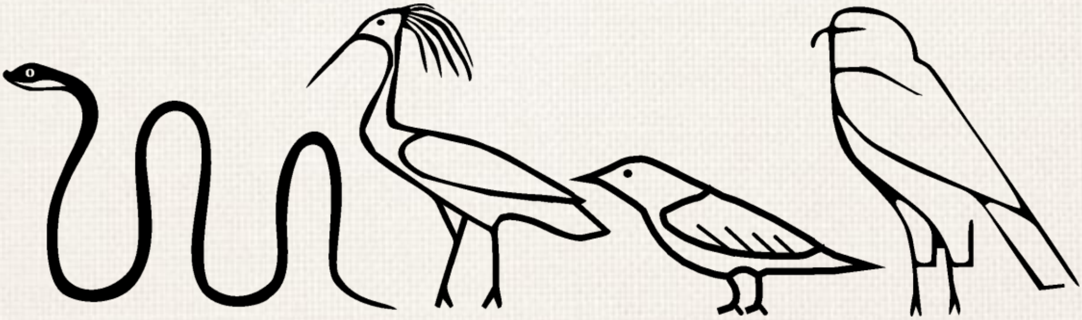
Tesis Doctoral

Dinamismo En La Distribución De Las Especies: Avances Metodológicos Y Aplicaciones

Darío Chamorro Sierra

2021



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Memoria presentada para optar al grado de Doctor en Biología

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DECLARACIÓN DE AUTORÍA Y ORIGINALIDAD DE LA TESIS PRESENTADA PARA OBTENER EL TÍTULO DE DOCTOR

D. DARÍO CHAMORRO SIERRA

Estudiante del programa de doctorado DIVERSIDAD BIOLÓGICA Y MEDIO AMBIENTE de la Universidad de Málaga, autor de la tesis, presentada para la obtención del título de doctor por la Universidad de Málaga, titulada: DINAMISMO EN LA DISTRIBUCIÓN DE LAS ESPECIES: AVANCES METODOLÓGICOS Y APLICACIONES.

Realizada bajo la tutorización de DR. ANTONIO ROMÁN MUÑOZ GALLEGO y dirección de DR. ANTONIO ROMÁN MUÑOZ GALLEGO Y CAT. RAIMUNDO REAL GIMÉNEZ.

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ACREDITAN QUE:

D. **Darío Chamorro Sierra**, doctorando en el Programa de Doctorado en Diversidad Biológica y Medio Ambiente, ha realizado, en el Departamento de Biología Animal de la Facultad de Ciencias de la Universidad de Málaga, las investigaciones que le han conducido a la redacción de la presente Memoria de Tesis Doctoral, titulada "**DINAMISMO EN LA DISTRIBUCIÓN DE LAS ESPECIES: AVANCES METODOLÓGICOS Y APLICACIONES**".

La presente memoria, que recoge los resultados obtenidos y su interpretación, reúne los requisitos necesarios para ser sometida al juicio de la Comisión correspondiente. Por tanto, como directores de la tesis, autorizamos su exposición y defensa para optar al Grado de Doctor por la Universidad de Málaga.

Además, las publicaciones que avalan la mencionada tesis no han sido utilizadas en tesis doctorales anteriores.

Y para que así conste, en cumplimiento de las disposiciones vigentes, firmamos la presente acreditación en Málaga, a 03 de diciembre de 2020.

Fdo.: Raimundo Real Giménez Fdo.: Antonio-Román Muñoz Gallego

TESIS DOCTORAL

DINAMISMO EN LA DISTRIBUCIÓN DE LAS ESPECIES: AVANCES METODOLÓGICOS Y APLICACIONES

PHD THESIS

DYNAMISM OF THE SPECIES DISTRIBUTION: METHODOLOGICAL ADVANCES AND APPLICATIONS

2021

por/by:

DARÍO CHAMORRO SIERRA

dirigida por/supervised by:

Dr. ANTONIO ROMÁN MUÑOZ GALLEGO

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PROGRAMA DE DOCTORADO EN DIVERSIDAD BIOLÓGICA Y MEDIO AMBIENTE

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Dissertation to fulfil the requirements for the degree of Doctor in Biology, with mention of International Doctor

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Dr. Antonio Román Muñoz Gallego, Universidad de Málaga.
Prof. Dr. Raimundo Real Giménez, Universidad de Málaga.

Miembros del Tribunal / Examining Committee:

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Prof. Dr. Serge Gofas – Universidad de Málaga, España.
Dr. Pelayo Acevedo– Consejo Superior de Investigaciones Científicas, España.
Dr. Pedro Tarroso – Centro de Investigação em Biodiversidade e Recursos Genéticos (CIBIO/InBio) da Universidade do Porto, Portugal.

Informes de expertos externos / Reports from external experts:

Dr. José Carlos Brito –Universidade do Porto, Portugal.
Dr. José Carlos Guerrero – Universidad de la República, Uruguay.

Dr. Urtzi Enriquez – Institute of Vertebrate Biology, Czech Academy of Science, República Checa.

Esta es la tesis doctoral nº **21** 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.

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Scientia
Biodiversitatis
Biogeografía, Diversidad y Conservación

INDICE GENERAL / TABLE OF CONTENTS

AGRADECIMIENTOS Y MOTIVACIÓN PERSONAL

Fue en Mayo de 1992 cuando esta aventura dio comienzo, y es que los valores por el respeto y el conocimiento de la naturaleza se me inculcaron literalmente desde la cuna, cuando a los escasos días de vida un osito de peluche (*Mimosín*, el cual aún conservo) me hizo compañía y despertó mi curiosidad hacia el mundo de los animales. Si bien es cierto que no conservo recuerdos nítidos de aquella época, sí que sé a través de mis padres Ángeles e Isidro, que mi amor por esas criaturas fue nato. Ellos siempre me apoyaron y nutrieron mi interés por la zoología, a través de innumerables documentales, juguetes, libros, juegos educativos, revistas y un sinfín de excursiones al campo. A ellos les debo todo esto y mucho más. Gracias también a esta afición conjunta con mi hermano Gabriel, que siempre me preguntaba sobre animales y plantas, algo que me motivaba aún más a comprender los secretos que guardan las criaturas vivientes.

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14 / Febrero / 2021

"El amor desinteresado por todas las criaturas vivas, el más noble atributo del ser humano, está fuera de nuestra comprensión"

~ Charles R. Darwin

CAPÍTULO 0

ORGANIZACIÓN DE LA TESIS

OUTLINE OF THE THESIS

"La prueba de todo conocimiento es el experimento.

El experimento es el único juez de la verdad científica"

~ Richard P. Feynman

0 ORGANIZACIÓN DE LA TESIS

La presente tesis doctoral consta de diez capítulos que abordan diferentes aspectos del dinamismo de la distribución de las especies y de cómo la modelización biogeográfica aporta nueva información y marcos teóricos que ayudan a desentrañar los patrones de los rangos de distribución, sus peculiaridades y sus cambios. Para ello se han seleccionado cinco casos (taxones) cuya investigación proporciona información sobre los patrones biogeográficos y nuevos enfoques teórico-prácticos que pueden ser utilizados en la gestión y conservación de las especies bajo el contexto de planeta cambiante. Estas especies seleccionadas son a su vez representantes de grupos de especies que comparten patrones biogeográficos, por lo que al estudiar las especies seleccionadas, se estudian las características comunes para todo el grupo, permitiendo un análisis en profundidad que permite detallar los mecanismos que condicionan su dinámica, algo que se vería oscurecido si se analizaran muchas especies al mismo tiempo.

La organización general de la tesis se explica a continuación:

En el **capítulo 1** se ofrece una introducción general a esta tesis doctoral. En primer lugar, se presenta una definición completa de la ciencia que estudia la distribución de las especies – la biogeografía –, abarcando desde su etimología hasta las ramas del conocimiento que estudia. Esta parte ayuda a comprender la gran versatilidad de esta ciencia para proporcionar información que sea relevante en distintas áreas del conocimiento. En segundo lugar, se realiza un recorrido por la historia de la biogeografía a lo largo de los siglos, señalando algunos de los acontecimientos más relevantes que han supuesto un avance en la explicación de la distribución de los seres vivos en el planeta y, por tanto, han promovido el desarrollo de esta ciencia. Esta parte es útil para contextualizar la tesis y destacar la importancia y el interés de los diferentes procesos que se van a estudiar a lo largo de la misma. La primera parte de este recorrido histórico abarca los orígenes del estudio de la distribución de la especie, desde las pinturas rupestres prehistóricas y las primeras obras de filósofos de la Edad Antigua, como Aristóteles y Plinio el Viejo, hasta las "primeras ideas biogeográficas" escritas por monjes y frailes durante la Edad Media. A continuación, se describen los acontecimientos y escritos más importantes de la Edad de los Descubrimientos, que promovieron un interés creciente por el origen de las especies y las diferencias entre las faunas de los distintos continentes, el cual inspiró los primeros ensayos de biogeografía *sensu stricto*. A continuación se presenta una compilación de ensayos que contribuyeron al desarrollo de la biogeografía como ciencia durante el siglo XIX, como la regionalización de Wallace y la teoría de la evolución de Darwin, así como los primeros escritos sobre ecología. La explicación de las cuatro escuelas de biogeografía que convergen en el siglo XX se presenta después, a saber, el dispersalismo, la panbiogeografía, la biogeografía filogenética y la vicarianza cladística. A continuación, se describen los avances más relevantes de la biogeografía ecológica como el origen de la macroecología y la biogeografía de islas de MacArthur y Wilson, así como los objetivos de este campo. Concluyendo esta primera parte de la introducción, se presenta un cronograma resumen de la historia de la biogeografía.

Después de la reseña histórica, se ofrece 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). Esta parte resalta la gran diversidad de patrones de distribución que presentan las especies en todo el mundo. Seguidamente, se muestra una breve introducción al dinamismo de las distribuciones de las especies, que es el hilo conductor de esta tesis doctoral y el objetivo principal que se va a abordar desde diversas perspectivas a lo largo de los diferentes capítulos. En ella se explica el motivo que hace que las distribuciones sean espacio-temporalmente dinámicas, realizando una analogía con la física cuántica. A continuación, se muestra una breve sección en la que se introducen los límites espaciales (pero también temporales) 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. En la siguiente sección se presenta una concisa descripción de las diferentes formas de representar la distribución de las especies, haciendo especial hincapié en las dificultades para obtener datos y para reflejar la dinámica y las fluctuaciones del proceso. En esta parte se describen los métodos más utilizados para representar los rangos de distribución de las especies, así como sus limitaciones. Al mismo tiempo, se explica el uso de los Modelos de Distribución de Especies (SDMs, de sus siglas en inglés *Species Distribution Models*) como herramientas biogeográficas, y sus ventajas sobre las herramientas anteriormente citadas. También se proporciona la clasificación de los SDMs según los objetivos que abordan y la forma en la que se expresan, así como las diferencias entre los SDMs estadísticos y los mecanicistas. A continuación, se discute la incertidumbre de las distribuciones de las especies y la utilidad de la lógica difusa para comprender la naturaleza. En esta sección también se presenta una breve explicación de por qué los SDMs son herramientas útiles para tratar los problemas derivados de la incertidumbre, y por qué los métodos de lógica difusa en los SDMs son cada vez más utilizados. Seguidamente, se ofrece una descripción y justificación del principal método utilizado en la tesis, los SDMs obtenidos mediante la función de favorabilidad. En esta parte se hace hincapié en su importancia en biogeografía, señalando su capacidad para analizar la incertidumbre y la dinámica asociadas a la distribución de las especies. A continuación, se presentan los pasos más comunes de la realización de un modelo de favorabilidad, así como las diferentes aplicaciones de los modelos de favorabilidad. Al final del **capítulo 1**, se explica el uso de los modelos de favorabilidad en esta tesis doctoral y el uso de diferentes taxones como representantes de grupos que comparten patrones biogeográficos particulares, siendo el Busardo Moro del Atlas como un ejemplo de especies que se desplazan hacia el norte por efecto del cambio climático (**capítulos 3** y **4**), el Carricero Común como aves migradoras transaharianas que modifican su fenología debido al aumento de las temperaturas invernales (**capítulo 5**), las tres víboras ibéricas como especies parapátricas (**capítulo 6**) y el Ibis Eremita como especie en peligro crítico de extinción con una distribución relicta cuya dinámica parece haber cambiado recientemente (**capítulo 7**).

El **capítulo 2** contiene los objetivos generales que se abordaron durante el desarrollo de esta tesis doctoral, relacionados con el conocimiento biogeográfico del dinamismo de las áreas de distribución de las especies. Estos objetivos tienen la intención de mejorar los aspectos conceptuales y teórico del estudio de las distribuciones, tratan de desarrollar las herramientas para su análisis y también de profundizar en la información sobre las especies estudiadas, que fueron seleccionadas como ejemplos de grupos de especies con patrones biogeográficos concretos. En pocas palabras, los principales objetivos son: (1) estudiar los patrones de distribución en el marco geográfico de la península ibérica y las zonas circunmediterráneas; (2) identificar los factores condicionantes del dinamismo de las distribuciones por medio de modelos biogeográficos; (3) proporcionar avances conceptuales y metodológicos para futuros estudios biogeográficos; (4) destacar la utilidad de la función de favorabilidad en la biogeografía dinámica; y (5) proponer, cuando sea posible, aplicaciones prácticas para la ordenación y conservación de las especies. Además, en este capítulo también se enumeraron los diferentes objetivos específicos abordados en los diferentes capítulos de esta tesis doctoral. Estos son: (6) identificar los factores ambientales que favorecen el establecimiento de aves típicamente africanas en la península ibérica y determinar la potencialidad de esta zona para albergar nuevas especies; (7) detectar y cuantificar el desequilibrio producido por el cambio climático entre la las zonas climáticamente favorables para las especies y su distribución mediante SDMs y operaciones de lógica difusa; (8) medir la tasa de desplazamiento latitudinal de las zonas favorables por la influencia del cambio climático actual en el contexto intercontinental del norte de África y el sur de Europa; (9) poner de manifiesto el cambio fenológico de aves migradoras transaharianos en Europa, que se convierten en presaharianas o incluso sedentarias en Iberia, y analizar el efecto del aumento de las temperaturas invernales en este fenómeno; (10) identificar los lugares más favorables de la península ibérica para la invernada de aves transaharianas insectívoras como zonas cuyo monitoreo podrían mejorar el conocimiento disponible sobre las alteraciones fenológicas debidas al cambio climático reciente; (11) crear un marco teórico y metodológico para estudiar las interacciones bióticas y ambientales entre las especies con distribuciones parapátricas, evaluando el peso relativo del ambiente y de la competencia interespecífica en estas particulares distribuciones; (12) identificar las zonas en las que es más probable que se produzca la exclusión competitiva o la coexistencia simpátrica entre especies parapátricas; (13) obtener información sobre la distribución histórica de las especies para demostrar que éstas no sobreviven necesariamente en las zonas ambientalmente más favorables; y (14) demostrar la importancia de considerar la estructura espacial de las especies en los modelos de distribución, en combinación con factores ambientales, con miras a detectar posibles patrones de distribución que podrían ser de gran provecho en la conservación de las especies amenazadas desde una perspectiva dinámica.

A medida que las temperaturas aumentan por el impacto del cambio climático, se está produciendo un aumento de las condiciones mediterráneas en el sur de Europa, lo que parece estar modificando la fenología así como las distribuciones de las especies. El Busardo Moro del Atlas, un ave sedentaria típicamente africana (es decir, aves cuyo límite de distribución septentrional estaba en el norte de África, en las mismas costas, pero que no criaba en Europa), ha colonizado recientemente Iberia a través del Estrecho de Gibraltar. En el **capítulo 3** se estudian los factores que condicionan su distribución, previa y posterior a la colonización del país europeo. En este capítulo se ha tratado de explicar la distribución autóctona de esta especie y de predecir las zonas favorables en las zonas ibéricas recientemente colonizadas mediante la elaboración de modelos geoespaciales, tratando de identificar los factores más influyentes en este proceso. Se aplicó la función de favorabilidad a las presencias y ausencias de zonas reproductoras tanto en el norte de Marruecos y como el sur de la península ibérica, junto con un conjunto de variables que describen el clima, la topografía, la actividad humana, la vegetación y las tendencias puramente espaciales. Uno de los modelos fue creado con los lugares de cría conocidos en el norte de Marruecos y se utilizó para pronosticar zonas de cría adecuadas en Europa extrapolándolo al sur de Iberia. Se construyó un segundo modelo con todos los datos disponibles para el norte de Marruecos y la península ibérica para explicar la distribución actual de los lugares de cría. Ambos modelos se evaluaron en base a criterios de discriminación, clasificación y parsimonia, y la influencia de cada factor se analizó utilizando la partición de la varianza. Las temperaturas estables y las precipitaciones abundantes pero estacionalmente distribuidas mostraron el mayor poder de predicción de los modelos. Esto indica una estrecha relación entre la distribución de la especie y el clima en el área de estudio, y sugiere que esta especie encuentra los ambientes más favorables en el bioma mediterráneo. La topografía y la vegetación, específicamente los acantilados y bosques cercanos a las zonas de caza, muestran una selección de hábitat para la reproducción dentro de las zonas climáticamente favorables. Así, se demuestra que el cambio en el límite de distribución de esta especie en expansión se ve favorecido por las nuevas condiciones climáticas de la península ibérica, más mediterráneas. También se detectan áreas susceptibles de ser ocupadas, que actuarían como áreas de expansión de su área de distribución y posibles fuentes de colonización de nuevas zonas en un futuro próximo. Se llega a la conclusión de que la península ibérica proporciona nuevas zonas adecuadas para la especie y facilitar su expansión hacia el norte. Este resultado, junto con el creciente número de registros disponibles, sugiere que esta especie podría pronto extenderse por toda Europa. Dado que el caso del Busardo Moro del Atlas no es un caso único, estos resultados pueden ser útiles para determinar si una expansión hacia el norte del bioma mediterráneo podría acarrear cambios en la distribución de aves que hasta ahora se han limitado a África.

En el **capítulo 4** se desarrollan en profundidad los conceptos teóricos y metodológicos sobre el análisis de las respuestas biogeográficas de las especies al cambio climático, que es un cambio biogeográfico importante y generalizado. Concretamente, el estudio se centra en el desequilibrio entre los taxones y un clima cambiante. La mayoría de los modelos de distribución de especies asumen un equilibrio entre la distribución con el ambiente, lo que dificulta su aplicabilidad al análisis de este cambio. Sin embargo, combinando SDMs basados en la favorabilidad climática con la teoría de los conjuntos borrosos, es posible evaluar la respuesta al cambio climático. Esto se hizo en este capítulo con el mismo taxón que en el capítulo anterior, el Busardo Moro del Atlas. A diferencia del capítulo anterior, en éste el área de estudio es todo el contexto geográfico del taxón, el Paleártico Occidental, ya que el análisis del dinamismo se centra ahora en su distribución completa. De esta manera, se predice el potencial de colonización del continente europeo por el Busardo Moro del Atlas en los diferentes escenarios de cambio climático. Como fuentes de incertidumbre se utilizaron las trayectorias de concentración representativa (RCPs, de sus siglas en inglés *Representative Concentration Pathways*) y los Modelos de Circulación Global (GCMs, de sus siglas en inglés *Global Circulation Models*) empleados para predecir los valores de las variables climáticas en los dos períodos de tiempo en el futuro: 2041-2060 y 2061-2080. En total, se obtuvieron ocho modelos de favorabilidad para cada período. Para clarificar los resultados, se realizó una predicción conjunta de los ocho modelos para cada período de tiempo mediante el cálculo de los valores medios de favorabilidad climática en cada Unidad Geográfica Operativa (OGU, de sus siglas en inglés *Operative Geographical Unit*). Posteriormente, la incertidumbre de estas predicciones conjuntas se calcularon para cada período de tiempo mediante la diferencia de la unión difusa de los ocho modelos (es decir, el valor máximo de favorabilidad de cualquiera de ellos en cada OGU) y su intersección difusa (como la unión difusa pero con el valor mínimo) en cada OGU. Luego se utilizaron cuatro operaciones de lógica difusa para evaluar los cambios predichos en la distribución reproductora en relación con el presente, siendo el incremento (I), la superposición (O), el mantenimiento (M) y el cambio previsto (S) de la favorabilidad. Además, se realizó una evaluación de la variación latitudinal de la distribución reproductora de la especie mediante el análisis de las diferencias de baricentro entre el baricentro latitudinal de las OGU con reproducción confirmada y los baricentros latitudinales de favorabilidad climática de las OGU con reproducción confirmada o las que se encuentran dentro del rango longitudinal en el que se reproduce el Busardo Moro del Atlas. Comparando los baricentros actuales y los previstos, se obtuvieron tres índices: el desequilibrio latitudinal (es decir, la diferencia entre los baricentros geográficos y climáticos latitudinales en las OGUs en las que se registra reproducción del busardo), el desplazamiento de favorabilidad para el período 2041-2060 (es decir la diferencia entre el baricentro latitudinal de favorabilidad climática actual y el previsto para el período 2041-2060, dentro de la región longitudinal donde el taxón cría, dividido por el número de años entre ambos períodos de tiempo), y el desplazamiento de favorabilidad para el período 2061-2080 (de manera similar, pero entre los períodos 2041-2060 y 2061-2080). Los resultados muestran zonas climáticamente favorables en el presente y en el futuro. Con este enfoque, se pone de manifiesto la existencia de un desequilibrio espacial y temporal entre la distribución de la especie con el clima actual de 4 km. Este desequilibrio está atrayendo a la especie hacia el norte a una velocidad de alrededor de 1.3 km/año, en otras palabras, la especie tarda 3 años en ocupar nuevas zonas climáticamente favorables. Se espera que esta velocidad disminuya a 0.5 km/año en el período 2060-2080. Además, confirmamos que el cambio que se produce es latitudinal hacia el norte, en lugar de un movimiento longitudinal o una ampliación de todo el rango de distribución. En este capítulo se mejoran las herramientas conceptuales y metodológicas tradicionalmente utilizadas para evaluar la respuesta de las especies al cambio climático, lo que resulta de gran interés a la hora de elaborar planes de gestión para la conservación de la biodiversidad en un contexto de cambio global.

En el **capítulo 5** se estudia un patrón biogeográfico recientemente alterado por el cambio climático, similar al de los capítulos anteriores pero con un dinamismo diferente: los cambios en las migraciones de larga distancia de las aves que se han estado produciendo durante las últimas décadas. En este capítulo, se analiza desde una perspectiva biogeográfica el caso del Carricero Común, como ejemplo de la alteración fenológica de una especie migratoria transahariana (es decir, una especie que se reproduce en Europa y cruza el desierto del Sahara para pasar el invierno en África) que se ha registrado recientemente en la península ibérica. En este capítulo se recopila toda la información disponible sobre los datos de anillamiento y recuperación de esta especie en la península durante el invierno, para luego investigar la influencia del clima mediante la elaboración de modelos biogeográficos. La base de datos de registros de anillamiento invernal se construyó con datos de 1959 a 2015, proporcionados por el Centro de Migración de Aves (CMA) de la SEO/Birdlife, la Oficina de Anillamiento de la Sociedad de Ciencias Arantzadi (OAA) para el área española y la Central Nacional de Anilhagem/CEMPA (ICNF) para el territorio portugués. Los datos de recuperación de anillas fueron proporcionados por EURING. Las recuperaciones de aves anilladas se clasificaron en "reproductoras" (si se anillaron en la temporada de cría anterior (mayo a julio) a su recuperación) y "no reproductoras" (si se anillaron fuera de la temporada de cría anterior). Se construyó un modelo de favorabilidad para identificar las zonas más favorables de la península ibérica y los factores explicativos más relevantes de esta distribución. Algunas aves ibéricas invernaban en las zonas de cría, o en sus alrededores, lo que podría indicar un posible proceso de sedentarización. Carriceros que crían en Gran Bretaña fueron recuperados invernando al norte de Iberia, mientras que individuos de Europa Central y Europa del Este muestran una tendencia a invernar en regiones del sur de la península y en la costa mediterránea, respectivamente. Las zonas más favorables se localizaron en las costas meridionales y orientales de la península ibérica y en algunos lugares de la costa atlántica septentrional de España. La temperatura mínima invernal fue el factor más relevante para la invernada de esta especie en Europa, por lo que las crecientes temperaturas invernales en esta zona alteran el dinamismo del límite sur de su distribución reproductora. El análisis espacial mostró la orientación de las trayectorias de vuelo de la especie desde sus zonas de cría hasta sus zonas de invernada, mientras que la topografía reflejó la selección de hábitat a escala fina. Como el caso del Carricero Común no es único, los resultados muestran el papel de la península ibérica como nuevo lugar de invernada para las especies que suelen invernar en la región subsahariana, modificando su estrategia de invernada de migradores transaharianos a presaharianos, y el reciente aumento de la temperatura como la causa principal, como también ocurre para otras especies cuyo rango de distribución está cambiando, por ejemplo el Busardo Moro del Atlas (capítulos 3 y 4).

El patrón que se analiza en el **capítulo 6** es la parapatría entre varios taxones cuya distribución está estrechamente relacionada con el ambiente. Concretamente, este capítulo trata del equilibrio dinámico entre las interacciones bióticas competitivas y el entorno en el que tienen lugar, que se produce en este tipo de límites de distribución. La parapatría es estudiada tradicionalmente por pares de áreas de distribución, pero un patrón más complejo está presente en la península ibérica, donde se distribuyen tres especies de víboras parapátricas con afinidades biogeográficas distintas: la eurosiberiana *Vipera seoanei*, la para-mediterránea *V. aspis* y la mediterránea *V. latastei*. En este capítulo el principal objetivo es evaluar si esta particular parapatría entre tres especies está causada principalmente por condiciones ambientales, acontecimientos históricos, competencia interespecífica entre ellas o una combinación de estos factores. Para ello se aplicó el concepto de favorabilidad para producir unidades de distribución conmensuradas no afectadas por la prevalencia de las diferentes especies en la península ibérica. En primer lugar, se tuvo en cuenta la estructura espacial de la distribución para cada especie mediante la favorabilidad espacial, que fue usada para seleccionar el área donde se realizaron los modelos ambientales posteriores (área espacialmente relevante). Estos modelos ambientales fueron posteriormente extrapolados a toda el área de estudio a fin de identificar zonas ambientalmente adecuadas para las especies. A continuación, se comparó la favorabilidad de cada especie con la favorabilidad compartida de más de una especie en sus áreas de solapamiento, identificando las zonas en las que se predice que se produzca la coexistencia simpátrica, la segregación ambiental o la exclusión competitiva. Desde el punto de vista ambiental, *V. aspis* y *V. latastei* están más relacionadas entre sí que con *V. seoanei*, lo que podría ser una consecuencia de la relación filogenética de estas especies (*V. aspis* y *V. latastei* son especies hermanas, mientras que *V. seoanei* está más emparentado con especies eurosiberianas del clado *Pelias* como *V. berus*). Los resultados muestran que cada especie está mejor adaptada a las condiciones ambientales de su lado del límite de distribución, lo que le da una cierta ventaja competitiva sobre las demás. Este hecho conduce a la formación de "barreras de exclusión competitiva" que impiden la expansión de las demás especies. Estas barreras explican la distribución de *V. aspis*, que presenta áreas favorables desocupadas en Iberia al otro lado de las "barreras de exclusión competitiva" formadas con las otras dos especies. También explican la ausencia de *V. latastei* en la parte nororiental y noroccidental de la península ibérica, ocupada por las otras dos especies. Sin embargo, para *V. seoanei* parece ser que su adaptación a los ambientes eurosiberianos es el factor más limitante de su distribución. Se han identificado algunas zonas de coexistencia simpátrica sostenible, principalmente en el curso alto del río Ebro. Estos resultados apoyan teorías filogenéticas sobre la localización de los refugios del Pleistoceno para estas especies y su posterior expansión al resto de la península ibérica. La alteración de este equilibrio dinámico entre el medio ambiente y la competencia interespecífica que mantiene la parapatría, por ejemplo por cambios en las condiciones climáticas, podría dar lugar a una alteración biogeográfica, como ya ocurre con el Carricero Común en el capítulo 5.

En el **capítulo 7** se exponen nuevas ideas para la conservación de una de las especies de aves más amenazadas del planeta, el Ibis Eremita. Esta especie estuvo ampliamente distribuida por Europa y el norte de África, pero a día de hoy las únicas colonias naturales se encuentran en los valles del río Souss-Massa en la región de Agadir en Marruecos. Los programas de introducción de individuos nacidos en cautiverio "Proyecto Eremita" y LIFE+, en España y Austria, respectivamente, se apoyaron principalmente en estudios de hábitat adecuado para la reproducción de la especie en la ubicación de sus actuales colonias. Sin embargo, estas colonias no tienen que estar necesariamente en los hábitats más favorables para la especie, sino en aquellos en los que ha podido permanecer. Los objetivos que se abordan en este capítulo son analizar la distribución histórica de las colonias reproductoras marroquíes mediante enfoques espaciales y ambientales, evaluar la favorabilidad ambiental de las colonias actuales en base a datos históricos de reproducción y a su ubicación actual, identificar las posibles zonas cuya conservación podría beneficiar la supervivencia de la especie y proponer el uso de modelos biogeográficos en la política de gestión y conservación de la especie en el contexto hispano-marroquí. Para ello, se realizaron SDMs de favorabilidad utilizando la presencia de colonias reproductoras durante el siglo XX en Marruecos y las presencias actuales en Marruecos y España. Las colonias reproductoras del siglo XX mostraron un patrón espacial con una alta conectividad entre las colonias de Agadir y las colonias de la costa mediterránea a través de las cordilleras del Medio y Alto Atlas. Desde el punto de vista ambiental, ambas costas del Estrecho de Gibraltar, así como otras zonas de la península ibérica, se identificaron como zonas favorables para la reproducción de los ibis durante el siglo XX, a pesar de su ausencia en estas zonas. En Marruecos, sólo las colonias de Agadir estaban situadas en zonas favorables. En la actualidad, la favorabilidad ambiental está situada en la costa atlántica de Marruecos, en el entorno de las colonias actuales y hacia el sur, lo que podría favorecer el establecimiento de nuevas colonias en esta zona en un futuro próximo (como ya ha ocurrido en 2017). Las colonias introducidas en España, así como las establecidas naturalmente en 2017 en Marruecos, están situadas en zonas ambientalmente favorables según su distribución histórica. Teniendo en cuenta las colonias actuales, se muestra una conectividad potencial de las zonas intermedias y de alta favorabilidad entre las colonias naturales e introducidas. Esto plantea la posibilidad de la creación de una estructura dinámica metapoblacional que podría beneficiar a la especie, algo que abre la puerta a una nueva perspectiva en la conservación de esta y otras especies en peligro de extinción.

En el **capítulo 8** se realiza una discusión general de los métodos utilizados como herramientas biogeográficas, relacionándolo con los contenidos y contextualizándolo en el escenario de cambio global actual. En este capítulo se destacan los objetivos y logros de la presente tesis doctoral. También se justifica en el mismo capítulo el uso de los factores ambientales seleccionados para cada caso de estudio, destacando la inclusión de los factores de usos del suelo o de actividad humana en los capítulos 3 y 6, pero excluyéndolos del capítulo 5, por no tener suficiente resolución para el caso de estudio, y para los capítulos 4 y 7, a fin de poder extrapolar los modelos a otras regiones donde estos factores son demasiado distintos. Después se discute el efecto del clima en las relaciones biogeográficas de las especies, ya que este factor es el más relevante para explicar la distribución de las especies estudiadas en la presente tesis doctoral. A continuación, se discute la conclusión de esta tesis que, al menos en mi humilde opinión, resulta más interesante: el desequilibrio entre las especies y las condiciones ambientales (o climáticas) donde habitan. Esta parte es especialmente importante porque pone de manifiesto el uso de este tipo de SDMs para comprender cómo las especies responden al cambio climático desde un punto de vista biogeográfico. Después se defiende el uso de la favorabilidad por dos razones principales. La primera es por ser obtenida a partir de una regresión logística, un algoritmo que usa la información de las presencias y las ausencias. La segunda razón es que los modelos de favorabilidad son conmensurables, es decir, pueden compararse incluso si las especies tiene prevalencias diferentes en el área de estudio. Esta es de imperiosa necesidad en los casos de estudio donde se comparan diferentes modelos, de la misma o diferente especie, o para aplicar métodos de lógica difusa. Luego se contrasta el concepto de favorabilidad con el concepto de nicho y sus aplicaciones en nuevos horizontes para la biogeografía, como la diversidad oscura. Finalmente, al final de este capítulo se discute la utilidad de la información sobre el dinamismo de la distribución de las especies obtenida a partir de los modelos biogeográficos en los planes de manejo y conservación de las especies, para anticiparse a los cambios de manera más eficiente.

Las conclusiones obtenidas a lo largo de todos los capítulos anteriores se recogen en el **capítulo 9**. Las conclusiones generales están relacionadas con el carácter difuso del límite entre África y Europa, con la eficacia de los SDMs para describir, explicar y predecir los rangos de las especies y su dinamismo, con los avances conceptuales y metodológicos que propone esta tesis doctoral, y con los beneficios de incluir la información obtenida mediante esta metodología en los programas de gestión y conservación. Más concretamente, en el **capítulo 3** se concluye que el clima es el principal factor que favorece la colonización de Europa por aves típicamente africanas y que la península ibérica es un lugar propicio para que estas especies se establezcan y propaguen. Del **capítulo 4** se concluye que la generación de áreas favorables en el norte atrae la distribución de la especie, generando un desequilibrio con el ambiente que puede medirse mediante modelos de favorabilidad junto a operaciones de lógica difusa y análisis de baricentro. Además, en este capítulo se proporcionan dos índices, el desequilibrio latitudinal y la tasa de desplazamiento de la favorabilidad. En el **capítulo 5** se concluye que parte de poblaciones de aves migradoras transaharianas están acortando su distancia migratoria, convirtiéndose en presaharianos o incluso residentes, debido a los inviernos más cálidos de la península ibérica, su nuevo lugar de invernada, especialmente las costas mediterráneas y atlánticas. Del **capítulo 6** se concluye que el marco conceptual y metodológico presentado en esta tesis doctoral es realmente eficaz para analizar el origen y mantenimiento de la parapatría, determinando el peso relativo del ambiente y la exclusión competitiva, e identificando la existencia de "barreras de exclusión competitiva" entre las víboras ibéricas. En el **capítulo 7**, las conclusiones más importantes son las relacionadas con la información que proporcionan los enfoques ambientales y espaciales históricos, junto con los actuales, para los programas de gestión y conservación de especies, tales como la detección de la conectividad entre las colonias naturales e introducidas que podrían establecer una dinámica metapoblacional en el futuro, probablemente beneficiando la conservación de la especie. Con todo lo anterior, los modelos de distribución permiten enfrentar la incertidumbre en el desarrollo futuro de las distribuciones de las especies, aportando ideas y explicaciones que podrían direccionar hipótesis, a la vez que pueden ser actualizar con nueva información, generando una dinámica de trabajo que favorece en última instancia el avance en el conocimiento de los fenómenos biogeográficos de la naturaleza.

Por último, en el **capítulo 10** se recoge por orden alfabético la bibliografía utilizada para redactar la presente tesis doctoral. Al final del capítulo se detallan las contribuciones científicas que avalan la presente tesis doctoral, así como otras contribuciones científicas obtenidas durante la realización de la tesis, y un breve *currículum vitae* del doctorando.

0 OUTLINE OF THE THESIS

This doctoral thesis is made up of ten chapters that deal with different aspects of the dynamism of the distribution of the species and how the biogeographic modelling analysis provides new information and theoretical frameworks that unravel the patterns and mechanism of the distribution ranges, peculiarities and changes. For this purpose, there have been selected five cases (taxa) whose research supplies new information on the distribution patterns, providing new theoretical and methodological approaches that can be used in the management and conservation of species in the context of the changing planet. These selected species are also representatives of groups of species that share biogeographical dynamic patterns, hence their study allow us to delve into the characteristics of their patterns without being obscured by the effect of analysing many species at the same time, detailing the mechanism that conditions their dynamic.

The general organization of this thesis, chapter by chapter, is explained below with a concise summary of each one.

Chapter 1 provides a general introduction to this doctoral thesis. Firstly, a succinct definition of the science that studies the distribution of species – the biogeography – is presented, from its etymology to the branches of knowledge it covers. This part helps us to understand the wide variety of cases in which this science could provide relevant information. Secondly, it is shown a compilation of the historic overview of the development of the biogeography over the centuries, pointing out some of the most relevant events that have led an important advance in explaining the distribution of living beings on the planet, and therefore, that promoted the development of the science. This part is useful to contextualize the thesis and to highlight the importance and interest of the different processes that are going to be studied during this doctoral thesis. The first part of this historical overview covers the rudimentary origins of the study of the distribution of the species, from the prehistoric cave paintings and the first works of ancient history philosophers, such as Aristotle and Pliny the Elder, to the "biogeographic theories" written by monks, priests and friars during the Middle Ages. Next, it is described the most important events and writings of the Age of Discovery that entailed an increasing interest in the origin of species and the differences among faunas of different continents, which inspired the first essays of biogeography *sensu stricto*. Then, it is presented a compilation of essays that contributed the development of the biogeography as a science during the 19th century, such as Wallace's world regionalisation and Darwin's evolution theory, as well as the first writings in ecology. The explanation of the four schools of biogeography that converge in the 20th century is presented afterwards, namely the dispersalism, the panbiogeography, the phylogenetic biogeography and the cladistics biogeography. After that, there are described the most relevant advances in ecological biogeography, such as the origin of macroecology and the MacArthur and Wilson's island biogeography, as well as the aims of this field. Summarizing this first part of the introduction, a timeline figure about the history of the biogeography is shown.

After the section of the historic overview of biogeography, it is given a brief explanation on the characteristics of the distributions of the species and how scientist classify them according to the spatial segregation of individuals or populations (uniform, clumped or random distributions), to the continuity of the species range (continuous, discontinuous or disjunct distributions), and to the global range extension (cosmopolitan, relictual and/or endemic distributions). This part remarks the high diversity of distributional patterns that species present all over the world. Then it presents a brief introduction to the dynamism of the species distributions, which is the golden thread that runs through this doctoral thesis and the chief aim it is going to be addressed from diverse perspectives over the different chapters. In it, it is explained the cause that makes the species distributions spatiotemporally dynamic and its analogy with quantum physics. Next it is shown a short section introducing to the spatial (but also temporal) limits in the species range and why the specific dynamic of the distribution edges are important to characterise the species distribution shifts. In the next section, a concise description of the different ways to represent the species distribution is presented, with great emphasis on the difficulties to obtain the data and reflect the dynamics and fluctuations in the process. In this part, it is described the most common methods used to represent the species distribution ranges and their limitations, at the same time that it is explained the use of Species Distribution Models (SDMs) as biogeographical tools, and what benefits provide this method that the previous tools cannot do. It is also provided with the classification of the SDMs according to the aims they addressed and the way they are expressed, as well as the differences between statistical and mechanistic SDMs. Following that, it is discussed the uncertainty of the species distributions and the utility of the fuzzy logic to understand nature, which is fuzzy and blurred rather than clear. In this section it is also presented a brief explanation of why the SDMs are useful tools to deal with these problems derived from uncertainty, and why the fuzzy logics methods, which could be used in certain types of SDMs, are experienced a significant increment in use. Then, it is given a description and succinct justification of the main method used in the thesis, the species distribution models using favourability function. This part emphasizes their relevance in biogeography and points out its capacity to analyse the uncertainty and the dynamics associated with the distribution of species. Next, the most common steps of doing a favourability model are presented together with a diagram of the process, as well as different applications of the favourability models. At the end of **chapter 1**, it is explained the use of favourability models in this doctoral thesis and the use of different taxa as representatives of groups that share particular biogeographical patterns, being the Atlas Long-legged Buzzard as an example of species that move northwards due to the effect of climate change (**chapters 3** and **4**), the Eurasian Reed Warbler as trans-Saharan migratory birds that change their phenology due to increasing winter temperatures (**chapter 5**), the three Iberian vipers as parapatric species (**chapter 6**) and the Northern Bald Ibis as critically endangered species with a relict distribution whose dynamics seems to have recently changed (**chapter 7**).

Chapter 2 contains the general objectives that were addressed during the development of this doctoral thesis, related to the biogeographical knowledge of the dynamism of the species distribution areas. These aims have the intention of improving the conceptual and theoretical aspects of the study of distributions, try to develop the tools for their analysis and they are also used to delve into the information about the studied species, which were selected as models of species with comparable biogeographical patterns. Briefly, the main aims are (1) to study the distribution patterns within the geographical framework of the Iberian Peninsula and Mediterranean areas; (2) to identify the conditional factors of the distribution dynamics by means of biogeographical models; (3) to provide conceptual and methodological advances for future biogeographical studies;

(4) to enhance the usefulness of the favourability function in dynamic biogeography; and (5) to propose, when possible, practical applications for management and conservation of species. In addition, this chapter also listed the specific aims that were addressed throughout the different chapters of this doctoral thesis. Those are: (6) to identify the environmental factors that favours the establishment of typical African birds in the Iberian Peninsula and to determine the potentiality of this area to host new species; (7) to detect and to quantify the disequilibrium produced by climate change between the species distribution and the climatically favourable areas for them using species distribution models and fuzzy logic; (8) to measure the rate of the latitudinal displacement of the favourability areas by the influence of current climate change in the intercontinental context of North of Africa and southern Europe; (9) to demonstrate the phenology change of Trans-Saharan migrants in Europe, which become Pre-Saharan or even sedentary in the Iberian Peninsula, and to analyse the effect of the increment of the winter temperatures in this phenomenon; (10) to identify the most favourable places of the Iberian Peninsula for the wintering of insectivores Trans-Saharan birds as places where the monitoring studies could improve the knowledge of phenological alterations due to recent climate change; (11) to create a theoretical and methodological framework to study the biotic and environmental interactions between species with parapatric distributions, assessing the relative weight of the environment and competition in these particular distributions; (12) to identify the areas where competitive exclusion or sympatric coexistence between parapatric species is more probable to occur; (13) to obtain information on the historical species distribution to show that species do not necessarily remain relict in the most environmentally favourable areas; and (14) to demonstrate the importance of considering the spatial structure of species in the

distribution models, in combination with environmental factors, with a view to detecting potential distribution patterns that could be of great applicability in the conservation of threatened species from a dynamic perspective.

As temperatures are becoming warmer under the impact of climate change, a gain in Mediterranean conditions is being produced in southern Europe, which is modifying the phenology as well as the distributions ranges of species. The sedentary African Long-legged Buzzard, a typically African bird (i.e. birds whose northern limit of distribution was in North Africa, on the same coasts, but which did not reach Europe), has recently colonized Europe across the Strait of Gibraltar. In **chapter 3** there are studied the factors that condition its distribution, pre- and post-colonization of the European country. In this chapter the aim was to explain the native distribution of this species and to predict favourable areas in newly colonized parts of Europe using geospatial modelling, trying to identify the most influential factors in this process. It was applied the favourability function, a generalized linear model describing environmental favourability, for the presence and absence of breeding areas in northern Morocco and the Southern Iberian Peninsula, according to a set of variables describing climate, topography, human activity, vegetation, and purely spatial trends. One model was built using some known breeding sites in Northern Morocco and was used to forecast future suitable breeding areas in Europe by an extrapolation. A second model was built with all the available data for northern Morocco and Europe to explain the current distribution of breeding sites. Both models were assessed according to discrimination, classification and parsimony criteria, and the influence of each factor was analysed using variation partitioning. Steady temperatures and abundant but seasonally distributed precipitation showed the strongest predictive power in the models. This indicates a close relationship between the species' distribution and the climate in the study area and suggests that this species finds the most favourable environments in the Mediterranean biome. Topography and vegetation, specifically cliffs and woods near hunting zones, point to a fine-scale habitat selection for breeding. Thus, it is shown that the change in the limit of distribution of this expanding species is favour by the new climatic conditions of the Iberian Peninsula, more Mediterranean. It also detects susceptible areas of occupation in the Iberian Peninsula, which would act as areas of expansion of its range and as possible sources for the colonisation of new areas in a near future. It was concluded that the Iberian Peninsula could provide newly suitable areas for the species and facilitate its northward expansion. This result, together with the increasing number of records available, suggests that this species could soon spread throughout Europe. As the case of the African Long-legged Buzzard is not a unique event, these results may be useful to determine whether a northward expansion of the Mediterranean biome could be followed by distribution shifts of bird species that have so far been restricted to Africa.

In **chapter 4**, the theoretical and methodological concepts on the analysis of the biogeographical responses of species to climate change, which is a major and generalized biogeographic change, are further developed. Specifically, the work focuses on the disequilibrium between taxa and a changing climate. Most species distribution modelling approaches assume equilibrium of the distribution with the environment, which hinders their applicability to the analysis of this change. However, combining species distribution models based on climatic favourability with fuzzy set theory, it is possible to assess the response to climate change, which was done in this chapter with the same taxon as the previous chapter, the Atlas Long-legged

Buzzard. Unlike in chapter 3, in this chapter the study area is now the entire geographical context of the taxon, the Western Palearctic, as the analysis of dynamism is focused on its complete distribution. In this way, the potential for colonization of the European continent by the Atlas Long-legged Buzzard is predicted under the different scenarios of climate change. As sources of uncertainty, they were used the Representative Concentration Pathway (RCP) and the Global Circulation Model (GCM) that had been used to predict the values of the climatic variables in the two periods of time, namely 2041–2060 and 2061–2080. In total, eight favourability models for each period were obtained. An ensemble forecasting of the models was then obtained for each period of time by calculating the mean values of the eight future climatic favourability models at each Operative Geographical Unit (OGU). Subsequently, the uncertainty of the ensemble forecasting models was calculated by the difference at each OGU of the fuzzy union of the eight models (i.e. the maximum value of favourability of either of them at the OGU) and their fuzzy intersection (as a fuzzy union but using the minimum value), for each period of time. Then, four fuzzy logic operations were used to assess changes in the expected breeding distribution, being the measures of the increment in favourability (I), favourability overlap (O), favourability maintenance (M), and the predicted shift in favourability (S) in relation to the present. In addition, an assessment of the latitudinal variation of the species breeding range was performed by the analysis of the barycentre differences between the latitudinal barycentre of the OGUs with reported breeding and the latitudinal barycentres of climatic favourability of the OGUs with reported breeding or those which are within the longitudinal range where the Atlas Long-legged Buzzard is reported to breed. Comparing the present and the forecasted barycentres, three indices were obtained: the latitudinal disequilibrium (i.e. the difference between the geographic and climatic latitudinal barycentres in the OGUs where the buzzard is reported to breed), the favourability displacement for the 2041-2060 period (i.e. the difference between the latitudinal climatic favourability barycentre at present inside the longitudinal breeding range and that forecast for the period 2041 to 2060, divided by the number of years between the compared periods), and the favourability displacement for the 2061-2080 period (similarly, but between the 2041-2060 and the 2061-2080 periods). The results show climatically favourable areas in the present and for the future. With this approach, there is a spatial and temporal disequilibrium of the species distribution with the current climate of 4 km. This disequilibrium is driving the species range northwards at a speed of around 1.3 km/year, or in other words, it takes 3 years for the species to occupy new climatically favourable areas. This speed is expected to decelerate to 0.5 km/year in the 2060–2080 period of time. In addition, we confirmed that the change that occurs is latitudinally northwards, rather than a widening of the entire range or a longitudinal movement. This chapter improves the conceptual and methodological tools traditionally used to assess the response of species to climate change, which is of great interest when making management plans for biodiversity conservation in a context of global change.

