. <https://atlasaves.seo.org/ave/collalba-gris/>
- Campbell, M. & Botha, A.** 2018. A clear and present danger: Impacts of poisoning on a vulture population and the effect of poison response activities. *Oryx* **52**: 552–558.
- Capel, J.J.** 1981. *Los climas de España*. Oikos-Tau SA Ediciones, Barcelona.
- Carranza, S., Harris, D.J., Arnold, E.N., Batista, V. & Gonzalez de la Vega, J.P.** 2006. Phylogeography of the lacertid lizard, *Psammodromus algirus*, in Iberia and across the Strait of Gibraltar. *J. Biogeogr.* **33**: 1279–1288.
- Carvalho, S.B., Brito, J.C., Crespo, E.G., Watts, M.E. & Possingham, H.P.** 2011. Conservation planning under climate change: Toward accounting for uncertainty in predicted species distributions to increase confidence in conservation investments in space and time. *Biol. Conserv.* **144**: 2020–2030.
- Case, T.J. & Taper, M.L.** 2000. Interspecific competition, environmental gradients, gene flow, and the coevolution of species' borders. *Am. Nat.* **155**: 583–605.
- Castro, A., Muñoz, A.-R. & 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. & Zbinden, N.** 2012. The altitudinal frontier in avian climate impact research. *Ibis (Lond. 1859)*. **154**: 205–209.

- Chamberlain, D.E., Negro, M., Caprio, E. & 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. & Girardello, M.** 2016. Identifying key conservation threats to Alpine birds through expert knowledge. *PeerJ* **4**: e1723.
- Chamorro, D., Olivero, J., Real, R. & Muñoz, A.-R.** 2016. El cambio del clima y la barrera biogeográfica del estrecho de Gibraltar para las aves africanas. In: *Avances en biogeografía. Áreas de distribución: entre puentes y barreras* (J. Gómez Zotano, J. Arias García, J. A. Olmedo Cobo, & J. L. Serrano Montes, eds), pp. 172–180. Tundra Ediciones, Almenara (Castellón, Spain).
- Chamorro, D., Olivero, J., Real, R. & Muñoz, A.-R.** 2017. Environmental factors determining the establishment of the African Long-legged Buzzard *Buteo rufinus cirtensis* in Western Europe. *Ibis (Lond. 1859)*. **159**: 331–342.
- Chamorro, D., Nieto, I., Real, R. & Muñoz, A.-R.** 2019. Wintering areas on the move in the face of warmer winters. *Ornis Fenn.* **96**: 41–54.
- Chamorro, D., Real, R. & Muñoz, A.-R.** 2020. Fuzzy sets allow gaging the extent and rate of species range shift due to climate change. *Sci. Rep.* **10**: 16272.
- Chamorro, D., Martínez-Freiría, F., Real, R. & Muñoz, A.-R.** 2021. Understanding parapatry: How do environment and competitive interactions shape Iberian vipers' distributions? *J. Biogeogr.* **48**: 1322–1335.
- Charmantier, A., McCleery, R.H., Cole, L.R., Perrins, C., Kruuk, L.E.B. & Sheldon, B.C.** 2008. Adaptive phenotypic plasticity in response to climate change in a wild bird population. *Science (80- )*. **320**: 800–803.
- Charmantier, A. & Gienapp, P.** 2014. Climate change and timing of avian breeding and migration: Evolutionary versus plastic changes. *Evol. Appl.* **7**: 15–28.
- Chedad, A., Bendjoudi, D., Beladis, I., Guezoul, O. & Chenchouni, H.** 2021. A comprehensive monograph on the ecology and distribution of the House Bunting (*Emberiza sahari*) in Algeria. *Front. Biogeogr.* **13**: e47727.
- Chen, I.-C., Shiu, H.-J., Benedick, S., Holloway, J.D., Chey, V.K., Barlow, H.S., Hill, J.K. & Thomas, C.D.** 2009. Elevation increases in moth assemblages over 42 years on a tropical mountain. *Proc. Natl. Acad. Sci. U. S. A.* **106**: 1479–1483.
- Chen, I.-C., Hill, J.K., Ohlemüller, R., Roy, D.B. & Thomas, C.D.** 2011. Rapid range shifts of species associated with high levels of climate warming. *Science (80- )*. **333**: 1024–1026.
- Cheviron, Z.A. & Brumfield, R.T.** 2012. Genomic insights into adaptation to high-altitude environments. *Heredity (Edinb)*. **108**: 354–361.

- Chu, J.J., Gillis, D.P. & Riskin, S.H.** 2022. Community science reveals links between migration arrival timing advance, migration distance and wing shape. *J. Anim. Ecol.* **91**: 1651–1665.
- Chuine, I., Morin, X. & Bugmann, H.** 2010. Warming, photoperiods, and tree phenology. *Science (80-. )*. **329**: 277–278.
- Climate Change - NASA Science.** 2024. <https://science.nasa.gov/climate-change/>. Date accessed: 27-11-2024.
- Cohen, J.** 1960. A coefficient of agreement for nominal scales. *Educ. Psychol. Meas.* **20**: 37–46.
- Coll, J.R., Aguilar, E. & Ashcroft, L.** 2017. Drought variability and change across the Iberian Peninsula. *Theor. Appl. Climatol.* **130**: 901–916.
- Collins, W.J., Bellouin, N., Doutriaux-Boucher, M., Gedney, N., Halloran, P., Hinton, T., Hughes, J., Jones, C.D., Joshi, M., Liddicoat, S., Martin, G., O&apos;Connor, F., Rae, J., Senior, C., Sitch, S., Totterdell, I., Wiltshire, A. & Woodward, S.** 2011. Development and evaluation of an Earth-System model – HadGEM2. *Geosci. Model Dev.* **4**: 1051–1075.
- Conklin, J.R., Lisovski, S. & Battley, P.F.** 2021. Advancement in long-distance bird migration through individual plasticity in departure. *Nat. Commun.* **12**: 4780.
- Copete, J.L., Lorenzo, J.A., Amengual, E., Bigas, D., Fernández, P., López-Velasco, D., Rodríguez, G. & García-Tarrasón, M.** 2015. Observaciones de aves raras en España, 2012 y 2013. *Ardeola* **62**: 453–508.
- Coppack, T., Pulido, F., Czisch, M., Auer, D.P. & Berthold, P.** 2003. Photoperiodic response may facilitate adaptation to climatic change in long-distance migratory birds. *Proc. R. Soc. London. Ser. B Biol. Sci.* **270**: S43–S46.
- Correia, R.A., Franco, A.M.A. & Palmeirim, J.M.** 2015. Role of the mediterranean sea in differentiating European and North African woodland bird assemblages. *Community Ecol.* **16**: 106–114.
- Corso, A.** 2009. Successful mixed breeding of Atlas Long-legged Buzzard and Common Buzzard on Pantelleria, Italy, in 2008. *Dutch Bird* **31**: 224–226.
- Cortés-Avizanda, A., Jovani, R., Carrete, M. & Donazar, J.A.** 2012. Resource unpredictability promotes species diversity and coexistence in an avian scavenger guild: A field experiment. *Ecology* **93**: 2570–2579.
- Cortés-Avizanda, A., Jovani, R., Donazar, J.A. & Grimm, V.** 2014. Bird sky networks: How do avian scavengers use social information to find carrion? *Ecology* **95**: 1799–1808.
- Cotton, P.A.** 2003. Avian migration phenology and global climate change. *Proc. Natl. Acad. Sci. U. S. A.* **100**: 12219–12222.

- Cox, C.B., Moore, P.D. & Ladle, R.J.** 2016. *Biogeography: An Ecological and Evolutionary Approach*. Wiley-Blackwell, Oxford.
- Cramp, S. & Simmons, K.E.L.** 1983. *Handbook of the Birds of Europe, the Middle East and North Africa. The Birds of the Western Palearctic. Vol III. Waders to Gulls*. Oxford University Press, Oxford.
- Cramp, S. & Perrins, C.M.** 1994. *Handbook of the Birds of Europe, the Middle East and North Africa: The Birds of the Western Palearctic. Volume VIII: Crows to Finches*. Oxford University Press, Oxford.
- Crawford, R., Tree, A., Whittington, P., Visagie, J., Upfold, L., Roxburg, K., Martin, A. & Dyer, B.** 2008. Recent distributional changes of seabirds in South Africa: Is climate having an impact? *African J. Mar. Sci.* **30**: 189–193.
- Croll, J.** 1864. On the physical cause of the change of climate during geological epochs. *Philos. Mag.* **28**: 121–137.
- Dale, V.R., Bolton, M., Dornelas, M., Magurran, A.E., Dennis, R., Broad, R., Riddiford, N.J., Harvey, P. V., Riddington, R., Shaw, D.N., Parnaby, D. & Reid, J.M.** 2024. Among-species variation in six decades of changing migration timings explained through ecology, life-history and local migratory abundance. *Glob. Chang. Biol.* **30**: e17400.
- Darlington, P.J.** 1957. *Zoogeography: The geographical distribution of animals*. John Wiley & Sons, Inc., New York.
- Darwin, C.R.** 1859. *On the origin of species by means of Natural Selection, or the preservation of favoured races in the struggle for life*. John Murray, London, UK.
- de Gabriel Hernando, M., Fernández-Gil, J., Roa, I., Juan, J., Ortega, F., de la Calzada, F. & Revilla, E.** 2021. Warming threatens habitat suitability and breeding occupancy of rear-edge alpine bird specialists. *Ecography (Cop.)*. **44**: 1191–1204.
- de Gabriel Hernando, M., Roa, I., Fernández-Gil, J., Juan, J., Fuertes, B., Reguera, B. & Revilla, E.** 2022. Trends in weather conditions favor generalist over specialist species in rear-edge alpine bird communities. *Ecosphere* **13**: e3953.
- de Jong, P., Tanajura, C.A.S., Sánchez, A.S., Dargaville, R., Kiperstok, A. & Torres, E.A.** 2018. Hydroelectric production from Brazil's São Francisco River could cease due to climate change and inter-annual variability. *Sci. Total Environ.* **634**: 1540–1553.
- De Juana, E. & Comité Ibérico de Rarezas de la Sociedad Española de Ornitología (SEO).** 1994. Observaciones homologadas de aves raras en España y Portugal. Informe de 1992. *Ardeola* **41**: 103–117.
- De Juana, E. & Comité de Rarezas de la Sociedad Española de Ornitología (SEO).** 1997. Observaciones de aves raras en España, año 1995. *Ardeola* **44**: 119–141.

- De Juana, E.** 2006. Escribano sahariano, *Emberiza sahari*. In: *Aves raras de España: Un catálogo de las especies de presentación ocasional*, p. 285. Lynx Edicions, Barcelona, Spain.
- de Zwaan, D.R., Drake, A., Greenwood, J.L. & Martin, K.** 2020. Timing and intensity of weather events shape nestling development strategies in three alpine breeding songbirds. *Front. Ecol. Evol.* **8**: 570034.
- de Zwaan, D.R., Scridel, D., Altamirano, T.A., Gokhale, P., Kumar, R.S., Sevillano-Ríos, S., Barras, A.G., Arredondo-Amezcu, L., Asefa, A., Carrillo, R.A., Green, K., Gutiérrez-Chávez, C.A., Lehtikoinen, A., Li, S., Lin, R.S., Norment, C.J., Oswald, K.N., Romanov, A.A., Salvador, J., Weston, K.A. & Martin, K.** 2022. GABB: A global dataset of alpine breeding birds and their ecological traits. *Sci. Data* **9**: 627.
- Defila, C. & Clot, B.** 2005. Phytophenological trends in the Swiss Alps, 1951–2002. *Meteorol. Zeitschrift* **14**: 191–196.
- Del Junco, O. & González, B.** 1969. La nueva especie de vencejo en el Paleártico: *Apus caffer*. *Ardeola* **13**: 115–127.
- DeMars, C.A., Gilbert, S., Serrouya, R., Kelly, A.P., Larter, N.C., Hervieux, D. & Boutin, S.** 2021. Demographic responses of a threatened, low-density ungulate to annual variation in meteorological and phenological conditions. *PLoS One* **16**: e0258136.
- DERA.** 2013. *Datos Espaciales de Referencia de Andalucía*. Instituto de Estadística y Cartografía de Andalucía, Consejería de Economía y Conocimiento.
- Dessler, A.E.** 2021. *Introduction to Modern Climate Change*, Third edit. Cambridge University Press, Cambridge, UK.
- Di Marco, M. & Santini, L.** 2015. Human pressures predict species' geographic range size better than biological traits. *Glob. Chang. Biol.* **21**: 2169–2178.
- Dies, J.I., Lorenzo Gutiérrez, J.A., Gutiérrez, R., García, E., Gorospe Rombouts, G., Martí-Aledo, J., Gutiérrez, P., Vidal, C., Sales, S. & López Velasco, D.** 2010. Observaciones de aves raras en España, 2008. *Ardeola* **57**: 481–516.
- Dies, J.I., Lorenzo, J.A., Gutiérrez, R., García, E., Gorospe, G., Martí-Aledo, J., Gutiérrez, P., Vidal, C., Sales, S. & López Velasco, D.** 2011. Observaciones de aves raras en España, 2009. *Ardeola* **58**: 441–480.
- Dimitrijević, M.S.** 2020. Milutin Milanković and climate changes leading to ice ages. *ChemTexts* **6**: 23.
- Diniz-Filho, J.A.F., Mauricio Bini, L., Fernando Rangel, T., Loyola, R.D., Hof, C., Nogués-Bravo, D. & Araújo, M.B.** 2009. Partitioning and mapping uncertainties in ensembles of forecasts of species turnover under climate change. *Ecography (Cop.)*. **32**: 897–906.

- Dirnböck, T., Essl, F. & Rabitsch, W.** 2011. Disproportional risk for habitat loss of high-altitude endemic species under climate change. *Glob. Chang. Biol.* **17**: 990–996.
- Doadrio, I.** 2001. *Atlas y Libro Rojo de los Peces Continentales de España*. Ministerio de Medio Ambiente-CSIC, Madrid.
- Donahue, M.J. & Lee, C.T.** 2008. Colonization. In: *Encyclopedia of Ecology* (S. E. Jorgensen & B. Fath, eds), pp. 672–678. Elsevier.
- Donázar, J.A. & Fernández, C.** 1990. Population trends of the Griffon Vulture *Gyps fulvus* in Northern Spain between 1969 and 1989 in relation to conservation measures. *Biol. Conserv.* **53**: 83–91.
- Donázar, J.A.** 1993. *Los Buitres Ibéricos: Biología y Conservación* (J. M. Reyero, ed). Madrid, Spain.
- Dormann, C.F., Purschke, O., Márquez, J.R.G., Lautenbach, S. & Schröder, B.** 2008. Components of uncertainty in species distribution analysis: A case study of the great grey shrike. *Ecology* **89**: 3371–3386.
- Drobinski, P., Da Silva, N., Bastin, S., Mailler, S., Muller, C., Ahrens, B., Christensen, O.B. & Lionello, P.** 2020. How warmer and drier will the Mediterranean region be at the end of the twenty-first century? *Reg. Environ. Chang.* **20**: 78.
- Du, L., Zeng, Y., Ma, L., Qiao, C., Wu, H., Su, Z. & Bao, G.** 2021. Effects of anthropogenic revegetation on the water and carbon cycles of a desert steppe ecosystem. *Agric. For. Meteorol.* **300**: 108339.
- Duarte, C.M., Alonso, S., Benito, G., Dachs, J., Montes, C., Pardo, M., Ríos, A.F., Simó, R. & Valladares, F.** 2006. *Cambio global. Impacto de la actividad humana sobre el sistema tierra*. Consejo Superior de Investigaciones Científicas (CSIC), Madrid.
- Duckworth, R.A. & Badyaev, A.V.** 2007. Coupling of dispersal and aggression facilitates the rapid range expansion of a passerine bird. *Proc. Natl. Acad. Sci.* **104**: 15017–15022.
- Dufour, P., Lees, A.C., Gilroy, J. & Crochet, P.-A.** 2024. The overlooked importance of vagrancy in ecology and evolution. *Trends Ecol. Evol.* **39**: 19–22.
- Dunn, E.H., Hussell, D.J.T., Kren, J. & Zoerb, A.C.** 2022. Northern Wheatear (*Oenanthe oenanthe*). In: *Birds of the World* (P. G. Rodewald & B. K. Keeney, eds). Cornell Lab of Ornithology, Ithaca, NY, USA.
- EEA.** 2012. *Climate change, impacts and vulnerability in Europe*. European Environment Agency, Copenhagen.

- Efrat, R., Hatzofe, O. & Nathan, R.** 2019. Landscape-dependent time versus energy optimizations in pelicans migrating through a large ecological barrier. *Funct. Ecol.* **33**: 2161–2171.
- El Khamlichi, R., Iglesias-Lebrija, J.J., Amhaouch, Z., Rousselon, K. & Álvarez, E.** 2022. First African white-backed vulture (*Gyps africanus*) tagged with GPS transmitter in North Africa and first record in Algeria. *Go-South Bull.* **19**: 23–28.
- Eldredge, N.** 1995. *Reinventing Darwin: Great Evolutionary Debate*. Weidenfeld & Nicolson, London, UK.
- Elith, J., Leathwick, J.R. & Hastie, T.** 2008. A working guide to boosted regression trees. *J. Anim. Ecol.* **77**: 802–813.
- Elith, J. & Leathwick, J.R.** 2009. Species distribution models: Ecological explanation and prediction across space and time. *Annu. Rev. Ecol. Evol. Syst.* **40**: 677–697.
- Elorriaga, J. & Muñoz, A.-R.** 2010. First breeding record of North African Long-legged Buzzard *Buteo rufinus cirtensis* in continental Europe. *Br. Birds* **103**: 399–401.
- Elorriaga, J. & Muñoz, A.-R.** 2013. Hybridisation between the Common Buzzard *Buteo buteo buteo* and the North African race of Long-legged Buzzard *Buteo rufinus cirtensis* in the Strait of Gibraltar: prelude or preclude to colonisation? *Ostrich* **84**: 41–45.
- Elósegui Aldasoro, J.** 1985. *Navarra. Atlas de aves nidificantes (1982-1984)*. Caja de Ahorros de Navarra.
- Elsen, P.R. & Tingley, M.W.** 2015. Global mountain topography and the fate of montane species under climate change. *Nat. Clim. Chang.* **5**: 772–776.
- England, M.D.** 1963. Observations on the Black-winged Kite in Portugal with preliminary notes on its status. *Br. Birds* **56**: 444–452.
- Engler, J.O., Stiels, D., Schidelko, K., Strubbe, D., Quillfeldt, P. & Brambilla, M.** 2017. Avian SDMs: Current state, challenges, and opportunities. *J. Avian Biol.* **48**: 1483–1504.
- Engler, R., Randin, C.F., Thuiller, W., Dullinger, S., Zimmermann, N.E., Araújo, M.B., Pearman, P.B., Le Lay, G., Piedallu, C., Albert, C.H., Choler, P., Coldea, G., De Lamo, X., Dirnböck, T., Gégout, J.C., Gómez-García, D., Grytnes, J.A., Heegaard, E., Høistad, F., Nogués-Bravo, D., Normand, S., Puşcaş, M., Sebastià, M.T., Stanisci, A., Theurillat, J.P., Trivedi, M.R., Vittoz, P. & Guisan, A.** 2011. 21st century climate change threatens mountain flora unequally across Europe. *Glob. Chang. Biol.* **17**: 2330–2341.
- 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, Lisboa.

- Espinosa, D., Aguilar, C. & Escalante, T.** 2001. Endemismo, áreas de endemismo y regionalización biogeográfica. In: *Introducción a la Biogeografía en Latinoamérica: Teorías, Conceptos, Métodos y Aplicaciones* (J. Llorente-Bousquets & J. J. Morrone, eds), pp. 31–37. Las Prensas de Ciencias, Facultad de Ciencias, UNAM, México, D.F.
- ESRI.** 2016. ArcGIS [software GIS]. Version 10.4.1.
- Essl, F., Staudinger, M., Stöhr, O., Schratt-Ehrendorfer, L., Rabitsch, W. & Niklfeld, H.** 2009. Distribution patterns, range size and niche breadth of Austrian endemic plants. *Biol. Conserv.* **142**: 2547–2558.
- Estrada, A., Real, R. & Vargas, J.M.** 2008. Using crisp and fuzzy modelling to identify favourability hotspots useful to perform gap analysis. *Biodivers. Conserv.* **17**: 857–871.
- Estrada, A., Delgado, M.P., Arroyo, B., Traba, J. & Morales, M.B.** 2016. Forecasting large-scale habitat suitability of European bustards under climate change: The role of environmental and geographic variables. *PLoS One* **11**: 1–17.
- Estrada, A. & Real, R.** 2021. A stepwise assessment of parsimony and fuzzy entropy in species distribution modelling. *Entropy* **23**: 1014.
- Estrada, J., Pedrocchi, V., Brotons, L. & Herrando, S.** 2004. *Atles dels ocells nidificants de Catalunya 1999-2002*. Institut Català d'Ornitologia (ICO)/Lynx Edicions, Barcelona.
- Evans, P.R. & Lathbury, G.W.** 1973. Raptor migration across the Straits of Gibraltar. *Ibis (Lond. 1859)*. **115**: 572–585.
- Fa, J.E., Olivero, J., Farfán, M.Á., Márquez, A.L., Vargas, J.M., Real, R. & Nasi, R.** 2014. Integrating sustainable hunting in biodiversity protection in central Africa: Hot spots, weak spots, and strong spots. *PLoS One* **9**: e112367.
- Farr, T.G. & Kobrick, M.** 2000. Shuttle radar topography mission produces a wealth of data. *Eos, Trans. Am. Geophys. Union* **81**: 583–585.
- Feldman, M.J., Imbeau, L., Marchand, P., Mazerolle, M.J., Darveau, M. & Fenton, N.J.** 2021. Trends and gaps in the use of citizen science derived data as input for species distribution models: A quantitative review. *PLoS One* **16**: e0234587.
- Ferrero, J.J.** 1996. Situación del Elanio azul (*Elanus caeruleus*) en el Mediterráneo. In: *Biología y Conservación de las Rapaces Mediterráneas* (J. Muntaner & J. Mayol, eds), pp. 101–115. SEO/BirdLife, Madrid.

- Ficetola, G.F., Marta, S., Guerrieri, A., Cantera, I., Bonin, A., Cauvy-Fraunié, S., Ambrosini, R., Caccianiga, M., Anthelme, F., Azzoni, R.S., Almond, P., Alviz Gazitúa, P., Ceballos Lievano, J.L., Chand, P., Chand Sharma, M., Clague, J.J., Cochachín Rapre, J.A., Compostella, C., Encarnación, R.C., Dangles, O., Deline, P., Eger, A., Erokhin, S., Franzetti, A., Gielly, L., Gili, F., Gobbi, M., Hågvar, S., Kaufmann, R., Khedim, N., Meneses, R.I., Morales-Martínez, M.A., Peyre, G., Pittino, F., Proietto, A., Rabatel, A., Sieron, K., Tielidze, L., Urseitova, N., Yang, Y., Zaginaev, V., Zerboni, A., Zimmer, A., Diolaiuti, G.A., Taberlet, P., Poulenard, J., Fontaneto, D., Thuiller, W. & Carteron, A. 2024.** The development of terrestrial ecosystems emerging after glacier retreat. *Nature* **632**: 336–342.
- Fiedler, W. 2003.** Recent changes in migratory behaviour of birds: A compilation of field observations and ringing data. In: *Avian Migration* (P. Berthold, E. Gwinner, & E. Sonnenschein, eds), pp. 21–38. Springer, Heidelberg, Berlin.
- Fielding, A.H. & Bell, J.F. 1997.** A review of methods for the assessment of prediction errors in conservation presence/absence models. *Environ. Conserv.* **24**: 38–49.
- Filippi-Codaccioni, O., Moussus, J.-P., Urcun, J.-P. & Jiguet, F. 2011.** Advanced autumn migration of the Common Crane *Grus grus* over Western Pyrenean passes. *Acta Ornithol.* **46**: 37–45.
- Fischer, T. 1902.** The Iberian Peninsula. In: *The international geography* (H. R. Mill, ed), pp. 368–385. D. Appleton and Company, Ithaca, NY, USA.
- Flack, A., Nagy, M., Fiedler, W., Couzin, I.D. & Wikelski, M. 2018.** From local collective behavior to global migratory patterns in white storks. *Science (80- )*. **360**: 911–914.
- Fletcher, K., Howarth, D., Kirby, A., Dunn, R. & Smith, A. 2013.** Effect of climate change on breeding phenology, clutch size and chick survival of an upland bird. *Ibis (Lond. 1859)*. **155**: 456–463.
- Flousek, J., Telenský, T., Hanzelka, J. & 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, Madrid.
- Font, I. 2000.** *Climatología de España y Portugal*. Universidad de Salamanca, Salamanca.
- Foote, E. 1856.** Circumstances affecting the heat of the sun's rays. *Am. J. Sci. Arts* **22**: 382.
- Forstmeier, W. 2002.** Benefits of early arrival at breeding grounds vary between males. *J. Anim. Ecol.* **71**: 1–9.

- Fourier, J.** 1824. Remarques générales sur les températures du globe terrestre et des espaces planétaires. *Ann. Chemie Phys.* **27**: 136–167.
- Freeman, B.G., Scholer, M.N., Ruiz-Gutierrez, V. & Fitzpatrick, J.W.** 2018. Climate change causes upslope shifts and mountaintop extirpations in a tropical bird community. *Proc. Natl. Acad. Sci. U. S. A.* **115**: 11982–11987.
- Gaggiotti, O.E., Jones, F., Lee, W.M., Amos, W., Harwood, J. & Nichols, R.A.** 2002. Patterns of colonization in a metapopulation of grey seals. *Nature* **416**: 424–427.
- 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.
- Gantenbein, B. & Largiadèr, C.R.** 2003. The phylogeographic importance of the Strait of Gibraltar as a gene flow barrier in terrestrial arthropods: a case study with the scorpion *Buthus occitanus* as model organism. *Mol. Phylogenet. Evol.* **28**: 119–130.
- García-Carrasco, J.-M., Muñoz, A.-R., Olivero, J., Segura, M. & Real, R.** 2021. Predicting the spatio-temporal spread of West Nile virus in Europe. *PLoS Negl. Trop. Dis.* **15**: e0009022.
- García-Carrasco, J.M., Muñoz, A.R., Olivero, J., Segura, M. & Real, R.** 2022. Mapping the risk for West Nile virus transmission, Africa. *Emerg. Infect. Dis.* **28**: 777–785.
- García-Carrasco, J.M., Muñoz, A.R., Olivero, J., Segura, M., García-Bocanegra, I. & Real, R.** 2023a. West Nile virus in the Iberian Peninsula: Using equine cases to identify high-risk areas for humans. *Eurosurveillance* **28**: 2200844.
- García-Carrasco, J.-M., Muñoz, A.R., Olivero, J., Segura, M. & Real, R.** 2023b. An African West Nile virus risk map for travellers and clinicians. *Travel Med. Infect. Dis.* **52**: 102529.
- García-Carrasco, J.-M., Souviron-Priego, L., Muñoz, A.-R., Olivero, J., Fa, J.E. & Real, R.** 2024. Present and future situation of West Nile virus in the Afro-Palaeartic pathogeographic system. *Arch. Anesthesiol. Crit. Care* **4**: 527–534.
- García-Navas, V., Sattler, T., Schmid, H. & Ozgul, A.** 2020. Temporal homogenization of functional and beta diversity in bird communities of the Swiss Alps. *Divers. Distrib.* **26**: 900–911.
- García, L.V.** 2003. Controlling the false discovery rate in ecological research. *Trends Ecol. Evol.* **18**: 553–554.
- Gauch, H.G.** 1982. *Multivariate Analysis in Community Ecology*. Cambridge University Press, Cambridge.
- Gervais, C.R., Champion, C. & Pecl, G.T.** 2021. Species on the move around the Australian coastline: A continental-scale review of climate-driven species redistribution in marine systems. *Glob. Chang. Biol.* **27**: 3200–3217.

- Gil-López, M.J., Segarra-Moragues, J.G., Casimiro-Soriguer, R. & Ojeda, F.** 2022. From the Strait of Gibraltar to northern Europe: Pleistocene refugia and biogeographic history of heather (*Calluna vulgaris*, Ericaceae). *Bot. J. Linn. Soc.* **198**: 41–56.
- Gil-Velasco, M., Rouco, M., Ferrer, J., García-Tarrasón, M., García-Vargas, F.J., Gutiérrez, A., Hevia, R., López, F., López-Velasco, D., Ollé, À., Rodríguez, G., Sagardía, J. & Salazar, J.A.** 2017. Observaciones de aves raras en España, 2014. *Ardeola* **64**: 161–235.
- Gil-Velasco, M., Rouco, M., García-Tarrasón, M., García-Vargas, F.J., Hevia, R., Illa, M., López, F., López-Velasco, D., Ollé, À., Rodríguez, G., Rodríguez, M. & Sagardía, J.** 2019. Observaciones de aves raras en España, 2017. *Ardeola* **66**: 169–204.
- Gil, J.A. & Pérez, C.** 2018. Distribución, hábitat y población reproductora del gorrión alpino (*Montifringilla Nivalis*) en el Pirineo Central (Aragón-España). *Pirineos* **173**: e039.
- Gil, J.A.** 2022. Gorrión alpino, *Montifringilla nivalis*. In: *III Atlas de las aves en época de reproducción en España* (B. Molina, A. Nebreda, A. R. Muñoz, J. Seoane, R. Real, J. Bustamante, & J. C. del Moral, eds). SEO/BirdLife, Madrid. <https://atlasaves.seo.org/ave/gorrión-alpino/>
- Glasmachers, T. & Igel, C.** 2010. Maximum likelihood model selection for 1-norm soft margin svms with multiple parameters. *IEEE Trans. Pattern Anal. Mach. Intell.* **32**: 1522–1528.
- Gobiet, A., Kotlarski, S., Beniston, M., Heinrich, G., Rajczak, J. & Stoffel, M.** 2014. 21st century climate change in the European Alps-A review. *Sci. Total Environ.* **493**: 1138–1151.
- Goded, M., Ursul, G., Baz, A. & Wilson, R.J.** 2024. Changes to butterfly phenology versus elevation range after four decades of warming in the mountains of central Spain. *J. Insect Conserv.* **28**: 935–949.
- Gómez-García, D., Aguirre de Juana, Á.J., Jiménez Sánchez, R. & Manrique Magallón, C.** 2023. Shrub encroachment in Mediterranean mountain grasslands: Rate and consequences on plant diversity and forage availability. *J. Veg. Sci.* **34**: e13174.
- González-Hernández, A., Nieto-Lugilde, D., Peñas, J. & Alba-Sánchez, F.** 2021. Lean pattern in an altitude range shift of a tree species: *Abies pinsapo boiss.* *Forests* **12**: 1451.
- González-Oreja, J.A.** 2003. Aplicación de análisis multivariantes al estudio de las relaciones entre las aves y sus hábitats: Un ejemplo con paseriformes montanos no forestales. *Ardeola* **50**: 47–58.

- Goosse, H.** 2015. *Climate System Dynamics and Modelling*. Cambridge University Press, Cambridge.
- Gordo, O. & Sanz, J.J.** 2006. Climate change and bird phenology: A long-term study in the Iberian Peninsula. *Glob. Chang. Biol.* **12**: 1993–2004.
- Gordo, O.** 2007. Why are bird migration dates shifting? A review of weather and climate effects on avian migratory phenology. *Clim. Res.* **35**: 37–58.
- Gouveia, S.F., Rubalcaba, J.G., Soukhovolsky, V., Tarasova, O., Barbosa, A.M. & Real, R.** 2020. Ecophysics reload—exploring applications of theoretical physics in macroecology. *Ecol. Modell.* **424**: 109032.
- Grangé, J.-L.** 2008. Biologie de reproduction de la Niverolle Alpine *Montifringilla nivalis* dans les Pyrénées occidentales françaises. *Nos Oiseaux* **55**: 67–82.
- Green, R.E., Donázar, J.A., Sánchez-Zapata, J.A. & Margalida, A.** 2016. Potential threat to Eurasian griffon vultures in Spain from veterinary use of the drug diclofenac. *J. Appl. Ecol.* **53**: 993–1003.
- Gregory, R.D. & van Strien, A.** 2010. Wild bird indicators: Using composite population trends of birds as measures of environmental health. *Ornithol. Sci.* **9**: 3–22.
- Grinnell, J.** 1922. The role of the ‘Accidental’. *Auk* **39**: 373–380.
- Griesinger, J.** 1996. Autumn migration of Griffon Vultures *Gyps fulvus* in Spain. In: *Biología y Conservación de las Rapaces Mediterráneas* (J. Muntaner & J. Mayol, eds), pp. 401–410. SEO/BirdLife, Madrid.
- Groves, C.R., Game, E.T., Anderson, M.G., Cross, M., Enquist, C., Ferdaña, Z., Girvetz, E., Gondor, A., Hall, K.R., Higgins, J., Marshall, R., Popper, K., Schill, S. & Shafer, S.L.** 2012. Incorporating climate change into systematic conservation planning. *Biodivers. Conserv.* **21**: 1651–1671.
- Grytnes, J.-A., Kapfer, J., Jurasinski, G., Birks, H.H., Henriksen, H., Klanderud, K., Odland, A., Ohlson, M., Wipf, S. & Birks, H.J.B.** 2014. Identifying the driving factors behind observed elevational range shifts on European mountains. *Glob. Ecol. Biogeogr.* **23**: 876–884.
- Guisan, A. & Zimmermann, N.E.** 2000. Predictive habitat distribution models in ecology. *Ecol. Modell.* **135**: 147–186.
- Guisan, A. & Thuiller, W.** 2005. Predicting species distribution: Offering more than simple habitat models. *Ecol. Lett.* **8**: 993–1009.
- Günther, A.** 1858. On the geographical distribution of reptiles. *Proc. Zool. Soc. London* **26**: 373–398.
- Gwinner, E.** 1996. Circadian and circannual programmes in avian migration. *J. Exp. Biol.* **199**: 39–48.

