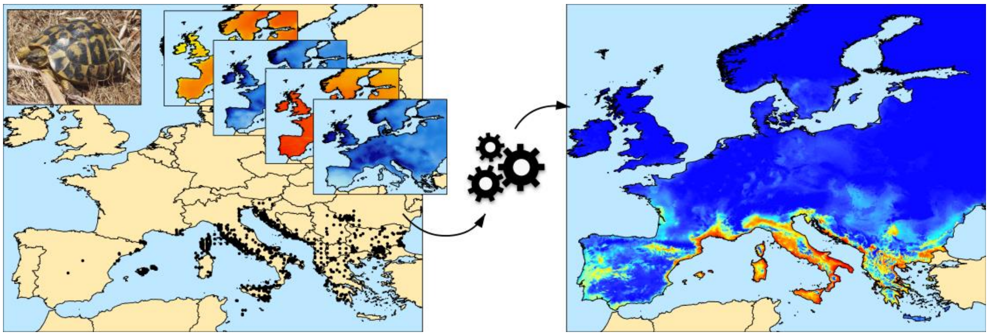
Tesis Doctoral



Aplicación de Modelos de Nicho Ecológico y Sistemas de Información Geográfica para la conservación de la biodiversidad

APPLICATION OF ECOLOGICAL NICHE MODELS AND GEOGRAPHICAL INFORMATION SYSTEMS IN BIODIVERSITY CONSERVATION

Cristian Madeira de Medeiros

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APPLICATION OF ECOLOGICAL NICHE MODELS AND GEOGRAPHICAL INFORMATION SYSTEMS IN BIODIVERSITY CONSERVATION

Memoria presentada por el Licenciado en Biología Cristian Madeira de Medeiros para optar al grado de Doctor en Biología por la Universidad de Salamanca

Vº Bº del Director

José Ángel Sánchez Agudo

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INFORME DEL DIRECTOR DE LA TESIS

El Dr. José Ángel Sánchez Agudo como director de la Tesis Doctoral titulada *“Aplicación de Modelos de Nicho Ecológico y Sistemas de Información Geográfica para la Conservación de la Biodiversidad”* realizada por D. CRISTIAN MADEIRA DE MEDEIROS en el Departamento de Botánica y Fisiología Vegetal de la Universidad de Salamanca, informa favorablemente el depósito de la misma, dado que reúne las condiciones necesarias para su defensa.

Lo que firmo en Salamanca a 16 de marzo de 2018.

Aos meus pais

A Karoline

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Sin siquiera haberme planteado alguna vez el enfrentarme al desafío que conlleva hacer una Tesis Doctoral, a menudo pensaba en la sección de agradecimientos que las encabezaba, y es que era lo que más me gustaba leer de toda Tesis que pasaba por mis manos, porque suelen ser textos bonitos y divertidos; me imagino que alguien más por ahí también tendrá este *hobby*. Después, desde el día que empecé la mía, he soñado sobre cuándo sería el día que me tocaría estar escribiendo estas líneas. Finalmente ha llegado el momento y espero no defraudar a nadie.

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A todas y a todos, ¡gracias! / A todas e a todos, obrigado!

“Born to lose, live to win”

(Ian Fraser ‘Lemmy’ Kilmister 1945-2015)

RESUMEN

Como consecuencia de la situación actual de deterioro ambiental global, la biodiversidad está sufriendo un importante menoscabo, por tanto se hace preciso diseñar estrategias eficaces con las que actuar de forma urgente en todos los frentes abiertos para intentar conservarla. Así, en esta tesis se presentan varias propuestas novedosas de trabajo sobre casos concretos relacionados con diversas problemáticas que existen actualmente en la conservación de especies. La metodología es transversal a todos los capítulos y consiste en la aplicación de una combinación de *Modelos de Nicho Ecológico (MNE)* y *Sistemas de Información Geográfica (SIG)*, para analizar/interpretar cuestiones sobre la distribución y conservación de especies. Los capítulos comprenden los siguientes temas: (i) comparación mediante MNE de bases de datos biológicas georreferenciadas correspondientes a una especie invasora; (ii) aplicación de los MNE en el estudio de los patrones de distribución de especies amenazadas; (iii) análisis del efecto de la marginalidad geográfica poblacional en la idoneidad de hábitat y; (iv) evaluación de los patrones de idoneidad de hábitat en las áreas de distribución de especies endémicas europeas correspondientes a distintos grupos de organismos. Los resultados aquí alcanzados sirven como base teórica sobre la que apoyarse a la hora de diseñar estrategias de conservación.

ABSTRACT

Due to the current situation of global environmental degradation, biodiversity is suffering an important damage, thus it is necessary to design efficient strategies in order to protect it. In this way, this thesis project presents novel proposals to address specific issues currently related to species conservation field. The methodology is transversal to all the chapters and consists on the application of Ecological Niche Models (ENM) jointly with the Geographic Information Systems (GIS), in order to analyze / interpret questions about the distribution and conservation of species. The chapters include the following topics: (i) comparison between geo-referenced biological databases corresponding to an invasive species using ENM; (ii) application of the ENM in the study of the distribution patterns of threatened species; (iii) to analyze the effects of geographical marginality on habitat suitability; (iv) evaluation of habitat suitability patterns in the distribution areas of European endemic species, corresponding to different groups of organisms. The results achieved here, serve as a theoretical basis on which to rely when designing conservation strategies.

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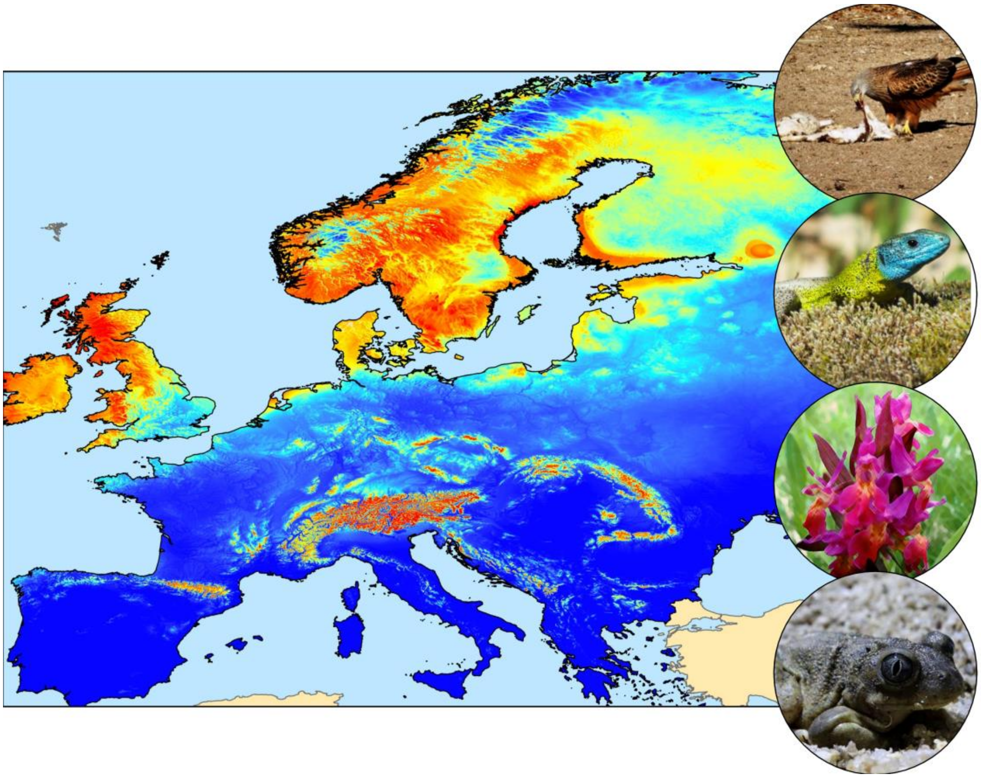

Fotos animales: Cristina Mimbrañes, Ricardo Córdoba Cámara y Thomas Lahlafi

I. INTRODUCCIÓN GENERAL

I.1. Marco epistemológico.

La conservación de la *biodiversidad* es el hilo que enhebra los capítulos que constituyen esta tesis doctoral, puesto que en cada uno de ellos se presentan propuestas metodológicas novedosas, que tratan de resolver situaciones concretas relacionadas con diversas problemáticas que existen actualmente en torno a la conservación de especies. La metodología es, por tanto, transversal a todos los capítulos y consiste en la aplicación de una combinación de *Modelos de Nicho Ecológico* y *Sistemas de Información Geográfica,* para resolver/analizar/interpretar cuestiones sobre la distribución de especies.

Esta memoria consta, además de la introducción y las conclusiones, de cuatro capítulos cuyo contenido está estructurado en formato de publicación científica; tres de ellos han sido ya enviadas a revistas indexadas[2,3] y están actualmente en revisión; el último está en el proceso final de edición previa a su envío. Sus títulos son los siguientes:

> *"How reliable is the untrained eye in the identification of an invasive species? The case of alien bee-hawking Yellow-legged hornet in Iberian Peninsula"*. Enviado a *Biological invasions*, en revisión desde octubre de 2017.

Además he colaborado con los siguientes trabajos:

[2] *"How effective are the protected areas to preserve endangered plant species in a climate change scenario? The case of three Iberian endemisms"*. Enviado a *Land Use Policy*, en revisión desde febrero de 2018 (con K.F. Ribeiro y J.A.S. Agudo).

[3] *"Seed germination of Carex lainzii Luceño, E. Rico & T. Romero: an endemic Spanish endangered species"*. Enviado a *Lazaroa*, en revisión desde octubre de 2017 (con K.F. Ribeiro, J.S. Sánchez y J.A.S. Agudo)

“Behavioural, ecological and human factors explain wintering red kite (Milvus milvus Linnaeus, 1758) distribution in the Iberian Peninsula: consequences and opportunities for conservation of European raptors”. Enviado a *Diversity & Distributions*, en revisión desde febrero de 2018.

“Living on the edge: do central and marginal populations of plants differ in habitat suitability?” Enviado a *Plant Ecology*, en revisión desde octubre de 2017.

“Assessing niche similarities between central and marginal populations of European endemic species”. Se está editando para el envío a *Biodiveristy and Conservation*.

I.2. La biodiversidad

En el Convenio sobre la Diversidad Biológica (CDB) se define *biodiversidad* (originalmente “diversidad biológica”) como la variedad de organismos vivos de cualquier tipo incluidos en los ecosistemas terrestres y ecosistemas acuáticos (marinos y dulceacuícolas), así como las interacciones ecológicas en las que participan; ello incluye la diversidad dentro de una misma especie (diversidad genética), diversidad entre las distintas especies de organismos y diversidad de los ecosistemas. Todos los niveles de la biodiversidad son necesarios para la supervivencia de las especies y por consiguiente de los seres humanos (Primack & Ros, 2002; Secretaría del Convenio sobre la Diversidad Biológica, 2010).

Desde un punto de vista antrópico, la biodiversidad, aporta una gran variedad de valores cuantificables, beneficios y servicios ecosistémicos que son de importancia fundamental para la sociedad: servicios de aprovisionamiento (p.ej. medicamentos, comida, combustibles, tejidos, etc.), reguladores (p.ej. depuración del aire y del agua, regulación del clima), culturales (p.ej. estéticos, religiosos, turísticos) (Secretaría del Convenio sobre la Diversidad Biológica, 2010). Aparte de contener un sinfín de valores esenciales para las poblaciones humanas, la biodiversidad tiene un valor intrínseco; todas las especies y las comunidades biológicas a las cuales pertenecen tienen valor propio, independientemente del valor que la sociedad humana les atribuya, su valor no es conferido ni revocable, sino que surge por su historia evolutiva y por sus papeles ecológicos únicos, o incluso del mero hecho de su existencia, por lo cual, todas las especies deben de ser conservadas (Primack & Ros, 2002; Soulé, 1985).

I.2.1. Factores de amenazas a la biodiversidad

Mantener la biodiversidad es uno de los principales objetivos de la Biología de la conservación, que hoy más que nunca, se justifica por el vertiginoso aumento en la tasa de extinción de especies y la degradación mundial de los ecosistemas (Millennium Ecosystem Assessment, 2005; Myers, Mittermeier, Mittermeier, da Fonseca, & Kent, 2000; Primack & Ros, 2002; Secretaría del Convenio sobre la Diversidad Biológica, 2010). Una gran cantidad de problemas afectan la biodiversidad mundial, por citar algunos: (i) pérdida, degradación y fragmentación de hábitats naturales; (ii) sobreexplotación de los recursos biológicos; (iii) contaminación, a través de acumulación o vertido de nutrientes en el medio ambiente; (iv) impactos de especies exóticas invasoras sobre ecosistemas y especies autóctonas; (v) el cambio climático y la acidificación de los océanos, asociados con la acumulación de gases de efecto invernadero en la atmósfera (J. O. Engler et al., 2017; Millennium Ecosystem Assessment, 2005; Secretaría del Convenio sobre la Diversidad Biológica, 2010, 2014).

El principal y más peligroso efecto de esta situación es la reducción de la biodiversidad global, puesto que gran parte de las especies de todos los grupos conocidos están, en promedio, al borde de la extinción (Primack & Ros, 2002; Secretaría del Convenio sobre la Diversidad Biológica, 2010). Debido a ello, queda clara la necesidad de plantear y ejecutar medidas para la conservación y gestión de la biodiversidad (p.ej. establecimiento de nuevas áreas de protección y/o proteger las áreas protección ya existentes). En este sentido, la *Biología de la Conservación* reúne conocimientos científicos multidisciplinares que tienen como principal objetivo el tratar de mitigar esa pérdida de la biodiversidad (Primack & Ros, 2002).

I.3. Biología de la conservación

Esta rama científica se inició en los últimos años del siglo XX, como una “disciplina de crisis” (Soulé, 1985) que desde sus comienzos tiene una vocación multidisciplinar, adoptando conocimientos de varias ciencias (p.ej. biología, ecología, economía, sociología, derecho) con la finalidad de responder a la “crisis de la biodiversidad” (Primack & Ros, 2002; Soulé, 1985). La biología de la conservación tiene como objetivos principales: (i) investigar y describir la diversidad del mundo vivo; (ii) entender los efectos de las actividades humanas sobre las especies, comunidades y ecosistemas; y (iii) desarrollar métodos interdisciplinarios prácticos encaminados a la protección y recuperación de la biodiversidad (Primack & Ros, 2002).

Desde mediados de la década de 1980, esta disciplina tuvo una gran eclosión que tuvo como manifestación visible la creación de un gran número de nuevas revistas científicas especializadas en este campo (sumándose a *Biological Conservation*, en activo desde 1968), como por ejemplo, *Biodiversity and Conservation* (1992), *Conservation Biology* (1987), o más recientemente *Conservation Letters* (2008). A pesar del avance que ha experimentado en los últimos años – en el sentido de su asentamiento definitivo como disciplina autónoma y su importante repercusión en determinados temas – el desfase entre la producción de conocimiento científico y la aplicación de las propuestas desarrolladas es muy notorio. De hecho, la mayor parte de las acciones de conservación se deciden en base a experiencias previas o presunciones del propio gestor y no como resultado de evidencias extraídas de investigaciones científicas (Pullin, Knight, Stone, & Charman, 2004). En este sentido, la presente memoria doctoral pretende dar el paso desde la fundamentación teórica de propuestas metodológicas a su aplicación efectiva en los problemas de conservación que afronta, sirviendo como una plantilla sobre la que diseñar acciones prácticas de conservación.

I.4. El nicho ecológico

El marco teórico de los Modelos de Nicho Ecológico se basa, obviamente, en el concepto de nicho (Guisan & Zimmermann, 2000; Sillero, 2011; Soberón, 2007, 2010; Soberón, Osorio-Olvera, & Peterson, 2017; Soberón & Peterson, 2005), cuya primera definición fue la de Grinnell (1917), que estaba interesado en la forma en que el medio ambiente o hábitat regulaba la distribución de diferentes especies. Grinnell entendía el nicho como una subdivisión de las condiciones idóneas del hábitat que permiten que individuos de una especie puedan sobrevivir y reproducirse. Este concepto está basado en la importancia de las variables ambientales (climáticas y topográficas) definidas a una escala geográfica relativamente grosera (Benito, 2009; Guisan & Zimmermann, 2000; Sillero, 2011; Soberón, 2007). A esas variables Grinnell las denomina escenopoéticas, variables no interactuantes, es decir, que son independientes de la especie.

Años más tarde, Elton (1927) revisa el concepto de nicho y enfatiza la importancia de los roles funcionales de las especies en la comunidades, especialmente relacionados a la posición de la especie en la cadena alimentaria. El concepto de Elton se basa en las variables a que él denominó bionómicas (p.ej. recursos o competencia intraespecífica); las variables interactuantes, es decir, que pueden ser modificadas por la especie (Sillero, 2011).

Posteriormente, en 1957, Hutchinson utilizando características de los nichos descritos por Grinnell y Elton para redefinir el concepto nicho, describiéndole como un hipervolumen *n*-dimensional en el espacio ecológico multidimensional dentro del cual una especie puede mantener poblaciones viables. Este concepto engloba tanto las variables escenopoéticas como a las bionómicas. Años más tarde Hutchinson describe dos niveles del nicho: el nicho fundamental y el nicho realizado. Nicho fundamental es el espacio multidimensional determinado por todas las variables ambientales (bióticas y abióticas) donde la especie puede mantener una población viable y persistir a lo largo del tiempo. El nicho realizado es un subconjunto del nicho fundamental, en el que las especies están restringidas por las interacciones interespecíficas (Benito, 2009; Sillero, 2011).

I.5. Sistemas de Información Geográfica

En términos generales, un Sistema de Información Geográfica (SIG) puede ser descrito como: *software* especialmente diseñado para capturar, analizar, almacenar, mostrar y mapear información referenciada geográficamente (Sillero, Martín-Alfageme, & Celaya, 2002; Supatimusro, Areerachakul, & Poomsripanon, 2013; Teixeira, 2016). Un SIG permite al usuario ver, comprender, cuestionar, interpretar y visualizar las relaciones, patrones y tendencias de los fenómenos de interés a través – esencialmente – de mapas (ESRI, 2015; Supatimusro et al., 2013; Teixeira, 2016). Con el uso de SIG es posible una verificación clara y objetiva, rápida y precisa de la distribución temporal y espacial de los taxones y de sus áreas de ocurrencia; son extremadamente útiles para análisis de patrones biogeográficos y para comunicar eficazmente los resultados a los gestores.

I.5.1. Datos ambientales

En un SIG los datos pueden ser almacenados en forma de "capas de información" (o *information layers*) estas capas pueden ser divididas según su tipo de estructura: vectorial y en rejilla (o *ráster*).

-*Datos de tipo vectorial*: son datos que se adjuntan a objetos cuyas coordenadas espaciales se definen con precisión. Estos objetos pueden ser puntos, o tener forma de líneas o polígonos según las características de la información que incorporen. Así, los puntos suelen servir para almacenar datos de observaciones o capturar una ubicación (p.ej., registro de ocurrencia de una especie). Las líneas y los polígonos – en ecología – normalmente se utiliza para representar información biológica o de paisaje (p.ej. ríos, carreteras, parcelas de cultivo, tipos de vegetación o usos del suelo). A estos datos se asocian los "atributos" que pueden ser de cualquier tipo: (i) numéricos continuos (p.ej. precipitación); (ii) discretos (p.ej. datos de conteo); y (iii) categóricos (p.ej. tipos de suelo). Además se pueden añadir otros tipos de datos como nombres, fechas, etc. Los datos vectoriales son bastante adecuados para almacenar datos cualitativos como las coberturas de usos del suelo, tipos de vegetación, infraestructuras humanas, limites administrativos, etc.

-*Datos de tipo ráster*: se divide el área de estudio en celdas (o "píxeles") isométricas (normalmente cuadrados). Cada capa contiene un tipo de información – normalmente de tipo cuantitativo que muestra una variación espacial gradual (p.ej. temperatura, altitud, distancia, profundidad) – adjunta a cada píxel. Los datos de tipo ráster permiten un mejor desempeño a la hora de manejar y analizar una gran cantidad de datos. Estos datos son los más idóneos para representar las características ambientales y, por lo tanto, los más adecuados para ser utilizados en proceso de modelado.

I.6. Modelos predictivos

Comprender los procesos subyacentes a la extensión y a los límites de las distribuciones de especies ha fascinado a los científicos desde el comienzo de la investigación ecológica y forma una parte fundamental de la biogeografía (J. O. Engler et al., 2017). El área de distribución de una especie está determinada por factores que operan con diferentes intensidades y a diferentes escalas tanto espaciales como temporales (Hortal, Roura-Pascual, Sanders, & Rahbek, 2010). Por lo tanto, una especie habita aquellas zonas en las que las condiciones abióticas le son favorables, donde la comunidad de especies permite su coexistencia, y en los lugares accesibles que pudieron ser colonizados tanto en tiempos evolutivos como ecológicos (Soberón & Peterson, 2005). Todos esos factores interactúan dinámicamente para producir la compleja entidad que representa el rango geográfico que es único de cada especie (Brown, Mehlman, & Stevens, 1995). No hay dos especies con el mismo rango de distribución; algunas pueden presentar patrones de distribución similares, otras ser completamente diferentes (Sillero, 2006). El rango geográfico es, por tanto, una expresión espacial de la ecología y biología evolutiva de las especies (Brown et al., 1995). Cambios en los rangos de distribución son fenómenos bastante recurrentes a lo largo de la historia de la vida en la Tierra (Hampe & Jump, 2011). Los rangos de distribución se desplazan, contraen, expanden y fragmentan en respuesta a los cambios de las condiciones ambientales globales (p.ej. cambio climático, depredación, competencia por recursos; Guisan et al., 2013). Los organismos están constantemente moviéndose de un lugar a otro en diferentes escalas geográficas y a diferentes escalas temporales. Durante los últimos años se ha incrementado el interés en comprender la distribución de la biodiversidad mundial debido a la urgente necesidad de protegerla contra las multifacéticas amenazas citadas anteriormente (J. O. Engler et al., 2017). De este modo, el estudio de los patrones de distribución, tiene una gran importancia para proporcionar información relevante que puede ser utilizada para guiar planes de manejo y de conservación de las especies (Guisan & Thuiller, 2005). Por ello, desde un punto de vista aplicado, obtener información fiable sobre la distribución de las especies es una cuestión fundamental.

El incremento actual de la potencia computacional y, consecuentemente, la mayor efectividad y rapidez en almacenar y compartir datos a través de la *web*, ha permitido el surgimiento de diferentes iniciativas destinadas a compilar y visualizar datos masivos de información biológica a nivel global (Dhillon & Sidhu, 2013). En la última década, solamente GBIF[4] ha publicado registros de presencia para más 590 000 especies (Costello, Michener, Gahegan, Zhang, & Bourne, 2013). Con este aumento de la disponibilidad de datos de ocurrencia a gran escala (a parte de GBIF se puede citar, por ejemplo, VertNet[5], SpeciesLink[6]) y al mismo tiempo de datos ambientales (p.ej. WorldClim[7], CHELSA[8], SoilGrids[9]) asociados con el desarrollo de innumerables herramientas computacionales o estadísticas para almacenar, gestionar y compartir estos datos, ha proporcionado el surgimiento de modelos estadísticos que vinculan los datos de ocurrencia de

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[4] www.gbif.org
[5] www.vertnet.org
[6] www.splink.org.br
[7] www.worldclim.org
[8] www.chelsa-climate.org
[9] www.soilgrids.org

especies con la información ambiental espacial, que finalmente se utilizan para predecir las distribuciones de las especies en el espacio y el tiempo (J. O. Engler et al., 2017; Jiménez-Valverde, Lira-Noriega, Peterson, & Soberón, 2010; Peterson, 2006). Estos modelos pueden ser de tipo mecánico o correlativo y son citados en la literatura con una gran variedad de nombres, como por ejemplo: Modelos de Distribución de Especies (*Species Distribution Model*s), Modelos de Nicho Ecológico (*Ecological Niche Models*), Modelos de Envueltas Bioclimáticas, Modelos Predictivos del Hábitat (*Predictive Habitat Distribution Models*) (J. O. Engler et al., 2017; Guisan & Thuiller, 2005; Guisan & Zimmermann, 2000; Peterson, 2006; Sillero, 2011). Los resultados de estos modelos son conocidos como mapas de distribución potencial o mapas de idoneidad de hábitat (*potential habitat distribution maps*; *habitat suitability maps*) (Guisan & Thuiller, 2005; Guisan & Zimmermann, 2000). Algunos autores argumentan que esas diferencias terminológicas no son meramente semánticas, sino conceptuales (para una discusión más detallada ver Sillero, 2011; Soberón, 2007, 2010; Soberón et al., 2017; Soberón & Peterson, 2005; Warren, 2012). No es pretensión de esta tesis discutir esas diferencias, por lo que hemos decidido seguir la terminología propuesta por Sillero (2011): Modelos de Nicho Ecológico (MNE).

En la actualidad están disponibles un número significativo de algoritmos matemáticos (algoritmos de modelado *sensu* Peterson et al., 2011) que pueden utilizar datos de solo presencia, presencia-ausencia o abundancia (Elith et al., 2006; Elith & Graham, 2009; Guisan & Thuiller, 2005; Peterson et al., 2011). Dichos datos pueden ser provenientes de muestreos de campo aleatorios o estratificados o registros obtenidos desde de colecciones de museos o herbarios, base de datos digitales o literatura especifica (Guisan et al., 2013; Guisan & Thuiller, 2005). Los datos ambientales (o variables predictoras) pueden ejercer un efecto directo o indirecto sobre el taxón objeto de estudio (Guisan & Thuiller, 2005). De manera general, se puede dividir aquellos factores que habitualmente determinan las distribuciones de las especies en tres grandes grupos: (i) las capacidades dispersoras de la especie (bien por sus propios movimientos o por la dispersión de propágulos); (ii) tolerancia ambiental (la gran mayoría en el sentido fisiológico: p.ej. clima, composición del suelo, agua); (iii) presencia o ausencia de factores bióticos (p.ej. polinizadores, dispersores de semillas, competidores, enfermedades; Guisan & Thuiller, 2005; Soberón, 2007; Soberón et al., 2017; Soberón & Peterson, 2005).

Esencialmente, los algoritmos de modelado pueden ser diferenciados por las siguientes características: (i) los tipos de datos biológicos que el método requiere (es decir, sólo datos de presencias, presencias y ausencias reales, presencias y *background*, y presencias y pseudoausencias) (Brotons, Thuiller, Araújo, & Hirzel, 2004; Peterson et al., 2011); (ii) el enfoque metodológico subyacente (p.ej. algoritmos basados en métodos de regresión, clasificación, máquinas de aprendizaje o estadísticas Bayesiana) (Peterson et al., 2011). Asimismo, se puede clasificar a los algoritmos de muchas maneras diferentes. En los siguientes párrafos los modelos están clasificados según sus requisitos de datos biológicos, lo cual es una consideración muy práctica al seleccionar un método (Peterson et al., 2011). Los requisitos de diferentes algoritmos con respecto al tipo de datos de entrada son los siguientes:

-*Métodos de solo presencia*: se basan únicamente en los registros de presencia, sin necesidad de referencia a otras muestras o cualquier otra información extraída del área de estudio (Peterson et al., 2011). Por ejemplo: las envueltas ambientales como BIOCLIM (Nix, 1986) los métodos de distancia como DOMAIN (Carpenter, Gillison, &

Winter, 1993) y las máquinas de soporte vectorial (*Support Vector Machines, SVM*) (Guo, Kelly, & Graham, 2005).

-*Métodos de presencia y ausencia*: se basan, como su nombre indica, en datos de presencia y ausencia, es decir, contrastan los sitios en los que la especie está presente con los de donde está ausente (Peterson et al., 2011). Dependiendo de la disponibilidad de los datos de ausencia, esas ausencias pueden ser reales o simuladas. A continuación se detallan los posibles datos de ausencia:

-*Ausencias reales*: hacen alusión a lo que son: datos de ausencia confirmados, es decir, un área idónea y accesible para la especie pero en el que la especie no está (Barbet-Massin, Jiguet, Albert, & Thuiller, 2012; Brotons et al., 2004; Peterson et al., 2011). Son datos muy difíciles de conseguir de manera precisa, sobre todo para especies crípticas o con gran movilidad. Aparte de que, para la obtención de datos de ausencia fiables, se necesita un esfuerzo de muestreo mucho más elevado cuando son comparados con los datos de presencia (Barbet-Massin et al., 2012; Brotons et al., 2004).

-*Pseudoausencias*: emulan los datos de ausencias reales. Normalmente sólo se muestrean, de manera aleatoria, los sitios en los que se conoce la presencia de la especie, dentro del área de estudio. Teniendo cuidado de que no se incluyan los píxeles en los que la especie ocupa o podría ocupar (Peterson et al., 2011). El proceso de generación de pseudoausencias debe seguir algunas reglas: tener en cuenta las distancias espaciales y ambientales con respecto a las presencias y las demás pseudoasencias (para mayores detalles ver Barbet-Massin et al., 2012; Hanberry, He, & Palik, 2012).

-*Datos de background*: el *background* – muchas veces confundidos con las pseudoausencias – puede ser definido sintéticamente como un muestreo exhaustivo del área de estudio, es decir, un intento de caracterizar las condiciones ambientales del área de estudio. Son datos ambientales extraídos de todo el área de estudio (o por lo menos una muestra significativa) que pueden incluso solapar con las presencias de la especie (ver Phillips et al., 2009).

I.6.1. Algoritmos de modelado

Entre los algoritmos de modelado que utilizan como entrada datos de presencia y ausencia están los modelos lineales generalizados (GLM; McCullagh & Nelder, 1989), los modelos aditivos generalizados (GAM; Hastie & Tibshirani, 1990), las técnicas multirrespuesta (MARS; Multivariate Adaptive Regression Splines; Elith & Leathwick, 2007), las técnicas de clasificación (CART; Classification and Regression Trees; De'ath & Fabricius, 2000), los árboles de regresión y clasificación (Random Forests; Breiman, 2001; BRT; Boosted Regression Trees; Elith, Leathwick, & Hastie, 2008), las redes neuronales (ANN; Artificial Neural Networks; Hilbert & Ostendorf, 2001) y los algoritmos genéticos (Pearson, Dawson, Berry, & Harrison, 2002). Aunque todas las técnicas citadas arriba están diseñadas originalmente para funcionar con presencias y ausencias reales, aceptan datos de presencia-pseudoausencia o presencia-*background* (Elith et al., 2006; Peterson et al., 2011). El enfoque de máxima entropía (Maxent; Phillips, Anderson, Dudík, Schapire, & Blair, 2017; Phillips, Anderson, & Schapire, 2006; Phillips, Dudík, & Schapire, 2004; Phillips & Dudík, 2008) y el análisis factorial de Nicho Ecológico (ENFA; Ecological Niche Factor Analysis; Hirzel, Hausser, Chessel, & Perrin, 2002) están diseñados para trabajar con datos de presencia-*background*. Finalmente está GARP

(Stockwell & Peters, 1999), que es un algoritmo genético diseñado para utilizar presencias-pseudoausencias.

La generación de MNE es un proceso computacionalmente complejo, que necesita gran variedad de datos, técnicas, paquetes de software y hardware apropiado. Sin embargo, todos los métodos citados anteriormente comparten en gran medida un conjunto de principios similares (Guisan & Zimmermann, 2000; Sillero, 2006): (i) captura y preparación de la muestra de presencia (la etapa que más consume tiempo pero la más importante para obtener resultados fiables; Jiménez-Valverde et al., 2010); (ii) preparación (i.e. uniformizar las extensiones y resoluciones) y selección de las variables ambientales bien sea estadísticamente (p.ej. reducción de la autocorrelación espacial) o mediante al conocimiento previo de la biología de la especie; (iii) selección y parametrización de algoritmos de modelado; (iv) calibración del modelo (también llamado de entrenamiento); (v) proyección al espacio geográfico y; (vi) análisis, interpretación de los resultados y aplicación. La salida de un modelo está compuesta por un mapa de tipo ráster del área de estudio compuesto por *n* píxeles isométricos. Ésta, describe las características de cada píxel de manera cuantitativa (p.ej. topografía, clima, influencia humana). Dependiendo de la calibración del modelo, las salidas podrán ser interpretadas en forma de probabilidades de presencia/ausencia o áreas idóneas/no idóneas para la ocurrencia de la especie.