In **chapter 5** it is studied a biogeographical pattern recently altered by climate change, similar as in the previous chapters but with a very different dynamism: the changes in bird long-distance migrations that have been produced for several decades. In this chapter it is analyses from a biogeographical perspective the case of the Eurasian Reed Warbler, as an example of the phenology alteration of a Trans-Saharan migratory species (i.e. a species that breeds in Europe and crosses the Sahara desert to spend the winter in Africa, especially at Western and Central Africa) that has been recorded recently wintering in the Iberian Peninsula. This chapter compiled all the available information on the ringing and recovery data of this species in the Iberian Peninsula in winter, in order to later investigate the influence of climate through biogeographical modelling. The database of wintering ringing records was built with data from 1959 to 2015, provided by the Centro de Migración de Aves (CMA) of the SEO/Birdlife, the Ringing Office of the Society of Sciences Arantzadi (OAA) for the Spanish area and the Central Nacional de Anilhagem/CEMPA (ICNF) for the Portuguese territory. Ringing-recovery data were provided by EURING. The birds that were recovered were classified in 'Breeder' (if they were ringed in the previous breeding season (May to July) they were recovered) and 'Non-Breeder' (if they were ringed out of the previous breeding season). The favourability model was constructed to identify the most favourable areas in Iberia and the most relevant explanatory factors of this distribution. Some Iberian birds wintered in breeding areas, or nearby, which could indicate a potential process of sedentarization. British Eurasian Reed Warblers winter in Iberia more northerly than individuals from Central Europe, and Eastern birds show a tendency to winter on the Mediterranean coast. The best areas are located in the southern and eastern coasts of the Iberian Peninsula and in some locations on the northern Atlantic coast of Spain. The minimum winter temperature is the most relevant factor affecting sites suitable for the wintering of this species in Europe, thus the increasingly warm temperatures in winter in this area alter the dynamism of the southern limit of their breeding distribution. Spatial trends analysis suggested the orientation of the flight paths of the species from their breeding areas to their wintering areas. Topography refined the model in that it is associated with habitat selection at a fine-scale. As the case of the Eurasian Reed Warbler is not unique, the results show the role of the Iberian Peninsula as a new wintering site for species usually wintering in the sub-Saharan region, modifying their wintering strategy from Trans-Saharan to Pre-Saharan migrants, and the role of the recent increment in the temperatures as the main cause, as it occurs for other species whose distribution ranges are shifting, such as the Atlas Long-legged Buzzards (chapters 3 and 4).

The pattern analysed in **chapter 6** is the parapatry among several taxa whose distribution is closely related to the environment. Specifically, this chapter deals with the dynamic equilibrium between competitive biotic interactions and the environment in which they take place, which occurs in this type of boundaries. Parapatry is traditionally studied by pairs of ranges but a more complex pattern is present in the Iberian Peninsula, where three parapatric viper species with distinct biogeographical affinities are distributed: the Euro-Siberian *Vipera seoanei*, the para-Mediterranean *V. aspis* and the Mediterranean *V. latastei*. In this chapter the main aim was to assess if this particular parapatry between three species it is mainly caused by environmental conditions, historical events, interspecific competition among them or, in case of a combination of these factors, in which degree they affect. To do that, it was applied the concept of favourability for occurrences to produce commensurate distribution units unaffected by the different species prevalence in the Iberian Peninsula. First, the spatial structure of the species distribution was taken into account performing a polynomial trend-surface analysis for each species that was converted in spatial favourability, which was used to select the training area were the subsequent environmental models were performed. Environmental models were extrapolated from the spatially relevant area to all the study area in order to identify areas where the species could potentially inhabit according to their environmental conditions. Then, the favourability of each species was compared with the favourability for occurrences of more than one species together at their overlapping ranges, identifying the areas in which sympatric coexistence, environmental segregation and competitive exclusion are predicted to occur. Environmentally, *V. aspis* and *V. latastei* are more related than with *V. seoanei*, which could be a consequence of the phylogenetic relationship of these species (*V. aspis* and *V. latastei* are sister species, whereas *V. seoanei* is more related to Euro-Siberian species from the Pelias clade such as *V. berus*). The results show that each species is better adapted to the environmental conditions on its side of the distribution limit, which gives them a certain competitive advantage over the others. This fact leads to the formation of "competitive exclusion barriers" that prevent the progress of the other species. These barriers are very important to explain the distribution of *V. aspis*, which has fragmented unoccupied favourable areas in Iberia on the other side of the "competitive exclusion barriers" formed with the other two species. They also explain the absence of *V. latastei* in the north-eastern and north-western part of the Iberian Peninsula, occupied by the other two species. However, for *V. seoanei* it seems to be its adaptation to Euro-Siberian environments what limits its distribution. Few areas of sustainable coexistence were detected, mainly in the high-course of the Ebro River. These results support phylogenetic theories about the location of Pleistocene refuges for these species and their subsequent expansion to the rest of the Iberian Peninsula. The alteration of this dynamic equilibrium between the environment and the interspecific competition that maintains the parapatry, for example by changes in climatic conditions, could lead to biogeographic alteration, as already occurs with the Eurasian Reed Warbler in chapter 5.

Chapter 7 sets out new ideas in the conservation of one of the most threatened bird species on the planet, the Northern Bald Ibis. This species was widely distributed in Europe and North Africa, but today the only natural colonies are found in the valleys Souss-Massa in Agadir region of Morocco. The introduction programmes of born-in-captivity individuals 'Proyecto Eremita' and LIFE+, in Spain and Austria, respectively, were supported by studies of suitable habitat for the species reproduction, which are mainly based on the location of its current colonies. However, these colonies do not necessarily have to be in the most favourable habitats for the species, but in those where it has been able to remain. The aims addressed in this chapter are to analyse the historical distribution of Moroccan breeding colonies by spatial and environmental approaches, to evaluate the environmental favourability of current Northern Bald Ibis colonies based on historical data of confirmed reproduction and their current location, to identify potential areas whose conservation could benefit the species' survival, and to propose the use of biogeographical modelling in the politics of management and conservation of the species in the Spanish-Moroccan context. To this end, species distribution models of favourability were performed using the presence of breeding colonies during the 20th century in Morocco and current presences in Morocco and Spain. The breeding colonies of the 20th century showed a spatial pattern with high connectivity between the colonies of Agadir and the colonies of the Mediterranean coast through the Middle and High Atlas mountain ranges. Environmentally, both coasts of the Strait of Gibraltar, as well as other areas of the Iberian Peninsula, were identified as favourable areas for the reproduction of the ibis during the 20th century despite the fact that the ibises did not breed there. In Morocco, only the colonies of Agadir were located in favourable areas. At present, the environmental favourability is located on the Atlantic coast of Morocco, in the surroundings of the current colonies and towards the south, which could favour the establishment of new colonies at this area in the near future (as it has already happened in 2017). The Spanish introduced colonies, as well as those naturally established in 2017 northwards of the main colonies in Morocco, are located in environmentally favourable areas according to their historical distribution. Taking into account these current colonies, it is shown the potential connectivity of intermediate and high favourability areas between the natural and introduced colonies. This raises the possibility of the creation of a dynamic metapopulation structure that could benefit the species, something that opens the door to a new standpoint of the conservation of this and others endangered species.

A general discussion is made in **chapter 8**, discussing the methods used as biogeographical tools and relating the contents by contextualizing them in the current scenario of global change. In this chapter, the aims and achievements of the present doctoral thesis are emphasized. It is also justified in the same chapter the use of the selected environmental factors for each study case, highlighting the inclusion of land cover or human activity factors in the chapters 3 and 6, but excluding them from the chapter 5, for not having enough resolution for the study case, and for chapters 4 and 7, in order to be able to extrapolate the models to other regions where these factors are too dissimilar. Then it is discussed the effect of clime in species biogeographical relations as this factor is the most relevant for explaining the distribution of the species of this doctoral thesis. The most interesting conclusion of this thesis – at least in my opinion – is discussed next: the disequilibrium between species and the environmental (or climatic) conditions where they inhabit. This part is especially important because it highlights the use of this kind of species distribution models to shed some light on how species are responding to climate change from a biogeographic point of view. Next it is defended the use of the favourability for two main reasons. The first one is because it is obtained by probability values from a logistic regression, which is an algorithm that takes into consideration the information provided by the presence and also by the absences. Contrary to the popular belief, all algorithms are affected by the false absences (including the only-presence models), so the models that include the information of 'what makes a species not occurring in one area' (but always having in mind the possibility of presenting false absences in the dataset) provides more information about the distribution of the species. The second reason is that favourability models are commensurable, i.e. they can be compared even if the species have different prevalence in the study area. This is a key reason of why favourability is selected, most of all in the study cases when different models, of the same or different species, are compared, or when fuzzy logic methods are going to be applied. Then it is compared the favourability concept with the niche concept and their applications in new horizons for the biogeography, such as the dark diversity. Finally, at the end of this chapter is discussed the utility of the information about the species distribution dynamism obtained from the biogeographical models in the management and conservation plans of nature and the species, gaining an important advantage to anticipate the changes, facing them more efficiently with the available resources.

The conclusions obtained throughout all the previous chapters are grouped in **chapter 9**. The general conclusions are related to the fuzzy nature of the limit between Africa and Europe, to the efficacy of the species distribution models to describe, explain and predict the species ranges and their dynamism, to the conceptual and methodological advances that this doctoral thesis propose, and to the benefits of including the information obtain by this methodology to the management and conservation programs. More specifically, from **chapter 3** it is concluded that the clime is the main factor favouring the colonization of Europe by typical African birds and that the Iberian Peninsula is a propitious place where these species can establish and propagate through Europe. From **chapter 4** it is concluded that the generation of favourable areas northwards attracts the species distribution, generating disequilibrium with the environment that is measure by favourability models together with fuzzy logic operations and barycentre analysis. Moreover, two indices are provided in this chapter, the latitudinal disequilibrium and the favourability displacement rate. From **chapter 5** it is concluded that populations of trans-Saharan migrants are shortening their migration distance, becoming Pre-Saharan or even residents, due to the warmer winters in the Iberian Peninsula, which is the place where these species winter, especially the Mediterranean and Atlantic coasts and the Ebro valley. From **chapter 6** it is concluded that the conceptual and methodological framework presented in this doctoral thesis is truly efficient to analyse the origin and maintenance of parapatry, determining the relative weight of the environment and the competitive exclusion, and identifying the existence of 'competitive-exclusion barriers' between Iberian vipers. From **chapter 7**, the most important conclusions are those related with the information that is provided by the historical environmental and spatial approaches, together with the current ones, for the species management and conservation programs, such as the detection of spatial connectivity through environmental favourable areas between natural and introduced colonies that could establish a metapopulation dynamic in the future, likely benefiting the species conservation. With all of the previous together and having in mind the resources available for biodiversity conservation, it is concluded that distribution models allow us to face the uncertainty in the future development of species distributions by providing ideas and explanations that could point the hypotheses, at the same time as they can be updated with new information collected, generating a working dynamic that favours progress in the knowledge of the biogeographical phenomena of nature.

Finally, **chapter 10** alphabetically listed the bibliography used to write the present doctoral thesis that was referenced in the text. At the end of the chapter, it is detailed the scientific contribution of this doctoral thesis, those articles that guarantee its scientific quality, as well as other scientific contributions which were not included on it. It was also included a brief *curriculum vitae* of the PhD candidate.

CAPÍTULO 1

INTRODUCCIÓN GENERAL

GENERAL INTRODUCTION

"Lo que sabemos es una gota de agua,
lo que ignoramos es el océano"

~ Isaac Newton

1 INTRODUCCIÓN GENERAL

1.1 Biogeografía

1.1.1 Definición

La palabra “Biogeografía” proviene de la unión de tres palabras griegas (Adrados & Somolinos 2010):

- *βίος* [bios], que significa “vida” y hace alusión a los seres vivos y sus características y cualidades, como en “biodiversidad” o “biología”;
- *γῆ* [gé], que proviene de Gea, diosa griega de la tierra y la naturaleza y se usa para designar estructuras o características propias de la tierra y el suelo, los países o el espacio físico en general, como ocurre en “geología”, “geografía” o “geometría”;
- *γράφω* [grapho], que hace referencia a la escritura y el dibujo, como en “biografía” o “gráfico”.

Por tanto, etimológicamente se puede interpretar como “la disciplina de elaborar escritos o gráficos (mapas) sobre la disposición de los seres vivos en la Tierra”. No obstante, esta definición no recoge todos los objetivos que en la actualidad se abarcan desde la biogeografía. Una mejor definición nos da la Real Academia de la Lengua Española (RAE) quien define la biogeografía como la “parte de la biología que se ocupa de la distribución geográfica de animales y plantas” (https://dle.rae.es/biogeografia). Sin embargo, sigue sin ser completamente precisa, ya que aparte de la distribución geográfica, otros aspectos de los seres vivos (no sólo de animales y plantas) son también estudiados bajo la biogeografía, como son la distribución temporal, causas de los cambios, interacciones bióticas, etc.

Una definición simple pero más precisa es la aportada por Lomolino *et al.* (2006a), la cual indica que la biogeografía es la ciencia que se encarga de comprender y documentar los patrones de distribución de los seres vivos en el espacio y en el tiempo, respondiendo a la pregunta de cómo varía la diversidad biológica a lo largo de la superficie de la Tierra. Se trata de una disciplina de síntesis, nutriéndose 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. 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. Por ello, también recoge características propias de la geografía y la cartografía (Lomolino *et al.* 2006a).

Según el objetivo del estudio biogeográfico, se habla de biogeografía descriptiva, causal o aplicada (Müller 1979a). La primera explica la diversidad de los seres vivos atendiendo a la corología (comprensión de las áreas de distribución), faunística (inventario de especies de una región), biogeografía sistémica (distribución espacial de ciertas categorías de organismos como los mamíferos o las plantas vasculares) y biogeografía biocenótica (distribución y dinámica de las comunidades vivas), entre otras disciplinas (Müller 1979a). La biogeografía causal es aquella que busca explicaciones para la distribución o patrones de distribución de las especies, bien del tipo ecológico o histórico, o que intenta desarrollar métodos empíricos para analizar las distribuciones (Lomolino *et al.* 2006a). La biogeografía aplicada es la última en surgir, y se basa en aplicar los conocimientos de la biogeografía causal y descriptiva de manera útil y práctica para la relación del ser humano con la naturaleza (Pérez 2013). Independientemente del tipo de biogeografía, ésta se puede especializar en algún acontecimiento concreto de la historia de la vida en la Tierra, dando como resultado diferentes "subdisciplinas". Por ejemplo, si se tiene especial interés por conocer las distribuciones históricas de los taxones se habla de paleobiogeografía (López Martínez 1989), si se tiene interés en conocer la distribución territorial de las comunidades vegetales se habla de fitogeografía o corología vegetal (Rivas-Martinez 1987) o si el interés es el estudio de los patrones espacio-temporales que presentan las enfermedades se habla de patogeografía (Murray *et al.* 2018).

Una reciente rama de la biogeografía enfoca su interés en la aplicación de los análisis biogeográficos sobre las dinámicas de distribución de las especies a los problemas relacionados con la conservación de la biodiversidad (Whittaker *et al.* 2005). Se trata de la biogeografía de la conservación, que tiene como parte de sus objetivos el diseño de herramientas que permitan el uso eficiente de grandes cantidades de información y que evalúen la incertidumbre y el nivel de sesgo de los datos y de los modelos obtenidos (Ladle & Whittaker 2011). En la presente tesis doctoral, el análisis de las distribuciones de las especies estudiadas aporta resultados que, más allá de tener un enfoque teórico sobre su dinámica biogeográfica, pueden apoyar a las acciones de conservación y gestión eficaz de dichas especies, bajo el contexto de cambio global y dinamismo propio de las especies.

1.1.2 Recorrido histórico por la biogeografía

1.1.2.1 Orígenes

La biogeografía *sensu lato* puede ser considerada tan antigua como la propia humanidad. Ya en el Paleolítico, los primeros seres humanos estudiaban las migraciones de los animales que les servían de sustento, e identificaban las plantas que les servían y dónde se encontraban. No sólo lo memorizaban y trasmitían entre sí, sino que lo dejaban registrado en pinturas rupestres, con el fin de recordar la disposición de dichas especies y cursos de agua en un territorio y de trasmitírselo a futuras generaciones, pudiendo ser interpretado como interés por una biogeografía primigenia (Papavero *et al.* 1995a).

Durante la Edad Antigua, Aristóteles (384-322 a.C.) dio pinceladas en el campo de la biogeografía en su obra *Historia animalium*, donde recoge una clasificación primaria de 540 seres vivos y sus localizaciones (Llorente-Bousquets *et al.* 2001). Otro filósofo de la época, Teofrasto (371-287 a.C.), realiza lo mismo centrándose en las plantas y en las causas de su distribución, en sus obras *De historia plantarum* y *De causis plantarum* (Papavero *et al.* 1995a). Estos autores sentaron las bases sobre las que muchos otros comenzaron a darle importancia a la distribución de las especies, como Plinio el Viejo (23-79 d.C.) quién en su obra *Naturalis historia* recoge un compendio de fábulas y hechos sobre los seres vivos, que a pesar de confundir la realidad con la ficción en ciertas ocasiones, describe fielmente la realidad geográfica para muchas especies (Zunino & Zullini 2003).

En la Edad Media, los pensadores de la época eran principalmente monjes que relacionaron todo hecho biogeográfico con la información de la Biblia. Así pues, grandes pensadores como san Agustín en *Confesiones* (398) o santo Tomás de Aquino en *Summa contra gentiles* (1260) predicaban sobre el origen de los seres vivos en el paraíso terrenal por la acción directa de Dios, que en un primer lugar habían sido repartidos por la Tierra mediante la intervención de ángeles y, secundariamente, habían sido dispersados por el arca de Noé tras el diluvio universal (Papavero *et al.* 1995f, Zunino & Zullini 2003). En Oriente, cabe destacar a Al-Biruni (973-1048) quien defendía que las especies tienden a extender su área de distribución y a ocupar el mayor espacio posible, siendo una inspiración para posteriores teorías dispersionistas (Zunino & Zullini 2003).

1.1.2.2 La edad Moderna

El inicio de la Edad Moderna estuvo marcado por las expediciones y los grandes descubrimientos, que despertaron la curiosidad de los naturalistas de la época. Mientras que en el resto de Europa los estudios de biogeografía se centraban en descripciones de las especies euroasiáticas que habían sido descubiertas en las expediciones, con anotaciones sobre sus distribuciones, como la de Marco Polo por Asia o Diogo Cão por la costa de África, los naturalistas españoles centraron su atención en la naturaleza del continente americano (Papavero *et al.* 1995b). En 1526 Gonzalo Fernández de Oviedo y Valdés publicó su obra *Sumario de la natural historia de las Indias* y en 1565 Nicolás Bautista Monardes publicó *Historia medicinal de las cosas que se traen de nuestras Indias Occidentales*, donde se reflejan anotaciones sobre diferencias entre las faunas y floras de los distintos continentes (Papavero *et al.* 1995b). Todos estos escritos promovieron un mayor interés científico en las expediciones, siendo la primera dedicada a fines científicos la de Francisco Hernández de Toledo en 1570. Este autor documenta numerosas especies de animales y plantas, sus aplicaciones para la medicina y sus distribuciones por el nuevo continente (López Piñero & Pardo Tomás 1996).

En 1590 el jesuita José de Acosta publicó *Historia natural y moral de las Indias*, una obra que sentó las bases racionales de la zoogeografía al comparar la fauna europea con la del nuevo continente de una forma religiosa pero lógica (Zunino & Zullini 2003), planteando hipótesis sobre los rasgos endémicos de las especies que hacían a éstas muy diferentes de las del viejo continente, y sobre su posible dispersión (Papavero *et al.* 1995b).

Otros autores que contribuyeron a la biogeografía durante esta primera parte de la Edad Moderna son Enrico Martínez, Walter Raleigh e Isaac de la Peyrière. Enrico Martínez publicó en 1606 el *Reportorio de los tiempos, y* *historia natural desta Nueva España* donde teoriza la llegada de especies al continente americano mediante unos puentes intercontinentales y terrenos emergidos que posteriormente desaparecieron (Papavero *et al.* 1995b). El corsario inglés Raleigh publica en 1614 la obra titulada *History of the world* donde postulaba que las especies que habían llegado a América se habían tenido que ir transformando paulatinamente para adaptarse a las nuevas condiciones del lugar (Papavero *et al.* 1995c, Llorente-Bousquets *et al.* 2001). Por su parte, de la Peyrière trata con escepticismo la teoría del diluvio universal y la dispersión secundaria en su obra *Systema theologicum de preadamitaum hypothesi* de 1655, comenzando así una confrontación ideológica entre los que apoyaban esta teoría religiosa (como Atanasio Kircher) y los que no (Papavero *et al.* 1995c).

Con todo lo anterior se sentaron las bases que más tarde serían usadas por los biogeógrafos. Sin embargo, no es hasta el siglo XVIII cuando se comienza a hablar de biogeografía *sensu stricto*. Si bien el primero en usar las palabras “zoología geográfica” fue Eberhard von Zimmermann en *Specimen* ***zoologiae geographicae*** *quadrupedum domicilia et migrationes sistens*” de 1777, los naturalistas más destacables del siglo fueron Carl von Linné (Linneo), Georges Louis Leclerc (Conde de Buffon) y Alexander von Humboldt.

Linneo, en sus obras *Systema naturae*, *Phisophia botánica* y *Oratio de telluris habitabilis incremento*, sostenía que todas las especies habían sobrevivido al diluvio universal en una montaña paradisiaca con todos los hábitats de la Tierra a lo largo de su recorrido altitudinal (monte Ararat), y desde donde se dispersaron una vez se retiraron las aguas (Papavero *et al.* 1995d).

Leclerc por su lado, aseguraba que si bien el hombre había sido creado en el Edén, los animales y las plantas eran criaturas de la Tierra, que se habían formado en una región del noroeste de Europa (centro de origen) y desde allí se habían ido dispersando mediante puentes intercontinentales, "degenerándose" a medida que se iban aislando en las nuevas regiones del Nuevo Mundo (Papavero *et al.* 1995e). Esto supuso el primer principio de la biogeografía, la llamada Ley de Buffon, que influyó fuertemente en el desarrollo de la ciencia del siglo XVIII (Lomolino *et al.* 2006b).

A finales del siglo XVIII, von Humboldt se embarca en numerosas expediciones por Europa, América y Asia Central que le sirvieron para publicar a comienzos del siglo XIX varios ensayos claves para la biogeografía y especialmente para la fitogeografía, como *Essai sur la géographie des plantes*, donde recoge que la flora se distribuye en altitud siguiendo un patrón bandeado (cinturones florísticos) equivalente a la manera en la que se distribuyen los vegetales desde el Ecuador al Ártico (Humboldt 1807).

1.1.2.3 El siglo XIX

Es en este siglo cuando se comienza a usar el término "Biogeografía". El zoólogo alemán Hermann Jordan lo utiliza en su obra de 1883, aunque en la versión original escribe mal el título ("*biographie*") mientras que el término en inglés "*biogeography*" aparece en la obra del mastozoólogo Clinton Hart Merriam en 1892, sin embargo, ninguno de los autores describe el término, por lo que ya se utilizaba antes aunque no apareciera en ninguna obra (Ebach 2015). La aceptación de que el clima de la Tierra cambia con frecuencia y el empleo del registro fósil para inferir los climas del pasado supuso un avance importante en la ciencia del siglo XIX, pues hasta las conclusiones de Charles Lyell y Adolphe Brongniart alrededor de 1830, la Ley de Buffon era la que regía por la época (Ospovat 1977). Sin embargo, estos autores demostraron que no sólo existían varios centros de origen de las especies, sino que también hubo varios periodos de creación a lo largo de la historia de la Tierra (Lomolino *et al.* 2006b). Por su parte, Augustin de Candolle y Philip Lutley Sclater aportaron grandes ideas que serían posteriormente usadas como conceptos biogeográficos por otros autores como Charles Darwin y Alfred Wallace (Darwin 1859, Wallace 1876, Papavero & Llorente-Bousquets 1995a).

De Candolle en sus obras como *La phytographie, ou l'art de décrire les végétaux considérés sous différents points de vue*, afirmaba que las plantas se distribuían de una manera determinada por factores propios y externos, pues estaban en un estado de "guerra" permanente entre ellas (interaccionaban y respondían), y destacó la importancia de ciertos factores en la dispersión de las especies y la existencia de barreras naturales que la impedían (Papavero & Llorente-Bousquets 1995b). Otra de sus grandes aportaciones a la biogeografía fue una de las primeras clasificaciones de las regiones botánicas del planeta (Llorente-Bousquets *et al.* 2001).

El ornitólogo Sclater publicó obras sobre la geografía de los animales, como *The geography of mammals* (1899) donde recoge información precisa sobre la distribución de los mamíferos, y fue pionero en la proposición de una división del planeta en seis regiones zoogeográficas (Sclater 1858).

Darwin, postuló su teoría de la evolución en la segunda mitad del siglo XIX mediante su obra *On the Origin of Species by Means of Natural Selection, or the Preservation of Favoured Races in the Struggle for Life*, lo que supuso una revolución científica para la biología. En la edición de 1872, añadió dos capítulos dedicados a la distribución geográfica de los seres vivos y a su dispersión mediante descendencia con modificaciones, que posteriormente se diferencia como especie mediante el aislamiento (Darwin 1872).

Wallace por su parte, invirtió el rol que había tenido la biogeografía hasta entonces, haciéndola el objetivo principal de sus estudios y no una prueba que respaldase otras teorías como la de la evolución (Zunino & Zullini 2003). Por ello Wallace es considerado el padre de la biogeografía moderna, así como por sus aportaciones a la ciencia, entre las que destacan en biogeografía: estudiar las barreras geográficas, medir los efectos del ser humano sobre la naturaleza y plantear la idea de que el pasado geológico del planeta influyó en la distribución actual de las especies (Llorente-Bousquets *et al.* 2001). En su obra más destacada, "*The Geographical Distribution of Animals*" de 1858, clasifica las zonas emergidas de la Tierra en regiones zoogeográficas que aún en la actualidad se siguen utilizando o han sido usadas como base para crear otras nuevas (v.g. Darlington 1957, Udvardy 1975). En esta obra también habla de zonas de transición biogeográfica (concretamente de la línea de Wallace, entre Asia y Oceanía), señalando que las barreras no son algo definido, sino que pueden ser graduales y difusas (Wallace 1876, 1890).

Otros científicos del siglo XIX postularon reglas (patrones) de variación de caracteres morfológicos en los individuos o poblaciones a lo largo de gradientes geográficos, entre las que cabe destacar la de Carl Bergmann sobre la tendencia de los animales endotérmicos a tener un mayor tamaño corporal en las regiones de climas fríos, la de Joel Asaph Allen sobre la minimización del área expuesta al ambiente en las extremidades de los animales que viven en regiones más frías, y la de David Starr Jordan sobre el cada vez mayor número y menor tamaño de vértebras de los peces teleósteos al alejarse latitudinalmente del ecuador (Lomolino *et al.* 2006b).

Estos autores ya no se centran en la historia de la distribución de las especies, sino en patrones ecológicos y fisiológicos que varían a lo largo de su rango geográfico, lo que supuso el comienzo de una nueva rama en la biogeografía durante el siglo siguiente – la biogeografía ecológica – que se separó de la tradicional o histórica (Hesse *et al.* 1951, Dansereau 1957).

1.1.2.4 Biogeografía histórica

Como hemos visto en el apartado anterior, la biogeografía histórica, tradicional o evolutiva es la que se venía estudiando desde el principio, encargándose de explicar dónde se han originado y cómo se han distribuido los seres vivos por el planeta y reconstruir las extinciones (Darlington 1957, Lomolino *et al.* 2006a). Durante el siglo XX se desarrollan cuatro grandes corrientes de biogeografía histórica que trataban de explicar la distribución a gran escala de los seres vivos.

El Dispersionismo era la corriente que regía desde el principio, ya que era la recogida en los escritos religiosos cristiano-judeo-islámicos (Papavero *et al.* 1995a), donde el Creador había originado a todas las especies y estas se habían ido dispersando por el mundo. Algunos autores como Linneo y el conde de Buffon, interpretaron y matizaron las enseñanzas de la Biblia, explicando cómo habían sido estos procesos de dispersión (Papavero *et al.* 1995d, 1995e). Más tarde fue asimilando los avances científicos sobre la historia de la vida a medida que naturalistas como Darwin y Wallace buscaban explicaciones y patrones de dispersión desde un punto de vista más científico y menos teológico (Llorente-Bousquets *et al.* 2001, Morrone 2009). El principio clave del dispersionismo postula que las especies surgen en un lugar –centro de origen– desde el que se van propagando (Morrone *et al.* 1996).

A mitad del siglo XX, coincidiendo con el Dispersionismo, surge la Panbiogeografía con León Croizat (Croizat 1958, 1982) apoyándose en la Teoría de la Deriva Continental de Alfred Wegener de 1912. Esta corriente se caracterizaba por emplear la vicarianza, es decir, la separación de taxones contiguos por la formación de discontinuidades en el ambiente físico, como la explicación para las distribuciones de las biotas del mundo (Croizat 1958, 1982, Morrone & Crisci 1990). Se convierte por tanto en la primera teoría que buscaba identificar grandes procesos vicarancistas a través de patrones entre varios grupos de organismos diferentes, no siendo una simple recreación de la historia como hacían los dispersionistas (Croizat 1982, Morrone & Crisci 1990, Morrone 2009).

En la segunda mitad del siglo XX, influenciada por el Dispersionismo y en contraparte a la Panbiogeografía, surge la Biogeografía Filogenética de la mano de Willi Henning (Henning 1966, Llorente-Bousquets *et al.* 2001). Ésta postula que la evolución ocurre en los márgenes de las distribuciones, de tal manera que las especies primitivas son las que permanecen en los centros de orígenes mientras las más modernas se alejan, lo que se denomina la regla de progresión (Henning 1966).

En contraparte a la Biogeografía Filogenética, varios autores recogen las ideas de Croizat y las desarrollan desde otro enfoque, formando la biogeografía por Vicarianza Cladista (Nelson & Platnick 1981, Llorente-Bousquets *et al.* 2001). En esta corriente reconstruyen la historia convirtiendo las filogenias de varios taxones en cladogramas de las áreas habitadas por ellos, ya que asumen que la historia de las áreas debe ser igual que las de las especies que las habitan, y buscan un consenso entre todas las opciones posibles (Nelson & Platnick 1981). Existen diferentes maneras de consensuar, como retener sólo las áreas comunes a todos los cladogramas

(Rosen 1978) o permitir cualquier combinación posible que no contradiga ningún cladograma (Wiley 1988). Sin embargo, las más aceptadas son aquellas que recurren a métodos más analíticos, como el BPA (*Brooks' Parsimony Analysis*), que resuelve las incongruencias necesarias recurriendo a translocaciones y extinciones (Brooks 1985).

A finales del siglo XX y principios del XXI, surge también la Filogeografía. Su concepto es similar a la Biogeografía Filogenética, pero trabaja a nivel poblacional o de especie, con dendrogramas de haplotipos, para reconstruir la historia reciente de las poblaciones (Avise 2000). Por tanto, no recurren a centros de origen pero sí a refugios, como los estudios sobre refugios glaciares en Europa para varias especies (v.g. Hewitt 2004, Ursenbacher *et al.* 2006, Gómez & Lunt 2007, Martínez-Freiría *et al.* 2020).

1.1.2.5 Biogeografía ecológica

Aunque los primeros trabajos de biogeografía ecológica aparecen durante el siglo XIX, de la mano de Bergmann, Allen y Jordan, no es hasta la primera mitad del siglo XX cuando ganan especial importancia, gracias a las recopilaciones de obras sobre patrones ecogeográficos de Hesse, Allee y Schmidt (1951) y Niethammer (1958) para los animales y de Dansereau (1957) para las plantas. Gracias a estas recopilaciones, se estableció como una ciencia propia con aportaciones de gran interés para otras tales como la biología evolutiva (Blackburn & Gaston 2006, Lomolino *et al.* 2006b) o la ecología (McIntosh 1985), y que aún en la actualidad aporta información importante a nuevas disciplinas como la biogeografía de la conservación (Ladle & Whittaker 2011) o la patogeografía (Murray *et al.* 2018).

Esta disciplina se encarga de representar la distribución de los organismos y las variaciones geográficas de diversidad en términos de interacciones entre los organismos y el ambiente físico y biótico en el que habitan (Lomolino *et al.* 2006a). Por ello está muy relacionada con la macroecología, la disciplina que se encarga de estudiar la relación entre patrones ecológicos tales como diversidad, abundancia o características entre los organismos (especies, poblaciones, individuos, etc.) y el ambiente a gran escala (Brown 1995). Sin embargo, a diferencia de la macroecología, en la biogeografía ecológica el componente espacial es un factor crucial en las cuestiones ecológicas (Blackburn & Gaston 2006, Murray *et al.* 2018).

Uno de los trabajos más influyentes de la biogeografía ecológica del siglo XX es el de Robert H. MacArthur y Edward O. Wilson (1963), quienes desarrollaron una nueva teoría para explicar las distribuciones de las especies en las islas en base a su tamaño y cercanía al continente. Esto hizo que muchos autores enfocaran sus estudios en conocer qué aspectos condicionan la distribución de los seres vivos (Lomolino *et al.* 2006a). Algunos se interesaron en ver el rol que tenía el ambiente abiótico, otros evaluaban el papel de las interacciones bióticas, mientras que otros trabajaban en aspectos más teóricos, como en saber si los procesos de distribución son estocásticos o deterministas (Darlington 1957, MacArthur 1984, Brown 1995). Los avances de la tecnología (como los Sistemas de Información Geográfica) y el desarrollo de métodos experimentales y matemáticos para cuantificar y analizar las cuestiones biogeográficas o ecológicas, supusieron un incremento exponencial de los trabajos enfocados a los aspectos ecológicos de las distribuciones de las especies desde la última década del siglo XX (Hengeveld 1993, Lomolino *et al.* 2006a).

En la Figura 1.1. se representa un cronograma resumen de algunos de los acontecimientos más relevantes en la historia de la biogeografía vistos en el capítulo 1 de la presente tesis doctoral.

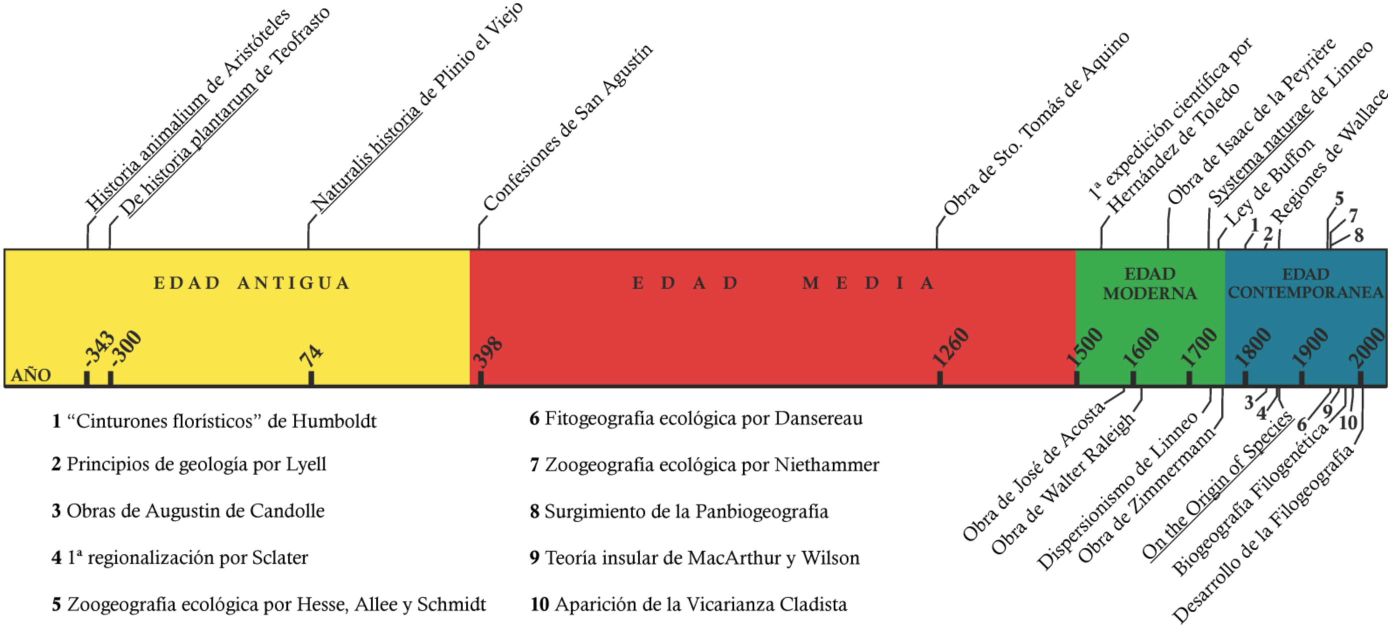

Figura 1.1: Cronograma de algunos de los acontecimientos más relevantes en la historia de la biogeografía.

1.2 La distribución de las especies

1.2.1 Características y tipos

Algunos autores postulan que las especies tienden a incrementar su número de individuos de tal manera que acaban por ocupar todo el territorio disponible, creando así distribuciones con formas lo más simples posible (Darwin 1872, Rapoport 1975). Aun así, los individuos y poblaciones no siempre se distribuyen de manera uniforme debido a la existencia de una serie de barreras y factores condicionantes en el entorno (Rapoport 1975). Existen factores abióticos como la temperatura o la humedad, bióticos como la historia natural de la especie o la movilidad de los individuos, así como factores antrópicos debidos a la actividad del ser humano (Real *et al.* 2003, Lomolino *et al.* 2006c, Di Marco & Santini 2015, Newbold *et al.* 2015). Estos pueden actuar de manera similar a una barrera geográfica o condicionando la distribución de una especie al afectar positiva o negativamente su supervivencia, reproducción, dispersión, etc. (Antúnez & Mendoza 1992, Duarte 2006, Ferreira 2011, Lyman 2016).

Las distribuciones tienen varias clasificaciones (Figura 1.2) (Espinosa *et al.* 2001, Molles 2008). 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.

Atendiendo a la continuidad de la distribución se clasifican en:

- Continua, cuando presenta poblaciones que se distribuyen de manera continuada por el espacio.
- Discontinua, si presenta poblaciones separadas debido a extinciones locales de algunas de sus poblaciones.
- Disyunta, cuando aparecen poblaciones separadas por alguna barrera geográfica o ambiental difícil de superar de manera natural.

Teniendo en cuenta la extensión global, hablamos de distribuciones o especies cosmopolitas cuando están presentes en todos los continentes de la Tierra a excepción de la Antártida, distribuciones o especies relictas cuando en el pasado ocupaban grandes áreas pero en la actualidad están confinadas en espacios de menor tamaño, o endémicas cuando sólo están presentes en cierta región (Espinosa *et al.* 2001, Molles 2008).

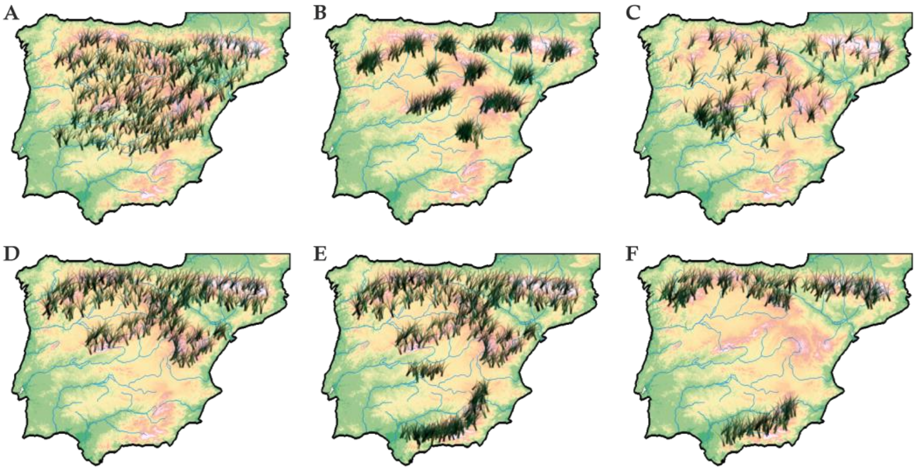

Figura 1.2. Tipos de distribución según la manera en la que los individuos/poblaciones ocupan el espacio: **(A)** uniforme, **(B)** agrupada y **(C)** aleatoria; o de la continuidad de la distribución completa: **(D)** continua, **(E)** discontinua y **(F)** disyunta.

1.2.2 Dinamismo de las áreas de distribución

Todas las distribuciones de las especies tienen en común que no son estáticas. Los individuos realizan desplazamientos diarios, estacionales, anuales, migraciones locales, dispersiones, ritmos, ciclos biológicos complejos, etc. (Müller 1979b). Además, las metapoblaciones tienen dinámicas concretas, pues los individuos se desplazan entre poblaciones, haciendo que varíe el número de individuos de las poblaciones, llegando incluso a hacer desaparecer algunas (extinción poblacional) y reaparecer otras mediante colonizaciones de ambientes adecuados que estaban despoblados (Levins 1969, Hanski 1999). Estos continuos cambios en la localización de los organismos son la razón de que las distribuciones se consideren dinámicas, lo que dificulta considerablemente conocer a priori la localización exacta de todos los individuos de la especie en cada momento (Real *et al.* 2017). Mediante el uso de emisores es posible observar la localización de algunos individuos en cada momento, pero hasta la fecha es muy difícil hacerlo para todos los individuos de una especie, e imposible para muchas especies (Recio *et al.* 2011), por lo que su uso para determinar la distribución completa de una especie es todavía escaso. En la actualidad se está avanzando mucho en esta línea 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.

Algo análogo a lo que ocurre con las distribuciones de las especies, también se encuentra en la mecánica cuántica: hasta que un objeto cuántico no se observa directamente (se mide), no se puede conocer su localización exacta (Zurek 1991). 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 no está ni presente ni ausente en ninguna localidad, sino parcialmente presente (y ausente) en todas, 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). No es descabellado creer que las especies, al ser seres físicos y por ello tener propiedades de las leyes físicas, comparten características comunes con los objetos cuánticos, como es el caso de sus distribuciones (Real *et al.* 2017). Así pues, 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 (Real *et al.* 2017, Gouveia *et al.* 2020). La distribución de las especies, por tanto, es algo dinámico, que cambia constantemente a diferentes escalas, y debe ser tenido 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.

1.2.3 Los límites biogeográficos

Desde un punto de vista ecológico, la distribución de una especie, en ausencia de barreras geográficas, acaba cuando la suma de los procesos de emigración y mortalidad en las poblaciones supera en número las inmigraciones y nacimientos de los individuos (Gaston 1990), o dicho de otra manera, cuando los factores bióticos y/o abióticos limitan la supervivencia, reproducción y *fitness* de los individuos (Hoffmann & Blows 1994). Esto se debe a que en los bordes, las condiciones ambientales para los individuos son generalmente más desfavorables que en el centro de sus distribuciones, haciendo que la densidad de individuos decrezca (Brown 1984, Brown *et al.* 1995, Lomolino & Channell 1995). Puede deberse a interacciones bióticas negativas para la especie, como la competencia (Darwin 1859), a que el flujo de genes proveniente de las poblaciones del centro de la distribución evite la adaptación de las periféricas a las condiciones de los bordes (Kirkpatrick & Barton 1997) o a que, simplemente, la especie carezca de la variación genética que le permita adaptarse a las condiciones al otro lado del margen (Case & Taper 2000).

A menos que los márgenes de las distribuciones de las especies estén delimitados por barreras geográficas importantes que impidan su dispersión, solo pueden ser considerados de una manera aproximada, como límites difusos, y nunca como algo fijo (Müller 1979b). Esto es así porque el propio dinamismo de las áreas de distribución, debido a los movimientos de los individuos y a sus dinámicas poblacionales modifican constantemente la forma de las distribuciones, y por ende, sus límites (Holt & Keitt 2000). Eventualmente, las poblaciones de los márgenes del área de distribución se debilitan o desaparecen (extinciones locales marginales) o son repobladas con individuos de otras poblaciones (colonizaciones), generando una dinámica específica de los bordes distribucionales que modifica su forma constantemente (Eldredge 1995). El hecho de que la dinámica de los bordes parezca ser más cambiante que la del centro de las distribuciones, hace que muchos autores sugieran que la especiación para la mayoría de los organismos se produce principalmente en los límites (Brussard 1984, Hoffmann & Blows 1994). Así, entendiéndose los límites como algo plástico y fluido, es importante conocer su 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, la introducción de especies o las interacciones bióticas, entre otras.

1.3 Representando las distribuciones: los SDMs

La representación de la distribución de una especie más básica es la simple georreferenciación de los individuos que se han observado en un territorio (presencias). Sin embargo, este tipo de representación presenta ciertos problemas que, en función de la especie estudiada, pueden ser más o menos relevantes. En primer lugar, asume que la especie está sólo en las localidades donde se ha observado y ausente en las que no, lo que determina un aspecto estático a la distribución, y no contempla que la especie no se haya detectado en algunas zonas o que se mueva a otras (Hengeveld 1992, 1993, Gouveia *et al.* 2020). Si bien repetidas observaciones de una misma área y su comparación pueden acercarnos al dinamismo de las distribuciones, una sola representación no puede mostrarlo (Hengeveld 1992). Además, la observación de los individuos en general presenta sesgos (diferente esfuerzo de muestreo, detectabilidad de la especie, escasez de recursos o poca experiencia de los observadores, etc.) que distorsionan más el alcance real de las distribuciones (Cochran 1977).

Las representaciones en forma de manchas (Figura 1.3A, p.ej. IUCN 2018) incluyen en su interior todas las presencias de la especie asumiendo la presencia de la especie en cada localidad contenida dentro del polígono. También están las mallas (Figura 1.3B, p.ej. cuadrículas UTM) que dividen el espacio en polígonos, cada uno de los cuales se representa de manera diferente en función de si contiene presencias de la especie o no. Este método es útil para la elaboración de Atlas y el diseño de expediciones, pero la asunción de que las especies ocupan por igual todo el terreno dentro de cada polígono es errónea, ya que en áreas heterogéneas los individuos tienen preferencias por ciertas zonas, y además existen fluctuaciones temporales en la densidad de los individuos (MacArthur 1984, Real *et al.* 2001).

Figura 1.3. Ejemplos de representaciones de la distribución de *Aquila fasciata* en forma de: **(A)** mancha (IUCN 2018), **(B)** cuadrículas UTM 10x10 km con presencia de la especie (Martí & del Moral 2003), y **(C)** modelo de favorabilidad ambiental (Muñoz *et al.* 2005).

En mi humilde opinión, las mejores representaciones de la distribución de una especie, por su semejanza con la realidad, son aquellas que de alguna manera recogen el carácter dinámico de la misma. Éstas deben establecer las localidades y ambientes que condicionan dicha distribución, a la vez que tener interiorizados los procesos históricos que han llevado a la especie a establecerse en dicho lugar, representando, de la manera más fielmente posible, la distribución de la especie en el presente, y que informa de la que tuvo en el pasado reciente y la que posiblemente tendrá en el futuro inmediato (Müller 1979a, Guisan & Thuiller 2005, Ladle & Whittaker 2011, Acevedo & Real 2012, Eglington *et al.* 2015).

Uno de los problemas a lidiar por la biogeografía es por tanto el derivado de la dinámica variable que presentan las distribuciones de las especies (Hengeveld 1992, 1993). ¿Cómo sacar el máximo rendimiento de un conjunto de datos de distribución incompleto y estático para representar el dinamismo de las áreas de distribución? Un trabajo de monitorización continuo, p.ej. una sucesión de atlas de la misma zona, podría recoger este carácter dinámico. Sin embargo este proceso es largo, costoso e inviable para muchas especies. Otra posibilidad es emplear Modelos de Distribución de Especies (SDMs, por sus siglas en inglés *Species Distribution Models*). Un

SDM es la representación simplificada de la distribución de una especie (Figura 1.3C) en base a parámetros eco-físico-geográficos que simulan la interacción de esa especie con el entorno que habita (Real *et al.* 2017). Para ello buscan patrones biogeográficos que identifiquen y caractericen zonas donde es más "probable" que la especie se encuentre, entendiendo así cómo funciona el sistema complejo 'especie-ambiente' y prediciendo su comportamiento (Real *et al.* 2006, 2017).