- Hagemeijer, W.J.M. & Blair, M.J.** 1997. *The EBCC Atlas of European Breeding Birds: Their Distribution and Abundance*. T & A D Poyser, London.
- Hahn, S., Bauer, S. & Liechti, F.** 2009. The natural link between Europe and Africa - 2.1 billion birds on migration. *Oikos* **118**: 624–626.
- Hällfors, M.H., Heikkinen, R.K., Kuussaari, M., Lehikoinen, A., Luoto, M., Pöyry, J., Virkkala, R., Saastamoinen, M. & Kujala, H.** 2024. Recent range shifts of moths, butterflies, and birds are driven by the breadth of their climatic niche. *Evol. Lett.* **8**: 89–100.
- Hallman, T.A., Guélat, J., Antoniazza, S., Kéry, M. & Sattler, T.** 2022. Rapid elevational shifts of Switzerland's avifauna and associated species traits. *Ecosphere* **13**: e4194.
- Hannah, L., Midgley, G.F. & Millar, D.** 2002. Climate change-integrated conservation strategies. *Glob. Ecol. Biogeogr.* **11**: 485–495.
- Hannah, L.** 2011. Climate change, connectivity, and conservation success. *Conserv. Biol.* **25**: 1139–1142.
- Harley, C.D.G.** 2011. Climate change, keystone predation, and biodiversity loss. *Science (80- )*. **334**: 1124–1127.
- Harris, J.B.C., Dwi Putra, D., Gregory, S.D., Brook, B.W., Prawiradilaga, D.M., Sodhi, N.S., Wei, D. & 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 Biol. Sci.* **375**: 20190106.
- Hays, J.D., Imbrie, J. & Shackleton, N.J.** 1976. Variations in the Earth's Orbit: Pacemaker of the Ice Ages. *Science (80- )*. **194**: 1121–1132.
- Helm, B., Van Doren, B.M., Hoffmann, D. & Hoffmann, U.** 2019. Evolutionary response to climate change in migratory Pied Flycatchers. *Curr. Biol.* **29**: 3714–3719.
- Hengeveld, R.** 1992. *Dynamic biogeography*. Cambridge University Press, Cambridge.
- Hernández, Á.** 2009. Summer-autumn feeding ecology of Pied Flycatchers *Ficedula hypoleuca* and Spotted Flycatchers *Muscicapa striata*: The importance of frugivory in a stopover area in north-west Iberia. *Bird Conserv. Int.* **19**: 224–238.
- Hickling, R., Roy, D.B., Hill, J.K., Fox, R. & Thomas, C.D.** 2006. The distributions of a wide range of taxonomic groups are expanding polewards. *Glob. Chang. Biol.* **12**: 450–455.

- Hijmans, R.J., Cameron, S.E., Parra, J.L., Jones, P.G. & Jarvis, A.** 2005. Very high resolution interpolated climate surfaces for global land areas. *Int. J. Climatol.* **25**: 1965–1978.
- Hijmans, R.J. & Graham, C.H.** 2006. The ability of climate envelope models to predict the effect of climate change on species distributions. *Glob. Chang. Biol.* **12**: 2272–2281.
- Hitch, A.T. & Leberg, P.L.** 2007. Breeding distributions of North American bird species moving north as a result of climate change. *Conserv. Biol.* **21**: 534–539.
- Hockey, P.A.R., Sirami, C., Ridley, A.R., Midgley, G.F. & Babiker, H.A.** 2011. Interrogating recent range changes in South African birds: Confounding signals from land use and climate change present a challenge for attribution. *Divers. Distrib.* **17**: 254–261.
- Hof, A.R. & Allen, A.M.** 2019. An uncertain future for the endemic Galliformes of the Caucasus. *Sci. Total Environ.* **651**: 725–735.
- Hoffmann, A.A. & Blows, M.W.** 1994. Species borders: Ecological and evolutionary perspectives. *Trends Ecol. Evol.* **9**: 223–227.
- Holt, B.G., Lessard, J.-P., Borregaard, M.K., Fritz, S.A., Araújo, M.B., Dimitrov, D., Fabre, P.-H., Graham, C.H., Graves, G.R., Jönsson, K.A., Nogués-Bravo, D., Wang, Z., Whittaker, R.J., Fjeldså, J. & Rahbek, C.** 2013. An update of Wallace's zoogeographic regions of the world. *Science (80- )*. **339**: 74–78.
- Holt, R.D. & Keitt, T.H.** 2000. Alternative causes for range limits: A metapopulation perspective. *Ecol. Lett.* **3**: 41–47.
- Holt, R.D.** 2003. On the evolutionary ecology of species' ranges. *Evol. Ecol. Res.* **5**: 159–178.
- Holt, R.D. & Keitt, T.H.** 2005. Species' borders: A unifying theme in ecology. *Oikos* **108**: 3–6.
- Horton, K.G., Morris, S.R., Van Doren, B.M. & Covino, K.M.** 2023. Six decades of North American bird banding records reveal plasticity in migration phenology. *J. Anim. Ecol.* **92**: 738–750.
- Hosmer, D.W. & Lemeshow, S.** 1980. Goodness of fit tests for the multiple logistic regression model. *Commun. Stat. - Theory Methods* **9**: 1043–4069.
- Hosmer, D.W. & Lemeshow, S.** 1989. *Applied Logistic Regression*. John Wiley & Sons, Inc., New York.
- Hosmer, D.W. & Lemeshow, S.** 2005. Assessing the fit of the model. In: *Applied Logistic Regression*, pp. 143–202. John Wiley & Sons, Inc., New York.

- Huntley, B., Collingham, Y.C., Green, R.E., Hilton, G.M., Rahbek, C. & Willis, S.G.** 2006. Potential impacts of climatic change upon geographical distributions of birds. *Ibis (Lond. 1859)*. **148**: 8–28.
- Huntley, B., Green, R.E., Collingham, Y.C. & Willis, S.G.** 2007. *A climatic atlas of European breeding birds*. Durham University, RSPB and Lynx, Barcelona.
- Huntley, B., Collingham, Y.C., Willis, S.G. & Green, R.E.** 2008. Potential impacts of climatic change on European breeding birds. *PLoS One* **3**: e1439.
- I.G.N.** 1999. *Mapa de carreteras. Península Ibérica, Baleares y Canarias*. Instituto Geográfico Nacional/Ministerio de Fomento, Madrid.
- 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.** 2013. Glosario. In: *Cambio Climático 2013. Bases físicas. Contribución del Grupo de trabajo I al Quinto Informe de Evaluación del Grupo Intergubernamental de Expertos sobre el Cambio Climático* (T. F. Stocker, D. Qin, G.-K. Plattner, M. Tignor, S. K. Allen, J. Boschung, A. Nauels, Y. Xia, V. Bex, & P. M. Midgley, eds). Cambridge University Press, Cambridge, UK and New York, USA.
- 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* (H.-O. Pörtner, D. C. Roberts, M. Tignor, E. S. Poloczanska, K. Mintenbeck, A. Alegría, et al. eds). Cambridge University Press, Cambridge, UK and New York, USA.
- Issa, N. & Muller, Y.** 2015. *Atlas des oiseaux de France métropolitaine: Nidification et présence hivernale*. Delachaux et Niestlé, Paris.
- Iverson, A.R., Schaefer, J.L.B., Skalos, S.M. & Hawkins, C.E.** 2023. Global positioning system (GPS) and platform transmitter terminal (PTT) tags reveal fine-scale migratory movements of small birds: A review highlights further opportunities for hypothesis-driven research. *Ornithol. Appl.* **125**: 1–16.
- Jaafar, H.H. & Sujud, L.H.** 2024. High-resolution satellite imagery reveals a recent accelerating rate of increase in land evapotranspiration. *Remote Sens. Environ.* **315**: 114489.
- Jackson, A.L., Ruxton, G.D. & Houston, D.C.** 2008. The effect of social facilitation on foraging success in vultures: A modelling study. *Biol. Lett.* **4**: 311–313.
- Janc, A., Dambrine, C., Lambert, P., Lassalle, G., Lepage, M., Lobry, J., Pierre, M., Kristiansen, T., Butenschön, M. & Cabral, H.N.** 2024. Fish distribution shifts due to climate change in the Northeast Atlantic: Using a hierarchical filtering approach on marine-estuarine opportunist species. *Estuar. Coast. Shelf Sci.* **310**: 109013.

- Jankowski, J.E., Robinson, S.K. & Levey, D.J.** 2010. Squeezed at the top: Interspecific aggression may constrain elevational ranges in tropical birds. *Ecology* **91**: 1877–1884.
- Janzen, F.J.** 1994. Climate change and temperature-dependent sex determination in reptiles. *Proc. Natl. Acad. Sci. U. S. A.* **91**: 7487–7490.
- Jary, Z. & Marks, L.** 2024. Quaternary History. In: *Landscapes and Landforms of Poland. World Geomorphological Landscapes* (P. Migoń & K. Jancewicz, eds), pp. 19–31. Springer, Cham.
- Jenni, L. & Kéry, M.** 2003. Timing of autumn bird migration under climate change: Advances in long-distance migrants, delays in short-distance migrants. *Proc. R. Soc. B Biol. Sci.* **270**: 1467–1471.
- Jetz, W., Wilcove, D.S. & Dobson, A.P.** 2007. Projected impacts of climate and land-use change on the global diversity of birds. *PLoS Biol.* **5**: e157.
- Joger, U., Fritz, U., Guicking, D., Kalyabina-Hauf, S., Nagy, Z.T. & Wink, M.** 2007. Phylogeography of western Palaearctic reptiles - Spatial and temporal speciation patterns. *Zool. Anz.* **246**: 293–313.
- Johnston, A., Hochachka, W.M., Strimas-Mackey, M.E., Ruiz Gutierrez, V., Robinson, O.J., Miller, E.T., Auer, T., Kelling, S.T. & Fink, D.** 2021. Analytical guidelines to increase the value of community science data: An example using eBird data to estimate species distributions. *Divers. Distrib.* **27**: 1265–1277.
- Jones, M.C. & Cheung, W.W.L.** 2018. Using fuzzy logic to determine the vulnerability of marine species to climate change. *Glob. Chang. Biol.* **24**: e719–e731.
- Jørgensen, P.S., Böhning-Gaese, K., Thorup, K., Tøttrup, A.P., Chylarecki, P., Jiguet, F., Lehikoinen, A., Noble, D.G., Reif, J., Schmid, H., van Turnhout, C., Burfield, I.J., Foppen, R., Voříšek, P., van Strien, A., Gregory, R.D. & Rahbek, C.** 2016. Continent-scale global change attribution in European birds - Combining annual and decadal time scales. *Glob. Chang. Biol.* **22**: 530–543.
- Karl, T.R. & Trenberth, K.E.** 2003. Modern global climate change. *Science (80-)*. **302**: 1719–1723.
- Ke, C., Gong, L.-X., Geng, Y., Wang, Z.-Q., Zhang, W.-J., Feng, J. & Jiang, T.-L.** 2024. Patterns and correlates of potential range shifts of bat species in China in the context of climate change. *Conserv. Biol.* **39**: e14310.
- Kebede Kassaw, A.-A., Melese Yilma, T., Sebastian, Y., Yeneneh Birhanu, A., Sharew Melaku, M. & Surur Jemal, S.** 2023. Spatial distribution and machine learning prediction of sexually transmitted infections and associated factors among sexually active men and women in Ethiopia, evidence from EDHS 2016. *BMC Infect. Dis.* **23**: 49.

- Keller, V., Herrando, S., Voříšek, P., Franch, M., Kipson, M., Milanesi, P., Martí, D., Anton, M., Klvaňová, A., Kalyakin, M.V., Bauer, H.-G. & Foppen, R.P.B.** 2020. *European Breeding Bird Atlas 2: Distribution, Abundance and Change*. European Bird Census Council & Lynx Edicions, Barcelona.
- Kemp, A.C., Christie, D., Kirwan, G.M. & Sharpe, C.** 2020a. Rüppell's Griffon (*Gyps rueppelli*), version 1.0. In: *Birds of the World* (J. del Hoyo, A. Elliott, J. Sargatal, D. Christie, & E. de Juana, eds). Cornell Lab of Ornithology, Ithaca, NY, USA.
- Kemp, A.C., Christie, D., Kirwan, G.M., Garcia, E. & Sharpe, C.** 2020b. White-backed Vulture (*Gyps africanus*), version 1.0. In: *Birds of the World* (J. del Hoyo, A. Elliott, J. Sargatal, D. Christie, & E. de Juana, eds). Cornell Lab of Ornithology, Ithaca, NY, USA.
- Kilzer, R., Willi, G. & Kilzer, G.** 2011. *Atlas der Brutvögel Vorarlbergs*. Bucher, Hohenems.
- Kirkpatrick, M. & Barton, N.H.** 1997. Evolution of a species' range. *Am. Nat.* **150**: 1–23.
- Kleespies, M.W., Friedrich, T., Marg, O., Völker, C. & Schiwy, S.** 2024. Assessing the unseen consequences: Influence of an extreme weather event on environmental perceptions and connection to nature. *Environ. Sci. Eur.* **36**: 122.
- Knaus, P., Antoniazza, S., Wechsler, S., Guélat, J., Kéry, M., Strebel, N. & Sattler, T.** 2018. *Swiss Breeding Bird Atlas 2013–2016. Distribution and population trends of birds in Switzerland and Liechtenstein*. Swiss Ornithological Institute, Sempach, Switzerland.
- Kokko, H.** 1999. Competition for early arrival in migratory birds. *J. Anim. Ecol.* **68**: 940–950.
- Körner, C. & Ohsawa, M.** 2006. Mountain Systems. In: *Ecosystems and human well-being: Current state and trends* (R. Hassan, R. Scholes, & N. Ash, eds), pp. 681–716. Island Press, Washington, DC.
- Körner, C.** 2007. The use of 'altitude' in ecological research. *Trends Ecol. Evol.* **22**: 569–574.
- Kortessalmi, P., Pääkkönen, S., Valkonen, J.K. & Nokelainen, O.** 2023. Bean Goose migration shows a long-term temporal shift to earlier spring, but not to later autumn migration in Finland. *Ornis Fenn.* **100**: 61–68.
- Kropf, M., Kadereit, J.W. & Comes, H.P.** 2003. Differential cycles of range contraction and expansion in European high mountain plants during the Late Quaternary: Insights from *Pritzelago alpina* (L.) O. Kuntze (Brassicaceae). *Mol. Ecol.* **12**: 931–949.

- Kunnasranta, M., Miettinen, E., Melin, M., Meller, A., Väänänen, V.M., Huitu, O. & Holmala, K.** 2024. The performance of alternative GPS tracking devices: A case report on wild boars (*Sus scrofa*). *Anim. Biotelemetry* **12**: 27.
- La Marca, W., Elith, J., Firth, R.S.C., Murphy, B.P., Regan, T.J., Woinarski, J.C.Z. & Nicholson, E.** 2019. The influence of data source and species distribution modelling method on spatial conservation priorities. *Divers. Distrib.* **25**: 1060–1073.
- La Sorte, F.A. & Jetz, W.** 2010. Projected range contractions of montane biodiversity under global warming. *Proc. R. Soc. B Biol. Sci.* **277**: 3401–3410.
- Ladle, R.J. & Whittaker, R.J.** 2011. *Conservation Biogeography*. Blackwell Publishing Ltd, Oxford.
- Lazo-Cancino, D., Rivera, R., Paulsen-Cortez, K., González-Berríos, N., Rodríguez-Gutiérrez, R. & Rodríguez-Serrano, E.** 2020. The impacts of climate change on the habitat distribution of the vulnerable Patagonian-Fuegian species *Ctenomys magellanicus* (Rodentia, Ctenomyidae). *J. Arid Environ.* **173**: 104016.
- Lees, A.C. & Gilroy, J.J.** 2021. *Vagrancy in Birds*. Helm, London.
- Legendre, P.** 1993. Spatial autocorrelation: Trouble or new paradigm? *Ecology* **74**: 1659–1673.
- Legendre, P. & Legendre, L.** 1998. *Numerical Ecology*, Second Eng. Elsevier, Amsterdam.
- Lehikoinen, A. & Jaatinen, K.** 2012. Delayed autumn migration in northern European waterfowl. *J. Ornithol.* **153**: 563–570.
- Lehikoinen, A., Green, M., Husby, M., Kålås, J.A. & Lindström, Å.** 2014. Common montane birds are declining in northern Europe. *J. Avian Biol.* **45**: 3–14.
- Lehikoinen, A., Brotons, L., Calladine, J., Campedelli, T., Escandell, V., Flousek, J., Grueneberg, C., Haas, F., Harris, S., Herrando, S., Husby, M., Jiguet, F., Kålås, J.A., Lindström, Å., Lorrillière, R., Molina, B., Pladevall, C., Calvi, G., Sattler, T., Schmid, H., Sirkiä, P.M., Teufelbauer, N. & Trautmann, S.** 2019. Declining population trends of European mountain birds. *Glob. Chang. Biol.* **25**: 577–588.
- Lehikoinen, E. & Sparks, T.H.** 2010. Changes in migration. In: *Effects of Climate Change on Birds* (A. P. Møller, W. Fiedler, & P. Berthold, eds), pp. 89–112. Oxford University Press, Oxford.
- Leng, S., Sun, R., Yang, X. & Chen, L.** 2023. Global inequities in population exposure to urban greenspaces increased amidst tree and nontree vegetation cover expansion. *Commun. Earth Environ.* **4**: 464.
- Lenoir, J., Gégout, J.C., Marquet, P.A., de Ruffray, P. & Brisse, H.** 2008. A significant upward shift in plant species optimum elevation during the 20th century. *Science (80- )*. **320**: 1768–1771.

- Llorente-Bousquets, J., Papavero, N. & Bueno, A.** 2001. Síntesis histórica de la biogeografía. In: *Introducción a la biogeografía en Latinoamérica: teorías, conceptos, métodos y aplicaciones* (J. Llorente-Bousquets & J. J. Morrone, eds), pp. 4–15. Las Prensas de Ciencias, Facultad de Ciencias, UNAM, México.
- Lobo, J.M., Jiménez-Valverde, A. & Real, R.** 2008. AUC: A misleading measure of the performance of predictive distribution models. *Glob. Ecol. Biogeogr.* **17**: 145–151.
- Logeais, J.-M.** 2015. Première nidification de l'Élanion blanc *Elanus caeruleus* en Maine-et-Loire. *Crex* **13**: 45–50.
- Lok, T., Overdijk, O. & Piersma, T.** 2015. The cost of migration: Spoonbills suffer higher mortality during trans-Saharan spring migrations only. *Biol. Lett.* **11**: 20140944.
- Lok, T., Veldhoen, L., Overdijk, O., Tinbergen, J.M. & Piersma, T.** 2017. An age-dependent fitness cost of migration? Old trans-Saharan migrating spoonbills breed later than those staying in Europe, and late breeders have lower recruitment. *J. Anim. Ecol.* **86**: 998–1009.
- Lomolino, M.V. & Channell, R.** 1995. Splendid isolation: Patterns of geographic range collapse in endangered mammals. *J. Mammal.* **76**: 335–347.
- Lomolino, M.V., Riddle, B.R. & Brown, J.H.** 2006a. What is biogeography? In: *Biogeography* (M. V. Lomolino, B. R. Riddle, & J. H. Brown, eds), pp. 4–9. Sinauer Associates, Inc., Sunderland, Massachusetts.
- Lomolino, M.V., Riddle, B.R. & Brown, J.H.** 2006b. *Biogeography*. Sinauer Associates Inc., Sunderland, Massachusetts.
- Lomolino, M.V., Riddle, B.R. & Brown, J.H.** 2006c. Distributions of species. In: *Biogeography* (M. V. Lomolino, B. R. Riddle, & J. H. Brown, eds), pp. 65–96. Sinauer Associates, Inc., Sunderland, Massachusetts.
- López-Ramírez, S., Chamorro, D., Real, R. & Muñoz, A.-R.** 2023. Southern Europe is becoming climatically favourable for African birds: Anticipating the establishment of a new species. *Front. Zool.* **20**: 18.
- López-Ramírez, S., Márquez, A.L., Real, R. & Muñoz, A.-R.** 2024a. Evaluating the expansion of African species into Europe driven by climate change. *Divers. Distrib.* **30**: e13840.
- López-Ramírez, S., Real, R. & Muñoz, A.-R.** 2024b. The northern wheatear is reducing its distribution in its southernmost European range and moving to higher altitudes. *J. Avian Biol.* **2024**: e03217.
- López-Ramírez, S., García-Carrasco, J.-M., Real, R. & Muñoz, A.-R.** 2025. Climate-driven shifts in trans-Saharan bird migration illustrated by the spotted flycatcher (*Muscicapa striata*). *Sci. Rep.* **15**: 35201.

- López-Ramírez, S. & Muñoz, A.-R.** 2025. Climate change drives range contraction and shapes species distribution in an alpine passerine: Caution required when comparing atlas data. *Glob. Ecol. Conserv.* **60**: e03620.
- Lovejoy, T.E. & Hannah, L.** 2005. *Climate Change and Biodiversity*. Yale University Press, New Haven, CT.
- Lu, X., Ke, D.H., Zeng, X.H. & Yu, T.L.** 2009. Reproductive ecology of two sympatric Tibetan snowfinch species at the edge of their altitudinal range: Response to more stressful environments. *J. Arid Environ.* **73**: 1103–1108.
- Lustenhouwer, N. & Parker, I.M.** 2022. Beyond tracking climate: Niche shifts during native range expansion and their implications for novel invasions. *J. Biogeogr.* **49**: 1481–1493.
- Mac Arthur, R.H.** 1972. *Geographical Ecology: Patterns in the Distribution of Species*. Harper & Row, New York.
- Maciel-Mata, C.A., Manríquez-Morán, N., Octavio-Aguilar, P. & Sánchez-Rojas, G.** 2015. Geographical distribution of the species: A concept review. *Acta Univ.* **25**: 3–19.
- Maclean, I.M.D., Austin, G.E., Rehfisch, M.M., Blew, J., Crowe, O., Delany, S., Devos, K., Deceuninck, B., Günther, K., Laursen, K., Van Roomen, M. & Wahl, J.** 2008. Climate change causes rapid changes in the distribution and site abundance of birds in winter. *Glob. Chang. Biol.* **14**: 2489–2500.
- Maggini, R., Lehmann, A., Kéry, M., Schmid, H., Beniston, M., Jenni, L. & Zbinden, N.** 2011. Are Swiss birds tracking climate change?: Detecting elevational shifts using response curve shapes. *Ecol. Modell.* **222**: 21–32.
- Maggini, R., Lehmann, A., Zbinden, N., Zimmermann, N.E., Bolliger, J., Schröder, B., Foppen, R., Schmid, H., Beniston, M. & Jenni, L.** 2014. Assessing species vulnerability to climate and land use change: The case of the Swiss breeding birds. *Divers. Distrib.* **20**: 708–719.
- Mantyka-Pringle, C.S., Martin, T.G. & Rhodes, J.R.** 2012. Interactions between climate and habitat loss effects on biodiversity: A systematic review and meta-analysis. *Glob. Chang. Biol.* **18**: 1239–1252.
- Marcano-Delgado, M., Ramírez, J., Real, R. & Muñoz, A.-R.** Integration of critically endangered Rüppell's Vultures with Griffon Vultures in a newly colonized European region. *J. Ornithol.* In press.
- Marchamalo, J.** 2002. Cigüeña Blanca (*Ciconia ciconia*). In: *Atlas de las aves invernantes de Madrid 1999-2001* (J. C. del Moral, B. Molina, J. de la Puente, & J. Pérez-Tris, eds), pp. 84–85. SEO-Monticola y Comunidad de Madrid, Madrid.

- Marjakangas, E.L., Bosco, L., Versluijs, M., Xu, Y., Santangeli, A., Holopainen, S., Mäkeläinen, S., Herrando, S., Keller, V., Voříšek, P., Brotons, L., Johnston, A., Princé, K., Willis, S.G., Aghababayan, K., Ajder, V., Balmer, D.E., Bino, T., Boyla, K.A., Chodkiewicz, T., del Moral, J.C., Mazal, V.D., Ferrarini, A., Godinho, C., Gustin, M., Kalyakin, M., Knaus, P., Kuzmenko, T., Lindström, Å., Maxhuni, Q., Molina, B., Nagy, K., Radišić, D., Rajkov, S., Rajković, D.Z., Raudoniki, L., Sjeničić, J., Stoychev, S., Szép, T., Teufelbauer, N., Ursul, S., van Turnhout, C.A.M., Veleviski, M., Vikstrøm, T., Wilk, T., Voltzit, O., Øien, I.J., Sudfeldt, C., Gerlach, B. & Lehikoinen, A.** 2023. Ecological barriers mediate spatiotemporal shifts of bird communities at a continental scale. *Proc. Natl. Acad. Sci. U. S. A.* **120**: e2213330120.
- Márquez, A.L., Real, R., Olivero, J. & 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. & Del Moral, J.C.** 2003. *Atlas de las Aves Reproductoras de España*. Dirección General de Conservación de la Naturaleza- Sociedad Española de Ornitología, Madrid.
- Martín, B., Torralvo, C.A., Elias, G., Tomás, J., Onrubia, A. & Ferrer, M.** 2019. Are Western European ospreys (*Pandion haliaetus*) shortening their migration distances? Evidence from trends of the wintering population in the Iberian Peninsula. *Eur. J. Wildl. Res.* **65**: 72.
- Martin, K. & Wiebe, K.L.** 2004. Coping mechanisms of alpine and arctic breeding birds: Extreme weather and limitations to reproductive resilience. *Integr. Comp. Biol.* **44**: 177–185.
- Martin, K., Altamirano, T.A., de Zwaan, D.R., Hick, K.G., Vanderpas, A. & Wilson, S.** 2021. Avian ecology and community structure across elevation gradients: The importance of high latitude temperate mountain habitats for conserving biodiversity in the Americas. *Glob. Ecol. Conserv.* **30**: e01799.
- Martínez-Meyer, E., Díaz-Porras, D., Peterson, A.T. & Yáñez-Arenas, C.** 2013. Ecological niche structure and rangewide abundance patterns of species. *Biol. Lett.* **9**: 20120637.
- Marx, W., Haunschild, R. & Bornmann, L.** 2021. Heat waves: A hot topic in climate change research. *Theor. Appl. Climatol.* **146**: 781–800.
- Massimino, D., Johnston, A. & Pearce-Higgins, J.W.** 2015. The geographical range of British birds expands during 15 years of warming. *Bird Study* **62**: 523–534.
- Matthäus, L., Kugelschafter, K. & Fietz, J.** 2023. Influence of ambient temperature on the phenology of the greater mouse-eared bat (*Myotis myotis*). *Ecol. Evol.* **13**: e10081.

- McGinness, H.M., Lloyd-Jones, L.R., Robinson, F., Langston, A., O'Neill, L.G., Rapley, S., Jackson, M. V., Hodgson, J., Piper, M., Davies, M., Martin, J.M., Kingsford, R., Brandis, K., Doerr, V. & Mac Nally, R.** 2024. Satellite telemetry reveals complex mixed movement strategies in ibis and spoonbills of Australia: Implications for water and wetland management. *Mov. Ecol.* **12**: 74.
- McKechnie, A.E., Rushworth, I.A., Myburgh, F. & Cunningham, S.J.** 2021. Mortality among birds and bats during an extreme heat event in eastern South Africa. *Austral Ecol.* **46**: 687–691.
- McSweeney, C.F., Jones, R.G., Lee, R.W. & Rowell, D.P.** 2015. Selecting CMIP5 GCMs for downscaling over multiple regions. *Clim. Dyn.* **44**: 3237–3260.
- Mekonen, S.** 2017. Birds as biodiversity and environmental indicator. *J. Nat. Sci. Res.* **7**: 28–34.
- Mekonnen, M.M. & Hoekstra, A.Y.** 2016. Four billion people facing severe water scarcity. *Sci. Adv.* **2**: e1500323.
- Melendez, L. & Laiolo, P.** 2014. The role of climate in constraining the elevational range of the Water Pipit *Anthus spinoletta* in an alpine environment. *Ibis (Lond. 1859)*. **156**: 276–287.
- Mellone, U.** 2020. Sea crossing as a major determinant for the evolution of migratory strategies in soaring birds. *J. Anim. Ecol.* **89**: 1298–1301.
- Mendoza, M. & Araujo, M.B.** 2022. Biogeography of bird and mammal trophic structures. *Ecography (Cop.)*. **2022**: e06289.
- Merilä, J. & Hendry, A.P.** 2014. Climate change, adaptation, and phenotypic plasticity: The problem and the evidence. *Evol. Appl.* **7**: 1–14.
- Meza Mori, G., Cotrina-Sanchez, A., Bandopadhyay, S., Rojas-Briceño, N.B., Torres Guzmán, C., Coronel Castro, E. & Oliva, M.** 2023. Does climate change impact the potential habitat suitability and conservation status of the national bird of Peru (*Rupicola peruvianus*)? *Biodivers. Conserv.* **32**: 2323–2344.
- Milankovitch, M.** 1941. *Kanon der Erdbestrahlungen und seine Anwendung auf das Eiszeitenproblem [El canon de la radiación terrestre y su aplicación al problema de la edad de hielo]*. H. V. Hötzbrinck, Belgrade.
- Mill, H.R.** 1902. *The International Geography*. D. Appleton and Company, Boston.
- Molina, B., Nebreda, A., Muñoz, A.-R., Seoane, J., Real, R., Bustamante, J. & Del Moral, J.C.** 2022. *III Atlas de aves en época de reproducción en España*. SEO/BirdLife, Madrid.
- Møller, A.P., Rubolini, D. & Lehikoinen, E.** 2008. Populations of migratory bird species that did not show a phenological response to climate change are declining. *Proc. Natl. Acad. Sci.* **105**: 16195–16200.

- Møller, A.P., Rubolini, D. & Saino, N.** 2017. Morphological constraints on changing avian migration phenology. *J. Evol. Biol.* **30**: 1177–1184.
- Molles, M.C.** 2008. Population distribution and abundance. In: *Ecology: concepts and applications*, pp. 210–230. McGraw-Hill Higher Education, Boston.
- Morán-Tejeda, E., Herrera, S., López-Moreno, J.I., Revuelto, J., Lehmann, A. & Beniston, M.** 2013. Evolution and frequency (1970–2007) of combined temperature-precipitation modes in the Spanish mountains and sensitivity of snow cover. *Reg. Environ. Chang.* **13**: 873–885.
- Moreau, R.E.** 1972. *The Palaearctic-African bird migration systems*. Academic Press, London and New York.
- Morganti, M. & Pulido, F.** 2012. Invernada de aves migradoras transaharianas en España. In: *Atlas de aves en invierno en España 2007–2010* (SEO/BirdLife, ed), pp. 59–64. Ministerio de Agricultura, Alimentación y Medio Ambiente-SEO/BirdLife, Madrid.
- Moritz, C. & Agudo, R.** 2013. The future of species under climate change: Resilience or decline? *Science (80- )*. **341**: 504–508.
- Moura, C.J., Collins, A.G., Santos, R.S. & Lessios, H.** 2019. Predominant east to west colonizations across major oceanic barriers: Insights into the phylogeographic history of the hydroid superfamily Plumularioidea, suggested by a mitochondrial DNA barcoding marker. *Ecol. Evol.* **9**: 13001–13016.
- Müller, P.** 1979. El área de distribución y su dinámica. In: *Introducción a la Zoogeografía*, pp. 23–52. Editorial Blume, Barcelona.
- Muñoz, A.-R., Real, R., Barbosa, A.M. & 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. & Real, R.** 2006. Assessing the potential range expansion of the exotic monk parakeet in Spain. *Divers. Distrib.* **12**: 656–665.
- Muñoz, A.-R. & Real, R.** 2013. Distribution of Bonelli's Eagle *Aquila fasciata* in southern Spain: Scale may matter. *Acta Ornithol.* **48**: 93–101.
- Muñoz, A.-R., Márquez, A.L. & Real, R.** 2013. Updating known distribution models for forecasting climate change impact on endangered species. *PLoS One* **8**: 65462.
- Muñoz, A.-R., Márquez, A.L. & 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. & Real, R.** 2015b. Environmental favourability as a cost-efficient tool to estimate carrying capacity. *Divers. Distrib.* **21**: 1388–1400.

- Muñoz, A.-R., Ramírez, J. & Real, R.** 2024a. A critically endangered African vulture starts breeding in Europe: Escaping from extinction or entering a genetic amalgamation trap? *Ardeola* **71**: 131–135.
- Muñoz, A.-R., Ramírez, J., Guerrero, M. & Zufiaur, F.M.** 2024b. Confirmed cases of Rüppell's Vulture *Gyps rueppelli* breeding in Senegal: Advocating systematic sampling to reassess the conservation status of the species in West Africa. *Ostrich* **95**: 56–63.
- Muñoz, A.-R., Delgado, D., Ortega, P., Ortega, J., Sepúlveda, A., Barón, P., Bratek, E., Elorriaga, J., Malia, C., Owen, R., Puerta, M., Cerezo, A., Ramírez, J., Seminario, Y. & González, M.** 2025. Bridging continents: The expansion and establishment of the House Bunting (*Emberiza sahari*) from North Africa to Europe. *Birds* **6**: 29.
- Myers, N., Mittermeier, R.A., Mittermeier, C.G., da Fonseca, G.A.B. & Kent, J.** 2000. Biodiversity hotspots for conservation priorities. *Nature* **403**: 853–858.
- Myneni, R.B., Keeling, C.D., Tucker, C.J., Asrar, G. & Nemani, R.R.** 1997. Increased plant growth in the northern high latitudes from 1981 to 1991. *Nature* **386**: 698–702.
- Navarrete, J.** 2022. Bulbul naranjero, *Pycnonotus barbatus*. In: *III Atlas de las aves en época de reproducción en España* (B. Molina, A. Nebreda, A. R. Muñoz, J. Seoane, R. Real, J. Bustamante, & J. C. del Moral, eds). SEO/BirdLife, Madrid. <https://atlasaves.seo.org/ave/bulbul-naranjero/>
- Newton, I.** 2023. *The migration ecology of birds* (2nd edition). Elsevier & Academic Press, Amsterdam.
- Newton, I.** 2025. Migration mortality in birds. *Ibis (Lond. 1859)*. **167**: 106–123.
- Niamir, A., Skidmore, A.K., Muñoz, A.-R., Toxopeus, A.G. & Real, R.** 2019. Incorporating knowledge uncertainty into species distribution modelling. *Biodivers. Conserv.* **28**: 571–588.
- Niethammer, G.** 1957. Zur Vogelwelt der Sierra Nevada. *Bonner Zool. Beiträge* **8**: 230–247.
- Nieto, I., Chamorro, D., Palomo, L.J., Real, R. & Muñoz, A.-R.** 2018. Is the Eurasian Reed Warbler *Acrocephalus scirpaceus* a regular wintering species in the Iberian Peninsula? Ringing data say yes. *Acta Ornithol.* **53**: 61–68.
- O'Neill, D., Shaffrey, L., Neumann, J., Cheffings, C., Norris, K. & Pettorelli, N.** 2024. Investigating odonates' response to climate change in Great Britain: A tale of two strategies. *Divers. Distrib.* **30**: e13816.
- Ogonowski, M.S. & Conway, C.J.** 2009. Migratory decisions in birds: Extent of genetic versus environmental control. *Oecologia* **161**: 199–207.