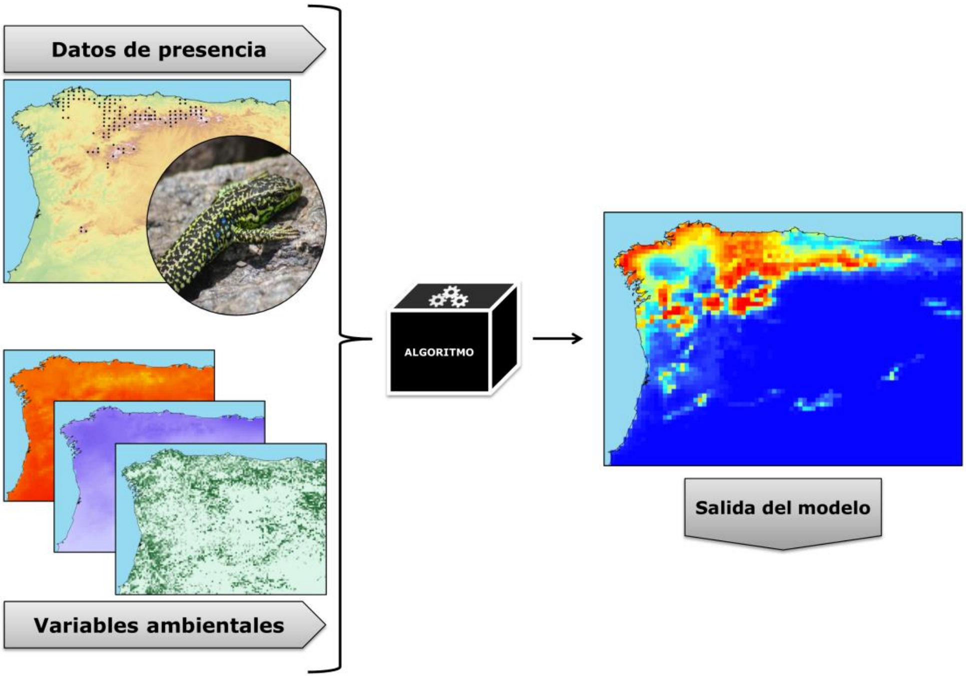

FIGURA 3 Ejemplo del proceso de modelado. Puntos de presencia de *Iberolacerta monticola*. (Foto: J.R. Peralta-Rincón)

I.6.2. Aplicaciones de los modelos

Los MNE son espacialmente representados y manejados por los SIG (Sillero, 2006), por lo tanto, son capaces de sintetizar el conocimiento disponible de una manera sistemática, racional y transparente (Addison et al., 2013). De este modo, los "buenos" modelos tienen un gran potencial para sustentar la toma de decisiones – que muchas veces son realizadas frente a la incertidumbre ambiental – relacionadas a la conservación (Addison et al., 2013; Margules & Pressey, 2000).

Los MNE son herramientas ampliamente utilizadas para comprender la ecología, la distribución espacial de las especies y asimismo, apoyar su conservación (Bahn & Mcgill, 2007; Guisan et al., 2013; Guisan & Thuiller, 2005). En los últimos años el número de publicaciones que usan estas herramientas ha crecido exponencialmente (Guisan et al., 2013); a continuación se ofrece un breve listado ejemplificando algunas aplicaciones de los MNE relacionados a problemas de conservación: (i) identificar (micro-)refugios biogeográficos (Ashcroft, Gollan, Warton, & Ramp, 2012); (ii) evaluar los potenciales efectos del cambio global en la distribución de las especies (Araújo, Alagador, Cabeza, Nogués-Bravo, & Thuiller, 2011; Benito, Lorite, & Peñas, 2011; Benito Garzón, Sánchez De Dios, & Sainz Ollero, 2008; Botkin et al., 2007; Cuyckens, Christie, Domic, Malizia, & Renison, 2016; Draper Munt, Muñoz-Rodríguez, Marques, & Moreno Saiz, 2016; R. Engler et al., 2009; Koo et al., 2017; Sillero & Carretero, 2013; Thuiller, Lavorel, Araújo, Sykes, & Prentice, 2005); (iii) evaluar el riesgo potencial por la introducción de especies invasoras (Barbet-Massin et al., 2013; Barbet-Massin, Rome, Villemant, & Courchamp, 2018; Bosch, Mardones, Pérez, de la Torre, & Muñoz, 2014; Kriticos, Sutherst, Brown, Adkins, & Maywald, 2003; Kumar, Neven, Zhu, & Zhang, 2015; Padalia, Srivastava, & Kushwaha, 2014; Peterson, 2003; Peterson & Vieglais, 2001; Villemant et al., 2011); (iv) seleccionar áreas prioritarias para conservación de las especies o evaluar la ya existentes (Araújo & Williams, 2000; Domíguez-Vega, Monroy-Vilchis, & Balderas-Valdivia, 2012; Giorgi et al., 2014; Hannah et al., 2007; Joshi, Charles, Ravikanth, & Aravind, 2017; Lessmann, Muñoz, & Bonaccorso, 2014; Loyola et al., 2013; Margules & Pressey, 2000; Ortega-Huerta & Peterson, 2004); (v) evaluar los riesgos de extinción (Araújo, Williams, & Fuller, 2002; Kissling, 2013; Tracewski et al., 2016); (vi) determinar lugares óptimos para la reintroducción de especies amenazadas (Hirzel et al., 2004; Li, Li, Li, Ma, & Zhai, 2002; McShea et al., 2005); (vii) localizar nuevas poblaciones de especies raras y/o amenazadas (Guisan et al., 2006; Lomba et al., 2010; Siqueira, Durigan, Marco Júnior, & Peterson, 2009). Debido a que los recursos para la conservación de la biodiversidad suelen ser escasos, los MNE surgen como una opción viable para buscar la mitigación de varios problemas relacionados a la conservación

(Araújo & Williams, 2001; Channell, 2004) (los ejemplos citados en el párrafo anterior y otros muchos más). Por un lado, porque son baratos, dependiendo de su magnitud no requieren ordenadores de alto rendimiento; además de que, según su magnitud, los procesos de modelado pueden ser considerados rápidos (Benito, 2009). Por otro lado, como son representaciones útiles y simplificadas de los complejos sistemas existentes en el mundo real, pueden ser utilizados para, de manera satisfactoria, testar hipótesis o experimentos e incluyen cualquier forma útil de abstracción para ayudar al pensamiento (Addison et al., 2013). Además, los MNE permiten simular el paso de grandes periodos de tiempo en cuestión de minutos (o horas) y pueden ser actualizados para incorporar nuevo conocimiento o capacidades tecnológicas (Benito, 2009).

I.6.3. Limitaciones e incertidumbres de los modelos

A continuación se comentan algunas de las limitaciones más recurrentes relacionadas con la disciplina de los MNE (una revisión más profunda puede ser encontrada en: Guisan & Thuiller, 2005; Guisan & Zimmermann, 2000). Obtener datos de distribución que sean fiables y de calidad es algo crucial a la hora de generar modelos. La disponibilidad de tales datos no siempre es una realidad, resultando así la primera limitación ante la que se encuentra un investigador a la hora de abordar un trabajo de modelado. Problemas con la precisión de la georreferenciación y los sesgos significativos en el tiempo y en el espacio, debido a diferencias en el esfuerzo de muestreo, pueden comprometer los resultados de cualquier modelo que utilice datos dichos problemas (Jiménez-Valverde et al., 2010). Aún relacionado con los datos de presencia está el problema de la autocorrelación espacial, que aparte de inflar el valor predictivo de los modelos, puede provocar que los modelos sobrepredigan el área potencial de distribución de la especie estudiada (Chapman, 2010; Guisan & Zimmermann, 2000).

Además, generalmente los procesos a micro-escala que moldean la distribución de las especies (p.ej. las interacciones bióticas o las condiciones microclimaticas experimentadas por las plantas de alta montaña; Körner & Hiltbrunner, 2017; Normand et al., 2009; Sinclair, White, & Newell, 2010) tienden a ser obviados a la hora de la generación de los modelos (Guisan & Thuiller, 2005); especialmente aquellos a gran escala, porque actualmente esos datos son escasos y normalmente – cuando están disponibles – son a una escala geográfica muy reducida o no tienen la calidad o precisión necesarias (Guisan & Zimmermann, 2000). Asimismo, generar tales datos es bastante complejo una vez que para definir el ambiente biótico de una especie (es decir, sus interacciones bióticas positivas y negativas) es necesario tener un conocimiento profundo de su biología y aunque se cumpla ese requisito, algunos fenómenos esenciales pueden ser omitidos (Benito, 2009; Soberón, Llorente, & Oñate, 2000). Otro problema que puede afectar a los resultados de las predicciones de los MNE es el posible desajuste que puede haber entre la “resolución” con la que se tomaron los datos de presencia (p.ej., el tamaño de la parcela en los muestreos de campo o el tamaño de la cuadrícula en los de atlas) con la que tienen las variables que están disponibles. En un mundo ideal, ambas deberían ser iguales, pero tal coherencia no siempre es posible (Guisan & Thuiller, 2005).

Finalmente en la mayoría de los casos, cualquier representación del nicho ecológico puede ser solamente parcial, ya que es extremadamente difícil considerar todos los ejes del nicho multidimensional (Martínez-Gutiérrez, Martínez-Meyer, Palomares, & Fernández, 2018; Yañez-Arenas, Guevara, Martínez-Meyer, Mandujano, & Lobo, 2014).

I.7. OBJETIVOS Y ESTRUCTURA DE LA TESIS

En este contexto teórico y metodológico explicado, esta tesis tiene como objetivo general aportar nuevas evidencias sobre la utilidad potencial de los Modelos de Nicho Ecológico para abordar cuestiones y problemas relativos a la conservación de especies. Este objetivo general se desglosa a su vez en objetivos específicos que son abordados de forma específica en cada capítulo:

1) Estudio de la problemática de las especies invasoras mediante MNE

Capítulo 2: *"How reliable is the untrained eye in the identification of an invasive species? The case of alien bee-hawking Yellow-legged hornet in Iberian Peninsula"*

Como se ha expuesto previamente, una de las amenazas más graves actualmente para la biodiversidad son las invasiones biológicas. Por ello es fundamental disponer de información fiable de los patrones de distribución de las especies invasoras a la hora de poder plantear medidas eficaces para su manejo. En este sentido se ha desarrollado en este capítulo, una metodología experimental que tiene como objetivo comparar la fiabilidad de los datos de presencia de la avispa asiática tomados por voluntarios no expertos (p.ej., entomólogos aficionados, apicultores), frente a los datos tomados por personal experto (p.ej., personal técnico e investigadores de servicios ambientales). Dicho de forma sencilla, la idea es valorar de forma objetiva la validez del ojo inexperto para el diseño de sistemas de alerta temprana de especies invasoras.

2) Aplicación de los MNE en el estudio de los patrones de distribución de especies amenazadas

Capítulo 3: *"Behavioural, ecological and human factors explain wintering red kite (Milvus milvus Linnaeus, 1758) distribution in the Iberian Peninsula: consequences and opportunities for conservation of European raptors"*

¿Qué ocurre con los requisitos ambientales de distribución de las especies migratorias? ¿Son iguales en todos los espacios que ocupan de forma temporal? Los MNE se aplican con eficiencia en especies sedentarias pero raramente han tenido una aplicación en especies que cambian sus dominios de presencia según periodos estaciones, como es el caso de las aves migratorias. En este capítulo estudiamos los requisitos de aparición invernal en el territorio ibérico de un ave de interés como es el milano real, cuyas poblaciones en la última década han tenido un marcado declive. Conocer cuáles son los factores que determinan sus áreas de invernada puede ser un paso importante para el desarrollo de estrategias de conservación eficaces.

3) Análisis del efecto de la marginalidad geográfica poblacional en la idoneidad de hábitat

Capítulo 4: *"Living on the edge: do central and marginal populations of plants differ in habitat suitability?"*

En este capítulo proponemos un nuevo marco metodológico para evaluar cuantitativamente las diferencias en la idoneidad de hábitat de las poblaciones de una especie que se encuentran en el borde de su rango de distribución con respecto a las que están en el centro. Esta cuestión puede tener una gran transcendencia en el ámbito de la conservación ya que las poblaciones "marginales" tienen un valor importante por constituir los frentes de avance o retracción del área de una especie, estando sometidas, habitualmente, a mayores amenazas, siendo su diversidad genética, por lo general mayor.

4) Evaluación de los patrones de idoneidad de hábitat en las áreas de distribución de especies endémicas europeas correspondientes a distintos grupos de organismos, testando la hipótesis de centro-periferia

Capítulo 5: *"Assessing niche similarities between central and marginal populations of European endemic species"*

En este último capítulo retomamos el contexto metodológico-conceptual del capítulo anterior, ahondando en el proceso estadístico de comparación de los resultados de los MNE, en este caso aplicándose a numerosas especies endémicas europeas correspondientes a varios grupos de organismos de comportamientos, hábitos y ecologías muy diversas, a fin de determinar su validez de cara a determinar diferencias entre poblaciones marginales y centrales.

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CAPÍTULO II

¿Qué tan fiable es el ojo inexperto en la identificación de una especie invasora? El caso de la avispa asiática en la Península Ibérica

Resumen

Las invasiones biológicas causan graves daños a los ecosistemas nativos, por lo tanto, es extremadamente importante tomar medidas para contener el progreso de las invasiones existentes y también prevenir nuevas. En el presente capítulo empleamos los Modelos de Nicho Ecológico (ENM) para comparar dos conjuntos de datos independientes para una especie exótica invasora: la avispa asiática (*Vespa velutina*) en la Península Ibérica. Un conjunto de datos contiene los registros de presencias recopilados por personas expertas (p.ej., personal técnico e investigadores de servicios ambientales); y el otro los registros recopilados por personas no expertas (p.ej., entomólogos aficionados, apicultores). El objetivo principal es evaluar la eficacia y la fiabilidad del conjunto de datos gestionados por los no expertos al compararlo con el conjunto de datos gestionados por expertos. Con ambos conjuntos de datos construimos dos modelos predictivos independientes utilizando el enfoque de Máxima Entropía (Maxent) y utilizamos sus resultados para realizar comparaciones por pares. Los patrones de áreas potenciales predichas, la prueba de *jackknife* para la importancia de las variables y las curvas de respuesta para cada variable, mostraron un alto grado de similitud entre los modelos (es decir, conjuntos de datos). Basándonos en nuestros resultados podemos concluir que, los registros de ocurrencia (es decir, alertas de presencia para esta especie) reunidos por no expertos pueden utilizarse como una herramienta adicional en el diseño de estrategias de control para *V. velutina* en su rango invadido. Los modelos derivados de ambos conjuntos de datos muestran un alto grado de similitud, por lo tanto, ambos tendrían la misma confiabilidad para ser utilizados en estrategias de manejo para esta especie.

How reliable is the untrained eye in the identification of an invasive species? The case of alien bee-hawking Yellow-legged hornet in Iberian Peninsula

Abstract

Biological invasions cause great damage to native ecosystems, therefore, it is extremely important to take measures to contain the progress of existing invasions and prevent new ones. In this chapter, we used the Ecological Niche Models (ENM) approach to compare two independent datasets for the invasive alien species the Yellow-legged hornet (*Vespa velutina*) in the Iberian Peninsula. One dataset compiles occurrence records gathered by expert people (e.g. environmental services' technical staff and researchers); and the other compiles occurrence records gathered by non-expert people (e.g. amateur entomologists, beekeepers). The main aim is to assess the effectiveness and reliability of the dataset managed by non-experts when comparing it to the dataset managed by experts. With both datasets we built two independent predictive models applying the maximum entropy approach (Maxent) and used its outputs to compare them. The patterns of potential predicted areas, the jackknife test for importance of variables and the response curves created for each variable, showed a high degree of concordance and similarity between models. Based on the results, the occurrence records (i.e. presence alerts for this species) gathered by non-experts can be used as an additional tool in the designing of control strategies for *V. velutina* in its invaded range. The two models derived from both datasets show a high degree of similarity, thus both would have the same reliability to be used in management strategies for this species.

II.1. INTRODUCTION

Human activities are modifying the composition of biological communities and leading to an increase in rates of biological invasion and species extinction from local to global scale (Hooper et al., 2005). The number of species moved unintentionally by humans across biogeographical barriers has increased dramatically due to globalization (i.e. expansion of transport and global trade) in the last few centuries (IUCN, 2000; Mack et al., 2000).

Due to their reproductive and dispersal strategies, social insects such as ants, bees and wasps are considered the most successful invaders of new territories around the world (Moller, 1996; Villemant et al., 2011). However, *Vespa velutina* Lepeletier, 1836, after its introduction and establishment in France, became the first exotic Vespidae which achieved a successful invasion in Europe (Beggs et al., 2001; Villemant et al., 2011). Similarly to other invasions caused by other Vespidae species, the *V. velutina* invasion generates a series of ecological, economic and social impacts (Beggs et al., 2001). Although the full impact of *V. velutina* is not yet known, some aspects raised concerns on population: the predation of domestic honeybees (*Appis mellifera*) and the local entomofauna, the damage caused to orchards during autumn (due feeding habits) associated to the fact that hornet’s stings are potentially deadly to allergic people. However, in areas colonized by *V. velutina*, no significant increase in Hymenoptera stings was reported during the first 5 years following the introduction (de Haro et al., 2010). As a consequence, beekeepers and some citizens have begun to actively search for *V. velutina* nests as a method of control, often carrying insufficient information or without necessary rigor, which has led to a destruction of a large number of individuals and colonies of *Vespa crabro* Linnaeus, 1758 or even other Vespidae (*Vespula* or *Dolichovespula* spp.). Disproportionate and unconscious actions, might contribute even more to the threats caused by *V. velutina* and its establishment (Balmori, 2015; Beggs et al., 2001; López, González, & Goldarazena, 2011; Monceau, Bonnard, & Thiéry, 2014; Robinet, Suppo, & Darrouzet, 2017; Rome, Perrard, Muller, & Villemant, 2011; Villemant et al., 2011; Villemant, Rome, & Haxaire, 2010).

Currently, there are over 200 million records of biodiversity data available online to researchers worldwide (Jiménez-Valverde, Lira-Noriega, Peterson, & Soberón, 2010). Data coming from these databases are known to be relevant therefore they have to play a key role in the field of conservation biology (Fagan & Kareiva, 1997). This type of data contain valuable information and are commonly cited in literature as part of Ecological Niche Models (ENM) input data (e.g. Bosch, Mardones, Pérez, de la Torre, & Muñoz, 2014; Bosso, Rebelo, Garonna, & Russo, 2013; Jiao, Zeng, Sun, & Lei, 2016; Kumar, Neven, Zhu, & Zhang, 2015). In general, ENM are powerful tools used widely to predict potential species habitat suitability based on relationships between species observations and environmental predictors (Domíguez-Vega, Monroy-Vilchis, & Balderas-Valdivia, 2012; Guisan et al., 2013; Guisan & Zimmermann, 2000). These are important prevention tools when used to identify new potential suitable areas of future biological invasions helping the experts on fast development of species conservation strategies (Balmori, 2015; Godown & Peterson, 2000; Guisan & Zimmermann, 2000; Kriticos, Sutherst, Brown, Adkins, & Maywald, 2003; Villemant et al., 2011).

Over the last years, there has been an increase in new initiatives in the Bioinformatics field seeking to maintain, share and communicate biological information on a global level (Dhillon & Sidhu, 2013). Jointly, the number of web users has increased sharply as well as the data collected by these users

(Bonney et al., 2009; Goodchild, 2007; Roy et al., 2012), mainly helped by the implementation of specific applications for computers and especially for mobile phones, many of them are designed to compile invasive species data (Adriaens et al., 2015; Teacher, Griffiths, Hodgson, & Inger, 2013). These voluntary contributions have as a strong point the fact of being an important source of information to help us understand the natural environment (Roy et al., 2012). The large range in volunteer experience level is pointed out by many authors as a factor that could directly affect the data quality and thus would be an important drawback when applying these data in scientific research (Bonney et al., 2009; Goodchild, 2007; Jiménez-Valverde et al., 2010; Roy et al., 2012).

To date, there is still no specific application in order to monitor *V. velutina*'s distribution, however, for this species, a digital database has been created, compiled and managed with data collected by volunteers with different levels of experience. Their scientific relevance often makes it difficult to develop predictive models that are required for decisions concerning its management. For example, the spatial distribution of *V. velutina* can change continuously, and it is sometimes not feasible to obtain data capturing such dynamics at large spatial scales, despite the need for such data to validate the developed predictive models. To compensate for the lack of data, an effective approach could be to construct frameworks that can extract useful data from monitoring and pest-control activities conducted by volunteers. Public participation has the potential to accumulate large amounts of long-term data required for this which may otherwise be difficult to collect (Kadoya, Ishii, Kikuchi, Suda, & Washitani, 2009). In this sense, we explored the use of ENM (*sensu* Sillero, 2011) to evaluate the quality and reliability of a data source of presence of an invasive bee created with information collected by volunteers in the north of the Iberian Peninsula by comparing it with a database created and managed by technical personnel from official bodies. Using each data set individually, we constructed two independent predictive models and used the predictions of each model to compare them. Through these analyses, we aimed to investigate the potential of using data generated in participatory monitoring programs for predicting future invasions and controlling the spread of invasive species.

II.2. METHODS

II.2.1. Study area

We selected the north of the Iberian Peninsula as our study area. This area is located in the southwestern Palearctic, bordered by the Atlantic Ocean and the Mediterranean Sea and isolated from rest of Europe by the Pyrenees mountain range. The heterogeneous climate of the area is divided by two major climate zones: the Atlantic climate, characterized by mild summers and cold, rainy winters; and the Mediterranean climate with mild winters and hot, dry summers. The orography is formed by the Pyrenees, Cantabrian, central and northern Iberian mountain ranges and the Galician Massif as well as several isolated mountains (Rebelo & Jones, 2010; Sillero, Brito, Skidmore, & Toxopeus, 2009).

II.2.2. Study species

Vespa velutina is one of the 22 currently recognized *Vespa* genus species; most of them having their native distribution restricted to Asia (Perrard, Pickett, Villemant, Kojima, & Carpenter, 2013; Rome et al., 2011). *V. velutina* is widespread in Asia. Its natural range stretches from India to Indonesia, also expanding widely in central and southern China and in Korea it was introduced by accident in the 2000s (Kim, Choi, & Moon, 2006; Rome et al., 2011).

The first record of this species in the European continent was obtained in the French department of Lot-et-Garonne in 2004 (Arca et al., 2015; Beggs et al., 2001; Monceau et al., 2014; Rome et al., 2013; Villemant et al., 2011). Individuals acclimated to the southwest of France, most likely came from gravid females that could have been introduced by accident from China through the international horticultural trade (Villemant et al., 2011, 2010). This species was detected for the first time in the Iberian Peninsula in August 2010, in the village of Amaiur, province of Navarra (Castro & Pagola-Carte, 2010). In addition, many other records were reported in October of the same year to the east of the province of Gipuzkoa (López et al., 2011). In 2011, the species was seen in northern Portugal, in the province of Minho (Grosso-Silva & Maia, 2012). From 2012 to 2014, the presence of the species was noted along the whole of the north of Spain ranging from the north of the province of Lugo to the north of Catalonia (Balmori, 2015; Rome et al., 2013). In 2011 a single observation was recorded in Belgium (Rome et al., 2013; Rome, Muller, & Villemant, 2012). The following year the species was detected in northwest of Italy (near to the French border) for the first time, its first nests were found in 2013 and since then continues expanding its range (Bertolino, Lioy, Laurino, Manino, & Porporato, 2016; Demichelis, Manino, Minuto, Mariotti, & Porporato, 2014). The species continues to spread through Europe with further nests observations in Germany (Rome et al., 2015) and recently in Great Britain (Franklin et al., 2017; Keeling, Franklin, Datta, Brown, & Budge, 2017).

The Yellow-legged hornet is a generalist predator with a varied diet; which can attack several insect orders and even spiders to feed their larvae, while the adults exclusively feed on sweetened liquids (Beggs et al., 2001;

López et al., 2011; Villemant et al., 2011, 2010). Due to the overlap of their prey, *V. velutina* could start to compete with its only European congeneric: *V. crabro*. This could result in a conservation problem of the European hornet, a species considered threatened in many European countries (Villemant et al., 2011).

Aiming to combat and control *V. velutina* in the geographical area of the Iberian Peninsula, Portugal maintains a plan of action and control against *V. velutina* since October 2014 and the latest version available is dated January 2015 (ICNF, 2015; http://www.icnf.pt/portal/naturaclas/patrinatur/especies/n-indig/vesp-velutina#plano-acao). Spain has its own control strategy of the species since April 2015 (MAGRAMA, 2014; http://www.magrama.gob.es/es/biodiversidad/publicaciones/pbl-fauna-flora-estrategias-eei-vespa.aspx).

II.2.3. Occurrence data

We compiled the *V. velutina* occurrence data (latitude and longitude) into two different datasets: *Official* and *Web dataset* in the study area.

Official dataset **(*N* = 5627):** we contacted the Spanish Ministry of Agriculture, Food and Environment (MAGRAMA) to gather the *V. velutina* presence records in Spain. As of February 2015, 8 of the 15 Autonomous Communities had reported to MAGRAMA *V. velutina* occurrence in their territories. The Spanish protocol is as follows: when a new nest is detected a call to the emergency phone number is made (it is considered as a warning network). Then, trained technicians move to the locality to check the species' occurrence, if confirmed the nest is destroyed and the record is consequently validated. Hence, the reported data consist in the georeferenced records of the nests removed and destroyed by the trained technicians of each community. Georeferenced data of nests in Portugal were gathered from the "*Instituto da*

Conservação da Natureza e das Florestas (ICNF)" available on *SOS Vespa* platform (www.sosvespa.pt). In Portugal, official institutions receive notifications of sightings of *V. velutina*' nests through the referred platform. Then, trained technicians validate this information. If necessary, these same professionals are sent to act in removing and destructing the nest.

***Web dataset* (*N* = 2619):** occurrence data were available on the web page managed by "Instituto Vasco de Investigación y Desarrollo Agrario" (NEIKER-Tecnalia) (www.avisosneiker.com) and also from the monitoring maps of the Yellow-legged hornet in Europe, with a special emphasis on the Iberian Peninsula (*Vespa velutina* in Europe as of December, 2016; https://www.google.com/maps/d/viewer?ll=41.574361%2C-2.900391&msa =0&spn=13.257017%2C28.54248&mid=zQZZvCfJcXQo.k0cLRXyow4C0), created and managed by the page called *"Mel de Selva"*. The latter is an open and collaborative platform which recompile all notifications across the Europe (with no expert validation or supervision).

As part of the methodology, we have established as a reference the *Official dataset* in order to be used for comparison with the *Web dataset* to assess the reliability and usefulness of the latter one. We do not intend to imply that the *Official dataset* is superior only because these data come from official bodies, but it is used simply as a reference of recognized validity to confront these data obtained by volunteers with different levels of experience (Llaneza & Núñez-Quirós, 2009).

Normally, presence records that are too close have the same combinations of values for the environmental variables which violate the assumption of independence between observations. To reduce the clustering (spatial bias), we randomly removed occurrence records that were within a radius of five grid squares of another (about 5 km) (Guisan & Zimmermann, 2000; Zohner, Benito, Fridley, Svenning, & Renner, 2017). The five grid square distance was chosen based on previous studies with other eusocial wasps from the Vespinae subfamily, where it is indicated that the foraging range of these species vary between 50 m and 1.2 km, although there are a few records of individuals who were found 8 km from their nests (Edwards, 1980; Matsuura & Yamane, 1990). So far, the foraging distance of *Vespa velutina* remains unknown (Monceau et al., 2014). To avoid pseudoreplication, records with duplicated coordinate values (i.e. latitude and longitude) were located and removed using R duplicated function (R Core Team, 2015; Zohner et al., 2017). This filtering decreased the number of records for *Official dataset* to 314 and for *Web dataset* to 630 occurrence records (Fig. 1). Although both datasets are the result of an extensive search of the occurrence of *V. velutina* within the study area, it is important to emphasize that datasets may not represent the full range of environmental conditions in which the species can be found outside of the study area (e.g. other introduced areas). Thus, our estimates will always be a conservative representation of the full potential of the species.

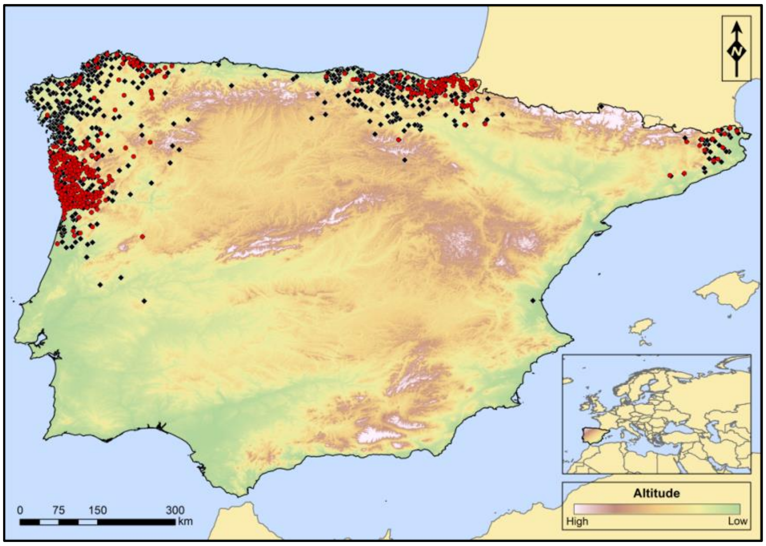

FIGURE 1 Occurrence data, per dataset, of *Vespa velutina* in the study area. Red dots: *Official* (N = 314) and black diamonds: *Web* (N = 630)

II.2.4. Environmental variables

Our initial variable set was composed of 23 variables as predictors, related to climatic and topographic conditions, land-cover and human influence (Appendix Table A1). All GIS work was conducted using ArcGIS Desktop 10 version 10.0 (ESRI, 2010). Bioclimatic variables were available from the WorldClim climatic database at 30 arc-seconds spatial resolution (approximately 1km at the equator) (Hijmans, Cameron, Parra, Jones, & Jarvis, 2005). Topographic variables were derived from the Digital Elevation Model (DEM) available from CGIAR-CSI database at 3 arc seconds spatial resolution (approximately 90 m at the equator) (Jarvis, Reuter, Nelson, & Guevara, 2008). The slope was calculated in degrees using “slope” function by ArcGIS program (ESRI, 2010). From each grid cell all over a DEM, it calculates the inclination of slope. Topographic diversity was calculated using the “focal statistics” function (ESRI, 2010), which calculates for each DEM grid cell the diversity of elevation values considering all cells within a 3 km radius. The Human Influence Index was available from SEDAC database (Socioeconomic Data and Applications Center) at 1 km spatial resolution. This variable contains information about the human population pressure (population density) and infrastructures (built-up areas, night-time lights), and human access (coastlines, roads, railroads, navigable rivers) (WCS & CIESIN, 2005). The land-cover data were available on Corine Land Cover (CLC) 2006 programme database at 1 km spatial resolution (European Environment Agency, 2006; www.eea.europa.eu). It contains information about the soil occupation all over Europe containing a hierarchical classification divided into three levels with 44 classes of land use and land cover. Using the “reclassify” function, we reclassified the 44 classes into seven new classes: artificial areas (1), agricultural areas (2), forest areas (3), scrublands or herbaceous vegetation (4), open areas with little or no vegetation (5), wetlands (6) and water bodies (7). Variables gathered originally at different resolutions were resampled at 1km spatial resolution.

To minimize multicollinearity among environmental variables, a hierarchical clustering with *complete linkage* method was used. From the resulting correlation tree, variables were selected based on a cut-off or threshold minimum of 0.5. In each one of the eight groups of variables with node <0.5, only one variable was selected based on its correlation and its previous applications in insects ENM studies (Appendix Fig. A1). In addition to the above procedure, we calculated the variance inflation factor (VIF; R package HH). The VIF for predictor *i* is 1/(1-R_*i*^2), where R_*i*^2 is the R^2 from a regression of predictor *i* against the remaining predictors. Values of VIF >5 are considered evidence of collinearity: the information carried by a predictor having such a VIF is contained in a subset of the remaining predictors (Benito et al., 2017; Heiberger, 2017). Although, isothermality (BIO3) and mean temperature of wettest quarter (BIO8) presented VIF values <5 we chose to remove them from the sample rather than temperature seasonality (BIO4), minimum temperature of the coldest month (BIO6) and precipitation of driest month (BIO14), because of their potential biological significance to species and also these variables were previously applied in *V. velutina* distribution models (Bessa, Carvalho, Gomes, & Santarém, 2016; Villemant et al., 2011) (Appendix Table A2). The categorical variable land cover type could not be tested using the linear regression method. Finally, seven variables were selected: temperature seasonality (BIO4), minimum temperature of the coldest month (BIO6), annual precipitation (BIO12), precipitation of driest month (BIO14), human influence index (HFP), land-cover (LC), and topographic diversity (TD).

II.2.5. Model settings and model evaluation

In order to compare *Official* and *Web datasets*, we calculated realized niche models (*sensu* Sillero, 2011) for *V. velutina* (hereafter *Official* and *Web*) using the free software Maxent (Maxent 3.3.3 software package; https://www.cs.princeton.edu/~schapire/maxent/) (Phillips, Anderson, & Schapire, 2006; Phillips, Dudík, & Schapire, 2004; Phillips & Dudík, 2008). It estimates the probable distribution of maximum entropy (i.e. closest to the uniform) by combining an only-presence dataset with environmental variables (Phillips et al., 2006, 2004). The advantage in applying the ENM approach to compare two independent data sets is that it allows to incorporate not only the species spatial distribution to the analysis but also to consider the constraints imposed by environmental predictors in the occurrence records.