Según el objetivo del estudio, un modelo biogeográfico puede ser:

- Descriptivo: se usa para identificar los límites y la complejidad interna del área de distribución.
- Explicativo: analiza el papel de los diferentes factores que determinan la distribución de las especies.
- Predictivo: deduce la distribución de la especie en zonas donde no hay registros de la especie en función de ciertos parámetros.

Según su forma de expresión nos encontramos con:

- Modelo imaginario: el que se crea en la mente, una hipótesis o idea sobre algún patrón de distribución.
- Modelo verbal: el que se crea cuando se formula esa idea en el lenguaje oral o escrito, en relación a los datos y variables de las que se dispone.
- Modelo matemático: es la función matemática obtenida mediante algún algoritmo (fórmula) que relaciona la distribución de una especie con las variables predictoras.
- Modelo cartográfico: es la representación gráfica sobre un mapa de los modelos obtenidos.

Metodológicamente, existen dos grupos principales de SDMs que contribuyen a desvelar los patrones que subyacen tras la distribución de las especies: mecanicistas y estadísticos. Los modelos mecanicistas son el resultado del método reduccionista del conocimiento de las distribuciones, es decir, se basan en relaciones hipotéticas de causa y efecto entre diferentes variables y la supervivencia de una especie, a partir de la teoría existente o los resultados obtenidos en los laboratorios (Guisan & Zimmermann 2000). Los problemas que presentan este tipo de modelos son su falta de visión holística, la inviabilidad de aplicación para muchos taxones y regiones al carecer de los experimentos fisiológicos o conocimientos ecológicos necesarios, su poca capacidad de ser modelos predictivos y la gran susceptibilidad de cometer errores por patrones inusuales en los resultados de los experimentos en los cuales se basan los modelos (Guisan & Zimmermann 2000, Bolker 2007, Real *et al.* 2017). Los SDMs estadísticos, por el contrario, se basan en la observación de correlaciones entre la distribución de una especie y las variables usadas que, de manera directa o indirecta sobre los individuos, condicionan a gran escala la manera en la que se distribuyen (visión holística), permitiendo predecir dónde es más "probable" que ésta esté (Guisan & Zimmermann 2000, Real *et al.* 2017).

1.3.1 La Incertidumbre y la Lógica Difusa en los SDMs

Algunos autores asumen que no existe la incertidumbre intrínseca en los ecosistemas ecológicos (i.e. la libertad de decisión de los individuos). Esta visión determinista de los ecosistemas postula que si se conociesen todas las variables que afectan a la distribución de la especie, se sabría exactamente la posición de cada individuo en todo momento (Regan *et al.* 2002). Contrariamente, otros autores postulan que los ecosistemas no actúan de una manera completamente predecible y determinista, sino que además de la incertidumbre asociada a la falta de conocimiento del sistema biológico, una incertidumbre intrínseca propia de los seres vivos (Real *et al.* 2017). De esta forma, la distribución de las especies responde a una serie de factores que la condicionan, que los SDMs son capaces de identificar, siempre bajo un umbral de incertidumbre derivado de la propia especie, individuos o condiciones ambientales en un momento concreto. 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 esa especie. Por ello, los biogeógrafos han buscado maneras de tener en cuenta la incertidumbre y el carácter dinámico en las distribuciones durante las últimas décadas, lo que les ha llevado al empleo de los conjuntos borrosos y su consiguiente lógica difusa (Robertson *et al.* 2004, Van Broekhoven *et al.* 2006, Estrada *et al.* 2008, Real *et al.* 2008, 2009, Olivero *et al.* 2011, Barbosa 2015, Chamorro *et al.* 2020).

Un conjunto difuso es un grupo de objetos del mundo físico que no presentan un criterio de pertenencia definido, sino que cada objeto tiene un grado de pertenencia a dicho conjunto (Zadeh 1965). Esto hace que el conjunto no presente un límite definido, sino gradual, lo que refleja mucho mejor el carácter continuo de la naturaleza (Salski 2006), como son las distribuciones de las especies, especialmente en sus márgenes. El conjunto difuso está caracterizado por una función de pertenencia, que es la que asigna a cada objeto su grado de pertenencia al conjunto, siendo éste un valor comprendido entre 0 (pertenencia mínima) y 1 (pertenencia máxima) (Zadeh 1965). A diferencia de la lógica probabilística tradicional, en la lógica difusa los elementos no son absolutamente "verdaderos" ni "falsos", sino verdaderos y falsos hasta cierto punto, lo que indica que cada clase existe en cierto grado para cada elemento del conjunto (Olivero *et al.* 2011). A modo de ejemplo, si usamos la categoría “persona alta”, una persona que mida 1.65 m podría considerarse alta en ciertas regiones del mundo, pero una persona que mida 1.80 m sería más alta que la anterior y una de 2.10 m aún mayor. Aquí la lógica clásica no tendría sentido, pues siempre depende de dónde pongamos el umbral del criterio “alto”. Sin embargo, en la lógica difusa las tres personas tienen un grado de pertenencia al conjunto difuso “persona alta”, que será mayor en el caso de la persona de 2.10 m y menor en la que mide 1.65 m. El empleo de la lógica difusa ante estas situaciones nos ahorra el establecer un umbral a los criterios que estamos empleando, que siempre están, en mayor o menor medida, influidos por la percepción del observador (en el ejemplo usado, en Noruega pondrían el umbral de “alto” por encima del que pondrían en Ecuador, dado que la percepción de ambos observadores sobre la altura de las personas está influida por las regiones que habitan, y en Escandinavia son más altos que en Sudamérica).

En biogeografía, la lógica difusa se puede aplicar a la distribución de los individuos de una especie (ya que como los objetos cuánticos, se pueden expresar en forma de probabilidad (Real *et al.* 2017), como hemos visto en el apartado 1.2.2.), a la similitud entre regiones o biotas (Olivero *et al.* 2011, Barbosa 2015) y a los SDMs, como es el caso de la función de favorabilidad (Real *et al.* 2006, Acevedo & Real 2012).

1.3.2 La Elección del SDM: La Favorabilidad

El listado de métodos empleados en la realización de SDMs es enorme (en la Tabla 1.1 se recogen algunos de los algoritmos más empleados en la elaboración de SDMs) y la elección de cuál de ellos utilizar debe hacerse en función de los objetivos del estudio y de los datos de partida (Guisan &

Zimmermann 2000, Franklin 2009: 105-112). Los casos analizados en la presente tesis presentaban una serie de características que impedían el uso de cualquier SDM. La mayoría de las especies estudiadas no tienen áreas de distribución muy extensas, requieren de modelos explicativos y predictivos fiables para poder proyectarse al futuro o para poder extraer conclusiones de buena calidad, y además, se precisa que se pudieran comparar entre sí, independientemente de la prevalencia de cada especie en el área de estudio. Por ello, se optó por el empleo de la Función de Favorabilidad (FF) (Real *et al.* 2006).

Tabla 1.1. Algunos algoritmos frecuentemente empleados en los SDMs.

Familia del SDM	Nombre del algoritmo matemático
Modelos Lineales Generalizados (GLM)	Regresión lineal normal Regresión logística (binomial) Regresión exponencial Regresión de Poisson
Algoritmos robóticos (*machine learning*)	GARP MaxEnt Random forests Árboles de decisiones Redes neuronales artificiales
Métodos de envolturas ambientales	BIOCLIM HABITAT
Métodos de distancias ambientales	DOMAIN ENFA
Métodos híbridos	Modelos Aditivos Generalizados Modelos espaciales autorregresivos Regresión adaptativa multivariante

1.3.2.1 Características de la Favorabilidad

Algunas de las características inherentes a la FF han influido en la elección de este método frente a otros. Cabe destacar las siguientes:

- El concepto de favorabilidad ya está implícito en el primer principio sobre la probabilidad de Pierre-Simone (Laplace 1825: 12) como la proporción de casos favorables en relación al conjunto total de casos. Esto indica que la favorabilidad puede ser obtenida en función de la probabilidad y la prevalencia (proporción de casos).
- Se obtiene de una regresión logística (GLM), que sigue una distribución binomial, por lo que admite datos que se puedan introducir de manera binaria, como son los datos de presencias (1) y ausencias (0) que están disponibles en la mayoría de atlas, webs, etc.
- Al no verse afectados por el efecto de la prevalencia de los datos, diferentes modelos de favorabilidad pueden ser comparados aunque se trate de diferentes especies.
- Al ser una función de la correlación entre las variables ambientales y la distribución de la especie, expresa la manera en la que ésta responde a las condiciones ambientales de cada región, siendo equiparable al concepto de nicho ecológico de respuesta (interacción) de las especies como funciones de condiciones de hábitat (Maguire 1973).
- En este sentido, la FF puede considerarse como la análoga a la función de onda de los objetos cuánticos para las especies biológicas, englobando el nicho y reflejando la respuesta de la distribución de la especie con el ambiente.
- La FF define un valor de favorabilidad –del intervalo [0,1]– para cada unidad geográfica del área de estudio, que indica cuán favorable o desfavorable es para la especie esa localidad.

- La favorabilidad puede ser analizada desde la lógica difusa, permitiendo realizar todas las operaciones difusas (combinaciones, uniones, intersecciones…) entre diferentes modelos.
- El observador controla el procedimiento de la modelación en todo momento, haciéndolo conocedor del porqué de sus resultados y permitiendo decidir qué hacer con los datos.

1.3.2.2 ¿Cómo se hace un modelo de favorabilidad?

Todo comienza con un planteamiento de una o varias hipótesis que generamos al observar la naturaleza (modelo imaginario). Con esta idea en la cabeza, se seleccionan las presencias y ausencias de las especies que se van a analizar y el conjunto de variables predictivas. Estas variables se seleccionan en base al criterio de expertos y estudios previos, pues deben responder a hipótesis (modelos verbales) sobre el efecto de cada una sobre la distribución de la especie. El siguiente paso consiste en la preparación de los datos para el posterior análisis matemático (minimización de la autocorrelación espacial de los datos, chequeo de la calidad y cantidad, tratamiento de variables, etc.). El algoritmo empleado con mayor frecuencia es la regresión logística binaria, la cual produce una combinación lineal de variables (y o *logit*) que calcula la probabilidad de presencia de la especie (P) en base a una selección de variables ambientales significativas y de la prevalencia de presencias/ausencias (modelo matemático):

$$y = a + b_1x_1 + b_2x_2 + \cdots + b_nx_n \qquad P = \frac{e^y}{1 + e^y}$$

donde a es el término independiente, b los coeficientes y x las variables ambientales de la combinación lineal *logit* obtenida por una regresión logística, y su relación con la probabilidad (P) siendo e la base del logaritmo neperiano.

Estos valores de probabilidad (*P*) son posteriormente convertidos en valores de Favorabilidad (*F*) mediante la ecuación (1) de Real *et al.* (2006):

$$F = \frac{\frac{P}{1-P}}{\frac{n^{\underline{o}}\ presencias}{n^{\underline{o}}\ ausencias} + \frac{P}{1-P}} \qquad (1)$$

Posteriormente, la favorabilidad se representa gráficamente mediante un sistema de información geográfica (modelo cartográfico). Con los datos de distribución se realiza una evaluación del modelo en base a criterios estadísticos y matemáticos (calibración, discriminación, clasificación…). Dicho modelo puede ser también validado al observar si sus predicciones se cumplen y en qué grado (p.ej. con presencias no utilizadas en el análisis). Con variables de otras áreas o periodos de tiempo, el modelo matemático puede ser extrapolado. Esquema resumen en la Figura 1.4.

1.3.2.3 ¿Qué aplicaciones tiene?

Los modelos de favorabilidad han sido utilizados para determinar patrones biogeográficos que puedan aportar información y pautas en la conservación y la gestión de la naturaleza (Muñoz *et al.* 2005, Estrada *et al.* 2018, Aximoff *et al.* 2020), y para profundizar el conocimiento sobre los cambios en las distribuciones bien por cambios climáticos (Muñoz *et al.* 2013), usos del suelo (Romero *et al.* 2012) o invasiones (Muñoz & Real 2006). Más reciente es el empleo de la favorabilidad para la búsqueda de los patrones biogeográficos que se esconden tras los brotes de enfermedades infecciosas (Olivero *et al.* 2017a, Murray *et al.* 2018).

En la presente tesis los modelos de favorabilidad han sido empleados para ahondar en el conocimiento de la dinámica que presentan las distribuciones, seleccionando una serie de especies a modo de representantes de grupos que comparten un patrón biogeográfico concreto. Estas son el Busardo Moro del Atlas como ejemplo de especies que se desplazan hacia el norte por el efecto del cambio climático, el Carricero Común ejemplo de aves migradoras transaharianas que modifican su fenología por las crecientes temperaturas invernales, las Víboras ibéricas como ejemplo de especies parapátricas y el Ibis Eremita como modelo de especies críticamente amenazadas con una distribución relicta cuya dinámica parece haber cambiado recientemente.

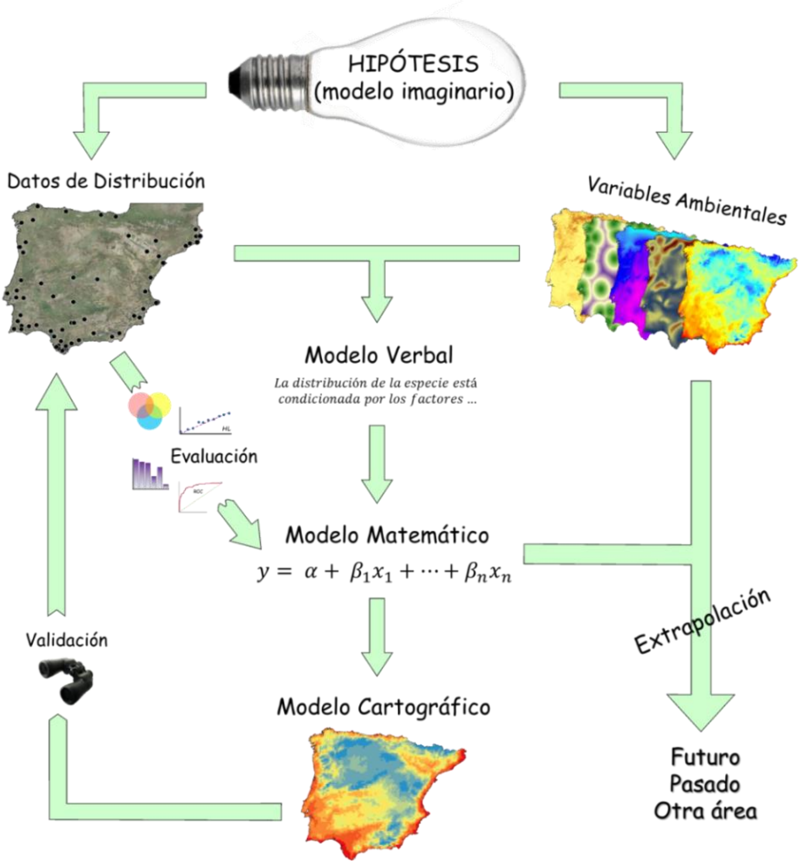

Figura 1.4. Esquema general de los pasos en la realización de un modelo de favorabilidad, desde la idea o hipótesis hasta la representación cartográfica de la distribución de la especie, y los consecutivos pasos de evaluación y validación del modelo así como la posible extrapolación del mismo.

CAPÍTULO 2

OBJETIVOS DE LA TESIS DOCTORAL

AIMS OF THE DOCTORAL THESIS

> *"Lo importante es no dejar de hacerse preguntas"*
>
> ~ Albert Einstein

2 OBJETIVOS DE LA TESIS DOCTORAL

En la presente tesis doctoral se ha indagado en el conocimiento biogeográfico del dinamismo de las áreas de distribución de las especies, con la intención de mejorar aspectos teóricos en el estudio de las distribuciones, de avanzar en aspectos metodológicos para su análisis y de profundizar en el conocimiento de las especies tratadas, las cuales han sido elegidas como representantes de otras especies que comparten patrones biogeográficos similares.

Los objetivos generales en la presente tesis doctoral han sido:

1. Profundizar en los patrones de distribución de las especies en el marco geográfico de la península ibérica y áreas circunmediterráneas, como límites difusos entre los continentes de África y Europa, con especial interés en las interacciones con el ambiente donde se encuentran.
2. Elaborar modelos explicativos y predictivos de la distribución de especies para identificar los factores que condicionan la dinámica que presentan sus distribuciones.
3. Aportar nuevos métodos e ideas a la comunidad científica que sirvan para su aplicación a futuros estudios en el ámbito de la biogeografía.
4. Poner de manifiesto la utilidad de los modelos de distribución de las especies y de la Función de Favorabilidad como herramientas de análisis bajo el marco conceptual de la biogeografía dinámica.
5. Proponer aplicaciones prácticas a los resultados obtenidos, con vistas a optimizar los planes de gestión y conservación de las especies en el contexto de planeta cambiante y dinámico.

Además de los objetivos generales anteriormente mencionados, se han planteado los siguientes objetivos específicos que han sido tratados a lo largo de los diferentes capítulos:

6. Identificar los factores que favorecen el establecimiento de aves típicamente africanas en la península ibérica y determinar el potencial de acogida de ésta para estas nuevas especies (capítulo 3).
7. Detectar y cuantificar el desequilibrio producido por el cambio climático entre la distribución de las especies y las zonas climáticamente favorables mediante los modelos de distribución y la lógica difusa (capítulo 4).
8. Calcular la tasa o velocidad a la que las zonas climáticamente favorables se desplazan latitudinalmente bajo la influencia del cambio del clima actual en el contexto intercontinental del norte de África y sur de Europa (capítulo 4).
9. Poner de manifiesto el cambio fenológico de especies migradoras transaharianas en Europa, a través del cual pasan a ser presaharianas, e incluso sedentarias en la península ibérica, analizando la influencia del incremento de la temperatura invernal en este fenómeno (capítulo 5).
10. Identificar las zonas de mayor favorabilidad ambiental en la península ibérica para la invernada de aves migradoras transaharianas insectívoras como lugares en los que potenciar los estudios de seguimiento para avanzar en el conocimiento de los cambios fenológicos debidos al cambio reciente del clima (capítulo 5).
11. Crear un marco de trabajo que permita estudiar las interacciones bióticas y con el ambiente entre especies con distribuciones

parapátricas, pudiendo determinar el peso relativo del ambiente y de la competencia en este tipo de distribuciones (capítulo 6).

12. Identificar las zonas más propicias para que ocurra exclusión competitiva o coexistencia simpátrica entre las especies con distribuciones parapátricas (capítulo 6).
13. Obtener información de la distribución histórica de las especies para evidenciar que las especies no necesariamente quedan de manera relicta en las zonas más favorables ambientalmente (capítulo 7).
14. Demostrar la importancia de considerar en los modelos de distribución la estructura espacial de las especies, en combinación con los factores ambientales, con vistas a detectar patrones de distribución potencial que pueden ser de gran aplicabilidad en la conservación de especies amenazadas bajo una perspectiva dinámica (capítulo 7).

2 AIMS OF THE DOCTORAL THESIS

During the development of this doctoral thesis, I have investigated the biogeographical knowledge of the dynamism of the species distribution areas, with the intention of improving the theoretical aspects of the study of distributions, the development of the tools for their analysis and delving into the knowledge of the studied species, which were selected as models of species with similar biogeographical patterns.

The general aims in this thesis have been:

1. To study the patterns of distributions within the geographical framework of the Iberian Peninsula and Mediterranean areas, as fuzzy boundaries between the continents of Africa and Europe, making emphasis in the species-environment interactions.
2. To produce explicative and predictive models of the species in order to identify the factors which condition the distribution dynamics.
3. To contribute to the scientific community providing methods and ideas that can be applied to future studies in the field of biogeography.
4. To highlight the usefulness of species distribution models and the Favourability Function as analytical tools under the conceptual framework of dynamic biogeography.
5. To propose practical applications of the obtained results with a view to optimising the management and conservation plans of species under the context of changing and dynamic planet.

In addition to the general aims previously mentioned, the following specific objectives were set, which have been studied throughout the different chapters of the thesis:

6. To identify the environmental factors that favours the establishment of typical African birds in the Iberian Peninsula and to determine the potentiality of this area to host new species (chapter 3).
7. To detect and to quantify the disequilibrium produced by climate change between the species distribution and the climatically favourable areas for them using species distribution models and fuzzy logic (chapter 4).
8. To measure the rate of the latitudinal displacement of the favourability areas by the influence of current climate change in the intercontinental context of North of Africa and southern Europe (chapter 4).
9. To demonstrate the phenology change of Trans-Saharan migrants in Europe, which become Pre-Saharan or even sedentary in the Iberian Peninsula, and to analyse the effect of the increment of the winter temperatures in this phenomenon (chapter 5).
10. To identify the most favourable places of the Iberian Peninsula for the wintering of insectivores Trans-Saharan birds as places where the monitoring studies could improve the knowledge of phenological alterations due to recent climate change (chapter 5).
11. To create a theoretical and methodological framework to study the biotic and environmental interactions between species with parapatric distributions, assessing the relative weight of the environment and competition in these particular distributions (chapter 6).

12. To identify the areas where competitive exclusion or sympatric coexistence between parapatric species is more probable to occur (chapter 6).
13. To obtain information on the historical species distribution to show that species do not necessarily remain relict in the most environmentally favourable areas (chapter 7).
14. To demonstrate the importance of considering the spatial structure of species in the distribution models, in combination with environmental factors, with a view to detecting potential distribution patterns that could be of great applicability in the conservation of threatened species from a dynamic perspective (chapter 7).

CAPÍTULO 3

FACTORES AMBIENTALES QUE PERMITEN EL ESTABLECIMIENTO DE ESPECIES AFRICANAS EN EUROPA OCCIDENTAL

ENVIRONMENTAL FACTORS DETERMINING THE ESTABLISHMENT OF AFRICAN SPECIES IN WESTERN EUROPE

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

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.* **159**: 331–342.

3 ENVIRONMENTAL FACTORS DETERMINING THE ESTABLISHMENT OF AFRICAN SPECIES IN WESTERN EUROPE

3.0 RESUMEN

Las temperaturas se están haciendo cada vez más cálidas por el efecto del cambio climático, lo que tiene efectos sobre la distribución y la fenología de las especies. El Busardo Moro del Atlas (*Buteo rufinus cirtensis*) es un ejemplo, ya que ha colonizado recientemente Europa a través del Estrecho de Gibraltar. Nuestro objetivo en este capítulo es explicar la distribución nativa de este taxón e identificar las áreas favorables para su reproducción en el sur de Europa, recientemente colonizado, mediante la modelación geoespacial y la identificación de los factores ambientales condicionantes de este proceso. Para ello aplicamos la función de favorabilidad usando variables ambientales relativas al clima, topografía, actividad humana, vegetación y tendencias espaciales, y las presencias y ausencias de zonas reproductoras en el norte de Marruecos y el sur de la península ibérica. Un primer modelo fue construido a partir de las zonas reproductoras conocidas del norte de Marruecos con la intención de ser extrapolado a Iberia y predecir las áreas adecuadas para su reproducción. Un segundo modelo fue construido teniendo en cuenta toda la información disponible del norte de Marruecos e Iberia, con el fin de explicar la distribución actual de las zonas reproductoras que usa. Ambos modelos fueron evaluados atendiendo a criterios de discriminación, clasificación y parsimonia, y la influencia de

cada factor ambiental fue analizada mediante la partición de la varianza. La estabilidad en las temperaturas y la alta abundancia de precipitaciones distribuidas estacionalmente mostraron el mayor poder de predicción en los modelos. Esto indica una estrecha relación entre la distribución de la subespecie y el clima, sugiriendo que los ambientes más favorables para su reproducción se encuentran dentro del bioma mediterráneo. La topografía y la vegetación, concretamente, la presencia de acantilados y bosques cercanos a áreas de campeo, apuntan a una selección de hábitat a escala fina para la cría. Se llegó a la conclusión de que la península ibérica ofrece nuevas áreas favorables para la especie, de modo que facilitaría su expansión hacia el norte. Este resultado, junto con el número creciente de registros de la especie en Europa, sugiere que este busardo podría propagarse por Europa en un futuro próximo. Dado que el caso del Busardo Moro Africano no es un evento único, nuestros resultados pueden ser útiles para determinar si una expansión hacia el norte del bioma mediterráneo podría acontecer cambios en las distribuciones de las especies de aves que hasta ahora se han limitado a África y en las comunidades de aves de las zonas recientemente colonizadas.

3.0 ABSTRACT

Winters have become warmer under the impact of climate change, which has modified the phenology as well as the distributions ranges of birds. The African Long-legged Buzzard *Buteo rufinus cirtensis* has recently colonized Europe via the Strait of Gibraltar. In this chapter, we aim to explain the native distribution of this species and to predict favourable areas in newly colonized parts of Europe using geospatial modelling to identify the most influential factors in this process. We applied the favourability function, a

generalized linear model describing environmental favourability, for the presence/absence of breeding areas in northern Morocco and the Southern Iberian Peninsula, according to a set of variables describing climate, topography, human activity, vegetation, and purely spatial trends. A model was built using some known breeding sites in Northern Morocco, and was used to forecast future suitable breeding areas in Europe. A second model was built with the available data for northern Morocco and Europe to explain the current distribution of breeding sites. Both models were assessed according to discrimination, classification and parsimony criteria, and the influence of each factor was analysed using variation partitioning. We concluded that the Iberian Peninsula could provide new suitable areas for the species and facilitate its northward expansion. This result, together with the increasing number of records available, suggests that this species could soon spread throughout Europe. Steady temperatures and abundant but seasonally distributed precipitation showed the strongest predictive power in the models. This indicates a close relationship between the species' distribution and climate in the study area, and suggests that this species finds the most favourable environments in the Mediterranean biome. Topography and vegetation, specifically cliffs and woods near hunting zones, point to a fine-scale habitat selection for breeding. As the case of the African Long-legged Buzzard is not a unique event, our results may be useful to determine whether a northward expansion of the Mediterranean biome could be followed by distribution shifts of bird species that have so far been restricted to Africa.

3.1 INTRODUCTION

Within recent decades, it has been demonstrated that the global climate is becoming warmer (IPCC 2014) with widespread effects on ecosystems and biodiversity (Karl & Trenberth 2003). Climate change is altering biological systems and has already affected the distribution and population dynamics of a number of species across a broad range of geographical locations and habitats (Walther *et al.* 2002, Parmesan & Yohe 2003, Root *et al.* 2003). Predicting the consequences of climate change on range shifts is a challenge because bird ranges are expected to shift in response to temperature changes (Thomas & Lennon 1999, Böhning-Gaese & Lemoine 2004, Massimino *et al.* 2015), both in latitude and elevation (Huntley *et al.* 2006, Virkkala *et al.* 2008, Chen *et al.* 2011, Auer & King 2014), and because distributional changes may cause alterations in community composition, especially at range margins (Hampe & Petit 2005). This topic is of particular relevance to southern Spain and northern Morocco, where an important biogeographic barrier separates North African and southern European fauna and flora. The Strait of Gibraltar delimits the northern and southern breeding ranges of many African and European taxa, respectively (Busack 1986, Gantenbein & Largiadèr 2003, Rodríguez-Sánchez *et al.* 2008, García-Mudarra *et al.* 2009), even though the distance between the African and European continents is only 14 km at its narrowest point.

The southernmost area of Spain has recently played an important role as a focal point for the colonization of Europe by African birds. This region has a long tradition of birdwatching, and ornithological observations have been carefully recorded for the last two centuries (Irby 1895, Verner 1909, Finlayson 1992, Barros & Ríos 2008). This area delimits the northern distribution of some African species; however, if they move further north they cross into Europe, where they come into contact with different species and, in some cases, encounter new habitats. Some African species that have successfully expanded their breeding range more widely throughout Spain, such as the Black-shouldered Kite *Elanus caeruleus*, the White-rumped Swift *Apus caffer*, and the Little Swift *Apus affinis* (Molina 2003), were first sighted in this area. Some other species have become regular visitors, such as Rüppell's Vulture *Gyps rueppellii* (Ramírez *et al.* 2011); the most recent arrival is the African Long-legged Buzzard *Buteo rufinus cirtensis*. There has been a significant increase in the number of records of this bird in recent years, with a marked southerly bias in their distribution (de Juana & Comite de Rarezas de la Sociedad Española de Ornitología 1997, 2002, 2003, 2005, 2006, Dies *et al.* 2007, 2011, Gutiérrez *et al.* 2012, 2013). In 2004, the African Long-legged Buzzard nested in Ceuta (Muñoz 2003, Ávila *et al.* 2004), one of the two Spanish cities in northern Morocco, and in 2009 it was confirmed that the species was breeding in mainland Spain and, therefore, continental Europe (Elorriaga & Muñoz 2010). Although the northward expansion of the species' range is short in terms of distance, it is a large step in biogeographical terms. There has been a recent increase in the geographic distribution of observations, with records further north in Spain (Gutiérrez *et al.* 2012, 2013) and also in southern Portugal (Comité Português de Raridades, SPEA (http://www.spea.pt/fotos/editor2/reg_nao_publicados_v7_2012_12_31.pdf, http://www.avesdeportugal.info/butruf.html, accessed 2016 Nov 30).

This bird illustrates the fact that species distributions are not fixed. Thomas *et al.* (2001) demonstrated that, even in the short term, climate may modify species distributions at their margins. As species distributions are affected by different factors such as history, climate, topography, human activities, ecological interactions and population dynamics (Lomolino *et al.* 2006c, Real *et al.* 2009), we estimated the ecological requirements of the African Long-legged Buzzard by linking its geographical distribution to different environmental predictor variables. Thus, we assessed the potential distribution of this species in the recently colonized area of southern Spain. Our aim was to simulate the ecological processes shaping the distribution of the species in order to predict the core areas for the colonization of Europe by this African raptor. We considered two complementary scenarios to identify favourable breeding areas for this species. To obtain a predictive model, we analysed the characteristics of the breeding areas in northern Morocco, and then extrapolated the environmentally favourable conditions to the European part of the study area. We then modelled the breeding distribution in both Morocco and Spain to obtain an explanatory model.

3.2 METHODS

3.2.1 The species

The Long-legged Buzzard is a medium-sized raptor with two allopatric subspecies, the nominal *B. r. rufinus,* a partial migrant whose distribution extends from south-eastern Europe to Mongolia, and *B. r. cirtensis,* which breeds in northern Africa and is sedentary (Cramp & Simmons 1980, del Hoyo *et al.* 1994). In Morocco, the African subspecies inhabits a range of environments, such as cliffs and forest areas, and mainly lives below 800 m (Thévenot *et al.* 2003). In northern Morocco it is locally common (Thévenot *et al.* 2003), whereas in Spain it is listed as a rarity (Dies *et al.* 2010).

3.2.2 Study area

The study area comprised all terrestrial lands in the Iberian Peninsula and Morocco between 38º 55’ N and 33º 23’ N (Figure 3.1). This area contains mainly Mediterranean biomes with similar ecological conditions on both sides of the Strait of Gibraltar, including large mountain ranges up to 3479 m in the Iberian Peninsula and 3360 m in Morocco. Although there is strong climatic heterogeneity in this area, the overall similarity in environmental conditions is important if our aim is to project the model from Morocco to the Iberian Peninsula because conditions outside the calibration range could lead to erroneously predicting favourability in the new area. Mean temperatures range from –3 ºC to 26 ºC, and mean annual precipitation ranges from less than 120 mm to more than 1050 mm (Hijmans *et al.* 2005). Temporal heterogeneity also influences the area, as seasonality is a main feature of the Mediterranean climate (summer has at least two drought months with high temperatures).

Figure 3.1. Study area location with the current African Long-legged Buzzard breeding presences in 10-km UTM squares. Black squares represent definite breeding presences. Black-edged squares indicate the area surveyed.

3.2.3 Distribution data

In comparison with other Palearctic raptors, little is known about the African Long-legged Buzzard. Data on the presence of breeding territories of the African Long-legged Buzzard in Morocco and Spain were obtained from regional road transects and specific surveys in potential breeding territories, and conducted during the nesting season (from April to July) in 2014 and 2015. We concentrated our efforts in those areas suitable for the species according to its habitat preferences. As it usually nests on cliffs (Cramp & Simmons 1980) we paid particular attention to gorges, crags and hillocks, although we also visited forested areas because the species commonly breeds in trees in the study area(Irby 1895, Elorriaga & Muñoz 2010). We initially detected the presence of the species through road surveys, and then further explored occupied areas. The surveys allowed large areas to be searched for breeding territories and were conducted by two or three observers experienced in detecting and identifying the species. A.R.M. directed every survey and one or two other observers assisted on the surveys. The routes (approximately 1500 km/year in Morocco and 215 km/year in Spain) followed improved and unimproved surface roads and were carried out over a 6–7 days each year in Morocco and 2–3 days each year in Spain. The fundamental units of the distribution data were 10×10 km UTM squares. The study area was divided into 2684 squares (1681 in the Iberian Peninsula and 1003 in Morocco). During the survey period we sampled 157 squares in Morocco and 39 in Spain. A territory was considered to be occupied when evidence of breeding was observed, such as displays or a pair in a suitable nesting habitat during the nesting season, permanent territory (two individuals in suitable habitats over the two years of survey), adults carrying nest materials or occupying a nest, and recently fledged young. We obtained breeding records for 24 squares for Africa and 6 for mainland Spain (see Figure 3.1), which is more complete than previous published information in public datasets such as GBIF or eBird, and includes all their sites for the breeding period.

Table 3.1. Environmental variables used to model the distribution of African Long-legged Buzzard grouped by their environmental factor.

Factor	Code	Variable	Source
Topography	*Alti*	Altitude (m)	1
	Slop	Slope (degrees)	1
Spatial Situation	*Lati*	Latitude (degrees N)	1
	Long	Longitude (degrees E)	1
Climate	*Prec*	Mean annual precipitation (mm)	2
	PVC	Precipitation variation coefficient (%)	2
	TRan	Annual temperature range (°C)	2
	TJul	Mean temperature in July (°C)	2
	TJan	Mean temperature in January (°C)	2
Human activity	*PopDen*	Population density (hab/km^2)	3
	DRoad	Distance to the nearest road (m)	4
Vegetation	*IrrCr*	Surface proportion of irrigated croplands	5
	DrCr	Surface proportion of dry croplands	5
	ExCr	Surface proportion of extensive croplands	5
	InCr	Surface proportion of intensive croplands	5
	Arti	Surface proportion of artificial areas	5
	Oak	Surface proportion of oak forest	5
	Nee	Surface proportion of needle-leaved forest	5
	MixFor	Surface proportion of mixed forest	5
	ForGra	Surface proportion of mosaic forest with grassland	5
	GraGro	Proportion of mosaic grassland with sparse groves	5
	Shr	Surface proportion of shrublands	5
	Spar	Surface proportion of sparse vegetation	5
	Bar	Surface proportion of bare areas	5

Data sources: 1 – (US Geological Survey 1996) 2 – (Hijmans *et al.* 2005), 3 – (Oak Ridge National Laboratory 2001), 4 – FAO/GIS (http://www.fao.org/geonetwork), 5 – Globcover (http://due.esrin.esa.int/page_globcover.php).

3.2.4 Predictor variables

We used 24 independent variables related to topography, vegetation, climate, human activity, and purely spatial trends (Table 3.1) to identify the factors that could affect the breeding location of African Long-legged Buzzards. These variables were chosen on the basis of their potential predictive and explanatory power, and were assumed to be correlated to a higher number of probable causal factors (Muñoz *et al.* 2005). We obtained mean values of these variables in 10×10 km UTM squares using the module *ZONAL* of ARCMAP10.1 (ESRI©2012) software, starting from 1 km^2 resolution raster layers. A spatial trend variable was used to create a purely spatial descriptor, following the trend surface approach (Legendre & Legendre 1998). This descriptor was added to the list of variables in the modelling process as described in Fa *et al.* (2014).

3.2.5 Distribution modelling

We modelled the presence/absence of breeding African Long-legged Buzzards using the Favourability Function (Real *et al.* 2006). Favourability outputs are specifically based on the environmental conditions that could facilitate a species' presence, irrespective of the proportion of presences in the data set (Real *et al.* 2006, Acevedo & Real 2012). This property of favourability models is essential to analyse the potential expansion of the African Long-legged Buzzard, as its current range is expected to have a lower size than the current extent of environmentally favourable areas. The Favourability Function also has further analytic potential, because models of different species can be compared and combined (Acevedo & Real 2012) and may improve existing biodiversity metrics (Real *et al.* 2006).

Favourability was calculated by performing a forward-backward stepwise logistic regression of presences/absences (dependent variable) on the set of predictor (independent) variables; the resulting probability values (*P*) were then transformed into favourability values (*F*) using the equation (1) as is specified as follows (Real *et al.* 2006):

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

where n_1 and n_0 are the number of presences and absences in the study area, respectively.

We constructed two different favourability models of the breeding distribution of African Long-legged Buzzards: the Iberia-Morocco Model (IMM), aimed at determining which environmental conditions could describe the distribution of current breeding areas on both sides of the Strait of Gibraltar; and the Only-Morocco Model (OMM), aimed at predicting which native areas have environmentally favourable conditions for breeding in northern Morocco, which was used to predict the potential breeding distribution in the Iberian Peninsula. The dependent variable for the IMM was the presence/absence of breeding areas on both sides of the strait, whereas the OMM only took this aspect into account in Morocco. The OMM was then extrapolated to the Iberian Peninsula using the equation (2) (Real *et al.* 2006), as described in Barbosa *et al.* (2003):

$$F = \frac{e^y}{(n_1/n_0) + e^y} \qquad (2),$$

where n_1 and n_0 are the numbers of presences and absences in Morocco (24 and 979, respectively), e is the base of the natural logarithms and y is a linear combination of the predictor variables that were found to be significant in the forward-backward stepwise selection process (i.e., y is the linear combination of variables – or *logit* – resulting from the above-mentioned logistic regression.

We used the False Discovery Rate (FDR; Benjamini & Hochberg 1995) to control for type I errors, which can arise from using a large number of variables. We only accepted those variables which were significantly related to the distribution of the species with $\alpha < 0.05$ under an FDR of $q < 0.05$. When Pearson's correlation between two variables within a model was ≥ 0.8, multicollinearity was avoided by retaining only the variable that most significantly predicted species presence (Fa *et al.* 2014). The significance of every variable that was entered in the models was assessed using Wald's (1943) test.

Favourability values range from 0 to 1, 1 indicating the most favourable conditions. However, it makes little sense to establish markedly different favourable areas using, for example, the values 0.48 and 0.52 (Hosmer & Lemeshow 2000a). Thus, we reclassified the areas into 'clearly favourable' areas (> 0.8), 'clearly unfavourable' areas (< 0.2), and different intervals of 'intermediate favourability' areas, according to the threshold criteria described in Muñoz *et al.* (2005).

3.2.6 Model evaluation and validation

In the first stage, the IMM and the OMM were calibrated using an 80% randomly selected subset of the recorded presences, so that the remaining 20% was set aside for cross-validation. This validation was based on model sensitivity towards the 20% subset, the limit for model acceptance being 0.75. In the second stage, if a model was validated, it was calibrated again using 100% of the recorded presences. This recalibrated model was employed henceforth if (1) the Spearman rank's correlation coefficient with the cross-validated model was higher than 0.95, and (2) it shared the most important predictor variables with the cross-validated model.

The classification capacity of the obtained models was evaluated using six indices (Fielding & Bell 1997, Barbosa *et al.* 2013) sensitivity (proportion of correctly classified presences), specificity (proportion of correctly classified absences), correct classification rate (CCR; proportion of presences and absences correctly classified), Cohen's Kappa (proportion of specific agreement), and over-prediction rate (OPR; proportion of observed absences in the predicted presence area). We used the Area Under the ROC Curve (AUC; Lobo *et al.* 2008) to assess the models' discrimination capacity, and the Akaike Information Criterion (AIC; Akaike 1974) to compare models based on parsimony analysis. The OMM was assessed before the extrapolation, using presences/absences in Morocco as the reference, and was also assessed after extrapolation to the Iberian Peninsula, using all the presences/absences in the study area.

We also validated the extrapolation of the OMM to the Iberian Peninsula by checking the favourability values obtained in squares north of the Strait of Gibraltar in which African Long-legged Buzzards have been recorded as breeding. Validation was considered positive if these squares where 'clearly favourable' ($F > 0.8$) for breeding.

3.2.7 Variation partitioning

Variation partitioning analysis (Legendre 1993) was used to analyse the explanatory dimension of the IMM and OMM, following the approach described in Muñoz *et al.* (2005). We grouped the variables included in the model into three main explanatory factors: topography, climate, and vegetation. We then computed how much of the variation in favourability explained by the model was accounted for by the pure effect of each factor (i.e., not affected by covariation with other factors in the model), and which proportion was clearly attributable to more than one factor. The negative combined effect of two factors could suggest that one of the factors was obscured by the other.

3.3 RESULTS

The variables entered in the cross-validated models were combined according to the following *logit* (y) equations:

$$\text{IMM: } y = -13.57 + 5.087 \times Oak + 11.89 \times PVC + 0.20 \times Slop$$

$$\text{OMM: } y = 1.85 + 0.0054 \times Prec - 0.037 \times TRan + 10.46 \times Nee$$

where Oak is the surface proportion of oak forest, PVC is the variation coefficient of precipitation, *Slop* is the slope, *Prec* is the mean annual precipitation, $TRan$ is the annual temperature range, and *Nee* is the surface proportion of needle-leaved forest. The variables are placed in the same order they were entered in the model in the stepwise process. Table 3.1 shows the variable units and Table 3.2 shows the Wald test values and significance. According to these values, climatic variables have the strongest predictive power in both models. The cross validation reported sensitivity values of 83.3% and 75% of the IMM and the OMM, respectively, towards the 20% presence subsets not used for model calibration.

The models calibrated with 100% of recorded presences provided the following *logit* (*y*) equations:

$$\text{IMM: } y = -13.29 + 5.78 \times Oak + 11.40 \times PVC + 0.25 \times Slop$$

$$\text{OMM: } y = 1.86 + 0.0062 \times Prec - 0.038 \times TRan + 7.86 \times Nee + 4.37 \times Shr$$

where *Shr* is the surface proportion of shrubland. Spearman rank's correlation coefficients of these models with the cross-validated models are 0.996 ($p < 0.01$) and 0.976 ($p < 0.01$), respectively. On the other hand, the two IMMs selected the same variable set, and all variables in the cross-validated OMM were included in the model calibrated using 100% of the recorded presences (Table 3.2). So, the latter model was employed henceforth.

Table 3.2. Variables included in the models, Wald test values, and significance (*p*). The variables are ranked according to their order of entrance in each model. Variables coded as in Table 1. The cross-validated model was calibrated using a randomly selected 80% subset of the recorded presences.

	Cross-validated model		**All-presences model**	
IMM	**Wald**	***p***	**Wald**	***p***
Oak	7.783	5.274×10^{-03}	12.511	4.046×10^{-04}
PVC	24.616	6.997×10^{-07}	27.620	1.476×10^{-07}
Slop	12.545	3.973×10^{-04}	21.211	4.115×10^{-06}
Constant	61.8603	3.687×10^{-15}	72.022	2.128×10^{-17}
OMM				
Prec	18.716	1.517×10^{-05}	21.329	3.868×10^{-06}
TRan	11.858	5.74×10^{-04}	14.493	1.407×10^{-04}
Nee	6.861	8.807×10^{-03}	3.942	4.710×10^{-02}
Shr	—	—	4.731	2.962×10^{-02}
Constant	0.514	4.733×10^{-01}	0.607	4.357×10^{-01}

Table 3.3. Measure of the indices: Cohen's Kappa, sensitivity, specificity, correct classification rate (CCR), over-prediction rate (OPR), area under the curve (AUC), and Akaike information criterion (AIC) of the models performed. IMM: Iberia Peninsula and Morocco Model; OMMo: Only Morocco Model original; OMMe: Only Morocco Model extrapolation to Iberian Peninsula.

	Kappa	Sensit.	Specif.	CCR	OPR	AUC	AIC
IMM							
	0.089	0.833	0.847	0.847	0.942	0.921	233.721
OMM							
OMMo	0.110	0.792	0.783	0.784	0.918	0.880	181.138
OMMe	0.00738	1.000	0.510	0.512	0.993	0.948	96.728

The OMM and the IMM showed a high and discrimination capacities (see Table 3.3). The IMM, however, showed higher sensitivity, specificity, and AUC values than the OMM, whereas the OMM extrapolation to the Iberian Peninsula showed a higher parsimony (i.e. lower AIC).

Favourability values for breeding African Long-legged Buzzards are shown in Figure 3.2, A (IMM) and B (OMM). After extrapolation to the Iberian Peninsula, the number of squares classified as "clearly favourable" in the OMM was almost four times higher than the number predicted by the IMM (469 and 119 squares, respectively). This difference was even more obvious in Portugal and eastern Spain (see Figure 3.2). The number of squares classified as having "intermediate favourability" values was fairly similar in both models (1395 squares for OMM and 1120 squares for IMM).

Validation analysis of the extrapolation of the OMM to the Iberian Peninsula confirmed that 100% (n=6) of the squares with presences of breeding African Long-legged Buzzards in the Iberian Peninsula showed environmental favourability values higher than 0.93.

The results of the variation partitioning analysis are shown in Figure 3.3. The pure influence of climate explained 88.7% of the variation in the IMM vs 50.3% in the OMM. However, the relative importance of the apparent effect of climate (i.e. the sum of pure influence and influence shared with other factors) was more than double in the OMM (92.6%) and 80.4% in the IMM, where the effect of climate was partially obscured by the influence of topography.

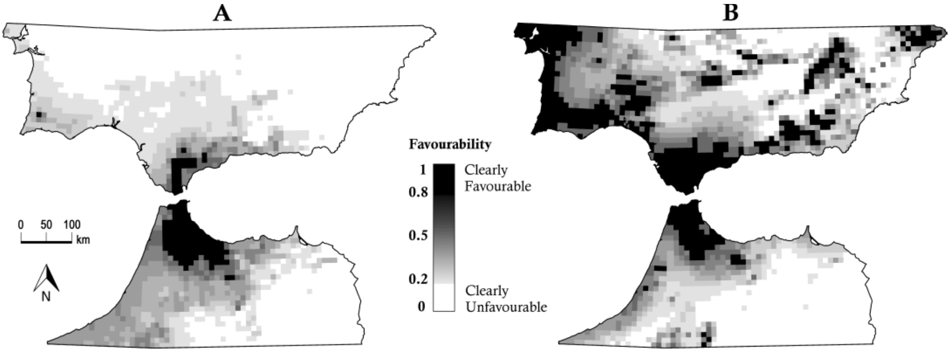

Figure 3.2. African Long-legged Buzzard favourability values in the Iberian Peninsula and Morocco, according to the IMM **(A;** based on all presences in the study area) and OMM **(B;** based on presences in Morocco alone and then extrapolated to the Iberian Peninsula).

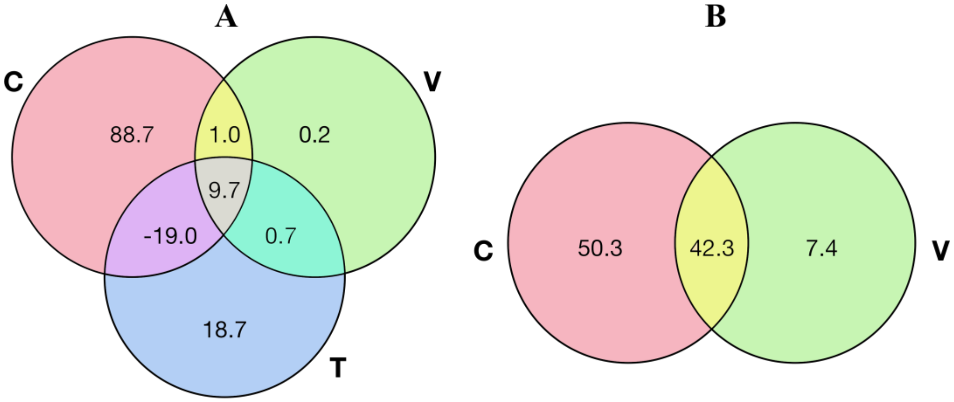

Figure 3.3. Results of the variation partitioning of IMM **(A)** and OMM **(B)**. Values shown in the diagrams are the percentages of variation explained exclusively by vegetation (V), topography (T), and climate (C), and by the combined effect of these factors.