- Oliva, M., Palacios, D., Fernández-Fernández, J.M., Rodríguez-Rodríguez, L., García-Ruiz, J.M., Andrés, N., Carrasco, R.M., Pedraza, J., Pérez-Alberti, A., Valcárcel, M. & Hughes, P.D.** 2019. Late Quaternary glacial phases in the Iberian Peninsula. *Earth-Science Rev.* **192**: 564–600.
- Onrubia, A.** 2021. Eurasian Griffon Vulture *Gyps fulvus*. In: *Migration Strategies of Birds of Prey in Western Palearctic* (M. Panuccio, U. Mellone, & A. Agostini, eds), pp. 55–67. CRC Press, Boca Raton, Florida.
- Oppel, S., Dobrev, V., Arkumarev, V., Saravia, V., Bounas, A., Kret, E., Velevski, M., Stoychev, S. & Nikolov, S.C.** 2015. High juvenile mortality during migration in a declining population of a long-distance migratory raptor. *Ibis (Lond. 1859)*. **157**: 545–557.
- Orta, J., Boesman, P.F.D., Kirwan, G.M. & Marks, J.S.** 2020. Long-legged Buzzard (*Buteo rufinus*), version 1.0. In: *Birds of the World* (J. del Hoyo, A. Elliott, J. Sargatal, D. Christie, & E. de Juana, eds). Cornell Lab of Ornithology, Ithaca, NY, USA.
- Ortiz-Bobea, A., Ault, T.R., Carrillo, C.M., Chambers, R.G. & Lobell, D.B.** 2021. Anthropogenic climate change has slowed global agricultural productivity growth. *Nat. Clim. Chang.* **11**: 306–312.
- Pachauri, R.K. & Meyer, L.A.** 2014. *Climate Change 2014: Synthesis Report. Contribution of Working Groups I, II and III to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change*. Geneva, Switzerland.
- Palomo, L.J., Gisbert, J. & Blanco, J.C.** 2007. *Atlas y Libro Rojo de los Mamíferos Terrestres de España*. Dirección General para la Biodiversidad-SECEM-SECEMU, Madrid.
- Paniagua, L.L., García-Martín, A., Moral, F.J. & Rebollo, F.J.** 2019. Aridity in the Iberian Peninsula (1960–2017): Distribution, tendencies, and changes. *Theor. Appl. Climatol.* **138**: 811–830.
- Pardo de Santayana, G., Sánchez, H., Mora, A., Gil-Velasco, M., López, F., López-Velasco, D., Ollé, À., García-Tarrasón, M., Illa, M. & Hernández, J.** 2021. *Observaciones de aves raras en España, Septiembre - Octubre, 2021*. Comité de Rarezas SEO/BirdLife, Madrid.
- Pardo de Santayana, G., Sánchez, H., López, F., López, D., Illa, M., Marco, J. & Rojas, A.** 2025. Observaciones de aves raras en España (Septiembre 2023 – Agosto 2024). *Ardeola* **72**: 141–148.
- Parmesan, C.** 1996. Climate and species' range. *Nature* **382**: 765–766.
- Parmesan, C. & Yohe, G.** 2003. A globally coherent fingerprint of climate change impacts across natural systems. *Nature* **421**: 37–42.

- Parris, K.M., Steven, R., Vogel, B., Lentini, P.E., Hartel, J. & Soanes, K.** 2023. The value of question-first citizen science in urban ecology and conservation. *Conserv. Sci. Pract.* **5**: e12917.
- Pärtel, M., Szava-Kovats, R. & Zobel, M.** 2011. Dark diversity: Shedding light on absent species. *Trends Ecol. Evol.* **26**: 124–128.
- Pautasso, M.** 2012. Observed impacts of climate change on terrestrial birds in Europe: An overview. *Ital. J. Zool.* **79**: 296–314.
- Pearson, R.G. & Dawson, T.P.** 2003. Predicting the impacts of climate change on the distribution of species: Are bioclimate envelope models useful? *Glob. Ecol. Biogeogr.* **12**: 361–371.
- Pepin, N., Bradley, R.S., Diaz, H.F., Baraer, M., Caceres, E.B., Forsythe, N., Fowler, H., Greenwood, G., Hashmi, M.Z., Liu, X.D., Miller, J.R., Ning, L., Ohmura, A., Palazzi, E., Rangwala, I., Schöner, W., Severskiy, I., Shahgedanova, M., Wang, M.B., Williamson, S.N., Yang, D.Q. & Mountain Research Initiative, E.D.W.W.G.** 2015. Elevation-dependent warming in mountain regions of the world. *Nat. Clim. Chang.* **5**: 424–430.
- Pernollet, C.A., Korner-Nievergelt, F. & Jenni, L.** 2015. Regional changes in the elevational distribution of the Alpine Rock Ptarmigan *Lagopus muta helvetica* in Switzerland. *Ibis (Lond. 1859)*. **157**: 823–836.
- Péron, G., Henry, P., Provost, P., Dehorter, O. & Julliard, R.** 2007. Climate changes and post-nuptial migration strategy by two reedbed passerines. *Clim. Res.* **35**: 147–157.
- Phillips, S.J., Anderson, R.P. & Schapire, R.E.** 2006. Maximum entropy modeling of species geographic distributions. *Ecol. Modell.* **190**: 231–259.
- Pleguezuelos, J.M., Márquez, R. & Lizana, M.** 2004. *Atlas y Libro Rojo de los Anfibios y Reptiles de España*. Dirección General de Conservación de la Naturaleza-Asociación Herpetologica Española, Madrid.
- Pocock, M.J.O., Tweddle, J.C., Savage, J., Robinson, L.D. & Roy, H.E.** 2017. The diversity and evolution of ecological and environmental citizen science. *PLoS One* **12**: e0172579.
- Podhrázký, M., Musil, P., Musilová, Z., Zouhar, J., Adam, M., Závora, J. & Hudec, K.** 2017. Central European Greylag Geese *Anser anser* show a shortening of migration distance and earlier spring arrival over 60 years. *Ibis (Lond. 1859)*. **159**: 352–365.
- Podolsky, A.L.** 2018. Applying songbird population dynamics models to conservation biology needs. *Theor. Appl. Ecol.* **2018**: 99–107.
- Popy, S., Bordignon, L. & Prodon, R.** 2010. A weak upward elevational shift in the distributions of breeding birds in the Italian Alps. *J. Biogeogr.* **37**: 57–67.

- Potvin, D.A., Välimäki, K. & Lehikoinen, A.** 2016. Differences in shifts of wintering and breeding ranges lead to changing migration distances in European birds. *J. Avian Biol.* **47**: 619–628.
- Pounds, J.A. & Crump, M.L.** 1994. Amphibian declines and climate disturbance: The case of the golden toad and the harlequin frog. *Conserv. Biol.* **8**: 72–85.
- Prieta, J.** 2022. Vencejo moro, *Apus affinis*. In: *III Atlas de las aves en época de reproducción en España* (B. Molina, A. Nebreda, A. R. Muñoz, J. Seoane, R. Real, J. Bustamante, & J. C. del Moral, eds). SEO/BirdLife, Madrid. <https://atlasaves.seo.org/ave/vencejo-moro/>
- Pulido-Pastor, A., Márquez, A.L., García-Barros, E. & Real, R.** 2018. Identification of potential source and sink areas for butterflies on the Iberian Peninsula. *Insect Conserv. Divers.* **11**: 479–492.
- Pulido-Pastor, A., Márquez, A.L., Guerrero, J.C., García-Barros, E. & Real, R.** 2021. Metapopulation patterns of iberian butterflies revealed by fuzzy logic. *Insects* **12**: 392.
- Pulido, F., Berthold, P., Mohr, G. & Querner, U.** 2001. Heritability of the timing of autumn migration in a natural bird population. *Proc. R. Soc. London. Ser. B Biol. Sci.* **268**: 953–959.
- Qi, Q. & Wang, Z.** 2024. Machine learning-based models to predict aquatic ecological risk for engineered nanoparticles: Using hazard concentration for 5% of species as an endpoint. *Environ. Sci. Pollut. Res.* **31**: 25114–25128.
- Radhakrishna Rao, C.** 1948. Large sample tests of statistical hypotheses concerning several parameters with applications to problems of estimation. *Math. Proc. Cambridge Philos. Soc.* **44**: 50–57.
- Ramírez, J., Simón, M., Solís, S., Pérez, C. & García, E.** 2002. Vencejo Moro, *Apus affinis*. Observaciones de aves raras en España. *Ardeola* **49**: 161.
- Ramírez, J., Muñoz, A.R., Onrubia, A., de la Cruz, A., Cuenca, D., González, J.M. & Arroyo, G.M.** 2011. Spring movements of Rüppell's Vulture *Gyps rueppelli* across the Strait of Gibraltar. *Ostrich* **82**: 71–73.
- Ramírez, J.** 2012. First record of Rüppell's Vulture *Gyps rueppelli* arriving in Morocco from Spain. *Go-South Bull* **9**: 44–45.
- Ramírez, J., Zufiaur, F.M. & Guerrero, M.** 2019. Spring migration of Eurasian Griffon Vultures across the Strait of Gibraltar: Number, timing and age composition. *Ardeola* **66**: 113–118.
- Randler, C.** 2021. Users of a citizen science platform for bird data collection differ from other birdwatchers in knowledge and degree of specialization. *Glob. Ecol. Conserv.* **27**: e01580.

- Ratte, H.T.** 1984. Temperature and insect development. In: *Environmental Physiology and Biochemistry of Insects* (K. H. Hoffmann, ed), pp. 33–66. Springer, Heidelberg, Berlin.
- Real, R., Guerrero, J.C., Antúnez, A., Olivero, J. & Vargas, J.M.** 2001. Geographic responses of amphibian species to environmental gradients in Southern Spain. I. Individualistic patterns. *Boletín la Real Soc. Española Hist. Nat. (Sección biológica)* **96**: 243–249.
- Real, R., Barbosa, A.M., Porrás, D., Kin, M.S., Márquez, A.L., Guerrero, J.C., Palomo, L.J., Justo, E.R. & Vargas, J.M.** 2003. Relative importance of environment, human activity and spatial situation in determining the distribution of terrestrial mammal diversity in Argentina. *J. Biogeogr.* **30**: 939–947.
- Real, R., Barbosa, A.M. & Vargas, J.M.** 2006. Obtaining environmental favourability functions from logistic regression. *Environ. Ecol. Stat.* **13**: 237–245.
- Real, R., Márquez, A.L., Estrada, A., Muñoz, A.R. & Vargas, J.M.** 2008. Modelling chorotypes of invasive vertebrates in mainland Spain. *Divers. Distrib.* **14**: 364–373.
- Real, R., Márquez, A.L., Olivero, J. & Estrada, A.** 2010. Species distribution models in climate change scenarios are still not useful for informing policy planning: An uncertainty assessment using fuzzy logic. *Ecography (Cop.)* **33**: 304–314.
- Real, R., Romero, D., Olivero, J., Estrada, A. & Márquez, A.L.** 2013. Estimating how inflated or obscured effects of climate affect forecasted species distribution. *PLoS One* **8**: e53646.
- Real, R., Barbosa, A.M. & Bull, J.W.** 2017. Species distributions, quantum theory, and the enhancement of biodiversity measures. *Syst. Biol.* **66**: 453–462.
- Recio, M.R., Mathieu, R., Denys, P., Sirguey, P. & Seddon, P.J.** 2011. Lightweight GPS-tags, one giant leap for wildlife tracking? An assessment approach. *PLoS One* **6**: e28225.
- Reif, J. & Flousek, J.** 2012. The role of species' ecological traits in climatically driven altitudinal range shifts of central European birds. *Oikos* **121**: 1053–1060.
- Resano-Mayor, J., Fernández-Martín, Á., Hernández-Gómez, S., Toranzo, I., España, A., Gil, J.A., de Gabriel, M., Roa-Álvarez, I., Strinella, E., Hobson, K.A., Heckel, G. & Arlettaz, R.** 2017. Integrating genetic and stable isotope analyses to infer the population structure of the White-winged Snowfinch *Montifringilla nivalis* in Western Europe. *J. Ornithol.* **158**: 395–405.
- Resano-Mayor, J., Bettega, C., Delgado, M.D.M., Fernández-Martín, Á., Hernández-Gómez, S., Toranzo, I., España, A., de Gabriel, M., Roa-Álvarez, I., Gil, J.A., Strinella, E., Hobson, K.A. & Arlettaz, R.** 2020. Partial migration of White-winged snowfinches is correlated with winter weather conditions. *Glob. Ecol. Conserv.* **24**: e01346.

- Robinson, R.A., Baillie, S.R. & Crick, H.Q.P.** 2007. Weather-dependent survival: Implications of climate change for passerine population processes. *Ibis (Lond. 1859)*. **149**: 357–364.
- Rocha-Méndez, A., Prieto-Torres, D.A., Sánchez-González, L.A. & Navarro-Sigüenza, A.G.** 2024. Climatic niche shifts and ecological sky-island dynamics in Mesoamerican montane birds. *Ecol. Evol.* **14**: 1–17.
- Rohde, R.A. & Hausfather, Z.** 2020. The Berkeley Earth land/ocean temperature record. *Earth Syst. Sci. Data* **12**: 3469–3479.
- Roiz, D., Ruiz, S., Soriguer, R. & Figuerola, J.** 2014. Climatic effects on mosquito abundance in Mediterranean wetlands. *Parasit. Vectors* **7**: 333.
- Romero, D., Olivero, J. & Real, R.** 2013. Comparative assessment of different methods for using land-cover variables for distribution modelling of *Salamandra salamandra longirotris*. *Environ. Conserv.* **40**: 48–59.
- Romero, D., Olivero, J. & Real, R.** 2019. Accounting for uncertainty in assessing the impact of climate change on biodiversity hotspots in Spain. *Anim. Biodivers. Conserv.* **42**: 355–367.
- Romo, H., García-Barros, E., Márquez, A.L., Moreno, J.C. & Real, R.** 2014. Effects of climate change on the distribution of ecologically interacting species: Butterflies and their main food plants in Spain. *Ecography (Cop.)*. **37**: 1063–1072.
- Root, T.L., Price, J.T., Hall, K.R., Schneider, S.H., Rosenzweig, C. & Pounds, J.A.** 2003. Fingerprints of global warming on wild animals and plants. *Nature* **421**: 57–60.
- Root, T.L. & Schneider, S.H.** 2006. Conservation and climate change: The challenges ahead. *Conserv. Biol.* **20**: 706–708.
- Rotics, S., Turjeman, S., Kaatz, M., Resheff, Y.S., Zurell, D., Sapir, N., Eggers, U., Fiedler, W., Flack, A., Jeltsch, F., Wikelski, M. & Nathan, R.** 2017. Wintering in Europe instead of Africa enhances juvenile survival in a long-distance migrant. *Anim. Behav.* **126**: 79–88.
- Rouco, M., Copete, J.L., De Juana, E., Gil-Velasco, M., Lorenzo, J.A., Martín, M., Milá, B., Molina, B. & Santos, D.M.** 2022. *Lista de las aves de España. Edición de 2022*. SEO/BirdLife, Madrid.
- Russo, D., Jones, G., Polizzi, M., Meola, V. & Cistrone, L.** 2024. Higher and bigger: How riparian bats react to climate change. *Sci. Total Environ.* **913**: 169733.
- Rutz, C.** 2008. The establishment of an urban bird population. *J. Anim. Ecol.* **77**: 1008–1019.

- Ryan, P.** 2020. House Bunting (*Emberiza sahari*). In: *Birds of the World* (J. del Hoyo, A. Elliott, J. Sargatal, D. Christie, & E. de Juana, eds). Cornell Lab of Ornithology, Ithaca, NY, USA.
- Salski, A.** 2006. Ecological applications of fuzzy logic. In: *Ecological Informatics* (F. Recknagel, ed), pp. 3–14. Springer, Berlin.
- Sander, M.M., Jähnig, S., Lisovski, S., Mermillon, C., Alba, R., Rosselli, D. & Chamberlain, D.** 2023. High nest failure but better nestling quality for early breeders in an alpine population of Northern Wheatear (*Oenanthe oenanthe*). *Ibis (Lond. 1859)*. **165**: 125–141.
- Santos, C.D., Silva, J.P., Muñoz, A.-R., Onrubia, A. & Wikelski, M.** 2020. The gateway to Africa: What determines sea crossing performance of a migratory soaring bird at the Strait of Gibraltar? *J. Anim. Ecol.* **89**: 1317–1328.
- Sassi, Y., Nouzières, B., Scacco, M., Tremblay, Y., Duriez, O. & Robira, B.** 2024. The use of social information in vulture flight decisions. *Proc. R. Soc. B Biol. Sci.* **291**: 20231729.
- Saunders, H.** 1871. A list of the birds of southern Spain. *Ibis (Lond. 1859)*. **13**: 205–225.
- Schano, C., Niffenegger, C., Jonas, T. & Korner-Nievergelt, F.** 2021. Hatching phenology is lagging behind an advancing snowmelt pattern in a high-alpine bird. *Sci. Rep.* **11**: 22191.
- Schmitt, T.** 2009. Biogeographical and evolutionary importance of the European high mountain systems. *Front. Zool.* **6**: 9.
- Sclater, P.L.** 1858. On the general geographical distribution of the members of the class Aves. *J. Proc. Linn. Soc. London. Zool.* **2**: 130–136.
- Scridel, D., Bogliani, G., Pedrini, P., Iemma, A., von Hardenberg, A. & Brambilla, M.** 2017. Thermal niche predicts recent changes in range size for bird species. *Clim. Res.* **73**: 207–216.
- Scridel, D., Brambilla, M., Martin, K., Lehtikoinen, A., Lemma, A., Matteo, A., Jähnig, S., Caprio, E., Bogliani, G., Pedrini, P., Rolando, A., Arlettaz, R. & Chamberlain, D.** 2018. A review and meta-analysis of the effects of climate change on Holarctic mountain and upland bird populations. *Ibis (Lond. 1859)*. **160**: 489–515.
- Scridel, D., Brambilla, M., de Zwaan, D.R., Froese, N., Wilson, S., Pedrini, P. & Martin, K.** 2021. A genus at risk: Predicted current and future distribution of all three Lagopus species reveal sensitivity to climate change and efficacy of protected areas. *Divers. Distrib.* **27**: 1759–1774.

- Scridel, D., Anderle, M., Capelli, F., Forti, A., Bettega, C., Alessandrini, C., Delgado, M.D.M., Pedrotti, L., Partel, P., Bogliani, G., Pedrini, P. & Brambilla, M. 2024. Coping with unpredictable environments: Fine-tune foraging microhabitat use in relation to prey availability in an alpine species. *Oecologia* **204**: 845–860.
- Sekercioglu, C.H., Schneider, S.H., Fay, J.P. & Loarie, S.R. 2008. Climate change, elevational range shifts, and bird extinctions. *Conserv. Biol.* **22**: 140–150.
- Senar, J.C. & Copete, J.L. 1995. Mediterranean house sparrows (*Passer domesticus*) are not used to freezing temperatures: An analysis of survival rates. *J. Appl. Stat.* **22**: 1069–1074.
- SEO/BirdLife. 2012. *Atlas de aves en invierno en España 2007–2010*. Ministerio de Agricultura, Alimentación y Medio Ambiente-SEO/BirdLife, Madrid.
- SEO/BirdLife, Comité de Rarezas. 2024. Observaciones de aves raras en España (Septiembre 2022 – Agosto 2023). *Ardeola* **71**: 183–194.
- Sepúlveda, A.J. & Ortega, J. 2023. Primera reproducción constatada del escribano sahariano en España. *Quercus* **466**: 45.
- Sergio, F., Tavecchia, G., Tanferna, A., Blas, J., Blanco, G. & Hiraldo, F. 2019. When and where mortality occurs throughout the annual cycle changes with age in a migratory bird: Individual vs population implications. *Sci. Rep.* **9**: 17352.
- Shi, J.-B., Li, D.-Q. & Xiao, W.-F. 2006. A review of impacts of climate change on birds: Implications of long-term studies. *Zool. Res.* **27**: 637–646.
- Sillero, N., Arenas-Castro, S., Enriquez-Urzelai, U., Vale, C.G., Sousa-Guedes, D., Martínez-Freiría, F., Real, R. & Barbosa, A.M. 2021. Want to model a species niche? A step-by-step guideline on correlative ecological niche modelling. *Ecol. Modell.* **456**: 109671.
- Sillett, T.S. & Holmes, R.T. 2002. Variation in survivorship of a migratory songbird throughout its annual cycle. *J. Anim. Ecol.* **71**: 296–308.
- Simberloff, D.S. & Wilson, E.O. 1969. Experimental zoogeography of islands: The colonization of empty islands. *Ecology* **50**: 278–296.
- Simmons, A.D. & Thomas, C.D. 2004. Changes in dispersal during species' range expansions. *Am. Nat.* **164**: 378–395.
- Sinervo, B., Méndez-de-la-Cruz, F., Miles, D.B., Heulin, B., Bastiaans, E., Villagrán-Santa Cruz, M., Lara-Resendiz, R., Martínez-Méndez, N., Calderón-Espinosa, M.L., Meza-Lázaro, R.N., Gadsden, H., Avila, L.J., Morando, M., De la Riva, I.J., Sepúlveda, P.V., Rocha, C.F.D., Ibargüengoytia, N., Puntriano, C.A., Massot, M., Lepetz, V., Oksanen, T.A., Chapple, D.G., Bauer, A.M., Branch, W.R., Clobert, J. & Sites, J.W. 2010. Erosion of lizard diversity by climate change and altered thermal niches. *Science* (80- ). **328**: 894–899.

- Soultan, A., Pavón-Jordán, D., Bradter, U., Sandercock, B.K., Hochachka, W.M., Johnston, A., Brommer, J., Gaget, E., Keller, V., Knaus, P., Aghababayan, K., Maxhuni, Q., Vintchevski, A., Nagy, K., Raudonikis, L., Balmer, D., Noble, D., Leitão, D., Øien, I.J., Shimmings, P., Sultanov, E., Caffrey, B., Boyla, K., Radišić, D., Lindström, Å., Veleviski, M., Pladevall, C., Brotons, L., Karel, Š., Rajković, D.Z., Chodkiewicz, T., Wilk, T., Szép, T., van Turnhout, C., Foppen, R., Burfield, I., Vikstrøm, T., Mazal, V.D., Eaton, M., Vorisek, P., Lehikoinen, A., Herrando, S., Kuzmenko, T., Bauer, H.-G., Kalyakin, M.V., Voltzit, O.V., Sjeničić, J. & Pärt, T. 2022. The future distribution of wetland birds breeding in Europe validated against observed changes in distribution. *Environ. Res. Lett.* **17**: 024025.
- Sparks, T.H. & Braslavská, O. 2001. The effects of temperature, altitude and latitude on the arrival and departure dates of the swallow *Hirundo rustica* in the Slovak Republic. *Int. J. Biometeorol.* **45**: 212–216.
- Spooner, F.E.B., Pearson, R.G. & Freeman, R. 2018. Rapid warming is associated with population decline among terrestrial birds and mammals globally. *Glob. Chang. Biol.* **24**: 4521–4531.
- Stafford, K., Farley, E., Ferguson, M., Kuletz, K. & Levine, R. 2022. Northward range expansion of subarctic upper trophic level animals into the Pacific Arctic region. *Oceanography* **35**: 158–166.
- Stiels, D., Bastian, H.V., Bastian, A., Schidelko, K. & 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.
- Stofberg, M., Amar, A., Sumasgutner, P. & Cunningham, S.J. 2022. Staying cool and eating junk: Influence of heat dissipation and anthropogenic food on foraging and body condition in an urban passerine. *Landsc. Urban Plan.* **226**: 104465.
- Strinella, E., Ricci, F. & Vianale, P. 2007. Uso dell'habitat nel Fringuello alpino (*Montifringilla nivalis*) in periodo riproduttivo in un'area sub-antropizzata: Campo Imperatore (Gran Sasso-Abruzzo). *Alula* **14**: 107–114.
- Strinella, E., Scridel, D., Brambilla, M., Schano, C. & Korner-Nievergelt, F. 2020. Potential sex-dependent effects of weather on apparent survival of a high-elevation specialist. *Sci. Rep.* **10**: 8386.
- Sullivan, B.L., Aycrigg, J.L., Barry, J.H., Bonney, R.E., Bruns, N., Cooper, C.B., Damoulas, T., Dhondt, A.A., Dietterich, T., Farnsworth, A., Fink, D., Fitzpatrick, J.W., Fredericks, T., Gerbracht, J., Gomes, C., Hochachka, W.M., Iliff, M.J., Lagoze, C., La Sorte, F.A., Merrifield, M., Morris, W., Phillips, T.B., Reynolds, M., Rodewald, A.D., Rosenberg, K.V., Trautmann, N.M., Wiggins, A., Winkler, D.W., Wong, W.-K., Wood, C.L., Yu, J. & Kelling, S. 2014. The eBird enterprise: An integrated approach to development and application of citizen science. *Biol. Conserv.* **169**: 31–40.

- Summers-Smith, D. & Bonan, A.** 2020. White-winged Snowfinch (*Montifringilla nivalis*). In: *Birds of the World* (J. del Hoyo, A. Elliott, J. Sargatal, D. A. Christie, & E. de Juana, eds). Cornell Lab of Ornithology, Ithaca, NY, USA.
- Sun, J., Qiu, H., Guo, J., Xu, X., Wu, D., Zhong, L., Jiang, B., Jiao, J., Yuan, W., Huang, Y., Shen, A. & Wang, W.** 2020. Modeling the potential distribution of *Zelkova schneideriana* under different human activity intensities and climate change patterns in China. *Glob. Ecol. Conserv.* **21**: e00840.
- Svenning, J., Gravel, D., Holt, R.D., Schurr, F.M., Thuiller, W., Münkemüller, T., Schiffers, K.H., Dullinger, S., Edwards, T.C., Hickler, T., Higgins, S.I., Nabel, J.E.M.S., Pagel, J. & Normand, S.** 2014. The influence of interspecific interactions on species range expansion rates. *Ecography (Cop.)*. **37**: 1198–1209.
- Taheri, S., Naimi, B. & Araújo, M.B.** 2016. Did British breeding birds move north in the late 20th century? *Clim. Chang. Responses* **3**: 5.
- Tayleur, C.M., Devictor, V., Gaüzère, P., Jonzén, N., Smith, H.G. & Lindström, Å.** 2016. Regional variation in climate change winners and losers highlights the rapid loss of cold-dwelling species. *Divers. Distrib.* **22**: 468–480.
- Taylor, B.** 2020. Spotted Flycatcher (*Muscicapa striata*). In: *Birds of the World* (J. del Hoyo, A. Elliott, J. Sargatal, D. Christie, & E. de Juana, eds). Cornell Lab of Ornithology, Ithaca, NY, USA.
- Teixeira, J., Ferrand, N. & Arntzen, J.W.** 2001. Biogeography of the golden-striped salamander *Chioglossa lusitanica*: A field survey and spatial modelling approach. *Ecography (Cop.)*. **24**: 618–624.
- Tellería, J.L., Asensio, B. & Díaz, M.** 1999. *Aves Ibéricas II: Paseriformes*. J. M. Reyero (ed), Madrid.
- Thévenot, M., Vernon, R. & Bergier, P.** 2003. *The Birds of Morocco: An annotated Checklist*. The Natural History Museum, Tring, UK.
- Thomas, C.D. & Lennon, J.J.** 1999. Birds extend their ranges northwards. *Nature* **399**: 213.
- Thomas, C.D., Bodsworth, E.J., Wilson, R.J., Simmons, A.D., Davies, Z.G., Musche, M. & Conradt, L.** 2001. Ecological and evolutionary processes at expanding range margins. *Nature* **411**: 577–581.
- Thorup, K. & Rabøl, J.** 2001. The orientation system and migration pattern of long-distance migrants: Conflict between model predictions and observed patterns. *J. Avian Biol.* **32**: 111–119.
- Thuiller, W., Lavorel, S., Araújo, M.B., Sykes, M.T. & Prentice, I.C.** 2005. Climate change threats to plant diversity in Europe. *Proc. Natl. Acad. Sci. USA* **102**: 8245–8250.

- Tingley, M.W., Monahan, W.B., Beissinger, S.R. & Moritz, C.** 2009. Birds track their Grinnellian niche through a century of climate change. *Proc. Natl. Acad. Sci. U. S. A.* **106**: 19637–19643.
- Tøttrup, A.P., Thorup, K. & Rahbek, C.** 2006. Changes in timing of autumn migration in North European songbirds populations. *Ardea* **94**: 527–536.
- Tyndall, J.** 1861. On the absorption and radiation of heat by gases and vapours, and on the physical connexion of radiation, absorption, and conduction.—The bakerian lecture. *London, Edinburgh, Dublin Philos. Mag. J. Sci.* **22**: 169–194.
- Udvardy, M.D.F.** 1969. *Dynamic zoogeography: with special reference to land animals.* Van Nostrand Reinhold, New York.
- Udvardy, M.D.F.** 1975. *A classification of the biogeographical provinces of the World.* International Union for Conservation of Nature (IUCN) and Natural Resources Morges, Switzerland.
- US Geological Survey.** 1996. GTOPO30. Land Processes Distributed Active Archive Center (LPDAAC), EROS Data Center, Washington D.C., available from <https://lta.cr.usgs.gov/GTOPO30>.
- Väli, Ü., Dombrovski, V., Treinys, R., Bergmanis, U., Daróczy, S.J., Dravecky, M., Ivanovski, V., Lontkowski, J., Maciorowski, G., Meyburg, B.-U., Mizera, T., Zeitz, R. & Ellegren, H.** 2010. Widespread hybridization between the Greater Spotted Eagle *Aquila clanga* and the Lesser Spotted Eagle *Aquila pomarina* (Aves: Accipitriformes) in Europe. *Biol. J. Linn. Soc.* **100**: 725–736.
- Vanderwerf, E.A. & Downs, R.E.** 2022. Factors affecting breeding success of White Terns (*Gygis alba*; Aves: Laridae) in urban environments of Honolulu, Hawaii. *Pacific Sci.* **76**: 33–41.
- Wald, A.** 1943. Tests of statistical hypotheses concerning several parameters when the number of observations is large. *Trans. Am. Math. Soc.* **54**: 426–482.
- Walker, B.L., Yappert, A.A., Brennan, C.L., Bossu, C.M. & Jones, A.W.** 2024. Field research guided by citizen science and monitoring data reveal a novel alpine breeding distribution and vegetation associations of a declining, habitat-specialist songbird in Colorado, USA. *Avian Conserv. Ecol.* **19**: 10.
- Wallace, A.R.** 1876. *The geographical distribution of animals: with a study of the relations of living and extinct faunas as elucidating the past changes of the Earth's surface.* Harper & Brothers, New York.
- Wallingford, P.D., Morelli, T.L., Allen, J.M., Beaury, E.M., Blumenthal, D.M., Bradley, B.A., Dukes, J.S., Early, R., Fusco, E.J., Goldberg, D.E., Ibáñez, I., Laginhas, B.B., Vilà, M. & Sorte, C.J.B.** 2020. Adjusting the lens of invasion biology to focus on the impacts of climate-driven range shifts. *Nat. Clim. Chang.* **10**: 398–405.

- Walther, G.-R., Post, E., Convey, P., Menzel, A., Parmesan, C., Beebee, T.J.C., Fromentin, J.-M., Hoegh-Guldberg, O. & Bairlein, F. 2002. Ecological responses to recent climate change. *Nature* **416**: 389–395.
- Weidensaul, S. 2012. Geolocators on raptors: Advantages and limitations of a new tracking technology. *J. Raptor Res.* **46**: 141–144.
- Weiskopf, S.R., Rubenstein, M.A., Crozier, L.G., Gaichas, S., Griffis, R., Halofsky, J.E., Hyde, K.J.W., Morelli, T.L., Morissette, J.T., Muñoz, R.C., Pershing, A.J., Peterson, D.L., Poudel, R., Staudinger, M.D., Sutton-Grier, A.E., Thompson, L., Vose, J., Weltzin, J.F. & Whyte, K.P. 2020. Climate change effects on biodiversity, ecosystems, ecosystem services, and natural resource management in the United States. *Sci. Total Environ.* **733**: 137782.
- Welbergen, J.A., Klose, S.M., Markus, N. & Eby, P. 2008. Climate change and the effects of temperature extremes on Australian flying-foxes. *Proc. R. Soc. B Biol. Sci.* **275**: 419–425.
- Weston, K.A., Taylor, S.S. & 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.
- Whittaker, R.J., Araújo, M.B., Jepson, P., Ladle, R.J., Watson, J.E.M. & Willis, K.J. 2005. Conservation biogeography: Assessment and prospect. *Divers. Distrib.* **11**: 3–23.
- Wiens, J.J. & Graham, C.H. 2005. Niche conservatism: Integrating evolution, ecology, and conservation biology. *Annu. Rev. Ecol. Evol. Syst.* **36**: 519–539.
- Woodward, J. 2014. Die eiszeit. In: *The Ice Age: A Very Short Introduction*, pp. 50–59. Oxford University Press, Oxford.
- Yu, H., Luedeling, E. & Xu, J. 2010. Winter and spring warming result in delayed spring phenology on the Tibetan Plateau. *Proc. Natl. Acad. Sci. U.S.A.* **107**: 22151–22156.
- Zadeh, L.A. 1965. Fuzzy sets. *Inf. Control* **8**: 338–353.
- Zajac, Z., Gomez, O., Gelati, E., van der Velde, M., Bassu, S., Ceglar, A., Chukaliev, O., Panarello, L., Koebler, R., van den Berg, M., Niemeyer, S. & Fumagali, D. 2022. Estimation of spatial distribution of irrigated crop areas in Europe for large-scale modelling applications. *Agric. Water Manag.* **266**: 107527.
- Žalakevičius, M. 2001. Bird numbers, population state, and distribution areas in the eastern Baltic region in the context of the impact of global climate change. *Acta Zool. Litu.* **11**: 141–162.
- Zamora, R. & 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.