We used all available occurrences of *V. velutina* from each dataset to calibrate two models (i.e. *Official* and *Web*) in north of Iberian Peninsula. We selected three feature classes (linear, quadratic and product), a regularization multiplier value of 1, a maximum of 5000 iterations and 20000 background points. We limited the background points to areas which we assume were surveyed (i.e. all provinces within the Iberian Peninsula with at least one species' occurrence record) for the species by providing Maxent with a background file with the same bias as the presence locations (Elith et al., 2010). The predictive performance of each model was assessed using 10 replicates with bootstrap procedure (80% of the data for calibration and 20% for evaluation) and the area under the receiver operating characteristic (ROC) curve, also known as AUC, which evaluates predictive ability in discriminating occurrence from background records and ranges from 0.5 (randomness) to 1 (perfect discrimination) (Fielding & Bell, 1997). The models calibrated in the north region were projected to all grid square (approximately 1 x 1 km) within the Iberian Peninsula to build an invasion risk map.

Also, we calculated the jackknife test of training gain values that estimate which variables were most important for the building of each model in order to assess the degree of similarity between the geographical distribution patterns generated by models.

The continuous outputs from Maxent were converted into binary maps (suitable or unsuitable habitats for species) using the 10th percentile training presence threshold (values above this threshold value are considered suitable for the species presence). This is a conservative value commonly used in ENM studies, especially for datasets that have been taken during long periods of time and by different experts, with different methodologies (Bosso et al., 2013; Rebelo & Jones, 2010). The surface total of potential predicted areas by each model was calculated using the "calculate geometry" ArcGIS default function (ESRI, 2010).

II.2.6. Models pairwise comparisons

To assess the degree of similarity between the *Official* and *Web* models, we compared the predicted suitability area by Maxent using different approaches. Firstly, following the approach proposed by Parolo et al. (2008), we calculated a global comparison using Spearman's *rho* correlation coefficient from both models to assess the degree of concordance between model outputs. Then, considering the two independent models as two different species, we used the ENMTools v1.4.4 program (http://purl.oclc.org/enmtools/) in order to measure the overlap between niches and consequently the level of similarity between both. ENMTools (Warren, Glor, & Turelli, 2010) uses statistical tests and comparative metrics of similarities which facilitate quantitative comparisons between ENM. One of its uses is precisely to measure the level of overlap between niches. Two metrics introduced by Warren et al. (2008) are implemented in this program: Schoener's *D* and the metric derived from the Hellinger distance, called *I*. The *D* and *I* values vary between 0 and 1 within the geographic space (higher value means higher niche overlap).

II.3. RESULTS

II.3.1. Models evaluation and pairwise comparisons

The models reached a better performance than random with high AUC values (>0.872; Fig. 2). The *Official* (AUC_{mean} training: 0.926 ± 0.006; AUC_{mean} test: 0.926 ± 0.014) performed slightly better than *Web* (AUC_{mean} training: 0.892 ± 0.008; AUC_{mean} test: 0.896 ± 0.008).

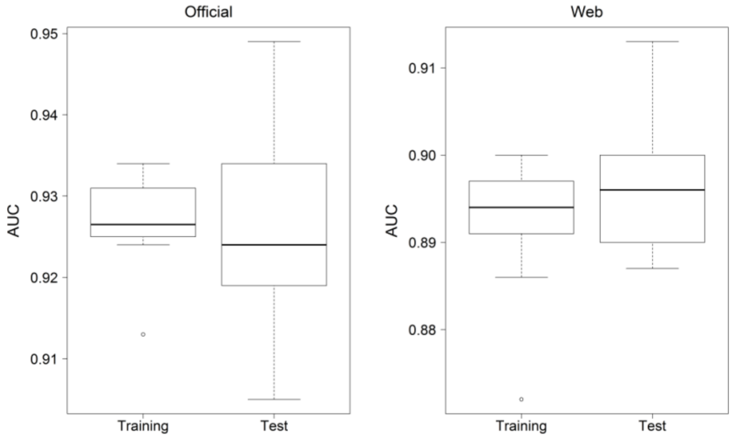

FIGURE 2 Boxplot of AUC training and testing values per dataset for Maxent (mean 10 replicates)

All approaches indicated a high degree of agreement between models. *Official* and *Web* were highly correlated (Spearman's *rho* = 0.973). Comparisons of *D* and *I* values based on both models were >0.7, suggesting a consistent overlapping trend (*D* = 0.785; *I* = 0.956). Both resulting models have similar spatial distribution patterns (Fig. 3). The mean surface of predicted area for *V. velutina* from *Official* was approximately 48000 km^2 (Figs 3 and A2 in Appendix). The largest suitable area is found in the territory extending continuously all over the Cantabrian Cornice to the southwest of Portugal. Other potential distribution areas are located in the extreme south and northeast of the Iberian Peninsula. For *Web*, the mean suitable area presented was approximately 70000 km^2 (Figs 3 and A3 in Appendix) and presented a distribution pattern clearly similar to that presented by *Official*. The regions where *Web* presented wider surface of predicted area than *Official* are northwest, northeast and south of the Iberian Peninsula.

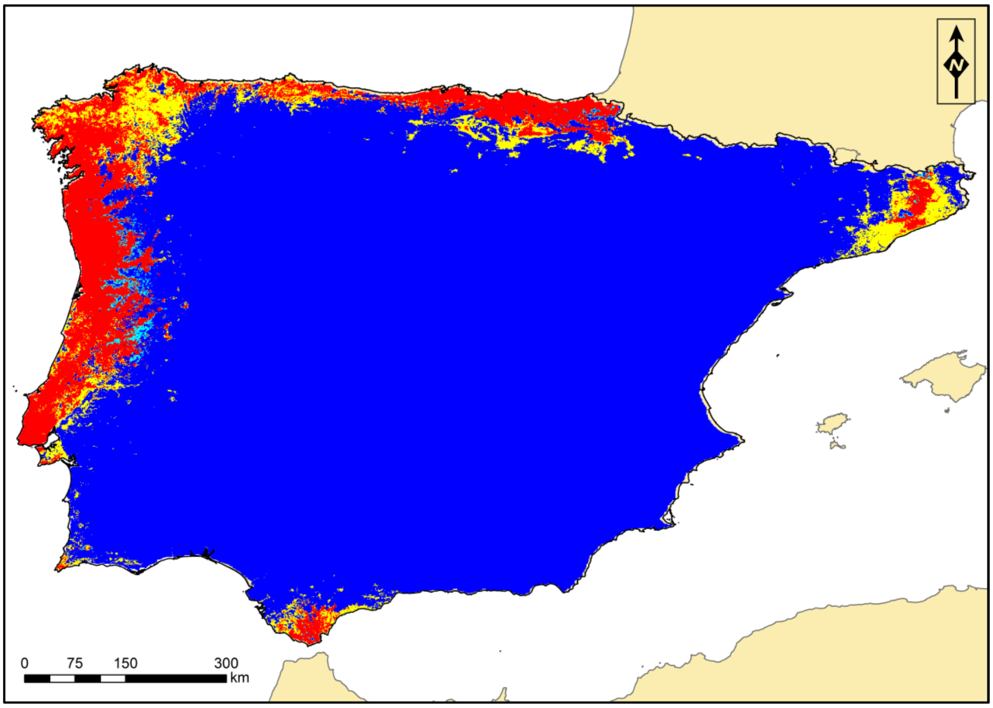

FIGURE 3 Predictions of the potential distributions of *Vespa velutina* with Maxent (10 replicates average): both models predict suitable (red); only *Official* predicts suitable (light blue); only *Web* suitable suitability (yellow) and none of the models predict suitable (blue). 10th percentile threshold average: *Official*: 0.241; *Web*: 0.221

II.3.1.1. Variables importance

The average value of model regularized training gain achieved for *Official* was 1.47 and *Web* was 1.14. The jackknife tests of variable importance showed that the minimum temperature of the coldest month (BIO6), temperature seasonality (BIO4) and annual precipitation (BIO12) had higher predictive power (i.e. high training gain; Fig. 4). For *Official* the probability of *V. velutina* presence was positively associated with increases of minimum temperature of coldest month (>3 ºC; Fig. 5a). *Web* showed a very similar pattern. For both models the probability of presence was higher in areas of low seasonality of temperatures (>4000; Fig. 5b). Finally, the probability of *V. velutina* presence predicted by both models was positively associated with increases of the annual precipitation (>900 mm; Fig. 5c).

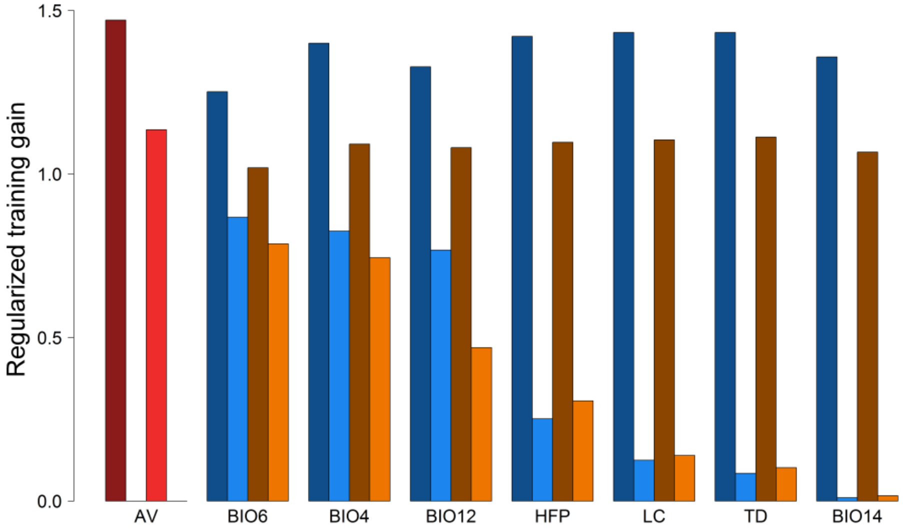

FIGURE 4 Jackknife test of variable environmental importance provided by the seven environmental variables considered to develop the Maxent model for *V. velutina*. Results are shown for all variables (*Official*: dark red and *Web*: light red); for all variables except the one selected (*Official*: dark blue and *Web*: dark orange) and for single variables (*Official*: light blue and *Web*: diagonal light orange). AV indicates the values for all variables, for variable codes see Table A1 in Appendix

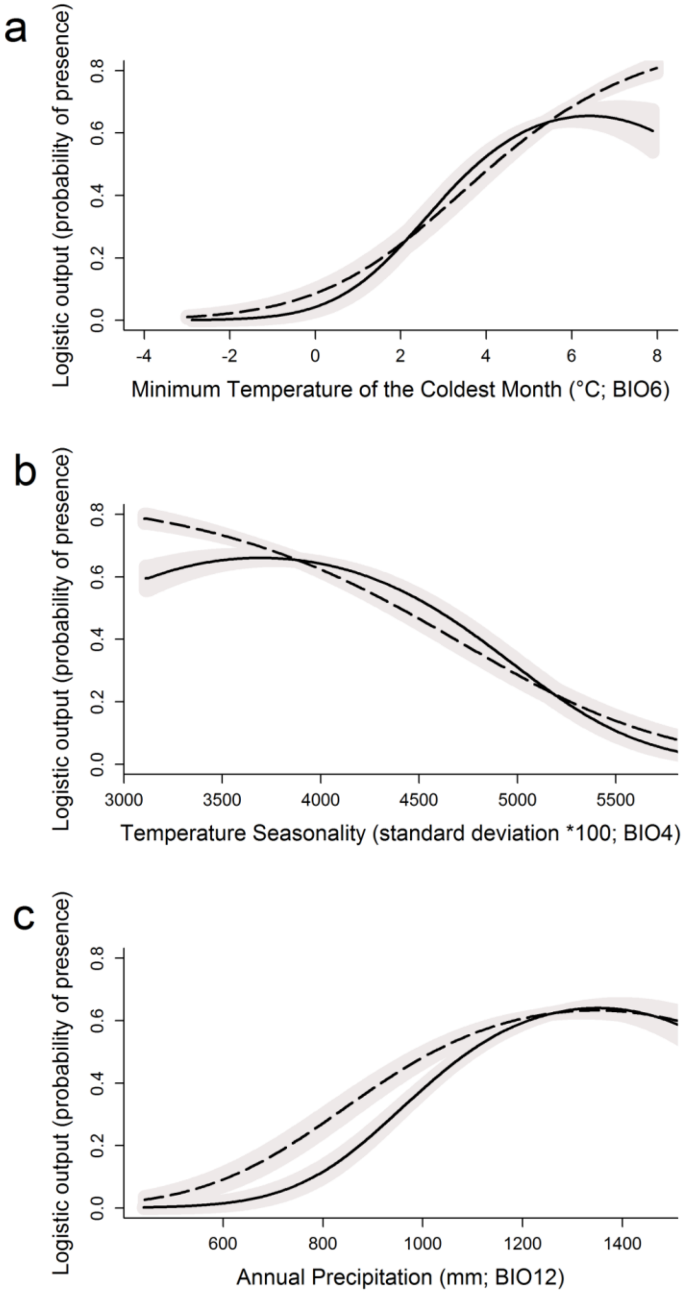

FIGURE 5 Response curves for the most important environmental variables. *Official* (black lines), *Web* (dashed black lines); Standard deviation (shaded light grey): (a) Minimum temperature of the coldest month (°C; BIO6), (b) Temperature seasonality (BIO4; standard deviation *100), (c) Annual precipitation (mm; BIO12)

II.4. DISCUSSION

II.4.1. Model comparisons

The approach applied in this work allows the spatially explicit comparison between the models, showing strong levels of similarity between them. As expected, the *Web* model predicted a larger area than *Official* model, which could be explained due the fact that the *Web* dataset contains twice more records than the *Official* dataset. It becomes clear when analyzing the mismatched regions between models (i.e. *Web* models predicted larger area than the *Official* ones) that they are located exactly in places for which there are more occurrence data from the *Web* dataset than from the *Official* dataset. Despite of that, the general patterns of predicted areas for both datasets are very similar showing a good level of concordance. Moreover, the high AUC values of *Official* and *Web* models would point towards a high accuracy in prediction performance for both. Also models show a very high value of Spearman's *rho* correlation coefficients among suitability maps which indicates an overall measure of a positive concordance beyond the simple visual analysis of suitability maps. This fact was reinforced likewise with the high values of niche overlap metrics (*D* and *I*) showed by both average models outputs. Thus, the application of the niche overlap technique introduced by Warren et al. (2008) for assessing the degree of similarity between two independent data sets of a single species represents a significant advance allowing strong inferring based on results. This approach takes into account possible spatial autocorrelation in environmental variables and hence offers stronger evidence of similarity between spatial patterns showed by different data sets (Wooten & Gibbs, 2012). It is also important to highlight the high degree of concordance in both models regarding the importance and the type of response to environmental predictors. Our models showed similar range of optimum values for the most three important variables.

The patterns of the predictions obtained in this study are very similar to those presented by Ibáñez-Justicia and Loomans (2011), Villemant et al. (2011) and Barbet-Massin et al. (2013) in Iberian Peninsula (all based only climate data) in which the Atlantic coastline (northern Spain and southern Portugal) and Mediterranean coastline (extreme south of Spain) were found as the most suitable climatic areas for *V. velutina*. Bessa et al. (2016), published the first study addressing the role of environmental and anthropogenic predictors in the distribution of *V. velutina* in this geographic area. In the same way as in our study, these authors used others variables (e.g. topography, land-cover types and human disturbance) besides of climate variables and their results were quite similar to ours.

II.4.2. Factors affecting the distribution of yellow-legged hornet in Iberian Peninsula

For *Official* and *Web* models, the environmental variables that appeared as most important contain information about temperature and precipitation. The average model training gain values increased when these variables were used in isolation (excepting BIO14). To date, temperature and precipitation appear as the most discriminating factors for *V. velutina* distribution in Iberian Peninsula. After the climate variables, human footprint was the variable with more importance reinforcing the idea presented by Bessa et al (2016) in which the expansion of *V. velutina* in its invaded range cannot be explained only by climatic predictors. According to these authors *V. velutina* would seek a balance between suitable climatic conditions (ensuring colony survival) and habitat structure (ensuring shelter and food resources) to fulfil its invaded range (Bessa et al., 2016). This might be the reason why the species is currently colonizing areas along the seaside in Iberian Peninsula, where suitable conditions for nesting (e.g. natural trees and humans constructions) and foraging (human wastes especially seafood products) can be easily found (Monceau & Thiéry, 2017). These activities seems to be the most relevant human action in order to favour the *V. velutina* spread out.

The areas predicted by models as suitable for the species in the north of the Iberian Peninsula are characterized by cold winters, low seasonality of temperatures and high levels of annual precipitation especially in coastal areas. Part of the native range of *V. velutina* is dominated by the tropical and subtropical climates in the cooler highland areas (Martin, 1995). However, throughout its native range, *V. velutina* also inhabits regions predominated by temperate climates stretching from the northeast of India to the southeast of China (Archer, 1994; Carpenter & Kojima, 1997; Martin, 1995), which may help to explain why at present, the species is occupying areas under influence of Atlantic climate in the north of the Iberian Peninsula. On the other hand, the models indicate the Iberian coastal areas in the extreme south under influence of Coastal Mediterranean climate as suitable climates for *V. velutina* where the species occurrence has not yet been reported. This may be because the range of minimum temperatures of the coldest month and the low levels of temperature seasonality in this region are very similar to some regions colonized by the species along the north and northwest coasts; the annual precipitation level is similar to most areas where the edge of the species distribution is found in the north of the Iberian Peninsula. Our results suggest that the potential invasion of *V. velutina* toward the south of the Iberian Peninsula could be more accessible along Iberian coastlines especially where the temperatures during the coldest month are above 0°C, with low levels of temperature seasonality and annual precipitation levels above 800 mm (Balmori, 2015). Equally previous studies (Barbet-Massin et al., 2013; Bessa et al., 2016; Ibáñez-Justicia & Loomans, 2011; Villemant et al., 2011), our models predicted areas in the south of the Iberian Peninsula as suitable for *V. velutina.* Since, there are evidences that species continues expanding its range careful monitoring should be realized in this region.

II..4.3. Effectiveness of data gathered by non-expert volunteers for invasive species monitoring

It is well known that ENMs are an important tool for invasive species management (Kadoya et al., 2009; Peterson, 2003; Peterson & Vieglais, 2001). Also the use of data collected by volunteers through participatory programs focused on the prediction of potential distribution of invasive insect species had been successfully applied at local (Kadoya et al., 2009) and global (Barbet-Massin et al., 2013; Villemant et al., 2011) scales. Reliable occurrence data are fundamental inputs for these tools and many times there are large amounts of species occurrence data without validation. Validate all records in a large dataset could be an impossible task and it would require too much time, while the officials databases are not updated as rapid as the volunteers sources. Being the latter is crucial when generating ENMs for invasive species management purposes, thus, a way to validate a large amount of records in a short period of time should be a priority. Kadoya et al. (2009) proposed an approach using ENMs to validate two datasets gathered by volunteers: built predictive models from independent datasets and used to validate one another. Our proposal was similar, but instead of using two datasets coming from volunteers, we used an official source as reference to build models and compared them with those obtained from volunteer data. In this way we succeeded assess the effectiveness of data gathered by volunteers for *V. velutina* in a relatively short period of time and without elevate costs.

As a validated data source, these data compiled by volunteers could be useful as complementary information to formulate scientific predictions of the potential distribution for this or other species in order to identify areas that should be regularly monitored to avoid further invasions. In addition, the present contribution can also directly and/or indirectly provide feedback on improvements to the data collection by volunteers, which, in turn, can improve both the validation and development of more precise invasion risk maps (Kadoya et al., 2009; Kadoya & Washitani, 2007). This relationship between technical personnel from official institutions and volunteers can be mutually beneficial, because such activities are linked to the conservation of biodiversity through the control of invasive species (Kadoya et al., 2009; Teacher et al., 2013).

In conclusion, no noticeable differences were observed between models derived from *Official* and *Web* datasets, both would have the same reliability in order to be used in management strategies for *V. velutina* in its invaded range. Initiatives like this should be encouraged since volunteer data are a powerful source to accumulate essential amounts of valuable data in short periods of time. These should be applied as ENM inputs to make predictions that are essentials for the management of invasive alien species.

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APPENDIX CHAPTER II

Table A1

Summary of initial set of environmental variables. The seven variables used in calibration of Maxent's models are marked with an asterisk (*)

Code	Variable	Source
BIO1	Annual Mean Temperature	WorldClim
BIO2	Mean Diurnal Range	WorldClim
BIO3	Isothermality	WorldClim
BIO4	Temperature Seasonality*	WorldClim
BIO5	Max Temperature of Warmest Month	WorldClim
BIO6	Min Temperature of Coldest Month*	WorldClim
BIO7	Temperature Annual Range	WorldClim
BIO8	Mean Temperature of Wettest Quarter	WorldClim
BIO9	Mean Temperature of Driest Quarter	WorldClim
BIO10	Mean Temperature of Warmest Quarter	WorldClim
BIO11	Mean Temperature of Coldest Quarter	WorldClim
BIO12	Annual Precipitation*	WorldClim
BIO13	Precipitation of Wettest Month	WorldClim
BIO14	Precipitation of Driest Month*	WorldClim
BIO15	Precipitation Seasonality	WorldClim
BIO16	Precipitation of Wettest Quarter	WorldClim
BIO17	Precipitation of Driest Quarter	WorldClim
BIO18	Precipitation of Warmest Quarter	WorldClim
BIO19	Precipitation of Coldest Quarter	WorldClim
LC	Land cover and Land Use*	CORINE
HFP	Human influence index*	SEDAC
SLP	Slope	Derived from DEM (CGIAR-CSI)
TD	Topographic diversity*	Derived from DEM (CGIAR-CSI)

Appendix 1: selection of variables

To select the variables we followed the approach proposed by Zohner et al. (2017): (1) compute the correlation matrix ("cor" function; R Core Team, 2015) between our initial set of environmental variables; (2) convert the correlation matrix into a distance matrix; (3) produce a dendrogram ("hclust" function; R Core Team, 2015) showing the correlation pattern among environmental variables; (4) select one variable for each cluster below the 0.5 threshold (Appendix Fig. A1) and; (5) calculate the variance inflation factor (R package HH; Heiberger, 2017). The VIF analysis is an iterative process in which the user removes predictors, till all predictors show VIF values below 5 (Zohner et al., 2017; Appendix Table A2).

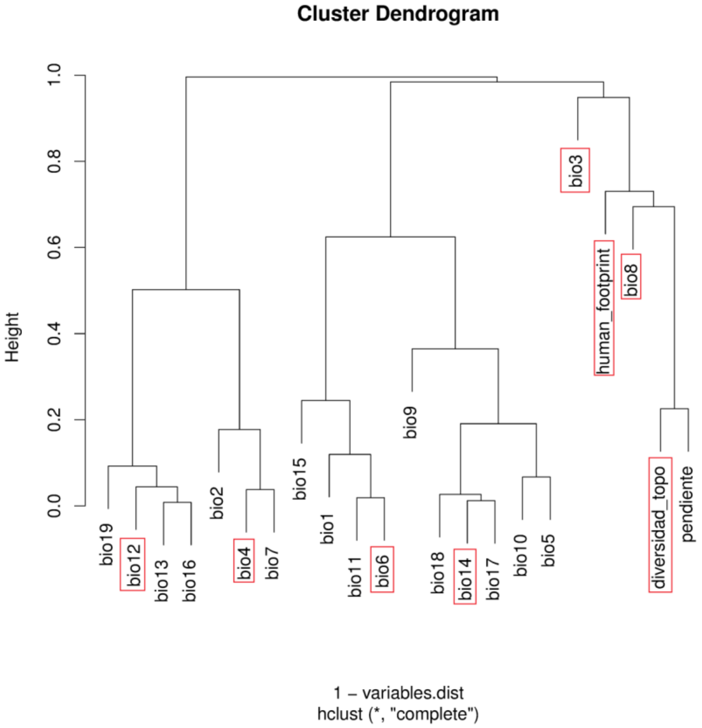

FIGURE A1 Hierarchical clustering dendrogram for the initial set of environmental variables. Red boxes indicate the variables finally selected for subsequent analyses

Table A2
Values of variance inflation factor (VIF) for the seven selected variables for each cluster < 0.5 threshold (excluding LC). VIF_1 indicates VIF values for the eight variables; VIF_2 indicates VIF values for the six remaining variables. Variables were removed, till all predictors showed VIF values < 5. See variable codes in Table A1

Code	VIF1	VIF2
BIO12	3.99	2.41
BIO4	5.96	3.60
BIO6	5.65	4.13
BIO14	5.29	3.68
BIO3	1.99	Removed
BIO8	2.18	Removed
TD	1.54	1.54
HFP	1.24	1.24

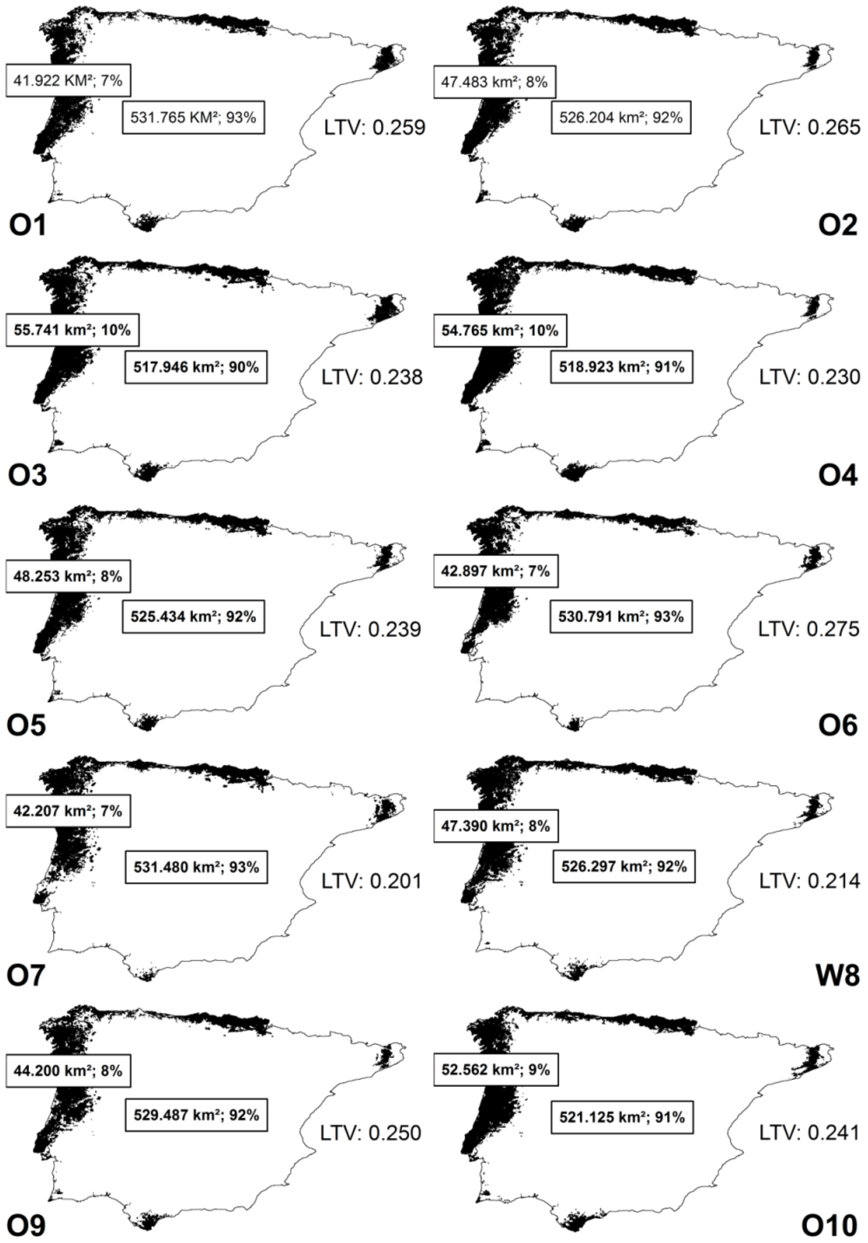

FIGURE A2 Surface of predicted area per replicate for *Vespa velutina* derived from *Official* dataset. Values are shown in square kilometres (km²) and percentage (%) of total study area. LTV indicate logistic threshold value

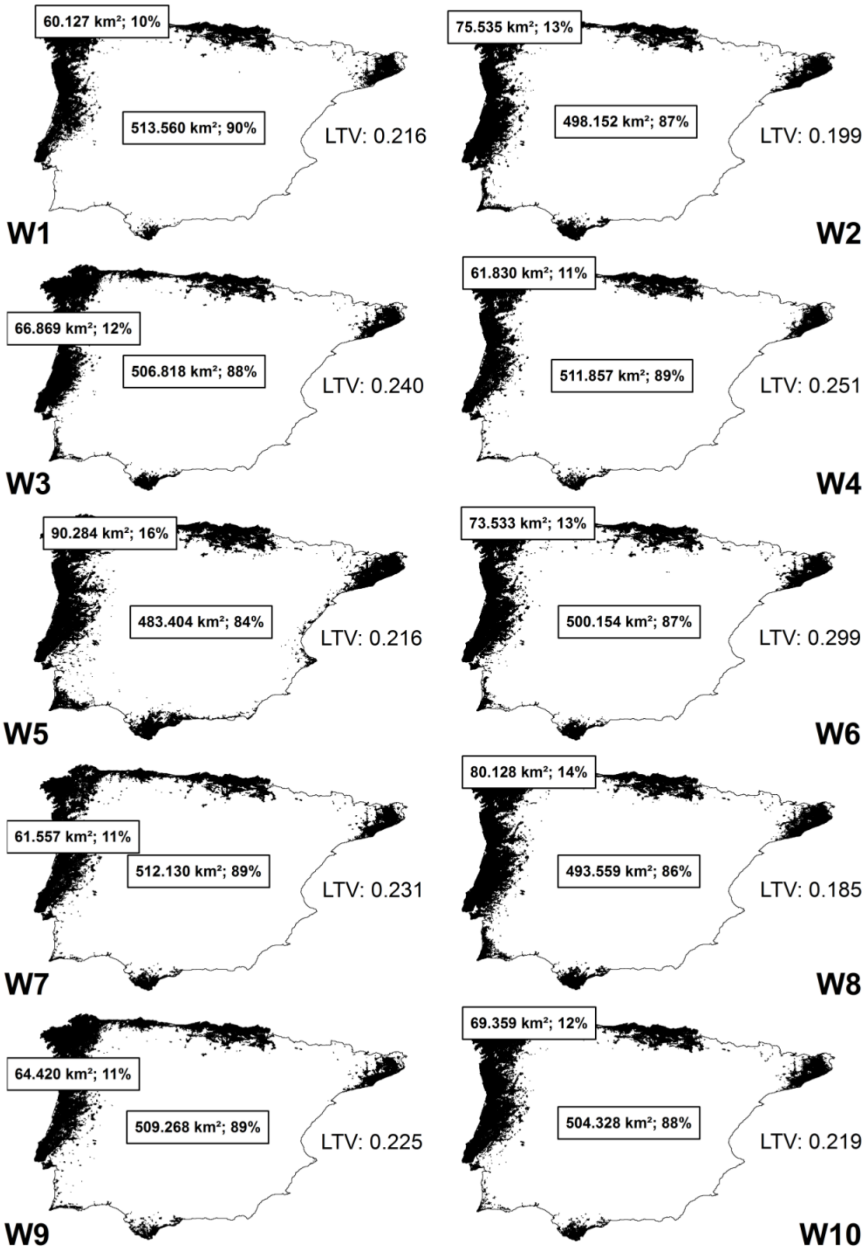

FIGURE A3 Surface of predicted area per replicate for *Vespa velutina* derived from *Web* dataset. Values are shown in square kilometres (km²) and percentage (%) of total study area. LTV indicate logistic threshold value

CAPÍTULO III

Fotos: Cristina Miñambres y Ricardo Córdoba Cámara

Factores comportamentales, ecológicos y humanos explican la distribución invernal del Milano Real (*Milvus milvus* Linnaeus, 1758) en la Península Ibérica: consecuencias y oportunidades para la conservación de las rapaces europeas

Resumen

El milano real es la única rapaz con distribución restringida a Europa y que actualmente está catalogada como casi amenazada a nivel mundial. Los milanos reales son altamente vulnerables al cambio climático y casi han desaparecido del extremo sur de su rango original. La población residente en la Península Ibérica convive con las grandes poblaciones del norte de Europa que migran aquí en invierno, por lo que las amenazas durante esta estación pueden ser un factor crítico para su conservación global. Se han aplicado *Boosted Regression Trees* (BRT) teniendo en cuenta factores climáticos, topográficos, de uso de la tierra y de influencia humana para modelar el nicho ecológico de los milanos invernantes en la Península Ibérica, comparando los resultados con modelos previos para poblaciones reproductoras en España y Alemania. Las aves invernantes ocupan un rango mayor que las aves residentes. La selección de hábitat de los migrantes es más similar a los milanos reproductores de Alemania que a las aves españolas residentes y su distribución es muy similar a los milanos negros reproductores en la Península Ibérica. Los factores relacionados con las actividades humanas son las variables que más explican la distribución de los migrantes. La población de milanos migratorios se concentra en tierras agrícolas del noroeste de España, donde ocurre la plaga del topillo común. En el resto de la zona de invernada, el modelo incluye asentamientos humanos rurales y factores de uso / hábitat de la tierra que reflejan principalmente la disponibilidad de los otros dos principales recursos alimenticios de invierno: ganado y carroña pequeña. La población de milanos reales invernantes ocupa parcialmente el nicho ecológico vinculado a los seres humanos que es dejado vacante en invierno por los milanos negros migradores del Sahara, como un ejemplo interesante de reemplazo ecológico estacional a gran escala y distribución de recursos en especies hermanas migratorias. La selección del hábitat de invierno está estrechamente asociada a tres grandes amenazas conocidas que actúan en la Península Ibérica: la gestión de la plaga de los topillos, los protocolos de eliminación de la carroña de ganado y el envenenamiento por plomo y el riesgo de disparo en las fincas de caza. La conservación global del milano real depende en gran medida de la implementación de varias mejoras potenciales en la gestión, algunas de ellas útiles para la conservación de otras aves rapaces migratorias europeas de cortos desplazamientos.