3.4 DISCUSSION

We have presented evidence for the existence of favourable areas for the African Long-legged Buzzard in the southern Iberian Peninsula, which could facilitate settlement and the northward expansion and colonisation of southwestern Europe by this African species. These results are supported by the finding that climate had the greatest predictive value for its distribution. If climate warming continues, further arrivals of African Long-legged Buzzards are to be expected in southern Spain, increasing the possibility that self-sustaining populations may become established in this area.

Favourability models are normally constructed to show the biological features that determine species distributions; biogeographic trends are shown when the relationship between environmental variables and presence/absence data is used to construct the models (Acevedo & Real 2012). A striking feature of our models is that they classify as highly favourable large areas for the African Long-legged Buzzard from which it is currently absent. Given that the species bred for the first time in mainland Spain in 2009, and also that it remains very scarce, the wide availability of unoccupied favourable areas may presage the future expansion of the species, which will probably occur within the most favourable areas detected by our models. They are well described by a small number of variables, and suggest that the suitable areas for the African Long-legged Buzzard are mainly determined by climate, which is the most influential factor in both of them (OMM and IMM). The information provided by the IMM provides a more cautious picture than the OMM. The IMM model indicates the potential expansion of the species in the near future, and may identify areas in which to monitor and better document the potential new population. On the other hand, the OMM model indicates the potential distribution of the species over the longer term, and characterizes the areas with the potential to host the species in the southern Iberian Peninsula that have the same environmental conditions that determine the distribution of the species in the Moroccan range. The fact that specificity in the OMM is not 1 means that this model defined high favourability conditions in some areas of Morocco where the presence of nesting sites was not detected by the survey method, although they may occur. The favourability function is capable of generalising beyond the observed presences with high reliability (Olivero *et al.* 2016), overcoming the effects of possible false absences in the data. When the data are extrapolated from Morocco to Europe, the occupied squares in Spain show high favourability values in all cases, which indicates that it is possible accurately to predict areas selected for the species when the model is extrapolated beyond the species' native range.

Climatic variables had the strongest predictive power, as indicated by the highest Wald test values, and also had the highest proportion of explained variation, which was more pronounced in the IMM because of the larger area under analysis. These results highlight the correlation between the species' distribution and temperature and precipitation. Thus, recent warming trends may have contributed to the northward shift of the species, and the subsequent colonization pattern of the Iberian Peninsula. However, climate is not the only factor that influences the environment. When analysing species distributions, more accurate models can be obtained when climate is combined with other factors, such as topography (Márquez *et al.* 2011, Muñoz & Real 2013). The effect of the factors that determine species distributions may differ depending on the spatial scale at which they act. Climate is a factor that typically changes over large areas, whereas topography and/or vegetation create finer-scale variation in climate that influences species distributions (Pearson & Dawson 2003, Muñoz & Real

2013). In our case, topography and/or vegetation influenced the species distributions on a smaller scale in the areas that were climatically favourable. Slope is related with cliff availability (Muñoz *et al.* 2005), and may act as a limiting resource for breeding in this cliff-nesting raptor (Thévenot *et al.* 2003), although it also breeds on trees in some areas of northern Morocco and southern Spain (Elorriaga & Muñoz 2010, 2013). Thus, the presence of mountainous areas and forests may favour the presence of the species and be an indicator of nest-site availability. Precipitation and temperature range were included in OMM, and their combination explains the selection of rainy areas with stable temperatures on the north coast of Morocco. Our model detected favourable areas in this region. According to Thévenot *et al.* (2003), the species is more abundant in Morocco between 0 m and 800 m above sea level, but is absent above 1000 m.

There was a high over-prediction rate when the OMM model was extrapolated to the Iberian Peninsula. That is, the African Long-legged Buzzard is absent from many of the areas in which the model predicted its presence in Spain and Portugal, although this does not necessarily mean that the model is erroneous (Barbosa *et al.* 2013). These unoccupied favourable areas in Europe may simply be suitable areas to which the species has not yet managed to disperse, partly due to the physical barrier of the Strait of Gibraltar. Distribution models are abstract constructions which need to be connected with natural history (Muñoz *et al.* 2015a). Rather than being a drawback, the over-predictions enable us to extract ecological inferences by comparing the observed and predicted (potential) species distributions. We draw attention to the existence of three continuous highly favourable areas, two centred on the African and European shores of the Strait of Gibraltar, and the other centred in the Portuguese Algarve, in which the species has been recently detected although breeding has not yet been confirmed. Despite the fact that the literature defines the species primarily as a cliff and crag nester, and rarely as breeding in trees (Cramp & Simmons 1980, Rodriguez *et al.* 2013), in mainland Spain, Ceuta (a Spanish enclave in northern Morocco), and the Moroccan Region Tangiers-Tetouan, all the nests found were located on trees. This aspect suggests that in the Portuguese Algarve, where the availability of cliffs is limited, the African Long-legged Buzzard could also act as a tree-nesting species, which is an adaptation that has also been observed in the case of Bonelli's Eagle *Aquila fasciata* (Ferreira 2011).

In recent decades, the Iberian Peninsula has been successfully colonised by other African bird species, such as the White-rumped Swift *Apus caffer* (del Junco & González 1969), the Black-shouldered Kite *Elanus caeruleus* (Ferrero 1996), the Little Swift *Apus affinis* (Ramírez *et al.* 2002) and the Common Bulbul *Pycnonotus barbatus*, which has been breeding in this region since 2013. More recently, there have been an increasing number of records of other species, such as Ruppell's Vulture *Gyps rueppellii*, the Lanner Falcon *Falco biarmicus*, the Cream-coloured Courser *Cursorius cursor,* and Moussier's Redstart *Phoenicurus moussieri*, among others. Although they are regularly observed, there have been no reports of them breeding (Copete *et al.* 2015). This general increase of African species in southern Europe is complemented by records during the present decade of White-backed Vulture *Gyps africanus* and Bateleur *Terathopius ecaudatus* (Dies *et al.* 2010, Copete *et al.* 2015), which constitute new taxa for Western Europe. In both cases, the initial records occurred around the Strait of Gibraltar, which indicates that this area has become a potential focal point for the colonisation of Europe by African species.

We used a modelling approach to explicitly analyse the relationship between the distribution of the African Long-legged Buzzard and environmental variables, which allowed us to form hypotheses about how it responds to environmental variability and to provide insights into its potential expansion to Europe in response to regional climate change (Muñoz *et al.* 2015b). Another African colonizer, the Black-shouldered Kite *Elanus caeruleus*, seems to have taken advantage of the gradual increase of cultivated areas in the Iberian Peninsula to expand its distribution in Western Europe (Balbontín *et al.* 2008). Although both species, Black-shouldered Kite and African Long-legged Buzzard, have probably colonized the Iberian Peninsula from Africa, observations of the former date back to the mid-19th century, while first regular observations of the latter date from the beginning of the 21st century (Elorriaga & Muñoz 2010). We support the idea that the African Long-legged Buzzard is in the Iberian Peninsula due to a modern colonization because there are no historical records in an area regularly visited by ornithologists during the last two centuries (e.g. Irby 1895, Verner 1909, Bernis 1980). Although some plumages of the African Long-legged Buzzard can look identical to Asian Long-legged Buzzard (*Buteo rufinus rufinus*), which is not an issue in our case, and could be confused with Steppe Buzzard (*Buteo buteo vulpinus*), a rarity in our study area (Rodriguez *et al.* 2013), typically plumaged birds are relatively easy to distinguish from Common Buzzard, because of the clear tendency they have to orange-reddish colour and pale appearance.

For the moment, those areas occupied by the African Long-legged Buzzard in Spain are in protected forested areas that have not suffered changes at the landscape scale during the last decades. Recently the African Long-legged Buzzard was found breeding in the Sicilian Channel (Corso 2009), tentatively suggesting a range expansion also in the Central

Mediterranean and the settlement of pioneering individuals in southern Europe. Curiously, both in Pantelleria Island (Italy) and southern Spain, the reproduction of pure African Long-legged Buzzards was followed by its hybridization with the Common Buzzard *Buteo buteo* (Corso 2009, Elorriaga & Muñoz 2013). The consequences of this phenomenon in the northward expansion process remain unknown and information is still very limited, although deserves particular attention. If hybrids were infertile, hybridization could slow down or even constitute a barrier against the expansion of the species into Europe. With respect to the nominate subspecies *B. r. rufinus*, it has also expanded its distribution towards the northwest during the last decades, climatic change being one of the possible factors influencing its spread (Mrlik & Landsfeld 2002).

As pointed out by Crick (2004), much work is needed in the area of understanding the effects of climate change on individual species, although we must keep in mind that the recent northward movement of the African Long-legged Buzzard could be attributed to different factors acting simultaneously, including climate change. Our results, for example, could be useful in direct sampling and monitoring studies of the species when planning field surveys, such that top priority could be given to the most favourable areas. This study has contributed to a better understanding of the northward shift of African species that cross the Mediterranean, and to assessing the role that the Straits of Gibraltar plays in both connecting and isolating bird populations, thus providing insight into the relationships between European and African biomes. If the climate continues to warm, we can expect further arrivals in Europe of potential colonist African bird species.

CAPÍTULO 4

CALCULANDO LA EXTENSIÓN Y TASA DE CAMBIO DE LAS DISTRIBUCIONES ALTERADAS POR EL CAMBIO CLIMÁTICO MEDIANTE LOS CONJUNTOS BORROSOS

FUZZY SETS ALLOW GAGING THE EXTENT AND RATE OF SPECIES RANGE SHIFT DUE TO CLIMATE CHANGE

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4 FUZZY SETS ALLOW GAGING THE EXTENT AND RATE OF SPECIES RANGE SHIFT DUE TO CLIMATE CHANGE

4.0 RESUMEN

La reciente modificación de la distribución de las especies en respuesta a un clima cada vez más cálido supone un cambio biogeográfico importante y generalizado. El principal impulsor de este cambio es el desequilibrio que se produce entre la distribución de las especies y su favorabilidad climática. La mayoría de los enfoques de modelización de la distribución de las especies suponen un equilibrio de la distribución con el medio ambiente, lo que dificulta su aplicabilidad al análisis de este cambio. Combinando los modelos de distribución de especies basados en la favorabilidad climática y usando la teoría de conjuntos borrosos, en este capítulo se evalúa la respuesta al cambio climático de una especie típicamente africana, el Busardo Moro del Atlas. Con este enfoque pone de manifiesto el desequilibrio latitudinal existente entre la distribución de la especie y el clima, que además se cuantifica en 4 km. Este desequilibrio ejerce un poder atrayente que desplaza a la especie hacia el norte, a una velocidad de alrededor de 1.3 km/año. Es decir, la especie tardaría 3 años en ocupar nuevas zonas climáticamente favorables. Se espera que esta velocidad se desacelere hasta 0.5 km/año en el periodo de 2060-2080. Además, se confirma que el cambio en el área de distribución del taxón estudiado es latitudinal hacia el norte, en lugar de producirse una ampliación de todo el rango de distribución o un movimiento longitudinal. Este estudio proporciona un nuevo marco teórico y una metodología que pueden ser utilizados para

evaluar la dinámica y los cambios biogeográficos de las distribuciones debidos al cambio del clima.

4.0 ABSTRACT

The recent modification of species distribution ranges in response to an increasingly warmer climate has constituted a major and generalized biogeographic change. The main driver of the shift in distribution is the disequilibrium of the species ranges with their climatic favourability. Most species distribution modelling approaches assume equilibrium of the distribution with the environment, which hinders their applicability to the analysis of this change. Using species distribution models based on climatic favourability combined with fuzzy set theory, we assessed in this chapter the response to climate change of a typically African species, the Atlas Long-legged Buzzard. With this approach we were able to quantify that there is a latitudinal disequilibrium of the species distribution with the current climate of 4 km, which is driving the species range northwards at a speed of around 1.3 km/year, i.e., it takes 3 years for the species to occupy new climatically favourable areas. This speed is expected to decelerate to 0.5 km/year in 2060–2080. In addition, we confirmed that the change that occurs is latitudinally northwards, rather than a widening of the entire range or a longitudinal movement. This study provides a new theoretical framework and methodology that can be used to assess biogeographic changes in dynamic distributions.

4.1 INTRODUCTION

Different environmental, biological, historical, and anthropogenic factors affect the distribution of species in space and time (Lomolino *et al.* 2006d). However, climate seems to be the most relevant factor for several taxa at large scales (Pearson & Dawson 2003, Mackey & Lindemayer 2011, Márquez *et al.* 2011, Chamorro *et al.* 2017, Sun *et al.* 2020). Throughout the last century, and especially over the last few decades, there have been global alterations leading to a warmer climate (IPCC 2014) with widespread effects on biological systems (Walther *et al.* 2002, Karl & Trenberth 2003, Root *et al.* 2003). This recent climate change has already caused expansions, reductions, or shifts in the distribution of many species (Thomas & Lennon 1999, Warren *et al.* 2001, Böhning-Gaese & Lemoine 2004, Hitch & Leberg 2007, Virkkala *et al.* 2008, Melles *et al.* 2011, Massimino *et al.* 2015, Borzée *et al.* 2019, Lazo-Cancino *et al.* 2019). In particular, climate shifts are modifying the margins of species distributions over short periods of time, a process that is more marked in vagile species such as birds (Thomas *et al.* 2001, Castro *et al.* 2008).

In general, it is only in recent decades that studies have addressed the reaction of birds to climate change in relation to modifications in their distribution (Huntley *et al.* 2006, Maclean *et al.* 2008, Elorriaga & Muñoz 2010) and phenology (Møller *et al.* 2008, Ambrosini *et al.* 2011, Nieto *et al.* 2018). These modifications are relevant not only for the species undergoing the changes, but also for the species residing in the new receiving areas. Distribution changes ultimately affect community composition, which adds uncertainty to the future status of natural populations and forces changes in species management and conservation programs (Root & Schneider 2006, Real *et al.* 2010).

The Strait of Gibraltar separates Africa and Europe. It is 14 km at its narrowest and thus also puts the two continents in close contact. It is a difficult-to-cross bridge for many migratory species, especially soaring birds (Evans & Lathbury 1972, Bijlsma 1987, Hahn *et al.* 2009), and is also an effective biogeographic barrier for many other taxa (Gantenbein & Largiadèr 2003, Carranza *et al.* 2006, García-Mudarra *et al.* 2009). However, this barrier is currently being overcome by some typical African birds: that is, taxa that until very recently had their northern distribution limit in Northern Africa (de Juana & Comité Ibérico de Rarezas de la Sociedad Española de Ornitología 1994, de Juana & Comite de Rarezas de la Sociedad Española de Ornitología 1997, Dies *et al.* 2010, Copete *et al.* 2015). These changes are putting into contact two different faunas in the European part of the Strait of Gibraltar, entailing changes in communities that are leading to new ecological interactions in this región (Elorriaga & Muñoz 2013). It is known that the southern part of the Iberian Peninsula is a suitable place for colonization by different African bird species (Chamorro *et al.* 2016) and that it plays a relevant role as a focal point in the colonization of Europe by these African species (Ramírez *et al.* 2011, Chamorro *et al.* 2017). However, the scientific basis for forecasting the future development of these distribution ranges has yet to be established. Issues that remain unaddressed include whether they are expanding or shifting their distributions, the spatial and temporal disequilibrium between the species ranges and their climatic favourability, the latitudinal rate of their change in distribution range, or whether these rates are expected to increase, decrease or remain constant in the future.

In biogeographic terms, a major change has been the recent colonization of Europe by one of these typical African birds, the Atlas Long-legged Buzzard (*Buteo rufinus cirtensis*). The species is divided into two subspecies, the Asian Long-legged Buzzard (*Buteo rufinus rufinus*), which breeds from the Balkans and Asia Minor eastwards to Mongolia and northwest India (Cramp & Simmons 1980), and the aforementioned Atlas Long-legged Buzzard, traditionally distributed from Mauritania and Morocco eastwards to Egypt (Figure 4.1A) (del Hoyo et al. 1994, Ferguson-Lees & Christie 2001). The Atlas subspecies used to breed as far as the African coast of the Strait of Gibraltar (Irby 1895, Muñoz 2003, Ávila *et al.* 2004). However, in 2009, the first breeding record was confirmed in continental Europe (Elorriaga & Muñoz 2010). (Chamorro *et al.* 2017) conducted a biogeographic study of the taxon and showed that climate is the most important factor affecting the distribution of the Atlas Long-legged Buzzard, suggesting that climate change is the main driver of this biogeographic change (see **chapter 1**). This assessment was based on the notion of climatic favourability, a typical fuzzy concept whose theoretical foundation rests on fuzzy set theory rather than on niche theory.

Since the beginning of the 2000s, fuzzy set theory and its corresponding fuzzy logic (Zadeh 1965) have been increasingly used in biogeography (e.g. Robertson *et al.* 2004, Real *et al.* 2009, Olivero *et al.* 2011, 2017b). 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 which assigns each object with a value ranging from zero to one (Zadeh 1965). Fuzzy sets have no sharply defined boundaries and so they better reflect the continuous character of nature (Salski 2006). Thus, fuzzy logic provides a conceptual framework that has a particular scope of applicability in the domains of biogeographic pattern classification and information processing. It is more successful than crisp approaches to managing typical fuzzy notions such as the presence of a species in a particular region, the identification of climatically favourable areas for reproduction, or climatic similarity between localities (Zadeh 1965, Acevedo & Real 2012, Real *et al.* 2017).

In this paper, we use fuzzy logic methods to analyse the dynamics of species distribution in the context of climate change, quantifying the extent of colonization as well as displacement rates in climatically favourable areas. We applied these methods to assess the favourability of the Western Palearctic for the Atlas Long-legged Buzzard, and to determine if the species is actually being pushed northward due to climate change. We projected the predictions to future climate change scenarios to forecast its response to different climatic conditions (i.e., whether its distribution will expand and at what rate). Thus, we attempt to provide information on the ongoing occupation of Europe and the northern Mediterranean basin by African birds. This information will be of interest for the environmental management of potentially affected areas.

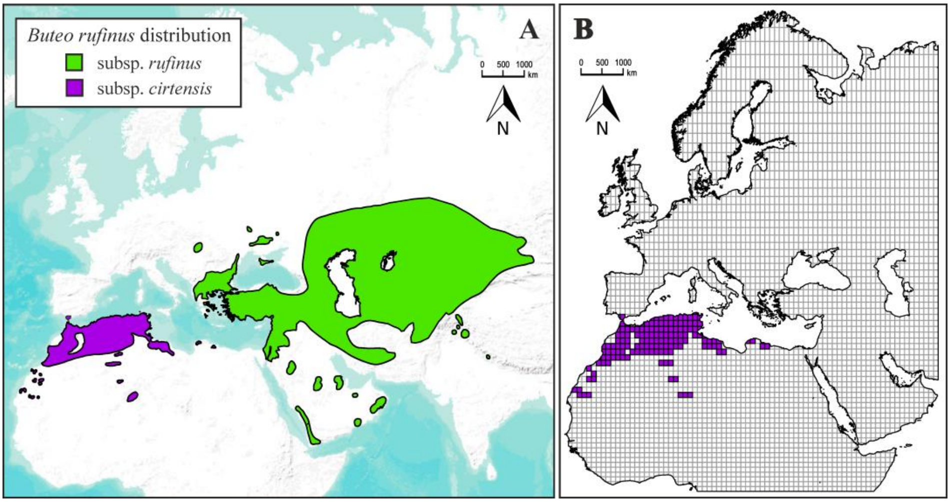


Figure 4.1. (A) *Buteo rufinus* distribution separated by the two accepted subspecies, modified from the IUCN shapefile. **(B)** Study area (1-degree latitude × 1-degree longitude grid cells) with the presences used for the modelling process are shown in violet.

4.2 METHODS

4.2.1 Study area

The study area was the European, Asian, and African zones from 20º00'W to 60º00'E and from 09º30'N to 70º00'N (Figure 4.1B). This area, which comprises the Western Palearctic and surrounding areas, fully covers the current breeding territories of the Atlas Long-legged Buzzard, as well as the western distribution of the Asian Long-legged Buzzard. Climatic heterogeneity is high, covering sub-tropical, desert, Mediterranean, Atlantic, and tundra climates (Mill 1902, Udvardy 1975, Font 2000). To analyse the distribution of the subspecies, the study area was converted into 1-degree latitude × 1-degree longitude grid cells (*n* = 3839) using the *Create Fishnet* and *Intersect* tools from ARCGIS. These cells were used as operational geographic units (OGUs) (Crovello 1981, Márquez *et al.* 2001).

4.2.2 Species distribution data

There is such little information on the Atlas Long-legged Buzzard that it is considered a gap in the knowledge of Western Palearctic birds (Cramp & Simmons 1980). In contrast to the Asian Long-legged Buzzard, it is mainly sedentary with some dispersal (Cramp 1992, del Hoyo *et al.* 1994). This middle-size raptor occupies different habitat types in North Africa, occurring well into the Sahara (Thévenot *et al.* 2003) and up to the Atlas Mountains, and breeding as high as *c* 2500 m above sea level (Barreau *et al.* 1987). It is relatively scarce in most of its breeding range, although it can be locally common in forest areas bordering open hunting grounds, such as the lakes area in the cedar forests of the Mid-Atlas (Rodriguez *et al.* 2013).

World atlases were used to obtain the distribution data to determine the breeding area of the Atlas Long-legged Buzzard (Cramp & Simmons 1980, Cramp 1992, del Hoyo *et al.* 1994). This information was updated using the IUCN red list (IUCN 2017), e-Bird (https://ebird.org/species/lolbuz1), and some personal records from Morocco and Spain (Chamorro *et al.* 2017). We identified the OGUs where the species had been reported as breeding at least once from 1980 to 2020. Thus, we obtained a binary target variable representing breeding/not breeding at each OGU (breeding: n_1= 146, not breeding: n_0= 3693, Figure 4.1B).

4.2.3 Predictor variables and future scenarios

A set of 21 environmental variables (Table 4.1) related to topography and climate between 1950 and 2000 were used in the biogeographic modelling procedure. These variables were digitized in raster format at a resolution of 1 km^2 pixels. Values of these variables at each OGU were obtained by averaging the values of the 1 km^2 pixels within them using the ZONAL function of ARCGIS 10.4.1 software.

Expected future values of the climatic variables were obtained for the periods 2041 to 2060 and 2061 to 2080 (Hijmans *et al.* 2005) (http://worldclim.org/). Four different Representative Concentration Pathways (RCP) were used to represent the extreme (2.6 and 8.5) and intermediate (6.0 and 4.5) trajectories of future CO_2 emissions, with different effects on precipitation and temperatura (IPCC 2014). We also used two different Global Circulation Models (GCM; HadGEM2-ES and NorESM1-M) to consider other sources of uncertainty regarding the future climate of the study área (Kirkevåg *et al.* 2008, Real *et al.* 2010, Collins *et al.* 2011). This process resulted in eight sets of expected values of the climatic variables for each period of time.

Table 4.1. Variables used to model the Atlas Long-legged Buzzard distribution grouped by environmental factor. Exc. is the procedure that excluded the variable, being † Spearman's correlation value, * FDR analysis and ‡ step-wise selection process.

Code	Variable	*Exc.*	Source
Topography			
Alti	Altitude (m)	—	1
Slop	Slope (degrees)	*	2
Alti2	Altitude squared (m^2)	‡	2
Climate			
MeanTemp	Annual Mean Temperature (ºC)	—	3
DiTempRange	Mean Diurnal Temperature Range (ºC)	—	3
Isoth	Isothermally (%)	†	3
TempSeason	Temperature Seasonality (standard deviation)	*	3
MaxTemp	Max. Temperature of Warmest Month (ºC)	†	3
MinTemp	Min. Temperature of Coldest Month (ºC)	†	3
TempAnRange	Temperature Annual Range (ºC)	‡	3
TempWetQ	Mean Temperature of Wettest Quarter (ºC)	—	3
TempDryQ	Mean Temperature of Driest Quarter (ºC)	†	3
TempWarmQ	Mean Temperature of Warmest Quarter (ºC)	†	3
TempColdQ	Mean Temperature of Coldest Quarter (ºC)	‡	3
Prec	Annual Precipitation (mm)	—	3
PrecWetMonth	Precipitation of Wettest Month (mm)	†	3
PrecDryMonth	Precipitation of Driest Month (mm)	—	3
PrecSeason	Prec. Seasonality (coefficient of variation)	*	3
PrecWetQ	Precipitation of Wettest Quarter (mm)	†	3
PrecDryQ	Precipitation of Driest Quarter (mm)	†	3
PrecWarmQ	Precipitation of Warmest Quarter (mm)	†	3
PrecColdQ	Precipitation of Coldest Quarter (mm)	†	3

Data sources: 1 – (US Geological Survey 1996), 2 – calculated from *Alti* with ARCGIS software, 3 – (Hijmans *et al.* 2005).

4.2.4 Model for the present

We performed a logistic regression of the binary target variable on each environmental variable separately. This is a supervised machine learning approach that assesses the predictive power of each variable according to the significance (α) of the score test of the corresponding regression. Multicollinearity between these variables was reduced by calculating the Spearman correlation coefficients r between them. For each pair of variables with $r > 0.8$, only the one with the highest individual predictive power was retained (Fa *et al.* 2014). On the basis of this subset of predictors, the False Discovery Rate (FDR, Benjamini & Hochberg 1995) was evaluated to control the increase in type I errors (i.e. familywise error rate), and therefore the likelihood of obtaining false significant results when a large number of variables are used in the modelling process (García 2003). Using the Benjamini & Yekutieli (2001) procedure for all forms of dependency between test statistics, only variables significantly associated with the distribution of the subspecies with $\alpha < 0.05$ under an FDR value of 0.05 were accepted in subsequent modelling procedures.

A comprehensive model for the current probability of breeding at every OGU according to their climatic conditions was obtained by multivariate forward-backward stepwise logistic regression of the target variable on the remaining subset of predictors. This procedure starts with a model with no predictor variable (i.e. the null model), which yields a constant probability of breeding at each OGU equal to the prevalence of the OGUs where breeding was reported in the whole OGU dataset. Then, a significant combination of predictors (*y* or *logit*) is built by adding the variables that provide the most significant contribution to the model obtained in the previous step (Hosmer & Lemeshow 1980, 2000b). If no predictor variable significantly adds to the null model then no environmental model is produced. Variables with an overall, broad scale, predictive power are entered first in the modelling procedure, while those that add significant nuances to the previous model are entered in subsequent steps. To avoid redundancy, variables that do not significantly add to the predictive power of the final model are not included, as their effect, if any, is effectively included in the model via correlated variables.

The effect of prevalence on the resulting probability values was discounted to extract the pure response of the buzzard to environmental conditions (Maguire 1973, Gouveia *et al.* 2020). This was done by obtaining favourability values (*F*) using the equation (2) (Real *et al.* 2006).

$$F = \frac{e^y}{\frac{n_1}{n_0} + e^y} \qquad (2),$$

where n_1 and n_0 are the number of OGUs where breeding was reported or not reported, respectively, e is the Euler's number, and y is the logit resulting from the performed logistic regression.

Favourability values range from 0 (minimum favourability) to 1 (maximum favourability). A local favourability value of 0.5 indicates that the local probability of breeding of this subspecies is the same as its prevalence in the study area, i.e., is the probability expected by a null model unaffected by environmental predictors, where breeding is neither favoured nor unfavoured by the environment. Hence, favourability refers to the degree to which the environmental conditions favour the breeding of the subspecies (Acevedo & Real 2012, Muñoz *et al.* 2015a), being a favourability value of 0.5 the threshold separating favourable from unfavourable areas. However, given the continuous and fuzzy character of favourability (Acevedo & Real 2012), 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 2000a). Thus, we classified the areas into 'high favourability' ($F \geq 0.8$), 'intermediate favourability' ($0.2 < F < 0,8$), 'low favourability' ($0.00001 \leq F \leq 0.2$), and 'very-low favourability' ($F < 0.00001$) (Chamorro *et al.* 2019).

4.2.5 Model assessment

The relative weight of each variable in the final model was assessed using the Wald test (Wald 1943). The discrimination capacity of the resulting model was evaluated using the Area Under the Receiver Operating characteristic Curve (AUC) (Lobo *et al.* 2008, Romero *et al.* 2012), which has an associated significance value. We used Cohen's Kappa Index 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 (Kappa is described as the proportion of specific agreement, whose values range from –1 to +1) (Cohen 1960). As described by Fielding & Bell (1997) and Barbosa *et al.* (2013), we also 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), 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). Good classification performance is shown by high Kappa, sensitivity, specificity, and CCR values and low over- and under-prediction rate values. Model calibration was assessed using the Hosmer & Lemeshow (1980) test, where non-significant values ($p > 0.05$) indicate a good fit between predicted and observed probabilities (i.e. a well calibrated model). The test was performed by dividing the probability range of the model into 10 bins of equal range and checking that each bin included at least 15 OGUs and at least 5 OGUs in which reported breeding was expected in all of them, requirements that should be fulfilled for reliable model calibration (Hosmer & Lemeshow 1980). Good calibration is very difficult to obtain when there are many OGUs because small relative differences between observed and predicted probabilities generate significant values in the statistic (Hosmer & Lemeshow 1980).

We evaluated the current potential for dispersion of the Atlas Long-Legged Buzzard using the potential change factor (Pch) in OGUs with breeding. This factor is the ratio between the OGUs with favourability value higher than 0.5 and OGUs with reported breeding. Values lower or higher than 1 indicate higher or lower potential regarding the actual breeding distribution of the buzzard, respectively (Muñoz & Real 2006).

4.2.6 Projection to future climatic scenarios

Future climatic favourability values (F_f) were obtained by replacing in the *logit* (y) of equation (2) the present values of the climatic variables 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 buzzard breeding (Real *et al.* 2006). Thus, the favourability function is the membership function that assigns each OGU their degree of membership value (Real *et al.* 2006). The uncertainty of the ensemble forecasting at each OGU was computed as the difference at each OGU between the fuzzy union of the eight models (the maximum value of favourability of either of them at the OGU) and their fuzzy intersection (the minimum value of favourability of either of them at the OGU) (Romero *et al.* 2019).

4.2.7 Assessment of latitudinal variation

In biogeography, the barycentre (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 (Daget 1977, Gauch 1982, Real *et al.* 2001). When applied to geographic coordinates, the barycentre is indicative of the geographic centre of the distribution range (Antúnez & Mendoza 1992). The latitudinal barycentre of the OGUs with reported breeding of the Atlas Long-legged Buzzard (B_{bre}) was obtained as the arithmetic mean of the latitudinal values at the centre of the OGUs. For the present and future models, the latitudinal barycentres of climatic favourability (B_{F}) were obtained by weighting the latitude with the favourability using equation (3):

$$B_{\mathrm{F}} = \frac{\sum(La \times F)}{\sum F} \qquad (3),$$

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 barycentre was applied to the following OGUs: 1) those with reported breeding of the buzzard (B_{FB}), and 2) all those with reported breeding or otherwise within the longitudinal range where the subspecies was reported to breed (B_{FLo}). The climatic favourability barycentre was also calculated using the future ensemble forecasting models for 2041 to 2060 (B_{F60}) and 2061 to 2080 (B_{F80}).

The difference between the geographic and climatic latitudinal barycentres in the OGUs where the buzzard was reported to breed (B_{bre} and B_{FB}) represents the latitudinal disequilibrium (Ldis = $B_{FB} – B_{bre}$) between current climatic favourability for breeding and the actual breeding areas. This latitudinal disequilibrium is northward if $B_{FB} > B_{bre}$, southward if the $B_{FB} < B_{bre}$ or in equilibrium if $B_{FB} = B_{bre}$. The difference between the latitudinal climatic favourability barycentre at present inside 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 forecasted to shift between the two periods. This shift is predicted to be northward if the barycentre for the future has a higher value than the present one. Similarly, we computed the difference between the latitudinal climatic favourability barycentres for the periods 2041 to 2060 and 2061 to 2080 ($B_{F80} – B_{F60}$). We obtained two average rates of latitudinal climatic Favourability Displacement (FD_{20-60} and FD_{60-80}, respectively) by dividing these distances by the number of years between the periods compared: that is, the years from 2020 until the end of the period 2041 to 2060 (40 years) and from 2060 until the end of the period 2061 to 2080 (20 years), 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 computed in latitudinal degrees and subsequently converted into kilometres considering the equivalence of the latitudinal degree at the equator (111.12 km).

4.2.8 Fuzzy logic assessment of other expected breeding distribution changes

Four fuzzy logic operations were used to forecast other impacts of climate change on Atlas Long-legged Buzzard climatic favourability (Real *et al.* 2010). These operations measure the increment in favourability (*I*), favourability overlap (*O*), favourability maintenance (*M*), and the predicted shift in favourability (*S*) in relation to the present (Real *et al.* 2010). Thus, they are collectively known as the IOMS framework (equations 4, 5, 6 and 7) (Kou *et al.* 2011):

$$I = \frac{c(F_f) - c(F_p)}{c(F_p)} \, (4), \qquad O = \frac{c(F_f \cap F_p)}{c(F_f \cup F_p)} \, (5), \qquad M = \frac{c(F_f \cap F_p)}{c(F_p)} \, (6),$$

$$S = \frac{Min[c(F_p) - c(F_f \cap F_p),\ c(F_f) - c(F_f \cap F_p)\,]}{c(F_p)} \qquad (7),$$

where c(*X*) is the cardinality of the fuzzy set *X*: that is, the sum of the degrees of membership of all the OGUs (i.e. favourability values) in the fuzzy set *X*, which is a measure of the size of the fuzzy set; F_p and F_f are the fuzzy sets of present and future favourable areas for the buzzard, respectively; $F_f \cap F_p$ is the fuzzy intersection between future and present favourability defined by the minimum of the two favourability values in each OGU, representing the present climatic favourability conditions that are expected to persist in the future; $F_f \cup F_p$ is the fuzzy union between future and present favourability, defined by the maximum of the two favourability values in the OGU; and Min is the minimum of the two values in square brackets. Positive values in I indicate a gain in overall climatically favourable areas, whereas negative values indicate a net loss of climatic favourability. O, M, and S range from 0 to 1. O values closer to 1 are obtained when a large proportion of favourable areas are shared in the present and future models, whereas a value of zero indicates total separation between climatically favourable areas at present and in the future. An M value of 1 indicates that the present favourable areas will be completely maintained in the future projections. The lower the M values the less the currently favourable areas are going to remain climatically favourable. Values of S indicate the degree to which the loss of presently favourable areas is expected to be replaced by other new favourable areas elsewhere.

4.3 RESULTS

The climatically favourable areas for the Atlas Long-legged Buzzard include Northern Africa, Sicily, the Middle East, and the Southwest of the Iberian Peninsula. The latter area is the only continental European region where the climate is highly favourable (Figure 4.2). In Africa, highly favourable areas are located in Morocco, the Mediterranean coasts of Algeria, Tunisia, Egypt, and two inland areas of Algeria (Tassili n'Ajjer national park and El Menia oasis) (Figure 4.2). In the Middle East, favourable areas are in the margins of the Mediterranean and Caspian seas, the Arabian Peninsula, Cyprus, Iran, and Turkey. These areas are currently occupied by its sister subspecies, the Asian Long-legged Buzzard (Figure 4.1A and Figure 4.2).

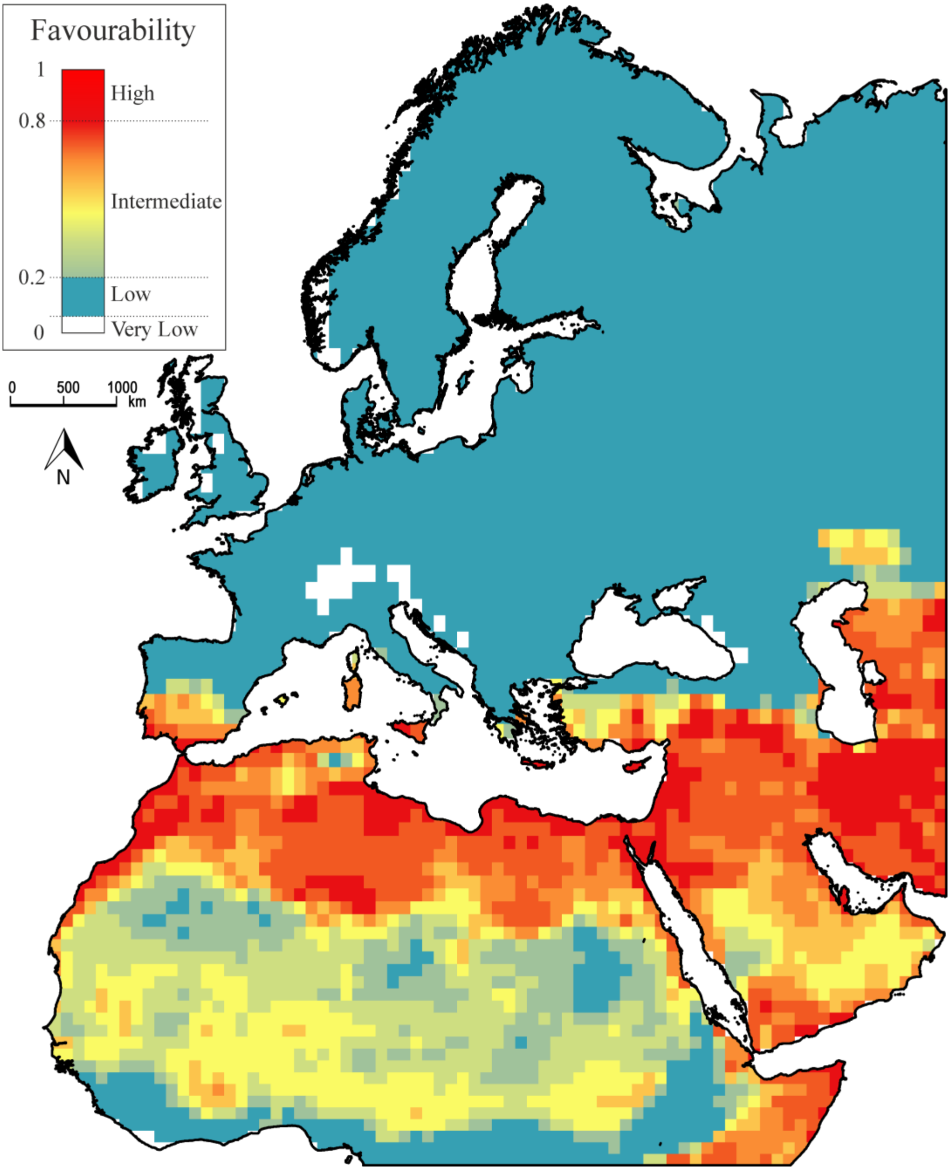


Figure 4.2. Cartographic representation of the current climatic favourability for Atlas Long-legged Buzzard breeding in each OGU of the study area. The mathematical model is shown in Table 4.2.

Table 4.2. Variables entered in the logistic regression model by the forward-backward step-wise selection process, ranked by their order of entrance. β 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 p the significance of the coefficients. Codes of the variables are the same as in Table 4.1.

Variable	**β**	**Wald**	***p***
PrecDryMonth	–0.2199	29.406	5.86×10^{-08}
TempWetQ	–0.1212	34.327	4.65×10^{-09}
DiTempRange	–0.4175	44.148	3.04×10^{-11}
Prec	0.0013	13.103	2.94×10^{-04}
MeanTemp	0.0980	7.874	5.01×10^{-03}
Alti	0.000477	5.603	1.79×10^{-02}
Constant	3.4712	20.707	5.35×10^{-06}

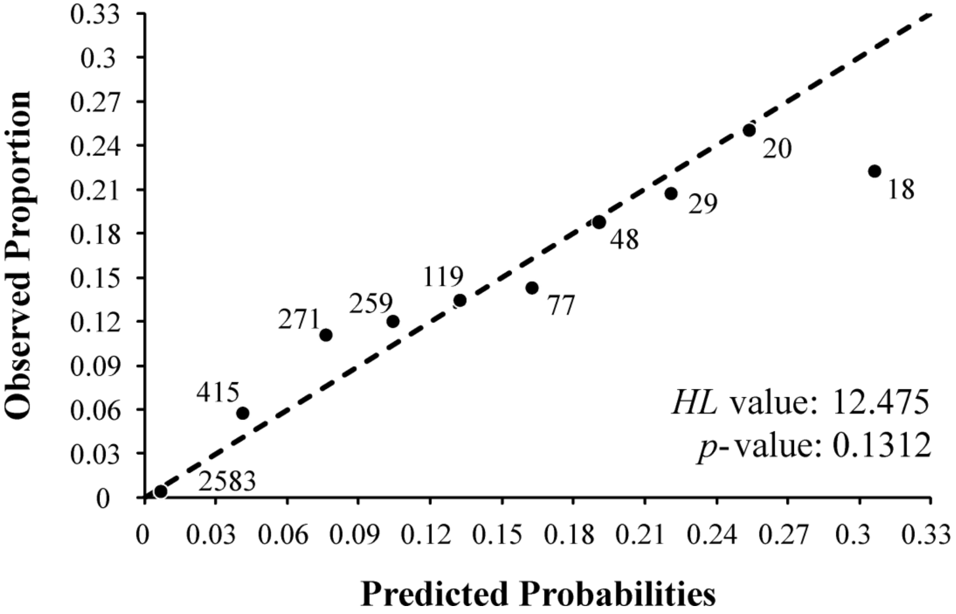


Figure 4.3. Graphic representation of the Hosmer and Lemeshow test values for each bin, with the number of cases at each bin.

Table 4.3. Assessment indices: Prevalence of the model (n_1/n), area under the curve (AUC), Cohen's Kappa, sensitivity, specificity, correct classification rate (CCR), under-prediction rate (UPR), over-prediction rate (OPR), and factor of potential change (Pch).

Index	Value	Index	Value	Index	Value
Prevalence	0.03701	Sensitivity	0.90411	UPR	0.00496
AUC	0.86542	Specificity	0.73941	OPR	0.88235
Kappa	0.15271	CCR	0.74550	Pch	7.68493

The climatic favourability model included six variables (Table 4.2). A small diurnal temperature range, cool temperatures during the wettest season, and scarce precipitation in the driest month are the most favourable conditions for Atlas Long-legged Buzzard breeding because these variables were the first to be entered in the stepwise procedure. In addition, under the Wald test, these variables have the most weighting in the model (Table 4.2).

The calibration test (Figure 4.3) showed that differences between expected and predicted values were nonsignificant ($p > 0.05$) over the whole range of expected probability values. The model had high classification power (Table 4.3), higher sensitivity than specificity, and a high over-prediction rate (OPR > 0.8). Discrimination capacity was high (AUC > 0.8) and highly significant ($p = 6.516 \times 10^{-51}$). The Pch value of the model was remarkably high (Table 4.3).

Figure 4.4 shows the ensemble forecasting for all possible future climatic scenarios for each period of time. Although forecast favourable areas did not differ substantially between the two periods of time, they differed from the present climatic favourability pattern. Current breeding areas in North Africa are expected to have lower favourability values in the future, but other areas are expected to increase their favourability values in Sicily, Sardinia, and the Iberian and Arabian peninsulas (Figure 4.2 and Figure 4.4).

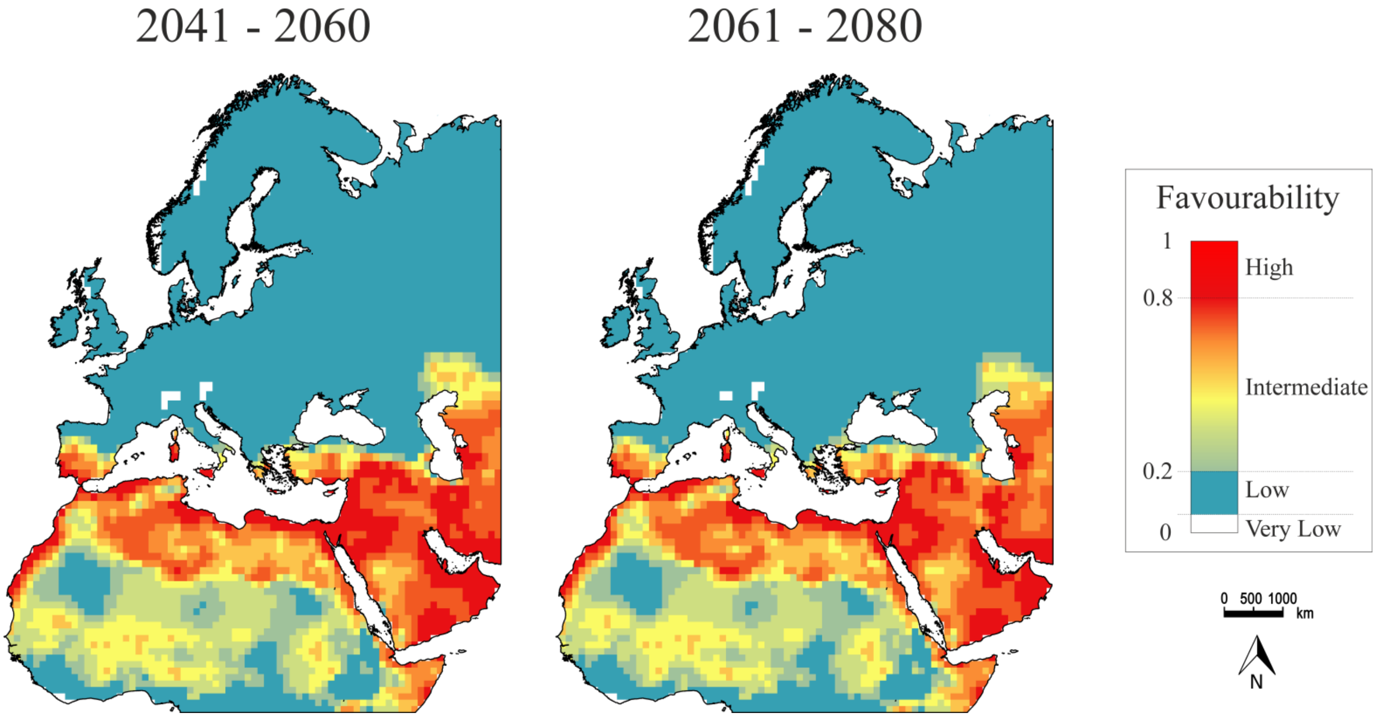


Figure 4.4. Atlas Long-legged Buzzard ensemble climatic favourability models for future periods of time.