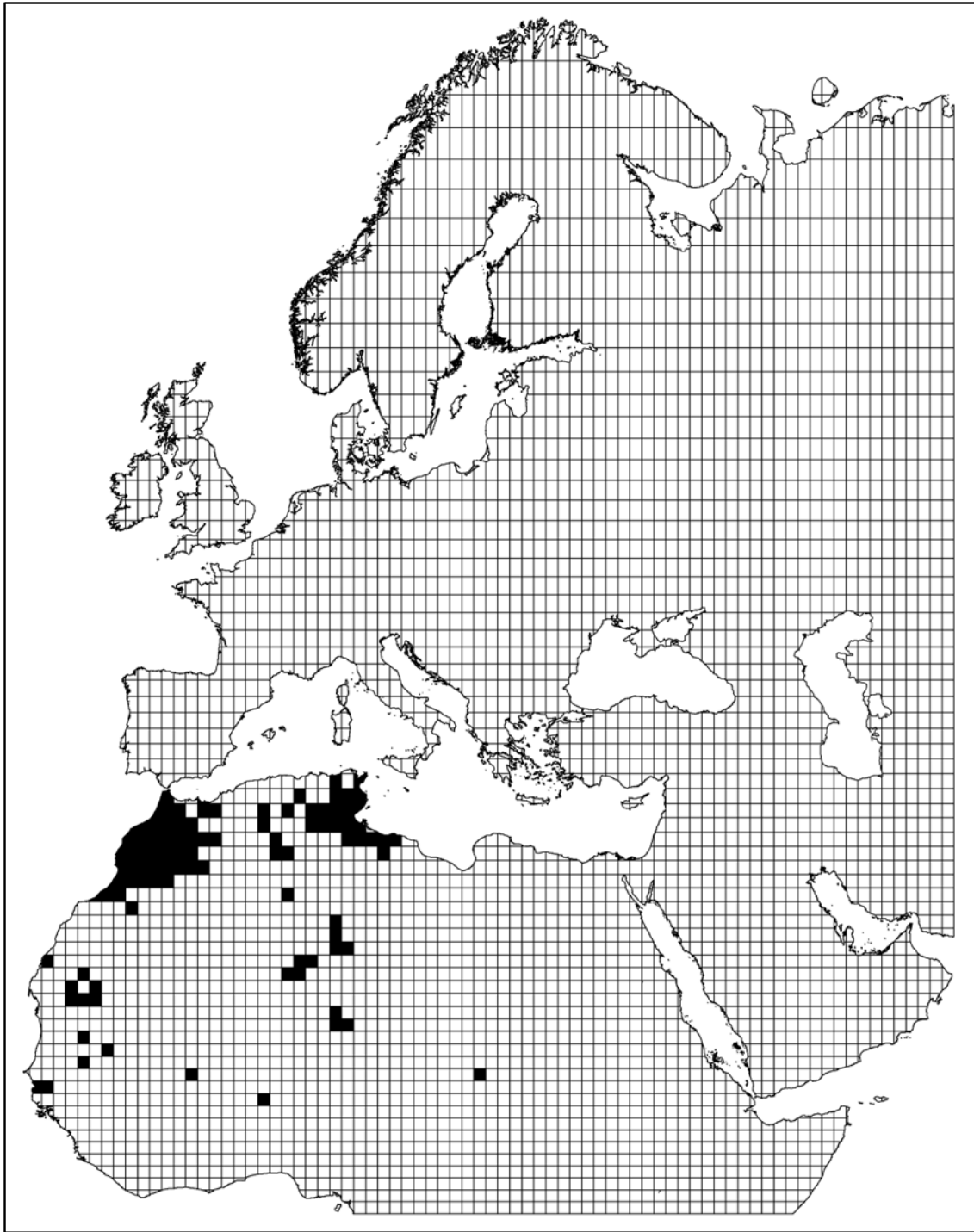
- Zanolla, M., Altamirano, M., Carmona, R., De la Rosa, J., Souza-Egipsy, V., Sherwood, A., Tsiamis, K., Barbosa, A.M., Muñoz, A.-R. & Andreakis, N.** 2018. Assessing global range expansion in a cryptic species complex: Insights from the red seaweed genus *Asparagopsis* (Florideophyceae). *J. Phycol.* **54**: 12–24.
- Zhu, B., Verhoeven, M.A., Velasco, N., Sanchez-Aguilar, L., Zhang, Z. & Piersma, T.** 2022. Current breeding distributions and predicted range shifts under climate change in two subspecies of Black-tailed Godwits in Asia. *Glob. Chang. Biol.* **28**: 5416–5426.
- Zulian, V., Miller, D.A.W. & Ferraz, G.** 2021. Integrating citizen-science and planned-survey data improves species distribution estimates. *Divers. Distrib.* **27**: 2498–2509.
- Zurek, W.H.** 1991. Decoherence and the transition from quantum to classical. *Phys. Today* **44**: 36–44.
- 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., Serradiaz, J.M., Thuiller, W., Yates, K.L., Zimmermann, N.E. & Merow, C.** 2020. A standard protocol for reporting species distribution models. *Ecography (Cop.)*. **43**: 1261–1277.
- Zuur, A.F., Ieno, E.N. & Elphick, C.S.** 2010. A protocol for data exploration to avoid common statistical problems. *Methods Ecol. Evol.* **1**: 3–14.

# CAPÍTULO 11

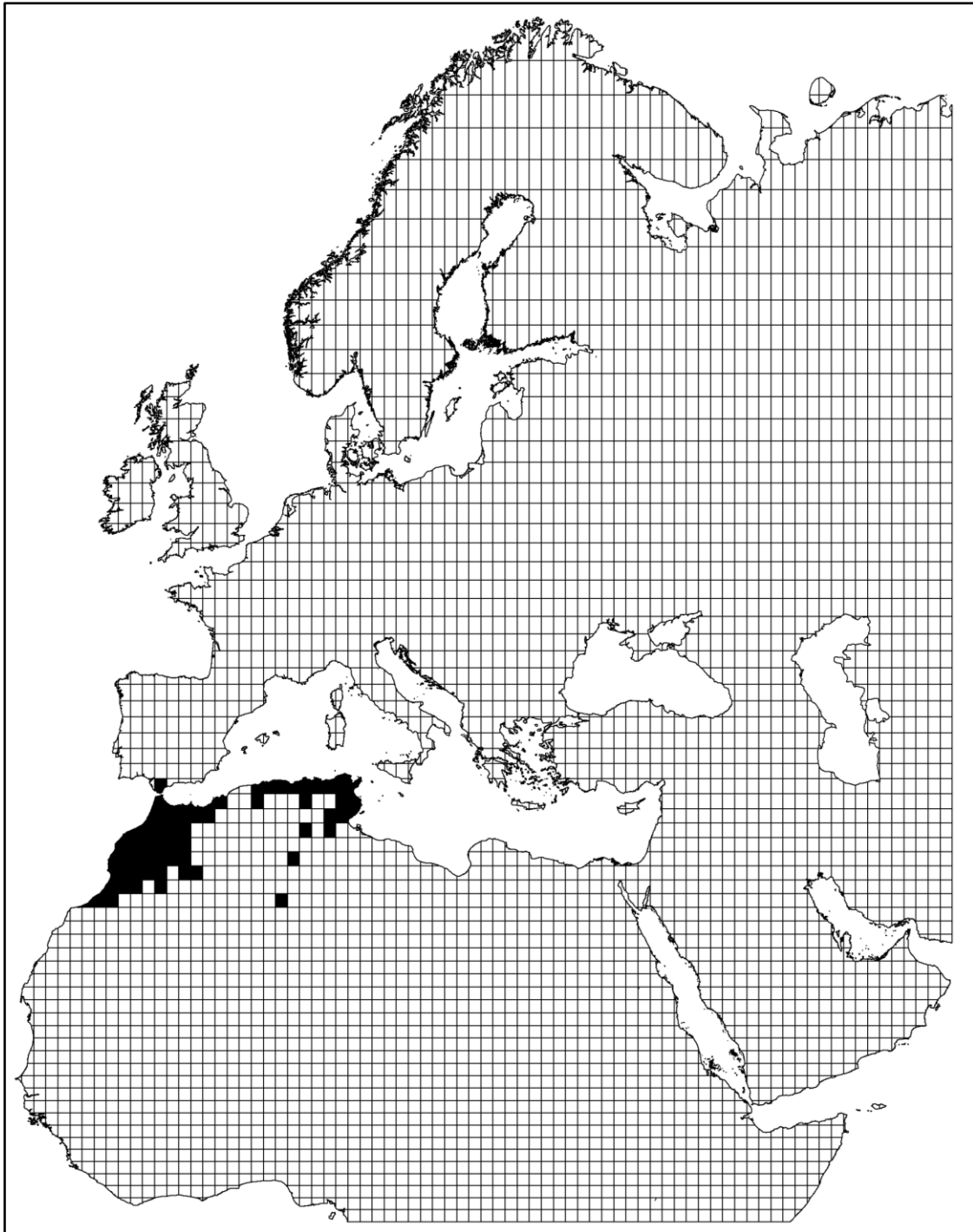
## Apéndices

## 11. Apéndices

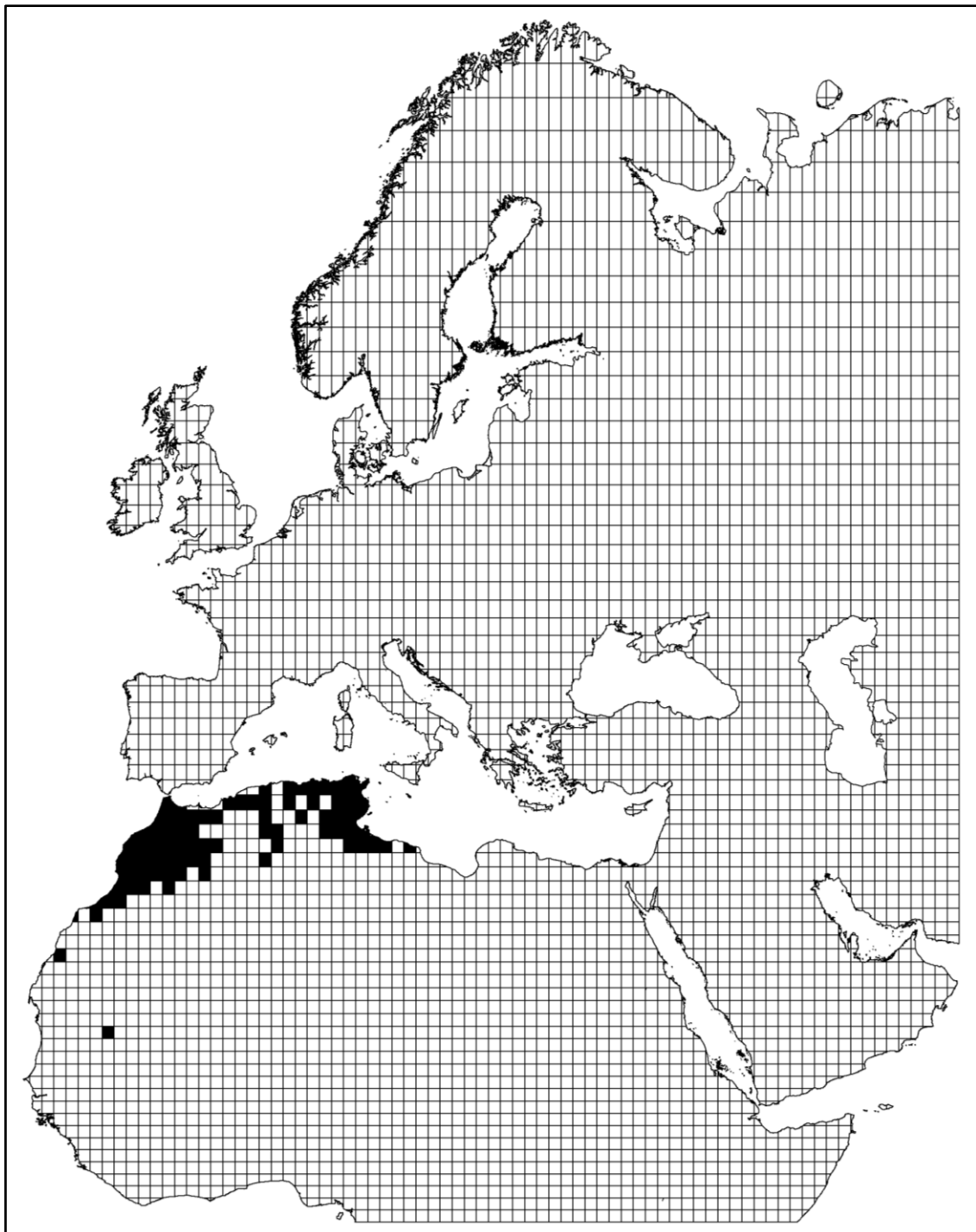
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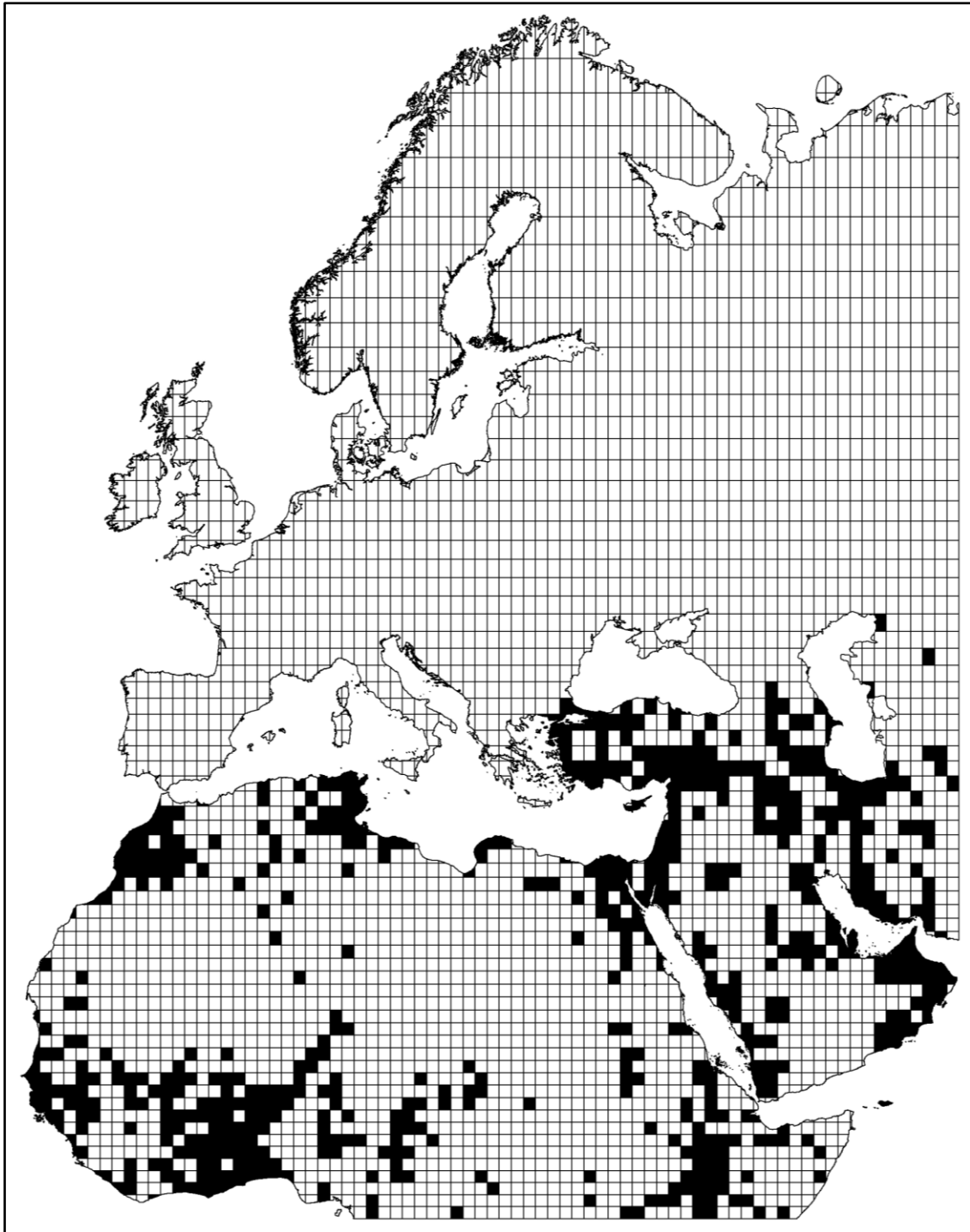
**Appendix 1.** Current House Bunting breeding presences in the study area (shown in black).  
Map projection: WGS\_1984\_World\_Mercator (ArcGIS 10.4.1).



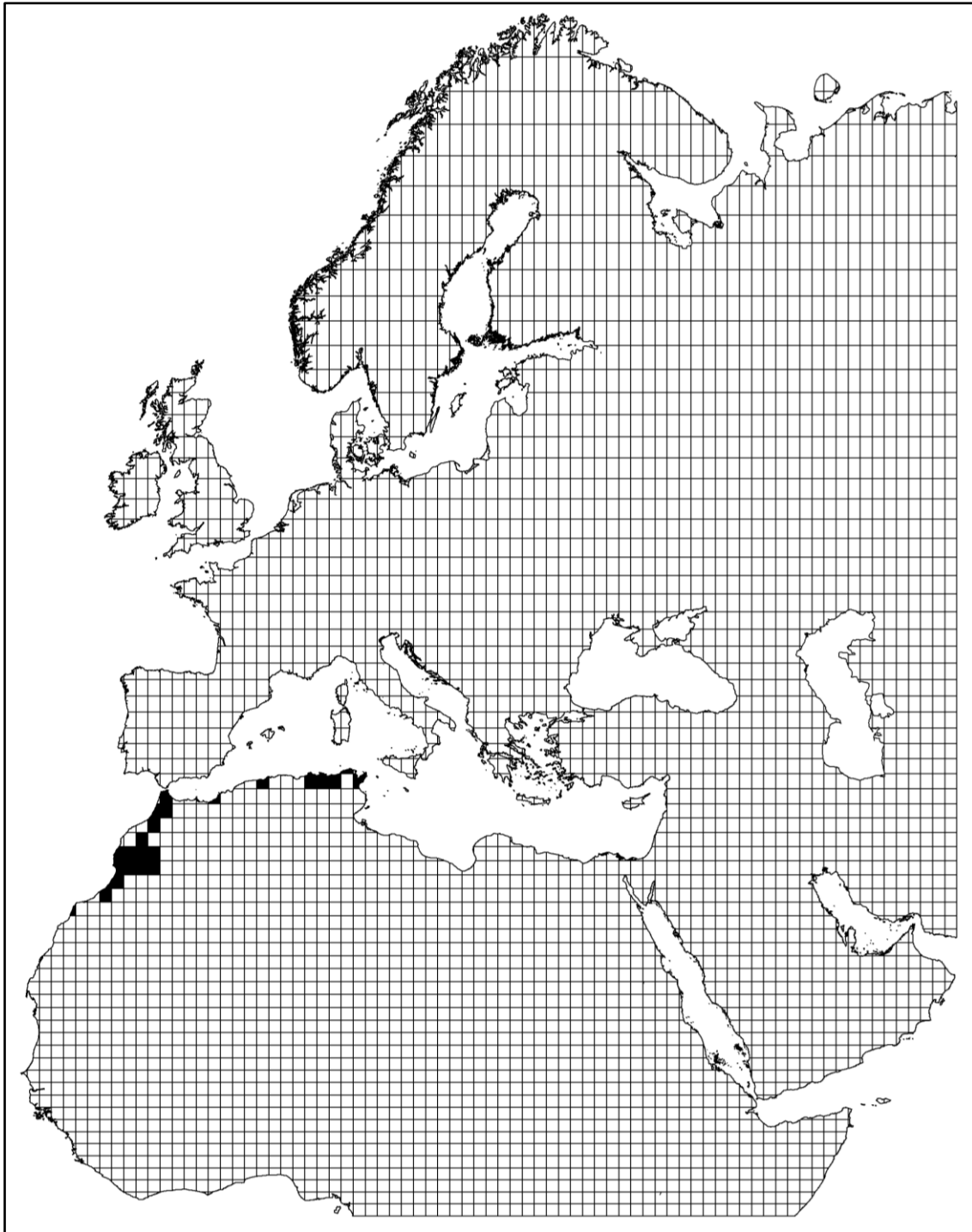
**Appendix 2.** Current Common Bulbul breeding presences in the study area (shown in black).  
Map projection: WGS\_1984\_World\_Mercator (ArcGIS 10.4.1).



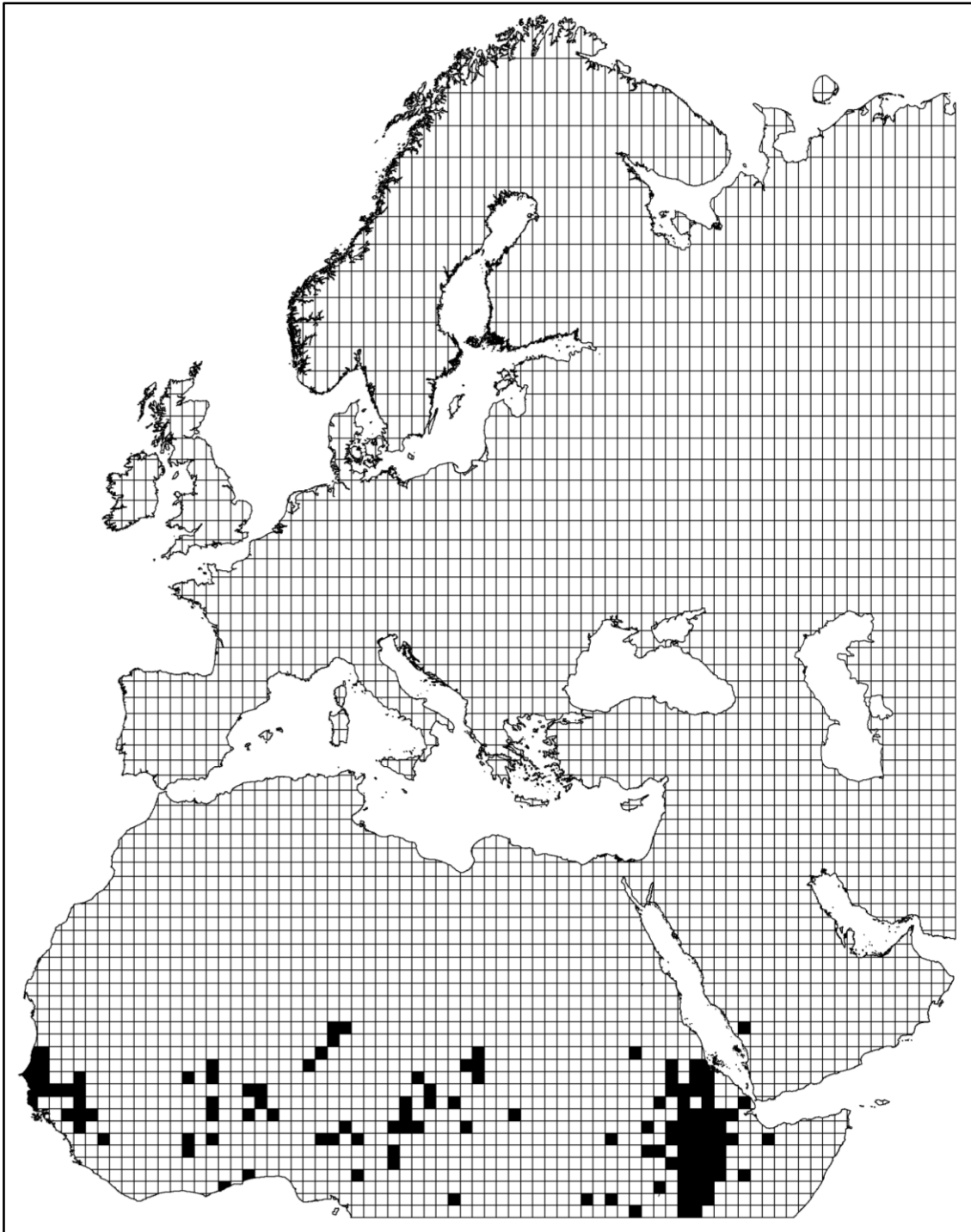
**Appendix 3.** Current Moussier's Redstart breeding presences in the study area (shown in black). Map projection: WGS\_1984\_World\_Mercator (ArcGIS 10.4.1).



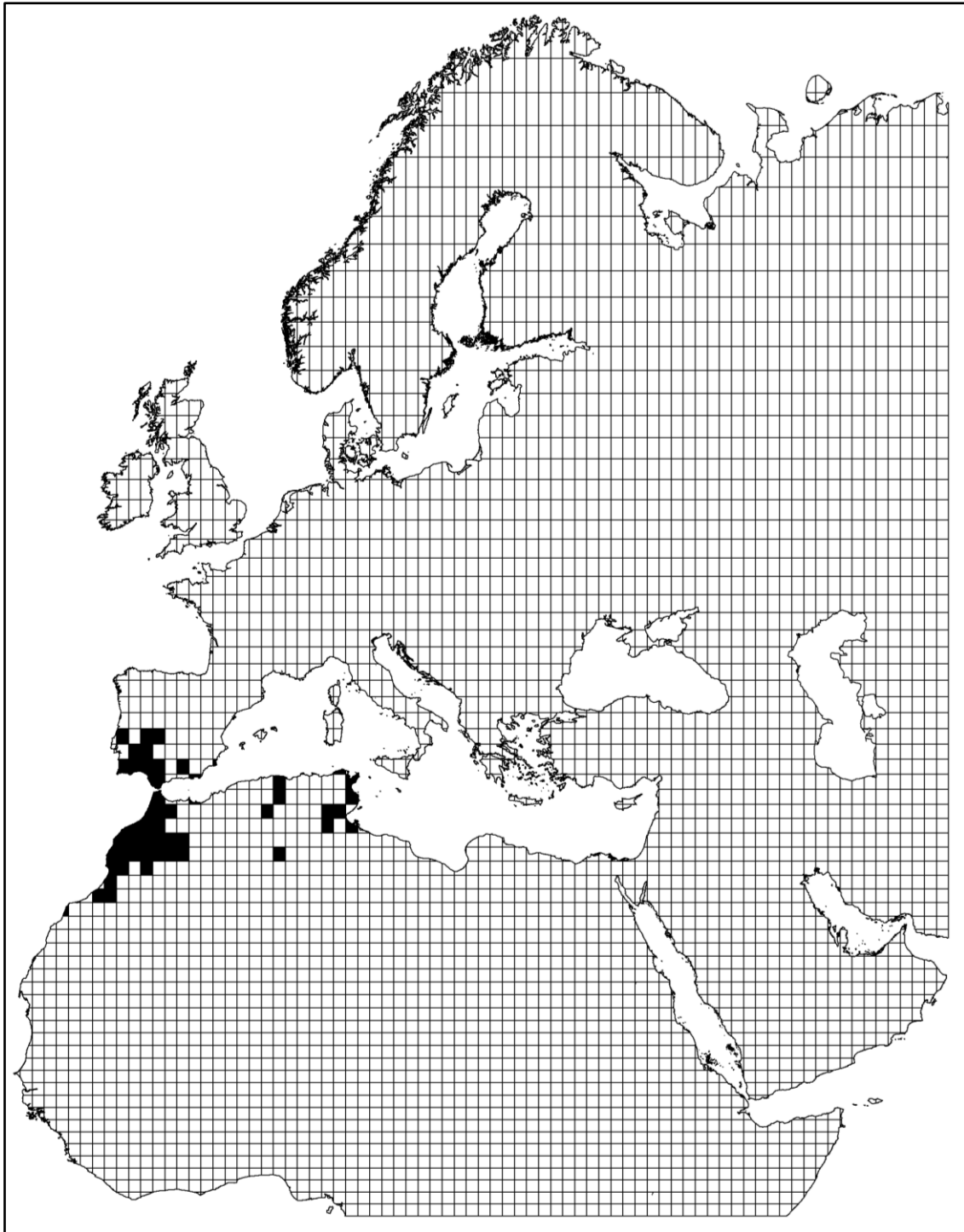
**Appendix 4.** Current Laughing Dove breeding presences in the study area (shown in black).  
Map projection: WGS\_1984\_World\_Mercator (ArcGIS 10.4.1).



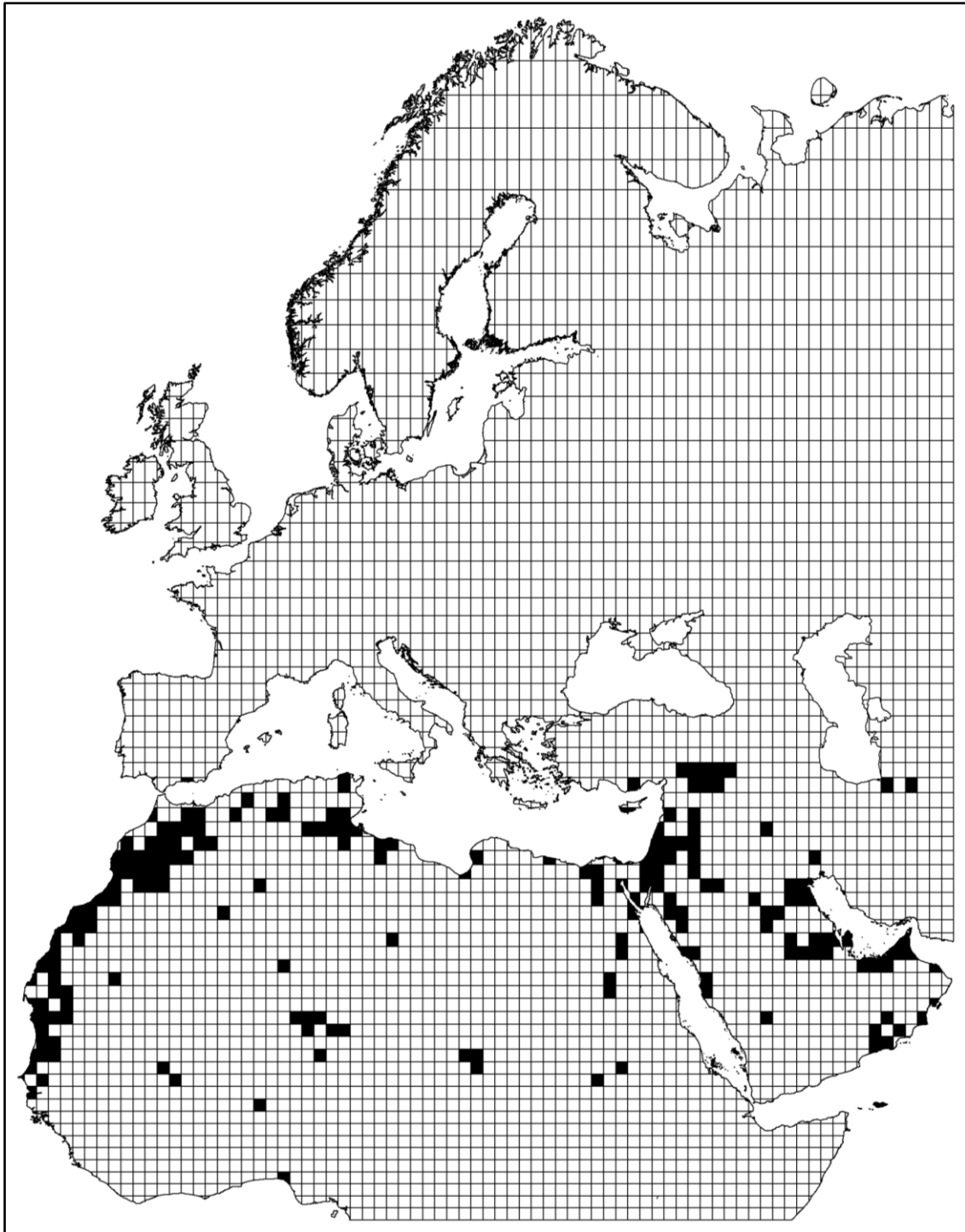
**Appendix 5.** Current Black-crowned Tchagra breeding presences in the study area (shown in black). Map projection: WGS\_1984\_World\_Mercator (ArcGIS 10.4.1).



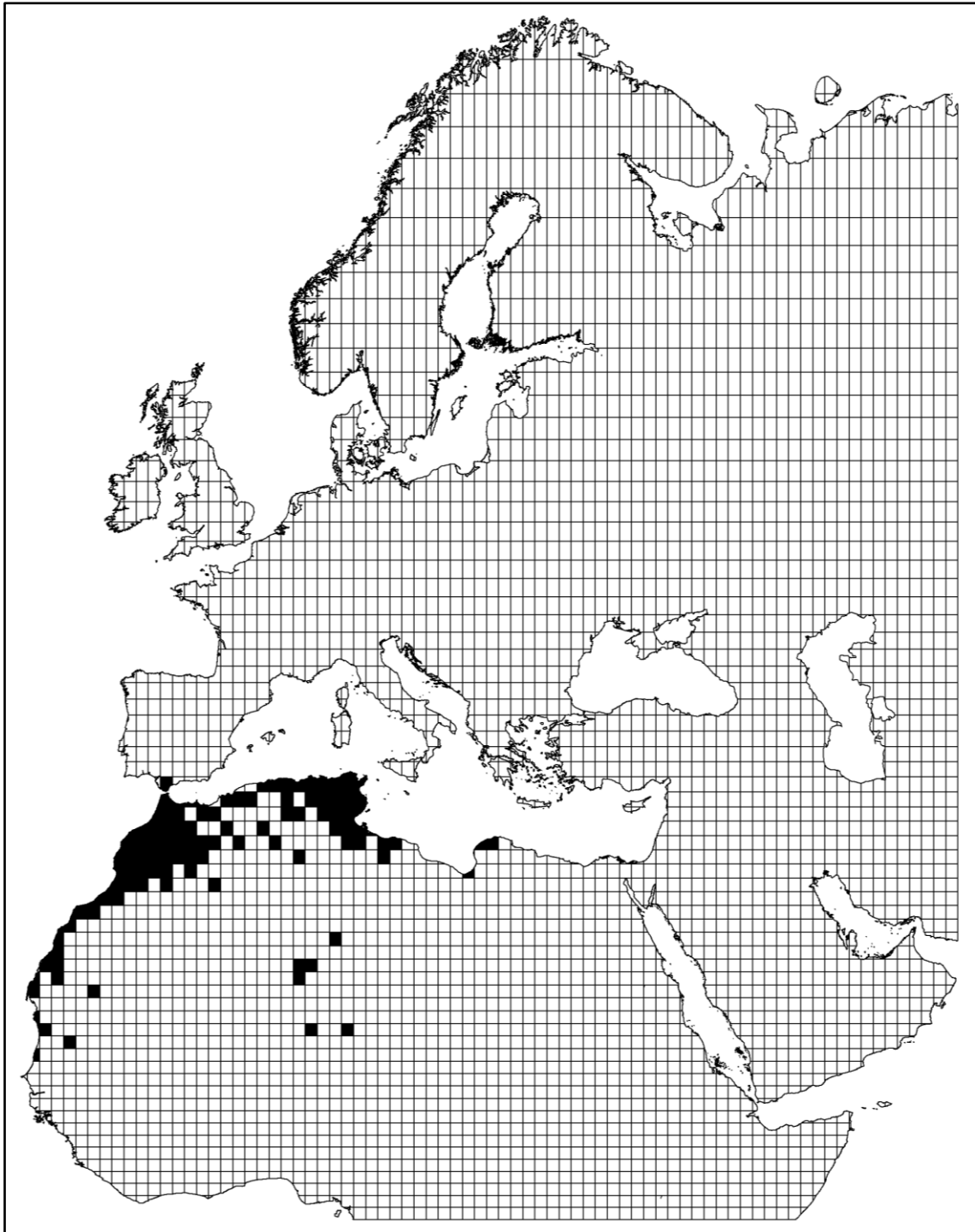
**Appendix 6.** Current Rüppell's Vulture breeding presences in the study area (shown in black).  
Map projection: WGS\_1984\_World\_Mercator (ArcGIS 10.4.1).