Behavioural, ecological and human factors explain wintering Red Kite (*Milvus milvus* Linnaeus, 1758) distribution in the Iberian Peninsula: consequences and opportunities for conservation of European raptors

Abstract

The red kite is the only raptor with distribution restricted to Europe, currently near threatened at global level. Red kites are highly vulnerable to global warming and they have almost disappeared from the southern edge of their original range. The resident population in Iberia coexists with biggest northern populations migrating there in winter, so threats during this season may be a critical factor for its global conservation. Boosted regression trees (BRT) considering climatic, topographic, land use and human factors are applied to modelling realized ecological niche of wintering red kites in Iberia, comparing results with previous models for breeding populations in Spain and Germany. Wintering birds occupy a larger range than resident birds. Habitat selection of migrants is more similar to German breeding kites than to resident Spanish birds and their distribution is pretty similar to breeding black kites in Iberia. Human-related factors are the main explanatory variables of migrant distribution. Migrant red kite population is concentrated in agrarian land of NW Spain where common vole outbreaks occur. In the rest of the wintering area, the model includes rural human settlements and land use/habitat factors reflecting mainly availability of the other two main winter food resources: livestock and small game carrion. Wintering red kite population partially occupy the human-related ecological niche left vacant in winter by cross-Saharan migrant black kites, as an interesting example of large-scale seasonal ecological replacement and resource distribution in migratory sister species. Winter habitat selection is tightly associated to three known major threats acting in Iberia: management of vole pests, livestock carrion disposal protocols and lead poisoning and persecution risk in game estates. Red kite global conservation is highly dependent on the implementation of several potential improvements in management, some of them useful for conservation of other European short-distance migratory raptors too.

III.1. INTRODUCTION

Many species are adversely affected by human activities at large spatial scales in what has been termed “biodiversity crisis” (Western, 1992). More specifically, large-size animals with low population density and K-strategy life history may be particularly prone to be affected by human impacts, including many raptors (González-Suárez, Gómez, & Revilla, 2013; Newton, 1998). Most research on ecology of this kind of species is often centered on breeding populations and season, although conservation problems may be as important during winter, the limiting season in temperate climates (Newton, 1998). In fact, many bird species in temperate biomes have migratory habits, so breeding and wintering areas can be completely different, as different threats acting on breeding season and winter can be (Kirby et al., 2008; Newton, 2004, 2008). In these migratory species, the knowledge of ecological limiting factors and identification of threats and conservation problems out of breeding season may be even more relevant than during breeding season (Bildstein, 2006; Kirby et al., 2008; Klaassen et al., 2014; Sanderson, Donald, Pain, Burfield, & van Bommel, 2006).

Several factors may be involved in the selection of wintering areas and habitat use by migratory birds. This must be viewed as a hierarchical process, from large-scale geographical, behavioral and ecological factors determining migration routes, departure dates and large-scale winter distribution, that are usually genetically fixed in the populations (Berthold, 1999), to micro-habitat use in wintering areas, that may be more variable and adaptable (Hutto, 1985). Food availability is a main factor explaining winter habitat use in migrant birds, particularly when many individuals gather in specific areas, exploiting seasonal or sporadic overabundance of food (Karr, 1976). Many short-distance migrant European birds stay all winter in the

Iberian Peninsula, where they may find resident populations of the same species (Senar & Borrás, 2004). In these cases, the question raises of which factor drives selection of wintering areas by migrant birds. On one hand, conspecific attraction may be a major force explaining wintering area selection in highly social species, such as black (*Milvus migrans*) and red kites, something known since centuries ago by hunters using decoys to attract waterfowl to shooters and used also more recently for conservation purposes (Smith & Peacock, 1990). Thus, a large coincidence between the distribution of wintering and resident birds should be expected if this is a major force driving wintering area selection. On the other hand, it is also expected that migratory species would search in the winter quarter favourable habitat and weather, which in short-distance migrants, may even be similar to those in the breeding area, so a coincidence between wintering and breeding landscapes and environmental conditions may be expected too. If habitat selection patterns during breeding season are similar in all populations, this would again match resident and wintering birds in the same areas. Both hypotheses are difficult to be distinguished because they have similar predictions, then. But in cases in which the migratory fraction of the population has a different habitat, food or weather selection pattern in its breeding area, as compared with resident populations in the wintering area, this difference would predict that wintering areas should be larger or different than breeding areas of resident birds, reflecting those differences in habitat selection patterns. Finally, when large migrant and resident populations co-exist in the same areas, behavioral mechanisms to reduce competition are expected to appear, such as differential habitat use or diet (e.g. Pérez-Tris & Tellería, 2002).

The red kite (*Milvus milvus*) provides a unique opportunity to test these hypotheses, because large-scale distribution modelling of the German and Spanish breeding populations have been published (Heuck, Brandl, Albrecht, & Gottschalk, 2013; Seoane, Viñuela, Díaz-Delgado, & Bustamante, 2003), German birds are expected to be the bulk of wintering red kites in Spain (the main migratory population is there; BirdLife International, 2017), and winter distribution and life history of wintering red kites in Spain are relatively well known too (Heredia, Alonso, & Hiraldo, 1991; Hiraldo, Heredia, & Alonso, 1993; Viñuela, Martí, & Ruiz, 1999). This is a raptor species with opportunistic habits, considered as generalist in terms of habitats requirements, associated to open, hilly and flat areas (often farmland landscapes) where they can forage and scavenge over a high variety of food resources, avoiding rugged landscape (Almeida et al., 2005; Mougeot, Garcia, & Viñuela, 2011; Seoane et al., 2003). In Germany, Heuck et al. (2013) provided also a country-scale distribution model, using climatic, topographic, and land use/habitat classification categories, but with a different statistical methodology. Both models are very similar in general terms, indicating that habitat selection was pretty similar in Germany and Spain, but two important differences emerge when revised in detail (Table A1 in Appendix). First, the German breeding population seems to be more associated to lowland flat areas (average height <300 m), including several river valleys, while the Spanish breeders are concentrated in foot hills at higher ranges, avoiding the bottom of large river valleys (Seoane et al., 2003; Viñuela et al., 1999). Second, German red kites avoided forests (average forest cover of 7-9%, in three kinds of forest) and selected areas with only isolated trees or tree lines. In contrast, optimal forest cover in Spain was around 40-60% (Seoane et al., 2003). Thus, breeding red kites in Germany are typical of mainly deforested areas or forest edge, while in Spain they use areas with higher forest cover, even selecting large forest patches (Olano, Beñaran, Laso, & Arizaga, 2016).

The Iberian Peninsula holds the main wintering ground of Red kites (Viñuela et al., 1999), so improving our knowledge of wintering habitat selection is of crucial importance for its global conservation (García, Viñuela, & Sunyer, 1998; Sunyer & Viñuela, 1994). Currently considered a near threatened species at global level (BirdLife International, 2016, 2017), and vulnerable or endangered in Portugal and Spain, respectively (Almeida et al., 2005; Viñuela, 2004). The species is experiencing a moderately rapid population decline (BirdLife International, 2016), and it is suspected that threats during winter in Spain may be a critical factor behind declines at continental scale (BirdLife International, 2017; Carter, 2001; Mougeot et al., 2011). This is considered one of the European bird species more vulnerable to global warming (Wormworth & Mallon, 2007) that has almost disappeared from the southern edge of its original range in Mediterranean latitudes indeed (BirdLife International, 2017; Molina, 2015).

Here, we present realised niche models (*sensu* Sillero, 2011) of wintering red kites in the Iberian Peninsula, considering climatic, topographic, land-use and human factors, to help improving our knowledge of which are the main elements determining the occurrence of the species in winter, an important first step for the development of any conservation strategy of the species at global level. We compare these winter models with those for breeding populations in Germany and Spain, and with black kite distribution in the study area. We discuss the implications of these results for conservation of this and other European raptors proposing specific management measures.

III.2. METHODS

III.2.1. Study area

The study was restricted to Iberian Peninsula territory (~580000 km²) which is located in southwestern Europe (Fig. 1), surrounded by the Mediterranean Sea and the Atlantic Ocean, with a mean altitude of ~660 m and a maximum height of 3479 m. Climate is mainly Mediterranean with continental influence, dry and with cold winters, especially in inland plateaux and mountainous regions while north and west coastal regions have oceanic influence, with wetter and milder weather,, this influence reaching inland regions of Portugal, Extremadura and Guadalquivir basin (AEMET, 2011; Bosch, Mardones, Pérez, de la Torre, & Muñoz, 2014; Casas-Grande, Del Pozo-Manrique, & Mesa-León, 2006; De Cara & Mestre, 2012). Finally, SE part of the peninsula has the most arid and hot weather.

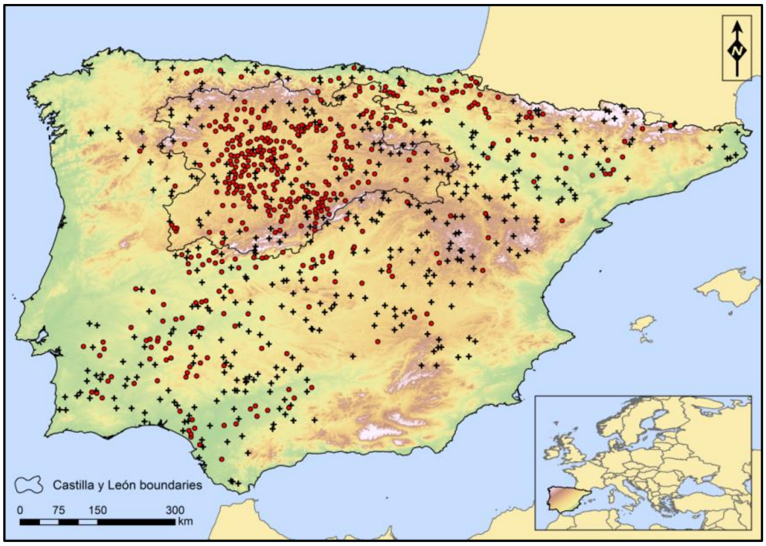

FIGURE 1 Study area and occurrence points of red kite winter roosting sites. White dots indicate the occurrence records and crosses indicate pseudo-absence records. Records within the *Castilla y León* boundaries were not included in the second model

III.2.2. Presence data

Red kite roost-sites records (presence data) were gathered across the Iberian Peninsula during 2013-2015. These data were extracted from the two most recent national red kite wintering populations census performed in Spain in the winter 2013-2014 (*n* = 431 roosting sites; Molina, 2015) and Portugal, where presence data were compiled during the winter 2014-2015 (*n* = 12 roosting sites; Leitão et al., 2015). The final dataset contained 443 winter roosts-sites (i.e. latitude and longitude) for red kite with only one record per grid square of 5 km (Fig 1).

III.2.3. Generation of pseudo-absences

Although the survey of roosting sites was satisfactory in most study areas, it was not complete in others, and additionally, even in well surveyed zones, we cannot discard that in such a large-scale survey performed by voluntaries, some roosting sites remained overlooked. Thus, this is a typical situation in which false absences could be expected, but after excluding zones where real absence is well known, considering random pseudo-absences would be highly advisable (Barbet-Massin, Jiguet, Albert, & Thuiller, 2012; Hanberry, He, & Palik, 2012). Random pseudo-absences were generated in ArcGIS 10.3.1 through the extension ‘create random points’ with the following constraints: (i) following the recommendations of Barbet-Massin et al. (2012) we generated the same number of pseudo-absences as available presences, (ii) random selection from all points within the studied area excluding available presence points, (iii) since pseudo-absences need to provide a reasonable representation of the environmental variation in the study area and to avoid spatial autocorrelation issues, we defined a minimum distance of 5 km between pseudo-absences and (iv) the pseudo-absences were not generated within 5 km radius from presences points, resulting in unique records per grid square of 5 km (Mateo, Croat, Felicísimo, & Muñoz, 2010). We limited the pseudo-absences points to areas surveyed for the species (i.e. all provinces within the Iberian Peninsula with at least one species' presence record). In this way, we would be providing pseudo-absences data with similar biases to those in the presence data by excluding large areas where the real absence of the species is pretty sure (Elith et al., 2010).

III.2.4. Environmental predictors

Our initial variable set was composed by 31 predictor variables (Table 1): 19 bioclimatic variables, two topographic (topographic diversity and slope), six land-use/land-cover types, two distances variables (distance to water and distance to dump sites), a human influence index and a proxy for expected dead livestock biomass available. All GIS work was conducted using ArcGIS 10.3.1 for Desktop (ESRI, 2015). Bioclimatic variables were available from WorldClim climatic database at 2.5 arc minutes spatial resolution (approximately 5 km2 at the equator; Hijmans, Cameron, Parra, Jones, & Jarvis, 2005). Topographic variables were derived from the Digital Elevation Model (DEM) available from CGIAR-CSI database at 3 arc seconds spatial resolution (Jarvis, Reuter, Nelson, & Guevara, 2008). Slope was calculated in degrees using 'slope' function. From each grid cell all over a DEM, it calculates the inclination of slope. Topographic diversity was calculated using the 'focal statistics' function which calculates for each DEM grid cell the diversity of elevation values considering all cells within a 3 km radius.

Six land-use/land-cover variables derived from Corine Land Cover (CLC) 2006 programme (European Environment Agency, 2014): agroforestry areas (PAF), arable land (PAL), forests (PF), pastures associated with crops (PP), tree cultures (PTC) and scrub/herbaceous vegetation (PSHV). For each category, the percent area coverage per grid cell was calculated using 'calculate geometry' and 'calculate field' tools. All land-use/land-cover rasters were generated at 5 km^2 spatial resolution. Dump sites (large official offal treatment dumps; DDS), water bodies and water courses (DW) categories were also derived from CLC 2006. Using 'Euclidean distance' function the variables "distance to roosts of pseudo-absences" were calculated. This function calculates the Euclidean distance to the closest vector entity.

No official records of carrion availability or location of carrion disposal sites are available for the study area. We have considered as a proxy the dead livestock biomass available (DLBA), that was calculated using the approach introduced by Morales-Reyes et al. (2016). The abundance data of the most important livestock species (cattle, sheep, goat and pig) per municipality in 2012 and the average weight per age class in Spain were obtained from Spanish Ministry of Agriculture, Food and Environment (MAGRAMA, 2012). The livestock species abundance data in Portugal were available from the latest update of Portugal Statistics database (INE, 2011). The annual mortality rate per age class and species generated by Government of *Castilla y Leon* in 2013 (as cited in Morales-Reyes et al., 2016), was applied to livestock species abundance data in order to estimate the potential dead biomass available for red kites per year all over Iberian Peninsula. The spatial distribution of dead livestock biomass available (tons per year) was represented according to the 5 km grid square. When a grid belonged to more than one municipality, the biomass availability was distributed proportionally to their areas. Finally, the Human Influence Index known as Human Footprint (HFP) dataset was available from SEDAC database

(Socioeconomic Data and Applications Center) at 1 km^2 spatial resolution (WCS & CIESIN, 2005). Predictors were gathered originally at different resolutions then resampled at 0.048º (approximately 5 km^2 at the equator) spatial resolution (Table 1).

Predictors considered to construct models were selected on the basis of a three-step procedure: (i) to minimize multicollinearity among environmental variables, a hierarchical clustering with *complete linkage* method was used. From the resulting correlation tree, variables were selected based on a cut-off or minimum threshold of 0.5. In each one of the groups of variables with node <0.5 only one was selected based on its correlation (Fig. S1 in Supplementary Information); (ii) complementary to the first step, we calculated the variance inflation factor (VIF; R package HH). The VIF for predictor *i* is 1/(1-R_*i*^2), where R_*i*^2 is the R^2 from a regression of predictor *i* against the remaining predictors. Values of VIF >5 are considered evidence of collinearity: the information carried by a predictor having such a VIF is contained in a subset of the remaining predictors (see Appendix 1 for details and Table A1; Benito et al., 2017; Heiberger, 2017); and (iii) we ran a step-wise simplification (by using the ‘gbm.simplify’ function) of preliminary exploratory models and the variables not reaching 2% relative importance were removed (see Elith, Leathwick, & Hastie, 2008). The predictor set was finally reduced to 10 variables (Table 1).

TABLE 1
Summary of environmental predictors. The 10 variables used in Boosted Regression Trees (BRT) models area marked with an asterisk (*; see Appendix 1)

Code	Description	Source
BIO1	Annual Mean Temperature	WorldClim
BIO2	Mean Diurnal Range	WorldClim
BIO3	Isothermality	WorldClim
BIO4	Temperature Seasonality	WorldClim
BIO5	Max Temperature of Warmest Month	WorldClim
BIO6	Min Temperature of Coldest Month*	WorldClim
BIO7	Temperature Annual Range	WorldClim
BIO8	Mean Temperature of Wettest Quarter*	WorldClim
BIO9	Mean Temperature of Driest Quarter	WorldClim
BIO10	Mean Temperature of Warmest Quarter	WorldClim
BIO11	Mean Temperature of Coldest Quarter	WorldClim
BIO12	Annual Precipitation	WorldClim
BIO13	Precipitation of Wettest Month	WorldClim
BIO14	Precipitation of Driest Month	WorldClim
BIO15	Precipitation Seasonality	WorldClim
BIO16	Precipitation of Wettest Quarter	WorldClim
BIO17	Precipitation of Driest Quarter	WorldClim
BIO18	Precipitation of Warmest Quarter	WorldClim
BIO19	Precipitation of Coldest Quarter*	WorldClim
HFP	Human Influence Index*	SEDAC
SLO	Slope (degrees)*	Derived from DEM (CGIAR-CSI)
TD	Topographic diversity	Derived from DEM (CGIAR-CSI)
DLBA	Dead livestock biomass available (t per 5km² grid cell)*	Derived from MAGRAMA and INE PT livestock species data
DDS	Distance to dump sites (landfill or mine dump sites, industrial or public) (m)*	Modified from CORINE
DW	Distance to water bodies and courses (m)*	Modified from CORINE
PAF	Agro-forestry areas (land mostly occupied by agriculture, with significant areas of natural vegetation and annual crops or grazing land under the wooded cover of forestry species.) percent coverage (%)*	Modified from CORINE
PAL	Arable land (non-irrigated and permanently irrigated land and rice fields) percent coverage (%)*	Modified from CORINE
PF	Forests (broad-leaved, coniferous and mixed forests) percent coverage (%)*	Modified from CORINE
PP	Pastures and annual crops associated with permanent crops percent coverage (%)*	Modified from CORINE
PTC	Olive groves, fruit trees and vineyards percent coverage (%)	Modified from CORINE
PSHV	Scrub / herbaceous vegetation (natural grasslands, moors and heathland) percent coverage (%)	Modified from CORINE

III.2.5. Boosted regression trees

We calculated the realized ecological niche (*sensu* Sillero, 2011) using Boosted Regression Trees (BRT) models to identify the environmental variables most relevant in explaining the presence and habitat selection pattern of winter population of red kites in Iberian Peninsula. BRT models were fitted in R version 3.4.2 (R Development Core Team, 2017) using ‘dismo’ package version 1.1-4 (Hijmans, Phillips, Leathwick, & Elith, 2017) and ‘gbm’ package version 2.1.3 (Ridgeway, 2017), supplemented with functions introduced by Elith et al. (2008). BRT is a technique which uses boosting and regression trees algorithms, exploring linear combinations of hundreds or thousands of trees into a single model, improving overall model accuracy (Elith et al., 2008). BRT model parameters were set to constrain overfitting and optimise the number of regression trees for each model. The maximum interaction depth (‘tree complexity’) were fitted over a range of values (1-10) and learning rate (0·1-0·0005) and a Bernoulli error distribution (Elith et al., 2008). Because using the same data for model testing and validation leads to over-fitting and deflates the estimated error rate, the optimal number of trees was determined using 10-fold cross-validation (CV) with a bag fraction of 0.75 as suggested by Elith et al. (2008). Model fit were assessed after 10-fold CV by the percentage of explained deviance (D^2) and by CV deviance values. Lower CV deviances indicate better performance than higher CV deviances. All models were fitted with the ‘gbm.step’ function and the model fitted with more than 1000 trees (as recommended by Elith et al., 2008) which achieved the highest D^2 value was further simplified in a backwards stepwise manner by using the ‘gbm.simplify’ function. The selection of predictors from the simplified model whose relative influence exceeded 2% were used to build a final model. The degree to which the fitted values discriminate between observed outcomes was measured using the area under the receiver operating curve (AUC) and the correlation coefficient through 5-fold cross-procedure. Then we calculated a suitability map to show the spatial pattern of probability of occurrence of red kite on the 5 km grid cell level for the Iberian Peninsula.

The relative influence (i.e. relative contribution or relative importance) of the explanatory variables was estimated based on the number of times the variable was selected for splitting, weighted by the squared improvement to the model as a result of each split, and averaged over all trees (Friedman, 2001; Friedman & Meulman, 2003). The contribution of each variable was scaled so that the sum added up to 100, with higher numbers indicating stronger influence on the response (Elith et al., 2008). A higher percentage of a variable indicates a stronger relative influence on the response. To better visualize fitted functions, we calculated the partial dependencies that shows the relationships between the response and one predictor variable while controlling for the average effects of all other predictors (Friedman, 2001; Friedman & Meulman, 2003).

The Spanish northwest (fundamentally *Castilla y León* territory, NW area hereafter) uses to hold more than half wintering population (Fig. 1 Cardiel, 2006; Molina, 2015; Viñuela et al., 1999), concentrated there in the last 30 years, probably because common vole (*Microtus arvalis*) outbreaks started to appear in this area since the early 1980s, and this is a main prey in central Europe (De Juana, De Juana, & Calvo, 1988; Hille, 1995; Luque-Larena et al., 2013; Sunyer & Viñuela, 1994, 1996). Vole outbreaks suppose plenty of easily accessible food, and this could be reflected both in the diet and winter distribution of the species, which could be using priority habitats with high vole abundance, such as highly deforested areas mainly occupied by cereal crops (García et al., 1998). During the winter 2013-2014 a vole outbreak started to develop in this area (Rodríguez-Pastor, Luque-Larena, Lambin, & Mougeot, 2016), so the data we are using could be strongly biased by this fact. For these reasons, we also built a second equivalent model (following the same procedure than above) excluding all distribution data within NW in order to identify the most relevant variables related with habitat selection of wintering red kite in Iberian Peninsula at large, but removing the expected important effect of a large-scale vole outbreak on winter distribution and habitat use. This exercise would allow a better understanding of why this species mostly concentrates its wintering ground in that region, to what point its habitat use is biased by vole outbreaks, and how is its habitat selection in the absence of this overabundant prey.

III.3. RESULTS

The selected final BRT model was fitted with: *lr* of 0.001, *tc* of 10 and with total of 4400 decision trees. All model replicates performed well with high AUC mean value: 0.81 (±0.01 SD; Table 2 and see suitability values predicted by the model in Fig. 2). Our predictions of most suitable areas for red kite (suitability >0.7) accumulate in NW Spain with other important areas in lowlands of Extremadura, and several river valleys (Ebro, Tajo, Guadiana and Guadalquivir).

TABLE 2
AUC and correlation coefficient values for each BRT replicate. A indicates the values for the model built with all occurrence records. B indicates the values for the model built excluding the Iberian NW subpopulation

	A			B		
	AUC	Correlation	p-Correlation	AUC	Correlation	p-Correlation
	0.80	0.53	4.04E-14	0.80	0.49	7.68E-08
	0.83	0.55	1.14E-15	0.75	0.43	3.36E-06
	0.81	0.52	8.75E-14	0.75	0.41	9.01E-06
	0.80	0.52	8.70E-14	0.80	0.49	4.97E-08
	0.80	0.52	1.37E-13	0.81	0.52	6.58E-09
mean	0.81	0.53	7.06E-14	0.78	0.47	2.50E-06
SD	0.01	0.01	5.16E-14	0.03	0.05	3.91E-06

The relative importance of the predictors in the BRT model and the correspondent partial dependence plots for each predictor and the probability of red kite presence are presented in Figs. 4 and 5, respectively. The human influence Index (HFP), contributed most to the models with a relative importance of 13.2%. The areas with human influence ranging from 30% to 70%, were preferred by wintering red kites as roosting sites. Slope (SLO) followed as the second most important predictor (relative importance of 12.5%), the areas with gentle slope (<20°) appeared as the most preferable habitat for roosting sites. Wintering red kite probability of presence increased regularly with the area covered by arable land (PAL) with a relative importance of 12.4%. The minimum temperature of the coldest month (BIO6) raised the species occurrence especially from 0 ºC to 5 ºC (relative importance of 11.9%). Mean temperature during winter (BIO8) between 0 °C and 1 ºC also favoured the species presence. Wintering red kites preferred to settle their communal roosting sites in areas with maximum distance to water bodies (DW) larger than 60 km. The probability of finding red kite roosting sites declines as the density of dead livestock biomass available declined (DLBA; <20 t per grid square). The red kite seemed to prefer roosting sites in areas within 70000 m from dump sites (DDS), with a peak of increase at very short distances (Fig. 5), although the species can be found roosting as far as 150000 m away from dump sites. Areas with moderate precipitation in the coldest quarter (BIO19), ranging from 150 to 4300 mm, were also positively selected. Finally, this species prefers habitats with high percentage of coverage of agro-forestry areas (PAF).

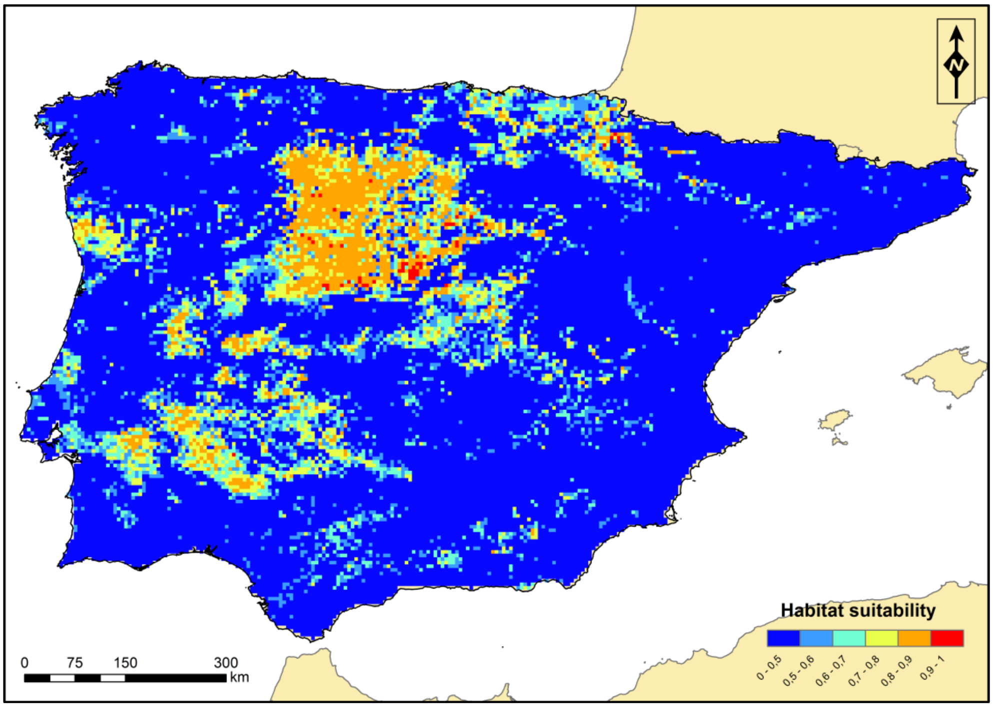

FIGURE 2 Roosting sites habitat suitability map of the red kite wintering population

Overall, the most suitable areas for roosting sites of wintering population of red kite were on arable land and lowland areas that had gentle slopes, with relatively low levels of precipitation and mild temperatures in winter, not too far from water bodies, relatively close to dump sites, in areas with a minimum density of dead livestock carcasses and affected by moderate human influence.

When the northern subpopulation is excluded, the model suggests that the wintering red kites prefer to choose roosting sites within areas with a minimum amount of trophic resources (DLBA >10 t per grid square; DDS <50 km), moderate human impact (HFP from 50% to 70%), temperatures above freezing (from 0 ºC to 10 ºC) and with gentles slopes (Figs. 4 and 6).