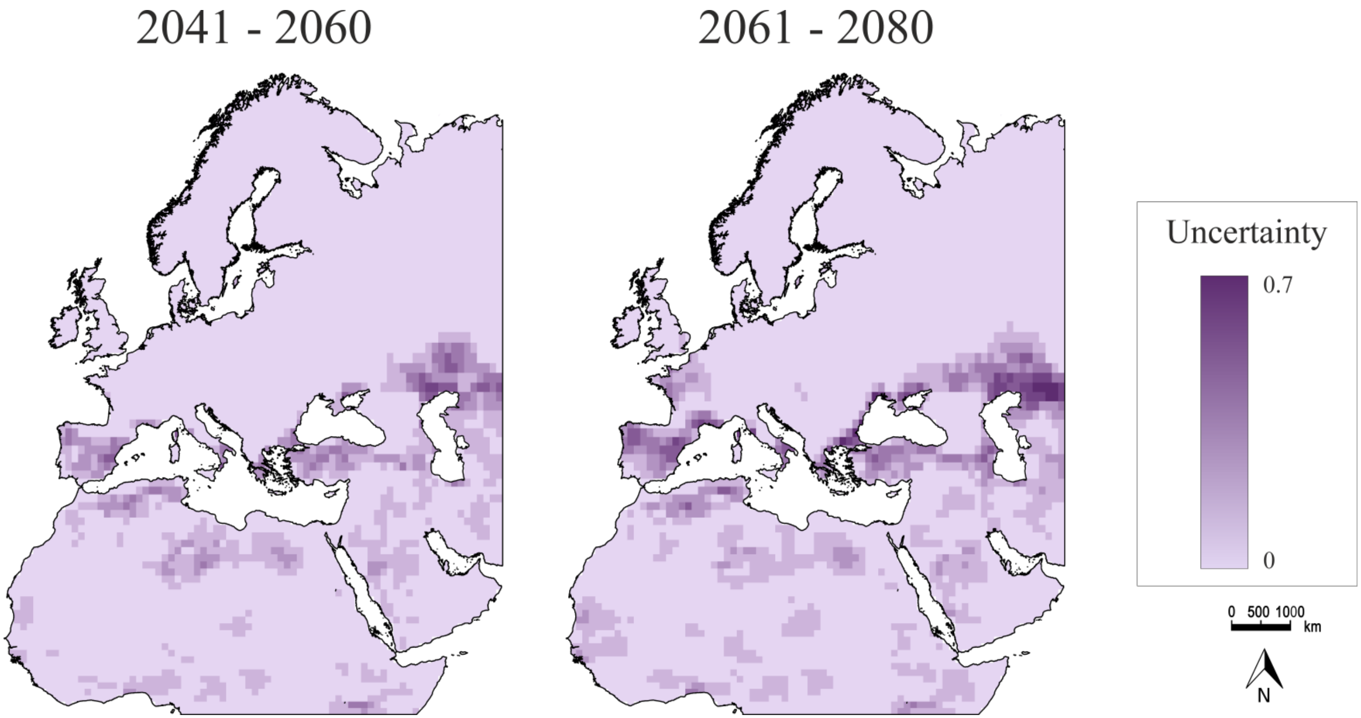


Figure 4.5: Climatic uncertainty for each period of time, associated with the different climate change scenarios analysed.

Figure 4.5 shows the uncertainty values associated with climate scenarios, showing a low mean uncertainty of less than 0.1. For the period 2061 to 2080, there is an increase in uncertainty values in some areas, such as on the Atlantic coast of France and the northern coast of the Black Sea, where in the period 2041 to 2060 the uncertainty values are much lower. The highest uncertainty values are in the northern half of the Iberian Peninsula, the northern edge of the Caspian Sea, the coast of the Balkan Peninsula, and Turkey, particularly for the period 2061 to 2080. Low uncertainty values are found in the south of the Iberian Peninsula and the coasts of north-western Africa.

Table 4.4 shows the results of the barycentre analysis. A northward disequilibrium of 0.039 degrees of latitude was detected between the latitudinal barycentre and the climatic favourability barycentre of the OGUs with reported breeding of the buzzard. A latitudinal degree is roughly equivalent to 111.12 km, and so this disequilibrium was equivalent to 4.3 km. Applying the same equivalence, the $FD_{20\text{-}60}$ rate value was 1.3 km/year. If this rate is assumed to be similar to the current one, then the latitudinal disequilibrium of 4.3 km between distribution and climatic favourability is equal to a temporal disequilibrium of a little more than 3 years. The $FD_{60\text{-}80}$ value was lower at 0.6 km/year.

Table 4.5 shows the fuzzy logic indicators of other expected effects of climate change for each possible scenario and the ensemble forecast at each period of time. Increment values are low ($I < 0.08$) but generally positive: however, some negative values are expected in lower CO_2 emissions scenarios (2.6, 4.5, and 6.0). Overlap values of present and future favourable areas are high ($O > 0.78$). Maintenance values for currently favourable areas are not expected to be complete (0.92 at most) although they are generally high (M > 0.87). In all cases, shift values are lower than 0.11 but higher than 0.08, indicating that between 8% and 11% of currently favourable areas for breeding are expected to be lost but could be replaced by new opportunities for breeding in emergent favourable areas elsewhere.

Table 4.4. Results of the latitudinal variation assessment in decimal degrees. Latitudinal barycentre of the actual breeding area (B_{bre}). Latitudinal climatic favourability barycentres of the OGUs with reported breeding of the buzzard (B_{FB}), latitudinal climatic favourability barycentres of the OGUs inside the longitudinal range, where the subspecies was reported to breed, for the current model (B_{Lo}), and the 2041-2060 (B_{F60}) and the 2061-2080 (B_{F80}) future ensemble forecasting models. 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.

Measure	Value
B_{bre}	29.706
B_{FB}	29.745
B_{FLo}	25.388
B_{F60}	25.868
B_{F80}	25.971
Ldis	0.039
FD_{20-60}	0.012
FD_{60-80}	0.0051

Table 4.5. Fuzzy logic indicators of the impact of climate change for each Global Circulation Model (GCM) and Representative Concentration Pathway (RCP) and the ensemble forecasting at each period of time: Increment (*I*), Overlap (*O*), Maintenance (*M*), Shift (*S*) and the cardinality of the favourability values for the future ($c\text{F}_f$).

Time	GCM	RCP	I	O	M	S	cF_f
2041 – 2060	HadGEM2–ES	2.6	–0.00198	0.818	0.899	0.0988	1225.341
		4.5	0.0260	0.815	0.910	0.0903	1259.751
		6.0	0.00871	0.822	0.906	0.0938	1238.474
		8.5	0.0470	0.816	0.920	0.0804	1285.514
	NorESM1–M	2.6	0.00845	0.817	0.903	0.0966	1238.160
		4.5	–0.00265	0.804	0.890	0.1071	1224.520
		6.0	–0.000816	0.807	0.893	0.1063	1226.776
		8.5	0.0251	0.808	0.905	0.0947	1258.708
	Ensemble		0.0137	0.821	0.908	0.0920	1244.647
2061 – 2080	HadGEM2–ES	2.6	–0.0155	0.821	0.895	0.0895	1208.728
		4.5	0.0213	0.807	0.903	0.0972	1254.035
		6.0	0.0190	0.808	0.902	0.0978	1251.171
		8.5	0.0783	0.785	0.914	0.0859	1324.008
	NorESM1–M	2.6	–0.0279	0.817	0.887	0.0852	1193.483
		4.5	–0.0189	0.804	0.883	0.0979	1204.510
		6.0	–0.0239	0.799	0.878	0.0983	1198.398
		8.5	0.01146	0.801	0.896	0.1042	1245.755
	Ensemble		0.00589	0.815	0.901	0.0994	1235.002

4.4 DISCUSSION

Five of the six significant predictive variables included in the favourability model were associated with climate (Table 4.2). In addition, the only non-climatic variable, altitude, was the last to be included in the model, suggesting a finer-scale effect. It also had the lowest weight in the model under the Wald test (Table 4.2). Consequently, the favourability model can be rightly considered to be a climatic favourability model. The requirements of this buzzard are matched with Mediterranean climatic conditions (Chamorro *et al.* 2017) as shown by the concentration of highly favourable areas for breeding in the Mediterranean basin and the generally low climatic favourability values in the European continent, which are especially low in the Alps, the Caucasus Mountains, and the British and Norwegian coasts. The main favourable climatic conditions are stability in daily temperatures, low temperatures during the wettest season, and low precipitation during summer (Table 4.2). The positive coefficient associated with altitude (Table 4.2) may be due to the fact that this species mainly nests in cliffs (Thévenot *et al.* 2003). However, in the Iberian Peninsula it nests in trees (Elorriaga & Muñoz 2010, 2013), which shows the plasticity of the species when choosing a nesting substrate. Such plasticity has also been demonstrated for other species (Muñoz *et al.* 2015b). This variable could also be indicative of climatic conditions that are closely correlated with altitude (Muñoz *et al.* 2005).

As our models were based on fuzzy set theory, they were able to measure the spatial and temporal disequilibrium between the buzzard breeding area and the climatic favourability for breeding. The mean climatically favourable condition occurs 4.3 km northwards of the mean latitudinal range of the buzzard breeding areas. The mere existence of this spatial disequilibrium demonstrates that, in order to be sound, favourability distribution models do not have to assume that the species must be in equilibrium with their environment, as models based on niche theory have customarily assumed (Guisan & Zimmermann 2000, Guisan & Thuiller 2005). In fact, a spatial disequilibrium is needed for the climatic conditions of the favourable areas to attract the buzzard and lead to changes in its breeding range (Acevedo & Real 2012, Real *et al.* 2017, Gouveia *et al.* 2020). The $FD_{20\text{-}60}$ value suggests that the buzzard range is not in temporal equilibrium with the current climate by a margin of about 3 years. This result suggests that, if climatic conditions stop changing, the buzzard range could attain equilibrium with the climate in approximately 3 years. 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 to 0.6 km/year from 2060 to 2080, suggesting that the colonization of the Western Palearctic will decelerate according to current climatic projections.

Fuzzy logic operations (IOMS framework, Table 4.5) indicate that the climatic favourability for the Atlas Long-legged Buzzard is shifting rather than broadening. An initial indicator of this change is that the Increment values are low and even negative in some cases. This result would not be expected if the expansion of the range was northward, as this would include the maintenance of favourable areas in their southern range and the addition of new favourable areas in the north (Thomas &

Lennon 1999). Maintenance values of only about 90% are mainly explained by the favourability loss in the southern limit of the current distribution, as in the Sahel region (Figure 4.4). However, the main indicator is that the Shift values are more than zero, and practically identical to the part of the current favourability area that is not expected to be maintained (Table 4.5). This result indicates that the loss of climatically favourable areas in the south are expected to be compensated for by the appearance of new favourable areas in the north, particularly in the coast of northern Morocco, the southern half of the Iberian Peninsula, as other study previously stated (Chamorro *et al.* 2017), and the Mediterranean islands of Sardinia and Sicily (Figure 4.4). This loss may effectively push the breeding distribution of the buzzard northward. High Overlap between present and future climatic favourability models indicates that the current and expected favourable areas are geographically close (Real *et al.* 2010), which could facilitate the movement of buzzards to the newly available zones that are currently unoccupied. There is a high degree of similarity between all predicted future scenarios. The forecasts for the 2061 to 2080 period have the highest uncertainty, which is normal when the forecast time period is further away from the present (IPCC 2014).

It should be noted that the Asian Long-legged Buzzard is currently occupying areas in the Middle East that have been identified as highly favourable for the Atlas Long-legged Buzzard (Cramp 1992). This situation is likely preventing the establishment of the Atlas Long-legged Buzzard because of possible competitive exclusion (Hardin 1960, Waters *et al.* 2013, Jowers *et al.* 2019). It may also be the main reason for the high over-prediction rate and high Pch of the climatic favourability model for the Atlas Long-legged Buzzard (Table 4.3 and Figure 4.2), and that the range shift is more likely to be northwards rather than eastwards. This forecast is supported by empirical data, such as the increasing number of records of the Atlas Long-legged Buzzard in northern Spain (Gutiérrez *et al.* 2012, 2013, Gil-Velasco *et al.* 2019) and Portugal (Jara *et al.* 2010) and its successful breeding since 2009 in the south of the Iberian Peninsula (Elorriaga & Muñoz 2010).

However, other factors could interfere in the northwards colonization process, by delaying or even stopping the Atlas Long-legged Buzzard dispersion. For instance, hybridization with the Common Buzzard (*B. buteo*) has already been detected in Pantelleria Island (Italy) and southern Spain (Corso 2009, Elorriaga & Muñoz 2013). These areas represent new contact zones where these closely related species currently meet. Hybridization in these areas is favoured because the Atlas Long-legged Buzzard is currently rare and, hence, its choice of mate is restricted. If the offspring were infertile, hybridisation would be acting as a synecological barrier against the expansion of the Atlas Long-legged Buzzard into Europe (Väli *et al.* 2010, Elorriaga & Muñoz 2013). Thus, some new climatically favourable areas could remain unoccupied by the Atlas Long-legged Buzzard in the future. It is therefore relevant to track its northward expansion into Europe by monitoring favourable areas on the distribution fronts, such as the Strait of Gibraltar, and in those areas detected as highly favourable in this study.

Many other African birds have already experienced or are currently experiencing a similar expansion pattern in the Iberian Peninsula. Some examples are the White-rumped Swift (*Apus caffer*), the Little Swift (*Apus affinis*), and the Common Bulbul (*Pycnonotus barbatus*), which is the most recent addition to the European avifauna and is already breeding (del Junco & González 1969, Ferrero 1996, Ramírez *et al.* 2002, Chamorro *et al.* 2017). Moreover, in the last decade, there has been an increasing number of reports of other African birds such as Rüppell's Vulture (*Gyps rueppellii*), Lanner Falcon (*Falco biarmicus*), Cream-coloured Courser (*Cursorius cursor*), Moussier's Redstart (*Phoenicurus moussieri*), and House Buntings (*Emberiza sahari*) (Copete *et al.* 2015, Chamorro *et al.* 2016, Gil-Velasco *et al.* 2019, Molina *et al.* 2019). Other species, such as the White-backed Vulture (*Gyps africanus*) and Bateleur (*Terathopius ecaudatus*) have also been recently reported in Europe for the first time (Dies *et al.* 2010, Copete *et al.* 2015). These reports may indicate that European Mediterranean areas, and particularly the Iberian Peninsula, should be prepared for the establishment of new African fauna in the near future.

These species could use these areas as stepping stones to expand into the rest of Europe. For example, this pattern was followed by the Black-shouldered Kite (*Elanus caeruleus*), which started breeding in Tarifa (southern Spain), then moved northwards, and became established in France in 2013 (Ferrero 1996, Ferrero & Onrubia 2004, Balbontín *et al.* 2008, Logeais 2015). Some typical Mediterranean birds are also moving northwards and reaching Central Europe, where they are breeding for the first time. This is happening, for example, in Switzerland, where typical Mediterranean species, such as the Short-toed Snake-eagle (*Circaetus gallicus*) and the European Bee-eater (*Merops apiaster*) have settled recently and experienced population growth (Knaus *et al.* 2018).

These observations indicate that a change in species composition is already occurring in Western Europe due to climate change.

Favourability models have proven to be useful tools to identify new potential areas for the arrival and establishment of new individuals in the near future (Muñoz & Real 2006, Pulido-Pastor *et al.* 2018). The practical usefulness of these tools must be coupled to a sound theoretical background (Niamir *et al.* 2019). Our results reflect the interaction between the Atlas Long-legged Buzzard and its environment within a dynamic biogeographic framework. The favourability function is well established in fuzzy set theory and it also represents the response function of the species to the environmental conditions (Muñoz *et al.* 2005, Real *et al.* 2009, Barbosa & Real 2012, Muñoz & Real 2013). This aspect may constitute a contact point between fuzzy set theory and niche theory. In our view, this contact point requires adding notions of graduality to the niche concept, such as those included in the Maguire (1973) niche concept (Gouveia *et al.* 2020). More theoretical work is needed on the relationships between fuzzy set theory and niche theory. This would allow forecasting that is simultaneously practical and theoretically comprehensive and, thus, useful for conservation management and the scientific understanding of the biogeographic processes underlying the species response to climate changes.

CAPÍTULO 5

ÁREAS DE INVERNADA EN MOVIMIENTO FRENTE A LOS INVIERNOS MÁS CÁLIDOS

WINTERING AREAS ON THE MOVE IN THE FACE OF WARMER WINTERS

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

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 Ornithologica*. **53**(1): 61–68.

Chamorro, D., Nieto, I., Real, R. & Muñoz, A.-R. 2019. Wintering areas on the move in the face of warmer winters. *Ornis Fennica*. **96**: 41–54.

5 WINTERING AREAS ON THE MOVE IN THE FACE OF WARMER WINTERS

5.0 RESUMEN

Durante las últimas décadas se han detectado cambios en la fenología de las especies migradoras y en la distancia de su migración. El Carricero Común *Acrocephalus scirpaceus* es una especie típicamente transahariana que ha sido recientemente registrada en invierno en la península ibérica. En este capítulo se recopiló toda la información disponible de los anillamientos y recuperaciones de esta especie en invierno en la península ibérica, para posteriormente investigar la influencia del clima en su invernada mediante la modelización biogeográfica. Así, se detectaron las zonas más favorables para su invernada y se identificaron los factores ambientales que explican esta distribución. Algunos de los carriceros ibéricos fueron encontrados invernando cerca de sus zonas de cría, lo que parece indicar un proceso de sedentarización. Por otro lado, las aves de las islas británicas se encontraban invernando más al norte que las procedentes de centro Europa, y las que venían del este europeo se encontraban en la costa del Mediterráneo. La presencia de inviernos suaves resulta ser el factor más relevante en la selección de los sitios adecuados para la invernada de esta especie en Europa. Éstos están situados en las costas meridionales y orientales de la península ibérica y en algunos lugares de la costa atlántica septentrional de España. El análisis de la tendencia espacial parece indicar la orientación de las principales rutas de migración de la especie desde sus zonas de cría hasta las de invernada mientras que el factor topográfico se asocia a una selección de hábitat a escala fina. Como el caso del Carricero Común no es único, los resultados muestran el papel de la península ibérica como un nuevo lugar de invernada para las especies insectívoras que suelen invernar en la región subsahariana, modificando así su estrategia de migración de aves transaharianas a presaharianas, y también señalan que el reciente aumento de la temperatura invernal es el principal causante de este fenómeno.

5.0 ABSTRACT

For several decades, there have been changes in the bird migration. The Eurasian Reed Warbler *Acrocephalus scirpaceus* is a Trans-Saharan migratory species, which has been recorded recently wintering in the Iberian Peninsula. This chapter compiled all the available information on the ringing and recovery data of this species in the Iberian Peninsula in winter, in order to later investigate the influence of climate through biogeographical modelling. The model was constructed to identify the most favourable areas in Iberia and the most relevant explanatory factors of this distribution. Some Iberian birds wintered in breeding areas, or nearby, which could indicate a potential process of sedentarization. British Eurasian Reed Warblers winter in Iberia more northerly than individuals from Central Europe, and Eastern birds show a tendency to winter on the Mediterranean coast. The minimum winter temperature is the most relevant factor affecting sites suitable for the wintering of this species in Europe. The best areas are located in the southern and eastern coasts of the Iberian Peninsula and in some locations on the northern Atlantic coast of Spain. Spatial trends analysis suggested the orientation of the flight paths of the species from their breeding areas to their wintering areas. Topography refined the model in that it is associated with habitat selection at a fine-scale. As the case of the Eurasian Reed Warbler is not unique, the results show the role of the Iberian Peninsula as a new wintering site for species usually wintering in the sub-Saharan region, modifying their wintering strategy from Trans-Saharan to Pre-Saharan migrants, and whether the recent increase in temperature is the main cause.

5.1 INTRODUCTION

Bird migration is an evolutionary adaption for finding sites with sufficient availability of resources during the non-breeding season to ultimately increase survival and breeding competence (Newton 2008). Besides the natural learning of juveniles from experienced individuals (Flack *et al.* 2018), the onset of migration, physiological adaptions, and the characteristics of migration (orientation, time, distance, stopovers, etc.) have a genetic basis (Berthold & Querner 1981, Berthold 1988, 1991, Berthold *et al.* 1992, Gwinner 1996). However, environmental changes can affect this genetic influence, allowing the species to modify their migratory behaviour according to the current conditions (Berthold & Querner 1981, Berthold 1988, Berthold *et al.* 1992, Ogonowski & Conway 2009). This flexibility imparts a variable response that ultimately benefits the persistence of the population if environmental conditions change in a brief period of time (Charmantier & Gienapp 2014). Individuals have two types of response mechanisms to the environment over the short term: the microevolutionary response to natural selection (Berthold *et al.* 1992, Berthold & Querner 1995, Pulido *et al.* 2001), and phenotypic plasticity (Charmantier *et al.* 2008, Charmantier & Gienapp 2014). The former mechanism is a 'non-labile' trait that is stable during the individual's lifetime, whereas phenotypic plasticity is mainly 'labile', changing repeatedly in order to fit the new environmental conditions, such as the behavioural or 'individual' plasticity (Charmantier & Gienapp 2014), but that also could be stable during an individual's lifetime if conditions maintain (Charmantier *et al.* 2008). These traits could influence the population distribution range or migration behaviour if individuals alter their phenology in response to environmental shifts, such as climate-driven changes (Huntley *et al.* 2006, Lehikoinen & Sparks 2010, Massimino *et al.* 2015, Potvin *et al.* 2016).

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

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

The winter survival of insectivorous species depends on the abundance of flying insects during the whole season, which is associated with mild temperatures (Lewington 2006). The Eurasian Reed Warbler, therefore, must have sufficient resources in some areas of the Iberian Peninsula to survive during winter, which would increase the wintering population size if these conditions persist. Based on this idea, our first aim is to demonstrate that the Eurasian Reed Warbler has become a regular wintering species in the Iberian Peninsula. To do that, we compiled wintering ringed records of the Eurasian Reed Warbler from Portugal and Spain with the information related to their ringing origin, distance of migration and spatial distribution. Then, we hypothesise that these birds have more suitable areas for their wintering in the Iberian Peninsula than they actually occupy based on the previous wintering distribution, and therefore, an increment in wintering populations is possible. To demonstrate this, we characterized the areas in which this trans-Saharan migrant currently winters by means of species distribution models, and identified areas with similar environmental conditions which could be wintering sites in the near future, as the modelling methodology could predict occupancy in a short-term future (Muñoz, A.-R., Carrasco, E. & Real, R. *in prep.*). Bearing in mind that these environmental conditions could directionally shift due to climate change, we also assessed the relevance of climate on the selection of the wintering sites. This study provides information of the current status and the future of the European populations of this species, which is an example of all Trans-Saharan migrants which are currently changing their phenology and wintering distribution.

5.2 METHODS

5.2.1 Study area

The study area was the Iberian Peninsula and the Balearic Islands (SW Europe). The Iberian Peninsula is a region with heterogeneous physiography and climate and covers nearly 600000 km^2. The Balearic archipelago covers almost 5000 km^2 and is located in the western Mediterranean Sea.

According to Font (2000), the study area can be divided into three climatic regions: Mediterranean, Atlantic, and Interior. The Mediterranean region includes the Balearic Islands and the southern and eastern strips of mainland Spain and is characterised by its hot and dry summers and mild winters. Mediterranean coasts have mild temperatures due to their regulation by the Mediterranean Sea. Winter temperatures range from 6 °C to 10 °C and barely reach an absolute minimum temperature of –7 °C in the North and –2 °C in the South. Some of these coasts, especially those in the provinces of Malaga and Granada, have special frost-free micro-climates that can support tropical fruit-tree crops such as avocados, papayas, mangos, and custard apples (Botas 2017). The Atlantic region includes northern and western Spain and Portugal and has mild-cold winters, cool summers, and abundant regular precipitation. Between Lisbon in Portugal and Galicia in Spain, the mean minimum temperature on the coast ranges between 5 °C to 11 °C, although the absolute minimum temperature can reach –7 °C. On the Spanish North Atlantic coast, the mean minimum temperature is around 6 °C, although oscillations are narrower because of the influence of the warmer water of the Bay of Biscay (Anadón *et al.* 2009). The interior region includes central mainland Spain, which has high temperatures in summer but low ones in winter because of irregular and scarce precipitation and the absence of sea influences. The absolute winter temperature can reach –15 °C in some regions and average minimum temperatures ranges between –2 °C to 8 °C. Topography has a marked influence on reducing the severe temperatures in the largest river valleys.

5.2.2 Species and distribution data

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

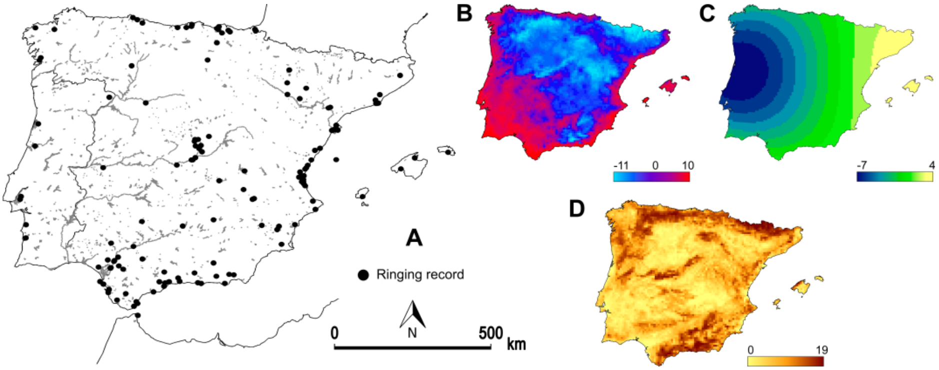


Figure 5.1. (A) Spatial distribution of all records of Eurasian Reed Warblers (black dots, $n = 414$) found during the strict wintering season (15 Nov. –31 Jan.) in the Iberian Peninsula, and the distributions of the mean winter minimum temperaturas **(B)**, spatial trend-surface analysis **(C)**, and slope **(D)** in the Iberian Peninsula and Balearic Islands.

The database of wintering ringing records was built with data from 1959 to 2015 provided by the Centro de Migración de Aves (CMA) of the SEO/BirdLife, the Ringing Office of the Society of Sciences Arantzadi (OAA) for the Spanish area and the Central Nacional de Anilhagem/CEMPA (ICNF) for the Portuguese territory. Ringing-recovery data were provided by EURING (www.euring.org). To avoid including data of early and late migrants, we only selected those records between the 15th November and 31st January, period considered as strictly wintering (Cramp 1992). To focus on wintering individuals we selected individuals in healthy conditions and with a ±1 week of precision in recoveries at the most, following more restrictive criteria than European Bird Census Council (https://www.ebcc.info/). Ringing on bad weather days is unusual, so these records cannot be attributed to aberrant individuals due to storms. For every bird we got information related to the specific location and date of ringing and/or recovery records. We considered as ‘breeders’ those birds that were ringed as adults in the previous reproductive season they were recovered, between May and July. We built the origin-destiny map plotting the positions of ringing and recoveries data.

To model the wintering distribution of the Eurasian Reed Warbler, a subset of ringing/recovery record from the previous database were selected for the period 1990-2015 (Figure 5.1A), imparting a contemporary connotation to the model. Sampling effort is one of the most relevant drawbacks of this type of data. For this reason, the presence and absence of the species was mapped using 10×10 km UTM grid cells of the Iberian Peninsula and Balearic Islands ($n = 5791$) to obtain favourability models, which mitigate the effect of prevalence and the false-absences (Acevedo & Real 2012).

5.2.3 Predictor variables

A set of 21 environmental variables related to spatial location, topography, and climate was used to identify the factors that influence the Eurasian Reed Warbler wintering in the Iberian Peninsula and Balearic Islands (Table 5.1). Topography and climate data were obtained by averaging the 1 km^2 pixel values obtained from the digitized variables in the 10×10 km UTM squares (i.e. Figure 5.1B & C), as described in Muñoz *et al.* (2005, 2015a). Climate data has average monthly precipitation and temperature data for 1971 to 2000 (AEMET 2011) which was the source with the highest resolution and reliability for the Iberian Peninsula. Using the spatial location variables of latitude (*La*) and longitude (*Lo*), we conducted a polynomial trend-surface analysis (Legendre & Legendre 1998), including the square and cube units and the interactions between them (i.e., La^2, Lo^2, La^3, Lo^3, $La \times Lo$, $La^2 \times Lo$, $La \times Lo^2$), that we used as a new variable (*Spat*) which describe more complex patterns (Legendre 1993). Thus, we attempted to show geographical trends in species distribution associated with historical events, migration routes, or species population dynamics (Figure 5.1D) by simultaneously assessing the climatic conditions in the context of spatial influences (Real *et al.* 2003, Márquez *et al.* 2004).

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

Table 5.1. Environmental variables used to model the distribution of Eurasian Reed Warblers grouped by their environmental factor. Variables marked with (*) had fulfilled the False Discovery Rate (FDR) and Spearman correlation criteria; Variance inflation Factor (VIF) values are showed for these variables.

Code	Variable	VIF	Source
Topography			
Alti	Altitude (m)		1
* *Slop*	Slope (degrees)	1.765	1
AltiR	Altitudinal range		1
SE	Southward exposure degree		2
WE	Westward exposure degree		2
Spatial Situation			
Lati	Latitude (degrees N)		3
Long	Longitude (degrees E)		3
* *Spat*	Trend-surface analysis (see Methods)	2.229	3
Climate			
* *Prec*	Mean winter precipitation (mm)	22.411	4
Tm	Mean winter temperature (°C)		4
* *Tn*	Mean winter minimum temperature (°C)	2.187	4
Tx	Mean winter maximum temperatures (°C)		4
* *DP01*	Days with precipitation ≥ 0.1 mm in winter	7.682	4
DP1	Days with precipitation ≥ 1 mm in winter		4
DP10	Days with precipitation ≥ 10 mm in winter		4
* *DP30*	Days with precipitation ≥ 30 mm in winter	12.156	4
D0T	Days with minimum temperature ≤ 0 °C in winter		4
* *DIS*	Winter direct irradiance at surface (kwhm^{-2}day^{-1})	3.451	4
SIR	Winter surface incoming radiation (kwhm^{-2}day^{-1})		4
PET	Mean annual potential evapotranspiration (mm)		4
AET	Mean annual actual evapotranspiration (mm)		4

Data sources: 1 – (US Geological Survey 1996), 2 – based on the DEM in Farr & Kobrick (2000), 3 – (IGN 1999), 4 – (AEMET 2011).

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

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

5.2.4 Statistical analysis

Logistic regression analysis was used to model the winter occurrence data based on presences-absences in the 10 × 10 km UTM grid cells. Logistic regression analysis yields a probabilistic output (*P*) predicting a dichotomous dependent variable (presence-absence in the present case) from the set of independent variables (Hosmer & Lemeshow 2000b). To eliminate the effect of prevalence, probability models were converted using the favourability function of Real *et al.* (2006):

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

where n_1 and n_0 are the number of presences and absences in the study area, respectively. Favourability values range from 0 (null favourability) to 1 (high favourability), and a favourability value of 0.5 indicates that the presence of the species is as probable as its prevalence in the corresponding study area. Hence, favourability refers to the environmental conditions that favour the presence of the species (Acevedo & Real 2012, Muñoz *et al.* 2015b). The use of a favourability value of 0.5 as a cut-off for the presence/absence of the species is unreliable when attempting to establish clearly demarcated favourable areas (Hosmer & Lemeshow 2000a). Thus, we reclassified the areas into ‘clearly favourable’ (F > 0.8), ‘clearly unfavourable’ (F < 0.2), and areas of ‘intermediate favourability’ (Muñoz *et al.* 2005).

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

5.2.5 Model assessment

We used several indices to assess model performance. The Area Under the receiver operating characteristic Curve (AUC) was used as a measure of discrimination capacity that could be a more accurate indicator when describing the distribution of the species in the different steps of the model (Hosmer & Lemeshow 2000a, Romero *et al.* 2012). The weight of each added variable and the estimation of the parameter in the equation were assessed using the Wald test (Wald 1943). Classification accuracy was tested using a set of widely recognized measures, whose values range from 0 to 1 (Fielding & Bell 1997, Barbosa *et al.* 2013). The measures used were as follows: the correct classification rate (CCR: the conditional probability of correctly classified presences and absences), sensitivity (the conditional probability of correctly classified presences), specificity (the conditional probability of correctly classified absences), the over-prediction rate (OPR: the proportion of observed and assumed absences in the predicted presence area), and the under-prediction rate (UPR: the proportion of observed presences in the predicted absence area). We also used Cohen's Kappa which is described as the proportion of specific agreement and whose values range from –1 to +1 (Cohen 1960). We assessed the factor predicted change in presences (Pch), where values greater than 1 predict an increase in distribution range (Muñoz & Real 2006).

5.3 RESULTS

A total of 414 wintering records were included in the database, 344 ringed birds and 70 recoveries (Table 5.2). Approximately 75% were captured along the Mediterranean coast (Catalonia, Community of Valencia, Murcia, Andalusia and Balearic Islands), whereas around 10% were captured on the

Atlantic coast. The remaining 15% were captured inland, mostly in great valleys and rivers, as Guadalquivir, Tajo and Ebro (Figure 5.1A). Monthly distribution of wintering records showed that the highest amount of data was recorded in the second half of November (245), followed by December (92) and January (77). Catalonia and Valencia Community were the areas with the highest number of records in November, whereas Andalusia and inland regions played the most important role during December and January, respectively.

According to the origin of birds, 37 individuals were considered as 'Breeders' (Table 5.2), of which 16 individuals were recovered during winter in the same Spanish place where they were ringed; 5 were recovered in different places of Spain, and 16 were birds from other European countries and recovered in the Iberian Peninsula (Figure 5.2). The origin of these birds seems to be related with the wintering area; British birds remained in Northern Spain, birds from Belgium and the Netherlands were recovered in South-Western and Southern Spain, respectively, and birds from Central and Eastern Europe (France, Germany, Poland and Czech Republic) were mainly recaptured in Eastern Spain and the central plateau of the Iberian Peninsula (Figure 5.2).

Table 5.2. Summary of winter Eurasian Reed Warbler recoveries in the Iberian Peninsula. We considered as 'Breeder' those birds ringed in the previous breeding season (May to July) they were recovered. As 'Non-Breeder' we considered those birds which were ringed out of the previous breeding season (August to April).

Eurasian Reed Warbler Data			**Recovered in**	
	Region	Consider as	Ringing Place	Different Place
Ringed in	Spain	Breeder	16	5
		Non-Breeder	14	10
	Portugal	Non-Breeder	2	—
	Other European Countries	Breeder	—	16
		Non-Breeder	—	7

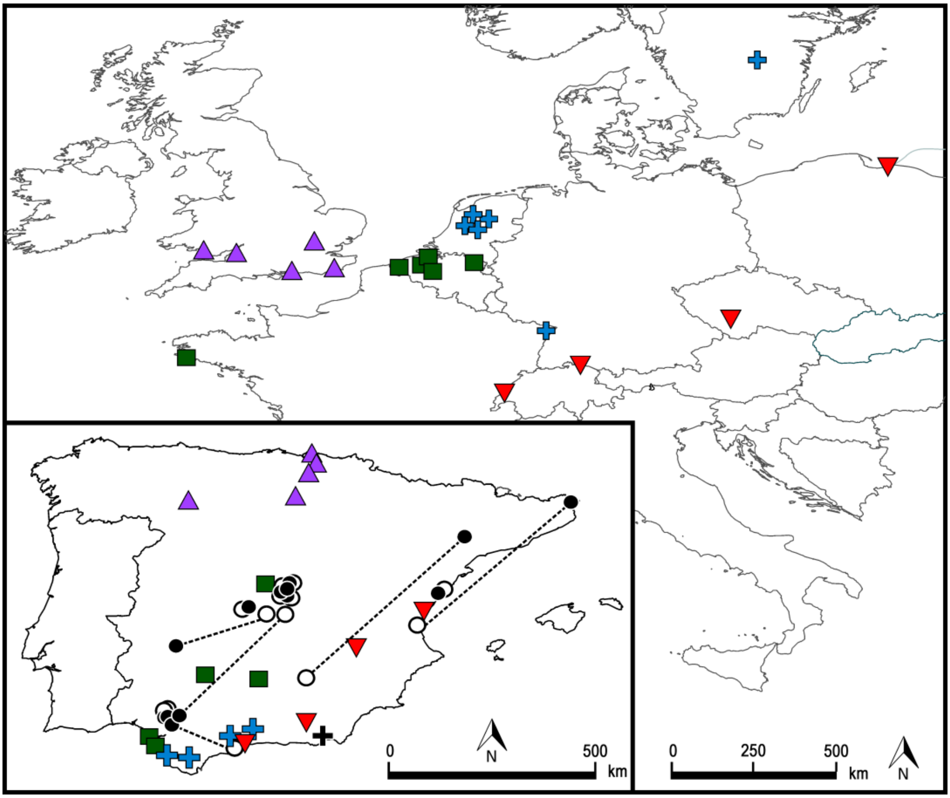


Figure 5.2. Origin and destination of the 23 birds ('Breeder' and 'Non-breeder' recoveries from other European countries) and the 21 Spanish recoveries considered as sedentary (only Spanish 'Breeder'). Trigonometric shapes link the country where the birds were ringed and the Spanish places where they were recovered. Black circles and hollow circles show the ringing and recovery places where sedentary birds were recorded, respectively, whose movements are linked by a broken line.

During modelling, 114 presences were considered in the study area. The predictive model of the wintering pattern of the Eurasian Reed Warbler in the study area included variables associated with climate, spatial location, and topography (Table 5.3). The model had high discriminative capacity (AUC > 0.8) and classification (CCR, sensitivity and specificity > 0.7) capacity and a positive kappa value. We also observed a high proportion of predicted presences in the study area in which the species was assumed to be absent (OPR > 0.9). However, the UPR had lower values (Figure 5.3). The spatial variable was calculated from the spatial trend-surface analysis:

$$Spat = 743.25 - 37.083La - 81.95Lo + 0.46La^2 + 0.24Lo^2 + 4.033La \times Lo - 0.011Lo^3 - 0.0501La^2 \times Lo$$

Table 5.3. Variables included in the modelling process and their coefficients (β), Wald test values, and significance (*p*). The variables are ranked according to their order of entrance. Codes are the same as in Table 5.1.

Variable	β	Wald	*p*
Tn	0.29	45.71	1.37×10^{-11}
Spat	0.56	35.33	2.78×10^{-9}
Slop	–0.17	11.39	7.35×10^{-4}
Constant	–2.090	15.86	6.82×10^{-5}

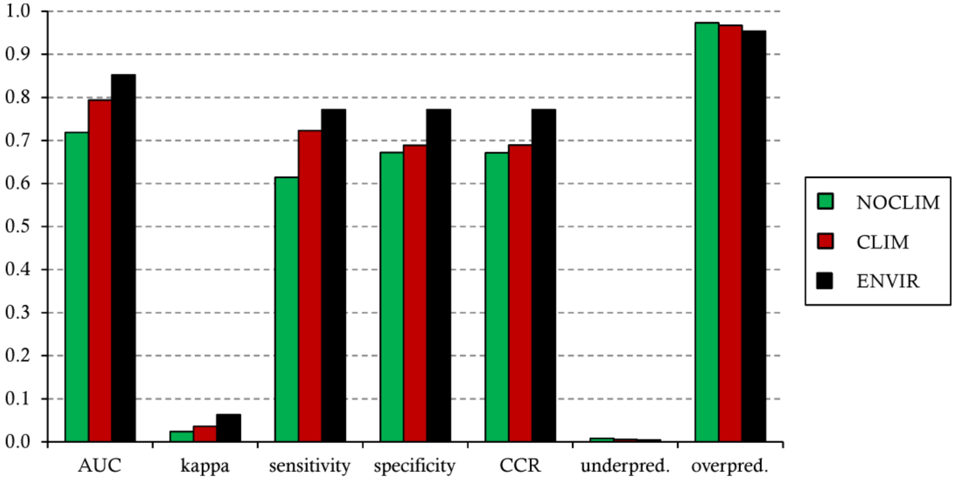


Figure 5.3. Assessment scores for the Eurasian Reed Warbler distribution environmental model in the Iberian Peninsula (**ENVIR**, black bar), model constructed using only the climatic variable (**CLIM**, red bar) and the non-climatic variables (**NOCLIM**, green bar) entered in the environmental model.

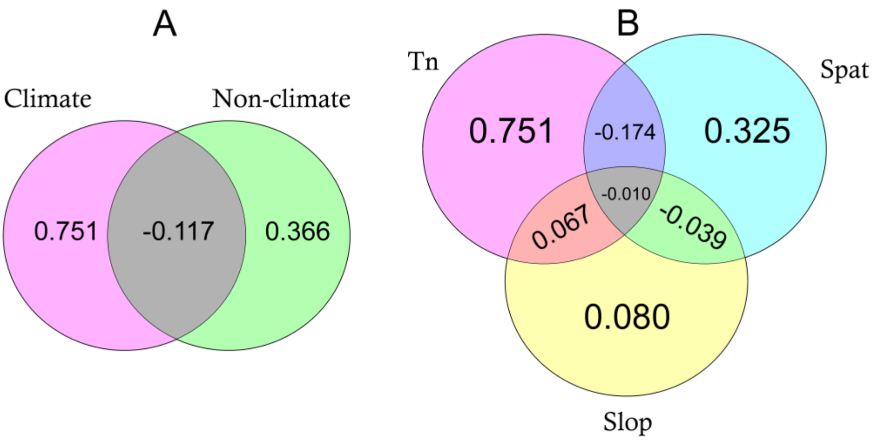


Figure 5.4. Variation partitioning of the environmental model using the factor climate vs the factor combined non-climatic variables **(A)** and the individually considered explanatory variables **(B;** codes in Table 5.1). Values within the circles represent the proportion of variation explained by the indicated factors and by their interactions.

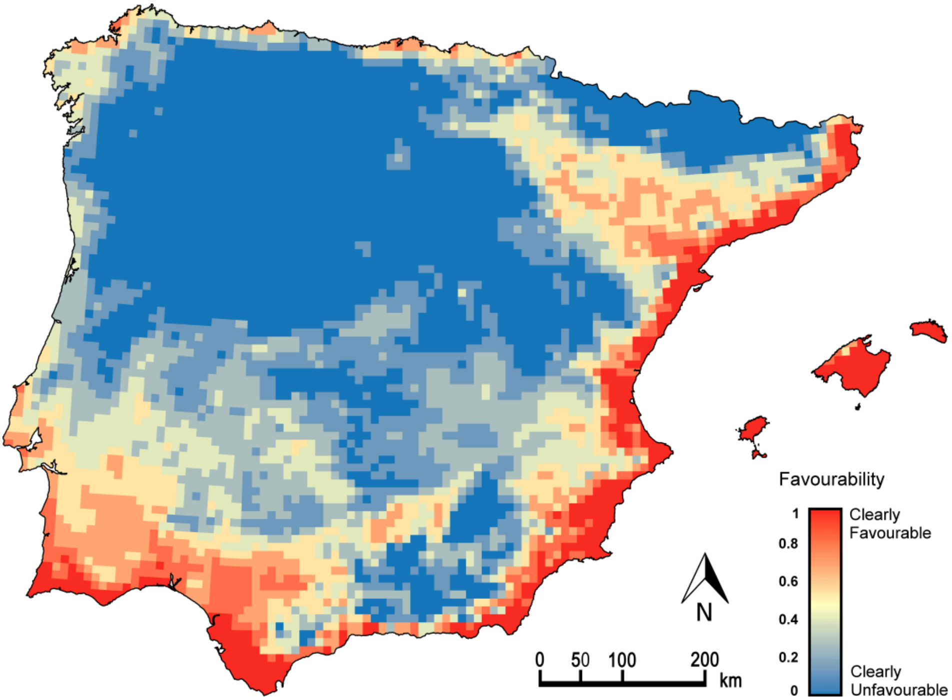


Figure 5.5. Distribution of favourable sites for the Eurasian Reed Warbler wintering.

The proportion of the variation only explained by climate (mean minimum temperature) was 0.751, showing that climate had the most significant influence on the wintering of the species in the Iberian Peninsula, whereas the proportion of the variation explained by non-climatic variables was 0.366 (Figure 5.4A). Spatial location and slope explained 0.325 and 0.080 of the variation of the model, respectively (Figure 5.4B).

The favourability map (Figure 5.5) showed that clearly favourable areas were on the Mediterranean coast, specific Atlantic coastal areas in the north and south of the Iberian Peninsula, and some estuaries (especially those with wide rivers), whereas clearly unfavourable areas were in northern inland regions and in mountainous areas. The intermediate favourability areas with the lowest values were located in southern inland areas of the Iberian Peninsula, whereas the values increased nearer to the coast, with the exception of some large valleys (i.e., the Guadalquivir valley in the south and the Ebro valley in the north). The Pch value for the model was 16.49.

5.4 DISCUSSION

The effect of climate on bird distribution patterns has been strongly studied since the beginning of 21st century (Žalakevičius 2001, Péron *et al.* 2007, Muñoz *et al.* 2013, Massimino *et al.* 2015, Eyres *et al.* 2017, Bay *et al.* 2018). The influence of climate change on bird migration and its consequences is a key topic within the ornithology community (Both & Visser 2001, Gordo & Sanz 2006, Lehikoinen & Sparks 2010, La Sorte *et al.* 2017). Although this was studied for the reproduction of the Eurasian Reed Warbler (Schaefer *et al.* 2006) and also on the breeding performance of the Great Reed Warbler *Acrocephalus arundinaceus* (Dyrcz & Halupka 2009), there is little information about the response to climate change during winter. First evidences of a regular wintering of Eurasian Reed Warblers in the Iberian Peninsula are presented in this research. Although the European population is mostly migratory and winters in sub-Saharan Africa (Dowsett-Lemaire & Dowsett 1987), occurrence data showed that the species is wintering for years.

Our model shows that almost 24% of the Iberian Peninsula is favourable for the Eurasian Reed Warbler during winter (although they only occupy 10% of that), and that more than 68% can be classified as ‘intermediate favourability’. These results support the idea that the Iberian Peninsula is already a new wintering area for this insectivorous long-distance migrant and it also corroborated our hypothesis of a potential increment in the wintering populations, possible due to the existence of unoccupied favourable areas. The obtained model is relatively specific in that it correctly classified absences (Figure 5.3); however, the fact that the specificity value was less than 1 shows that the model detected clearly favourable conditions in areas in which the species had not yet been detected, while preventing possible false absences with high reliability (Olivero *et al.* 2016). Sensitivity values (especially in the first step) and the high over-prediction rate may be explained by the detection of unoccupied favourable areas, although this possibility does not mean that the model is erroneous (Muñoz & Real 2006, Barbosa *et al.* 2013). The obtained Pch value indicates that there is more than twelve times the number of favourable areas than those with confirmed presences. According to this, we predict a potential increase in wintering areas for this species in a recent future if conditions persist. It should be noted that the sampling methodology did not cover the whole study area, and therefore many of the unoccupied regions predicted as clearly favourable could actually be occupied by the species.

According to the origin of wintering birds (Figure 5.2), our results show a potential process of sedentarization in Spanish birds, with individuals remaining in the breeding areas the following winter they were ringed, and also that some Eurasian Reed Warblers from Central and Northern Europe remain in the Iberian Peninsula during the winter period. It has long been thought that the wintering occurrence of the species in Southern Europe was sporadic, related to individuals in bad conditions, and mostly juveniles (Bermejo 2004, Robson & Barriocanal 2011). However, the species appears during winter in a consistent way what could be related with warmer winters. In fact, winter temperature was the variable with the greatest explanatory power in the model, when selecting those areas with the mildest winters (Table 5.3, Figure 5.5). Winters tend to be milder in our study area, especially since the beginning of the 21st century when the minimum temperatures have increased and fewer days with less than 0 °C have occurred (Brunet *et al.* 2007, IPCC 2014). During the last winters (2015-2016, 2016-2017) average temperature has increased 1.65 ºC and 0.6 ºC, respectively, with regard to the reference period (1981-2010) in the Iberian Peninsula (AEMET 2016, 2017). This lack of severe winters year after year have led to an increase in the number of flying insects, such as mosquitoes (Roiz *et al.* 2014), which are the Eurasian Reed Warbler prey. That constant food availability allows the birds to maintain their body conditions during the wintering season, losing less energy when they face the environment, what is also climatically less severe. Under these conditions, the individuals remaining in the Iberian Peninsula during winter have an increased likelihood of survival until the next breeding season, a decreased likelihood of fitness impoverishment, and an increased likelihood of producing more offspring (Kokko 1999, Forstmeier 2002, Alves *et al.* 2013). Thus, there could be an increase in the number of individuals that change their phenology (Arizaga *et al.* 2012, Andueza *et al.* 2014). Related to the rest of Europe, the scarcity of prey during winter for this species forces the individuals to move southwards to find sufficient food to survive (Lewington 2006). However, if these individuals find sufficient resources during winter in the Iberian Peninsula, before crossing the

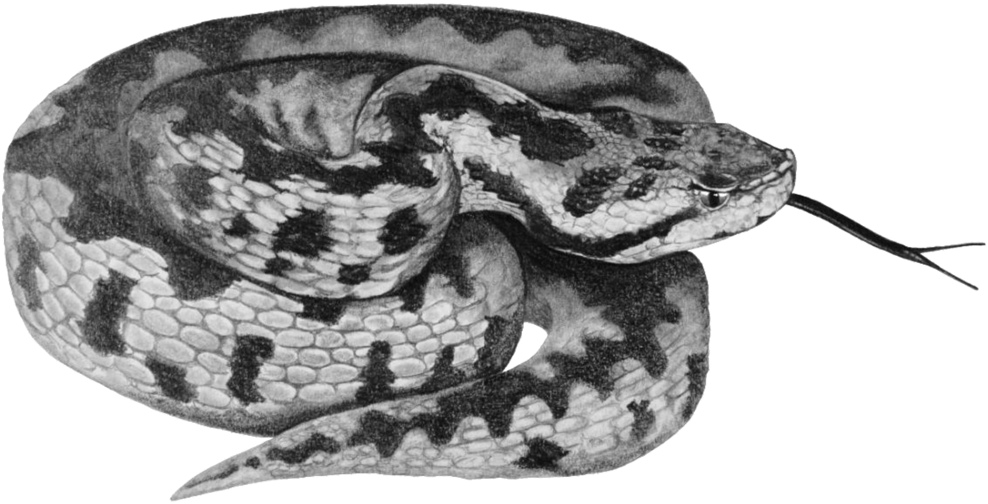
Strait of Gibraltar, they do not need to move to Africa and could stay in the Iberian Peninsula. Therefore, the next spring they will be able to select better breeding sites than individuals that did the long-distance migration due to their proximity to the sites. Furthermore, their mortality rates during migration will be lower, which will allow them to have more offspring (Alves *et al.* 2013) and that explain the abundant of recoveries of wintering birds in the Iberian Peninsula originating from central and northern Europe.