**Appendix 7.** Current Little Swift breeding presences in the study area (shown in black). Map projection: WGS\_1984\_World\_Mercator (ArcGIS 10.4.1).



**Appendix 8.** Current Cream-colored Courser breeding presences in the study area (shown in black). Map projection: WGS\_1984\_World\_Mercator (ArcGIS 10.4.1).



**Appendix 9.** Current Atlas Long-legged Buzzard breeding presences in the study area (shown in black). Map projection: WGS\_1984\_World\_Mercator (ArcGIS 10.4.1)

**Appendix 10.** Response of each of nine species of African birds to the different explanatory variables used in this study. Variable codes are shown in **Table 2.2.**

<b>Variable</b>	<i>E. sahari</i>	<i>P. barbatus</i>	<i>P. moussieri</i>	<i>S. senegalensis</i>	<i>T. senegalus</i>	<i>G. rueppelli</i>	<i>A. affinis</i>	<i>C. cursor</i>	<i>B. rufinus cirtensis</i>
Alti	L	L	L	L	L	L	L	L	L
Slope	L	U	U	U	U	U	U	L	U
Tmean	U	L	U	U	L	U	L	U	U
Rtday	U	L	L	U	L	U	L	U	U
Isot	L	L	L	U	L	U	L	U	L
Season	L	L	L	L	L	L	L	L	L
Tmax	U	L	U	U	L	U	L	U	U
Tmin	U	U	U	U	U	U	U	U	U
Rtan	L	L	L	L	U	U	U	L	U
Twet	L	U	U	L	U	U	U	L	U
Tdry	U	U	U	U	U	U	U	U	U
Twarm	U	L	U	U	L	U	L	U	U
Tcold	U	U	U	U	U	U	U	U	U
Prec	L	L	L	L	L	L	L	L	L
Pmax	L	L	L	L	L	L	L	L	L
Pmin	U	U	U	L	U	U	U	L	U
Cvp	L	U	U	L	L	L	L	L	L
Pwet	L	L	L	L	L	L	L	L	L
Pdry	U	U	U	L	U	L	U	L	U
Pwarm	L	U	U	L	U	L	U	L	U
Pcold	L	L	L	L	L	L	L	L	L

Note: L: Lineal; U: Unimodal

**Appendix 11.** Variables entered into the logistic regression model of the House Bunting via a forward–backward stepwise selection process, ranked by their order of entrance. The prefix “U\_” indicates that this variable had a U response for the species and is included in the model as a U variable. Variable codes are shown in **Table 2.2**.

Variable	$\beta$	S.E.	Wald	$p$	VIF
Pwarm	- 0.0163	0.00343	22.633	< 0.001	1.438
Alti	0.000621	0.000213	8.468	0.004	1.094
U_Tdry	1.238	0.334	13.740	< 0.001	1.533
Constant	0.978	1.060	0.851	0.356	

*Note:*  $\beta$ s are the coefficients in the logit function, S.E. is the standard error of these coefficients, Wald is the Wald’s statistics value (representing the relative importance of the variable in the model),  $p$  is the significance of the coefficients according to the Wald test and VIF is the variance inflation factor (used to quantify collinearity between variables in the model).

**Appendix 12.** Variables entered into the logistic regression model of the Common Bulbul via a forward–backward stepwise selection process, ranked by their order of entrance. The prefix “U\_” indicates that this variable had a U response for the species and is included in the model as a U variable. Variable codes are shown in **Table 2.2**.

Variable	$\beta$	S.E.	Wald	$p$	VIF
U_Slope	0.627	0.137	20.817	< 0.001	1.053
U_Twet	0.771	0.191	16.318	< 0.001	1.270
U_Tdry	0.487	0.296	2.699	0.1004	1.328
U_Pwarm	1.012	0.246	16.865	< 0.001	1.120
Constant	7.785	1.244	39.147	< 0.001	

*Note:*  $\beta$ s are the coefficients in the logit function, S.E. is the standard error of these coefficients, Wald is the Wald’s statistics value (representing the relative importance of the variable in the model),  $p$  is the significance of the coefficients according to the Wald test and VIF is the variance inflation factor (used to quantify collinearity between variables in the model).

**Appendix 13.** Variables entered into the logistic regression model of the Moussier's Redstart via a forward–backward stepwise selection process, ranked by their order of entrance. The prefix “U\_” indicates that this variable had a U response for the species and is included in the model as a U variable. Variable codes are shown in **Table 2.2**.

Variable	$\beta$	S.E.	Wald	$p$	VIF
U_Tdry	0.675	0.302	4.995	0.025	1.314
U_Twet	0.987	0.187	27.853	< 0.001	1.239
U_Slope	0.567	0.157	13.009	< 0.001	1.035
U_Pwarm	1.291	0.237	29.624	< 0.001	1.129
Constant	9.285	1.295	51.395	< 0.001	

Note:  $\beta$ s are the coefficients in the logit function, S.E. is the standard error of these coefficients, Wald is the Wald's statistics value (representing the relative importance of the variable in the model),  $p$  is the significance of the coefficients according to the Wald test and VIF is the variance inflation factor (used to quantify collinearity between variables in the model).

**Appendix 14.** Variables entered into the logistic regression model of the Laughing Dove via a forward–backward stepwise selection process, ranked by their order of entrance. The prefix “U\_” indicates that this variable had a U response for the species and is included in the model as a U variable. Variable codes are shown in **Table 2.2**.

Variable	$\beta$	S.E.	Wald	$p$	VIF
U_Tdry	0.737	0.126	33.931	< 0.001	3.015
U_Slope	1.206	0.145	69.209	< 0.001	1.528
U_Rtday	0.401	0.0647	38.399	< 0.001	2.039
Cvp	0.00731	0.00195	14.004	< 0.001	2.961
Twet	- 0.0636	0.00992	41.113	< 0.001	2.422
Season	- 0.00105	0.000287	13.304	< 0.001	3.406
Alti	- 0.000322	0.000127	6.366	0.012	1.465
Pmin	- 0.0183	0.00685	7.101	0.008	3.177
Pmax	0.00275	0.000821	11.191	< 0.001	4.071
Pcold	- 0.000924	0.000332	7.763	0.005	3.392
Constant	3.597	0.411	76.665	< 0.001	

Note:  $\beta$ s are the coefficients in the logit function, S.E. is the standard error of these coefficients, Wald is the Wald's statistics value (representing the relative importance of the variable in the model),  $p$  is the significance of the coefficients according to the Wald test and VIF is the variance inflation factor (used to quantify collinearity between variables in the model).

**Appendix 15.** Variables entered into the logistic regression model of the Black-crowned Tchagra via a forward–backward stepwise selection process, ranked by their order of entrance. The prefix “U\_” indicates that this variable had a U response for the species and is included in the model as a U variable. Variable codes are shown in **Table 2.2**.

Variable	$\beta$	S.E.	Wald	$p$	VIF
U_Slope	0.502	0.182	7.653	0.006	1.101
U_Twet	0.646	0.263	6.050	0.014	1.314
U_Tdry	0.712	0.262	7.366	0.007	1.270
Constant	5.036	1.637	9.467	0.002	

Note:  $\beta$ s are the coefficients in the logit function, S.E. is the standard error of these coefficients, Wald is the Wald's statistics value (representing the relative importance of the variable in the model),  $p$  is the significance of the coefficients according to the Wald test and VIF is the variance inflation factor (used to quantify collinearity between variables in the model).

**Appendix 16.** Variables entered into the logistic regression model of the Rüppell's Vulture via a forward–backward stepwise selection process, ranked by their order of entrance. The prefix “U\_” indicates that this variable had a U response for the species and is included in the model as a U variable. Variable codes are shown in **Table 2.2**.

Variable	$\beta$	S.E.	Wald	$p$	VIF
U_Isot	1.500	0.183	67.272	< 0.001	5.968
Cvp	0.0192	0.00460	17.324	< 0.001	2.299
U_Slope	2.764	0.306	81.760	< 0.001	1.237
U_Rtday	0.463	0.168	7.618	0.006	1.887
U_Twet	- 0.535	0.135	15.609	< 0.001	1.685
Pcold	- 0.00131	0.000477	7.581	0.006	1.313
U_Tdry	- 0.631	0.293	4.636	0.031	3.288
Constant	7.211	1.262	32.623	< 0.001	

*Note:*  $\beta$ s are the coefficients in the logit function, S.E. is the standard error of these coefficients, Wald is the Wald's statistics value (representing the relative importance of the variable in the model),  $p$  is the significance of the coefficients according to the Wald test and VIF is the variance inflation factor (used to quantify collinearity between variables in the model).

**Appendix 17.** Variables entered into the logistic regression model of the Little Swift via a forward–backward stepwise selection process, ranked by their order of entrance. The prefix “U\_” indicates that this variable had a U response for the species and is included in the model as a U variable. Variable codes are shown in **Table 2.2**.

Variable	$\beta$	S.E.	Wald	$p$	VIF
U_Twet	0.743	0.207	12.914	< 0.001	1.308
U_Tdry	0.460	0.267	2.969	0.085	1.348
U_Slope	0.373	0.184	4.117	0.042	1.091
U_Pwarm	1.036	0.236	19.264	< 0.001	1.114
Constant	7.100	1.317	29.050	< 0.001	

*Note:*  $\beta$ s are the coefficients in the logit function, S.E. is the standard error of these coefficients, Wald is the Wald's statistics value (representing the relative importance of the variable in the model),  $p$  is the significance of the coefficients according to the Wald test and VIF is the variance inflation factor (used to quantify collinearity between variables in the model).

**Appendix 18.** Variables entered into the logistic regression model of the Cream-colored Courser via a forward–backward stepwise selection process, ranked by their order of entrance. The prefix “U\_” indicates that this variable had a U response for the species and is included in the model as a U variable. Variable codes are shown in **Table 2.2**.

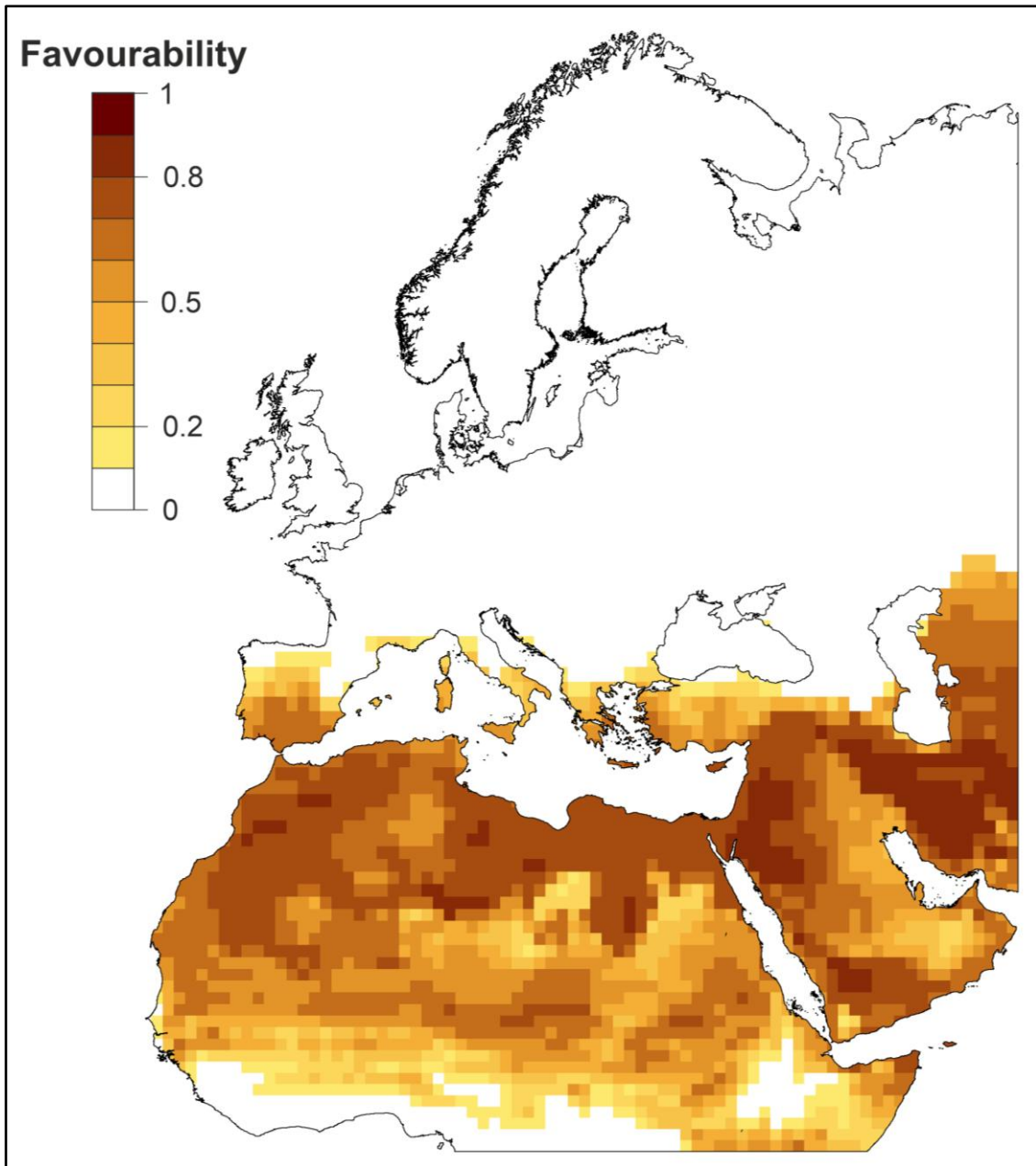
Variable	$\beta$	S.E.	Wald	$p$	VIF
Pwarm	- 0.00888	0.00273	10.546	0.0012	1.892
U_Isot	0.505	0.122	17.138	< 0.001	2.436
U_Tdry	0.731	0.160	20.797	< 0.001	2.023
Constant	0.952	0.497	3.671	0.055	

*Note:*  $\beta$ s are the coefficients in the logit function, S.E. is the standard error of these coefficients, Wald is the Wald’s statistics value (representing the relative importance of the variable in the model),  $p$  is the significance of the coefficients according to the Wald test and VIF is the variance inflation factor (used to quantify collinearity between variables in the model).

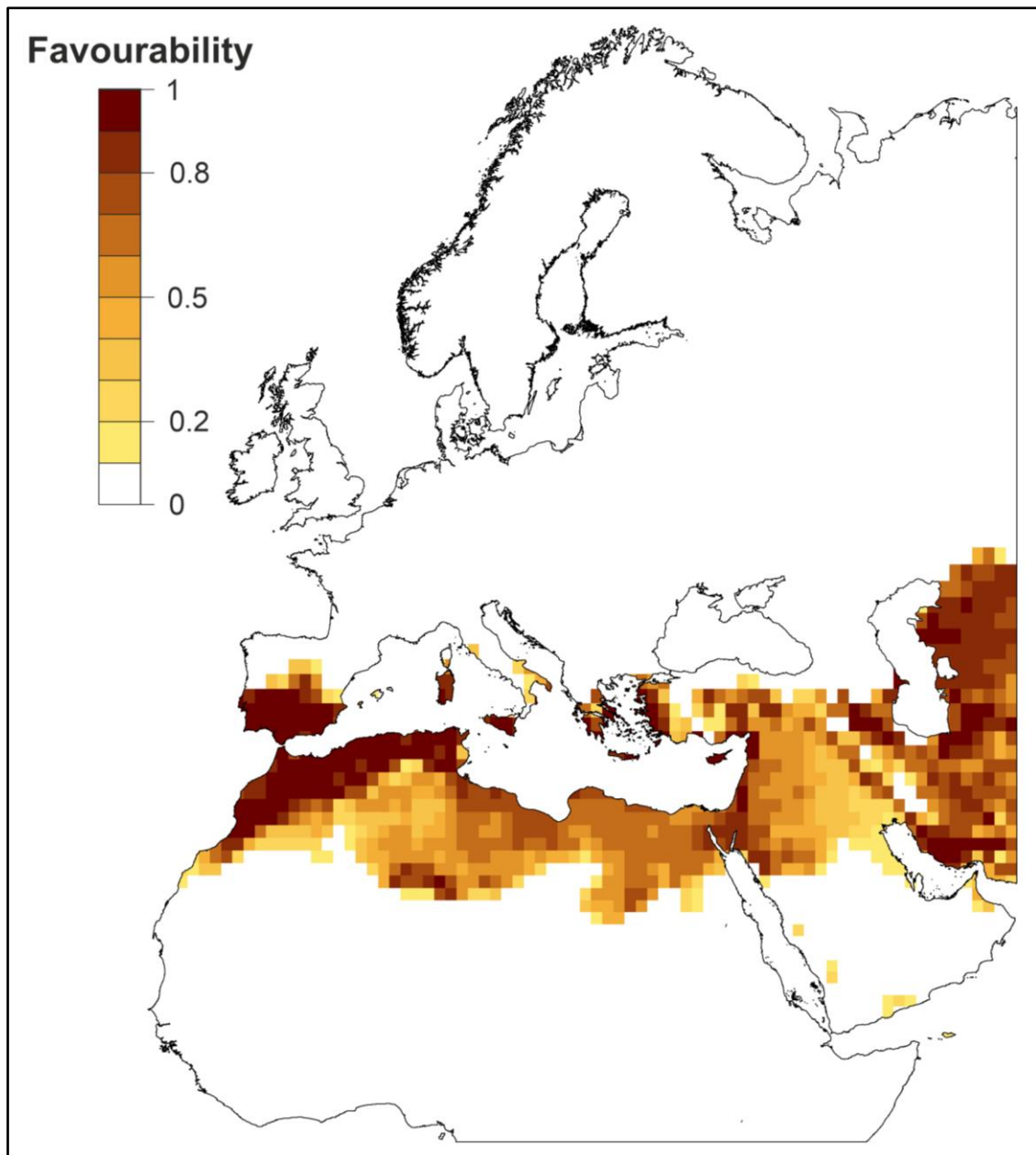
**Appendix 19.** Variables entered into the logistic regression model of the Atlas Long-legged Buzzard via a forward–backward stepwise selection process, ranked by their order of entrance. The prefix “U\_” indicates that this variable had a U response for the species and is included in the model as a U variable. Variable codes are shown in **Table 2.2**.

Variable	$\beta$	S.E.	Wald	$p$	VIF
U_Tdry	1.020	0.261	15.291	< 0.001	1.286
U_Twet	1.404	0.217	41.809	< 0.001	1.214
U_Slope	0.532	0.172	9.555	0.002	1.035
U_Pwarm	1.052	0.285	13.679	< 0.001	1.116
Constant	10.276	1.325	60.105	< 0.001	

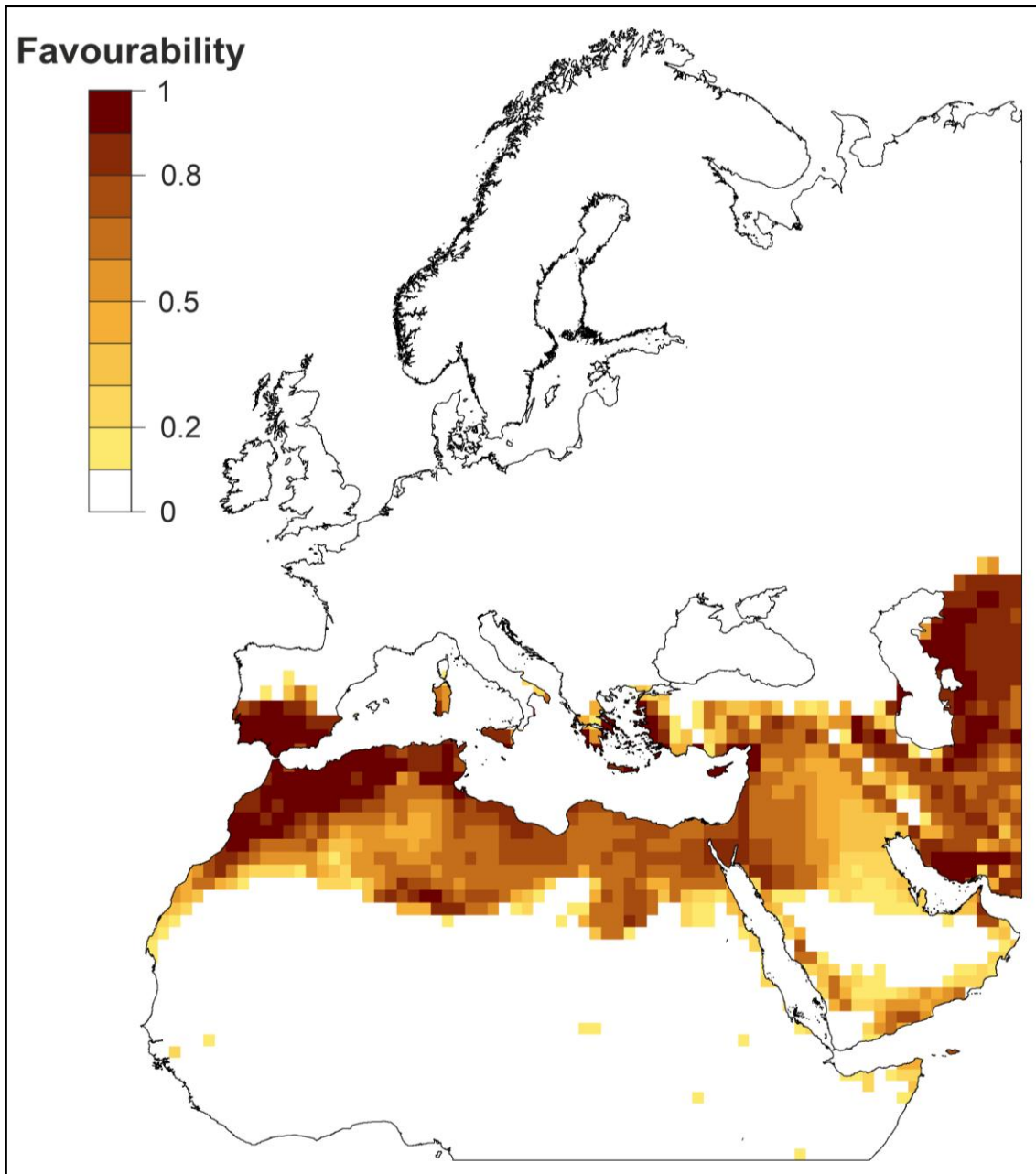
*Note:*  $\beta$ s are the coefficients in the logit function, S.E. is the standard error of these coefficients, Wald is the Wald’s statistics value (representing the relative importance of the variable in the model),  $p$  is the significance of the coefficients according to the Wald test and VIF is the variance inflation factor (used to quantify collinearity between variables in the model).



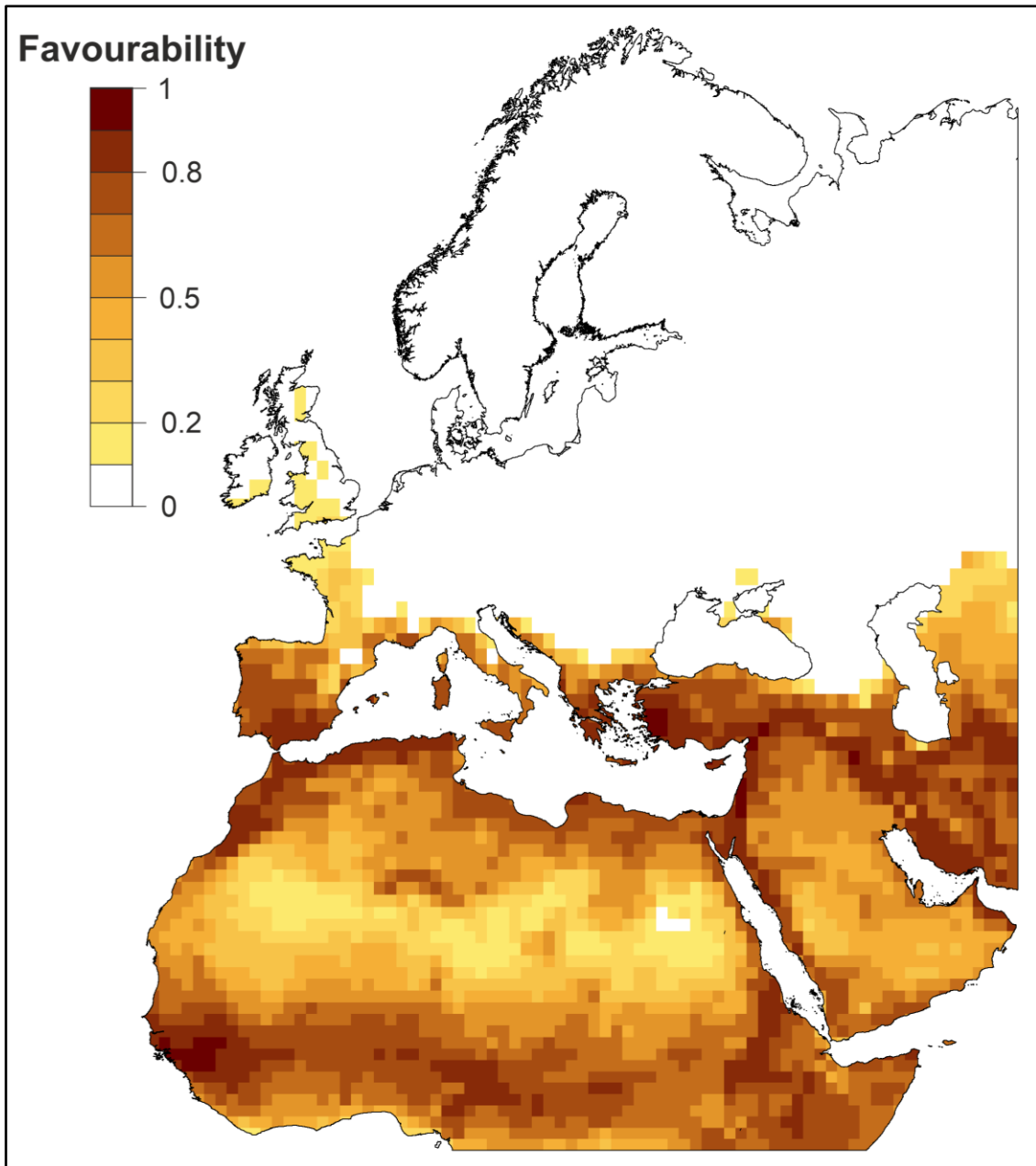
**Appendix 20.** Current climatic favourability for House Bunting breeding in each operational geographic unit of the study area.



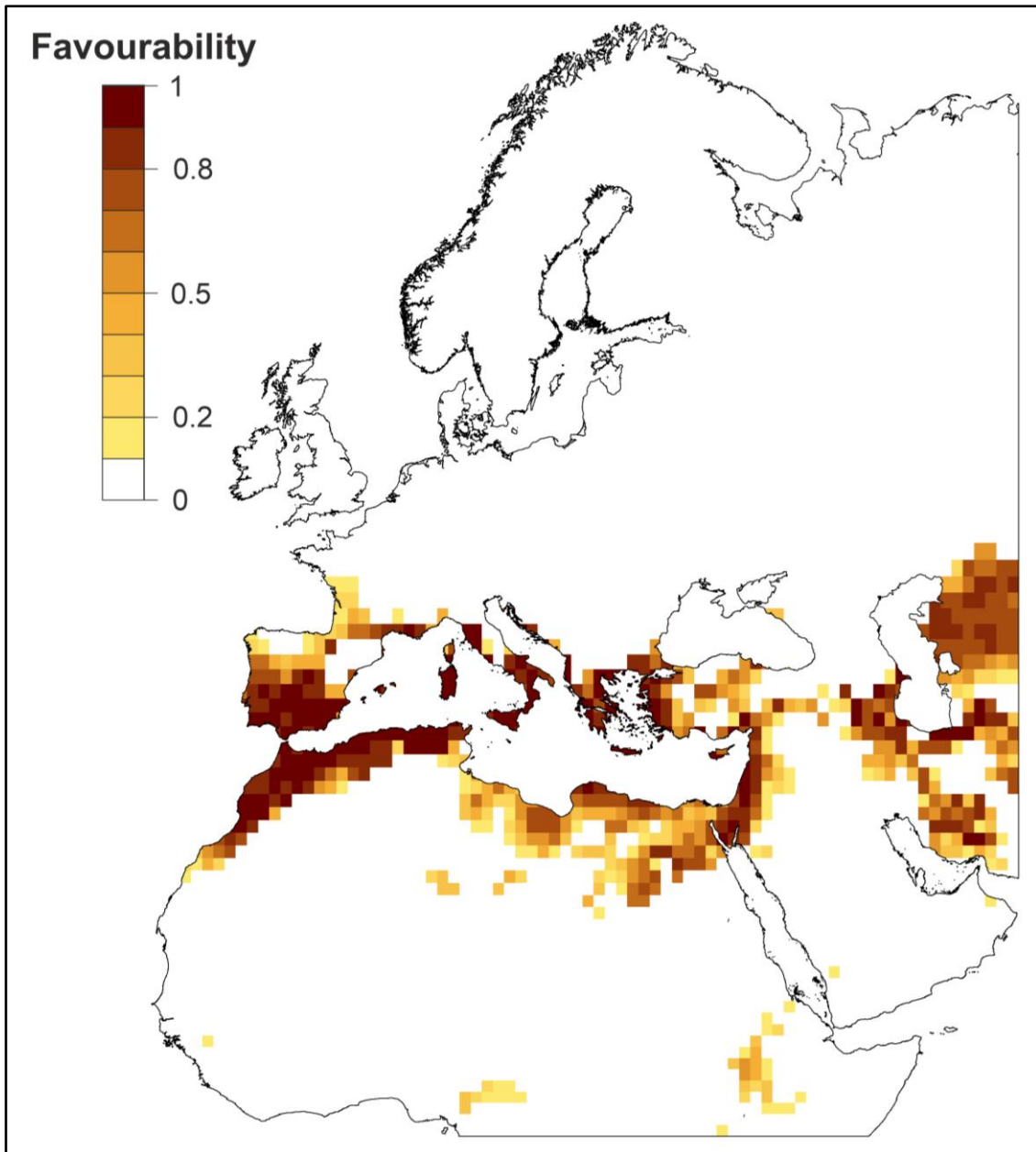
**Appendix 21.** Current climatic favourability for Common Bulbul breeding in each operational geographic unit of the study area.



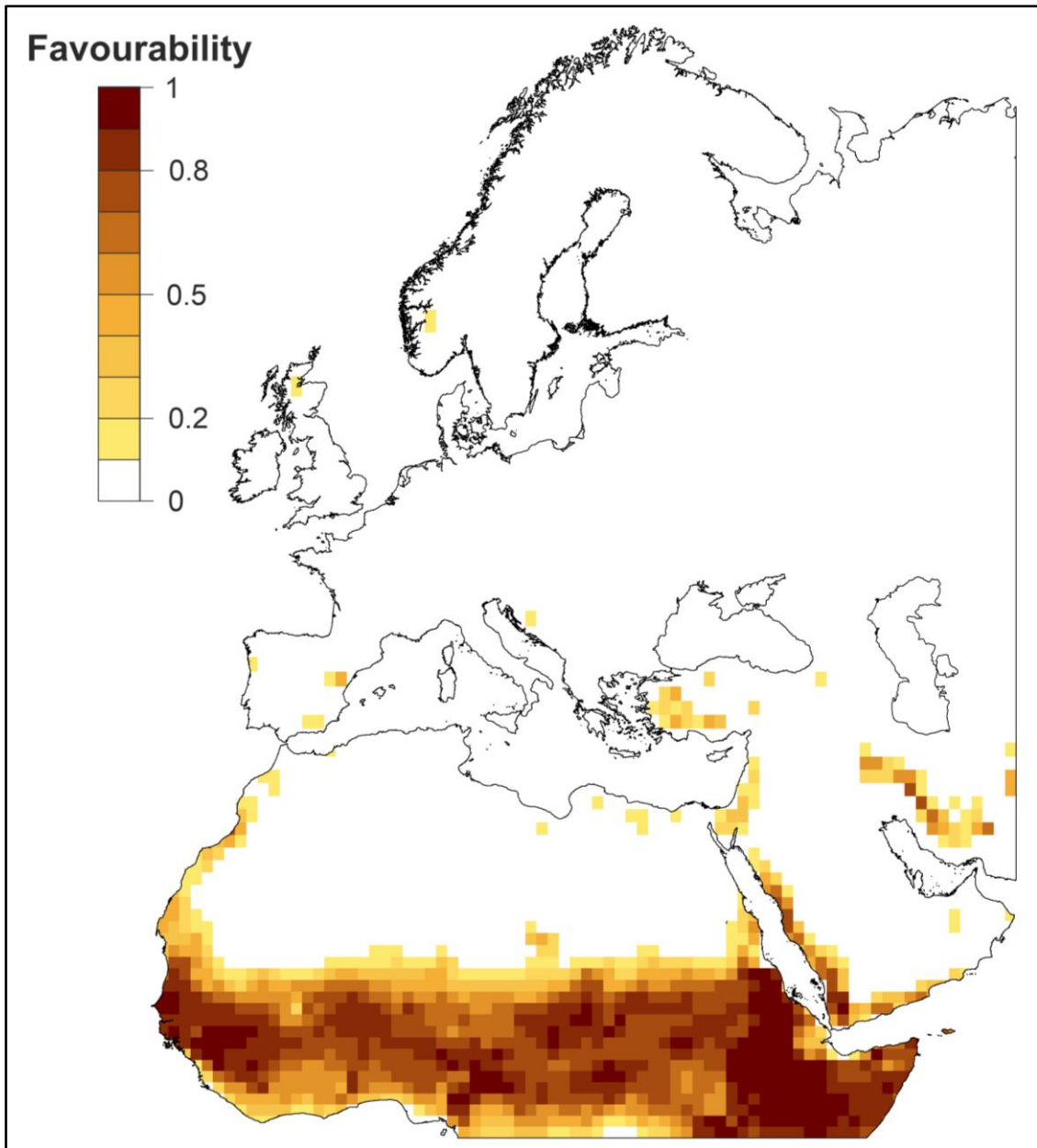
**Appendix 22.** Current climatic favourability for Moussier's Redstart breeding in each operational geographic unit of the study area.