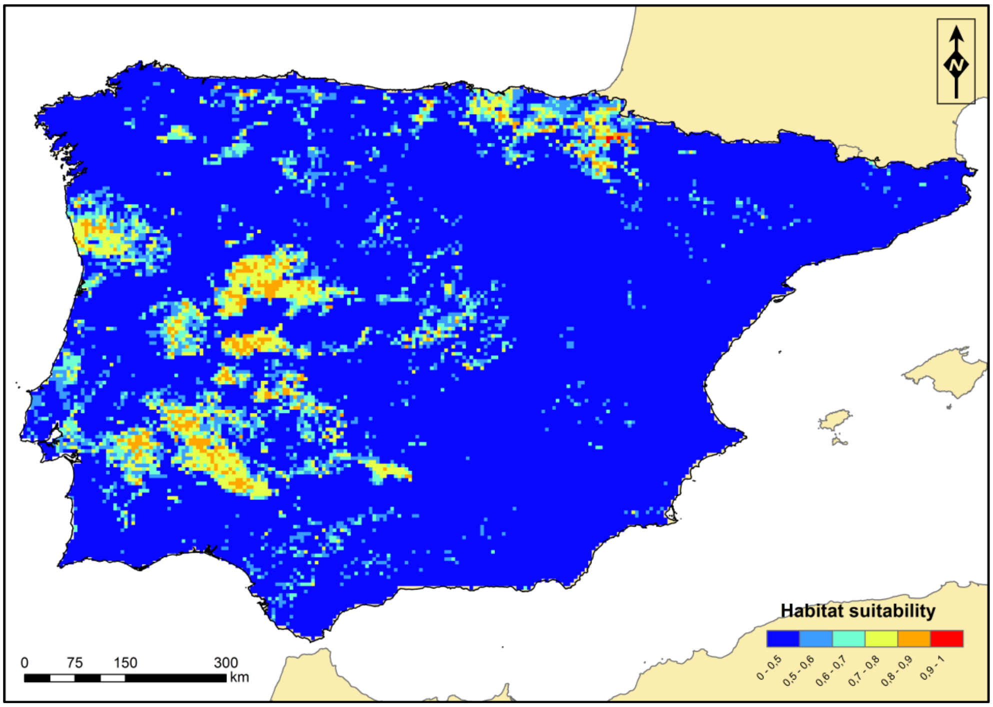

FIGURE 3 Roosting sites habitat suitability map of wintering red kite population. Model built excluding the occurrence records of NW Spain subpopulation in *Castilla y León*

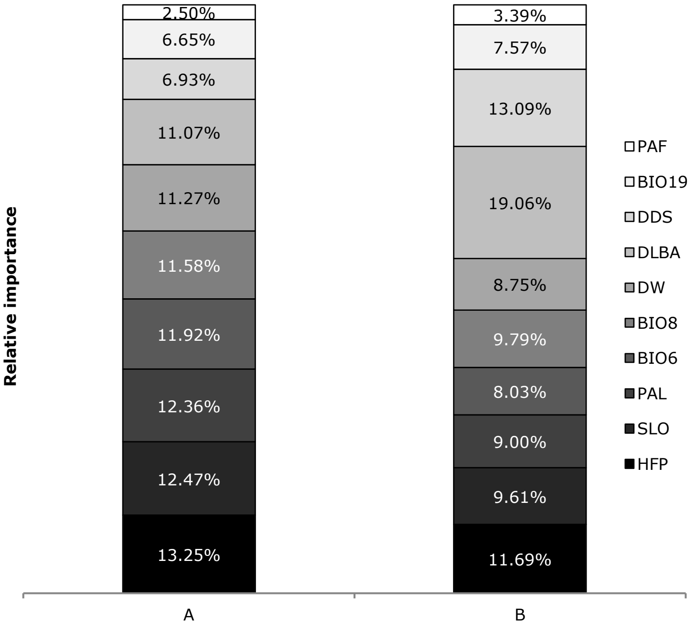

FIGURE 4 Relative importance of environmental predictors. A indicates the values for the model built with all occurrence records. B indicates the values for the model built excluding the occurrence of Iberian NW subpopulation. See variable codes in Table 1

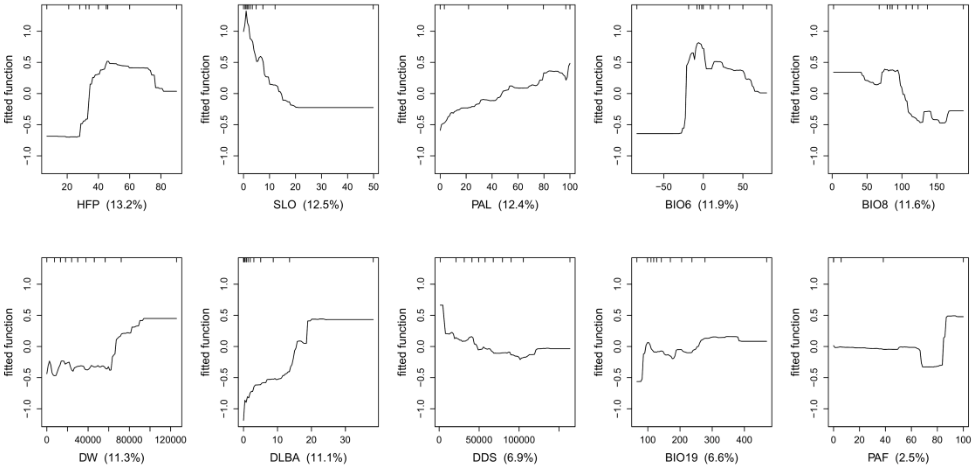

FIGURE 5 Partial dependence plots for the 10 variables used in BRT model built with all occurrence records. For variables explanation, codes and their units see Table 1. Rug plots at inside top of plots show distribution of sites across that variable

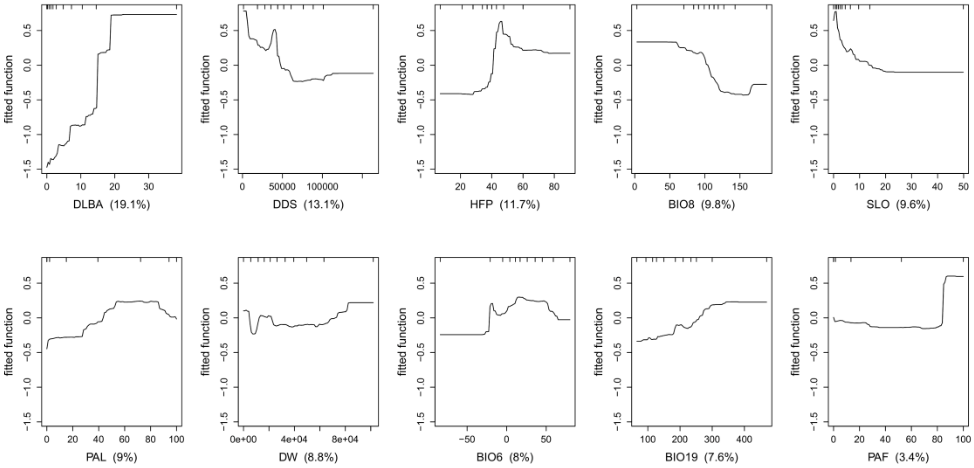

FIGURE 6 Partial dependence plots for the 10 variables used in BRT model built excluding the occurrence of Iberian NW subpopulation. For variables explanation, codes and their units see Table 1. Rug plots at inside top of plots show distribution of sites across that variable

III.4. DISCUSSION

III.4.1. Factors predicting distribution of roosting sites

Our results revealed that roosting sites distribution can be predicted in the Iberian Peninsula with high reliability (AUC values >0.8), by a combination of land use/land cover, topography, climate and human influence. The models indicated as the most suitable sites for wintering red kites those with a certain degree of human impact in flat or gentle landscapes occupied by extensively farmed and agroforestry land. The species is using in winter all available range of arable land coverage per 5 km grid square, usually avoiding the grid cells without this habitat.

Wintering red-kites in Spain can often be seen around small villages and farms, even selecting roosting sites not far from village edges (Viñuela et al., 1999), explaining the relevant effect of the human impact variable, so red kites are less frequent in areas with very high (large cities or industrial areas) or very low human impact (Fig. 5). Reduced presence of red kites in rugged mountain areas was also detected in the breeding populations (Heuck et al., 2013; Seoane et al., 2003), and may be related both to avoidance of large eagles species, the main red kite natural enemies, and reduced human presence (and thus food resources provided by livestock; Seoane et al., 2003). A large cover of agrarian land and flat landscape is typical of the main wintering area in the NW. When the occurrence data of NW Spain subpopulation are excluded, the relative importance of slope and “trophic” variables (DLBA and DDS) increases, corroborating the idea that topography and availability of food resources are fundamental requirements for wintering red kite’s habitat selection. This pattern is slightly different to that found for the breeding population of red kites in Spain (Seoane et al., 2003). Red kites during breeding season chooses pasturelands in undulated areas near mountains with moderate cover of forest, avoiding woody crops (olive trees, vineyards, almond and other fruit trees), but with low effect of arable land cover (Table A2 in Appendix; Seoane et al., 2003).

Red kite wintering distribution seems to be strongly correlated to specifics food resources commonly consumed such as common voles

(*Microtus arvalis*), common rabbits (*Oryctolagus cuniculus*), dump sites and availability of livestock carcasses. Other small to medium-sized mammals and birds represent secondary food source for red kite (García et al., 1998; Mougeot et al., 2011; Ortega & Casado, 1991; Sunyer & Viñuela, 1994). The common vole is widely distributed across the northern plateau where it is considered a pest in crop areas, due to population outbreaks during which densities may reach >1000 voles/ha in optimal habitat (such as alfalfa fields; Luque-Larena et al., 2013). Thus, in this part of Spain wintering red kites may find a common prey of breeding populations in central Europe, rodents in general (Heuck et al., 2013) and common voles in particular (Hille, 1995) in high density. Furthermore, it has been reported that relative abundance of common vole in the diet of wintering birds is correlated with arable land cover around roosting sites (García et al., 1998), probably because red kites catch most of consumed voles during autumn ploughing (as many as more than 50 kites have been observed following machinery while ploughing; Viñuela et al., 1999).

Interestingly, when winter distribution data from NW Spain are excluded, pattern of habitat selection in the rest of the Iberian Peninsula seems to change substantially, so it seems that selection of arable land is much stronger in NW, what gives support to the hypothesis of common vole abundance as a main driver of winter distribution of this species (Viñuela, 2012), and may explain the high suitability value in this region. In this second model without NW area, the abundance of livestock turned to be the most important factor explaining distribution (Fig. 6), what reinforces that where voles are absent, again food availability in the form of livestock carrion is a major driver explaining distribution.

The common rabbit is distributed all over the Iberian Peninsula and is the most important food resource for wintering red kites out of NW Spain

(García et al., 1998; Ortega & Casado, 1991). Both arable land and agroforestry areas are a main habitat for rabbits in Spain (Ferreira et al., 2014), its extent and relative quality largely determining rabbit abundances (Delibes-Mateos, Farfán, Olivero, & Vargas, 2010). Summarizing, our models indicated as most suitable areas for occurrence of wintering red kite lowland areas with high availability of prey (i.e. arable lands/agroforestry areas) and surrounded by others easily accessible food resources (i.e. livestock carrion or dump sites), confirming previous suggestions about the importance of food resources determining their distribution in winter (Viñuela, 2012; Viñuela et al., 1999) and supporting that food availability is a main factor explaining distribution and habitat use of migratory birds in wintering areas (Karr, 1976).

In the global model, the probability of finding a roosting site declined near rivers or other water bodies (<60 km), but after removing NW area, the pattern almost reversed (Fig. 5 and 6). Red kites in the northern plateau use to avoid valley bottoms for roosting, probably because of persistent winter fogs, very common in the Duero Valley and often maintained several hours after sunrise (Viñuela et al., 1999). But these fog banks usually do not reach slightly higher areas far from water, at the edges of valleys, due to thermal inversion. But this meteorological factor is not so common neither persistent in other wintering areas, where red kites apparently prefer the immediacy of water bodies for roosting, probably because adequate high trees are more common near rivers and lakes.

In the Iberian Peninsula the most discriminant factors for breeding distribution were climate (mean annual temperature ranging from 10 °C to 15 °C), topography (less rugged areas) and vegetation cover (with high values of index of plant productivity) (Seoane et al., 2003), but climate had not any clear effect in Germany. Germany holds the core breeding distribution area for the species, so weather conditions in the country during breeding season could be generally favourable, as compared to Mediterranean latitudes. Three climate variables were significant for our model for wintering birds, two containing information about temperature and the other about precipitation. This may be explained by the fact that red kite normally avoids rainy climates (Seoane et al., 2003), but in winter they would also be avoiding the coldest areas with more freezing weather. In fact, in the model excluding NW wintering area, a relatively humid and cold area during winter, the variable reflecting rainfall turned to be more important and positively affecting the probability of occurrence (Fig. 6 and Table A2 in Appendix).

III.4.2. Spatial and seasonal segregation of red and black kite populations

Winter distribution of red kites in Spain must be determined in first instance by migratory routes, which concentrate high numbers of migrants in the lowest mountain passes of western Pyrenees, given the clear trend to avoid high mountains and rugged terrain detected in both German and Spanish populations. From there, two main routes have been identified, constrained by the distribution of mountains: one heading southeast at the south face of Pyrenees occupying the Ebro valley and another one to SW through a narrow area between Cantabric and Iberian mountains, entering NW main wintering area (Cortés, 1988). From here, using low passes of central ridge, a fraction of migrating red kites enter the south part of the country, occupying lowlands in Extremadura and southern river valleys (Tajo, Guadiana and Guadalquivir). Conspecific attraction could explain co-existence in the breeding area of resident birds, but most migrants occupy areas were breeders are absent or scarce. All these lowland areas are unused by resident breeders due to climatic constraints (dry and hot summers reducing vegetal productivity; Seoane et al., 2003), but during winter they may be considered an optimal habitat for German red kites: flat, open and with increased vegetal productivity after autumn rainfall, similar to that occupied in their breeding range. Overall, most wintering red kites occupy lower and more arid areas than the resident population but keep avoiding the wettest N and NW coastal areas including most of Portugal, except the driest areas in the south of the country (Figs. 1 and A2 in Appendix). Interestingly, migrant red kites partially occupy the summer range of black kites, except those northern areas and most arid locations near Mediterranean coast (see Fig. A2 in Appendix). Furthermore, roosting sites and feeding points of wintering red kites often coincide with those used by black kites, so both resources are used all year long by both species in a good example of distribution of resources between migratory and sedentary populations of two sister raptor species.

Our results coincide with those reported by detailed small-scale studies of habitat use in Guadalquivir marshes, where resident breeding pairs kept their territory all year long, often using forested areas, while wintering birds used mostly the large, open and flat marshland area, and this difference was reflected in different diets too (Heredia et al., 1991; Viñuela et al., 1999). However, no aggressive behaviour potentially driving spatial segregation between resident and migrant birds has been detected. On the contrary, young and nonbreeding resident birds or even breeding pairs in territories at high altitude moving to lowlands may use winter roosts, mixing with wintering birds, and roosts are often located very near nesting trees of resident pairs (Heredia et al., 1991; Viñuela et al., 1999). Furthermore, wintering red kites used often sharable prey (e.g. carrion) rarely used by resident birds, that behave more as solitary foragers and hunters (Hiraldo et al., 1993). Thus, wintering red kites would occupy a larger distribution area than resident birds, because they use habitats rarely used by the latter, but more similar to those occupied by migrants in their breeding range than to those used by resident breeding birds, and this does not seem to be a consequence of competitive exclusion or spatial avoidance. However, differences between wintering birds, behaving as a “social searching network” looking for overabundant and sharable resources, and resident birds, behaving more as solitary hunters, would reduce competition and facilitate resource distribution between both sympatric populations (Pérez-Tris & Tellería, 2002).

III.4.3. Consequences for conservation: problems and opportunities

The main factors explaining distribution of wintering red kites, are related with human management and intimately linked to main known threats for the species: toxicological and sanitary risks and illegal predator persecution. In the NW area holding most migrant birds, chemical control with second-generation anti-coagulant rodenticides (SGARs) has been extensively and commonly used in the recent past (Luque-Larena et al., 2013; Olea et al., 2009), causing a clear reduction in red kites breeding numbers of treated areas (Mougeot et al., 2011). These slow-acting toxics leave rodent prey that has consumed the baits available to predators for long periods, and the toxic is accumulative and persistent, causing secondary exposure or death to rodent predators (López-Perea & Mateo, 2018). The red kites are particularly prone to SGAR poisoning, currently considered one of the main threats for the species (BirdLife International, 2017; Coeurdassier et al., 2012). In the winter 2013-2014 bromadiolone (an SGAR) was used to control vole populations and reached >25 % of common kestrels broods (*Falco tinnunculus*) in next boxes, even although rodenticide use was spatially limited and mitigation measures were applied (putting the bait inside burrows; see Martínez-Padilla et al., 2017). Furthermore, bromadiolone is usually applied in conditions of high vole abundance, that attract large numbers of several raptors species also wintering in this area (e.g. Short-eared owls *Asio flammeus*, Common buzzards *Buteo buteo* or Hen harriers *Circus cyaneus*; Jubete, 2011). Finally, typical treatment dates are in late winter and early spring, when vole populations start to invade cereal crops, in full wintering and migrating season. Consequently, integrated and ecologically-based vole management is urgently required to reduce the risk of exposure to SGARs for a significant part of the European population of red kites, but also for a high number of other migratory raptors (Coeurdassier et al., 2014; Paz et al., 2013). It is important to point out that models of the impact of global warming predict an 86 % loss of adequate habitat for red kites, so a range retraction to the north is expected and probably already ongoing (Wormworth & Mallon, 2007). Therefore, in the near future even a larger concentration of migrant birds in N Iberian Peninsula can be expected, due to disappearance of conspecific attraction and a retraction in suitable area in the southern part of current range.

Besides voles in NW, adequate management of food resources produced by livestock raising or other activities generating meat remains during winter in Spain turns to be crucial for the conservation of the European population or red kites (Viñuela, 2017). This food resource of prime importance can also be a source of possible sanitary problems due to disease transmission or veterinary drugs affections to carrion-eating birds (Blanco, 2015; Blanco, Cardells, & Garijo-Toledo, 2017; Green, Donázar, Sánchez-Zapata, & Margalida, 2016). As a possible solution to reduce this risk, leaving dead livestock in extensive exploitations out in the open, accessible to carrion-eating birds has been proposed as a potential solution for vultures (Cortés-Avizanda et al., 2016). Although red kites may also use this resource, they have only secondary access to remains left by vultures

(Álvarez, Arias de Reyna, & Hiraldo, 1976; Hiraldo, Blanco, & Bustamante, 1991), and they prefer gather in dumps with small meat remains (e.g. from chicken farms, or remains from slaughterhouses or meat processing factories; Viñuela et al., 1999), less often used by vultures than dumps with entire corpses. Thus, a well-designed network of feeding stations with good sanitary conditions must be considered a crucial element of any conservation strategy of the species, which may favour to other endangered raptors using similar resources, such as Egyptian vultures (*Neophron pernocpterus*). This kind of management technique has proven to be highly successful in the reintroduction programs in UK, and has also been successfully used in France (Carter, 2001).

Finally, the third crucial food resource for wintering birds, rabbits or other game (often wounded or shot unretrieved individuals; Mougeot et al., 2011; Ortega & Casado, 1991) is particularly used in southern populations, and may be associated to risks such as illegal hunting, illegal use of poisoning for predator control in game estates during late winter/early spring and lead poisoning, all of them important threats for the species in this geographical area (Hiraldo, Bustamante, & Viñuela, 1995; Villafuerte, Viñuela, & Blanco, 1998; Viñuela et al., 1999). Again, the provisioning of feeding points providing safe food resources could be an interesting strategy to mitigate the problem, providing alternative food resources to birds suspected to be in risky areas (e.g. with recent evidence of poisoning).

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APPENDIX CHAPTER III

Appendix 1: selection of variables

To select the variables we followed the approach proposed by Zohner et al. (2017): (i) compute the correlation matrix (“cor” function; R Core Team, 2015) between our initial set of environmental variables; (ii) convert the correlation matrix into a distance matrix; (iii) produce a dendrogram (“hclust” function; R Core Team, 2015) showing the correlation pattern among environmental variables; (iv) select one variable for each cluster below the 0.5 threshold (Fig. A1) and; (v) calculate the variance inflation factor (R package HH; Heiberger, 2017). The VIF analysis is an iterative process in which the user removes predictors, till all predictors show VIF values below 5 (Zohner et al., 2017; Table A1).

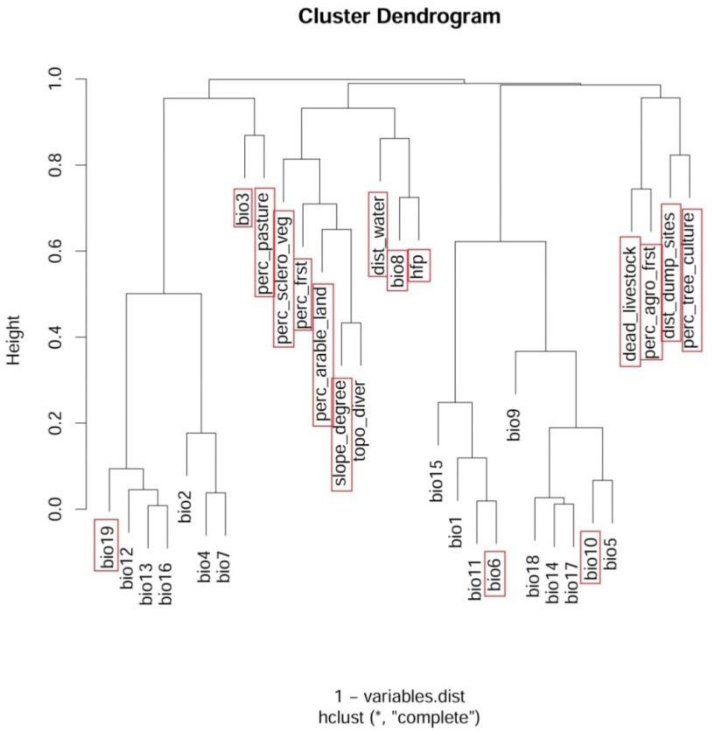

FIGURE A1 Hierarchical clustering dendrogram for the initial set of environmental variables. Red boxes indicate the variables finally selected for subsequent analyses

TABLE A1
Values of variance inflation factor (VIF) for the 16 selected variables for each cluster <0.5 threshold. VIF_1 indicates VIF values for the 15 variables; VIF_2 indicates VIF values for the 14 remaining variables. Variables were removed, till all predictors showed VIF values <5. For variable description see Table 1

Code	Variable	VIF_1	VIF_2
BIO3	Isothermality	1.323	1.256
BIO6	Min Temperature of Coldest Month	5.819	2.616
BIO8	Mean Temperature of Wettest Quarter	2.664	2.530
BIO10	Mean Temperature of Warmest Quarter	3.880	Removed
BIO19	Precipitation of Coldest Quarter	3.734	2.630
HFP	Human Influence Index	1.325	1.311
SLO	Slope	1.461	1.427
DLBA	Dead livestock biomass available	1.325	1.311
DDS	Distance to dump sites	1.184	1.108
DW	Distance to water bodies and courses	1.131	1.120
PAF	Agro-forestry areas	1.744	1.741
PAL	Arable land	2.672	2.672
PF	Forests	2.218	2.175
PP	Pastures and annual crops associated with permanent crops	1.603	1.596
PTC	Olive groves, fruit trees and vineyards	1.625	1.609
PSHV	Scrub / herbaceous vegetation	1.982	1.979

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Appendix 2: other supporting information

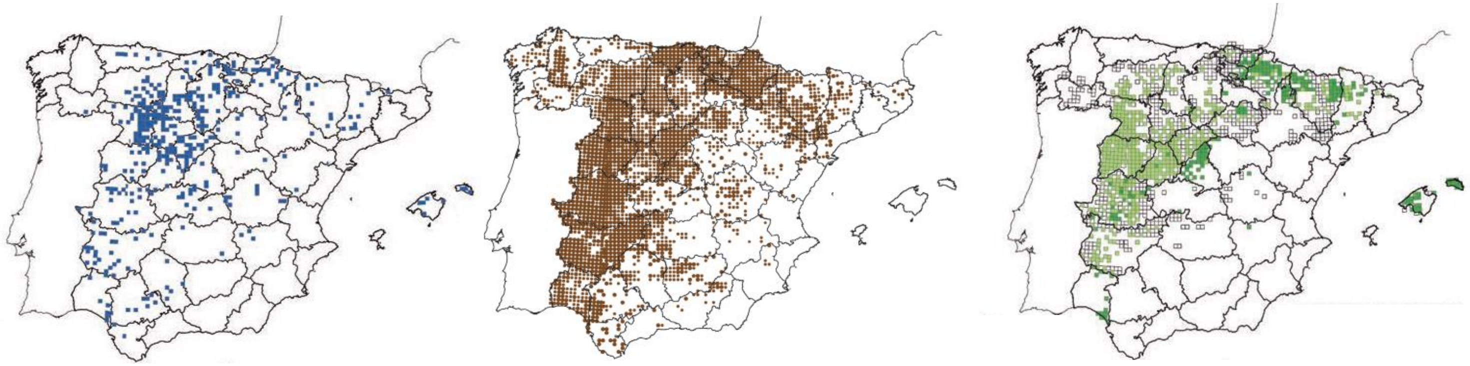

FIGURE A2 Probability of presence of wintering red kites (left map, location of roosting sites in winter 2013-2014; Molina, 2015), distribution of black kites during breeding season (central map, data from Spanish Bird Atlas; Blanco & Viñuela, 2004) and distribution of resident red kite breeding population (right map, dark green; confirmed breeding; light green; probable breeding: empty squares: sampled but the species was not found; Molina, 2015)

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TABLE A2

Comparison of models for breeding red kites in Spain (Seoane et al., 2003) and Germany (Heuck et al., 2013) and wintering red kites in Spain (this work). NC indicates that a given variable was not considered among the predictor variables. ++ indicates positive effect on probability of presence or abundance; -- indicates negative effect; MID indicates maximal presence probability or abundance at mid values of the predictor variable. Marked in red the four most important predictors in every model

	Breeding-Spain		Breeding-Germany (presence)	Winter-Spain	
	Presence	Abundance		All	Without NW
% of forest	MID	No effect	**--**[2]	No effect	No effect
% of pastureland	**++**	**++**	**++**	No effect	No effect
% of tree cultures	--	--	No effect	No effect	No effect
% irrigated crops	No effect	**--**	No effect[3]	**++**[3]	MID[3]
% non-irrigated crops	++	No effect			
% agroforestry areas	NC	NC	NC	++	++
% discontinuous urban fabric	NC	NC	**--**	NC	NC
Human influence index (HFI)	NC	NC	NC	**MID**	**MID**
Landscape diversity	NC	NC	++	NC	NC
Mean altitude	**MID**	**MID**	**--**	NC	NC
Mean slope	**--**	**--**	NC	**--**	--
Temperature[1]	--	No effect	No effect	**--**/++	--/**++**
Rainfall	No effect	No effect	NC	--[4]	--
Plant productivity (NDVI)	**MID**	No effect	NC	NC	NC
Distance to water bodies	NC	NC	NC	++	++
Distance to dump sites	NC	NC	NC	--	**--**
Dead livestock mass available	NC	NC	NC	++	**++**

[1]Yearly (Spain-breeding), spring (Germany) and coldest/wettest months (winter) averages; [2]Coniferous, deciduous and mixed forests; [3]Only "arable land" considered (i.e. no distinction between irrigated or not); [4]Driest areas avoided

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Heuck, C., Brandl, R., Albrecht, J., & Gottschalk, T. K. (2013). The potential distribution of the red kite in Germany. *Journal of Ornithology*, *154*(4), 911–921. https://doi.org/10.1007/s10336-013-0955-2

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CAPÍTULO IV

Viviendo al límite: ¿la idoneidad del hábitat difiere entre las poblaciones centrales y marginales de plantas?

Resumen

El desempeño de las poblaciones ubicadas en la periferia del rango de distribución de una especie puede diferir sustancialmente con respecto al de las poblaciones centrales. Aquí, desarrollamos un marco de modelado para estimar los nichos ecológicos (bioclimáticos) de 4 especies localmente amenazadas de plantas y medir la distancia de poblaciones marginales (geográficamente) al centroide del nicho ecológico de la especie con la finalidad de analizar si las poblaciones marginales están fuera de su nicho óptimo. Nuestros resultados muestran que para tres de las cuatro especies que tienen sus poblaciones localizadas en los márgenes de su distribución, están también en los márgenes de sus gradientes climáticos. Estos resultados apoyan la hipótesis de que la marginalidad dentro del conjunto de condiciones habitables (nicho ecológico) puede representar un factor determinante en la capacidad de algunas poblaciones de plantas, así como una explicación plausible del grado de estancamiento o regresión experimentado por las especies en aquellas regiones donde sus poblaciones están ubicadas en los márgenes de su nicho ecológico. Por último, este estudio espera ser una base teórica sobre la que avanzar, incluyendo otros factores (interacciones bióticas, topografía, influencia humana, dinámicas poblacionales, etc.), lo que permitirá una mejor interpretación de las complejas redes de factores que suceden en las poblaciones marginales.

Living on the edge: do central and marginal populations of plants differ in habitat suitability?

Abstract

The performance of populations at the edge of a specie's distribution range may differ substantially from central populations. Here, we develop a modelling framework to estimate ecological niches (i.e. climatic) of four locally endangered plant species and measure the distance of marginal (geographically) populations to the species' niche centroid in order to analyse whether marginal populations are outside of the optimal ecological niche of each species. Our results show that for three of the four studied species which have their populations located at the margins of their distribution ranges, are also at the margins of their climate gradients. These results would support the hypothesis that marginality within the set of habitable conditions (i.e. ecological niche) may represent an important determinant on performance of some plant populations, as well as a plausible explanation to the degree of stagnancy or regression experienced by species in those regions where their populations are at the margin of their ecological niche. Finally, this study aims to be a theoretical base from which to advance on, including other types of factors (e.g. biotic interactions, topography, human influence and population fluctuations through time), which will allow for a better understanding of the complex network of factors that occur in marginal plant populations.

IV.1. INTRODUCTION

From the beginning of biogeography as a true discipline, naturalists have acknowledged the importance of species population distribution patterns and the evolutionary significance of peripheral populations (Abeli, Gentili, Mondoni, Orsenigo, & Rossi, 2014). The distribution limits of a species are mainly established by its adaptive strategies to abiotic and biotic conditions and their interactions (Sexton, McIntyre, Angert, & Rice, 2009; Wiens, 2011). To explain their large scale biogeographic patterns, it is necessary to understand how species adapt to the environmental conditions at the margins of their distribution (Wiens et al., 2010), which is more noticeable in the case of species with low mobility, like most plants.

In a macroecological context, the effects of marginality on plant population performance have always been the object of study until recently (Abeli et al., 2014; Soulé, 1973). Several studies acknowledge two types of marginality: 1) ecological marginality: when the marginal populations experience different abiotic or biotic environments with respect to the species' optimum conditions, and 2) geographical marginality: when the marginal populations are separated from central ones by spatial distance (Abeli et al., 2014; Soulé, 1973). In many cases and depending on dispersal barriers, geographical marginality may or may not overlap with ecological marginality (Abeli et al., 2014; Lesica & Allendorf, 1995; Soulé, 1973).

From a conservation point of view, marginal populations are usually influenced by ongoing phenomena (e.g. climatic changes, inbreeding, genetic drift, human influence, etc.) leading to disturbances in their survival/persistence, thus they are thought to be less viable and more prone to extinction than the central ones (Channell, 2004; Lesica & Allendorf, 1995; Sexton et al., 2009). Assessing whether the species' population positions in their ecological niche are located at the margin of their optimal niches would be of great importance to gain a better understanding of the mechanisms driving the survival or decline of marginal plant populations and could accelerate the implementation of legal protection actions.

Species range shifts have been a recurrent phenomenon throughout the history of life on Earth (Hampe & Jump, 2011). As a consequence of changes in environmental conditions (climate changes, predation, resource competition, etc.) living organisms are in constant movement from one place to another at different geographical scales and at different temporal speeds. At the border of the range, some populations can be left behind during the range shifts, remaining far from the new centre of distribution, but possibly in suitable environmental conditions (i.e. microrefugium) surrounded by inhospitable regional climate (R. Gentili et al., 2015; Hampe & Jump, 2011). Thus, geographical marginality does not always correspond to ecological marginality. The process in which some are left behind during species migrations is closely linked to the concepts of refugia / macrorefugia / microrefugia and fragmentation/connectivity of a species' area of distribution. As a consequence of the change of these suitable areas (i.e. microrefugia), the species' distribution range may be fragmented and some isolated population may then become marginal populations (Bhagwat & Willis, 2008; Tzedakis, Lawson, Frogley, Hewitt, & Preece, 2002). The concept of refugia has been broadly classified as either macrorefugia or microrefugia (Ashcroft, Gollan, Warton, & Ramp, 2012; Rull, 2009). The term microrefugium (originally 'microrefuge') was introduced by Rull et al. (1988) describing it as small areas with local suitable environmental conditions, in which small populations are able to persist outside their main distribution area (the macrorefugium), protected from the unfavourable regional environmental conditions (Ashcroft et al., 2012; R. Gentili et al., 2015; Hampe & Jump, 2011; Rull, 2009). It is well known that the Mediterranean basin has provided suitable habitats and contained the most important microrefugia during the adverse cold climate of the Pleistocene glacial periods in Europe (R. Gentili et al., 2015; Gómez & Lunt, 2007). These microrefugia, by providing suitable environments during adverse climate periods, have contributed to the survival of several species' isolated populations (Birks & Willis, 2008; Hampe & Jump, 2011; Médail & Diadema, 2009). But, for how long are the populations in these microrefugia viable if environmental conditions continue to change around them? And is it possible to predict the fragility of a microrefuge and therefore determine the viability of the populations housed in it? Moreover, microrefugia are relevant for conservation proposals since they are important locations which hold ongoing ecological and evolutionary processes. These areas can offer: (i) shelter for species from climate variability and enhance the ability of species to persist when the climate is unsuitable elsewhere; (ii) genetic isolation that can enhance evolutionary processes; and (3) the enhancement of the diversity of environmental conditions and thus increase the potential for higher biodiversity (Ashcroft et al., 2012).

Usually, the empirical analyses of these patterns are based on small data sets, and worst of all, they usually do not encompass the entire extent of occurrence of a species and thus, it is difficult to obtain detailed population parameters at broad geographic scales which would allow for a better understanding of the processes limiting the species' geographic ranges (Diniz-Filho et al., 2009). Under this scenario, Ecological Niche Models (ENMs) offer a possible solution to this challenge, by combining species' occurrence data throughout its natural distribution range with relevant environmental variables to estimate their ecological niche and thus to make comparisons of central and marginal populations.

Roughly, the main factors which determine the species spatial distribution can be divided in three important groups: (i) the dispersal capacities of the species (either by own movements or by propagule dispersal); (ii) environmental tolerance (mostly in a physiological sense; e.g. climate, soil composition, water); and (iii) the presence or absence of biotic factors (e.g. pollinators, seed dispersors, competitors, diseases) (Guisan & Thuiller, 2005; Soberón, 2007; Soberón, Osorio-Olvera, & Peterson, 2017; Soberón & Peterson, 2005). Broad-scale variables (i.e. climate) at large extents are often available in low resolutions while fine-scale variables (i.e. demographic, soil textures, physiological and behavioural variables) which are the most relevant in microrefugia are usually – when available – at small extents and in high resolution (Soberón, 2007). Thus, incorporating biotic information to models at large extent is a critical issue.