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

Although climate models have been demonstrated to have a high explanatory power, more reliable models are obtained when climatic and non-climatic variables are used together (Márquez *et al.* 2011). Regarding the spatial factor, the trend-surface analysis showed directionality in the spatial favourability of the Iberian Peninsula for this species (Figure 5.1D). Eastern followed by northern and southern coastal areas were the most favourable areas, whereas the Portuguese and Spanish inland areas were the least favourable. Given the spatial location of the Iberian Peninsula (i.e., acting as a border between Africa and Europe), many individuals from different breeding grounds arrive there, follow the Mediterranean coast until reaching the south, and then fly on to Africa (Kennerley & Pearson 2010, BirdLife International and NatureServe 2015). The wintering areas in the northern Iberian Peninsula coast could be explained by the arrival of British birds in these areas as recoveries map showed (Figure 5.2), given that this region is the first land they encounter in their migration across the sea and it is favourable. The results of the trend-surface analysis demonstrate the favourability of sites in the northern Iberian Peninsula, while sites in the eastern and southern Iberian Peninsula are on the main migration routes of birds from Northern and Central Europe (Figure 5.2) (Moreau 1972, Åkesson et al. 1996, Åkesson & Walinder 2002, Procházka et al. 2016). These results support the relevance of the migration orientation, which has a strong genetic basis (Berthold & Helbig 1992). More specifically, the breeding origin of the individuals affects their arrival site because, as nocturnal migrants, they migrate on a broad front but maintain their orientation in order not to become lost (Bermejo 2012, Alves *et al.* 2013, Hasselquist *et al.* 2017). This trend into maintain the orientation during their migration could explain the absences in the south-western quarter of the Iberian Peninsula, although having mild winter temperatures (Font 2000), but being remote from the typical migration routes of the species (Moreau 1972, Kennerley & Pearson 2010, Andueza *et al.* 2014).

The slope of the terrain also influenced potential distribution during winter because it reduced the favourability of the mountain ranges, even when they were near to the coast, despite suitable temperatures in these areas. This type of effect also occurs in areas of the interior where, despite their being flat, the altitude of the plateaus makes the temperatures unsuitable to the species. However, slope and climate both increase favourability in sites close to the coast and in wide rivers and valleys where reed-bed communities are more abundant because the climate is suitable and the low slope allows water to accumulate, thus facilitating the presence of the species (Cramp 1992, Bermejo *et al.* 2003, Kennerley & Pearson 2010, Bermejo 2012). Hence, the topography factor is associated with the selection of optimal habitats for wintering by the Eurasian Reed Warbler.

This modelling approach shows that climate is a determinant factor in the wintering strategy changes this species is experiencing in Europe, although other environmental conditions are relevant at a regional scale. The Eurasian Reed Warbler could be considered as a model of many of other Trans-Saharan migrants that have begun to winter in the Iberian Peninsula in recent years. The relationship between climate and species phenology gives rise to some hypotheses concerning the way in which species have responded to environmental variability in recent decades, and also sheds some light on the response of species distributions to climate change (Péron *et al.* 2007, Muñoz *et al.* 2015b). If temperature increasing continues, we could assume that more individuals would shorten their migration distance, and thus the size of populations regularly wintering in Europe would increase. However, the future of these populations could be at risk if climatic conditions undergo sudden and severe changes, which would entail high mortality rates in the proportion of birds wintering in Europe. The results of this study could be useful when applying direct sampling methodologies by giving priority to the most favourable areas, thus facilitating the sampling and monitoring of the species during winter. Although more research is required, results also contribute to our understanding of the effect of climate, especially in relation to the uncertainty surrounding the effect of climate change on species phenology and distribution. It would be interesting to couple the effects of environmental changes with the demography of the species both in breeding and wintering quarters, and to identify the potential consequences of rising temperatures for population dynamics.



CAPÍTULO 6

COMPRENDIENDO CÓMO EL MEDIO AMBIENTE Y LAS INTERACCIONES COMPETITIVAS FORMAN Y MANTIENEN LAS DISTRIBUCIONES PARAPÁTRICAS

UNDERSTANDING HOW ENVIRONMENT AND COMPETITIVE INTERACTIONS FORM AND MAINTAIN PARAPATRY

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

Chamorro, D., Martínez-Freiría, F., Real, R. & Muñoz, A.-R. In press. Understanding parapatry: how do environment and competitive interactions shape Iberian vipers' distributions? *Journal of Biogeography*. Doi: 10.1111/jbi.14078.

6 UNDERSTANDING HOW ENVIRONMENT AND COMPETITIVE INTERACTIONS FORM AND MAINTAIN PARAPATRY

6.0 RESUMEN

La parapatría como patrón biogeográfico particular ha sido estudiada tradicionalmente por pares de especies, teniendo en cuenta sus áreas de distribución, pero en las víboras de la península ibérica se da un caso más complejo, ya que son tres las especies implicadas: la eurosiberiana *Vipera seoanei*, la para-mediterránea *V. aspis* y la mediterránea *V. latastei*. El objetivo principal de este capítulo es analizar el origen y el mantenimiento de estas distribuciones parapátricas y si sus causas se deben a condiciones ambientales, acontecimientos históricos, competencia interespecífica o una combinación de todas ellas. Para ello se aplicó el concepto de favorabilidad, para obtener unidades de distribución conmensurables, no afectadas por la prevalencia de las distintas especies en la península ibérica. Después se comparó la favorabilidad de cada especie con la favorabilidad de presencia de las otras especies conjuntamente, dentro de sus áreas de distribución solapadas. Así se identificaron las zonas en las que se prevé que se produzca la coexistencia simpátrica, la segregación ambiental o la exclusión competitiva. En el caso de estudio la exclusión competitiva resultó ser el principal impulsor del patrón de distribución parapátrico, mediada por cambios graduales en las condiciones ambientales que favorecen a cada especie. *V. aspis* presenta zonas favorables fragmentadas fuera de su área de

distribución actual, que parecen estar desocupadas debido a la exclusión competitiva de las otras víboras. *V. latastei* parece estar limitada por la competencia con las otras víboras, además de encontrar condiciones desfavorables en el noroeste de la península. *V. seoanei* parece impedir el establecimiento de las otras dos especies en el cuarto noroccidental de la península debido a su mejor adaptación a las condiciones ambientales de esa región. Se detectaron pocas zonas de coexistencia sostenible, principalmente en el curso alto del río Ebro. En resumen, cada especie está mejor adaptada a las condiciones ambientales de las zonas que habitan, pero la existencia de ecotonos las obliga a concurrir de forma simpátrica y a competir por los recursos en las zonas de contacto. Su patrón de parapatría es por tanto un resultado de la historia evolutiva de las especies y de las fuertes interacciones competitivas entre ellas, que han formado "barreras de exclusión competitiva”. No obstante, estas barreras dependen del medio ambiente, por lo que los cambios en el entorno podrían afectar rápidamente a los límites de distribución de estas especies.

6.0 ABSTRACT

Parapatry is traditionally studied by pairs of ranges but a more complex pattern is present in the Iberian Peninsula, where three parapatric viper species with distinct biogeographical affinities are distributed: the Euro-Siberian *Vipera seoanei*, the para-Mediterranean *V. aspis* and the Mediterranean *V. latastei*. We aimed to assess if it is mainly caused by environmental conditions, historical events, interspecific competition among them, or a combination of these factors. We applied the concept of favourability for occurrence to produce commensurate distribution units

unaffected by the different species prevalence in the Iberian Peninsula. We compared the favourability of each species with the favourability for occurrence of more than one species together at their overlapping ranges, identifying the areas in which sympatric coexistence, environmental segregation and competitive exclusion are predicted to occur. Competitive exclusion was the main driver of the parapatric pattern, mediated by gradual changes in the environmental conditions favouring each species. The para-Mediterranean *V. aspis* presented fragmented favourable areas out of its range that seemed to be unoccupied due to the competitive exclusion by the other vipers. The Mediterranean *V. latastei* seemed to be limited by the competition with the other viper species rather than by the environment. *V. seoanei* prevented the other two species establishment in the north-western quarter of the Iberian Peninsula due to its better adaption to the humid conditions of this region. Few areas of sustainable coexistence were detected, mainly in the high-course of the Ebro River. In summary, each species is better adapted for particular conditions, but the existence of ecotones forces them to occur sympatrically and compete for the resources. The parapatry pattern is a result of the evolutionary history of the species and of strong competitive interactions between them, which form ‘competitive-exclusion barriers’. However, these barriers are environmentally dependent, so changes in the environment could rapidly affect the species distribution limits.

6.1 INTRODUCTION

The term parapatry describes the distributional patterns in which species have separate but contiguous distributions with a very narrow overlap between distribution ranges (Bull 1991). Parapatric distributions may result from the contact between species that were previously isolated in separated geographical refuges from which they spread out (Bull 1991, Butlin *et al.* 2008), or from the fragmentation of the range of an ancestor species that progressively experienced reproductive isolation between populations and subsequent speciation (Burban *et al.* 2020).

The maintenance of the parapatry depends on preserving the greater fitness of each taxon on its side of the distribution boundary (Bull 1991). Greater fitness is affected by factors related to the capacity for dispersion, survival and reproduction of the individuals, including adaption to or avoidance of environmental conditions in one side of the distribution limit (Key 1981, Bolfíková *et al.* 2017), successful interspecific competition for resources in specific regions (Cowen *et al.* 2020), or different types of predation or parasite susceptibility on different sides of the boundary (Vorndran *et al.* 2002, Staines *et al.* 2020). Otherwise, parapatry tends to create a barrier that eventually produces allopatry (Bull 1991).

Parapatric distributions are traditionally studied by pairs of species. However, there is a more complex situation in the Iberian Peninsula, where three species of the genus *Vipera* (Serpentes: Viperidae) are present in parapatry with narrow overlapping areas between the three species (Martínez-Freiría *et al.* 2008) and also between specific pairs (Duguy *et al.* 1979, Bea 1985, Brito & Crespo 2002). These vipers likely evolved through allopatric speciation and are morphologically and ecologically similar

(Martínez-Freiría *et al.* 2015, 2020). *V. seoanei* Lataste, 1879 is almost an endemism of northern Iberia, inhabiting areas of Atlantic climate (Martínez-Freiría *et al.* 2015). It is phylogenetically included in the *Pelias* group, together with other Euro-Siberian species such as *V. berus* (Martínez-Freiría *et al.* 2015), which diverged from the remaining *Vipera* clades adapted to Mediterranean conditions more than 15 Mya. ago (Freitas *et al.* 2020). The Western Mediterranean vipers (the para-Mediterranean *V. aspis* (Linnaeus, 1758) and the Mediterranean *V. latastei* Boscá, 1878) form a monophyletic group that has become highly diversified since the late Miocene (Martínez-Freiría *et al.* 2020). *V. aspis* is distributed over western Europe, including the north-eastern region of Spain (Martínez-Freiría *et al.* 2020), whereas *V. latastei* occurs over most of the Iberian Peninsula except the northernmost region which is occupied by the other Iberian vipers (Martínez-Freiría *et al.* 2020). Both *V. aspis* and *V. latastei* inhabit Mediterranean areas with hot and dry summers, although the former also occurs in Atlantic climates (Martínez-Freiría *et al.* 2008, 2020, Sillero *et al.* 2014). Martínez-Freiría *et al.* (2008) showed that these species have similar ecological requirements at local-scale, with subtle difference. Thus, both the influence of the environment and the competitive interactions must be shaping their distributions and maintaining parapatry.

We aimed to assess the roles that environmental segregation, competitive exclusion and sustainable sympatric coexistence have in the maintenance of the parapatric distribution pattern of the three Iberian *Vipera* species. To this end we used biogeographical models reflecting the spatial favourability patterns, environmental favourability for each species and shared favourability between the three species. Given the environmental affinities of the three species and their respective occupation of Iberia and Western

Europe, three hypotheses about the cause of the parapatric pattern were made: Hypothesis (1) *V. aspis* is restricted to the Pyrenees by competitive exclusion rather than by environmental constrains, as occurs in other areas of Western Europe with ecological conditions similar to those of Iberia), Hypothesis (2) *V. seoanei* is limited to areas with Euro-Siberian conditions due to environmental constraints, and Hypothesis (3) *V. latastei* is absent from northeastern Iberia because of competition with *V. aspis* (i.e. due to their ecological affinities) and from the northwestern Iberia due to the environment. Hypothesis (1) would be confirmed if there are uninhabited favourable areas for *V. aspis* in locations more favourable for the other two species; Hypothesis (2) would be confirmed if climate is the most probable explanatory factor for the distribution of *V. seoanei* and if the areas where the other species could outcompete it are mainly in the Mediterranean biogeographical region and Hypothesis (3) would be confirmed if environmental favourability for *V. latastei* is low in northwestern Iberia but high in the uninhabited northeastern territories in which *V. aspis* is present.

6.2 METHODS

6.2.1 Study area

The Iberian Peninsula (Iberia) is a biogeographical unit (600,000 km^2) located at the southwestern limit of Eurasia (Figure 6.1a). It is separated from Africa by the Strait of Gibraltar and from the rest of Europe by the Pyrenees, both of which play important roles as geographic barriers (Joger *et al.* 2007). About three-quarters of Iberia are formed by the vast Inner Plateau (average altitude 760 m), which is ringed by several mountain systems (Figure 6.1b): the Pyrenees in the northeast, the Cantabrian

Mountains in the northwest, the Iberian System in the central-eastern region, the Central System in the middle of the Inner Plateau (dividing it into northern and southern halves), the Sierra Morena System in the south and the Baetic System in the southeast (Fischer 1902). Climate and geography divide the territory into two biogeographic regions (Figure 1b, Rivas-Martínez *et al.* 2017): the Euro-Siberian and the Mediterranean regions. The Euro-Siberian region follows the Atlantic coast from the Pyrenees to the middle of Portugal and is characterized by mild-to-cold winters, cool summers and abundant regular precipitation. The Mediterranean region occupies the rest of Iberia, and is characterized by hot dry summers and mild winters. Both regions have several climatic subdivisions due to the orography, providing Iberia with high environmental heterogeneity (Rivas-Martínez *et al.* 2017).

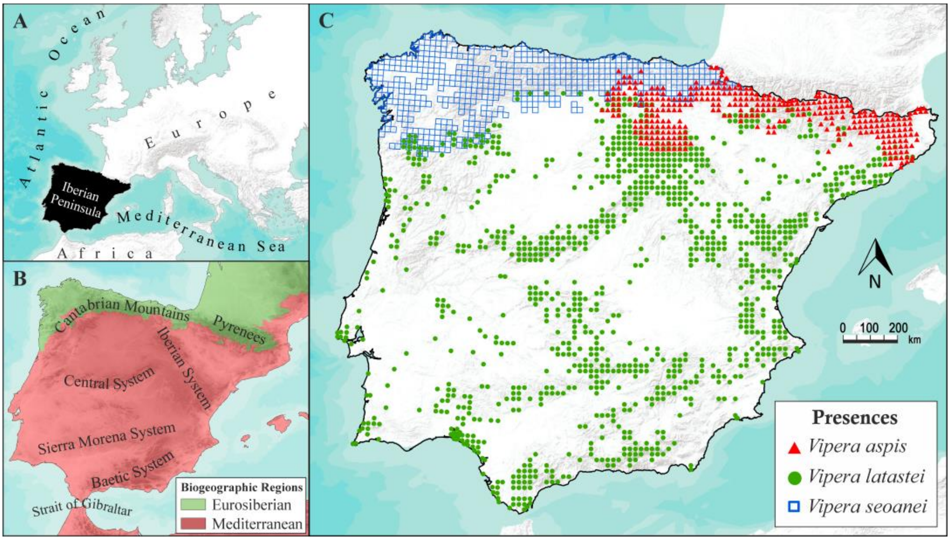


Figure 6.1. Spatial location of the Iberian Peninsula in the European continent **(A)**, biogeographic regions present in the Iberian Peninsula with the main mountain systems **(B)** and the presences distribution of the Iberian vipers into the UTM 10×10 km grid cell of the study area **(C)**.

6.2.2 Species data and predictors

Species distribution data were latticed using UTM 10×10 km cells as operational geographic units (OGUs, $n = 5{,}874$). The Iberian distributions of the three vipers were extracted from the distribution atlases of Spain (Pleguezuelos *et al.* 2002) and Portugal (Loureiro *et al.* 2008), and were supplemented with new data for Spain provided by the AHE (Asociación Herpetológica Española), recently published data (Martínez-Freiría et al., 2015, 2020) and also unpublished data newly collected (total number of OGUs with occurrences: *V. aspis* = 329, *V. latastei* = 1105, *V. seoanei* = 479, Figure 6.1c).

Thirty-eight variables related to spatial location, topography, climate, human activity and land-cover were used to model the distributions of the three species in the Iberian Peninsula (Table 6.1). Land cover variables were obtained separating each of the categories from the 1km^2 pixel CORINE Land Cover layer, and obtaining the proportions of coverage of all the variables at each OGU using the ZONAL function of ARCGIS package.

6.2.3 Environmental distribution modelling

The spatial structure of the species distribution was taken into account performing a polynomial trend-surface analysis (Legendre & Legendre 1998) for each species. This was achieved by conducting a logistic regression, which is a supervised-machine-learning algorithm, of the distribution of each species on the coordinates latitude (La), longitude (Lo) and their combinations up to the third potency (i.e., La^2, Lo^2, La^3, Lo^3, $La \times Lo$, $La^2 \times Lo$, $La \times Lo^2$). Spatial structure patterns can be associated with historical events and species population dynamics (Legendre 1993). The analyses provided the spatial probabilities of occurrence. These probabilities were converted into spatial favourability values using the function developed by Real *et al.* (2006) (see below). Spatial favourability values were used to delimit the relevant area for each species (Acevedo *et al.* 2012a) in which it is currently interacting with other species and their environment (Real *et al.* 2003, Márquez *et al.* 2004) by excluding the spatially unfavourable values ($F < 0.2$) from the training area in which the environmental model was performed for each species (Figure 6.2).

Table 6.1. Environmental variables used to model the viper distribution. *Exc.* Symbols show the variables excluded by the False Discovery Rate (FDR) and Spearman Correlation's rate analysis for * *V. aspis*, ‡ *V. latastei* and § *V. seoanei*, that were not used in the stepwise modelling.

Code	**Variable**	***Exc.***	**Source**
Topography			
Alti	Mean altitude (m)	§	1
Slop	Slope (degrees) (calculate from *Alti*)		1
Spatial situation			
La	Latitude (degrees)		2
Lo	Longitude (degrees)		2
Climate			
Tmean	Mean annual temperature (ºC)	* ‡	3
Tjan	Mean temperature in January (ºC)	* ‡ §	3
Tjul	Mean temperature in July (ºC)	§	3
Dt0	Mean No. annual days with min. temperature ≤ 0ºC	§	3
Dt20	Mean No. annual days with min. temperature ≥ 20ºC	‡ §	3
Dt25	Mean No. annual days with max. temperature ≥ 25ºC	* ‡ §	3
Dfog	Mean No. annual days of fog	*	3
Peva	Mean annual potential evapotranspiration (mm)	* ‡ §	3
Aeva	Mean annual actual evapotranspiration (mm)	§	3

Table 6.1. (*continued*)

Inso	Mean annual insolation (hours/year)	* ‡ §	3
Srad	Mean annual solar radiation (kwh/m^2/day)	* ‡	3
Prec	Mean annual precipitation (mm)	* ‡ §	3
Dp01	Mean No. annual days with precipitation ≥ 0.1 mm	* §	3
Dp1	Mean No. annual days with precipitation ≥ 1 mm	‡	3
Dp10	Mean No. annual days with precipitation ≥ 10 mm	* ‡	3
Dp30	Mean No. annual days with precipitation ≥ 30 mm	§	3
Hujul	Mean relative air humidity in July at 07:00 h. (%)	‡	3
Hujan	Mean relative air humidity in January at 07:00 h. (%)		3
Land cover			
Partif	Proportion of area occupied by artificial areas	* ‡ §	4
Ppast	Proportion of area occupied by pastures		4
Pcrop	Proportion of area occupied by permanent crops		4
Pagri	Proportion of area occupied by agriculture	§	4
Pscrub	Proportion of area occupied by scrubs		4
Psparse	Proportion of area occupied by sparse vegetation		4
Pmixfor	Proportion of area occupied by mixed forest	*	4
Poakfor	Proportion of area occupied by oak forest	‡	4
Pconfor	Proportion of area occupied by coniferous forest	§	4
Prock	Proportion of area occupied by rocks	‡ §	4
Psand	Proportion of area occupied by sands	* ‡	4
Psnow	Proportion of area occupied by snow	* ‡ §	4
Human activity			
Road	Distance to roads (km)	§	1
Pop	Mean population density (hab./km^2)	* ‡ §	5
Popmx	Maximum population density (hab./km^2)	* ‡ §	5
Popmn	Minimum population density (hab./km^2)	* ‡	5

Data sources:

1 – https://www.usgs.gov/centers/eros/science/usgs-eros-archive-digital-elevation-global-30-arc-second-elevation-gtopo30?qt-science_center_objects=0#qt-science_center_objects,
2 – https://www.ign.es/web/catalogo-cartoteca/resources/html/030963.html,
3 – http://www.aemet.es/es/serviciosclimaticos/datosclimatologicos/atlas_climatico,
4 – https://www.eea.europa.eu/data-and-maps/data/corine-land-cover-accounting-layers,
5 – https://landscan.ornl.gov/downloads/2000

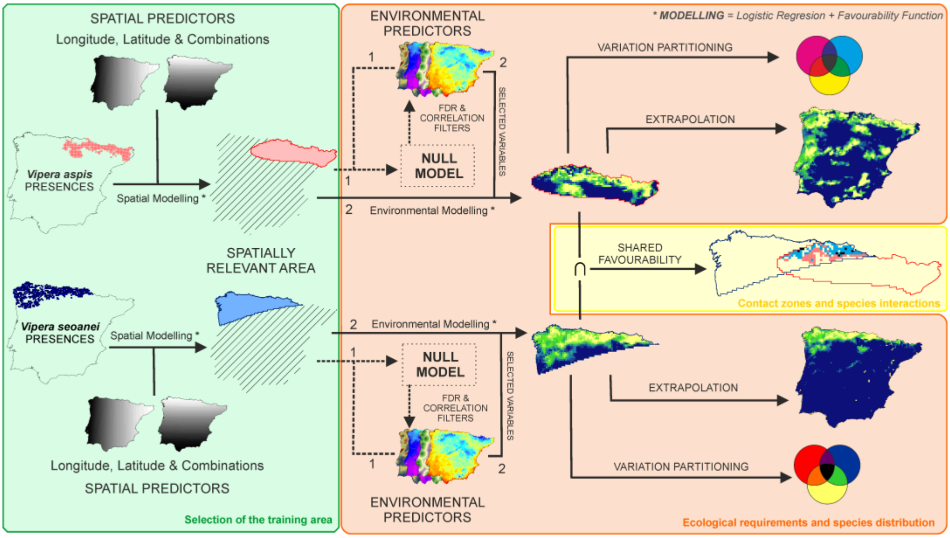


Figure 6.2. Graphical chart summarizing the methodological framework of this paper, using two species as example of all the steps used to obtain information about the ecology and competitive interactions between vipers. FDR (False Discovery Rate) was used to reduce the probability of committing type I error and correlation (Spearman's coefficient) was performed to address the multicollinearity between variables. Null model is the model with no variable in which variables that pass the FDR and correlation filters were added. Shared favourability is the intersection between the favourability of the two species into their overlapping spatially relevant area.

Topography, climate, land cover and human activity variables were used as predictors to obtain environmental models of the distribution of the three vipers into their relevant areas. Spearman correlation coefficients were calculated to address multicollinearity between these variables. For each pair of variables with r > 0.8, only one was retained according to their individual predictive power, which was assessed according to the significance (α) of the score test of univariate logistic regressions (Fa *et al.* 2014). The False Discovery Rate (FDR) was then determined to control for increases in the probability of type I errors when a large number of variables are used in modelling (Benjamini & Yekutieli 2001). Subsequent modelling procedures only accepted variables significantly associated with the distribution of the species with $\alpha < 0.05$ under an FDR value of less than 0.05 (Benjamini & Yekutieli 2001). To obtain a comprehensive environmental model for each species, we performed a multivariate forward-backward stepwise logistic regression of the distribution of each species in each relevant area on the remaining subset of variables (Figure 6.2). This procedure started with a model with no variable (the null model). A multivariate model was built by adding the variables that provided the most significant contribution to the model obtained in the previous step. Variables with broad-scale predictive power were entered in the first steps, whereas those that added significant nuances to the previous models were entered in subsequent steps. To avoid redundancy, variables that did not significantly add to the predictive power of the final model were excluded because their effect was effectively included in the model by the correlated variables.

Logistic regression analysis yields a probability of presence from the set of environmental variables (Hosmer & Lemeshow 2000b), which is affected by the prevalence of the species that is modelled in the dataset. As the main objective of this work was to compare different distributions, it is mandatory to use commensurate methods unaffected by different prevalence. Therefore, the effect of prevalence on the probability value was removed, thus obtaining favourability values with the equation developed by Real *et al.* (2006) equation:

$$F = \frac{e^{y}}{\frac{n_1}{n_0} + e^{y}} \qquad (2),$$

where n_1 and n_0 are the numbers of presences and absences, respectively, for each species and spatially relevant area, e is the Euler's number and y is the *logit* from the performed logistic regression, i.e., the linear combination of variables that were significant in the forward-backward stepwise selection process (Real *et al.* 2006). Favourability values (F) range from 0 (minimum favourability) to 1 (maximum favourability). A local favourability value of 0.5 indicates that the local probability of the presence of the species is the same as its prevalence in the training area (Real *et al.* 2006). Hence, favourability refers to the degree to which the environmental conditions are propitious for the presence of the species (Acevedo & Real 2012). Acevedo *et al.* (2012b) applied this framework to identify the biogeographical factors that conform pairs of parapatric distributions. However, favourability is a continuous and fuzzy concept (Acevedo & Real 2012). For this reason, it is unrealistic to use a favourability value of 0.5 as a cut-off for neatly distinguishing favourable from unfavourable areas (Hosmer & Lemeshow, 2000b:157–158). Thus, we reclassified the OGUs into 'favourable' ($F \geq 0.8$), 'intermediate favourability' ($0.8 > F > 0.2$) and 'unfavourable' ($F \leq 0.2$) for each species (Chamorro *et al.* 2017).

We identified the OGUs which the species could potentially inhabit according to their environmental conditions by extrapolating environmental models from the spatially relevant area to all the OGUs of Iberia (Figure 6.2) using equation (2) and maintaining the values of n_1 and n_0 of the relevant training area.

We grouped the variables included in each viper model into four main environmental factors (topography, climate, land-cover and human activity) and then we applied a variation partitioning procedure (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 the 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 one of the factors was obscured by the others (Chamorro *et al.* 2019).

6.2.4 Contact zones and species interactions

To identify where sustainable sympatric coexistence or competitive exclusion are expected to occur, the OGUs within shared spatially relevant areas (contact zones) were classified for each pair of species and the three species together using the Acevedo *et al.* (2010) methodological framework. Accordingly, the effect of an unfavourable environment ($F < 0.2$) for at least one species does not allow the establishment of that species, and therefore no interaction occurs (environmental segregation). However, an environment that is simultaneously favourable (optimal) for both species ($F > 0.8$) minimizes competitive interactions because the abundance of resources will allow weaker competitor to survive and persist in the same area (sympatric coexistence) despite the existence of competition (McPeek 2019). Only OGUs in which the shared favourability (i.e. the minimum environmental favourability values for both species) was intermediate ($0.2 < F < 0.8$) were identified as areas of 'competitive exclusion' (Figure 6.2). In these areas, the resources are abundant enough to sustain one species but not both. In this case, the species with the highest environmental favourability value in each OGU (i.e. the species best adapted to this particular environment) was identified as the best competitor in that OGU and likely excludes the others (Acevedo *et al.* 2007).

6.2.5 Modelling assessment

The weight of each variable and the estimation of the parameters in the *logit* equation were assessed using the Wald test (Wald 1943). The discrimination capacity of the models was evaluated using the Area Under the Receiver Operating Characteristic Curve (AUC; Hosmer & Lemeshow, 2000b). We evaluated the classification accuracy (using the favourability value 0.5 as classification threshold) with the correct classification rate (CCR: the conditional probability of correctly classified presences and absences), sensitivity (the conditional probability of correctly classified presences), specificity (the conditional probability of correctly classified absences), the over-prediction rate (OPR: the proportion of absences in the predicted presence area), and the under-prediction rate (UPR: the proportion of presences in the predicted absence area). We also calculated measures of model equilibrium such as PPI and PAI (potential presence increment and potential absence increment, respectively). All these measures are widely recognized and range from 0 to 1 (Barbosa *et al.* 2013). We used Cohen's Kappa index (Cohen 1960) to measure the degree to which the favourability of the OGUs with presences or absences in the dataset was higher or lower than 0.5, respectively (values range from –1 to +1). Model's calibration performance (reliability) were evaluated with the Hosmer & Lemesbow (1980) statistic (*HL*), where non-significant values ($p > 0.01$) mean a good fit between predicted and observed probabilities (good calibration), which is remarkably difficult to obtain with a large number of OGUs because small differences between observed and predicted probabilities generate significant changes in the statistic (Hosmer & Lemeshow 1980).

We assessed the biogeographical effect of the competitive interactions by creating a 4 × 4 matrix (classification matrix of interactions) of all the OGUs within contact zones using the following categories: environmentally unfavourable for at least one species, intermediate shared environmental favourability more favourable for competitor 1, intermediate shared environmental favourability more favourable for competitor 2, and environmentally favourable for both of them versus OGUs with the presence of both species, OGUs with the absence of both species, OGUs with the presence of competitor 1 but not competitor 2, and OGUs with the presence of competitor 2 but not competitor 1. Specific agreement between these categories was calculated using Cohen's Kappa coefficient (Cohen 1960).

6.3 RESULTS

In all three cases, we obtained significant environmental favourability models with high discrimination (AUC > 0.76) and classification capacities (CCR, sensitivity and specificity > 0.7 and a positive Cohen’s kappa value; Figure 6.3). Although under-prediction rates were generally low, they were higher for *V. seoanei*, whereas over-prediction was substantial for *V. latastei*, with 65% of the predicted favourable OGUs being unoccupied. The PPI was positive in all models, with a high value for *V. latastei*, indicating that potential occurrence areas according to environmental favourability exceed the currently occupied area. All models had a good calibration (Figure 6.3).

Figure 6.4a shows the spatially relevant areas for each species and Figure 6.4b their environmentally favourable areas. Hypothesis (1) was confirmed in the case of *V. aspis* because the model identified significant and clearly favourable OGUs in regions far from the nucleus of its known distribution range, such as the Central System or the Portuguese territory in which the species is absent (Figure 6.4b). Hypothesis (2) was confirmed in the case of *V. seoanei* because environmental favourability was constrained to the north-western quarter of the Iberian Peninsula from the coast to the Cantabrian Mountains. Hypothesis (3) was partly confirmed in the case of *V. latastei* because favourable OGUs are distributed over the main Iberian mountain systems, including the spatially relevant areas of the other species, but not in the north-westernmost part of Iberia (Figure 6.4a,b).

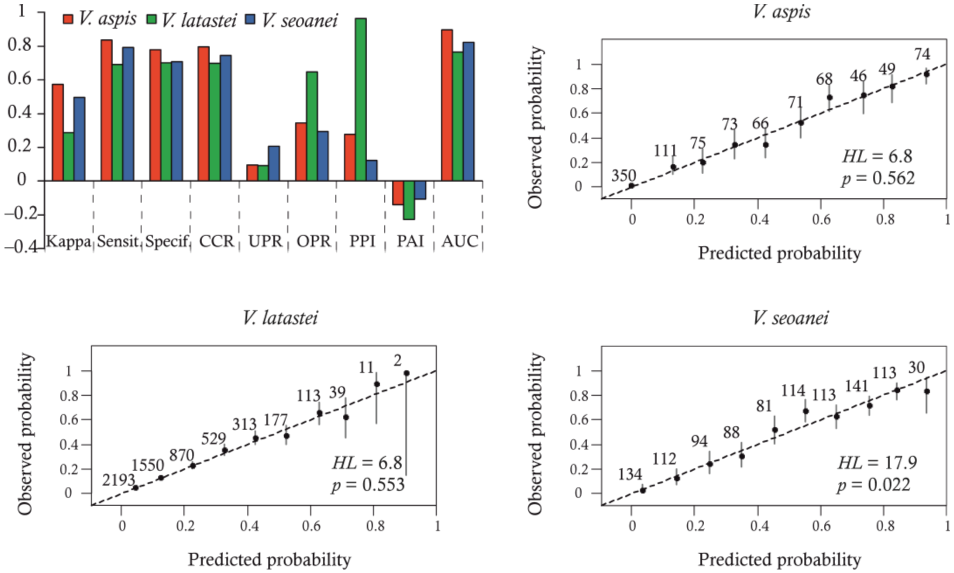


Figure 6.3. Assessment of environmental favourability models. Bar plot shows the classification and discrimination indices for each species models (Kappa: Cohen's Kappa index, Sensit.: sensitivity, Specif.; specificity, CCR: correct classification rate, UPR: under-prediction rate, OPR: over-prediction rate, PPI: potential presences increment, PAI: potential absences increment, AUC: area under the curve). Dot-line graphs show the calibration for each species model (HL: Hosmer and Lemeshow statistics, *p:* significance).

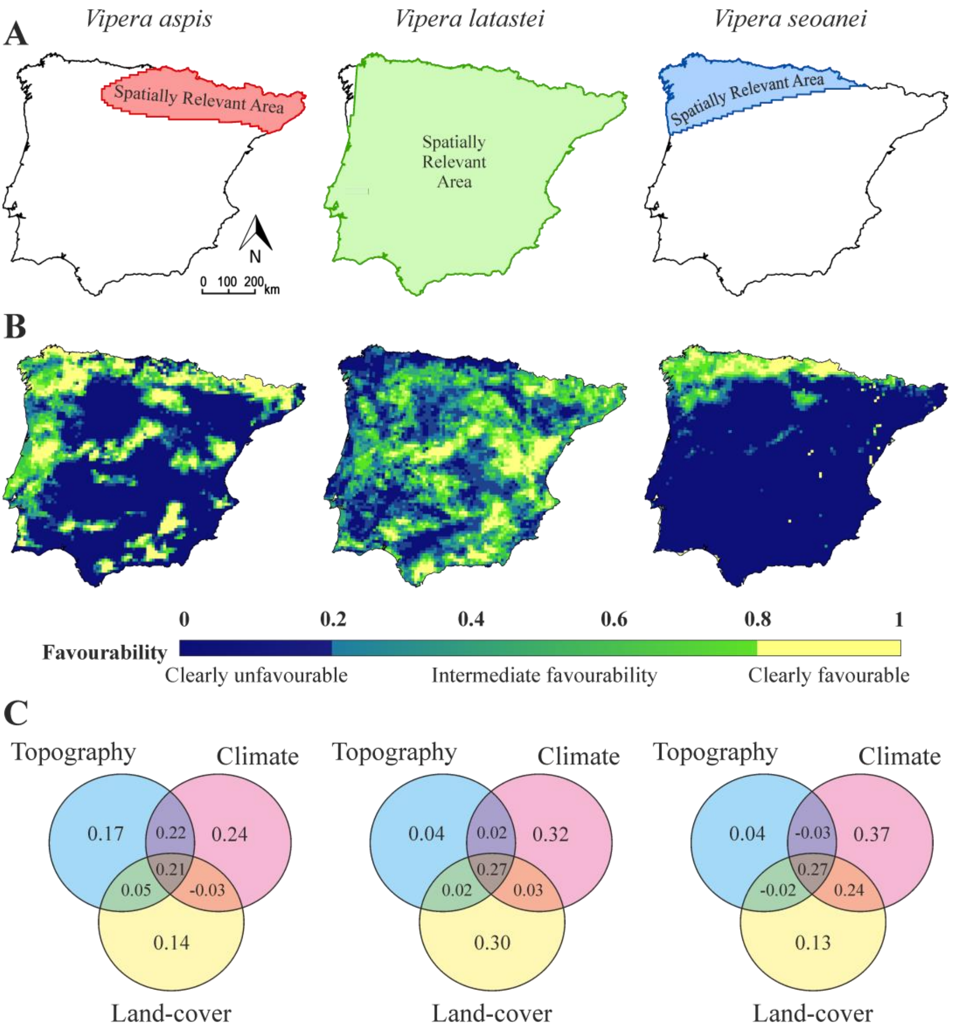


Figure 6.4. Spatially relevant areas **(A)**, favourability maps **(B)** and results of the variation partitioning **(C)** for each species. Favourability models were performed in their spatially relevant areas and then extrapolated to the rest of the Iberian Peninsula.

In all three cases, about one-third of the variation partitioning was explained by climate (Figure 6.4c), which was the environmental factor with the greatest explanatory power. For *V. seoanei*, climate explained more than the combined effect of the non-climatic factors (topography + land cover), which also confirms hypothesis (2). The shared effect of the three environmental factors explained about 20% for the three models (Figure 6.4c). *V. aspis* and *V. latastei* distributions are favoured by actual evapotranspiration and scarcity of frost days in high-altitude areas (Table 6.2). *V. seoanei* distribution is favoured by high precipitation and relative low solar irradiance in areas without a marked slope (Table 6.2). Human land-cover variables such as crops negatively affected the three species, especially *V. latastei* (Table 6.2).

In all cases, we identified areas across parapatric boundaries in which there are biogeographical effects of competitive interactions between vipers. In the case of *V. seoanei* and *V. latastei*, there are clear and continuous areas of competitive exclusion in which *V. seoanei* excludes *V. latastei* in the Euro-Siberian biogeographical region, whereas *V. latastei* outcompetes *V. seoanei* in the areas with Mediterranean conditions (Figure 6.5a). In the former case, average favourability values are generally higher for *V. seoanei* than those for *V. latastei* (Figure 6.5a). Only one OGU with potential sympatric coexistence was identified in the Pyrenees, but in fact both species are absent. However, the two species actually occur in 22 OGUs in which competitive exclusion is expected: *V. seoanei* is the best competitor in eight of these OGUs and *V. latastei* is the best competitor in the other 14. The interaction between the two species had a Kappa of 0.270 (Appendix S1).

The results showed that the contact zone of *V. seoanei* and *V. aspis* in the central sector of Northern Iberia has an area of competitive exclusion and 10 OGUs suitable for coexistence. Both species have been recorded in three of these OGUs. *V. seoanei* was more favoured in the coastal slopes of the Cantabrian Mountains, whereas *V. aspis* was more favoured in inner areas of the pre-Pyrenees (Figure 6.5b). Within the areas of shared intermediate favourability, *V. seoanei* was more favoured in the lower ranges (between 0.2 and 0.4) and the higher ranges (between 0.6 and 0.8), whereas *V. aspis* was more favoured in the mid-ranges (between 0.4 and 0.6; Figure 6.5b). The interaction between the two species had a Kappa value of 0.286 (see Appendix S2 for the classification matrix of interaction). Both species occurred in the OGUs predicted as areas of sustainable sympatric coexistence (3 OGUs), competitive exclusion (11 OGUs for *V. seoanei* as the best competitor, and 16 more favourable for *V. aspis*) and environmental segregation (2 OGUs).

V. aspis and *V. latastei* co-occur in the Pyrenees, the Iberian System and the upper reach of the River Ebro region in the Cantabrian Mountains. In these regions, *V. aspis* outcompetes its sister species in the northern areas, whereas *V. latastei* excludes *V. aspis* in the southern area (Figure 6.5c). Regarding shared favourability, the average intermediate values are higher for *V. aspis* than those for *V. latastei* (Figure 6.5c). Their interaction had a Kappa value of 0.436 (see Appendix S3 for the classification matrix). In all, 17 OGUs were identified as suitable for sympatric coexistence: in fact, both species are present in three of them. The other OGUs with the presence of both species were identified as 'competitive exclusion' areas, in which *V. aspis* is a better competitor in 29 OGUs and *V. latastei* in 26.

Regarding interspecific interactions between the three species, only one OGU with sustainable sympatric coexistence was detected in the central Pyrenees and 131 OGUs were identified as areas of competitive exclusion in the central-northern part of the Iberian Peninsula (Figure 6.5d). Favourability values for *V. aspis* were higher than for *V. seoanei* and both species had higher intermediate values than *V. latastei* in the shared favourability gradient (Figure 6.5d).

Table 6.2. Variables included in the modelling process with their coefficients (β), Standard Errors of them (E.T.), Wald test values, and significance (*p*) for each step. The variables are ranked according to their order of entrance. Codes are the same as in Table 6.1.

Variables	**β**	**E.T.**	**Wald**	***p***
V. aspis				
Slope	0.249	0.055	20.538	< 0.001
Poakfor	2.979	0.552	29.107	< 0.001
Ppast	–13.011	2.330	31.191	< 0.001
Dt20	–0.154	0.025	36.923	< 0.001
Aeva	0.011	0.0015	46.470	< 0.001
Dt0	–0.049	0.0062	62.311	< 0.001
Alti	0.0043	0.00066	43.599	< 0.001
Hujan	–0.158	0.025	40.967	< 0.001
Dp30	–0.155	0.043	13.080	< 0.001
Constant	6.233	2.130	8.563	< 0.005
V. latastei				
Alti	0.0014	0.00024	34.550	< 0.001
Dp01	–0.031	0.0028	120.649	< 0.001
Aeva	0.0029	0.00036	66.152	< 0.001
Pagri	–3.729	0.359	107.978	< 0.001
Pcrop	–2.120	0.176	144.346	< 0.001
Dt0	–0.012	0.0021	32.992	< 0.001
Slop	–0.072	0.020	12.649	< 0.001
Tjul	–0.197	0.037	28.675	< 0.001
Ppast	–4.853	1.190	16.629	< 0.001
Hujan	0.032	0.0095	11.187	< 0.005
Dp30	0.057	0.017	11.287	< 0.005
Dfog	–0.0079	0.0029	7.074	< 0.01
Constant	1.333	1.052	1.608	< 0.5
V. seoanei				
Srad	–2.276	0.309	54.421	< 0.001
Pcrop	–2.936	0.698	17.683	< 0.001
Pmixfor	–5.140	1.606	10.238	< 0.005
Dfog	0.018	0.0044	7.096	< 0.001
Psand	280.153	105.169	15.791	< 0.01
Tmean	–0.259	0.054	23.384	< 0.001
Slop	–0.144	0.038	14.550	< 0.001
Dp10	0.026	0.0084	9.658	< 0.005
Ppast	2.236	1.101	4.127	< 0.05
Constant	10.864	1.569	48.000098	< 0.001

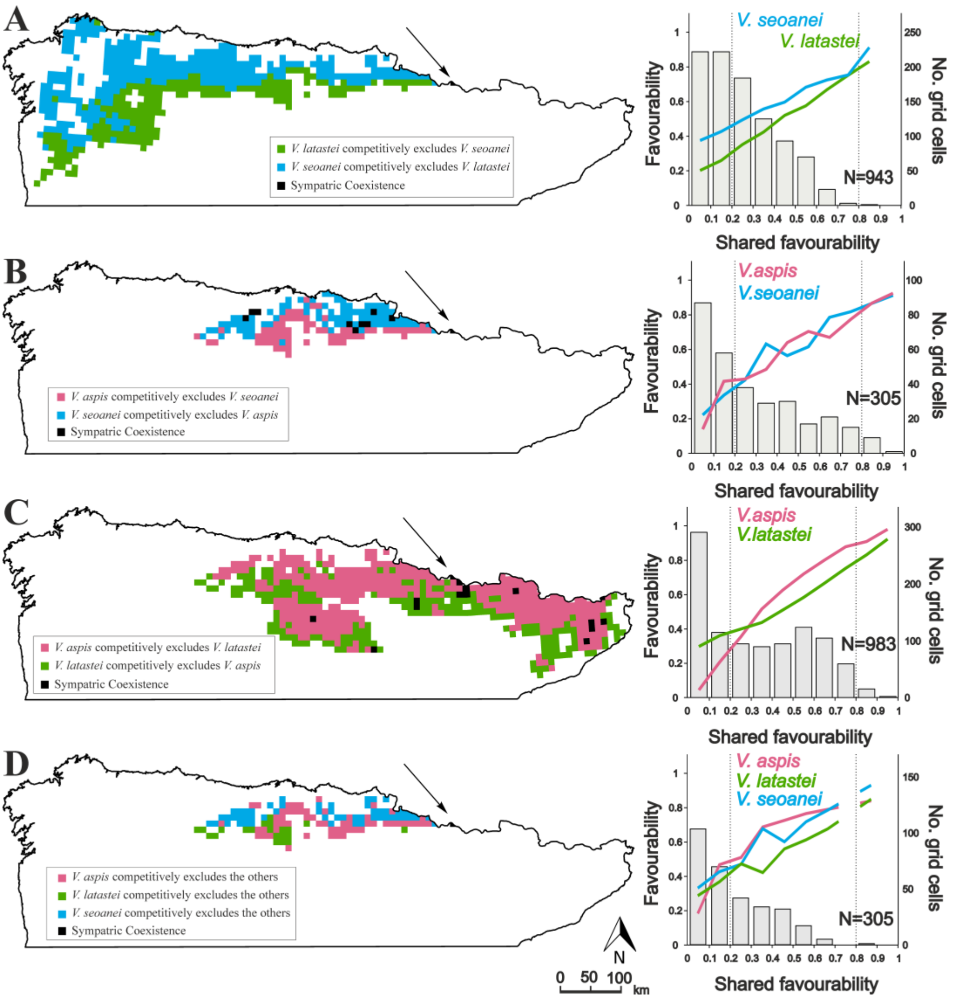


Figure 6.5. Areas where competitive exclusion and sympatric coexistence were identified for **(A)** *V. latastei* with *V. seoanei*, **(B)** *V. seoanei* with *V. aspis*, **(C)** *V. latastei* with *V. aspis* and **(D)** the three species together. White areas are those identified as ‘environmental segregation’. The arrow marks the common ‘sympatric coexistence’ area predicted for the four models. The graphs are the representation of the mean favourability of each species at the 10 intervals (0.1 widths) of shared favourability (i.e. the minimum favourability values for both species) within their contact areas. The histogram represents the number of OGUs in each shared favourability interval.