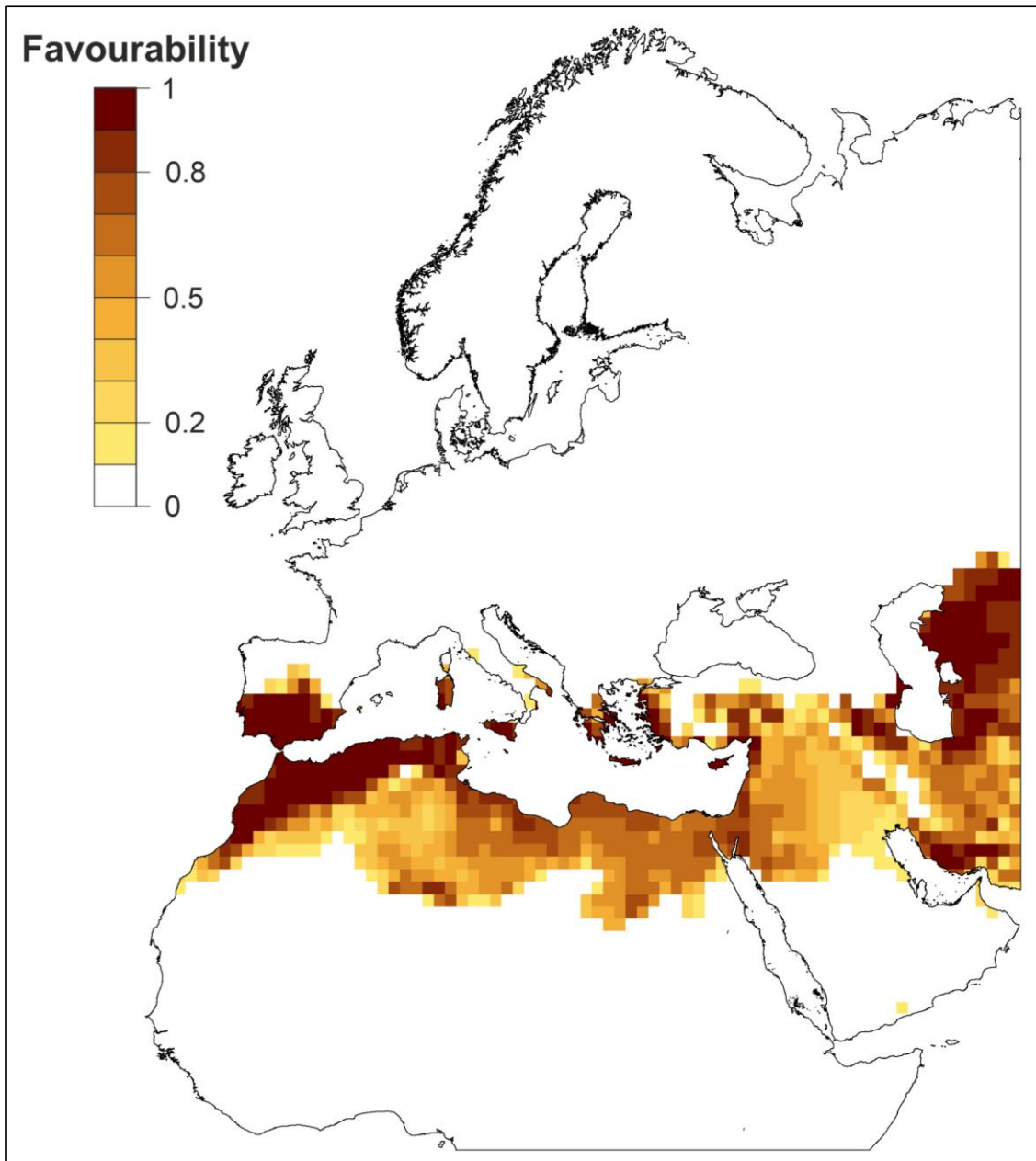
**Appendix 23.** Current climatic favourability for Laughing Dove breeding in each operational geographic unit of the study area.



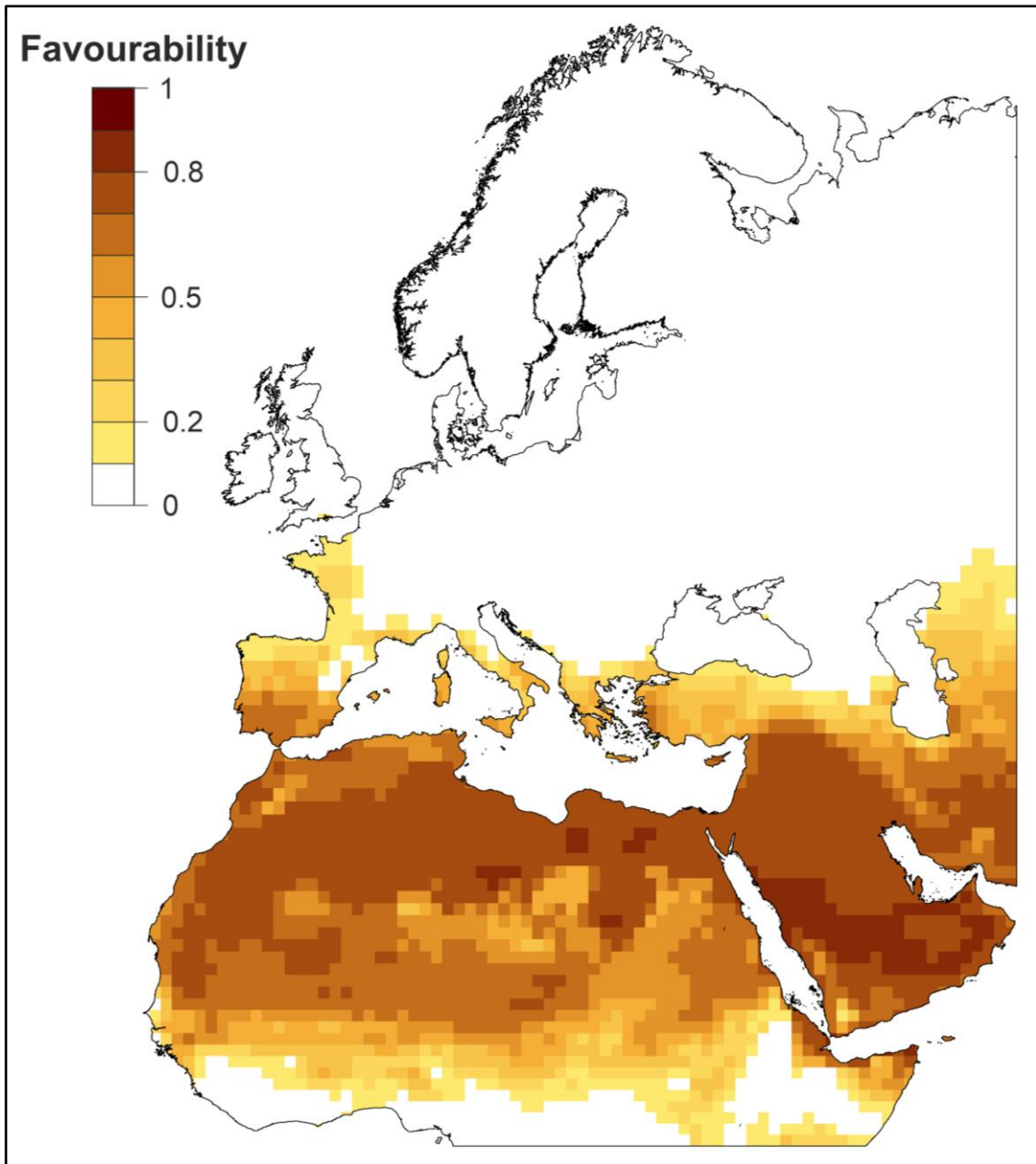
**Appendix 24.** Current climatic favourability for Black-crowned Tchagra breeding in each operational geographic unit of the study area.



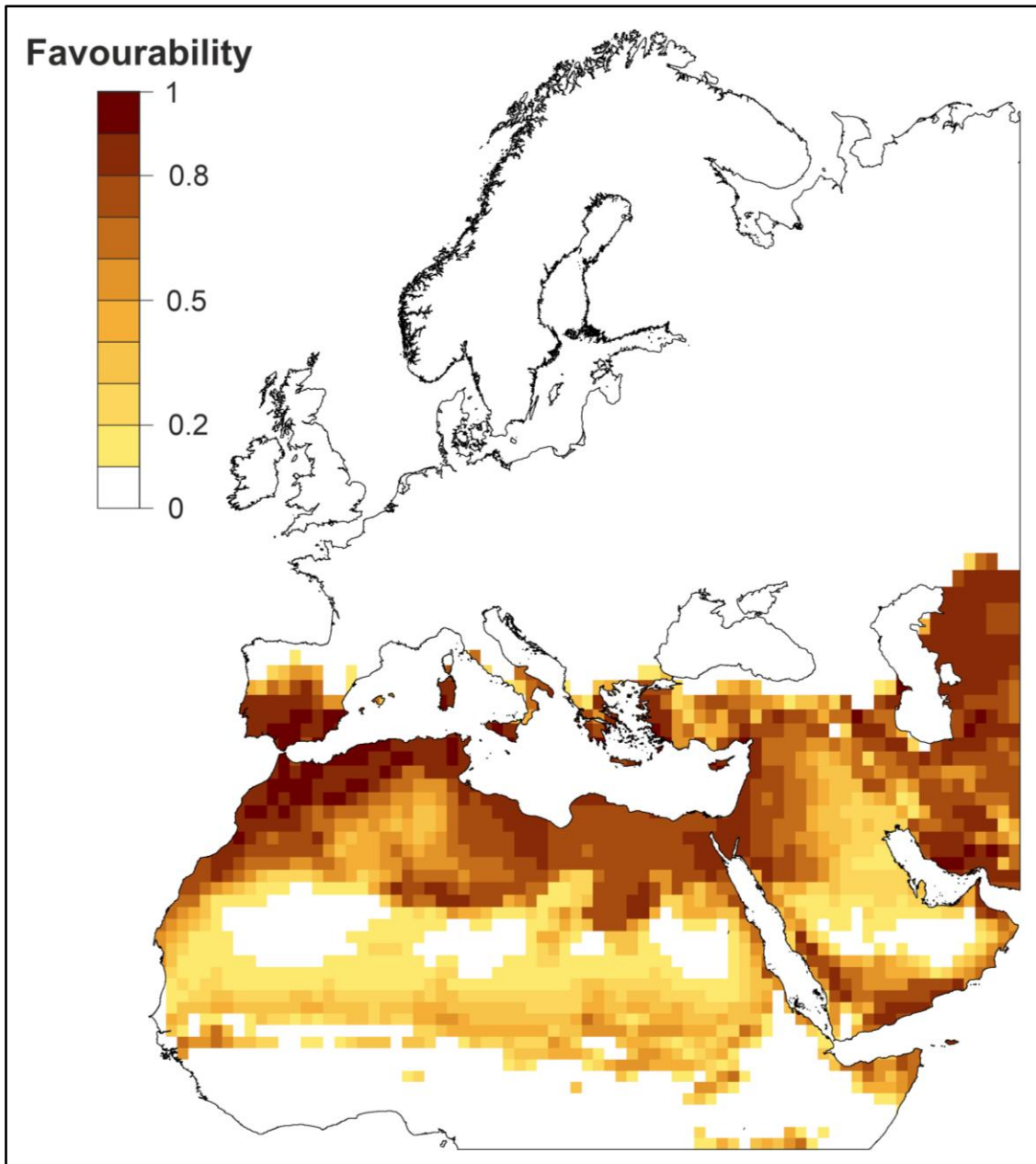
**Appendix 25.** Current climatic favourability for Rüppell's Vulture breeding in each operational geographic unit of the study area.



**Appendix 26.** Current climatic favourability for Little Swift breeding in each operational geographic unit of the study area.



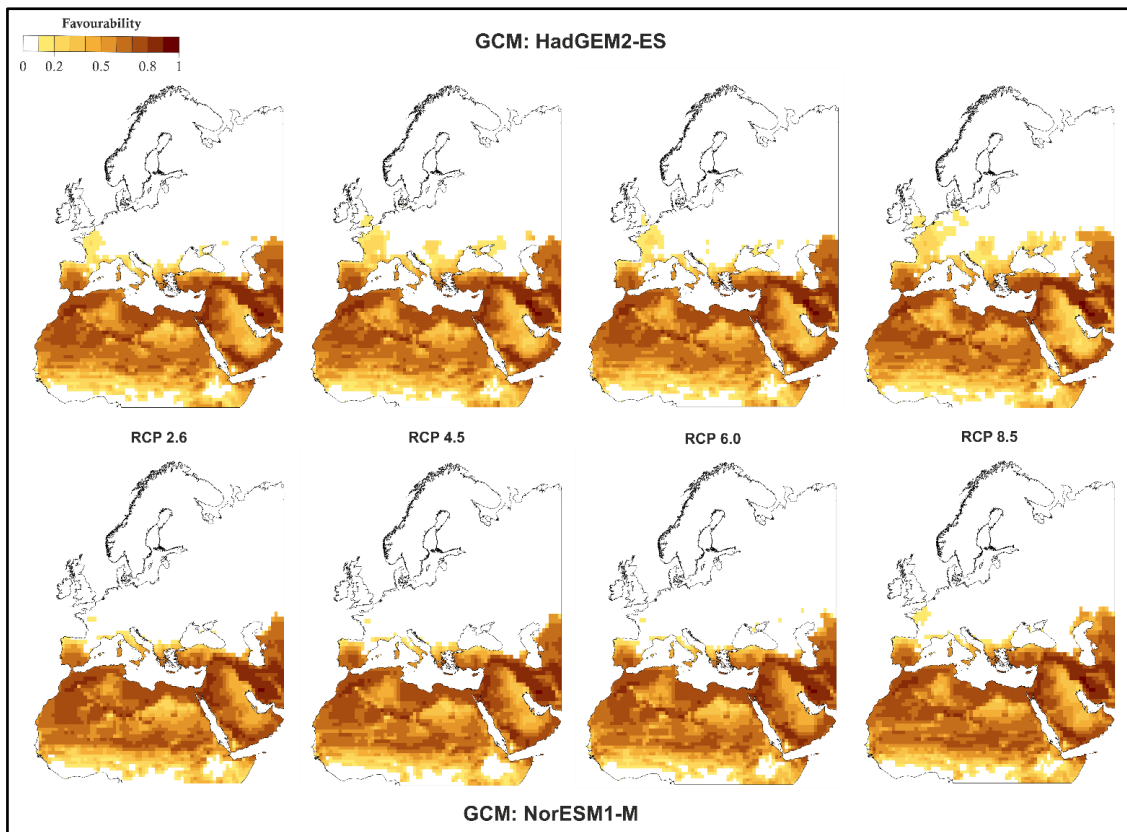
**Appendix 27.** Current climatic favourability for Cream-colored Courser breeding in each operational geographic unit of the study area.



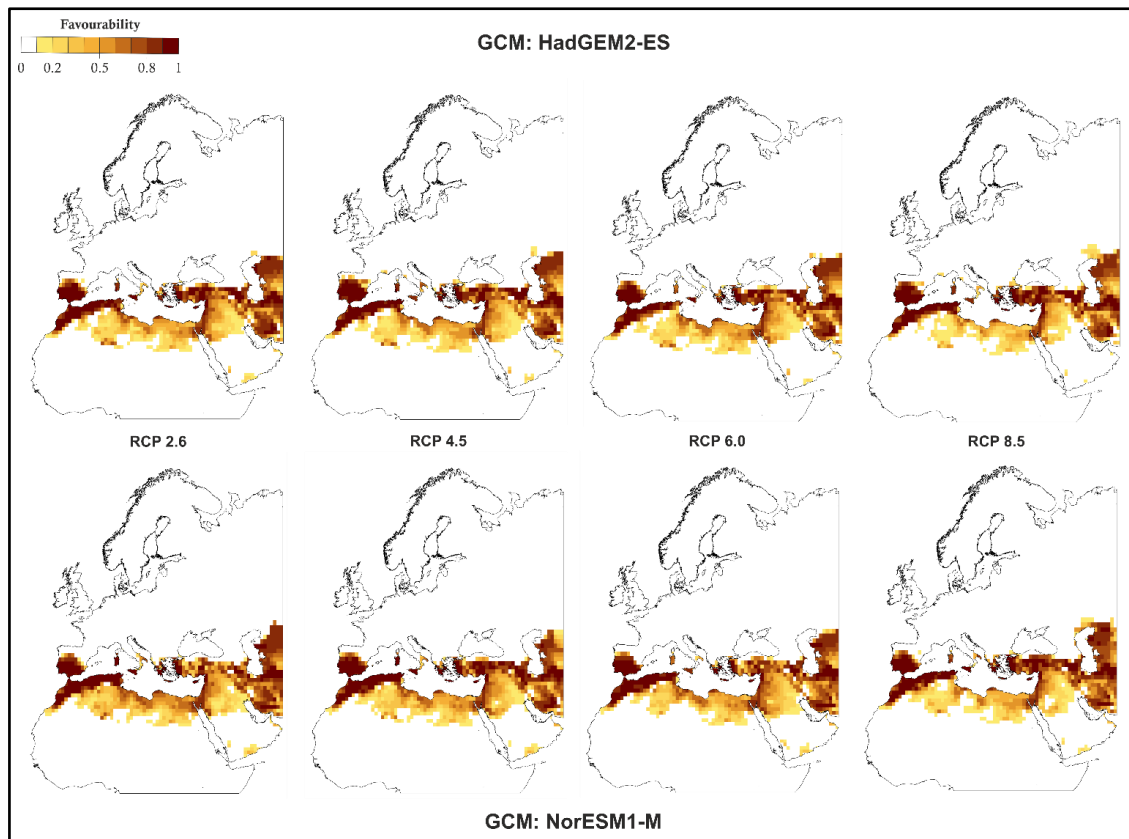
**Appendix 28.** Current climatic favourability for Atlas Long-legged Buzzard breeding in each operational geographic unit of the study area.

**Appendix 29.** Assessment of the climatic favourability models for each of the nine species according to their discrimination and classification capacities. Assessment indices: area under the curve (AUC), sensitivity, specificity, correct classification rate (CCR), over-prediction rate (OPR), under-prediction rate (UPR) and Cohen's Kappa index (Kappa).

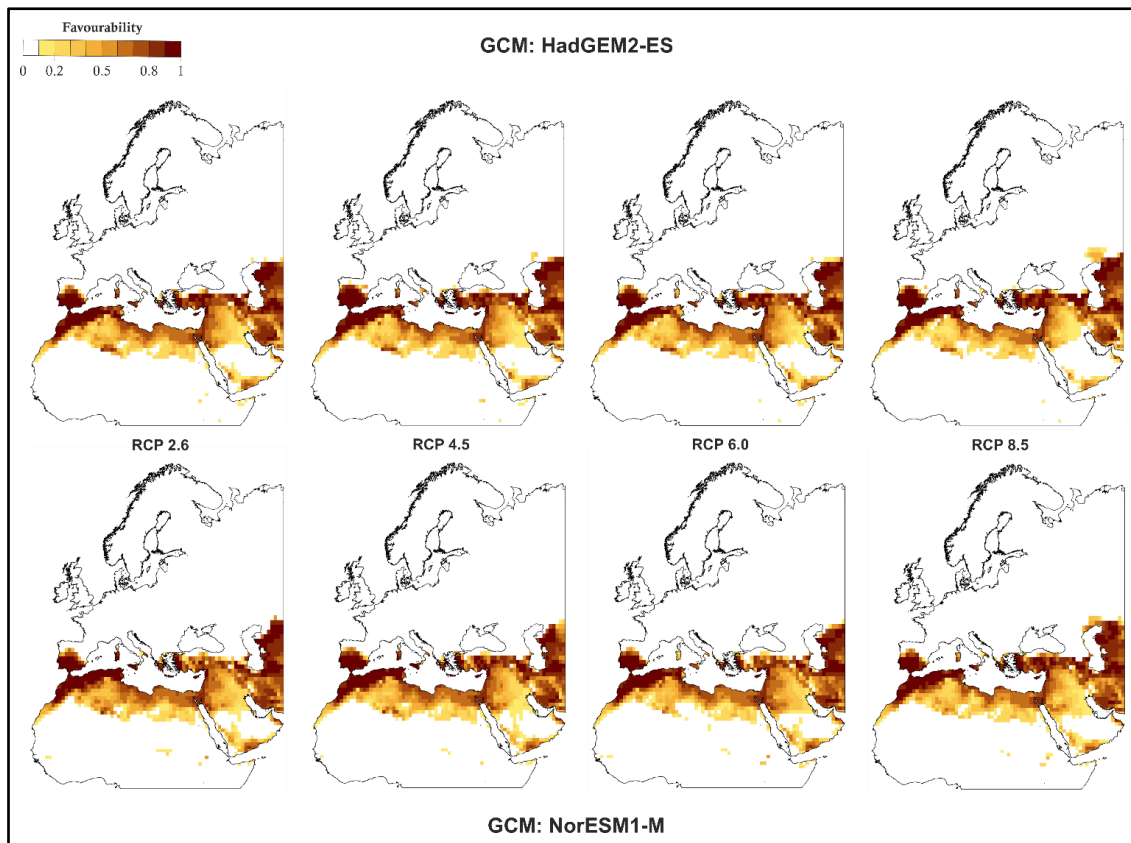
<b>Measure</b>	<i>E. sahari</i>	<i>P. barbatus</i>	<i>P. moussieri</i>	<i>S. senegalensis</i>	<i>T. senegalus</i>	<i>G. rueppelli</i>	<i>A. affinis</i>	<i>C. cursor</i>	<i>B. rufinus cirtensis</i>
AUC	0.830	0.957	0.949	0.833	0.967	0.954	0.960	0.821	0.911
Sensitivity	0.933	0.932	0.968	0.879	0.923	0.929	0.914	0.950	0.901
Specificity	0.607	0.842	0.818	0.639	0.882	0.843	0.854	0.635	0.765
CCR	0.615	0.843	0.822	0.678	0.882	0.845	0.855	0.651	0.769
OPR	0.943	0.905	0.892	0.680	0.953	0.845	0.919	0.874	0.897
UPR	0.0028	0.0014	0.0009	0.0354	0.0005	0.0026	0.0014	0.0044	0.0039
Kappa	0.064	0.145	0.161	0.304	0.078	0.226	0.127	0.143	0.140



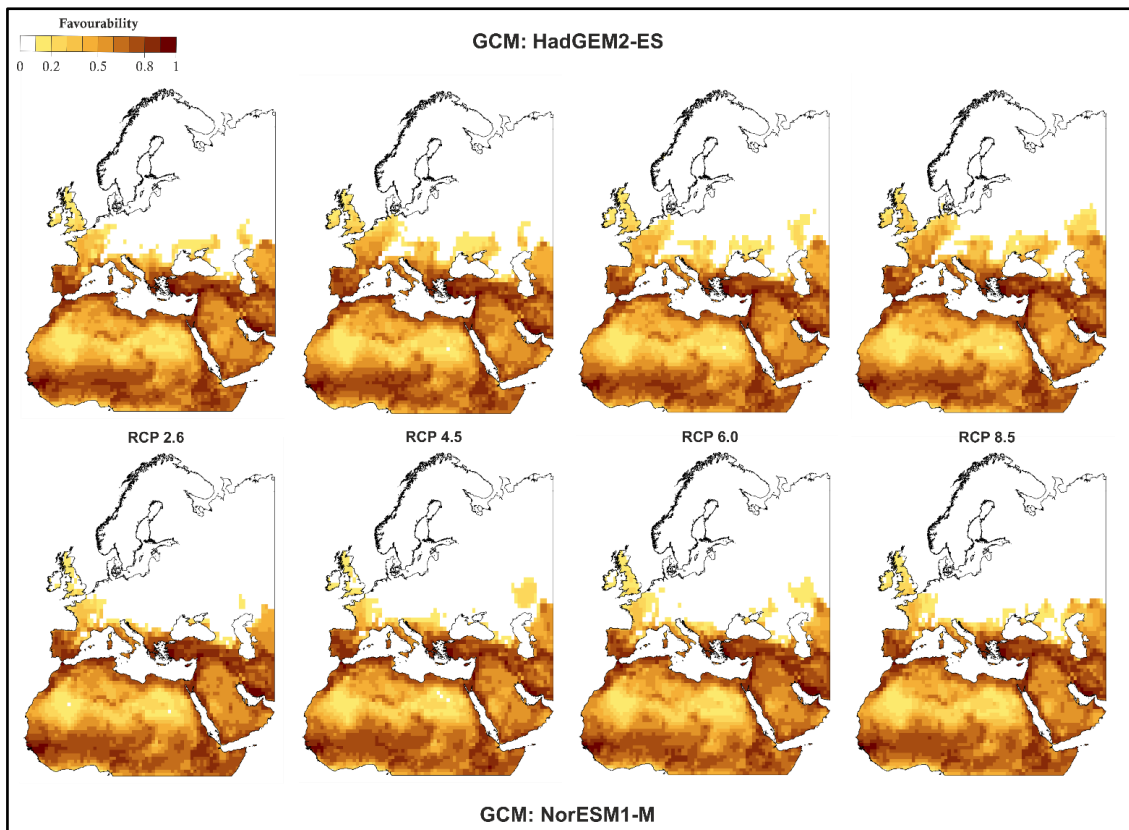
**Appendix 30.** Future climatic favourability for House Bunting breeding in each operational geographic unit of the study area, for the period 2041–2060, based on the results of the Global Circulation Models (GCMs) HadGEM2-ES and NorESM1-M, and the Representative Concentration Pathways (RCPs) 2.6, 4.5, 6.0 and 8.5.



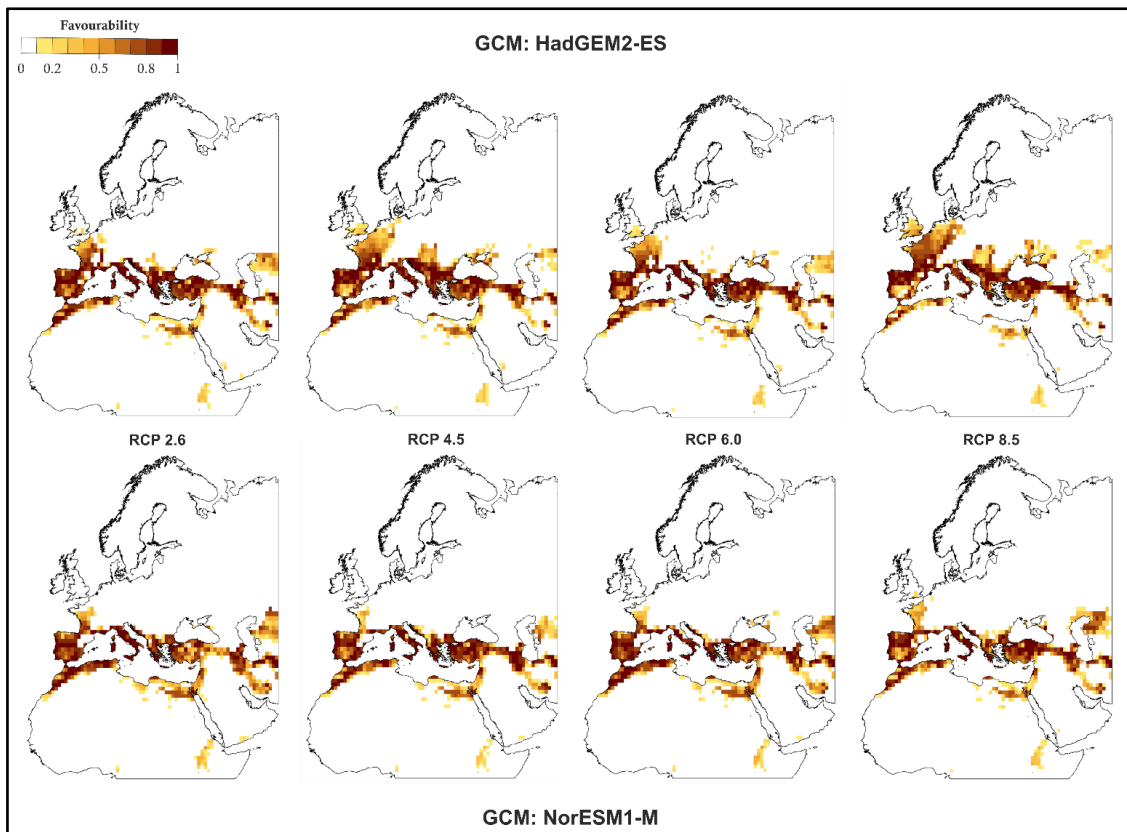
**Appendix 31.** Future climatic favourability for Common Bulbul breeding in each operational geographic unit of the study area, for the period 2041–2060, based on the results of the Global Circulation Models (GCMs) HadGEM2-ES and NorESM1-M, and the Representative Concentration Pathways (RCPs) 2.6, 4.5, 6.0 and 8.5.



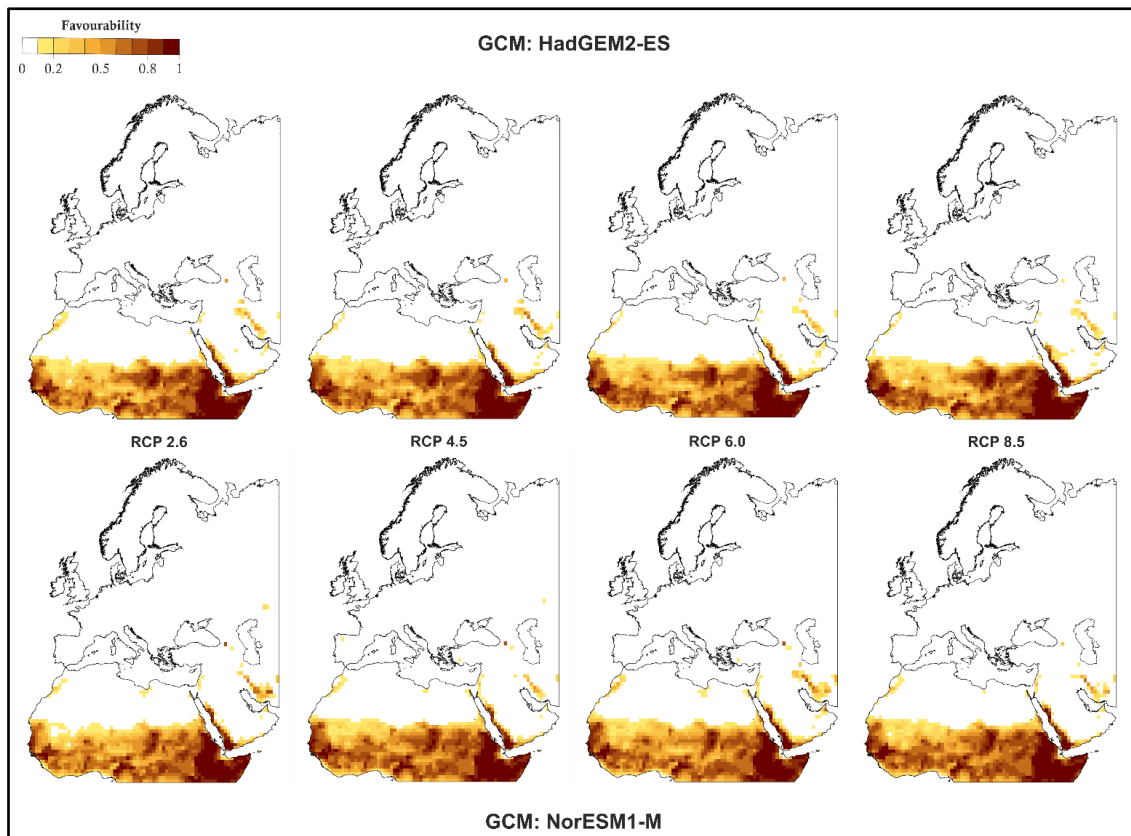
**Appendix 32.** Future climatic favourability for Moussier's Redstart breeding in each operational geographic unit of the study area, for the period 2041–2060, based on the results of the Global Circulation Models (GCMs) HadGEM2-ES and NorESM1-M, and the Representative Concentration Pathways (RCPs) 2.6, 4.5, 6.0 and 8.5.



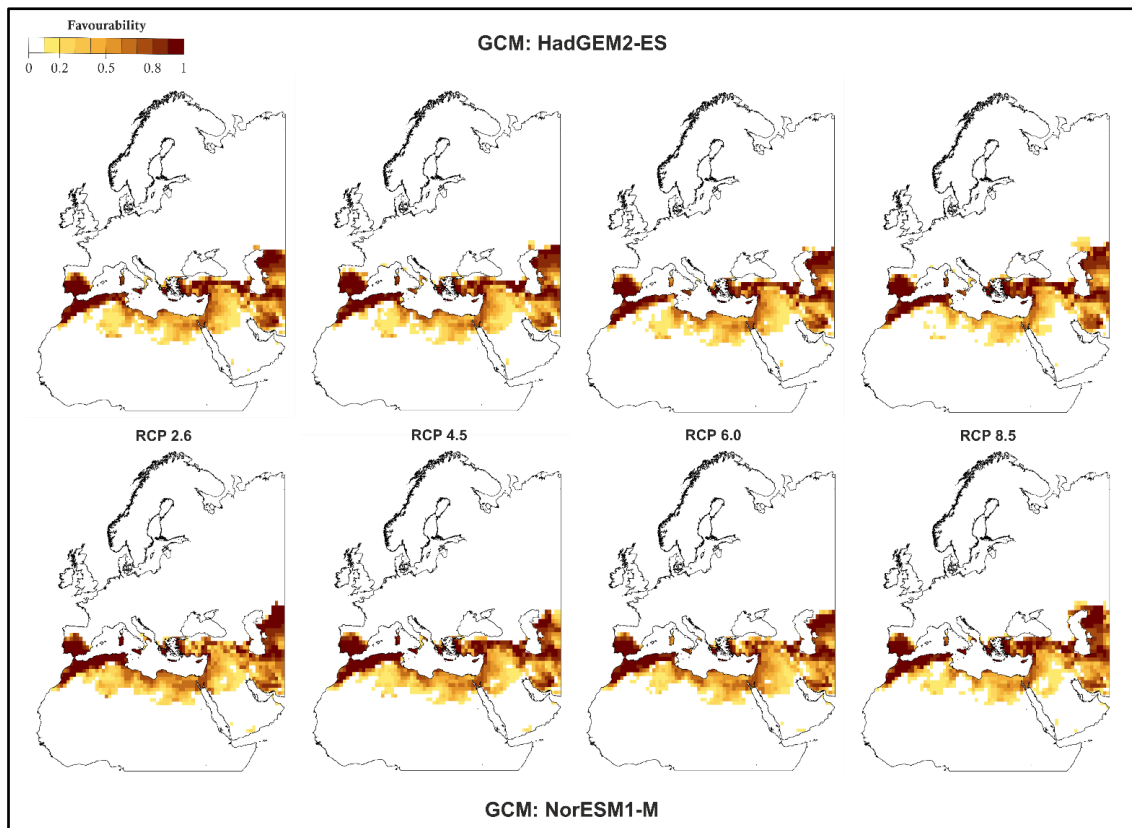
**Appendix 33.** Future climatic favourability for Laughing Dove breeding in each operational geographic unit of the study area, for the period 2041–2060, based on the results of the Global Circulation Models (GCMs) HadGEM2-ES and NorESM1-M, and the Representative Concentration Pathways (RCPs) 2.6, 4.5, 6.0 and 8.5.