The aim of this approach is to develop a preliminary tool based on ecological niche models to assess the potential distribution of marginal populations. This tool is used to determine if there are ecological differences for four selected plant species between the peripheral populations and the centroid of each of its ecological niches. It is expected that geographically marginal populations tend to occur in less suitable environments. To our knowledge this is the first time that niche models are used to quantify the weight of ecological marginality on geographically marginal plant populations.

IV.2. METHODS

IV.2.1. Study species

Four plants species of the European Flora were selected to carry out this study. Each of them has a different range of distribution but they all have in common that they reach the Iberian Peninsula marginally with only a few populations which constitute the western limit of their European distribution range. The Iberian Peninsula was established *a priori* as geographical marginal territory due to its latitude and peculiar characteristics (i.e. orographic and climatic). Also, this territory has historically been one of the major Mediterranean refugia for Central-European species (Rodolfo Gentili et al., 2015; Médail & Diadema, 2009). Moreover, due to the species' rarity within the Iberian territory they are included in the Red List of the Spanish Vascular Flora (Bañares, Blanca, Güemes, Moreno, & Ortiz, 2010; Moreno, 2008) and have legal conservation status at regional level in the Catalogue of Protected Flora in Castile and Leon (BOCYL, 2007).

Artemisia umbelliformis Lam. (Asteraceae) is a herbaceous perennial plant, it can be up to 25cm tall and is found in high montane rocks, in ventilated areas and under cryoturbation. It is a European endemism that was traditionally considered to be distributed along the Alps and north of the Apennines (Austria, France, Germany and Italy) with a few populations in the Pyrenees, the Cantabrian Mountains and the Sierra Nevada (Alonso-Redondo, Fernández-Cañedo, & Puente-García, 2011).

Drosera longifolia L. (Droseraceae) is a perennial and gregarious herb which inhabits central European localities with flooded mountain meadows and peat bogs on acidic substrates. The species is from the north and centre of Europe, north of Asia, Japan and north of America; it is very rare in the south of Europe where some populations reach the Basque Mountains and the north of Castile and Leon (Molina-Martín, 2011). In this study we consider *D. longifolia* as defined in *Flora iberica* (Paiva, 2003).

Empetrum nigrum L. (Empetraceae) is a creeping shrub with decumbent and radicant stems, it can grow up to 150 cm long. The main habitat for this species is the subalpine shrublands with *Calluna vulgaris* and *Vaccinium microphyllum*, in very shady environments with snow accumulation, lithosols and siliceous substrates. Its natural distribution range includes north of Europe, northwest of Asia, north of America and mountains in central and south of Europe. In the Iberian Peninsula there are only a few populations in the Pyrenees and the Cantabrian mountain range (Fernández-Cañedo, Del Egido-Mazuelas, & Puente-García, 2011). Here we have only considered the species' category, taking into consideration the deviation that can be generated by the few differences in the habitats of the two recognized subspecies: *Empetrum nigrum* subsp. *nigrum* L. and *Empetrum nigrum* subsp. *hermaphroditum* (Lange ex Hagerup) Böcher, since in the databases most of the records are only ascribed to the specific category.

Inula bifrons L. (Compositae) is a perennial hemicryptophyte, it can be up to 1m in height, growing in generally humid, limestone soils, under shady woods. It is distributed in temperate zones across the south of Europe: centre of Spain, south east of France, north west of Italy, Albania, Macedonia, Rumania and Bulgaria, being very scarce in all its areas (Santos-Vicente, Delgado-Sánchez, & Rico-Hernández, 2011).

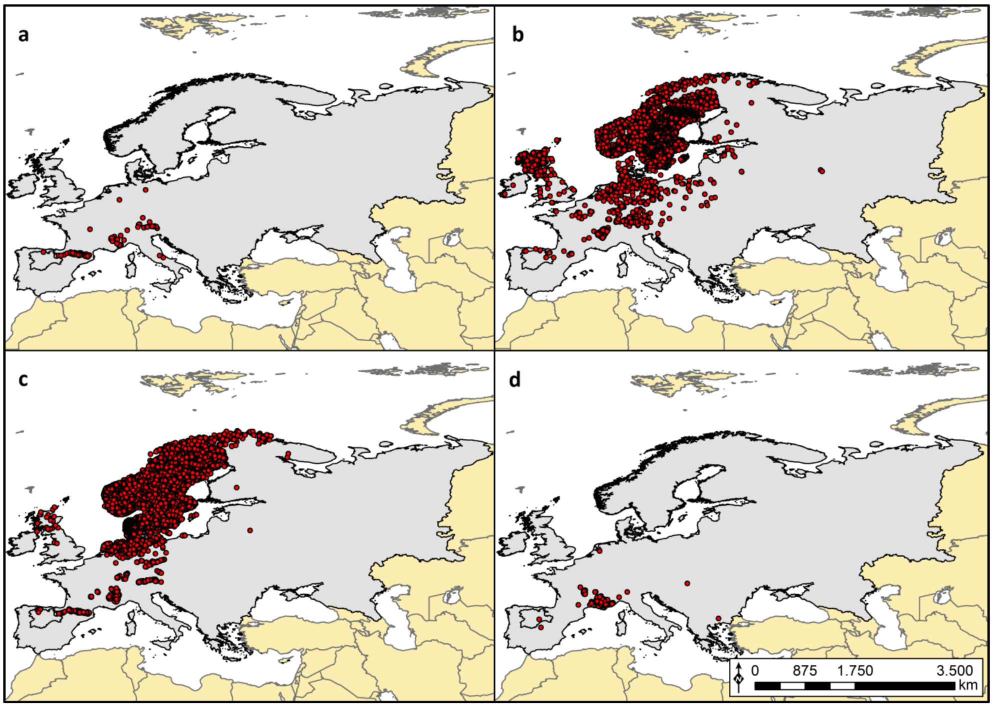

FIGURE 1 Occurrence records (red dots) per analysed species in the study area. (a) *Artemsia umbelliformis*, (b) *Drosera longifolia*, (c) *Empetrum nigrum* and (d) *Inula bifrons*

IV.2.2. Study area and dataset

The study area covers most of continental Europe including the British and Mediterranean Islands. The limits used are according to those defined by *Flora Europaea* (Tutin et al., 1964) excluding Iceland, Faroe Islands, Svalbard, Novaya Zemlya and Turkey. Partial territories in the Russian Federation west of the Urals were also included.

Species occurrence data (latitude and longitude) at continental level were obtained from the Global Biodiversity Information Facility (GBIF, 2017; www.gbif.org), and at community level from the ANTHOS database (www.anthos.es) through the National Node of Biodiversity Information Facility (GBIF España; www.gbif.es) and from the Catalogue of Protected Flora in Castile and Leon (BOCYL, 2007). All occurrence data were prepared carefully to detect and correct duplications and lack of precision or geographically discordant localities (Zohner, Benito, Fridley, Svenning, & Renner, 2017; see Figure 1). Since absence records were not available, we used an ecological niche modelling method developed for presence-only data (Phillips, Anderson, & Schapire, 2006; Phillips, Dudík, & Schapire, 2004; Phillips & Dudík, 2008) in order to calculate the realised ecological niche (sensu Sillero, 2011).

Climatic variables were obtained from CHELSA (Climatologies at high resolution for the earth's land surface areas) climatic database at 30 arc-seconds spatial resolution (approximately 1 km at the equator). These layers contain worldwide precipitation and temperature information, including minima, maxima, and ranges of values (Karger et al., 2017; http://chelsa-climate.org/). In order to avoid the cross-correlation within the selected variables, a multi-collinearity test was conducted using the Pearson correlation coefficient. Of the 19 bioclimatic variables available, we selected eight with cross-correlation coefficient values lower than 0.70. The final explanatory variables selected are shown in Table 1. All spatial information processing was handled using the Spatial Analyst Tool from ArcGIS 10.3.1 for Desktop (ESRI, 2015).

Table 1
List of climatic variables with a Pearson correlation lower than 0.70 obtained from CHELSA series (Karger et al., 2017; http://chelsa-climate.org/) and their relative contributions in Maxent models per species

		Species			
Code	Description	*Artemisia umbelliformis*	*Drosera longifolia*	*Empetrum nigrum*	*Inula bifrons*
BIO1	Annual Mean Temperature	4.796	5.195	0.372	9.784
BIO2	Mean Diurnal Range	17.253	*16.074*	**14.963**	**41.062**
BIO5	Max Temperature of Warmest Month	10.706	**67.259**	**74.942**	1.476
BIO8	Mean Temperature of Wettest Quarter	**23.369**	1.650	2.050	**14.618**
BIO15	Precipitation Seasonality	1.544	0.612	0.932	3.386
BIO16	Precipitation of Wettest Quarter	7.846	0.273	0.378	8.533
BIO17	Precipitation of Driest Quarter	**27.187**	0.630	0.418	8.577
BIO18	Precipitation of Warmest Quarter	7.301	8.308	5.945	12.566

IV.2.3. Niche characterization and distances to niche centroids

To estimate ecological niches of species and measure the distance to niche centroids (DNC) of each population, first we built ecological niche models for each species using Maximum Entropy modelling and then, we measured the multivariate Euclidean distance to niche centroids as in Yañez-Arenas et al. (2012).

For ecological niche modelling, we calculated the realised niche models (sensu Sillero, 2011) using the machine-learning technique called Maximum Entropy (Maxent) modelling (Phillips, Anderson, Dudík, Schapire, & Blair, 2017; Phillips et al., 2006, 2004; Phillips & Dudík, 2008). Maxent models were performed with Maxent 3.4.1 software (https://biodiversityinformatics.amnh.org/open_source/maxent/). We calculated the arithmetic mean through an iterative process and the standard deviation of a set of 10 Maxent models per species in cloglog format (Phillips et al., 2017) with default parameters using 10 replicates with bootstrap procedure (80% of the data for calibration and 20% for evaluation). The background points were set to 20 000 and all other settings were default values (Sillero & Carretero, 2013; Yañez-Arenas et al., 2012). The continuous outputs from Maxent were converted into binary maps (suitable or unsuitable habitats for species) using the conservative value of the 10th percentile training presence threshold (Bosso, Rebelo, Garonna, & Russo, 2013; Rebelo & Jones, 2010). Response curves were calculated to interrogate the relationship between the response and each explanatory variable. Finally, models were tested with the area under the curve (AUC) of the receiver operated characteristics (ROC) plot (Liu, Berry, Dawson, & Pearson, 2005). Random models have an AUC equal to 0.5; models with a good fit have AUC values close to 1 (Fielding & Bell, 1997). Here, we assume that the realised modelled niche is a good estimator of the fundamental niche, although we acknowledge that it is difficult to capture the true fundamental niche without physiological experiments for each species (Peterson et al., 2011).

To estimate the distances of environmental spaces of each population to the species' niche centroid, we followed Yañez-Arenas et al. (2012). In brief, we extracted values of environmental variables for all pixels where the species were predicted to be present according to the binary Maxent outputs. To avoid biases introduced by differences in scale among ecological dimensions (e.g. °C for temperature and mm for precipitation), we standardized each dimension (mean=0, variance=1). In this way, the multidimensional niche centroid is the point where values of all variables are 0, and calculations of the distances of environmental spaces of each population to the species' niche centroid become simple decompositions of Euclidean distances (Yañez-Arenas et al., 2012).

IV.3. RESULTS

Models developed for each species generally fit well with the knowledge of species' distributions (Figure 2) and their environmental preferences (Figure 3). Partial ROC analysis exhibited high average AUC ratios and low standard deviations for all models, indicating that all models performed reasonably well (Table 2).

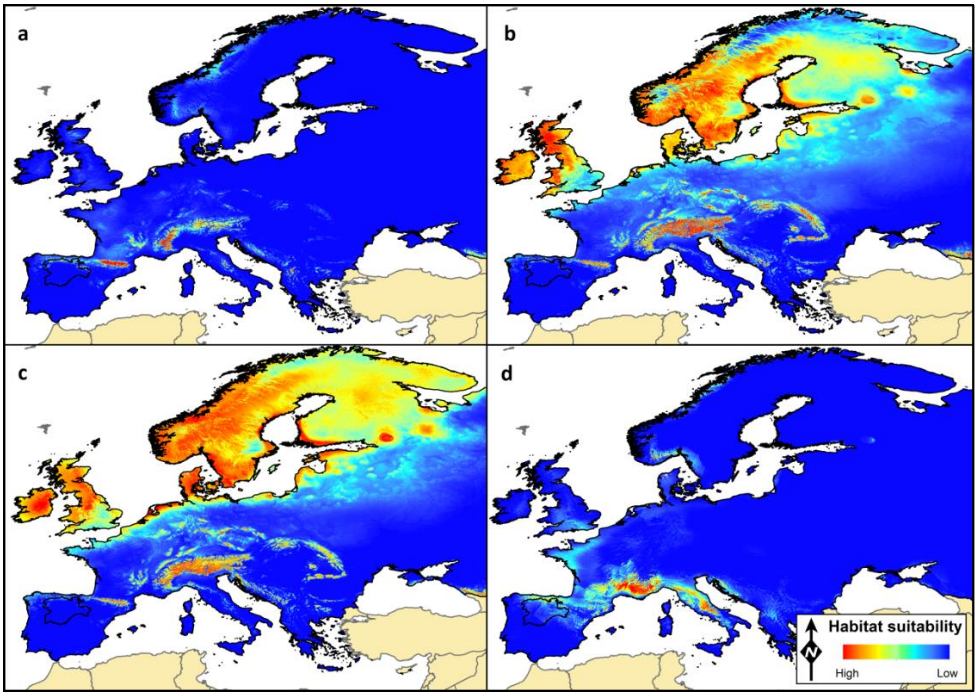

FIGURE 2 Maxent's potential distribution maps per analysed species. (a) *Artemsia umbelliformis,* (b) *Drosera longifolia*, (c) *Empetrum nigrum* and (d) *Inula bifrons*

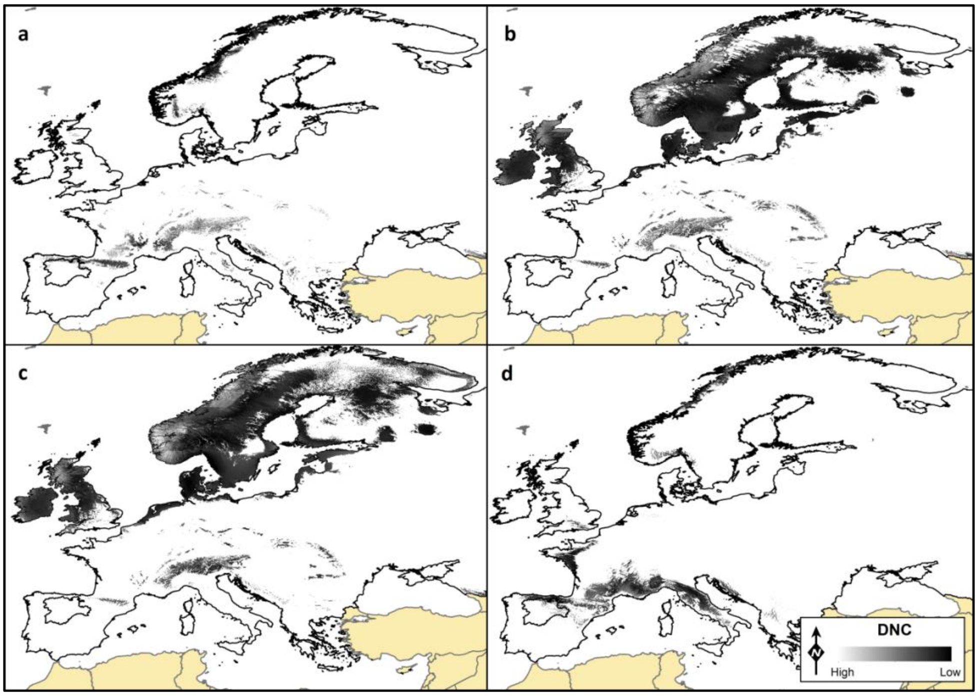

FIGURE 3 Distances to the ecological niche centroid maps per analysed species. (a) *Artemsia umbelliformis,* (b) *Drosera longifolia,* (c) *Empetrum nigrum* and (d) *Inula bifrons*

TABLE 2
AUC training and testing values for Maxent models (mean ± SD 10 replicates)

Species	AUC values	
	Training mean ± SD	Testing mean ± SD
Artemisia umbelliformis	0.987 ± 0.002	0.984 ± 0.004
Drosera longifolia	0.797 ± 0.000	0.798 ± 0.004
Empetrum nigrum	0.724 ± 0.000	0.724 ± 0.001
Inula bifrons	0.986 ± 0.003	0.983 ± 0.006

The variables that contributed most to the models were maximum temperature of warmest month, mean diurnal range, mean temperature of wettest quarter and precipitation of driest quarter (Table 2). The habitat suitability for both *D. longifolia* and *E. nigrum* was associated with colder environments and less seasonality (Figure 4). The habitat suitability for *A. umbelliformis* and *I. bifrons* was associated with wetter and less warm environments (Figure 5).

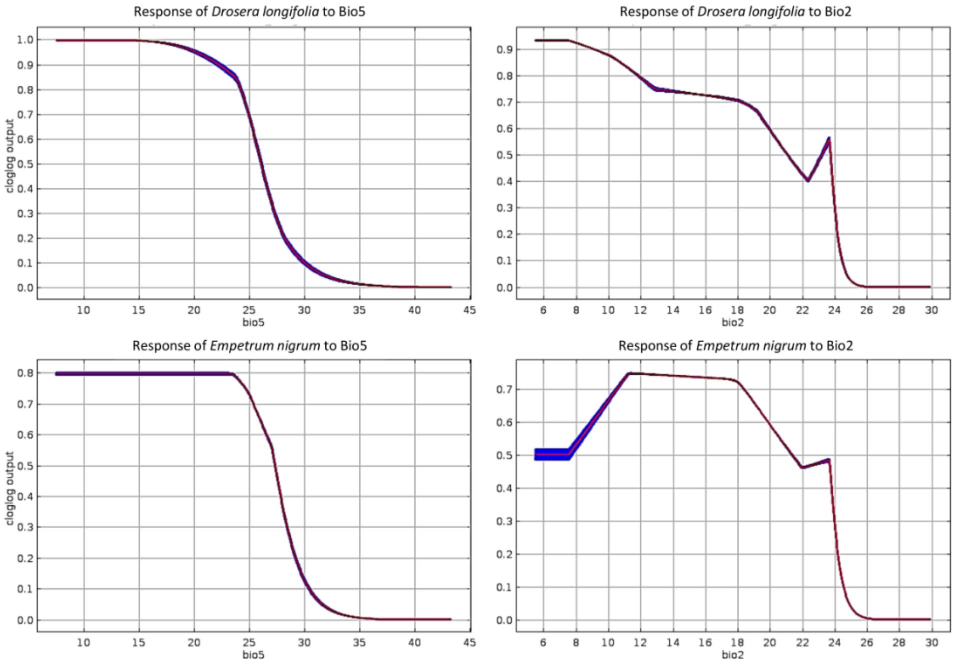

FIGURE 4 Response curves for the most important environmental variables in the ecological niche models for *Drosera longifolia* and *Empetrum nigrum*

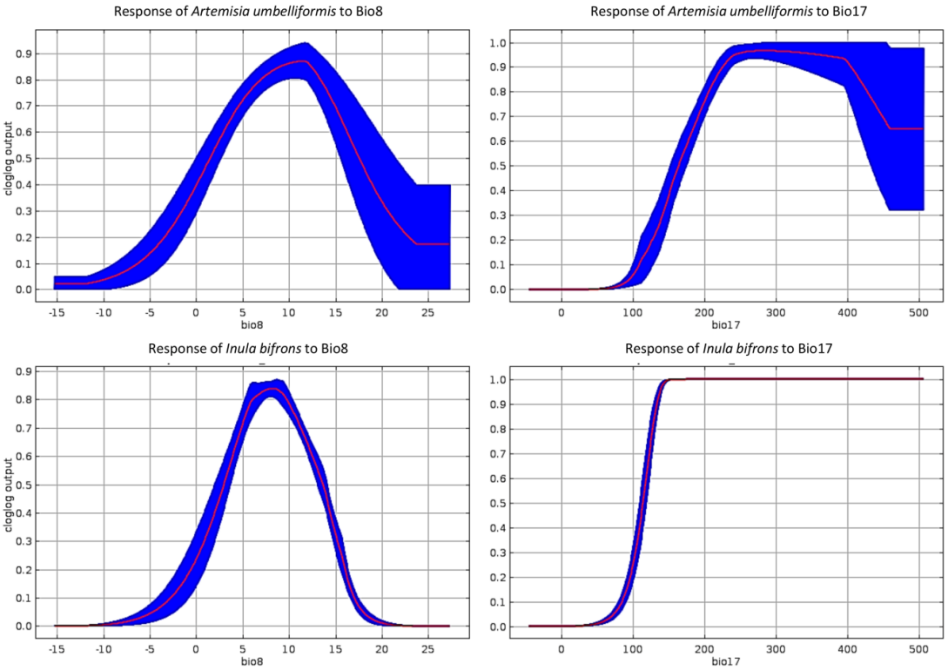

FIGURE 5 Response curves for the most important environmental variables in the ecological niche models for *Artemisia umbelliformis* and *Inula bifrons*

Three of the four populations in the northwest of the Iberian Peninsula were found in less suitable environments relative to each of the species' optimal climates (Table 3, Figure 3, 4, 6b, 6c 6d, 7b, 7c and 7d). *A. umbelliformis* was the only species whose marginal populations tended to occur in suitable environments near to the species' optimal climate (Table 3, Figure 3, 4, 6a and 7a).

TABLE 3
List of mean values of distance to the niche centroid (DNC) and habitat suitability per distribution and per species. NW IP indicates the scores reached by the populations located in the northwest of the Iberian Peninsula. Europe indicates the scores reached by the populations located out of the northwest of the Iberian Peninsula territory

Species	DNC$_{mean}$ value		Suitability$_{mean}$ value	
	NW IP	Europe	NW IP	Europe
Artemisia umbelliformis	0.654	0.528	0.870	0.792
Drosera longifolia	1.000	0.141	0.193	0.705
Empetrum nigrum	1.000	0.135	0.037	0.679
Inula bifrons	1.000	0.452	0.102	0.785

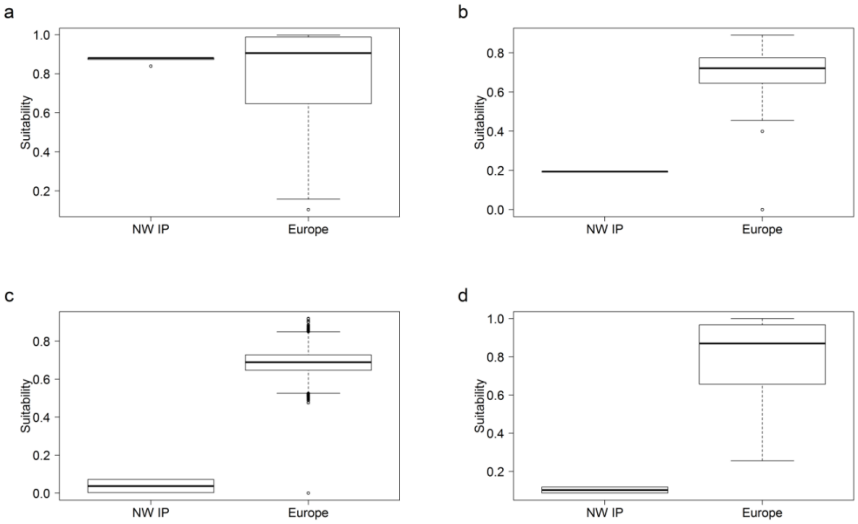

FIGURE 6 Suitability values for the occurrence records per analysed species. (a) *Artemsia umbelliformis*, (b) *Drosera longifolia*, (c) *Empetrum nigrum* and (d) *Inula bifrons.* NW IP represents the scores reached by the populations located in the northwest of the Iberian Peninsula. Europe represents the scores reached by the populations located out of the northwest of Iberian Peninsula territory

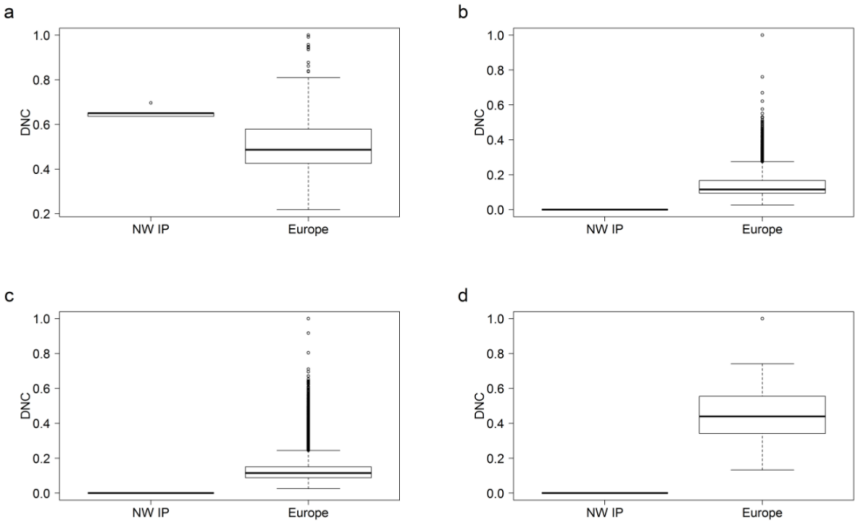

FIGURE 7 Distance to Niche Centroid (DNC) values for the occurrence records per analysed species. (a) *Artemsia umbelliformis*, (b) *Drosera longifolia*, (c) *Empetrum nigrum* and (d) *Inula bifrons.* NW IP represents the scores reached by the populations located in the northwest of the Iberian Peninsula. Europe represents the scores reached by the populations located out of the northwest of Iberian Peninsula territory

IV.4. DISCUSSION

In this study we apply the ecological niche model approach as an attempt to associate the effects of marginality – understood as the distribution of populations, geographically separated by long-distance from the main distribution core – on the performance of plant populations of a particular marginal territory (in this case the Iberian Peninsula). At the marginal range limit of a species' distribution, retractions (understood as the extinction of populations) and expansions (new colonisations) are responsible for the constant displacement of the limits of a species' range (Hampe & Jump, 2011). However this shift is rarely uniform and as a consequence of ecological irregularity of territories (which allows for the existence of microrefugia), randomness of dispersions, inequality in resource competencies or in predation phenomena, etc., some populations are often left behind remaining sometimes as relicts, isolated in small enclaves of suitable environmental conditions within an unsuitable regional climate (Hampe & Jump, 2011). We have selected the Iberian Peninsula as marginal territory since it is located at the end of the southern range of the European continent and due to its latitude and its peculiar orographic characteristics it has become one of the major Mediterranean refugia for Central-European species, especially during some past periods of strong glaciations (Rodolfo Gentili et al., 2015; Médail & Diadema, 2009). At the end of the glaciations, many of these species migrated north, although some of the remaining populations relegated to small refuges associated with scarce habitats, generally linked to mountainous systems (Rodolfo Gentili et al., 2015), which could be the case of most of our four studied species. Another main reason to put the focus on the Iberian Peninsula is because we have accurate data of selected species' presences for this territory which is essential to characterize ecologically potential microrefugia. The populations of *A.*

umbelliformis and *E. nigrum* are located in mountain peaks (Cantabrian Mountains above 2000 m a.s.l.; Alonso-Redondo et al. 2011; Fernández-Cañedo et al. 2011); *D. longifolia* populations reside in Laguna Larga de Neila, a glacial cirque surrounded by mountain peaks (*Sierra de la Demanda* about 2000 m a.s.l; Molina-Martín 2011); and I. bifrons populations are located on valley floors in relicts of *quejigal* woods (*Quercus faginea* Lam.; Santos-Vicente et al. 2011). All these areas provide a favourable microenvironment for small populations (i.e. microrefugia; Rull 2009). *A. umbelliformis*, *E. nigrum* and *D. longifolia* have populations inhabiting in the Pyrenees Mountains, which are also recognized (micro-)refugia (Médail & Diadema, 2009) reinforcing the idea that these populations were 'left behind' during range shifts (i.e. range contraction) of these species. Recently, Sanz et al. (2017) presented evidence that Pyrenees and Cantabrian Mountains acted as (micro-)refugia for *A. umbelliformis*.

Among the four analysed species, we have found a correspondence between ecological (i.e. climatic) and geographical marginality for three of them. These results would support the hypothesis that marginality within the set of habitable climate conditions (i.e. climate niche) could represent an outstanding factor on the performance of isolated plant populations (Lira-Noriega & Manthey, 2014). Less availability of suitable environments at the periphery could be translated into lower survival potential for the marginal populations (i.e. higher inbreeding phenomena).

The case of *A. umbelliformis* is the only one which showed no correspondence between geographic and ecological (i.e. climatic) marginality. Populations of this species located in the northwest of the Iberian Peninsula achieved low mean DNC values, that is to say, marginal and central distributions showed low dissimilarities between optimal climate niches. It is an expected result since the main distribution (i.e. central populations) of *A. umbelliformis* inhabits oceanic or continental climates and the marginal populations in the northwest of the Iberian Peninsula live in areas of strong oceanic influence (Rivas-Martínez, Rivas-Sáenz, & Penas-Merino, 2011).

The remaining species in which the ecological (i.e. climatic) marginality coincides with the geographical marginality: *D. longifolia*, *E. nigrum* and *I. bifrons* (Table 3; Figure 4b, c and d) have very specific habitat requirements (soil moisture, dampness, shading) that are only evident at fine scale – much finer than that used in this simulation – thus their characteristics were not included in our models. Based on Sinclair et al. (2010), we suspect that our predictions might be overestimating the species' distribution since the local scale features could be playing a key role in shaping their distribution ranges and they could be the reason why the three species are found in less suitable environments at the periphery. Moreover, accordingly to Körner and Hiltbrunner (2017), the microclimatic environment experienced by high altitude plants, especially those of small size, can be completely different from atmospheric temperatures, which is explained by the complex relationships between its lifeform (biotype), topography, snow accumulation and phases of its life cycle. Indeed, along the environmental gradient, the less suitable conditions are normally found close to the periphery (Normand et al., 2009). The central populations of *D. longifolia* and *I. bifrons* are located in regions with climatic conditions rather different from those of marginal populations. The central populations of *D. longifolia* are distributed across temperate climate -with oceanic and continental ombroclimate-, and boreal climate -with oceanic and subcontinental ombroclimates-. The core distribution of *I. bifrons* inhabits temperate climates and oceanic and continental ombroclimates. Furthermore the marginal populations of these species in the northwest of the Iberian

Peninsula inhabit temperate climates and oceanic and continental ombroclimates (Rivas-Martínez et al., 2011). This could explain why marginal populations of both species reach high mean DNC values and low mean suitability values. The high-latitude populations of *E. nigrum* are distributed across boreal climates and oceanic and subcontinental ombroclimates and the mid/low-latitude populations reside in temperate climates and oceanic and continental ombroclimates, even the populations in the northwest of the Iberian Peninsula (Rivas-Martínez et al., 2011). It seems clear that small scale factors, which our models are not capable of predicting, are acting locally and leading the species' distribution in marginal populations. Also, it is well accepted that high-latitude or altitude range limit should be controlled primarily by abiotic factors, whereas the low-limit should be determined primarily by biotic interactions (Hampe & Jump, 2011; Normand et al., 2009). Also, the optimal habitats for these three species are associated with colder, wetter and more seasonal environments and in the Iberian Peninsula they are linked to high mountain habitats with high water regimes and low temperatures. However, due to the warmer, less wet and more seasonal climates of this area in relation to northern European climates, the suitable environments of the Iberian populations seem to be lower than the mean values in the rest of their distribution. According to these results, marginality in the Iberian populations of these species is particularly highlighted.

Taking into account potential future scenarios of global warming (Tylianakis, Didham, Bascompte, & Wardle, 2008) and the requirements of the studied species, the persistence and/or performance of their populations may be significantly affected in the northwest of the Iberian Peninsula. Furthermore, Fernández-Cañedo et al. (2011), Molina-Martín (2011) and Santos-Vicente et al. (2011) have listed climate change as a potential threat for these species along with threats caused by the anthropogenic activities, basically because these populations inhabit very specific and restricted habitats. In addition, the populations of *E. nigrum* in the northwest of the Iberian Peninsula has been proposed to be categorized as "Vulnerable" in the Spanish Red List, under D2 IUCN criteria (Fernández-Cañedo et al., 2011; IUCN, 2001). Likewise *D. longifolia* and *I. bifrons* have been proposed to be included in the "Critically Endangered" category in the Spanish Red List under: [B1ab(ii, iv)+B2ab(ii, iii, iv) and [B1ac(iv)+2ac(iv); C2ab] IUCN criteria, respectively (IUCN, 2001; Molina-Martín, 2011; Santos-Vicente et al., 2011).