6.4 DISCUSSION

Iberian vipers represent an interesting example of parapatry in which each species is better adapted to particular environmental conditions on its side of the shared border. Well inside the distribution range each species finds favourable areas and minimizes competition with congeners. However, distribution limits are fuzzy, and in those border areas where interactions may occur, one of the species has the chance to outcompete the other if its ecological requirements are covered in a higher degree.

We found that the use of the favourability function for obtaining species distribution models was suitable to compare the biogeographical patterns of the three species for two main reasons: (a) it is not affected by the prevalence of the dataset, so different species with different amount of presences and absences can be commensurately compared (Acevedo & Real 2012); and (b) it produces an equation which is the response of the species to the environmental conditions, adding notions of graduality to the niche theory, such as those included in Maguire's (1973) definition of niche (Gouveia *et al.* 2020). With this function, Acevedo *et al.* (2010) established a framework to identify the locations where the competitive exclusion or sustainable coexistence could be expected within the distribution ranges of competing species. This framework may be applied to those cases where the struggle for resources could be a key-factor explaining species distributions, and also takes into consideration the influence of the environmental heterogeneity in the interspecific interactions (e.g. Ripple & Beschta 2006, de Fouw *et al.* 2020).

6.4.1 Ecological requirements and species distribution

On a broad scale, climate is usually the main factor explaining species distributions. This is particularly true in the case of reptiles, which are generally very sensitive to solar energy availability and precipitation (Guisan & Hofer 2003, Alatawi *et al.* 2020). It is also the case regarding the Iberian distributions of the three species studied. The main factors explaining the distribution of *V. seoanei* were those related with humid and fresh environments characteristic of the Atlantic climate, which concurs with what Martínez-Freiría *et al.* (2008) found at local scale. Therefore, the lack of favourable areas in the Mediterranean region (Figure 6.1b and Figure 6.4b) suggests that the species major adaptations for the humid conditions limited its distribution to areas under Atlantic influence. For the para-Mediterranean *V. aspis* and the Mediterranean *V. latastei*, the variables that explained their distributions were more similar between them than with *V. seoanei*, probably due to their closer phylogenetic relatedness (Martínez-Freiría *et al.* 2020). Some of these variables are related to their requirements of warm conditions at high-altitude areas (Martínez-Freiría *et al.* 2020), such as elevation, high actual evapotranspiration and scarcity of frost days (Table 6.2), similar to other Mediterranean species (Real *et al.* 1997, Brito *et al.* 1999). Other climatic variables had a lower explanatory power (see Wald's values in Table 6.2) and influenced the species distributions on a smaller scale (Chamorro *et al.* 2017). These variables are different for both species due to differences in the training area where the environmental models were performed for each species (Figure 6.4a). There are unfavourable areas for *V. latastei* in the north-western corner of Iberia (Figure 6.4a,b) due to their prevailing Atlantic climate, too humid and without enough radiation for the survival of Mediterranean species (Santos *et al.* 2006, Martínez-Freiría *et al.* 2020). However, *V.* aspis presents environmentally favourable areas into the Atlantic-influenced region (Figure 6.4b), which indicates a high tolerance to fresh environments, i.e. the species is not physiologically limited to Mediterranean conditions (Martínez-Freiría et al., 2008, 2020). We also found environmentally favourable areas for *V. aspis* in the Mediterranean Iberia where it has never been detected (Figure 6.4b), although the environmental conditions are similar to the conditions of other areas that the species inhabits, such as Italy or Sicily (Sillero *et al.* 2014). The absence of *V. aspis* in these environmentally favourable regions may indicate that the edge of its current range is better explained by the competition with the other species rather than by environmental limitations.

The locations of Pleistocene refugia from which these species expanded to Iberia are also relevant to explain their current distribution, as it is also important for many other herptiles (Gómez & Lunt 2007, Lucati *et al.* 2020). *V. aspis* is thought to have had Pleistocene refuges surrounding the Pyrenees from where it expanded to its current Iberian distribution (Martínez-Freiría *et al.* 2020). Despite having favourable areas at western and southern Iberia, it could not occupy them because *V. seoanei* and *V. latastei* likely had already occupied them due to having their Pleistocene refugia closer to these areas (Martínez-Freiría et al., 2015, 2020). Moreover, the fragmentation of the areas of southern Iberia favourable for *V. aspis* (Figure 6.4b), likely due to human activity in flatlands or valleys, could also hinder its expansion, as species are more probable to expand their distributions into continuous favourable areas where the abundance of resources facilitates the establishment of viable populations (Easteal *et al.* 1985).

The inclusion of human-altered habitats and agricultural land-uses (such as pastures and crops) in the models had a negative effect on the modelled distribution. This finding suggests that human influence is one of the strongest factors limiting the distribution of these species (Santos *et al.* 2006). However, human influence is a factor that sometimes cannot be directly measured (Niamir *et al.* 2016). Thus, high PPI values for all the viper models could be partially the result of a high number of environmentally favourable areas where humans are preventing the species from becoming established.

6.4.2 Contact zones and species interactions

Even though the general distribution patterns may be explained by the vipers' evolutionary history and ecological adaptions, they may not be sufficient to explain their parapatry. In the region of northern Iberia in which the favourable areas for the three vipers partially overlap, the distribution limits of each species are well defined by the most favourable conditions for the other two (except in a few areas in which environmental segregation is the prevailing phenomenon). This aspect suggests that interspecific competitive exclusion plays a relevant role in maintaining the parapatric distributions.

In the eastern part of the overlapping zone in the Pyrenees, *V. aspis* seems to be a better competitor than *V. latastei* in transition areas between montane and Mediterranean zones (Figure 6.1b). This finding is likely due to the better tolerance of *V. aspis* to fresh and humid conditions (Martínez-Freiría *et al.* 2008). However, *V. aspis* distribution is limited towards the south due to the occurrence of *V. latastei*, which is better adapted to pure Mediterranean conditions (Santos *et al.* 2006, Martínez-Freiría *et al.* 2008). *V. aspis* could expand its distribution through the Iberian Peninsula, but the existence of a 'competitive-exclusion barrier' by *V. lastastei* blocks *V. aspis* from the Mediterranean region. However, *V. aspis* outcompetes *V. latastei* at the Pyrenees. Thus the two species generate a dynamic unstable equilibrium of bidirectional competitive exclusions.

In the western Euro-Siberian areas, *V. seoanei* seems to be a better competitor than the others, forming a 'competitive-exclusion barrier' that prevents the establishment of the other species (Figure 6.5a,b). *V. aspis* is predicted to outcompete *V. seoanei* in some Euro-Siberian areas at the pre-Pyrenees with an ecotone to Mediterranean conditions (Figure 6.5b). There is a similar situation between *V. aspis* and other Euro-Siberian species, such as *V. berus* in northern Italy (Scali *et al.* 2011) or western France (Guiller *et al.* 2017). *V. latastei* only outcompetes *V. seoanei* in the southern limit of the Euro-Siberian region (Figure 6.5a), which is likely due to the environmental particularities of these areas – such as microclimates with strong Mediterranean conditions (Beck *et al.* 2018) – that give Mediterranean species an advantage in the struggle for resources (Santos *et al.* 2006, Martínez-Freiría *et al.* 2020). Thus, as suggested in previous studies (Martínez-Freiría *et al.* 2015), the specialization to Euro-Siberian conditions appears to be the factor that limit the current range of *V. seoanei*. Interspecific competition also affects the distribution of *V. seoanei*, but only in marginal areas within the overlapping zones (Figure 6.5a,b,d).

Darwin (1859) indicated that the edge of a species distribution is often determined by the border of a related species. Hardin (1960) considered that many parapatric species pairs with nearly identical ecological requirements were ecologically incompatible. In our study case, only a few OGUs were predicted as suitable for their sympatric coexistence. These species exhibit similarities in environmental requirements despite there being subtle difference between these requirements (Martínez-Freiría *et al.* 2008, 2020). Thus, it would be expected that their sympatric coexistence would be hindered by their sharing a common space, particularly when resources are limited (Gause 1934). This suggestion is in agreement with observations at finer scales. In this case, these species normally follow habitat segregation: *V. latastei* tends to occupy warmer and dryer habitats at lower altitudes, *V. aspis* tends to occupy warmer but humid habitats at lower altitudes and *V. seoanei* tends to occupy cooler and more humid habitats at higher altitudes. Nevertheless, some environmental conditions facilitate their sympatric coexistence (Martínez-Freiría *et al.* 2008). Our results pinpoint the location of the areas in which such environmental conditions favour the occurrence of sympatry. The finding that more OGUs with sympatric coexistence are predicted in areas in which *V. aspis* is in contact with *V. seoanei* or *V. latastei* is likely because the former species shows high tolerance regarding its ecological requirements, which means that more resources can be utilized and competitive effects are minimized (Sillero *et al.* 2014, McPeek 2019). However, *V. latastei* and *V. seoanei* only share one sympatric coexistence area, which may indicate that the resources common to both species are scarce.

It is striking that any two of these species inhabit less than 1% of areas predicted to have sustainable sympatric coexistence. This finding suggests that the best environmental conditions (i.e. those in which the potential effect of interspecific competition is reduced) are not in the areas in which these species are in contact. It may also suggest that there are other unaddressed factors that could affect the sympatric coexistence of the species (e.g. the presence of specific prey or resources; McPeek 2019). The sympatric areas with the presence of each pair of species were also identified as zones of coexistence for the species at finer-scale. This is the case for *V. latastei* and *V. aspis* at pre-Pyrenees, upper reaches of the River Ebro valley and northern Iberian System (Duguy *et al.* 1979, Martínez-Freiría *et al.* 2008, Zuazo *et al.* 2019) and for *V. seoanei* and *V. aspis* at the Basque Country (Bea 1985). However, the only area predicted as suitable for the sympatric coexistence of *V. latastei* and *V. seoanei* pair is in the western Pyrenees, where they do not occur. These results do not suggest that the species cannot be found together in sub-optimal areas that are not predicted as suitable for sustainable sympatric coexistence, such as the Peneda-Gerês National Park in northern Portugal (Brito & Crespo 2002). Studies at finer scales suggest that other factors such as temporal segregation could prevent competitive exclusion, thus allowing both species to remain in such areas and even hybridize during the breeding season when territoriality is weaker (Martínez-Freiría *et al.* 2010).

In summary, he results suggest that ‘competitive-exclusion barriers’, which are formed by strong ecological interactions and different environmental affinities, are the main factor that has led to and maintains the current parapatric pattern of Iberian vipers. Because competitive-exclusion equilibrium relies on environmental factors such as climate, which is currently undergoing rapid shifts, the species ranges will likely change in the near future (Bulgarella *et al.* 2014). These rapid changes could worsen the conservation status of the species given that low densities and high vulnerability to habitat and climate change are already threatening Iberian viper populations (Santos *et al.* 2006, Brito *et al.* 2011). Favourability models are useful tools to reveal the internal complexity of species distribution ranges (Real *et al.* 2003, Acevedo *et al.* 2014), to understand their origins and peculiarities (Acevedo *et al.* 2015) and forecast range dynamics (Muñoz & Real 2006, Chamorro *et al.* 2017, 2020). This study also demonstrates that this methodological approach is of practical use in the study of complex parapatric distributional patterns, provides information on the ecology of the species and helps to establish new directional hypotheses on the effect of competitive exclusion.

Appendix S1. Classification matrix of interaction between *V. latastei* and *V. seoanei* (nº OGUs)

		Categories of the occurrence data				
		Absence of both species	Presence of *V. latastei* but not *V. seoanei*	Presence of *V. seoanei* but not *V. latastei*	Presence of both species	TOTAL
Categories of favourability values	**Environmentally Unfavourable (for at least one species)**	267	21	156	0	**444**
	Intermediate shared environmental favourability more favourable for *V. latastei*	85	40	52	14	**191**
	Intermediate shared environmental favourability more favourable for *V. seoanei*	89	2	208	8	**307**
	Environmentally favourable for both of them	1	0	0	0	**1**
	TOTAL	**442**	**63**	**416**	**22**	**943**

Appendix S2. Classification matrix of interaction between *V. aspis* and *V. seoanei* (nº OGUs)

		Categories of the occurrence data				
		Absence of both species	Presence of *V. aspis* but not *V. seoanei*	Presence of *V. seoanei* but not *V. aspis*	Presence of both species	TOTAL
Categories of favourability values	**Environmentally Unfavourable (for at least one species)**	75	31	37	2	**145**
	Intermediate shared environmental favourability more favourable for *V. aspis*	13	28	10	16	**67**
	Intermediate shared environmental favourability more favourable for *V. seoanei*	16	8	48	11	**83**
	Environmentally favourable for both of them	3	0	4	3	**10**
	TOTAL	**107**	**67**	**99**	**32**	**305**

Appendix S3. Classification matrix of interaction between *V. latastei* and *V. aspis* (nº OGUs)

		Categories of the occurrence data				
		Absence of both species	Presence of *V. latastei* but not *V. aspis*	Presence of *V. aspis* but not *V. latastei*	Presence of both species	TOTAL
Categories of favourability values	**Environmentally Unfavourable (for at least one species)**	348	40	15	0	**403**
	Intermediate shared environmental favourability more favourable for *V. latastei*	81	57	32	26	**196**
	Intermediate shared environmental favourability more favourable for *V. aspis*	92	32	214	29	**367**
	Environmentally favourable for both of them	3	1	10	3	**17**
	TOTAL	**524**	**130**	**271**	**58**	**983**

CAPÍTULO 7

NUEVOS HORIZONTES EN LA CONSERVACIÓN DEL IBIS EREMITA USANDO LA FAVORABILIDAD

NEW HORIZONS FOR THE CONSERVATION OF THE NORTHERN BALD IBIS USING THE FAVOURABILITY

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

Chamorro, D., Benítez-Barrios, I., Real, R. & Muñoz, A.-R. Submitted. A biogeographical approach to the past and current distributions of the Western population of the Northern Bald Ibis: new horizons for its conservation.

7 NEW HORIZONS FOR THE CONSERVATION OF THE NORTHERN BALD IBIS USING THE FAVOURABILITY

7.0 RESUMEN

El Ibis Eremita (*Geronticus eremita*) es una de las especies de aves más amenazadas del planeta. En el pasado estuvo ampliamente distribuido por Europa y África, pero en la actualidad las únicas colonias naturales se encuentran en los valles Souss-Massa (Marruecos). Los programas de introducción de ejemplares nacidos en cautividad Proyecto Eremita y LIFE+, de España y Austria respectivamente, cuentan con estudios de hábitat adecuado para la reproducción de la especie, basados principalmente en la localización de sus colonias actuales. Sin embargo, estas colonias no necesariamente tienen por qué encontrarse en los hábitats más adecuados para la especie, sino en aquellos donde ha podido persistir. Los objetivos que se abordan en este capítulo son: (1) analizar la distribución histórica de las colonias reproductoras marroquís mediante aproximaciones espaciales y ambientales, (2) evaluar la favorabilidad ambiental que presentan las colonias actuales de Ibis Eremita en base a datos históricos de reproducción confirmada y su localización actual, (3) identificar zonas de interés cuya conservación pueda favorecer la supervivencia de la especie, y (4) proponer el uso de la modelación espacial en las políticas de gestión y conservación de la especie en el contexto sur de España-Marruecos. Para ello se realizaron

modelos de distribución de especies (SDMs) de favorabilidad con las presencias de las colonias reproductoras de la especie durante el siglo XX en Marruecos y las presencias actuales en Marruecos y en España, estas últimas derivadas del proyecto de introducción. Las colonias reproductoras del siglo XX mostraban un patrón espacial con alta conectividad entre las colonias de Agadir y las colonias de la costa del Mediterráneo, a través de las cordilleras del Medio y el Alto Atlas. Ambientalmente, ambas costas del Estrecho de Gibraltar, así como otras zonas de la península ibérica, fueron identificadas como zonas favorables para la reproducción del ibis en el siglo XX aunque la especie no criaba en ellas. Sin embargo, sólo las colonias de Agadir se encontraban en territorio ambientalmente favorable. Actualmente, la favorabilidad ambiental está localizada en la costa Atlántica de Marruecos, en los alrededores de las colonias actuales y hacia el sur, lo que podría favorecer el establecimiento en esa zona de nuevas colonias en un futuro próximo (como ya ocurrió en 2017). Las colonias introducidas en España, así como las establecidas naturalmente en 2017, al norte de las colonias principales en Marruecos, se encuentran en zonas ambientalmente muy favorables atendiendo a la distribución histórica. Teniendo en cuenta estas colonias, se observa una conectividad potencial de zonas favorables y de favorabilidad intermedia entre las colonias naturales y las colonias introducidas. Esto plantea la posibilidad de que se forme una estructura dinámica metapoblacional que podría beneficiar a la especie, algo que abre la puerta a nuevos enfoques en la conservación de esta y otras especies críticamente amenazadas.

7.0 ABSTRACT

The Northern Bald Ibis (*Geronticus eremita*) is one of the most endangered bird species on the planet. In the past, it was widely distributed through Europe and Africa, but today the only natural colonies are found in the valleys Souss-Massa (Morocco). The introduction programmes of born-in-captivity individuals 'Proyecto Eremita' and LIFE+, in Spain and Austria, respectively, were supported by studies of suitable habitat for the species reproduction, which are mainly based on the location of its current colonies. However, these colonies do not necessarily have to be in the most favourable habitats for the species, but in those where it has been able to remain. The aims addressed in this chapter are (1) to analyse the historical distribution of Moroccan breeding colonies by spatial and environmental approaches, (2) to evaluate the environmental favourability of current Northern Bald Ibis colonies based on historical data of confirmed reproduction and their current location, (3) to identify potential areas whose conservation could benefit the species' survival, and (4) to propose the use of biogeographical modelling in the politics of management and conservation of the species in the Spanish-Moroccan context. To this end, species distribution models (SDMs) of favourability were performed using the presence of breeding colonies during the 20th century in Morocco and current presences in Morocco and Spain. The breeding colonies of the 20th century showed a spatial pattern with high connectivity between the colonies of Agadir and the colonies of the Mediterranean coast through the Middle and High Atlas mountain ranges. Environmentally, both coasts of the Strait of Gibraltar, as well as

other areas of the Iberian Peninsula, were identified as favourable areas for the reproduction of the ibis during the 20th century despite the fact that the ibises did not breed there. In Morocco, only the colonies of Agadir were located in favourable areas. At present, the environmental favourability is located on the Atlantic coast of Morocco, in the surroundings of the current colonies and towards the south, which could favour the establishment of new colonies at this area in the near future (as it has already happened in 2017). The Spanish introduced colonies, as well as those naturally established in 2017 northwards of the main colonies in Morocco, are located in environmentally favourable areas according to their historical distribution. Taking into account these current colonies, it is showed a potential connectivity of intermediate and high favourability areas between the natural and introduced colonies. This raises the possibility of the creation of a dynamic metapopulation structure that could benefit the species, something that opens the door to a new standpoint of the conservation of this and others critically endangered species.

7.1 INTRODUCTION

The Northern Bald Ibis (*Geronticus eremita*) is an endangered species (BirdLife International 2018) which was, until the XVII century, widely distributed in northern Africa, the Middle East, and Central Europe (Pegoraro 1996). In the beginning of the 20th century, the remaining wild birds had been circumscribed to two disjointed genetically different populations in North-Western Africa (Morocco and Algeria) and the Middle East (Turkey and Syria) (Pegoraro *et al.* 2001). This fragmented distribution experienced an important reduction in the second half of the last century and evolved into the present situation (BirdLife International 2018). Factors such as poisoning via phytosanitary products, hunting, capture for zoos, changes in land use due to city growth, intensive agriculture, and livestock farming contributed to the ibis population's decline (Muñoz *et al.* 2002, Bowden *et al.* 2003, 2008, Böhm *et al.* 2020). Currently, the remaining wild populations persist only in the southwestern Atlantic coast of Morocco, where the species is primarily resident (Bowden *et al.* 2003, Böhm *et al.* 2020).

Due to this range contraction over the last century, European ex-situ conservation programs are attempting to reintroduce the species funded by the European Union's LIFE programme (http://waldrapp.eu/index.php/en/project/project-info), and also of the Environmental Agency of Andalusia, in Spain (Aguilera *et al.* 2012). Their main objectives are to reintroduce a migratory population in central Europe (the first attempt to reintroduce a continentally extinct migratory species), and to create a new sedentary population in Southern Spain, respectively. In Morocco, due to a successful protection campaign that included the declaration of the Souss-Massa National Park in 1991, the number of birds is increasing, and new breeding sites have recently been found (Aourir 2017). This conservation success suggests the possibility that the area currently occupied by the species may expand in the future, requiring the development of new management tools and conservation policies to ensure the future of the Northern Bald Ibis.

How a species utilizes the geographic space is one of the key issues in conservation biogeography (Whittaker *et al.* 2005). Differential habitat use can be inferred from the known distribution of the species by applying spatial modelling techniques. Species distribution models (SDMs) are being used to study the relationship between known occurrences of species and the characteristics of the ecological and environmental landscape, allowing the prediction of the most favourable areas for species presence (e.g. Chamorro *et al.* 2017, 2019, 2020). Generally, these approaches aim to characterize the species' ecological requirements and/or predict potential distributions using occurrence data and a set of predictor variables.

Our aims in this study are threefold. Firs, we aim to identify areas potentially favourable for the species based on climate and topography. Second, we aim to analyse the spatial structure of the past distribution of the species as an influential factor, while balancing the inertia promoted by previously considered factors (climate and topography). This may be particularly relevant in the case of this globally endangered, long-lived species, with their deferred maturity and philopatric behaviour. Finally, we discuss potential implications for reintroduction programs to at least partially restore its distribution range, as well as the potential role of the recently established breeding colony in Southern Spain, as these reintroduced ibises have already demonstrated the capacity to reach Morocco.

7.2 METHODS

7.2.1 Study area

The study area comprised the southern half of the Iberian Peninsula (Iberia) and Morocco between 38º55'N and 27º40'N (Figure 7.1), corresponding 407,660.05 km^2 to Morocco and 170,289.85 km^2 to Iberia. The Moroccan area is bordered by Algeria in the East, Western Sahara in the south, and the Atlantic Ocean in the west. The southern half of Iberia is surrounded by the Atlantic Ocean in the west and the Mediterranean Sea in the East, separated from Morocco by the Strait of Gibraltar. We selected Morocco as the last place that Northern Bald Ibis colonies remain in the wild, and we included the southern half of Iberia due to the "Proyecto Eremita" conservation programs. The climate is predominantly Mediterranean (Font 2000), but it is influenced by the Atlantic Ocean in the western coastal regions, the Sahara desert in southern Morocco, and the high mountain ranges of Morocco (Atlas and Rif) and Iberia (Baetic System and Sierra Morena) (Fischer 1902, Playfair 1902).

7.2.2 Species data and predictors

To model the Northern Bald Ibis's distribution, we used Google Earth software to georeference the locations of the confirmed breeding colonies during the 20th century. We sourced the locations from the BOU Checklist No. 20 (Thévenot *et al.* 2003) and some unpublished updates, along with data on the new breeding colonies established in 2017 from Aourir (2017) and the colonies of the Spanish-introduced individuals from "Proyecto Eremita" (López *et al.* 2015) (Figure 7.1). Then, they were transformed in a presence-absence matrix using a UTM 10×10 km grid cell as operational geographic units (OGUs, n = 5752), corresponding 4092 OGUs to Morocco and 1660 to the southern half of the Iberian Peninsula. OGUs with breeding colonies during the 20th century were considered as Extinct if they were no longer present (57), or Remaining if they were still present (4). Remaining OGUs were also considered from the 21st century, together with OGUs with Aourir (2017) colonies (*New* = 2) and OGUs with López et al. (2015) breeding colonies (*Introduced* = 2) (Figure 7.1).

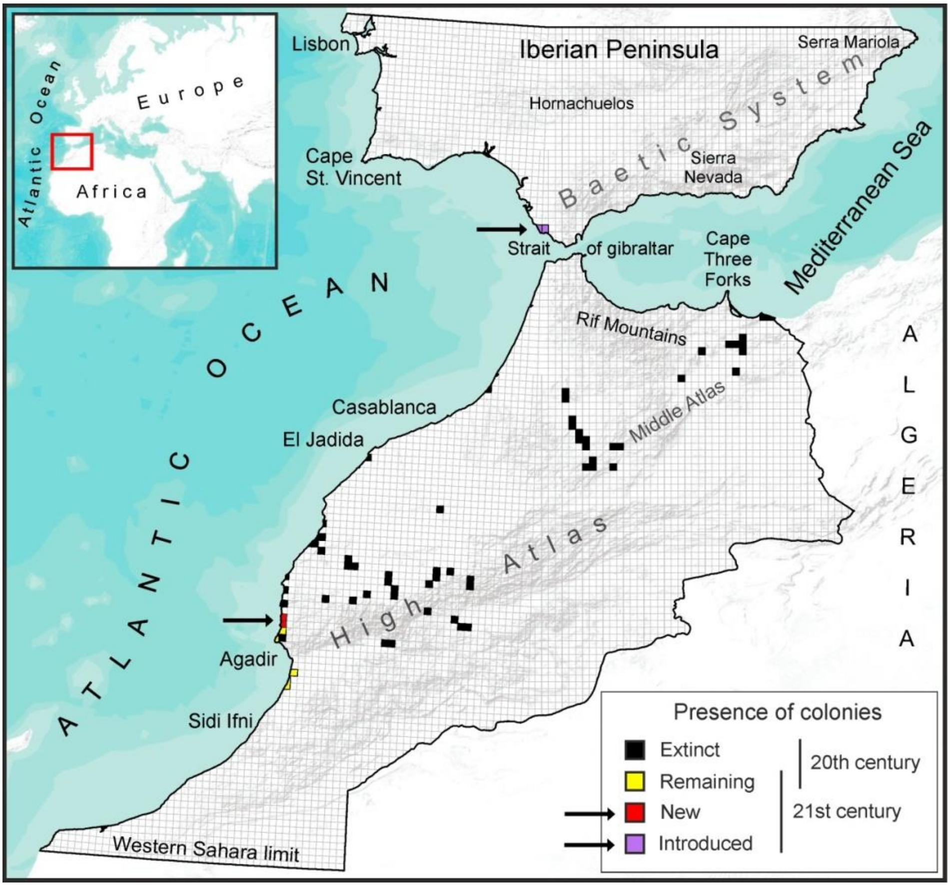


Figure 7.1. Presence distribution of the ibis breeding colonies at UTM 10×10 km cells: 20th century colonies = *Extinct* + *Remaining* colonies; 21st c. colonies = *Remaining* + *New* (Aourir 2017) +*Introduced* (from Eremita Project) colonies (López *et al.* 2015).

Table 7.1. Variables used to model the distribution of the Northern Bald Ibis colonies.

Code	Variable	Units	Source
Topography			
Alti	Altitude	m	1
Slop	Slope	degrees	2
Spatial coordinates			
La	Latitude	degrees N	3
Lo	Longitude	degrees E	3
Climate			
MeanTemp	Annual Mean Temperature	ºC × 10	4
DiTempRange	Mean Diurnal Temp. Range	ºC × 10	4
Isoth	Isothermally	%	4
TempSeason	Temperature Seasonality	Standard deviation	4
MaxTemp	Max. Temp. of Warmest Month	ºC × 10	4
MinTemp	Min. Temp. of Coldest Month	ºC × 10	4
TempAnRange	Temperature Annual Range	ºC × 10	4
TempWetQ	Mean Temp. of Wettest Quarter	ºC × 10	4
TempDryQ	Mean Temp. of Driest Quarter	ºC × 10	4
TempWarmQ	Mean Temp. of Warmest Quarter	ºC × 10	4
TempColdQ	Mean Temp. of Coldest Quarter	ºC × 10	4
Prec	Annual Precipitation	mm	4
PrecWetMonth	Precipitation of Wettest Month	mm	4
PrecDryMonth	Precipitation of Driest Month	mm	4
PrecSeason	Precipitation Seasonality	Coefficient of variation	4
PrecWetQ	Precipitation of Wettest Quarter	mm	4
PrecDryQ	Precipitation of Driest Quarter	mm	4
PrecWarmQ	Precipitation of Warmest Quarter	mm	4
PrecColdQ	Precipitation of Coldest Quarter	mm	4

Data sources: 1 – (US Geological Survey 1996), 2 – calculated from *Alti* with ARCGIS software, 3 – calculated from a georeferenced shapefile of the study area with ARCGIS software, 4 – (Hijmans *et al.* 2005).

Twenty-one environmental independent variables related to topography and climate and nine spatial variables were used to identify factors that could shape the location of the Northern Bald Ibis colonies (Table 7.1). These variables were chosen according to their potential predictive power, and were assumed to be correlated to a higher number of probable causal factors (Muñoz *et al.* 2005). We calculated mean values of these variables at each OGU using ZONAL function of ARCGIS software (Muñoz *et al.* 2005). Land-use variables were not taken into consideration due to the significant change in the landscape of the study area during the past century, which is not represented in the available land-use variables.

7.2.3 Distribution modelling

Environmental variables were selected before modelling the following steps. First, the multicollinearity between them was reduced by calculating the Spearman correlation coefficients, retaining only one variable of each pair with $r > 0.8$ according to the significance (α) of the score test of univariate logistic regressions (Fa *et al.* 2014). Then, the False Discovery Rate (FDR, Benjamini & Yekutieli 2001) for the subset of environmental variables that passed the Spearman test was evaluated to reduce the possibility of commit type I errors. Only variables significantly associated with the distribution of the species with significance $\alpha < 0.05$ under an FDR value below 0.05 were accepted in subsequent modelling steps (Benjamini & Yekutieli 2001).

Forward-backward stepwise logistic regression was the modelling algorithm selected for obtaining comprehensive models of the probability of breeding at every OGU according to predictors. This is a supervised machine learning approach that assesses the predictive power of each variable according to the significance (α) of the score test of the corresponding regression. It starts with a model with no predictors (i.e. a null model), which yields a constant probability of breeding at each OGU equal to the prevalence of the OGUs where colonies were reported in the dataset. Then, a significant combination of variables (*y* or *logit*) is built by adding the predictors that provide the most significant contribution to the model obtained in the previous step (Hosmer & Lemeshow 1980, 2000b), unless no predictor significantly adds to the null model, in which case no model is produced. Variables that do not significantly add to the predictive power of the final model are not included to avoid redundancy, as their effect, if any, is already included via correlated variables. The order of entrance in the modelling procedure of the variables is related to the scale of their influence. Those with an overall, broad-scale predictive power are entered first, while those that add significant nuances to the previous model are entered in subsequent steps.

The effect of prevalence on the resulting probability models was discounted to extract the pure response of the species to conditions that facilitate its breeding (Acevedo & Real 2012, Gouveia *et al.* 2020) via obtaining favourability values (*F*) using the Real *et al.* (2006) equation (2):

$$F = e^{y} + \left(e^{y} + {}^{n_1}/_{n_0}\right), \tag{2}$$

where n_1 and n_0 are the number of presences and absences, respectively, considered in the modelling procedure, *e* is the Euler's number and *y* is the *logit* from the performed logistic regression. Favourability values range from 0 (minimum) to 1 (maximum), where a local favourability value of 0.5 indicates that the local probability of breeding is the same as its prevalence (i.e. expected by a null model). Hence, favourability refers to the degree to which the conditions favour the establishment of a breeding colony of Northern Bald Ibis, with 0.5 as the threshold separating favourable from unfavourable areas (Acevedo & Real 2012, Muñoz *et al.* 2015a). However, given the continuous and fuzzy character of favourability (Acevedo & Real 2012), 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 2000a). Thus, we classified the areas into 'high favourability' ($F \geq 0.75$), 'intermediate favourability' ($0.2 < F < 0.75$) and 'low favourability' ($F \leq 0.2$).

Six different favourability models were constructed to clarify different aspects of the breeding distribution of Northern Bald Ibis (Table 7.2). Two of them were performed using the spatial variables latitude (*La*), longitude (*Lo*) and their combinations up to the third potency (i.e., La^2, La^3, Lo^2, Lo^3, $La \times Lo$, $La^2 \times Lo$, $La \times Lo^2$). This was made in order to detect purely spatial structured patterns that can be associated with historical events, species dynamics, migration routes or populations aggregation (Legendre 1993, Legendre & Legendre 1998, Chamorro *et al.* 2019). One was performed with the breeding colonies of the 20th and another with 21st centuries (SHM and SCM, respectively; Table 7.2). Two other models were built using topography and climate predictors to explain the factors that conditioned (now and in the past) the Northern Bald Ibis's-breeding area (Real *et al.* 2003). An environmental historical model (EHM) was obtained using the species 20th-century presences to identify potentially viable areas for the breeding of the species in the past (Chamorro *et al.* 2020). This was subsequently extrapolated to Iberia to detect environmentally favourable areas in this region (Chamorro *et al.* 2017). An environmental current model

(ECM) in the whole study area was performed to detect potentially favourable areas for the species according to their current situation, with birds on both sides of the Strait, using all OGUs present in the 21st century (Figure 7.1, Table 7.2), in order to analyse the connection between these areas. A model to explain the conditions where the species inhabits in the wild and to identify potentially breeding areas in the near future was performed using environmental and spatial variables in the OGUs of Morocco and the presences of the 20th century remaining at present (ERM, environmental remaining model). Finally, a combined spatial and environmental model (SEM) was obtained by computing the fuzzy intersection between SCM and ECM (i.e. the minimum value of favourability of either at each OGU). This was made in order to obtain an environmental conservative model that identified those areas of consideration for future reintroductions in Morocco. This could promote the potential establishment of a metapopulation structure with the Spanish introduced colonies. All models were evaluated according to discrimination and classification index (see Table 7.2 for a summary of models).

7.2.4 Model evaluation

We used several indices to assess model performance. The weight of each added variable and the estimation of the parameter in the equation were assessed using the Wald test (Wald 1943). The Area Under the receiver operating characteristic Curve (AUC), which has an associated significance value, was used as a measure of discrimination capacity (Lobo *et al.* 2008, Romero *et al.* 2012). Classification accuracy was tested using a set of widely recognized measures, whose values range from 0 to 1 (Fielding & Bell 1997, Barbosa *et al.* 2013). These measures were sensitivity (the conditional probability of OGUs with breeding colonies being classified as favourable), specificity (the conditional probability of OGUs without breeding colonies being classified as unfavourable), correct classification rate (CCR: the conditional probability of correctly classified OGUs), the over-prediction rate (OPR: the proportion of OGUs without breeding colonies in the area with favourability higher than 0.5), and the under-prediction rate (UPR: the proportion of OGUs with breeding colonies in the area with favourability lower than 0.5). Good classification performance is shown by high Kappa, sensitivity, specificity, and CCR values and low over- and under-prediction rate values. We also used Cohen’s Kappa Index to measure the degree to which the favourability of the OGUs with breeding or no-breeding colonies in the dataset was higher or lower than 0.5, respectively, whose values range from –1 to +1 (Cohen 1960).

Table 7.2. Favourability models constructed to clarify different aspects of the breeding distribution of Northern Bald Ibis. Models abbreviations are spatial historical model (SHM), environmental historical model (EHM), environmental remaining model (ERM), spatial current model (SCM), environmental current model (ECM) and spatial-environmental intersection model (SEM). *Area* is the study area where the model was performed, being Morocco (Mo.), Morocco extrapolated to the Iberian Peninsula (Mo./Ib.) or Morocco together with the Iberian Peninsula (MoIb.). *Factor* means the variables that were used in the modelling process. *Presences* is the class of breeding colonies that were used for each model. n_1 and n_0 are the number of OGUS with presence and absence for each model, respectively.

Model	Area	Factor	Presences	n_1	n_0
SHM	Mo.	Spatial	20th century	61	4031
EHM	Mo./Ib.	Environmental	20th century	61	4031
ERM	Mo.	Both	*Remaining*	4	4088
SCM	MoIb.	Spatial	21st century	8	5744
ECM	MoIb.	Environmental	21st century	8	5744
SEM	MoIb.	Both	21st century	8	5744

7.3 RESULTS

Two highly spatial favourable areas (according to historical data) were detected: one from El Jadida to Agadir (where the species is currently present) in the Atlantic coast, and another at the Mediterranean coast from including Cape Three Forks to the Algerian border and inland. Both favourable areas tend to connect with each other (SHM, Figure 7.2). EHM identified the areas currently occupied by the species as highly environmentally favourable, but also highlighted the Strait of Gibraltar and other areas in the Rif Mountains (Figure 7.3). Intermediate favourability areas occurred along the Atlantic coast and in the High and Middle Atlas. We identified highly favourable areas in Spain, which were mostly concentrated around the Strait of Gibraltar and the Sierra Nevada mountains and surroundings areas. We also found an isolated OGU in the Serra Mariola Natural Park (Alicante). We further identified favourable areas in Portugal in Cape St. Vincent and the area around Lisbon. EHM showed some continuity, and thus, potential connectivity, between the identified highly favourable areas and the intermediate favourability areas. Furthermore, all 21st-century breeding colonies were placed in highly favourable areas (Figure 7.3).

Highly favourable areas were identified in ERM north and south of Agadir (in which all known Moroccan breeding colonies are included), and from Sidi Ifni to the border with the Western Sahara (Figure 7.4). Furthermore, this model highlighted an area of intermediate favourability in the Moulouya River basin (North-eastern Morocco), completely isolated from current breeding colonies (Figure 7.4).

SCM showed an elongated ellipse of high favourability from Hornachuelos (Andalusia) to the Western Sahara along the Atlantic coast (Figure 7.5). On the other hand, ECM identified the natural colonies' current location and areas to the south as highly favourable, with an isolated OGU further north (south of Casablanca) in Morocco (Figure 7.5). It also showed highly favourable areas in the Atlantic coast of the Strait of Gibraltar, along with Sierra Nevada and, as before, one OGU in Serra Mariola Natural Park in Spain (Alicante), and in Cape St. Vincent and Lisbon (Portugal). ECM also detected a continuous area of intermediate favourability along the Atlantic coasts of Morocco and the south of the Iberian Peninsula, as well as other OGUs in the Strait of Gibraltar, High Atlas and Rif in Morocco, and the Baetic System in Spain. SEM restricted the highly and intermediate favourable areas to the Moroccan Atlantic coast and the Atlantic coast of the Strait of Gibraltar (Figure 7.5).

Details of the variables entering all models are shown in Table 7.3. Spatial descriptors up to the second potency were needed to describe the breeding distribution in the SCM, whereas spatial descriptors up to the third potency were needed for the SHM, and only climatic variables were entered in the environmental models. (Table 7.3). All models showed acceptable classification (under-prediction rates < 0.03 and high sensitivity) and discrimination (AUC rates > 0.67) capacity (

Table 7.4), being the EHM the one with the lowest classification and discrimination values.

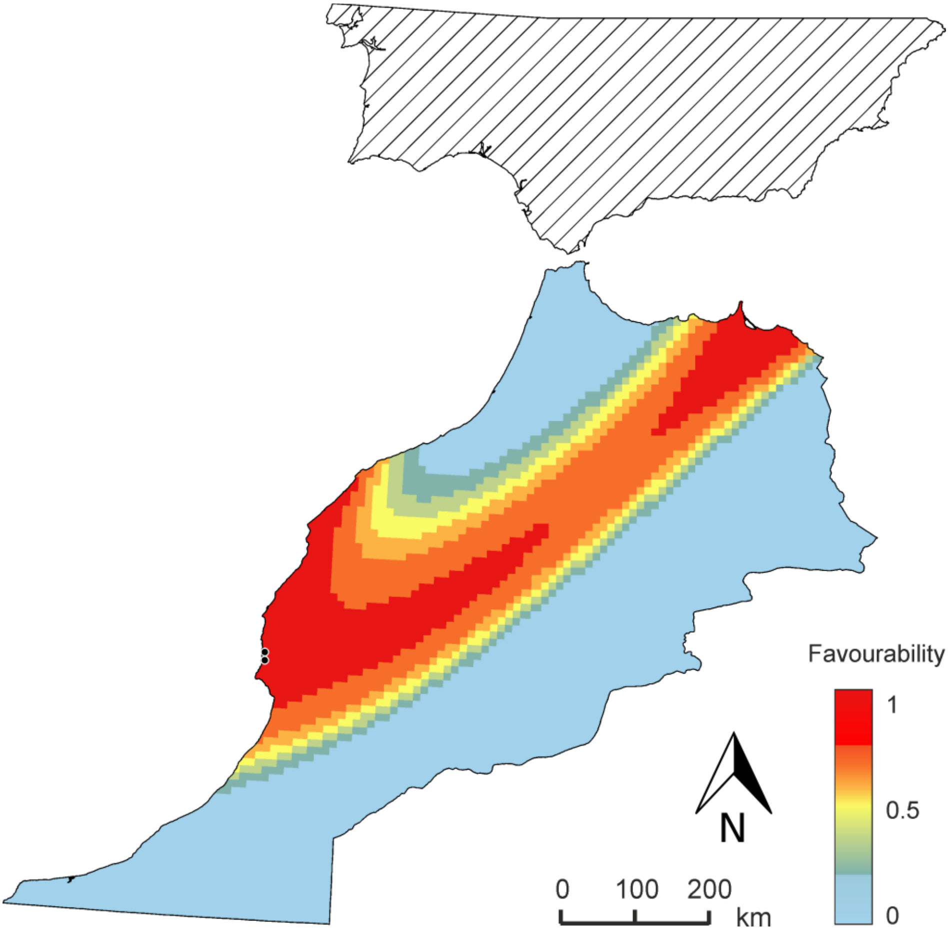


Figure 7.2. Representation of the favourability of the spatial historical model (SHM), built using the 20th century presences in Morocco.

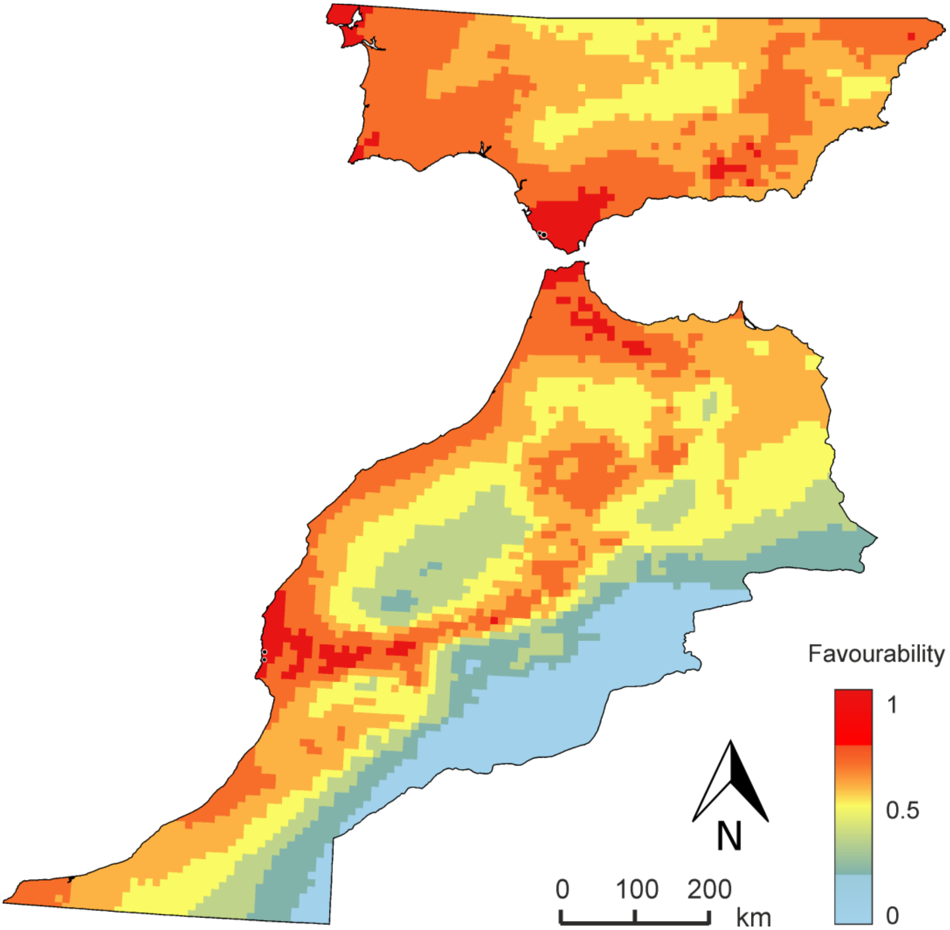


Figure 7.3. Representation of the favourability of the environmental historical model (EHM) built using the 20th century presences in Morocco and then extrapolated to the south of the Iberian Peninsula. Black dots represent the location of the *New* and *Introduced* colonies (López *et al.* 2015, Aourir 2017).

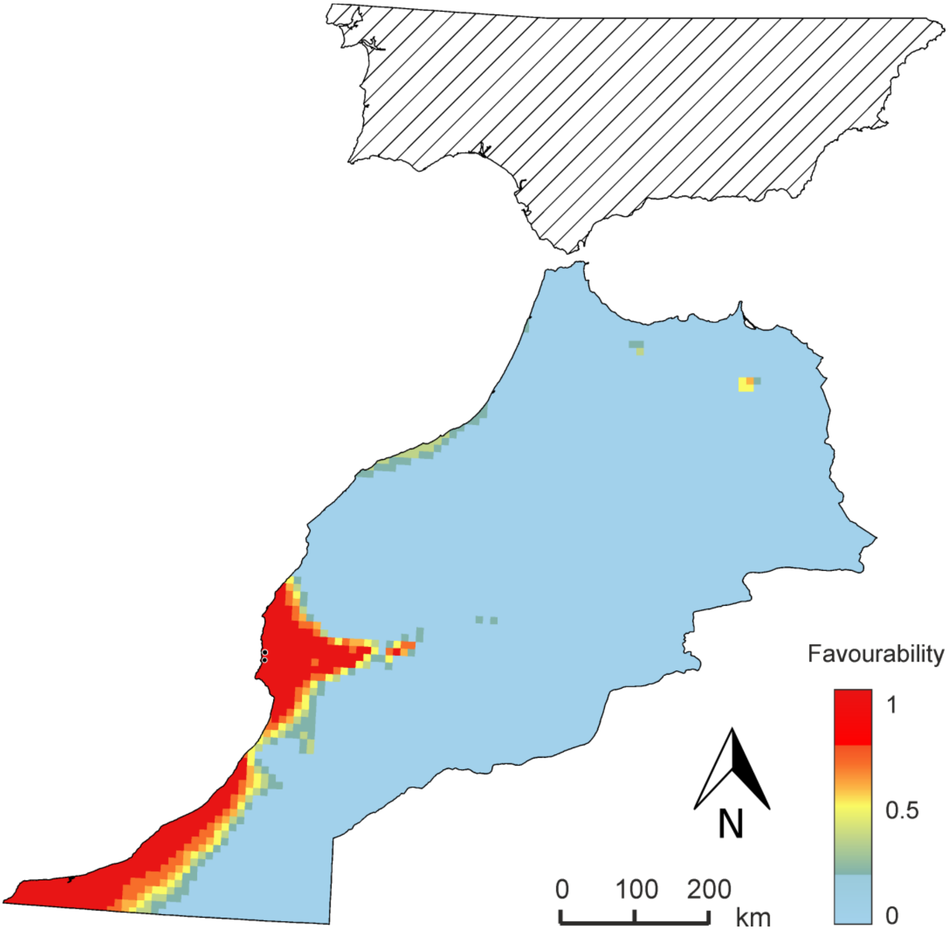


Figure 7.4. Representation of the favourability of the environmental remaining model (ERM), built using the Remaining presences in Morocco (presences from the 20th century still present in the wild). Black dots represent the location of the New colonies (Aourir 2017).