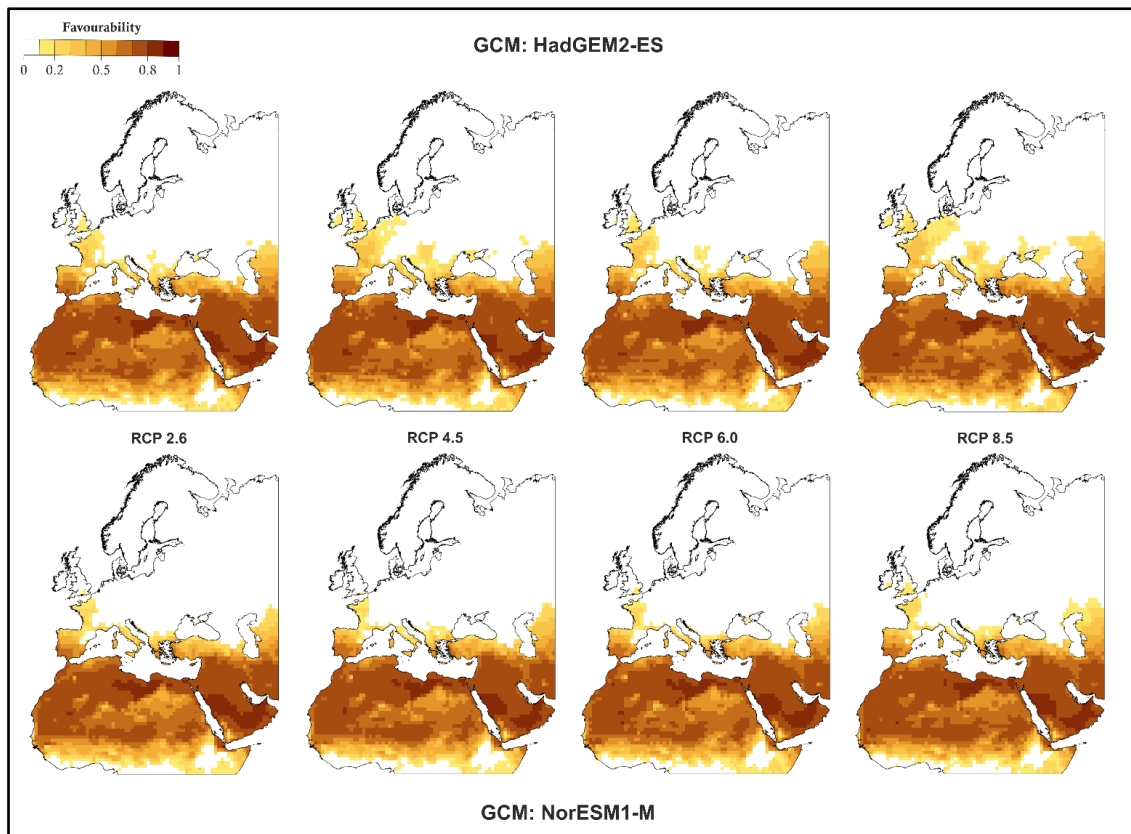
**Appendix 34.** Future climatic favourability for Black-crowned Tchagra breeding in each operational geographic unit of the study area, for the period 2041–2060, based on the results of the Global Circulation Models (GCMs) HadGEM2-ES and NorESM1-M, and the Representative Concentration Pathways (RCPs) 2.6, 4.5, 6.0 and 8.5.



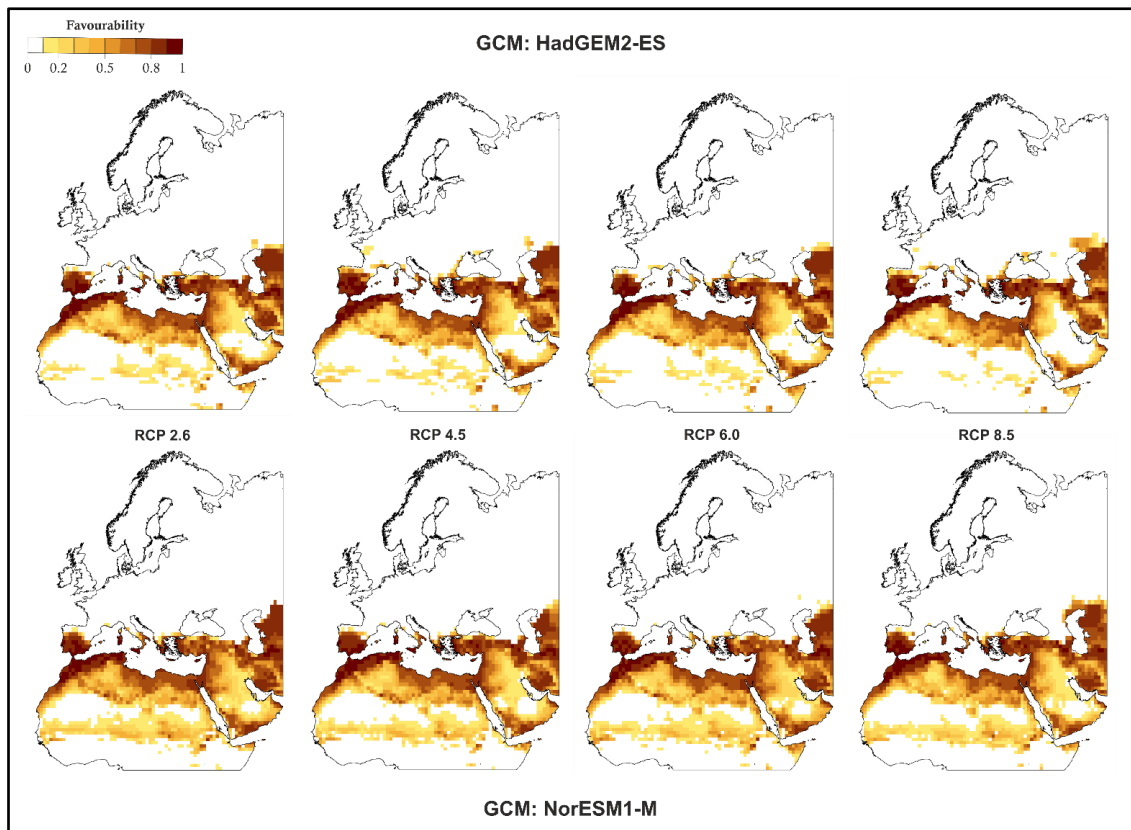
**Appendix 35.** Future climatic favourability for Rüppell's Vulture breeding in each operational geographic unit of the study area, for the period 2041–2060, based on the results of the Global Circulation Models (GCMs) HadGEM2-ES and NorESM1-M, and the Representative Concentration Pathways (RCPs) 2.6, 4.5, 6.0 and 8.5.



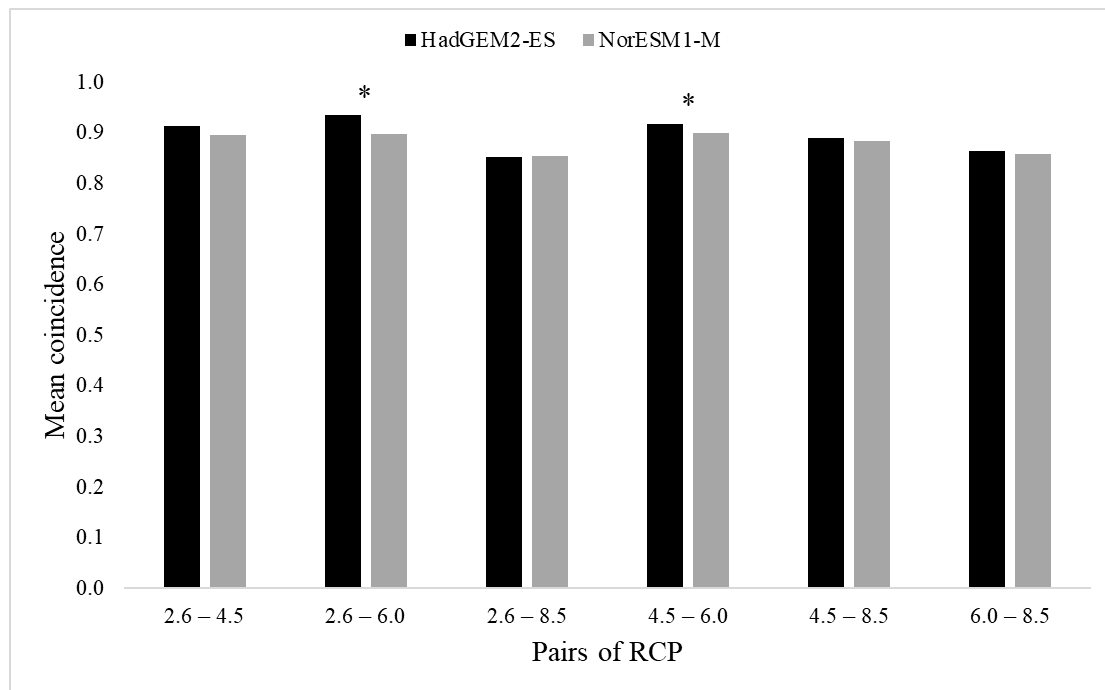
**Appendix 36.** Future climatic favourability for Little Swift breeding in each operational geographic unit of the study area, for the period 2041–2060, based on the results of the Global Circulation Models (GCMs) HadGEM2-ES and NorESM1-M, and the Representative Concentration Pathways (RCPs) 2.6, 4.5, 6.0 and 8.5.



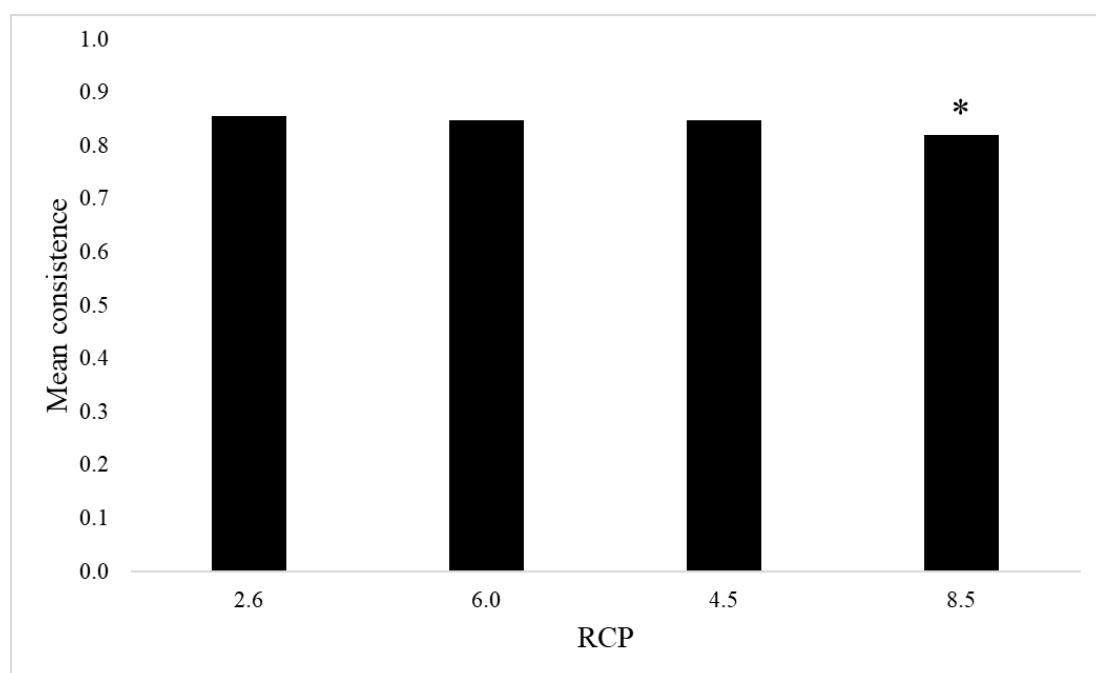
**Appendix 37.** Future climatic favourability for Cream-colored Courser breeding in each operational geographic unit of the study area, for the period 2041–2060, based on the results of the Global Circulation Models (GCMs) HadGEM2-ES and NorESM1-M, and the Representative Concentration Pathways (RCPs) 2.6, 4.5, 6.0 and 8.5.



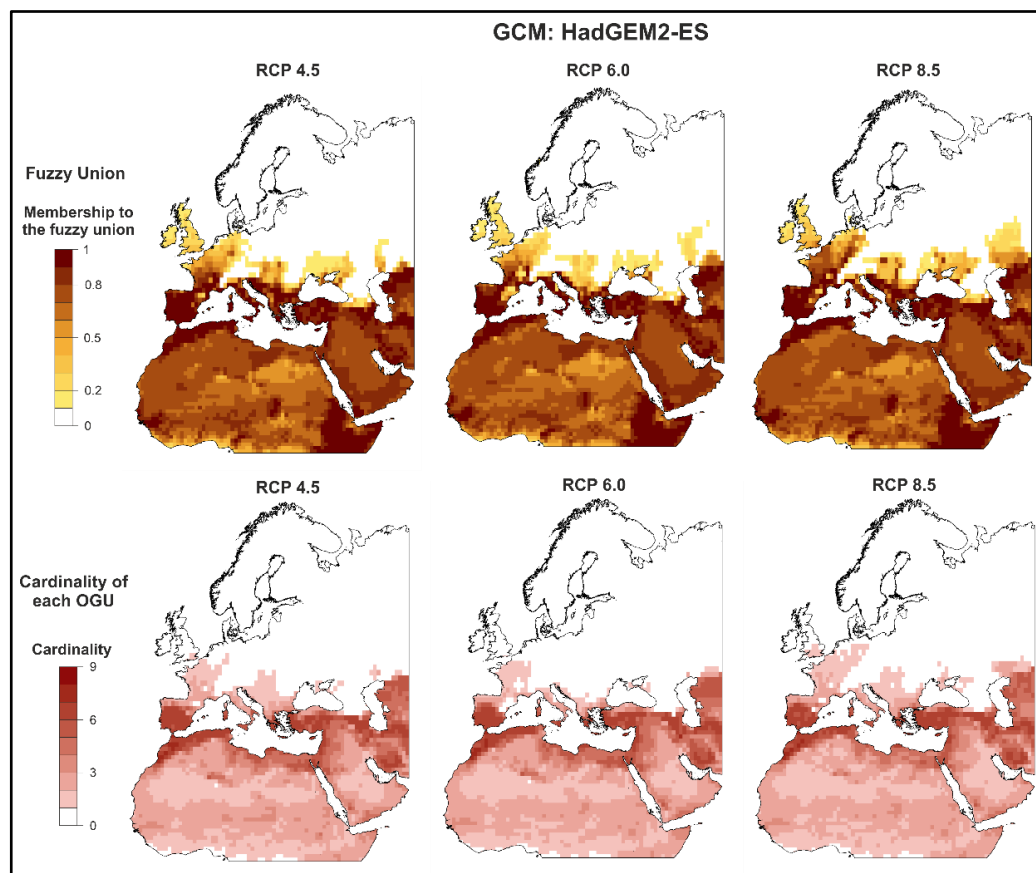
**Appendix 38.** Future climatic favourability for Atlas Long-legged Buzzard breeding in each operational geographic unit of the study area, for the period 2041–2060, based on the results of the Global Circulation Models (GCMs) HadGEM2-ES and NorESM1-M, and the Representative Concentration Pathways (RCPs) 2.6, 4.5, 6.0 and 8.5.



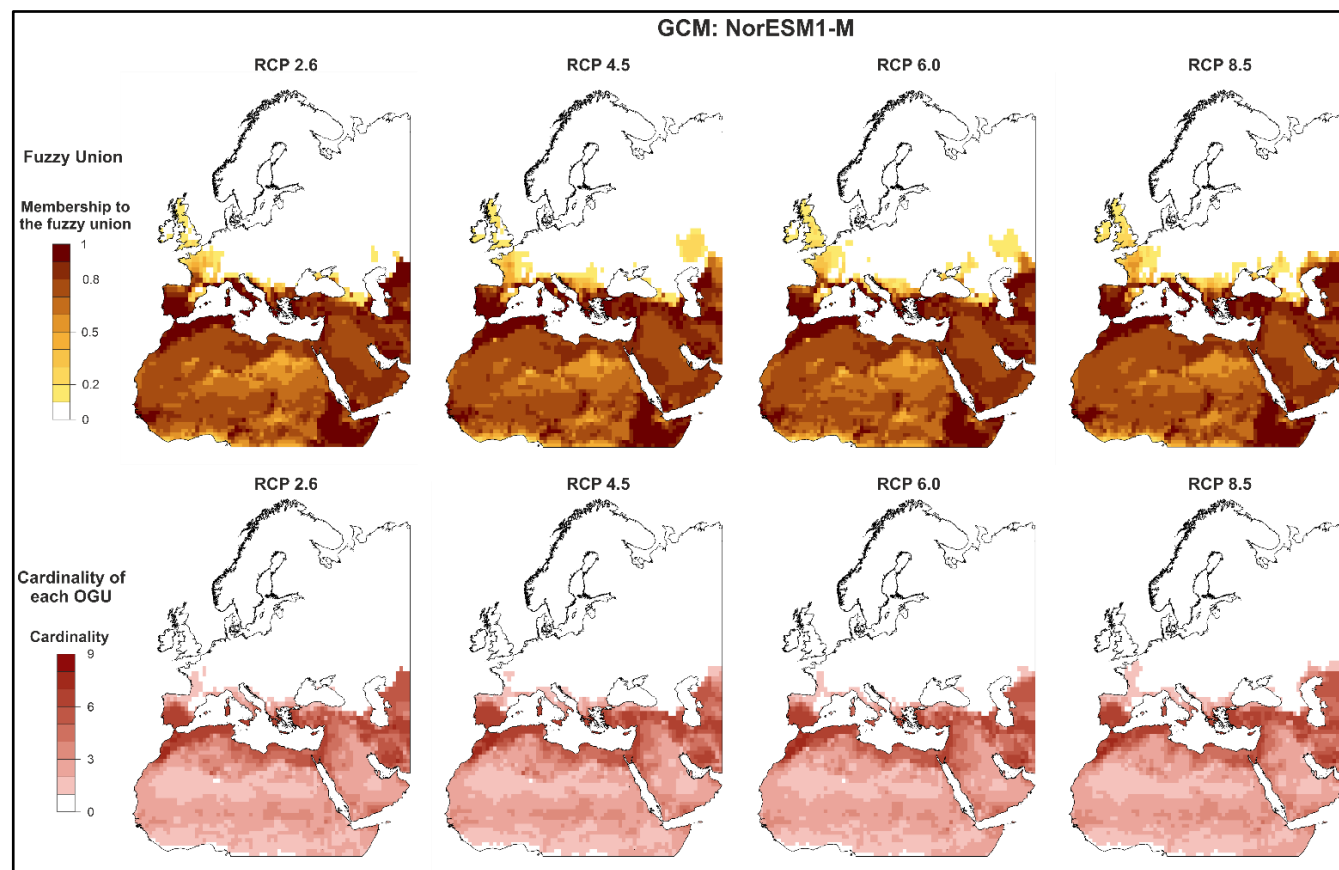
**Appendix 39.** Comparison of mean coincidence values of the nine studied bird species, using different pairs of Representative Concentration Pathways (RCPs) for each Global Circulation Model (GCM). Asterisks indicate a statistically significant difference in mean coincidences between the GCMs for that pair of RCPs.



**Appendix 40.** Comparison of mean consistence values of the nine studied bird species for each Representative Concentration Pathway (RCP), using different Global Circulation Models. Asterisks indicate a statistically significant difference in mean consistence values between a particular RCP and other groups.



**Appendix 41.** First row: Degree of membership of each Operational Geographic Unit (OGU) to the union of the fuzzy sets of OGUs that are expected to be climatically favourable for each species (meaning the degree to which the OGU is expected to be climatically favourable for any of them). Second row: cardinality of the fuzzy sets of species for which each OGU is expected to be climatically favourable (meaning the number of species for which the OGU is expected to be climatically favourable). These projections are based on the results of the Global Circulation Model (GCM) HadGEM2-ES and the Representative Concentration Pathways (RCPs) 4.5, 6.0 and 8.5 for the period 2041–2060.



**Appendix 42.** First row: Degree of membership of each Operational Geographic Unit (OGU) to the union of the fuzzy sets of OGUs that are expected to be climatically favourable for each species (meaning the degree to which the OGU is expected to be climatically favourable for any of them). Second row: cardinality of the fuzzy sets of species for which each OGU is expected to be climatically favourable (meaning the number of species for which the OGU is expected to be climatically favourable). These projections are based on the results of the Global Circulation Model (GCM) NorESM1-M and the Representative Concentration Pathways (RCPs) 2.6, 4.5, 6.0 and 8.5 for the period 2041–2060.

**Appendix 43.** Response of each African raptor to the different explanatory variables used in this study. Variable codes are shown in **Table 4.1**.

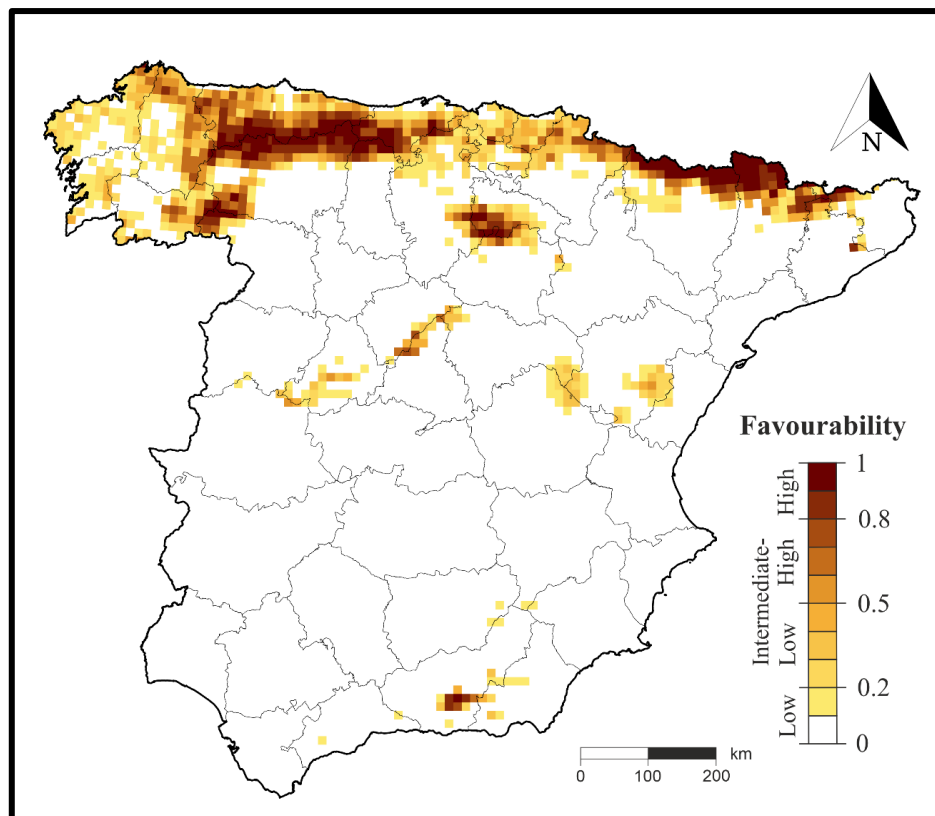
Variable	Atlas Long-legged Buzzard	Rüppell's Vulture	White-backed Vulture
Alti	M	M	U
Slope	U	U	U
Tmean	U	U	U
Rtday	U	U	U
Isot	U	U	U
Season	U	U	U
Tmax	U	U	U
Tmin	U	U	U
Rtan	U	U	U
Twet	U	U	U
Tdry	U	U	U
Twarm	U	U	U
Tcold	U	U	U
Prec	U	U	U
Pmax	U	U	U
Pmin	U	U	M
Cvp	U	U	U
Pwet	U	U	U
Pdry	U	M	M
Pwarm	U	U	U
Pcold	U	M	B

Note: M: Monotonic; U: Unimodal; B: Bimodal

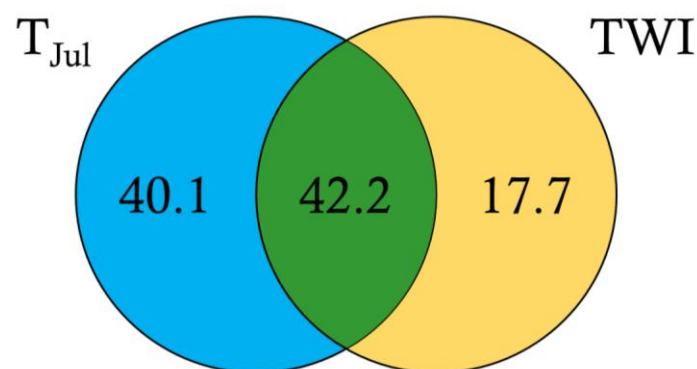
**Appendix 44.** Variables added to the logistic regression model considering only the III Spanish bird atlas data via a forward–backward stepwise selection process, ranked according to their order of entrance. Variable codes are shown in **Table 6.1**.

Variable	$\beta$	S.E.	Wald	$p$
T <sub>Jul</sub>	-0.787	0.157	25.145	< 0.001
TWI	-1.610	0.700	5.293	0.021
Constant	35.067	9.638	13.237	< 0.001

Note:  $\beta$ s are the coefficients in the *logit* function; S.E. is the standard error of these coefficients; Wald is the value of the Wald's statistic, representing the relative importance of the variable in the model;  $p$  is the significance of the coefficients according to the Wald test.



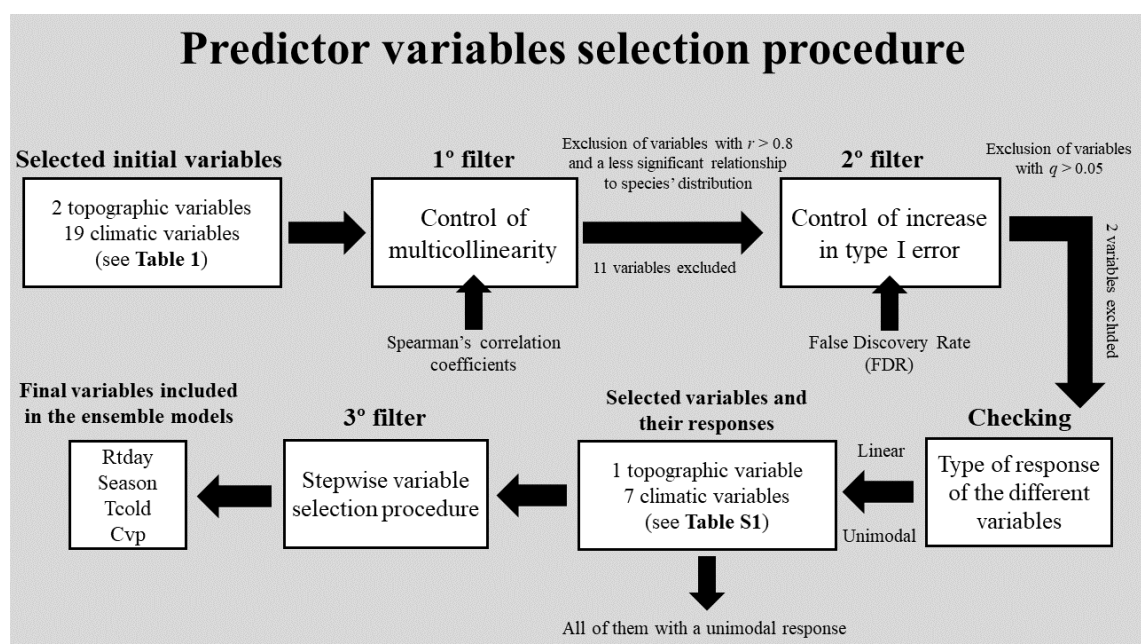
**Appendix 45.** Favourability values for the breeding of the White-winged Snowfinch in peninsular Spain, displayed for each UTM  $10 \times 10$  km grid cell, according to the environmental model considering only data from the III Spanish bird atlas. The mean environmental favourability values of the current Cantabrian and Pyrenean cores were 0.933 and 0.974, respectively.



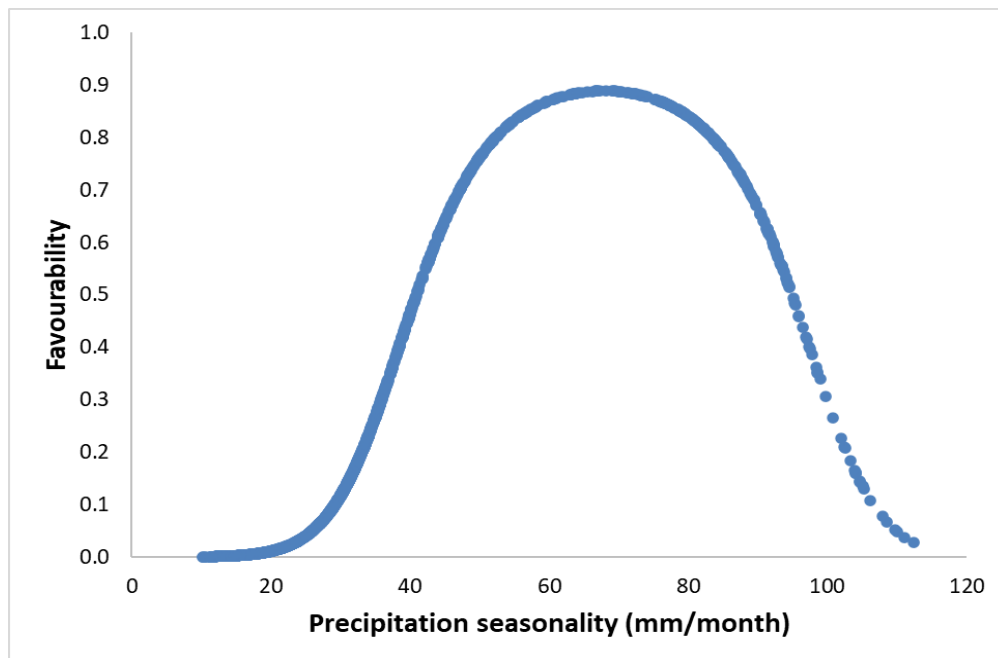
**Appendix 46.** Results of the variation partitioning of the environmental model considering only the III Spanish bird atlas data, using the two explanatory variables that entered the model: mean temperature in July ( $T_{Jul}$ ) and Topographic Wetness Index (TWI). Values shown in the diagram represent the percentages of variation explained exclusively by each variable and by their interaction.

**Appendix 47.** Response of the winter distribution of the spotted flycatcher in Europe and the Middle East to the different explanatory variables that passed the multicollinearity and false discovery rate filters. Variable codes are shown in **Table 7.1**.