As was said above *A. umbelliformis* was the only species whose marginal populations of the northwest of the Iberian Peninsula tended to occur in suitable climatic environments near to the species' optimal climate. In this region the species is more linked to high mountain habitats with very specific soil requirements rather than habitats with high precipitation regimes and low temperatures. Thus, the effects of ecological marginality on performance of its scarce populations could be related to the type of soil rather than population position within the species' climatic optimal. As suggested by Alonso-Redondo et al. (2011), management of the populations of this species in this area should prioritize the control of the anthropic activity that could result in a real threat. More recently, Sanz et al. (2017) found that populations residing in the northwest of the Iberian Peninsula are less genetically diverse than the central ones. This may lead these populations to decline because of genetic drift potentially leading to gene loss and inbreeding depression (Sanz et al., 2017).

Additionally, microrefugia have an intrinsic value for conservation in providing unusual and stable climates for species (Ashcroft et al., 2012) which can be extremely significant to marginal populations. It is also important to highlight that not all microrefugia hold relict populations (i.e. marginal; Ashcroft et al. 2012). Once a microrefugia is located, it should be targeted for inclusion in the reserve system (Ashcroft et al., 2012), especially those holding marginal populations. Our results for *A. umbelliformis* could reveal that the habitats occupied by this species in the northwest of the Iberian Peninsula could be considered as microrefugia. In the Iberian Peninsula, the Spanish legislation has created protected areas especially designed to conserve flora called “Plant Micro-reserves”. These reserves usually consist of small areas focused on the protection of some populations of species which have been included in regional red lists, especially those with major threatened status (BOCYL, 2007; Laguna, 2001; Laguna et al., 2004). In the northwest of the Iberian Peninsula (more specifically in Castile and Leon territory), the Flora's decree (63/2007) has incorporated the possibility of creating Plant Micro-reserves to protect vulnerable populations of some threatened species. Although the decree did not establish any specific area, the legal conditions were established to be able to do so. From that moment a work of selection of plant species and populations for which it was necessary to create these protected areas has been developed. Also documents with detailed information of this work were created by research teams. To this moment, two out of the four studied species have micro-reserves proposed: *A. umbelliformis* and *E. nigrum*. We believe that apart from considering the foreseeable disturbances caused by the climatic change in the distribution of species, the microrefugia locations should also be considered when planning the creation of new micro-reserves or enlarging those existing. If microrefugia protect persisting populations they may be able to recolonize the surrounding landscape when favourable conditions for their survival and reproduction return (Noss, 2001). Marginal populations of *E. nigrum*, *D. longifolia* and *I. bifrons* are also associated with anthropic activities that it would make them especially vulnerable. Thus, due to their biological value, it is highly recommended to carry out urgent conservation actions to protect their Iberian populations.

It is important to highlight again that we are aware of the limitations of our modelling approach. For instance, this approach is a correlative, static method which associates the species occurrence with a particular state of the environment, thus it does not capture the dynamic nature of population fluctuations through time (Botkin et al., 2007; Yañez-Arenas et al., 2012). Also, spatial autocorrelation may overestimate the potential species distribution and inflate the model’s predictive power (Chapman, 2010). However, we think that this niche-based distribution model is a suitable tool for a first-pass assessment of distribution patterns of species' populations in a spatially explicit fashion, with the potential to optimize evaluation efforts in the field, helping to prioritize the conservation efforts of the most vulnerable populations.

In conclusion, this study aims to be a theoretical basis on which to advance from, including other types of factors (e.g. biotic interactions, topography, soil conditions, human influence and population fluctuations through time; Sinclair et al. 2010), which will allow for a better understanding of the complex network of factors that occur in marginal plant populations (Abeli et al., 2014).

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CAPÍTULO V

Fotos animales: Juan Ramón Peralta Rincón y Thomas Lahlafi

Evaluación de las similitudes de nicho entre poblaciones centrales y marginales de especies endémicas europeas

Resumen

La conservación y la gestión de la biodiversidad requieren un conocimiento preciso de la distribución geográfica de las especies. En el presente trabajo, proponemos un proceso metodológico eficaz y estandarizado que comprende modelos de nichos ecológicos y métricas de similitudes de nichos, a fin de identificar las coincidencias entre la marginalidad ecológica y geográfica de 81 especies endémicas europeas. Como primer intento, hemos elegido varias especies de varios grupos de organismos (flora, reptiles y anfibios). Nuestros resultados muestran que las poblaciones de 35 de las 81 especies estudiadas ubicadas al margen de su rango de distribución también se encuentran en los límites de su nicho óptimo climático. Este trabajo pretende ser una base teórica para avanzar incluyendo otros tipos de factores (por ejemplo, interacciones bióticas, topografía, influencia humana y fluctuaciones de poblaciones a través del tiempo), lo que permitirá una mejor comprensión de la compleja red de variables que ocurre en poblaciones marginales. Nuestro proceso metodológico podría ser de interés para los gestores de la biodiversidad ya que sería un primer paso antes de decidir sobre qué especies y poblaciones se deben invertir los esfuerzos de conservación.

Assessing niche similarities between central and marginal populations of European endemic species

Abstract

Conservation and management of biodiversity require accurate knowledge on species geographic distribution. In the present work, we propose an effective and standardized framework which comprises ecological niche models and niche similarities metrics, in order to identify coincidences between ecological and geographic marginality of 81 Europeans endemic species. As a first attempt we have chosen several species (flora, reptiles and amphibians). Our results show that populations of 35 of the 81 studied species located at margin of their distribution range are also in the limits of their climatic optimal niche. This work aims to be a theoretical basis on which to advance including other types of factors (e.g. biotic interactions, topography, human influence and populations' fluctuations through time), which will allow a better understanding of the complex network of variables that occur in marginal populations. Our framework could be of interest for conservationist managers since it could be the first step before to decide about what species and populations invest the conservation efforts.

V.1. INTRODUCTION

Understanding the species population distribution patterns is one of the most important topics in ecology (Abeli, Gentili, Mondoni, Orsenigo, & Rossi, 2014; Sagarin, Gaines, & Gaylord, 2006; VanDerWal, Shoo, Johnson, & Williams, 2009) and consequently, the evolutionary significance of marginal populations (Abeli et al., 2014). The distribution range limits are fundamentally determined by species' adaptive capacity to abiotic and biotic factors and their interactions (Sexton, McIntyre, Angert, & Rice, 2009; Wiens, 2011).

Currently, most authors have been acknowledged two types of marginality: 1) ecological marginality when the marginal populations experience different abiotic or biotic environments with respect to the species' optimum condition, and 2) geographical marginality when the marginal populations are separated from central ones by spatial distance (i.e. disjunct populations; Abeli et al., 2014; Lesica & Allendorf, 1995; Soulé, 1973) In many cases depending on dispersal barriers, geographical marginality may or may not overlap with ecological marginality (Abeli et al., 2014; Lesica & Allendorf, 1995; Soulé, 1973).

Many studies have been focused on marginal populations under the assumption of the 'centre-periphery' hypothesis (CPH; *sensu* Pironon et al., 2017) which, in general terms, postulates that genetic variation and demographic performance of a species decreases from the centre to the edge of its geographic range (Pironon et al., 2017). This hypothesis is based on Hutchinson's (1957) idea that there is an "optimal" region within the species' niche (i.e. optimal conditions for the survival of the species) and less favourable towards to periphery (Brown, 1984; Pironon et al., 2017). Marginal populations are usually assumed to be smaller, with lower genetic diversity, less viable and more prone to extinction than the central ones (Abeli et al., 2014; Channell, 2004; Lesica & Allendorf, 1995; Sagarin & Gaines, 2002; Sagarin et al., 2006; Sexton et al., 2009; Vucetich & Waite, 2003). Originally, the CPH focused on species abundance and population genetic structure and over the years CPH has been generalized to other components (i.e. genetics, physiology, morphology, demography) predicting them to be higher and more constant at central populations. If CPH premises were confirmed, it would have important consequences for ecology, evolution and conservation biology (Pironon, Villellas, Morris, Doak, & García, 2015). However, empirical studies often contradict these assumptions (Abeli et al., 2014; Channell & Lomolino, 2000; Mandák, Bímová, Plačková, Mahelka, & Chrtek, 2005; Pironon et al., 2015; Sagarin & Gaines, 2002; Sagarin et al., 2006) and until present there is no ‘general rule’ or ‘rule of thumb’ for this issue.

From conservation perspective, the marginal populations could represent an important value in preserving biodiversity, either suffering some degree of threat (i.e. marginal populations with little chance of survival and/or genetically impoverished) or for its capacity for adaption or speciation due its higher levels of differentiation and greater persistence than central populations (Abeli et al., 2014; Channell, 2004). Thus, assessing whether the species’ population positions in their ecological niche are located at the margin of their optimal niches would have great importance to a better understand of the mechanisms driving the survival or decline of marginal populations and it could improve the implementation of legal protection actions.

Species range shifts have been a recurrent phenomenon throughout the history of life on Earth (Hampe & Jump, 2011). As a consequence of changes in environmental conditions (climate changes, predation, resource competition, etc.) living organisms are in constant movement from one place to another at different geographical scales and at different temporal speeds (Hampe & Jump, 2011). During the species' range shift, some populations living at the border of the range can be left behind. These populations could remain far from the new centre of distribution of the species and possibly inhabiting suitable environmental conditions surrounded by inhospitable regional climate (Gentili et al., 2015; Hampe & Jump, 2011). In this sense geographical marginality not always corresponds to ecological marginality. The process in which some populations living at the border range are left behind during species migrations is closely linked to the concepts of refugia / macrorefugia / microrefugia and fragmentation / connectivity of a species' distribution area. As a consequence of the change of small scale environmental favourable zones (i.e. microrefugia *sensu* Rull, 2009), species' distribution range may be fragmented and some isolated population then become marginal populations (Bhagwat & Willis, 2008; Tzedakis, Lawson, Frogley, Hewitt, & Preece, 2002). Refugia concept has been broadly classified as either macrorefugia or microrefugia (Ashcroft, Gollan, Warton, & Ramp, 2012; Rull, 2009). The term microrefugium (originally 'microrefuge') was introduced by Rull, Schubert & Aravena (1988) describing it as small areas with local suitable environmental conditions, in which small populations are able to persist outside their main distribution area (the macrorefugium), protected from the unfavourable regional environmental conditions (Ashcroft et al., 2012; Gentili et al., 2015; Hampe & Jump, 2011; Rull, 2009). Microrefugia have been contributed to survival of several species' isolated populations by providing suitable environments during adverse climate periods (Birks & Willis, 2008; Hampe & Jump, 2011; Médail & Diadema, 2009). Moreover, microrefugia are relevant for conservation proposes since they are important locations which hold ongoing ecological and evolutionary processes. These areas can offer: (i) shelter for species from climate variability and enhance the ability of species to persist when the climate is unsuitable elsewhere; (ii) providing genetic isolation that can enhance evolutionary processes; and (3) enhance the diversity of environmental conditions and thus increase the potential for higher biodiversity (Ashcroft et al., 2012).

Over the last years, many authors have pooled data in order to review the genetic and ecological data at range edges, and also have proposed multiples approaches and frameworks improving our understanding of the effects of marginality (see Abeli et al., 2014; Channell, 2004; Eckert, Samis, & Lougheed, 2008; Pironon et al., 2017; Sexton et al., 2009). Usually, the empirical analyses of these patterns are based on small data sets, and worst of all, they usually do not encompass the entire extent of occurrence of a species and thus, it is difficult to obtain detailed population parameters at broad geographic scales that allows a better understanding of the processes limiting species' geographic ranges (Diniz-Filho et al., 2009; Eckert et al., 2008). Lately, Ecological Niche Models (ENM) have become widely applied in biogeography and conservation fields (Carretero & Sillero, 2016). In fact, numerous studies have been used ENM tools in order to compare the response of the performance of different species according to geographic and climatic centre-periphery (Diniz-Filho et al., 2009; Fernández, Jordano, & Haeger, 2015; Gerst, Angert, & Venable, 2011; Martinez-Meyer, Diaz-Porras, Peterson, & Yanez-Arenas, 2013; Pironon et al., 2015; Yañez-Arenas, Martínez-Meyer, Mandujano, & Rojas-Soto, 2012). Thus, ENMs could offer a solution to this issue, by combining species' occurrences data throughout its natural distribution range with relevant environmental variables in order to estimate their ecological niche (*sensu* Sillero, 2011) and thus to make comparisons between central and marginal populations. In geographic broad scales studies, ENM, normally achieve successfully to characterize the coarse-scale processes, however the processes occurring at fine-scale (e.g. biotic interactions) may be overlooked (Sinclair, White, & Newell, 2010). Roughly, the main factors which determine the species spatial distribution can be divided in three important groups: (i) the dispersal capacities of the species (either by own movements or by propagule dispersal); (ii) environmental tolerance (mostly in a physiological sense; e.g. climate, soil composition, water); and (iii) the presence or absence of biotic factors (e.g. pollinators, seed dispersors, competitors, diseases; Guisan & Thuiller, 2005; Soberón, 2007; Soberón, Osorio-Olvera, & Peterson, 2017; Soberón & Peterson, 2005). Broad-scale variables (i.e. climate) at large extents are often available in low resolutions, and fine-scale variables (i.e. demographic, soils, physiological and behavioural) which are the most relevant in microrefugia are usually at small extents and in high resolution and normally are not available (Soberón, 2007). Thus incorporate biotic information to models at large extent is a critical issue.

In the present work, we have developed a preliminary model-based tool to assess the potential distribution of marginal populations. This framework is useful to determine if there are ecological differences between the marginal and central populations of 81 herpetofaunal and flora European endemisms. These groups of organisms have been chosen, as a first trial, according to their ability to move, assuming that this factor will be decisive in the results. We are also aware of the diversity existing within the chosen species, characterized by different ecologies, habits, adaptive capacities, etc.

V.2. METHODS

V.2.1. Study area

The study area covers most of continental Europe including the British and Mediterranean Isles. The limits used are according to those defined by *Flora Europaea* (Tutin et al., 1964) and the New atlas of European amphibians and reptiles (Sillero et al., 2014), excluding Iceland, Faroe Islands, Svalbard, Novaya Zemlya and Turkey. Partial territories in the Russian Federation west of the Urals were also included (Fig. 1).

V.2.2. Species data

Occurrence data (latitude and longitude) of 47 endemic herpetofaunal species (amphibians=20 and reptiles=27; Tables A1 and A2 in Appendix) were obtained from the Atlas of Amphibians and Reptiles in Europe with 10 km spatial resolution (Sillero et al., 2014). Records (latitude and longitude) of 34 endemic flora species (15 families; Tables A1 and A3 in Appendix) were obtained from the Global Biodiversity Information Facility (GBIF, 2017; www.gbif.org). However, since absence records were not available, we used ecological modelling methods using only presence data in order to calculate the realised ecological niche (*sensu* Sillero, 2011). The Total species datasets for both groups (fauna and flora) was split into two partial datasets according to their distribution pattern: Central and Marginal. Following the approach proposed by Osborne & Suárez-Seoane (2002), in order to provide an objective data partition rather than focusing on some arbitrarily selected origin, we calculated for each species the centroid or geometric centre of their geographical distributions. We defined a radius by calculating the standard deviation of the mean distance from the centroid of the species distribution dividing the data into two samples (Fig. 1). The underlying assumption for this decision is that environmental conditions change with the distance from the centroid of the distribution (Fernández et al., 2015). Models were built for each three datasets per species (Total, Central and Marginal; Table A1 in Appendix). All GIS work was realized using ArcGIS 10.3.1 for Desktop (ESRI, 2015).

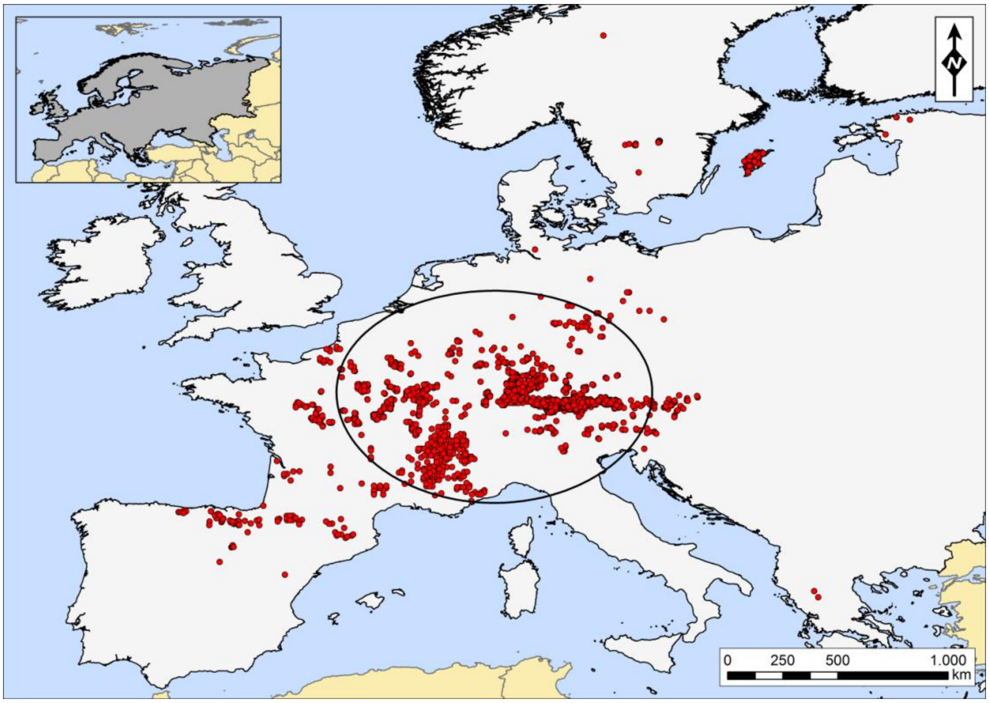

FIGURE 1 Example of species distribution map (*Gymnadenia odoratissima*) showing records corresponding to the Total (all points), Central (points inside the circle) and Marginal (points outside the circle) datasets. The study area is shown in the upper left rectangle

V.2.3. Environmental data and ecological niche models

Climatic variables were obtained from WorldClim climatic database at 30 arc seconds spatial resolution (approximately 1 km at the equator; Fick & Hijmans, 2017; www.worldclim.org). From the 19 bioclimatic variables available, we selected seven with a Pearson’s correlation coefficients lower than 0.75 (Tables 1, A4 and A5 in Appendix).

We calculated the realised niche models (*sensu* Sillero, 2011) using three datasets (Total, Central and Marginal) and three modelling presence-only methods: Maximum Entropy, BIOCLIM and DOMAIN. All these methods exclusively use presence records. Maximum Entropy models (Phillips, Anderson, Dudík, Schapire, & Blair, 2017; Phillips, Anderson, & Schapire, 2006; Phillips, Dudík, & Schapire, 2004; Phillips & Dudík, 2008) were performed with Maxent 3.3.3.k software (http://biodiversityinformatics.amnh.org/open_source/maxent/). BIOCLIM (Nix, 1986) and DOMAIN (Carpenter, Gillison, & Winter, 1993) models were performed with 'dismo' R package. All models were run with 20% of presence records from each dataset as training data.

TABLE 1
List of climatic variables with a Pearson's correlation coefficients lower than 0.75 obtained from WorldClim data (Fick & Hijmans, 2017; www.worldclim.org) used in BIOCLIM, DOMAIN and Maxent models

Description	Code
Mean Diurnal Range (Mean of monthly (max temp - min temp))	BIO2
Max Temperature of Warmest Month	BIO5
Min Temperature of Coldest Month	BIO6
Mean Temperature of Wettest Quarter	BIO8
Precipitation Seasonality (Coefficient of Variation)	BIO15
Precipitation of Driest Quarter	BIO17
Precipitation of Warmest Quarter	BIO18

V.2.4. Ecological niche models techniques

Maximum Entropy (Maxent) model is a general-purpose machine learning method, which is particularly well suited to noisy or sparse information and capable of dealing with continuous and categorical variables at the same time (Phillips et al., 2006, 2004). We calculated through an iterative process the arithmetic mean and the standard deviation of a set of 10 Maxent models per species in 'cloglog' format with default parameters using 20% of presence records from each dataset as testing data (Sillero & Carretero, 2013). Maxent identified the importance of each environmental variable by: (1) jack-knife analysis of the average AUC with training and test data; and (2) average percentage contribution of each variable to the models. For this purpose, variables were excluded in turn and a new model was created with the remaining variables; then a model was created using each individual variable.

BIOCLIM (Nix, 1986) defines the environmental envelope for the target species as a hyperbox, enclosing environmental factors within certain percentiles (e.g. 5%, 95%) of the observation records, and using mean and standard deviation for each environmental variable separately (assuming normal distribution). Each variable has its own envelope, represented by the interval [m–c×s, m+c×s], where ‘m’ is the mean; ‘c’ is the cut-off input parameter; and ‘s’ is the standard deviation.

DOMAIN (Carpenter et al., 1993) assigns a classification value to an unknown site based on the distance of its closest similar site in environmental space. The similarity metric is the only free parameter needed. Essentially, this model is analogous to a nearest neighbour classification, which is commonly used in spatial interpolation or image classification (Carretero & Sillero, 2016).

V.2.5. Model evaluation

All models were tested with the area under the curve (AUC) of the receiver operated characteristics (ROC) plot (Liu, Berry, Dawson, & Pearson, 2005). Random models have an AUC equal to 0.5; models with a good fit have AUC values close to 1. In addition, we calculated a set of 100 null models for each modelling method, following the methodology by Raes and Steege (2007). Null models were calculated in R (R Development Core Team, 2017). As the study area is the same for all species, we calculated the same null models for each modelling method, independently of species.

Therefore, AUC were compared between a specific modelling method and its corresponding null model, mixing all AUC scores.

V.2.6. Pairwise comparisons between models

Estimations of the species' realised niche for the different datasets were compared following the Broennimann et al. (2012) and Petitpierre et al. (2012) approach applying the procedures implemented in the ‘ecospat’ R package (Broennimann, Di Cola, & Guisan, 2016). Ecospat includes tools to support spatial analyses and modelling of species niches and distributions. It quantifies the niche overlap between two entities, either species or populations (e.g. native vs. invasive or two partial ranges as in this case). The package works in three steps (Warren, Glor, & Turelli, 2008): (1) it extracts environmental values to the records of the species pair (using the same variables of ENM calculations), transforms these values into densities by kernel smoothers, and represents them along the environmental axes of a PCA; (2) it measures the niche overlap along the gradients of the PCA; and (3) it applies statistical tests of niche equivalency and similarity. Niche overlap is calculated using the Schoener’s *D* metric as proposed by Warren et al. (2008), which varies from 0 (no overlap) to 1 (complete overlap; Carretero & Sillero, 2016).

Ecospat also performs niche equivalency and similarity tests. The niche equivalency test determines whether niches of two entities in two geographical ranges are equivalent. For it, the occurrences of both entities are merged and the resulting merged database is split into two datasets but with the same sample size than the original ones. The niche overlap statistic *D* is calculated for each pair of datasets. The process is repeated 100 times to guarantee that the null hypothesis can be rejected with high confidence. The simulated results are represented in a histogram: if the observed value of *D* is situated outside the density of 95% of simulated values, the null hypothesis of niche equivalency can be rejected. The niche similarity test examines whether the overlap between the observed niches of the two entities is different from the overlap between the observed niche of one entity and random niches from the other entity. Further, the environmental niche occupied in one entity should be more similar to the one occupied in the other range than would be expected by chance. Ecospat randomly shifts 100 times the entire observed density of occurrences in one entity and calculates the overlap of the simulated niche with the observed niche in the other entity. When the observed overlap is higher than 95% of the simulated values, the entity occupies environments in both ranges more similar to each other than expected by chance. Finally, Ecospat splits the niche into three components (Petitpierre et al., 2012): the proportion of the niche that is occupied in the second species of the comparison and shared with the first species (i.e. S; stability); the proportion of the niche in the first species that is not occupied in the second one (i.e. U; unfilling); and the proportion of the niche in the second species that is not occupied in the first one (i.e. E expansion; Carretero & Sillero, 2016). Values for S, U and E range from 0% to 100% and are typically said to be relevant at >10%, and although this threshold is partly arbitrary it allows for comparisons with other studies (e.g. Hill, Gallardo, & Terblanche, 2017; Parravicini, Azzurro, Kulbicki, & Belmaker, 2015; Petitpierre et al., 2012; Strubbe, Beauchard, & Matthysen, 2015). Finally, we extracted all suitability values per species and per dataset for the three modelling methods. Then, suitability values were compared between datasets, mixing all suitability values.

V.3. RESULTS

V.3.1. Model evaluation

We tested the hypothesis that the AUC values for each model were significantly different from that of a random null model (alpha = 0.05). AUC values from all modelling method were significantly higher than the values corresponding to its null model ($p < 0.001$). All models performed better than random reaching very high AUC values (>0.9); Maxent models performed well (AUC_{mean} 0.96 ± 0.03), followed by DOMAIN (AUC_{mean} 0.95 ± 0.05) and BIOCLIM (AUC_{mean} 0.94 ± 0.05; Fig. 2 and Tables A2 and A3 in Appendix).

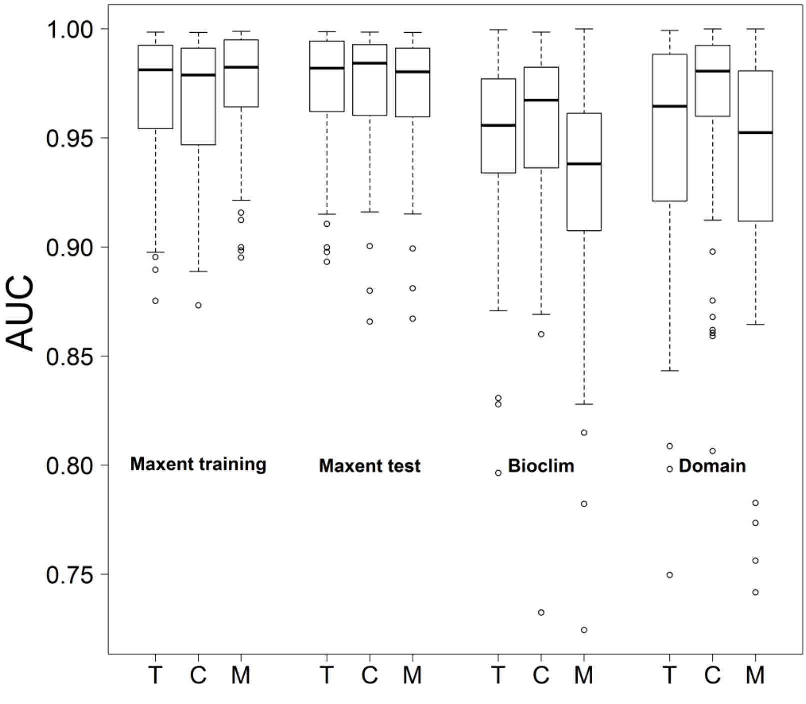

FIGURE 2 Boxplot of AUC values for Maxent, BIOCLIM and DOMAIN models per dataset: Total (T), Central (C) and Marginal (M)

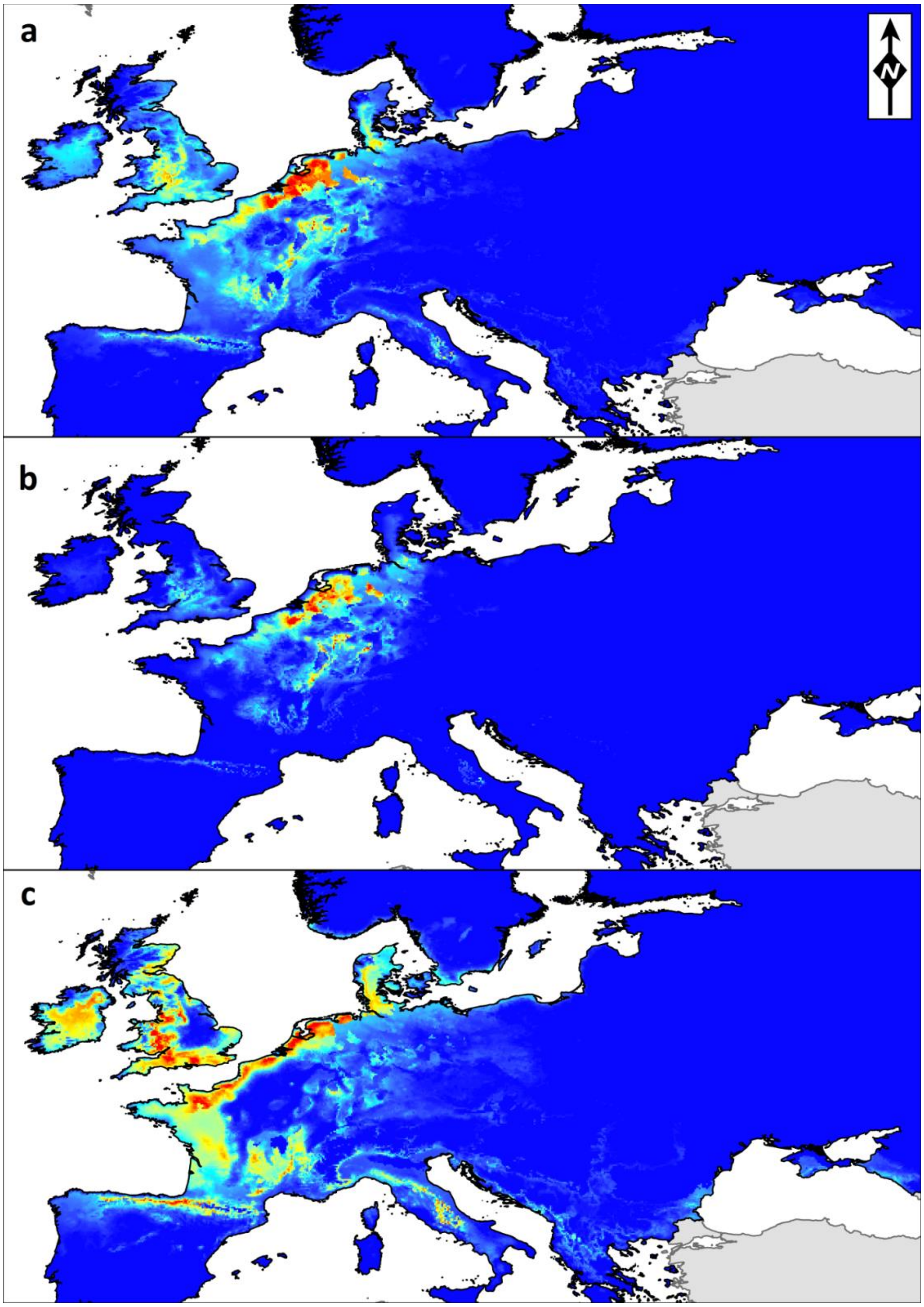

FIGURE 3 BIOCLIM models: example of (A) Total, (B) Central and (C) Marginal models for *Lissotriton helveticus*. Warmer colours indicate more suitability