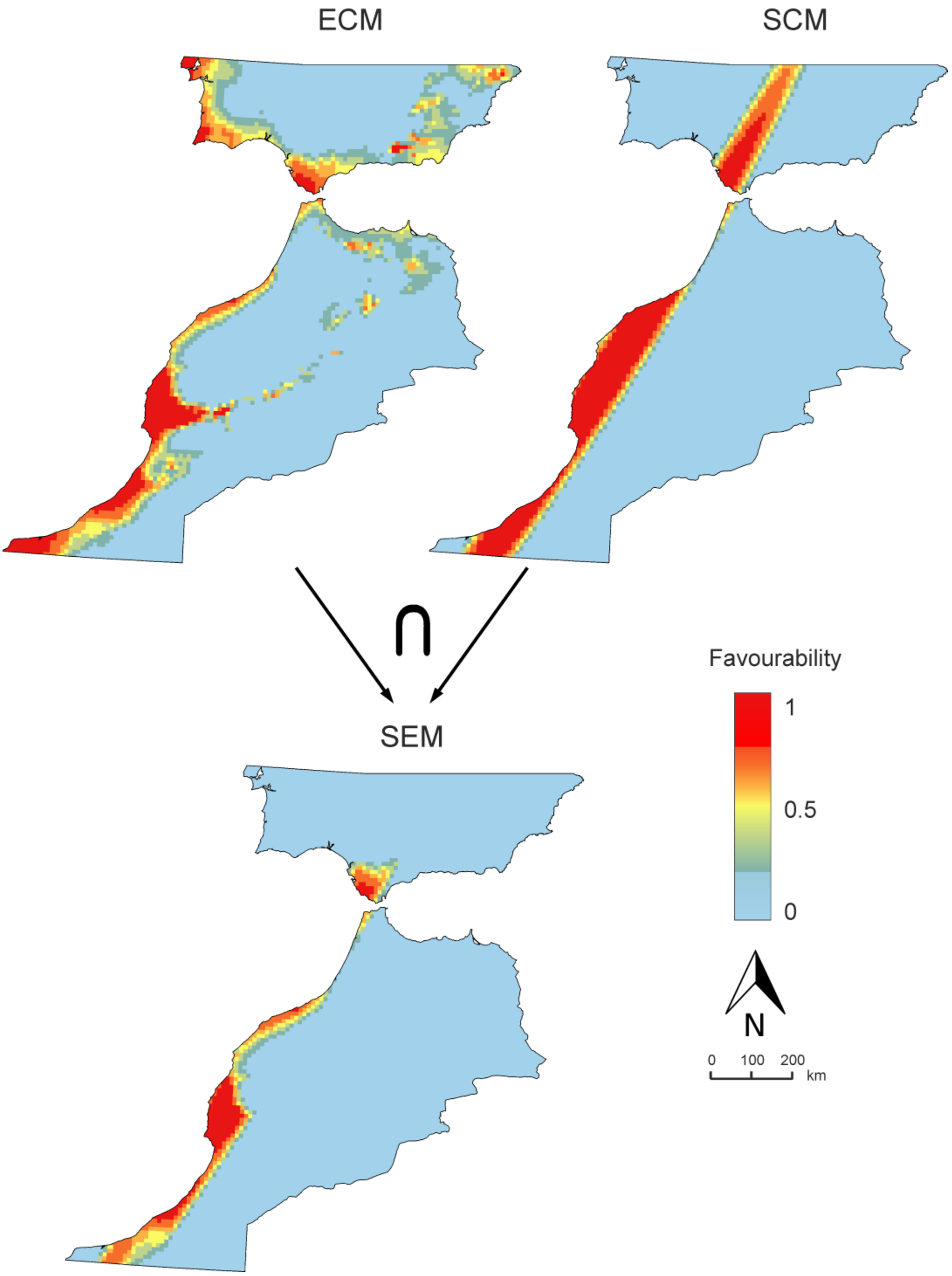


Figure 7.5. Representation of the current favourability models, built using the 21st century presences in Morocco together with the southern half of the Iberian Peninsula. SCM is the spatial current model, ECM the environmental current model and SEM the fuzzy intersection (∩) between them.

Table 7.3. Variables included in the modelling process with their coefficients (β), Wald test values, and significance (*p*) for each step. The variables are ranked according to their order of entrance. Codes are the same as in Table 7.1.

Variable	**β**	**Wald**	***p***
Spatial Historical Model			
Slope	2653.242	6.012	< 0.05
Poakfor	–2102.241	9.255	< 0.01
Ppast	–69.0951	5.459	< 0.05
Dt20	0.600	4.941	< 0.05
Aeva	–48.505	13.021	< 0.001
Dt0	–0.378	15.474	< 0.001
Alti	107.819	8.494	< 0.01
Hujan	–1.379	7.718	< 0.005
Dp30	1.249	12.423	< 0.001
Constant	–33980.806	6.595	< 0.05
Environmental Historical Model			
Prec	0.00156	6.740	< 0.01
MaxTemp	–0.0151	17.062	< 0.001
Constant	0.199	0.281	0.868
Environmental Remaining Model			
TempSeason	–0.00482	6.106	< 0.05
MinTemp	–0.0918	4.681	< 0.05
Constant	17.345	3.710	< 0.1
Spatial Current Model			
La	292.616	3.505	< 0.1
Lo	–437.706	3.442	< 0.1
La^2	–3.238	3.503	< 0.1
Lo^2	–7.292	3.387	< 0.1
La×Lo	9.641	3.430	< 0.1
Constant	–6623.417	3.514	< 0.1
Environmental Current Model			
MaxTemp	–0.0774	27.891	< 0.001
Constant	16.128	17.559	< 0.001

Table 7.4. Assessment indices obtained for the models: Kappa (Cohen's kappa index), sensitivity, specificity, correct classification rate (CCR), under-prediction rate (UPR), over-prediction rate (OPR) and area under the curve (AUC). Models abbreviations are spatial historical model (SHM), environmental historical model (EHM), environmental remaining model (ERM), spatial current model (SCM), environmental current model (ECM) and spatial-environmental intersection (SEM).

Model	Kappa	Sensit.	Specif.	CCR	UPR	OPR	AUC
SHM	0.0532	0.902	0.689	0.692	0.00215	0.958	0.866
EHM	–0.00399	0.672	0.224	0.230	0.0217	0.987	0.685
ERM	0.0216	1	0.918	0.918	0	0.988	0.974
SCM	0.0184	1	0.870	0.870	0	0.989	0.961
ECM	0.0226	1	0.892	0.892	0	0.987	0.977
SEM	0.0457	1	0.945	0.945	0	0.975	0.987

7.4 DISCUSSION

The Northern Bald Ibis is an iconic species that stands out amongst fauna threatened with extinction. While it is in the recovery process and numbers are increasing, the global population size is still very small and continues to require strong conservation measures (BirdLife International 2018). The only natural population occurs in Morocco, where effective action in the last two decades increased the number of individuals along with the promising onset of new breeding colonies (Aourir 2017). The identification of favourable areas in Morocco, accompanied by intense monitoring and protection, is paramount to the foundation of new breeding colonies and the spread of the species. Recovering as much of the Northern Bald Ibis's past distribution area in Morocco as possible should be a priority in the conservation strategy and development of conservation policies. This would help to avoid risks associated with local incidents that could potentially affect the already limited breeding colonies. For instance, in May of 1996, an acute mortality incident affected approximately 15% of the total population (Touti *et al.* 1999).

7.4.1 The spatial approach

Our spatial historical model (SHM) suggests that the past breeding distribution of the species could potentially have connected current occupied areas with now-extinct Mediterranean colonies, along the axis formed by the High and Middle Atlas and the Basin of the River Moulouya (Figure 7.2). This spatial approach predicts past geographical trends in the distribution of the Northern Bald Ibis, likely associated with its population dynamics, dispersal capacity and/or historical events. The ecological requirements of the species is of major interest (Schenker *et al.* 2020). However, the spatial organization of the distribution of this species should also be considered as it has deferred sexual maturity (Cramp 1977), and individuals show signs of dispersing, mostly in proximity to the current breeding sites, but some venturing greater distances (Bowden 2015). The spatial structure should also be considered in the modelling procedure because it could incorporate population-based spatial processes, since most natural ecological phenomena, as dispersal, display geographical patchiness (Legendre 1993). As proposed for other endangered species, an effort should be made to spatially organize reserve management in order to capture these biological dynamics across the landscape (Muñoz *et al.* 2013) and promote, the frequentation of favourable alternative breeding sites not limited to former breeding colonies.

The new spatial structure (SCM) drawn from the current breeding colonies (wild in Morocco and reintroduced in Spain) could provide a fresh perspective on the conservation of the species, and should inform the necessary conservation policies along the Moroccan Atlantic axis (Figure 7.5). The crossing of ibises from southern Spain to Africa suggests that both populations could contact naturally. This would likely be advantageous for both populations and, ultimately, for the conservation of the species. Even if this is not the case, it is still necessary to take it into account to apply more effective conservation measures.

7.4.2 The environmental approach

Most breeding colonies from the 20th century, especially those located along the High and Middle Atlas and inland, were in intermediate favourable areas according to our historical environmental approach (EHM, Figure 7.3). This could indicate that these colonies were acting as sinks of dispersal individuals from other colonies, such as those located in favourable areas of the Atlantic coast, which seems to show a spatial and environmental connection. The extinct colonies likely remained until the size of the other populations declined, and therefore did not produce enough dispersal individuals to reach them.

Our environmental-historical model (EHM) identified both sides of the Strait of Gibraltar and some areas at the Rif Mountains as favourable areas

(Figure 7.3). These areas are also present in the current model (ECM) but in lower proportion (Figure 7.5). Hence, the Strait of Gibraltar as a whole (including the Spanish and Moroccan coasts) stands out as a particular promising candidate for the hosting of the species, including birds from the introduction program in Spain and likely also from the natural colonies in Morocco. Thus, individuals from introduced colonies that cross the Strait of Gibraltar (Muñoz & Ramírez 2017) could establish new colonies in the favourable areas on the Moroccan coast, but also on the Iberian Peninsula.

Considering the remaining colonies in the wild (ERM), the highly favourable areas that have been identified to the north of Agadir (Figure 7.4), and these areas have seen the establishment of new colonies in recent years (Aourir 2017). This may be indicating the species-wide trend to move northwards in the future. The species could also move southwards to the highly favourable coastal line from Sidi Ifni to Western Sahara (Figure 7.4), another area that should be taken into consideration for conservation programs.

Although this environmental approach could be useful in identifying priority areas for conservation efforts, it must be acknowledged that human impact has not been taking into account in this study. Changes in land use, increases in pesticides in water bodies, and hunting of the species are the explanations for the ibis's population decline (Böhm *et al.* 2020). The Spanish-introduced colonies are located on a roadside in a populated area (López *et al.* 2015), suggesting this ibis are not disturbed by the presence of humans. This is the reason why its persecution could be a major handicap for its conservation. Thus, highly favourable areas could be negatively affected by human proximity in areas that are not under protection, where the introduced birds are most susceptible to being hunted.

7.4.3 Introduction programmes

The reestablishment of colonies in historically occupied areas is a work in progress taking place over the last two decades. The most important release projects were conducted in Austria (Fritz *et al.* 2017) and Spain (López *et al.* 2015). In Austria, the main objective was to introduce the species and establish a migratory pattern. In Spain, the original aim of testing of translocation techniques has been subsumed by a population rise that is currently close to being self-sustaining (Bowden 2015). Although the Spanish population remains largely sedentary, there are recent confirmed sightings of birds crossing to Africa, probably as part of a dispersal process (Muñoz & Ramírez 2017, Bowden *et al.* 2018). In addition to these recent and probably regular intercontinental movements, a female was captured in Guadalquivir marshlands on July 11th 1958 (the skin is kept in the collection of Estación Biológica de Doñana, nº 11723A). As the female was surely of Moroccan origin, we can assume that with populations growing in both Africa and Europe, it may be only a matter of time before they connect. This possibility should be considered in any action plans for the conservation of the species.

7.4.4 New insights for the conservation of the Northern Bald Ibis

At present, the International Single Species Action Plan for the conservation of the remaining populations recommends multiple actions intended to restore the Northern Bald Ibis to a favourable conservation status (Bowden 2015). These include increasing the population and breeding range and establishing new colonies (Böhm *et al.* 2020). Modelling techniques could forecast the favourable areas for the species, considering their ecological requirements and their dispersal capacity (as in the spatial approaches). According to our results, it would be advisable to take into account favourability maps that consider both the environmental and spatial factors, giving priority to those areas that best fit the environmental needs of the species within its dispersal radius, so that a metapopulation dynamic is favoured.

Ibis population decline is mainly related to human influence due to changes in the land use and agricultural methods (e.g. phytosanitary products, intensive crops, increment in the surface dedicated to livestock), as well as the direct persecution for consumption or captivity (Muñoz *et al.* 2002, Bowden *et al.* 2003, Böhm *et al.* 2020). Thus, human disturbance hinders the formation of a metapopulation dynamic, which adds uncertainty to our model's predictive capacity. It may be that favourable areas located close to large cities and industrial ports are actually unfavourable areas. The introduced colonies are less susceptible to human influence (López *et al.* 2015). This could create conflict if the ibises successfully establish themselves in non-protected favourable areas, a likely possibility given less than 5% of Moroccan terrestrial coverage is protected (https://www.protectedplanet.net/country/MAR). Hence, more protected areas (those the species currently inhabits as well as favourable areas where it could establish) and other protection resources in regions with large human presence (e.g. the surroundings of a city or industrial port) will facilitate the connection between introduced and wild ibis colonies.

Special attention should be paid to the Strait of Gibraltar, an environmentally favourable area where species establishment and continued population growth are expected as a result of the introduction project in Andalusia. Intercontinental movements will surely increase as the

Andalusian population grows, and this could be an opportunity for the species to re-colonize the north of Morocco. Taking into account the precarious conservation status of the Northern Bald Ibis, and the severe environmental impacts northern Morocco is suffering, the time has come to start a fruitful collaboration on both sides of the Strait.

CAPÍTULO 8

DISCUSIÓN GENERAL

GENERAL DISCUSSION

“En este mundo que habitamos, todo está sujeto a cambios continuos e inevitables”

~ Jean-Baptiste Lamarck

8 DISCUSIÓN GENERAL

El interés por conocer la distribución espacial y temporal de los seres vivos, sus causas y patrones comunes ha sido un tema que ha acompañado a la historia de la humanidad desde sus orígenes, bien con fines de aprovechamiento, científicos o de conservación (ver capítulo 1, Llorente-Bousquets *et al.* 2001). La biogeografía desempeña por tanto un papel importante en la sociedad, aportando conocimientos que mejoran la toma de decisiones no solo en temas de conservación de la biodiversidad, sino también en ámbitos cuya relación con el estado de la naturaleza no es tan clara o tan directa. Entre ellos están la salud pública, p.ej. conociendo cómo se origina y expande una enfermedad para tomar medidas frente a ella (Olivero *et al.* 2017a, b); el turismo, p.ej. estudiando la frecuencia de afloramientos de medusas en las playas (Bellido *et al.* 2020); o la política y la economía, p.ej. analizando las causas del tráfico ilegal de animales y sus consecuencias (Souviron-Priego 2018, Souviron-Priego *et al.* 2018). Sin embargo, la realidad no es tan sencilla. La distribución de los seres vivos está en constante cambio, tanto en el espacio como en el tiempo, y responde a dinámicas internas propias de la especie y a cambios en el ambiente (capítulo 1). Esta dinámica en las áreas de distribución genera una incertidumbre en los análisis biogeográficos y puede dificultar la toma de decisiones por parte de las administraciones competentes.

Mediante la presente tesis doctoral se ha pretendido explorar la capacidad descriptiva, predictiva y explicativa de los modelos de distribución de especies (SDMs), una de las herramientas actualmente más empleadas en biogeografía, para aportar aproximaciones de la realidad de la distribución espacio-temporal de los seres vivos (Elith & Leathwick 2009, Elith *et al.* 2010). Concretamente, se ha tratado de aportar nuevos enfoques y marcos conceptuales a cuestiones sobre cambios recientes en la distribución de las especies, a la par que desarrollar metodologías que mejoren las predicciones y permitan reflejar su dinamismo. Para ello se han empleado "especies representantes" de grupos que comparten patrones biogeográficos en sus distribuciones, analizando y profundizando en detalle sus peculiaridades. De esta manera, se aporta información que ayuda a entender el carácter dinámico de las distribuciones, aportando a su vez nuevos enfoques que pueden ser aplicados a la gestión y conservación de la biodiversidad.

Las especies están influenciadas por diferentes factores ambientales, como el clima, el tipo de suelo, la topografía, etc., además de por otros factores históricos, ligados a la actividad humana o biológicos propios de la especie (Antúnez & Mendoza 1992, Lomolino *et al.* 2006c). La inclusión de diferentes factores explicativos produce modelos más robustos y próximos a la realidad que aquellos que sólo emplean un factor, tradicionalmente el clima (Márquez *et al.* 2011). Sin embargo, debe tenerse en cuenta la escala del modelo, pues diferentes factores afectan de manera distinta atendiendo a la escala del estudio (Muñoz & Real 2013). Además, la inclusión de factores poco explicativos puede generar ruido en los resultados (Soultan & Safi 2017). Por ello, el proceso de elección de las variables debe ser altamente riguroso, teniendo en cuenta la capacidad explicativa de cada variable en la resolución a la que se realizará el modelo. Tanto en el estudio del establecimiento del Busardo Moro del Atlas en Europa (capítulo 3) como en el estudio de la parapatría de las víboras (capítulo 6), las variables relacionadas con el uso del suelo eran relevantes a la escala del estudio en cuestión para describir y explicar de la manera más precisa las distribuciones de las especies. En el primer caso mostraban la elección de hábitat de reproducción de la especie, algo que *a priori* parecía ser un limitante para su expansión por Europa, pero que tras el análisis resultó ser indicativo de la plasticidad en la elección de hábitat reproductivo que el busardo posee. Para el estudio de las víboras, las variables de uso del suelo reflejaban la gran sensibilidad de estas especies a la acción humana (capítulo 6), la cual limita su distribución (Santos *et al.* 2006, Niamir *et al.* 2016). Al contrario que en estos casos, para el estudio de la invernada del Carricero Común (capítulo 5), las variables disponibles de uso del suelo o vegetación tenían muy poca resolución, ya que esta especie es capaz de ocupar manchas de vegetación palustre de muy diferentes extensiones, desde grandes zonas húmedas hasta pequeñas formaciones de carrizo o enea (Kennerley & Pearson 2010). Dado que las variables disponibles no recogían puntos de vegetación tan pequeños, su inclusión contribuiría a infravalorar la distribución potencial de la especie (capítulo 5).

También es importante tener en cuenta el potencial predictor de las variables en aquellos estudios en los que se van a extrapolar los resultados. Si la similitud entre las variables del área donde se realiza el modelo y la de la zona a la que se va a extrapolar es alta (i.e. las variables empleadas en la extrapolación son las mismas y sus valores no se alejan del rango de valores del modelo original), los resultados serán robustos (capitulo 3, Werkowska *et al.* 2017). Si los valores difieren de manera notable o hay variables que en el área de extrapolación no están presentes, lo más idóneo sería excluir dichas variables del estudio. Lo mismo ocurre cuando las extrapolaciones se realizan entre distintos periodos de tiempo, donde, además, habría que añadir la incertidumbre de las predicciones de las variables (Romero *et al.* 2019). Por ello, excluir variables difíciles de predecir en el futuro, como la actividad humana o la cobertura del suelo, favorece la claridad de las predicciones (ver capítulo 4). También debe haber coherencia entre los datos de distribución y las variables utilizadas, pues variables que cambian rápida y considerablemente deben ser evitadas. Por ejemplo, para estudiar la distribución potencial del Ibis Eremita en Marruecos y el sur de la península ibérica en base a su distribución reproductora del siglo XX (capítulo 7), se excluyeron las variables de uso del suelo. Esta decisión se tomó porque las variables actuales no reflejan fielmente la realidad de la época de las presencias históricas, ya que el paisaje marroquí ha cambiado considerablemente durante el último siglo. Además, variables de uso del suelo presentes en Marruecos muy probablemente no estarían disponibles en el sur de la península ibérica, lo que comprometería la fiabilidad de las extrapolaciones y la comparación entre modelos (Barbosa *et al.* 2009, Werkowska *et al.* 2017).

El efecto del clima es muy importante en las relaciones biogeográficas de las especies (capítulos 3, 5 y 6), siendo de los factores más relevantes para explicar la distribución de las especies a grandes resoluciones de estudio (Muñoz & Real 2013, Chamorro *et al.* 2017). La adaptación de las especies a determinadas condiciones climáticas genera una estrecha relación especie-ambiente que condiciona su distribución (Martínez-Freiría *et al.* 2015). Dicho de otra forma, la distribución de las especies responde a las condiciones climáticas del ambiente en el que se encuentran, siendo el resultado de adaptaciones evolutivas y aclimataciones a las condiciones ambientales donde éstas se originan (ver capítulos 3 y 6, Martínez-Freiría *et al.* 2015, 2020). Cuando la especie se encuentra bajo las condiciones ambientales a las que se adaptó (óptimas), puede destinar más energía en otras tareas como la reproducción, cuidado de la descendencia o competir por los recursos con otras especies. Por el contrario, cuanto mayor sea la diferencia entre las condiciones ambientales donde se encuentra y aquellas que predominaron en el entorno durante su proceso evolutivo, para las que se adaptó, mayor será la cantidad de energía y recursos que deberá invertir en aclimatarse y asegurar así su supervivencia. En el estudio de las víboras ibéricas (capítulo 6), parece ser que las adaptaciones al ambiente en el que se encontraban los refugios del Pleistoceno de estas especies condicionaron su distribución potencial por la península. Pero la localización de dichos refugios, sumado a la disposición actual de los climas en la península ibérica (atlántico al norte y mediterráneo al sur), y a la gran similitud ecológica entre las especies, han favorecido la formación de 'barreras de exclusión competitiva' entre ellas. Estas barreras, dependientes de las condiciones ambientales, mayoritariamente climáticas, son las que establecen y mantienen la distribución parapátrica entre las tres especies (capítulo 6).

A algunas especies se las puede considerar en un estado de equilibrio con el clima en el que se encuentran, pero este equilibrio, si existe, sería dinámico, pues las oscilaciones e irregularidades en las condiciones climáticas obligan a las especies a estar continuamente adaptándose o aclimatándose (Kirkpatrick & Barton 1997, Merilä & Hendry 2014). Esto también ocurre en aquellas especies que no se encuentran en equilibrio con las condiciones ambientales, como las que se dan actualmente en la Tierra debido al cambio climático favorecido por la acción humana (Petit *et al.* 1999, Steffen *et al.* 2011, IPCC 2014). Las especies responden a estos cambios, pero no lo hacen de una manera simultánea a los cambios climáticos, por lo que se genera cierto desequilibrio espacio-temporal entre la distribución de las especies y las zonas donde las nuevas condiciones climáticas son favorables para ellas. Este desequilibrio sería la fuerza que podría favorecer que las especies ocupen las nuevas áreas disponibles, lo cual promovería los cambios en sus distribuciones (capítulo 4). Este hecho da un carácter añadido a los modelos de favorabilidad: tienen en cuenta y cuantifican el desequilibrio espacio-temporal entre las especies y el ambiente (capítulo 4, Acevedo & Real 2012, Gouveia *et al.* 2020), a diferencia de otros métodos en los que debe existir el equilibrio o éste se asume (Guisan & Zimmermann 2000, Guisan & Thuiller 2005).

En la presente tesis se ha optado por realizar modelos a partir de una regresión logística multivariante con datos de presencias y ausencias. Algunos autores sugieren que en la modelación biogeográfica se deben emplear técnicas que sólo tengan en cuenta las presencias de la especie, como ENFA (Engler *et al.* 2004), puesto que estos modelos no se ven afectados por las falsas ausencias, i.e. presencias no detectadas (Brotons *et al.* 2004). Sin embargo, esto es un error conceptual de gran calado y bastante extendido. Para empezar, la mayoría de métodos clasificados como de “solo presencia” no lo son en realidad, pues comparan las presencias con un fondo (*background*) u otro tipo de datos, que al no ser presencias, pasarían directamente a ser ausencias (Aranda & Lobo 2011, Barbet-Massin *et al.* 2012, Guillera-Arroita *et al.* 2014). Pero, además, aún las técnicas que verdaderamente son de “sólo presencia” están influenciadas por las falsas ausencias (Aranda & Lobo 2011). Como el resultado de los modelos depende de la cantidad de presencias que se usen, si de una especie no se tienen todas las presencias, lo cual es lo más habitual, presentará presencias que no han sido registradas, es decir, falsas ausencias. Si se pudieran realizar dos modelos, uno con las presencias registradas y otro con las reales, los resultados no serían iguales, por lo que el efecto de las falsas ausencias también se nota en el caso de los métodos considerados de “solo presencias”, aunque no utilicen las ausencias de la especie. Además, los factores que condicionan que una especie esté ausente de una zona concreta también suponen un tipo de información que puede ser muy importante en biogeografía y conservación (capítulos 6 y 7, Whittaker *et al.* 2005). Por ello los métodos que específicamente incluyen las ausencias en su diseño conceptual aportan más información y contribuyen en mayor medida a comprender los motivos que condicionan la distribución de las especies (Aranda & Lobo 2011, Acevedo & Real 2012, Acevedo *et al.* 2012a).

Otro de los motivos por el que se ha seleccionado la regresión logística es porque sus resultados son probabilidades (capítulo 1), a diferencia de otros métodos ampliamente utilizados, como por ejemplo MaxEnt (Phillips *et al.* 2006), que produce valores que se denominan, al igual que en otros métodos, *suitability* (Phillips *et al.* 2017). A partir de las probabilidades se pueden obtener los valores de favorabilidad (Real *et al.* 2006), los cuales no se ven afectados por el efecto de la prevalencia de los datos (Acevedo & Real 2012). Así, se obtienen modelos conmensurables, necesarios cuando se quieren realizar análisis comparativos de distribuciones (capítulo 6), y que pueden utilizarse para aplicar la lógica difusa a la distribución de las especies (capítulos 4 y 7), entre otras muchas aplicaciones (Real *et al.* 2017, Gouveia *et al.* 2020).

La favorabilidad expresa la manera en la que las especies responden a las condiciones ambientales de cada región (Acevedo & Real 2012). Por ello, el concepto de nicho ecológico de Maguire (1973) es equiparable a la favorabilidad, como la interacción o respuesta de las especies a las condiciones ambientales. Esto hace que su potencial explicativo y predictivo ayude a esclarecer hipótesis biogeográficas específicas, como por ejemplo sobre las causas de cambios en la fenología de las especies (capítulo 5), sobre sus distribuciones pasadas (capítulos 6 y 7) o su potencial de ocupación (capítulo 3, 4 y 7). Pero, además, su potencial predictivo permite también detectar aquellas zonas con condiciones ambientales adecuadas para las especies donde no se encuentran, bien porque algo las impidió llegar (como es el caso las víboras en Iberia, capítulo 6), bien porque aún no las han alcanzado pero que pueden hacerlo en un futuro próximo (capítulos 3, 4 y 7), o bien porque actualmente han desaparecido, e incluso porque en los muestreos realizados no han sido detectadas (Real *et al.* 2017, Gouveia *et al.* 2020). Esta característica permite crear el concepto de diversidad oscura, para recoger a aquellas especies que presentan áreas favorables desocupadas en una región, bien porque no están presentes en la actualidad o bien porque aún no han sido detectadas (Pärtel *et al.* 2011).

Incorporando la dinámica de las distribuciones (reflejada en los modelos de favorabilidad) y el potencial de ocupación de las especies en regiones donde no se encuentran (i.e. teniendo en cuenta la diversidad oscura de las áreas), podrían mejorarse considerablemente los planes de gestión y conservación de la naturaleza y de las especies en sí, obteniendo una gran ventaja para anticiparnos a los cambios y optimizar los recursos de los que se disponen para fomentar la conservación de la biodiversidad (capítulo 7, Estrada *et al.* 2018). Si a esto le sumamos un monitoreo de las zonas favorables, para determinar en qué medida se cumplen las predicciones de los modelos, y se actualizan los modelos en base a estos resultados, el rendimiento de la conservación de estas especies podría ser considerablemente superior al obtenido mediante los planes de conservación tradicionales. En esta tesis, se hace hincapié en cómo esta "conservación dinámica" podría dar esperanza a la supervivencia de una de las especies más amenazadas del planeta, el Ibis Eremita, ya que al proteger zonas donde la especie puede establecerse de manera natural, o mediante la ayuda humana, pese a que no está presente en ellas, podría fomentar el establecimiento de una nueva dinámica metapoblacional que impulse su supervivencia (capítulo 7).

Una de las propuestas más interesantes de la presente tesis es que los modelos de distribución (al menos los de favorabilidad) no asumen que las especies están en equilibrio con el clima, siendo este desequilibrio el causante de los cambios en las distribuciones de las especies. Además, con la presente tesis aportamos al marco conceptual y metodológico de la favorabilidad la noción de su capacidad para reflejar el dinamismo, pasado, actual o futuro, que presentan las distribuciones de las especies, y su potencial predictivo en los casos recientes con pocos datos disponibles. Estas representaciones se ajustan de una forma más adecuada a la complejidad de la naturaleza, facilitando una correcta toma de decisiones para optimizar la gestión y conservación de la biodiversidad en este gran planeta cambiante.

Futuras líneas de investigación.

Mediante la presente tesis doctoral se ha puesto en práctica conceptos y aplicaciones de la función de favorabilidad, la teoría de los conjuntos borrosos y otras herramientas de análisis biogeográfico. El abanico de aplicaciones sigue siendo muy amplio, con gran oportunidad para innovar en biogeografía. Diversas son las líneas de investigación que surgen a raíz de los resultados y nuevas preguntas que esta tesis ofrece.

En primer lugar, las especies seleccionadas para realizar el análisis biogeográfico de la dinámica de sus distribuciones y sus patrones, son ejemplos de grupos de taxones. Por tanto, un análisis en conjunto de dichos grupos podría ser una línea de investigación en el futuro, mostrando patrones más generales y ofreciendo así una perspectiva más holística del fenómeno analizado. Esto es de especial relevancia para las especies cuya dinámica está siendo alterada por el cambio climático, como es el caso del Busardo Moro del Atlas o del Carricero Común, es decir, de aves típicamente africanas colonizando el continente Europeo o de migradoras transaharianas con alteraciones en su fenología, respectivamente.

Gracias al descubrimiento de las barreras de exclusión competitiva, ambientalmente dependientes e inestables, cabe preguntarse qué posible repercusión tiene el cambio climático en la parapatría de estas especies, por lo que la proyección de los modelos al futuro y su estudio comparado puede ser otro posible objetivo a cumplir en un futuro a corto plazo.

La detección de zonas favorables para el ibis en el sur de Iberia nos ofrece también la posibilidad de considerar nuevas zonas de introducción de individuos en cautividad, en un principio descartadas por no parecerse a las zonas donde éste habita en estado salvaje en la actualidad. Un análisis más en detalle de esta zona, considerando además otros factores como el humano o grado de protección de la región, podría identificar nuevos lugares en los que la formación de colonias reproductoras sea más factible.

La actualización de los modelos con nuevos datos recogidos podría corroborar las tendencias desveladas en esta tesis, ofreciendo una imagen aún más dinámica de las distribuciones, y validando los resultados previamente obtenidos. Para ello, el monitoreo de las áreas favorables, así como el marcaje y seguimiento de individuos, permitiría mejorar los datos disponibles de las especies y observar los cambios graduales de la biodiversidad. Además, las herramientas propuestas en esta tesis se basan en conceptos cuya aplicación en otros ámbitos científicos puede suponer una innovación a la hora de estudiar otros fenómenos desde un punto de vista biogeográfico, como la evolución de las enfermedades.

CAPÍTULO 9

CONCLUSIONES FINALES

FINAL CONCLUSIONS

> *"El planeta estaba aquí mucho antes que nosotros y seguirá aquí después de nosotros. Lo que nos preocupa es salvarnos a nosotros mismos"*
>
> ~ Lynn Margulis

9 CONCLUSIONES FINALES

En la presente tesis doctoral se ha analizado la complejidad de las áreas de distribución de las especies desde el punto de vista de la biogeografía dinámica. Para ello se han utilizado ejemplos de especies con patrones espacio-temporales concretos y se ha puesto a prueba la modelación de las distribuciones en el marco teórico-práctico de la función de favorabilidad. Con ello se han respondido cuestiones biogeográficas sobre la situación actual de los cambios en las distribuciones de las especies estudiadas, y se han propuesto aproximaciones metodológicas que pretenden incorporar el dinamismo inherente a las especies en las técnicas de modelación.

Las principales conclusiones obtenidas son:

1. El límite entre los continentes de África y Europa, especialmente el situado en el estrecho de Gibraltar, es una barrera geográfica salvable para ciertos grupos de animales, como las aves. El cambio climático favorece la permeabilidad de dicha barrera al crear zonas favorables en Europa que atraen con más intensidad a las especies africanas.
2. Se han obtenido modelos de distribución para todas las especies estudiadas, siendo eficaces para describir la distribución de las especies, explicar sus condicionantes ambientales y predecir zonas de ocupación. Esto demuestra que los modelos de distribución son herramientas útiles para generar y responder hipótesis sobre la influencia de la heterogeneidad ambiental en la distribución de las especies.
3. En la presente tesis doctoral se introducen aportes conceptuales y metodológicos al conocimiento general del dinamismo de la distribución de las especies, como son el desequilibrio entre las especies

y el clima cambiante, las barreras de exclusión competitiva en especies parapátricas y los aportes a la conservación dinámica de las especies. Estas nuevas aportaciones pueden, además, ser aplicadas a otros estudios biogeográficos.

4. Se pone de manifiesto que la favorabilidad es la función de respuesta de las especies al ambiente en el que se encuentran, siendo capaz de reflejar el dinamismo inherente de las distribuciones e identificando zonas con condiciones adecuadas para las especies.
5. La información obtenida mediante los modelos de favorabilidad puede suponer una mejora en los planes de conservación de la biodiversidad ya que se adecúan al carácter dinámico de las distribuciones de las especies. Esta conservación dinámica de las especies puede ser de gran utilidad si tenemos en cuenta que permitiría optimizar los recursos disponibles con vistas a conservar la biodiversidad del planeta.
6. El factor climático ha resultado ser el que más potencial explicativo ha tenido para favorecer la colonización de Europa por las aves típicamente africanas, aunque la combinación de éste con otros factores, como la topografía o la vegetación, ha resultado necesaria para una mejora en los modelos, así como para una mejor interpretación de los mismo.
7. La península ibérica, debido a su gran similitud ambiental con el Norte de África y a su cercanía, presenta un elevado potencial para acoger fauna africana, permitiendo su establecimiento y posible propagación por el resto de Europa.
8. Alteraciones del ambiente, como el cambio climático, favorecen los cambios en las distribuciones de las especies. Se ha comprobado como en la zona circunmediterránea se están produciendo desplazamientos

latitudinales hacia el norte al generarse nuevas zonas favorables, que atraen a las especies africanas modificando su distribución en lo que supone un verdadero salto biogeográfico, la colonización de Europa.

9. Los modelos de favorabilidad, en combinación con operaciones de lógica difusa y análisis de baricentro de las distribuciones, han permitido la detección y cálculo del desequilibrio climático generado cuando el cambio climático altera la distribución de las especies. Esto demuestra que esta metodología no requiere para su uso que las especies estén en equilibrio con el ambiente, algo que no ocurre cuando las especies se están desplazando debido a cambios ambientales.
10. Para el estudio de las especies que se desplazan latitudinalmente debido a los efectos del cambio climático, se han generado dos nuevos índices. El desplazamiento latitudinal (*Ldis*) mide la distancia entre la distribución de la especie y el centro geográfico de sus zonas climáticamente favorables. El desplazamiento de la favorabilidad (*FD*) es una tasa que representa la distancia anual a la que se generan nuevas zonas favorables al norte de la distribución actual.
11. El hecho de que la favorabilidad no esté afectada por la prevalencia y su aplicabilidad en estudios de lógica difusa, aumenta su valor en los estudios en los que se comparan distribuciones y se analiza el potencial de ocupación de las especies. Así, se abre la puerta al empleo de la diversidad oscura para anticiparse a los cambios que puedan ocurrir en sus comunidades faunísticas.
12. Se pone de manifiesto que poblaciones de aves migradoras transaharianas están reduciendo su distancia de invernada, pasando a realizar migraciones de corta distancia desde el norte y el este de Europa hacia la península ibérica, donde invernan, e incluso

detectándose fenómenos de sedentarización en las que aves que crían en Iberia dejan de migrar.

13. Se demuestra además que los cambios fenológicos de estas migradoras de larga distancia se deben, casi exclusivamente, al aumento de las temperaturas invernales en la península ibérica. y a la aparición de zonas que reúnen las condiciones adecuadas para sobrevivir al periodo más frío del año. Al tratarse de especies insectívoras los cambios en el clima deben estar favoreciendo también a la actividad invernal de los invertebrados que componen su dieta.
14. Las zonas de mayor favorabilidad para la invernada de especies transaharianas en la península ibérica se localizan principalmente en la costa mediterránea, en el sur de la península, en el valle del Ebro y en regiones del norte de España.
15. Para determinar el peso relativo del ambiente y de la competencia entre especies parapátricas, se ha creado un marco teórico y metodológico. Este se realiza mediante la modelación puramente espacial, para la selección del área de estudio relevante, la modelación ambiental con la posterior extrapolación a toda el área de estudio, y el análisis de la favorabilidad compartida entre las especies. Este marco resulta de gran utilidad para desvelar la historia pasada de las distribuciones, apoyando o contrariando hipótesis filogenéticas o evolutivas
16. Se han identificado las zonas donde existe una mayor probabilidad de que se produzca exclusión competitiva o coexistencia simpátrica entre las víboras de la península ibérica, mostrando la existencia de 'barreras de exclusión competitiva' entre las distribuciones de las especies. Dichas barreras mantienen la parapatría.

17. La información aportada por la aproximación histórica espacial y ambiental de la distribución de las especies, junto con la aportada por la distribución actual, permite detectar patrones biogeográficos que se escapan si sólo se tienen en cuenta un único factor, como son las zonas potenciales de ocupación de la especie en un futuro próximo.
18. La información histórica de la distribución reproductora del Ibis Eremita arroja luz sobre el potencial de ocupación de esta especie en Marruecos y el sur de la península ibérica, mostrando que las zonas donde esta especie se ha mantenido no son las únicas adecuadas para su reproducción, lo que debe ser tenido en cuenta en los planes de conservación e introducción de ejemplares.
19. Al incluir las zonas donde se han introducido especies junto con las zonas donde se encuentran en estado salvaje, se pueden identificar estructuras espaciales que pueden ser de gran utilidad para la conservación de especies. En el caso del Ibis Eremita, se ha detectado una conectividad ambiental potencial entre las zonas naturales de cría y aquellas donde la especie ha sido introducida que podría favorecer el la creación de una nueva dinámica metapoblacional entre las colonias marroquís y españolas.
20. Los modelos de distribución permiten estrechar el abanico de incertidumbre del desarrollo futuro de las distribuciones de las especies al aportar ideas y explicaciones que pueden direccionar las hipótesis, a la par que se pueden actualizar con nueva información recogida, generando una dinámica de trabajo que favorece el avance en el conocimiento de los procesos biogeográficos de la naturaleza.

9 FINAL CONCLUSIONS

In this doctoral thesis, the complexity of the species distribution areas has been analysed from the perspective of dynamic biogeography. To this end, there were selected some examples of species with specific spatial-temporal patterns, and the distribution modelling has been tested in the theoretical and practical framework of the favourability function. With the obtained information, they have been answered biogeographical questions about the current situation of changes in the distributions of the studied species, and some methodological approaches were proposed which aim to incorporate the inherent dynamism of the species into the modelling techniques.

The main conclusions are:

1. The limit between the continents of Africa and Europe, especially the Strait of Gibraltar, is a geographical barrier that could be overcome by certain groups of animals, such as birds. Climate change favours the permeability of this barrier by creating favourable areas in Europe that strongly attract African species.
2. Distribution models have been obtained for all the studied species, which are highly effective in describing the distribution of the species, explaining the environmental characteristics that condition their distribution, and predicting areas of occupation. This shows that distribution models are useful tools for generating and responding to hypotheses on the influence of environmental heterogeneity on the distribution of species.

3. This doctoral thesis introduces conceptual and methodological contributions to the general knowledge of the dynamism of species distributions, such as the disequilibrium between species and the changing climate, the 'competitive-exclusion barriers' in parapatric species or contributions to the dynamic conservation of species. These new contributions can also be applied to other biogeographical studies.
4. It is brought to light that favourability is the response function of species to the environment in which they are found, being able to consider the inherent dynamism of distributions and identifying areas with suitable conditions for species.
5. The information obtained by favourability models could represent an improvement in biodiversity conservation plans as they are adjusted to the dynamic nature of species distributions. This dynamic conservation of species could be very useful if we take into account that it would allow for the optimization of the available resources with a view to conserving the planet's biodiversity.
6. The climatic factor has proved to be the one with the highest explanatory power for favouring the colonisation of Europe by typically African birds, although its combination with other factors, such as topography or vegetation, has entailed an improvement in the models, as well as a better interpretation of them.
7. The Iberian Peninsula, due to its great environmental similarity with North Africa and its proximity, has a high potential for hosting African fauna, allowing its establishment and possible propagation throughout the rest of Europe.
8. Alterations in the environment, like the current climate change, favour shifts in the distribution of species. It has been verified that in the

circum-Mediterranean area, northwards latitudinal shifts are occurring as new favourable areas are generated, which attract African species. This modifies their northern distribution, which implies a real biogeographical leap: the colonisation of Europe.

9. Favourability models, in combination with fuzzy logic operations and distribution barycentre analysis, have detected and calculated the climate disequilibrium generated when climate change alters the species distributions. This fact demonstrates that this methodology does not require equilibrium between the species and the environment for its use, which does not occur when species are shifting due to environmental changes.

10. For the study of species that latitudinally shift due to the effects of climate change, two new indices have been provided. The Latitudinal displacement (*Ldis*) measures the distance between the distribution of the species and the geographical centre of its climatically favourable areas. The Favourability Displacement (FD) is a rate that represents the annual distance at which new favourable areas are generated at north of the current distribution.

11. The fact that favourability is not affected by the prevalence of the dataset, together with its applicability in fuzzy logic studies, increases its value in investigations which aim to compare distributions or to analyse the potential occupation of the species. Hence, it opens the door to the use of dark diversity to anticipate changes that might occur in their fauna.

12. It is demonstrated that populations of trans-Saharan migratory birds are reducing their wintering distance, from northern and eastern areas of Europe to the Iberian Peninsula, where they winter, turning into short

distance migrants. It is even detected the phenomenon of sedentarisation, in which birds that breed in Iberia do not migrate.

13. It is also shown that the phenological changes of these long-distance migrants are almost exclusively caused by the increasingly warmer winters on the Iberian Peninsula, and the appearance of areas with the required conditions to the species survival during the coldest period of the year. Given that they are insectivorous species, the changes in the climate must also be favouring the winter activity of the invertebrates on which they feed.
14. The most favourable areas for trans-Saharan species to winter in the Iberian Peninsula are mainly located on the Mediterranean coast, in the south of the peninsula, in the Ebro valley and in few regions of northern Spain.
15. A theoretical and methodological framework has been created to address the role of the environmental conditions and the competitive interactions between parapatric species. This is done by means of purely spatial modelling, for the selection of the spatially relevant area, environmental modelling with subsequent extrapolation to the whole study area, and analysis of the shared favourability between the species. This framework is very useful for revealing the past history of distributions, supporting or contradicting phylogenetic or evolutionary hypotheses.
16. Areas where competitive exclusion or sympatric coexistence among Iberian Peninsula vipers are more likely to occur were identified, showing the existence of 'competitive-exclusion barriers' between the species distributions. These barriers are the reason of the maintenance of the parapatry.

17. The information provided by the spatial and environmental approaches of the historical distribution of the species, together with that given by the current distribution, detects biogeographical patterns, which could not be found if the study is focus only on one of these factors, for example, the potential areas of occupation of the species in the near future.
18. The historical breeding distribution of the Northern Bald Ibis sheds new light on its potential occupation in Morocco and the south of the Iberian Peninsula, showing that the locations where this species has remained are not the only favourable areas for its breeding, which must be taken into account for conservation and introduction plans.
19. By the inclusion of areas where species have been introduced, together with areas where they inhabits in the wild, it is possible to identify spatial structures that can be extremely useful for the conservation of species. In the case of the Northern Bald Ibis, a possible environmental connectivity has been detected between natural breeding colonies and those areas where the species has been introduced, which could favour the establishment of a new metapopulation dynamic between Moroccan and Spanish colonies.
20. Distribution models are handy methods to reduce the range of uncertainty in forecasting the future development of species distributions by providing ideas and explanations that could be used to formulate directional hypotheses, while at the same time they can be updated with new information collected. This generates a working dynamic that favours progress in the knowledge of nature biogeographical processes.

CAPÍTULO 10

REFERENCIAS BIBLIOGRÁFICAS

BIBLIOGRAPHY

"Cada esfuerzo por clarificar lo que es ciencia y de generar entusiasmo popular sobre ella es un beneficio para nuestra civilización global"

~ Carl E. Sagan

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Producción Científica Asociada A Esta Tesis Doctoral / Scientific Outputs Of This PhD Thesis

Artículos que avalan esta tesis doctoral / Articles from this PhD thesis:

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*. 159: 331–342. (**Q1**)

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Western population of the Northern Bald Ibis: new horizons for its conservation.

Otras publicaciones surgidas durante el desarrollo de la presente tesis doctoral, no incluidas en la memoria / Other publications which have been elaborated during the PhD thesis, but they are not included herein:

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. G. Zotano, J. Arias García, J. A. O. Cobo, & J. L. Serrano Montes, eds.), pp. 172–180. Tundra Ediciones, Castellón.

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BREVE *CURRICULUM VITAE* / BRIEF CV

Darío Chamorro Sierra nació en Asturias el 4 de Mayo de 1992. Cursó el Bachiller de Ciencias en donde desarrolló un interés especial por la naturaleza. En julio de 2008 fue beneficiario de una estancia para jóvenes investigadores en el Centro de Ciências do Mar do Algarve (CCMAR) donde desarrolló el programa ‘Bones (Ossos - como é o esqueleto dos organismos?)’. De 2010 a 2014 cursó el Grado en Biología en la Universidad de Oviedo. Durante este periodo se implicó en la organización y gestión universitaria, siendo representante de alumnos y miembro titular de las comisiones de docencia y reconocimiento de créditos de la Junta de la Facultad de Biología. Durante el curso 2013–2014 obtuvo una beca de colaboración con el departamento de Biología de Organismos y Sistemas, área de Ecología, con el proyecto titulado “Cambios recientes en la estructura de comunidades dominadas por grandes algas pardas”. De mayo a septiembre de 2014 realizó prácticas en el zoológico “El Bosque” de Oviedo. Comenzó sus estudios de máster en la Universidad de Málaga en el programa de Diversidad Biológica y Medio Ambiente en septiembre de 2014 y continuó con el programa de doctorado de mismo nombre al año siguiente, donde obtuvo una beca predoctoral (FPU15/00123) con el fin de completar su formación como PhD. Durante este periodo ha impartido docencia en la asignatura de Zoología y ha colaborado en la dirección de trabajos fin de grado y máster de Biología Animal. Ha realizado una estancia de investigación en el extranjero mediante la beca del Plan Propio de la Universidad de Málaga en el Centro de Investigação em Biodiversidade e Recursos Genéticos (CiBio) da Universidade do Porto (Portugal). Actualmente, tiene publicados cinco artículos en revistas científicas incluidas en el Science Citation index (SCI), además de otra en proceso. También ha publicado seis capítulos de libros y ha participado en dieciséis congresos científicos de ámbito internacional. Además, ha colaborado en diversas jornadas de divulgación científica como en ‘La Noche Europea de los Investigadores’ (2018) o en el ‘Simbiosis Festival’ (2017).

Mientras el planeta sigue su ciclo según la ley de gravitación, se están desarrollando las formas más bellas y maravillosas de la vida.

– Charles R. Darwin

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