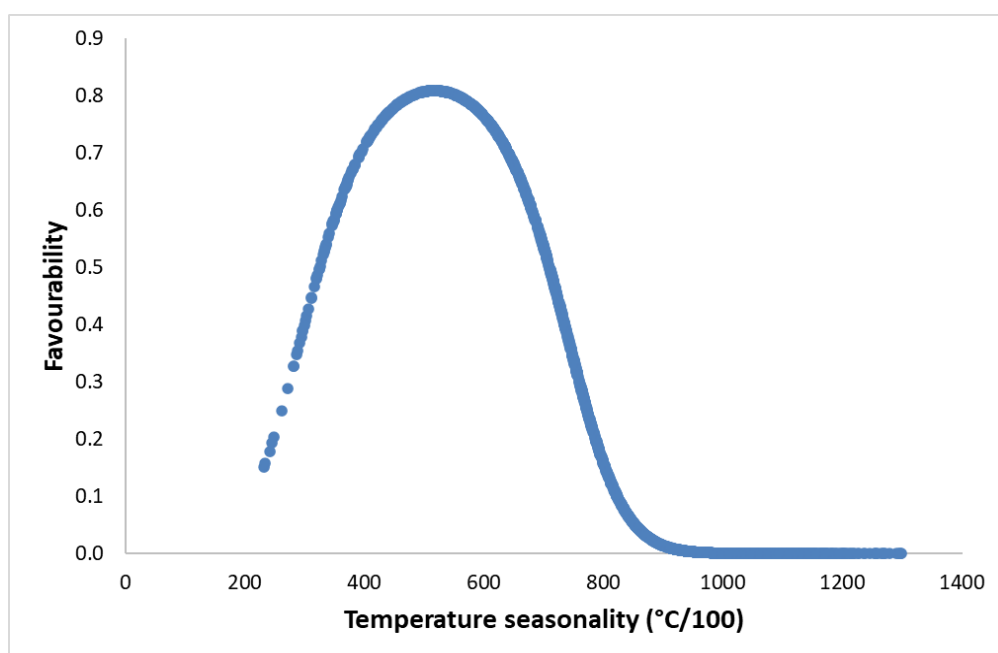
Variable	Type of response
Slope	Unimodal
Rtday	Unimodal
Isot	Unimodal
Season	Unimodal
Tcold	Unimodal
Pmin	Unimodal
Cvp	Unimodal
Pcold	Unimodal



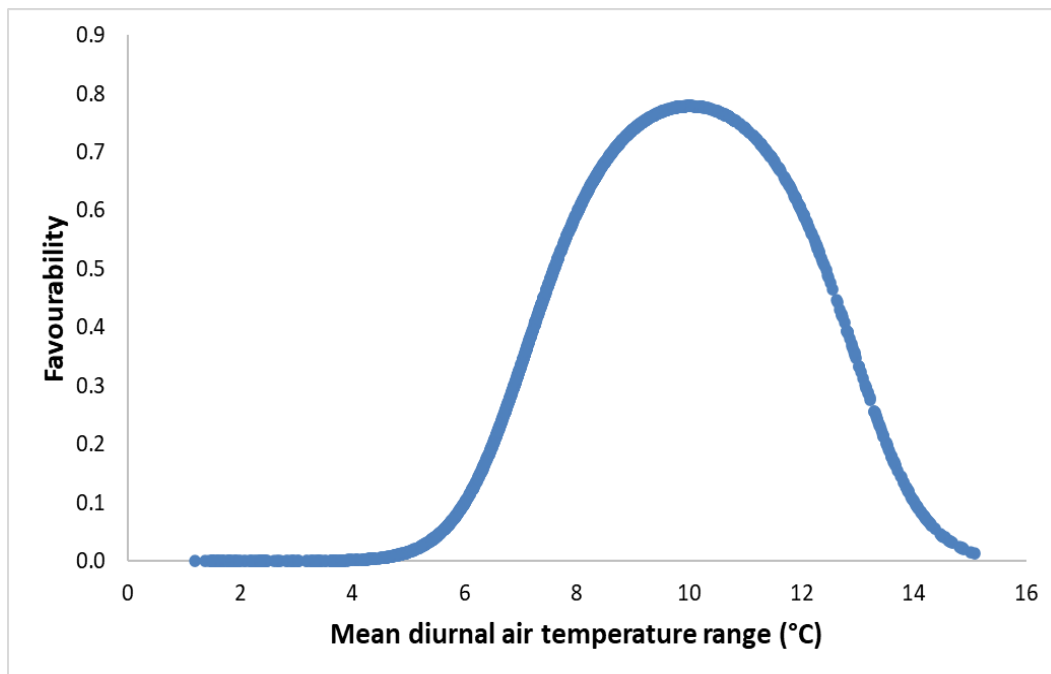
**Appendix 48.** Diagram summarising the different steps followed to select the environmental predictor variables included in the modelling process.



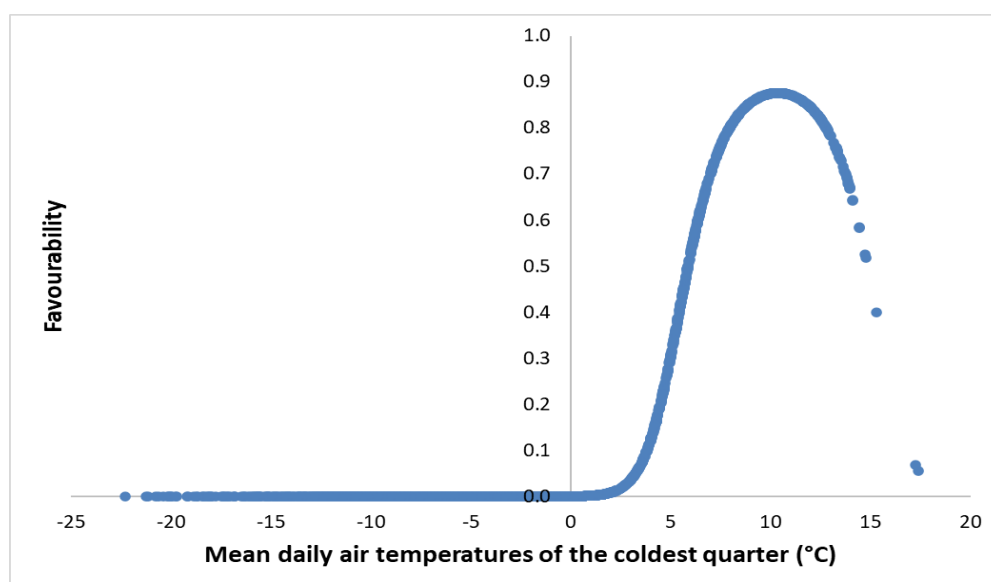
**Appendix 49.** Sensitivity of favourability function to the variable “Precipitation seasonality” in Europe and the Middle East. Points represent the 1887 OGUs of Europe and the Middle East. The logit function of the logistic regression that originated this response was  $Y = -15.527 + 0.0388 * C_{vp} - 0.0000286 * C_{vp}^2$ .



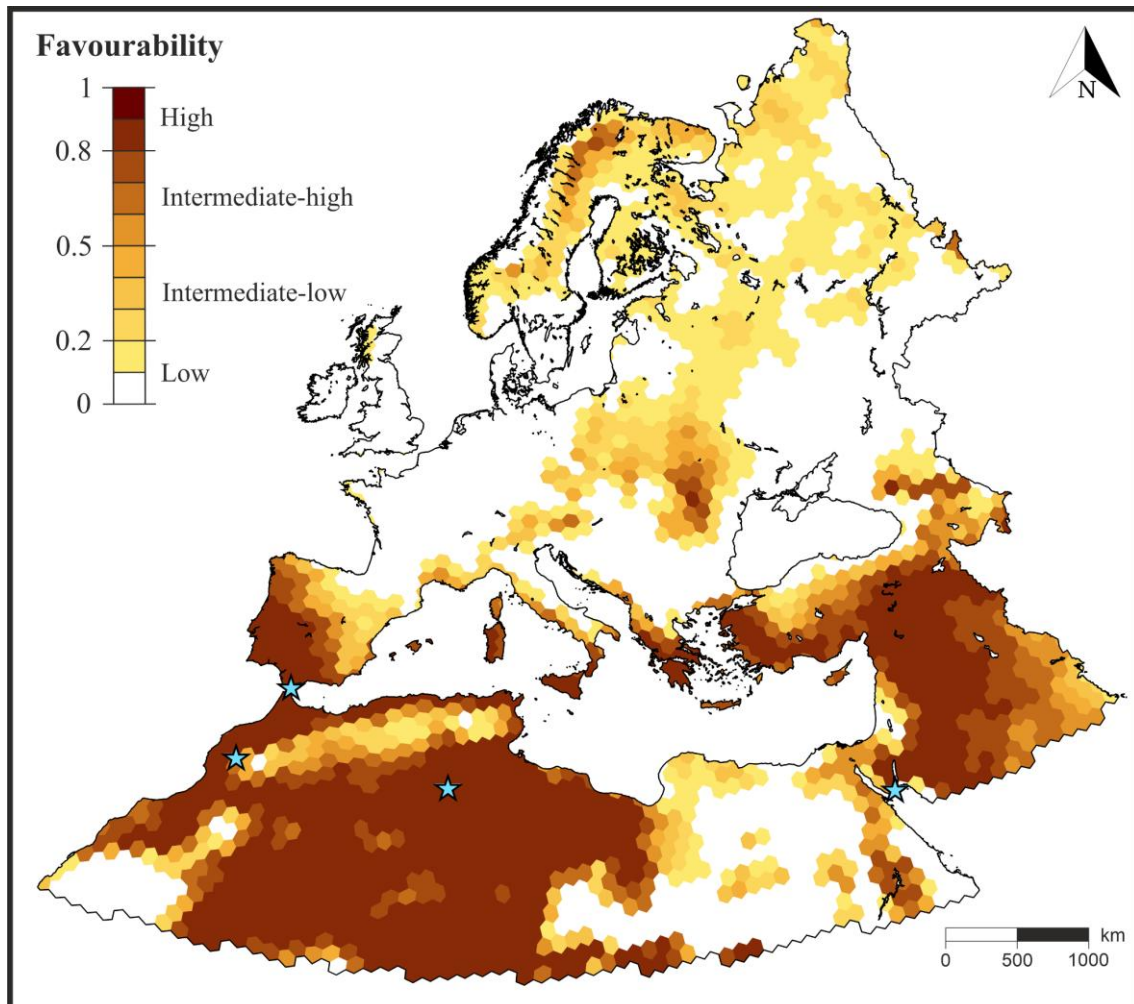
**Appendix 50.** Sensitivity of favourability function to the variable “Temperature seasonality” in Europe and the Middle East. Points represent the 1887 OGUs of Europe and the Middle East. The logit function of the logistic regression that originated this response was  $Y = -13.433 + 0.00403 * Season - 0.000000390 * Season^2$ .



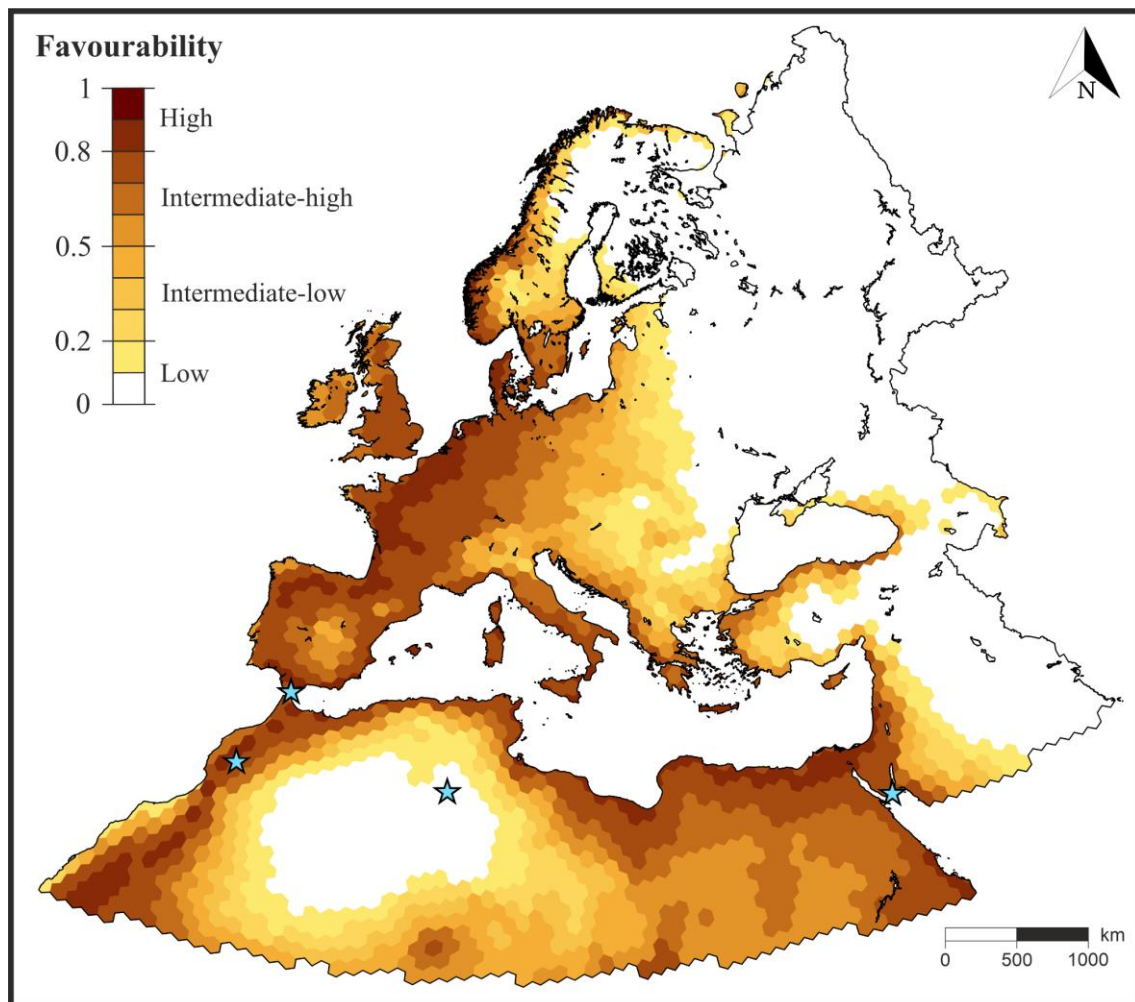
**Appendix 51.** Sensitivity of favourability function to the variable “Mean diurnal air temperature range” in Europe and the Middle East. Points represent the 1887 OGU’s of Europe and the Middle East. The logit function of the logistic regression that originated this response was  $Y = -24.761 + 0.431 \cdot R_{\text{tday}} - 0.00215 \cdot R_{\text{tday}}^2$ .



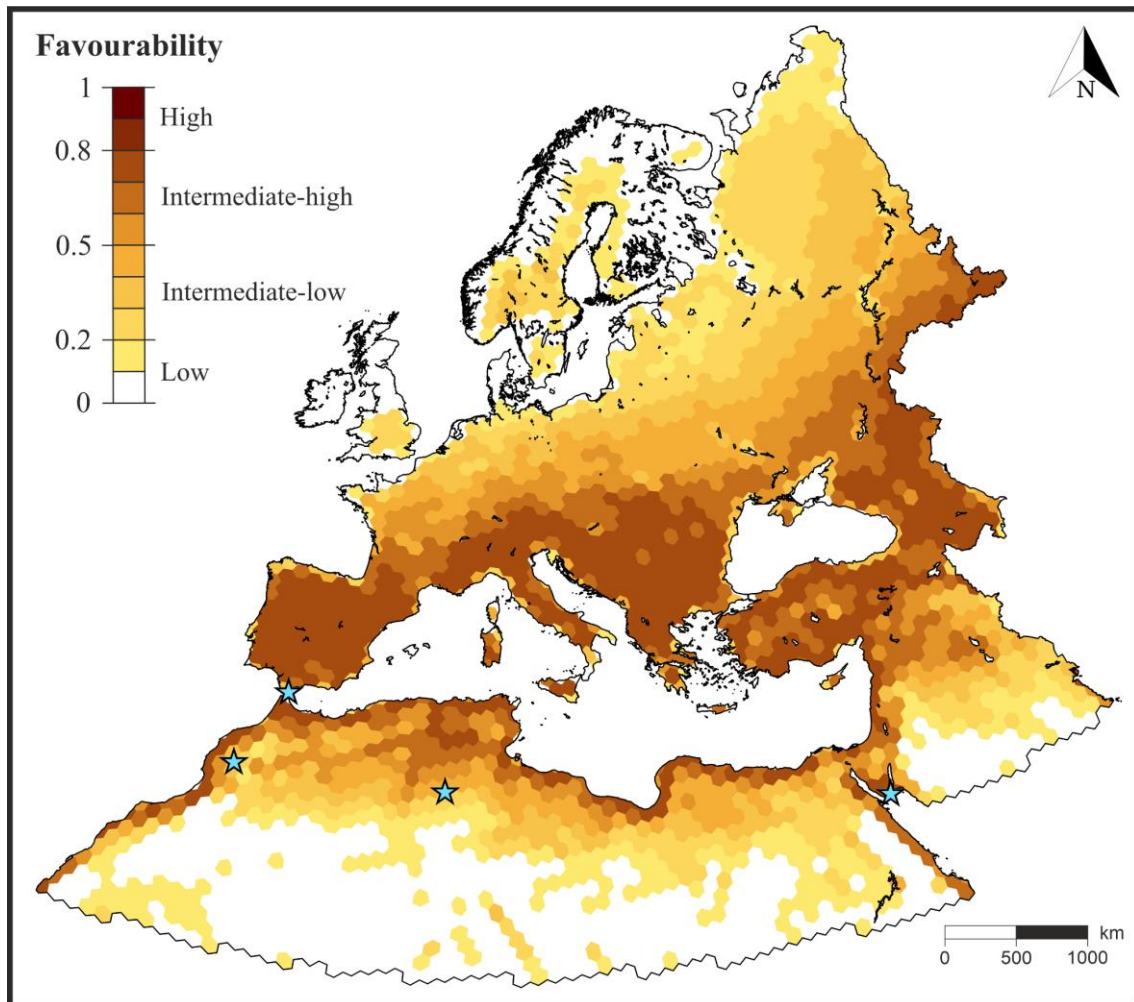
**Appendix 52.** Sensitivity of favourability function to the variable “Mean daily air temperatures of the coldest quarter” in Europe and the Middle East. Points represent the 1887 OGU’s of Europe and the Middle East. The logit function of the logistic regression that originated this response was  $Y = -7771.624 + 5.481 \cdot T_{\text{cold}} - 0.000967 \cdot T_{\text{cold}}^2$ .



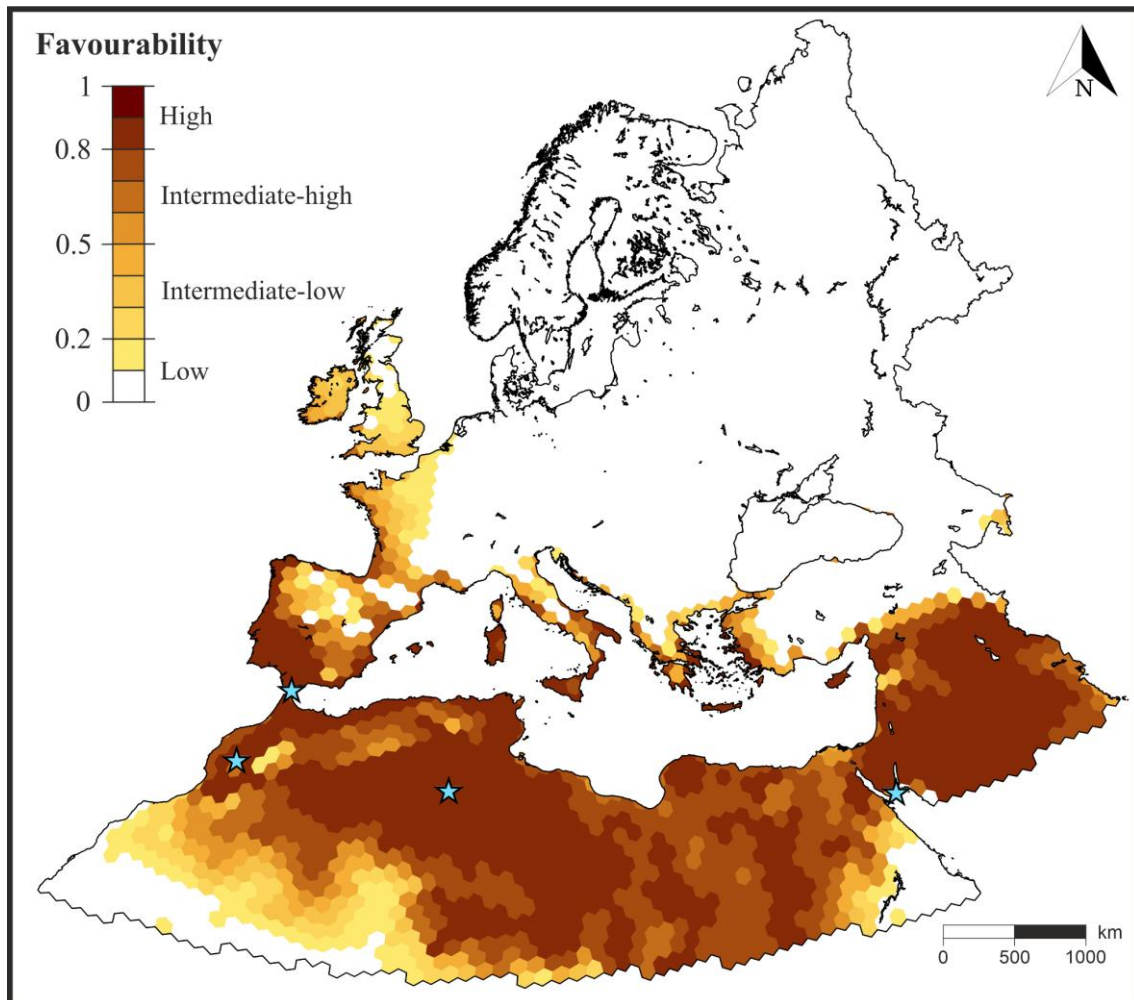
**Appendix 53.** Favourability values for the wintering of the spotted flycatcher in each operational geographic unit of the Western Palearctic according to the unimodal variable “Precipitation seasonality”. Blue stars represent confirmed wintering records of the species not included in the modelling process. Map projection: GCS\_WGS\_1984 (ArcGIS 10.4.1).



**Appendix 54.** Favourability values for the wintering of the spotted flycatcher in each operational geographic unit of the Western Palearctic according to the unimodal variable “Temperature seasonality”. Blue stars represent confirmed wintering records of the species not included in the modelling process. Map projection: GCS\_WGS\_1984 (ArcGIS 10.4.1).



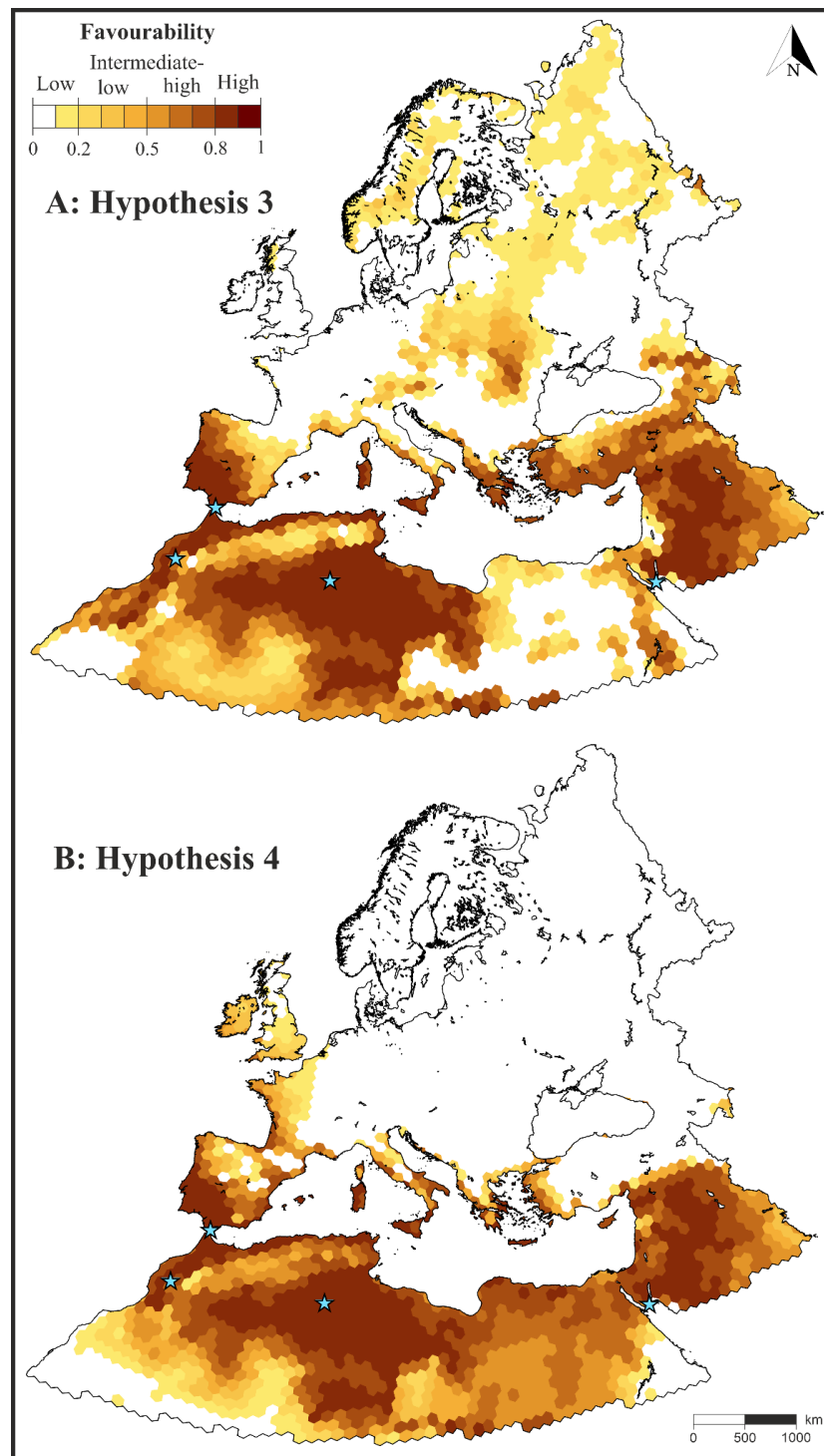
**Appendix 55.** Favourability values for the wintering of the spotted flycatcher in each operational geographic unit of the Western Palearctic according to the unimodal variable “Mean diurnal air temperature range”. Blue stars represent confirmed wintering records of the species not included in the modelling process. Map projection: GCS\_WGS\_1984 (ArcGIS 10.4.1).



**Appendix 56.** Favourability values for the wintering of the spotted flycatcher in each operational geographic unit of the Western Palearctic according to the unimodal variable “Mean daily air temperatures of the coldest quarter”. Blue stars represent confirmed wintering records of the species not included in the modelling process. Map projection: GCS\_WGS\_1984 (ArcGIS 10.4.1).

**Appendix 57.** Comparative assessment of the discrimination and classification capacities of the univariate models corresponding to the four unimodal variables that entered the ensemble model performed in Europe and the Middle East according to H1, and their extrapolation to North Africa. Assessment indices: area under the curve (AUC), sensitivity, specificity, correct classification rate (CCR), over-prediction rate (OPR), under-prediction rate (UPR), and Cohen’s kappa index (Kappa). Variable codes are shown in **Table 7.1**.

Measure	Europe and the Middle East				Europe, the Middle East and North Africa			
	Cvp	Season	Rtday	Tcold	Cvp	Season	Rtday	Tcold
AUC	0.890	0.859	0.816	0.918	0.798	0.825	0.800	0.853
Sensitivity	0.818	0.909	0.773	0.955	0.808	0.885	0.692	0.923
Specificity	0.776	0.675	0.645	0.789	0.651	0.609	0.694	0.624
CCR	0.777	0.678	0.646	0.791	0.652	0.612	0.694	0.627
OPR	0.959	0.968	0.975	0.949	0.978	0.979	0.979	0.977
UPR	0.00275	0.00159	0.00414	0.000679	0.00281	0.00180	0.00420	0.00117
Kappa	0.0579	0.0401	0.0264	0.0756	0.0240	0.0232	0.0230	0.0267



**Appendix 58.** Climatic favourability ( $F$ ) values for the wintering of the spotted flycatcher in each operational geographic unit of the Western Palearctic according to **A**: hypothesis 3 (H3: *temperature and precipitation are generally limiting for the wintering of the species*) and **B**: hypothesis 4 (H4: *the winter temperature, along with the combination of the other variables included in the model, limit the wintering of the species*). Blue stars represent confirmed wintering records of the species not included in the modelling process. Map projection: GCS\_WGS\_1984 (ArcGIS 10.4.1).

**Appendix 59.** Comparative assessment of the discrimination and classification capacities of the climatic favourability models according to H3 and H4 in Europe and the Middle East and their extrapolation to North Africa. Assessment indices: area under the curve (AUC), sensitivity, specificity, correct classification rate (CCR), over-prediction rate (OPR), under-prediction rate (UPR), and Cohen’s kappa index (Kappa).

Measure	Europe and the Middle East		Europe, the Middle East and North Africa	
	H3	H4	H3	H4
AUC	0.899	0.932	0.830	0.866
Sensitivity	0.818	0.955	0.808	0.923
Specificity	0.788	0.803	0.693	0.647
CCR	0.788	0.804	0.694	0.650
OPR	0.957	0.946	0.976	0.976
UPR	0.00272	0.000668	0.00263	0.00113
Kappa	0.0618	0.0819	0.0297	0.0295

**Appendix 60.** Assessment of the discrimination and classification capacities of the ensemble models in North Africa to compare the different hypotheses (H1, H2, H3 and H4). Assessment indices: area under the curve (AUC), sensitivity and specificity.

Measure	Hypotheses			
	H1	H2	H3	H4
AUC	0.628	0.462	0.551	0.495
Sensitivity	0.75	0	0.25	0.5
Specificity	0.647	0.943	0.677	0.597

## 12. Producción científica asociada a esta tesis doctoral

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A continuación, se detallan los artículos y capítulos de libro que avalan esta tesis doctoral:

- **López-Ramírez, S.**, Chamorro, D., Real, R. & Muñoz, A.-R. (2022). Cuantificando el desequilibrio latitudinal de las áreas de distribución de las especies como consecuencia del cambio climático. En *La naturaleza atlántica: hábitats, patrimonio y vulnerabilidad. II Congreso Iberoamericano y XII Congreso Español de Biogeografía* (Beato Bergua, S., Poblete Piedrabuena, M.A. & Rodríguez Pérez, C., Eds.). Delallama Editorial, Ribadesella (Asturias), pp. 127–136.
- **López-Ramírez, S.**, Chamorro, D., Real, R. & Muñoz, A.-R. (2023). Southern Europe is becoming climatically favourable for African birds: anticipating the establishment of a new species. *Frontiers in Zoology*, 20(1): 18. <https://doi.org/10.1186/s12983-023-00496-x> (D1)
- **López-Ramírez, S.**, Márquez, A. L., Real, R. & Muñoz, A.-R. (2024). Evaluating the expansion of African species into Europe driven by climate change. *Diversity and Distributions*, 30(6): e13840. <https://doi.org/10.1111/ddi.13840> (Q1)
- **López-Ramírez, S.**, Real, R. & Muñoz, A.-R. (2024). The northern wheatear is reducing its distribution in its southernmost European range and moving to higher altitudes. *Journal of Avian Biology*, 2024(5-6): e03217. <https://doi.org/10.1111/jav.03217> (Q1)
- **López-Ramírez, S.** & Muñoz, A.-R. (2025). Climate change drives range contraction and shapes species distribution in an alpine passerine: Caution required when comparing atlas data. *Global Ecology and Conservation*, 60: e03620. <https://doi.org/10.1016/j.gecco.2025.e03620> (Q1)
- **López-Ramírez, S.**, García-Carrasco, J.-M., Real, R. & Muñoz, A.-R. (2025). Climate-driven shifts in trans-Saharan bird migration illustrated by the spotted flycatcher (*Muscicapa striata*). *Scientific Reports*, 15(1): 35201. <https://doi.org/10.1038/s41598-025-19138-9> (Q1)
- Muñoz, A.-R., **López-Ramírez, S.**, García-Carrasco, J.-M. & Real, R. Contrasting mechanisms driving the northward expansion of African raptors into Europe (under review in *Journal of Zoology*).
- Muñoz, A.-R. & **López-Ramírez, S.** Africanisation of Southern Europe's avifauna is already underway (Submitted).

Otras publicaciones surgidas durante el desarrollo de la presente tesis doctoral, no incluidas en la presente memoria:

- Muñoz, A.-R., Márquez, A. L., Seoane, J., **López-Ramírez, S.**, del Moral, J. C., Molina, B., Nebreda, A., Bustamante, J. & Real, R. (2022). Material y métodos para la modelación ¿Por qué usar modelos de distribución en el nuevo Atlas? En *III Atlas de las aves en época de reproducción en España* (Molina, B., Nebreda, A., Muñoz, A.-R., Seoane, J., Real, R., Bustamante, J. & del Moral, J. C., Eds.). SEO/BirdLife, Madrid. <https://atlasaves.seo.org/metodologia-de-modelizacion/>
- **López-Ramírez, S.** & Muñoz, A.-R. (2022). A Local Approach to Better Understand the Spread and Population Growth of the Monk Parakeet as an Invasive Species. *Birds*, 3(3): 277–284. <https://doi.org/10.3390/birds3030018>
- **López-Ramírez, S.** & Muñoz, A.-R. (2023). Un enfoque local para comprender mejor la dispersión a gran escala y el crecimiento de las poblaciones de cotorra argentina como especie invasora. *Encuentros en la Biología*, 16(186): 11–14. <https://doi.org/10.24310/enbio.v16i186.17162>
- Navarro, I., **López-Ramírez, S.**, Real, R., Farfán, M. A. & Muñoz, A.-R. Enhancing conservation efforts through species distribution models: a case study of the threatened Bearded Vulture in Spain (under review in *Diversity and Distributions*).

### 13. Breve *curriculum vitae*

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Sandro López Ramírez es graduado en Biología con un Máster en Diversidad Biológica y Medio Ambiente por la Universidad de Málaga, obteniendo matrícula de honor en los Trabajos Fin de Grado y Fin de Máster. Ha continuado su formación en la Universidad de Málaga con el desarrollo de su tesis doctoral en el Departamento de Biología Animal tras haber obtenido una beca predoctoral FPU del Ministerio de Educación, Cultura y Deporte (FPU20/01360). Antes de comenzar la etapa predoctoral realizó seis meses de prácticas extracurriculares en la Reserva Ecológica de Ojén como guía de la naturaleza (septiembre 2019 – marzo 2020, 600 horas), donde posteriormente estuvo contratado a jornada completa otros cinco meses (julio – noviembre 2020). También participó en dos proyectos de investigación, ambos en la Universidad de Málaga, enfocados en la elaboración de modelos de distribución de aves y quirópteros: el primero de ellos para el III Atlas de las aves de España (financiado por SEO-BirdLife) y el segundo como indicador de riesgo para los parques eólicos de EDP renovables (financiado por Ecoacsa Reserva de Biodiversidad S.L.). En el periodo de cuarentena a causa del COVID-19, realizó los siguientes cursos online: “Técnicas de Marcaje y Seguimiento de Fauna Silvestre”, “Diseño de Estudios Faunísticos”, “Invasiones Biológicas, una amenaza creciente” (los tres de la Fundación General de la Universidad de Málaga) y “Primeros Auxilios en la Naturaleza” (Cruz Roja Española). Durante el desarrollo de su etapa predoctoral ha colaborado en 3 proyectos de investigación y publicado un total de 7 artículos científicos y 2 capítulos de libro. Los 5 artículos publicados que avalan la presente tesis doctoral han sido publicados en el primer cuartil (Q1), además de otros dos artículos que actualmente se encuentran en fase de revisión. También ha impartido horas de docencia en las prácticas de la asignatura de Zoología del grado en Biología y en Ciencias Ambientales de la UMA (180 horas en total) y ha participado en 11 congresos científicos de ámbito tanto nacional como internacional, obteniendo reconocimiento a la mejor ponencia en la temática de “Cambio Global: desafíos en un mundo cambiante” en el VI Congreso de Biodiversidad y Conservación de la Naturaleza (2023). Durante este periodo también ha complementado su formación con la asistencia a 46 conferencias, seminarios, talleres y cursos.



**NO PODEMOS PROTEGER  
EL MUNDO NATURAL HASTA  
QUE NO SEAMOS CAPACES  
DE ENTENDERLO**

**DAVID ATTENBOROUGH**