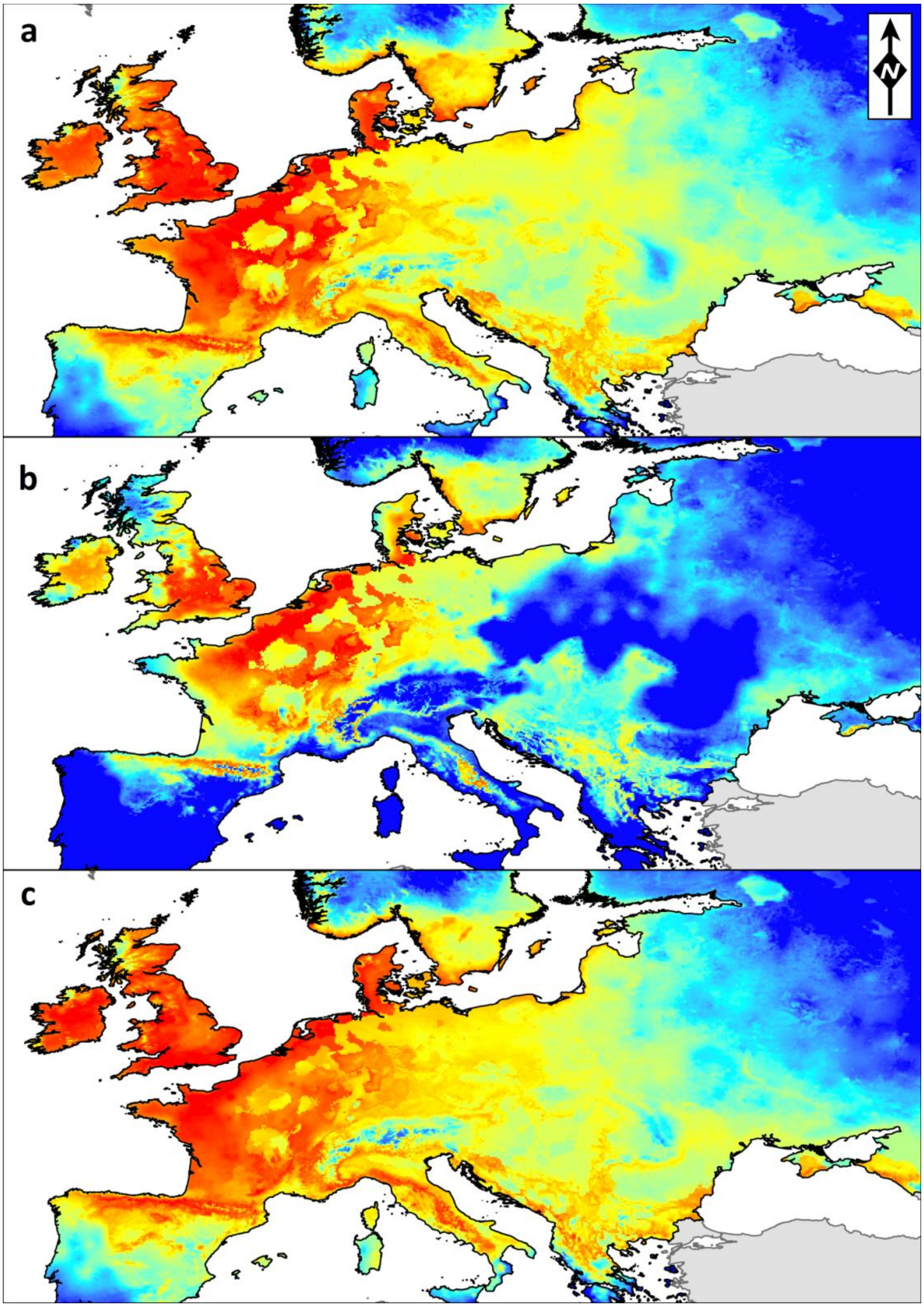

FIGURE 4 DOMAIN models outputs: example of (a) Total, (b) Central and (c) Marginal models for *Lissotriton helveticus*. Warmer colours indicate more suitability

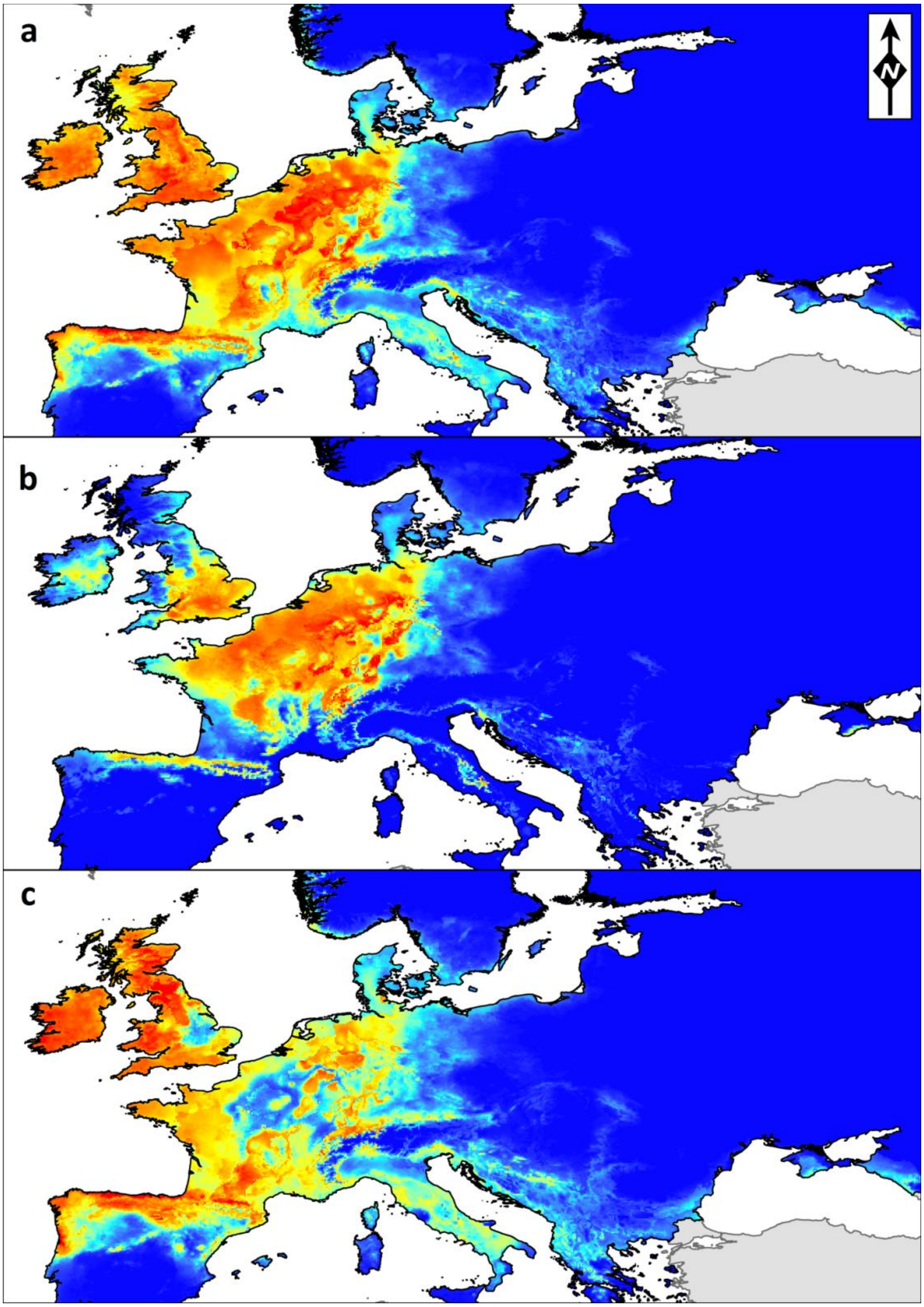

FIGURE 5 Maxent models outputs: example of (a) Total, (b) Central and (c) Marginal models for *Lissotriton helveticus*. Warmer colours indicate more suitability

In general, DOMAIN models predicted more suitable areas than Maxent and BIOCLIM respectively (examples in Figs. 3, 4 and 5). Also, in many cases for the three techniques, models built with Marginal datasets produced predicted suitable area pattern similar to models built with Total dataset. Models generated with these datasets, in general, predicted larger suitable areas than models generated with Central dataset for all species. We illustrated the three models outputs for *Lissotriton helveticus* that presented significant differences for predicted values of suitability between central and marginal populations (Figs. 3, 4 and 5 and A2 in Appendix).

V.3.2. Pairwise comparisons between models

Pairwise comparisons between datasets (Figs. 6 and 7 and Tables A6 and A7 in Appendix) provided inference statistical to the differences recorded. Climatic niche overlap analysis was carried out in a gridded climatic space formed by the first two axes of principal component analysis based on seven climatic variables. These first two axes accounted for 63.19% of the variation in the data (axis 1: 40.51%; axis 2: 22.68%; Figure A1 in Appendix).

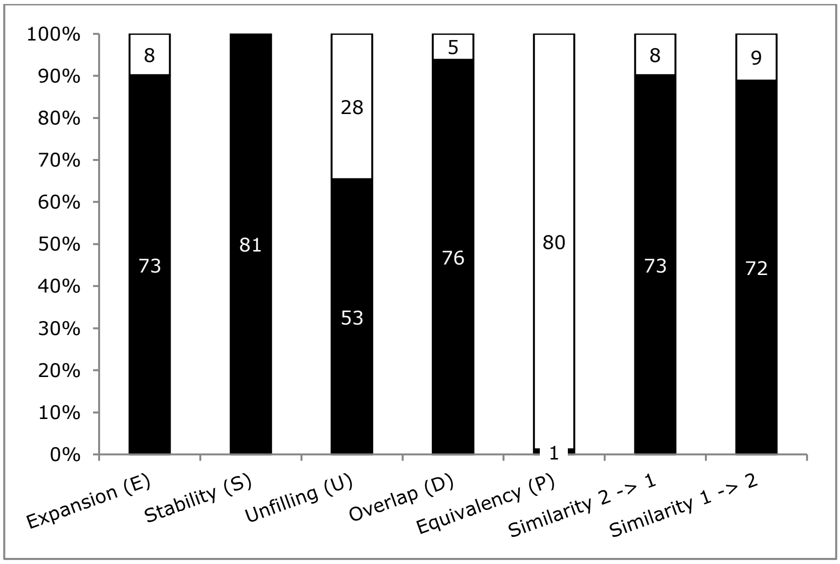

FIGURE 6 Pairwise comparisons of niches in climatic space (PCA) between datasets per species. Niche shift metrics: Expansion (E), Stability (S) and Unfilling (U). Values range from 0 to 1, with 1 being total niche expansion or unfilling and 0 reflecting no change between ranges. Black colour in these bars indicates that the amount of expansion or unfilling was above 10%. Niche equivalency and similarity tests with 100 replication between datasets per species. Black colour indicates significant values (*p* <0.05) in these bars

Tests detected niche expansion (>10%) for 73 of 81 studied species and all species and comparisons reached niche stability (>10%, except *Alisma wahlenbergii* and *Pulsatilla grandis* C-M <10%). Eight flora and nine fauna species presented niche unfilling (>10%) for all three comparisons (T-C, T-M and C-M). High climatic niche overlap (D >0.50) was observed for 10 flora and for 13 fauna taxa in C-M comparison. Niche equivalency hypothesis was rejected only for *G. odoratissima* (T-C comparison; *p*=0.01) indicating that the niches are not equivalent. The niche similarity hypothesis for C-M comparisons was rejected for 14 flora species and 21 fauna species (amphibians=12 and reptiles=12) indicating that its niches were not similar (*p* <0.05 in both directions; Figs 6 and 7; Tables A6 and A7 in Appendix).

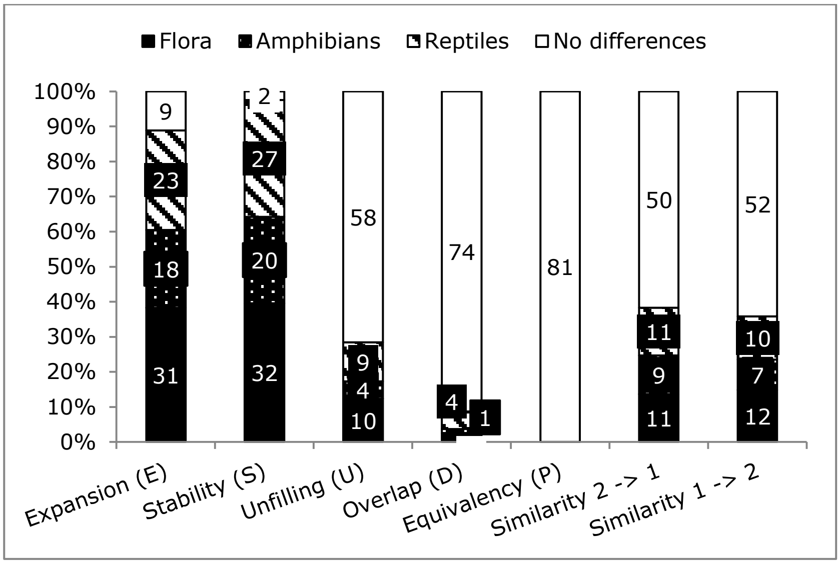

FIGURE 7 Pairwise comparisons of niches in climatic space (PCA) between C-M per species. Niche shift metrics: Expansion (E), Stability (S) and Unfilling (U). Values range from 0 to 1, with 1 being total niche expansion or unfilling and 0 reflecting no change between ranges. White colour in these bars indicates that the amount of expansion or unfilling was below 10%. Niche equivalency and similarity tests with 100 replication between datasets per species. White colour indicates significant values (*p* >0.05) in these bars

We illustrate results for two species, *Alisma wahlenbergii* and *Iberolacerta monticola*, one showed niche dissimilarities and other niche similarity between Central and Marginal distributions, respectively. *I. monticola* presented a high level of similarity between comparisons, even the comparison between C-M (E=0 .217, S=0.783, U=0.000, D=0.742, P=0.941 and Similarity=0.010 in both directions) indicating more similarity between climate niche occupied by species' central and marginal populations (Fig. 8, 9 and Table A6 in Appendix).

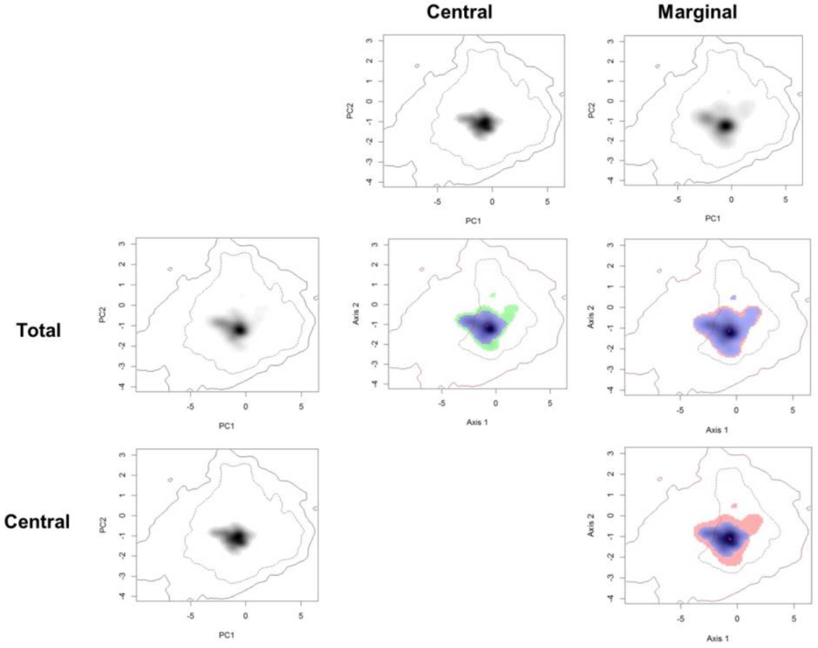

FIGURE 8 Niche overlaps and dynamics between datasets in climatic space (T-C, T-M and C-M): example for *Iberolacerta monticola*. On the first column, density plots of the species' datasets projected on the first two principal components (PCA1: 40.51% var; PCA2: 22.68 % var.) of the environmental space. The remaining plots indicate the pairwise comparisons between datasets and associated Expansion (red), Stability (blue) and Unfilling (green). Density of the occurrences of each subrange by cell is grey-shaded; solid and dashed contour lines illustrate 100% and 50% of the available environmental space, respectively

A. wahlenbergii showed differences between comparisons, especially the comparison C-M (E=0 .915, S=0.085, U=0.619, D=0.015, P=1.000 and Similarity=0.1782 in both directions) indicating less similarity between climate niche occupied by species' central and marginal populations (Fig. 10, 11 and Table A7 in Appendix).

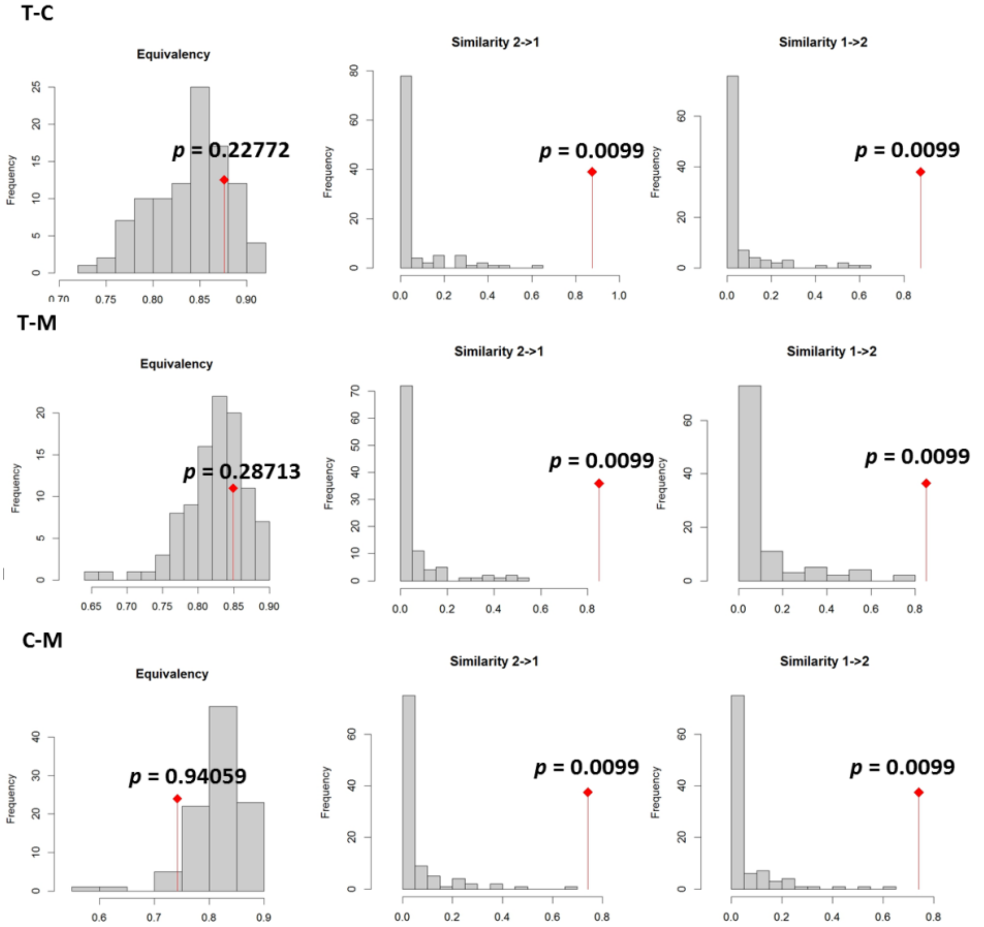

FIGURE 9 Niche equivalency and similarity tests between datasets (T-C, T-M and C-M): example for *Iberolacerta monticola*

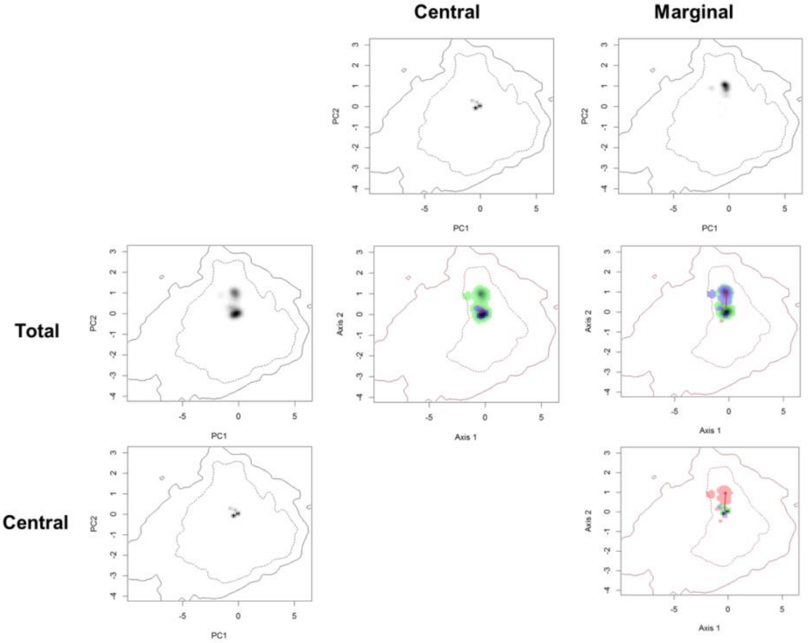

FIGURE 10 Niche overlaps and dynamics between datasets in climatic space (T-C, T-M and C-M): example for *Alisma wahlenbergii*. On the first column, density plots of the species' datasets projected on the first two principal components (PCA1: 40.51% var; PCA2: 22.68 % var.) of the environmental space. The remaining plots indicate the pairwise comparisons between datasets and associated Expansion (red), Stability (blue) and Unfilling (green). Density of the occurrences of each subrange by cell is grey-shaded; solid and dashed contour lines illustrate 100% and 50% of the available environmental space, respectively

As expected, most of studied taxa presented a high level of similarity for T-C and T-M comparisons, which could be explained by the fact that models built with Total dataset contained the Central and Marginal data. Among the 81 studied species, 65 (flora=30 and fauna=35) presented climatic niche similarities in at least four of seven metrics used for T-C comparison and 54 (flora=22 and fauna=32) for T-M comparison (considering Similarity <0.05 in at least one direction; Figs 6 and 7; Tables A6 and A7 in Appendix).

From 81 analysed taxa, 55 presented any difference of mean predicted suitability values between datasets comparisons. From those 55, 32 presented this difference in C-M comparison (Fig. 11). 44% of the taxa that presented niche dissimilarities also showed differences in predicted suitability values between central and marginal populations (Figs. 13 and A2, A3, A4, A5, A6, A7 and A8 in Appendix).

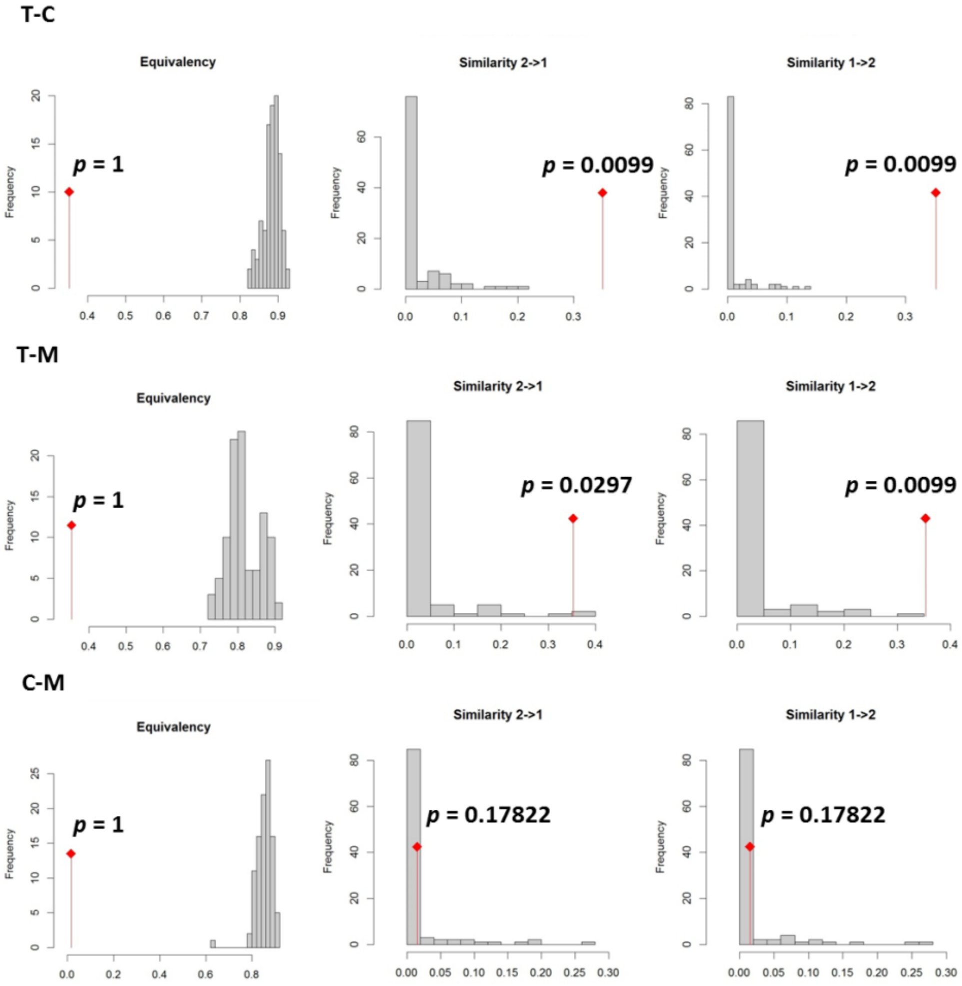

FIGURE 11 Niche equivalency and similarity tests between datasets (T-C, T-M and C-M): example for *Alisma wahlenbergii*

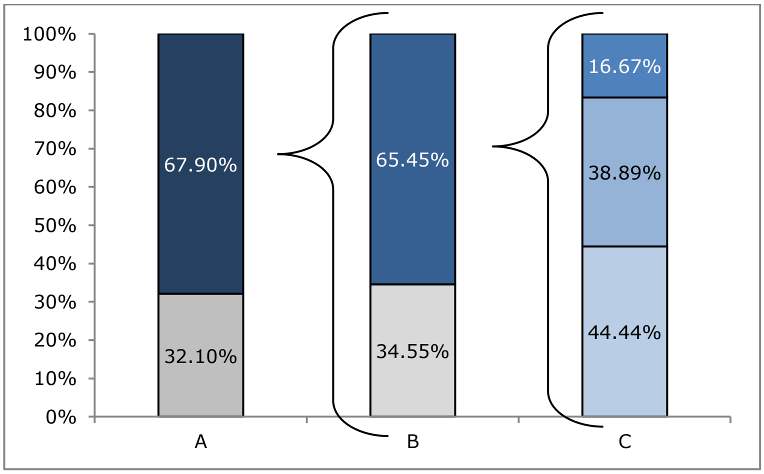

FIGURE 12 Pairwise comparisons (T-C; T-M; C-M) between suitability values. A: dark blue indicates the percent of species that presented differences in at least one pairwise comparison; in grey, species that show no difference between pairwise comparisons. B: in blue, species that presented differences in C-M comparison; in grey, species that presented other differences (T-C and T-M). C: shows the species that presented differences in C-M comparison (per group); dark blue (amphibians), mid blue (reptiles) and light blue (flora)

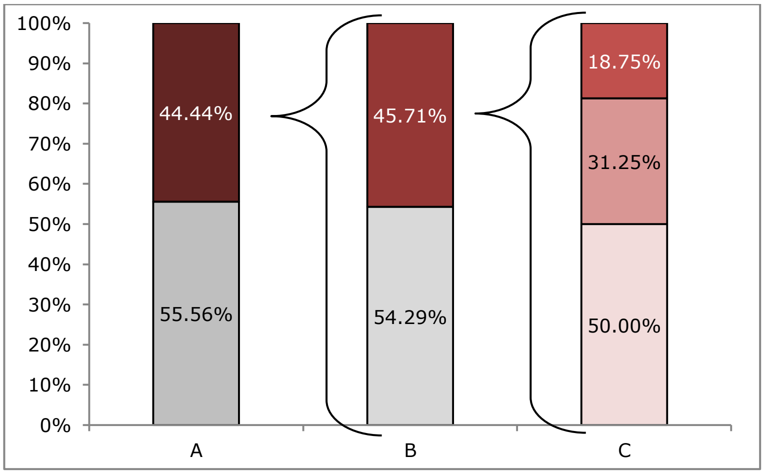

FIGURE 13 Suitability values for C-M comparison only for the species that showed differences in niche similarity test. A: dark red indicates the percent of species that presented dissimilarities between C-M pops; in grey species that show niche similarities. B: in red, species that presented niche dissimilarities and showed differences in suitability values between C-M pops; in grey, species that presented niche dissimilarities and showed no differences in suitability values between C-M pops. C: shows the species that niche dissimilarities and showed differences in suitability values between C-M pops (per group); dark red (amphibians), mid red (reptiles) and light red (flora)

DISCUSSION

The main aim of this study was to develop an effective framework, joining ecological niches models and multivariate analyses, in order to diagnose possible niche climate dissimilarities between species' central and marginal populations. More specifically we divided the species' occurrence records in three datasets and built models and also carried out pairwise comparisons between these datasets (Total, Central and Marginal).

Our results suggested that complex modelling techniques (e.g. Maxent) are better predictors than simple methods (e.g. Bioclim or Domain). However, we did not carry out any comparison since, the background data was not the same for all species and thus these comparisons would not be appropriated (Sillero & Carretero, 2013; VanDerWal, Shoo, Graham, & Williams, 2009). Besides of that, AUC values are sensitive to the proportion between the size of the species distribution range and the size of the study area: the larger this proportion, the higher the value of AUC (Lobo, Jiménez-Valverde, & Real, 2008; Sillero & Carretero, 2013) which can explain the very high mean AUC scores achieved by some studied species.

Based on niche similarity test, our results show that marginal populations of approximately 44% of studied taxa face different climatic situations with respect to the central populations (C-M comparison; Tables A6 and A7 in Appendix). It would support the hypothesis that marginality within the set of habitable climate conditions (i.e. climate niche) could represent an outstanding factor on performance of marginal populations (Lira-Noriega & Manthey, 2014). Using the same definitions of niche expansion and unfilling in previous multi-species studies (i.e. >10%; Hill et al., 2017; Parravicini et al., 2015; Petitpierre et al., 2012; Strubbe et al., 2015), we found niche expansion in 30 species which presented niche dissimilarities between C-M (i.e. Similarity >0.05 in at least one direction;

Tables A6 and A7 in Appendix). These results indicate alteration in species-climate relationships and that the marginal populations of these species inhabit different climate niches in comparison with its central populations. Also, more than a half of these 30 taxa, showed amounts of niche unfilling (Tables A6 and A7 in Appendix) suggesting that their marginal populations are not in climatic equilibrium and could have the potential to further expand their distributions because not all suitable climates are currently exploited (Hill et al., 2017; Petitpierre et al., 2012). Moreover, these results agree with previous works, which used ENM-based techniques showing that abundance values for animal populations usually decreases from the climatic centre towards marginal conditions (see Martinez-Meyer et al., 2013; Yañez-Arenas et al., 2012) and also corroborates the idea that abundance does not often follow a spatial radial pattern (i.e. maximum abundance is located at the geographic center of species' range and decreases towards the borders; Ureña-Aranda et al., 2015). In addition, Lira-Noriega & Manthey (2014) identified a clear pattern of negative relationship between genetic diversity and climatic centre distance for different taxa (insects, plants, birds, mammals and worms). We did not find differences between central and marginal populations for 56% of analysed species. Previous studies also did not find a clear pattern central-marginal related with climatic distance (e.g. Diniz-Filho et al., 2009; Gerst et al., 2011; Pironon et al., 2015). Those results reinforce the idea that there is no "universal rule" in order to identify this issue and corroborate with the idea that a correspondence between geographic and ecological marginality not always is true (Abeli et al., 2014; Lesica & Allendorf, 1995; Soulé, 1973).

Our results showed that in comparison with fauna taxa, a larger number of plants species presented differences between central and marginal populations. Lira-Noriega & Manthey (2014) found a similar pattern (i.e.

larger number of marginal populations in plant species in comparison with animals), these patterns could be explained by the capacity of mobility between target taxa. In this sense, populations of sedentary organisms (as plants) located at the range limits could be more prone to be converted into isolated/relicts populations. Unlike, animals when facing a great environmental stress situation, their primary strategy consists in escaping from such situations through thermoregulatory movements toward more favourable microhabitats (Hampe & Jump, 2011). Moreover, more than 45% of studied species that showed niche dissimilarities between central and marginal pops also are presented differences in predicted suitability values (Fig.12). Less suitable environments available at the periphery could be translated into lower survival potential for the marginal populations (i.e. higher inbreeding phenomena).

It is normal that during species' range shifts (i.e. contractions and retractions), populations located at the border limit of a species’ distribution could be converted into relict populations (Hampe & Jump, 2011). Jointly, the territorial ecological irregularities (i.e. randomness of dispersions, variability in resources, predation phenomena) these phenomena allow the existence of small enclaves of suitable environmental conditions within an unsuitable regional climate (i.e. microrefugia; Hampe & Jump, 2011). Although, not all microrefugia hold relict populations (i.e. marginal; Ashcroft et al., 2012), they have an intrinsic value for conservation in providing unusual and stable climates for species (Ashcroft et al., 2012) which can be extremely significant to marginal populations. Thus, once microrefugia are located, they should be targeted for inclusion in the reserve system (Ashcroft et al. 2012), especially those holding marginal populations. In addition, marginal populations may represent valuable resource in conserving biodiversity. Some studies showed that in some case, species' marginal populations persist better in the periphery than in the centre of their distribution and also some populations contain high genetic diversity which may represent opportunities to conserve species faced with high intensity and widespread changes to their environment (e.g. Channell, 2004; Channell & Lomolino, 2000; Lomolino & Channell, 1995; Vucetich & Waite, 2003). Also, poleward marginal populations may represent our best chance to conserve those species threatened by global climate change, since many studies have already documented poleward shifts in many species' distributions (Channell, 2004). In this sense, Velo-Antón, Martínez-Freiría, Pereira, Crochet, & Brito (2018) recently found a lineage diversification in spiny-footed lizard (*Acanthodactylus aureus*) facilitated by the existence of microrefugia climatically stable.

We believe that apart of considering the foreseeable disturbances caused by the climatic change in the distribution of species, the microrefugia locations also should be considered when planning the creation of new Protected Areas (PAs) or enlarging the existents ones. If microrefugia protect persisting populations they may be able to recolonize the surrounding landscape when favourable conditions for their survival and reproduction returned (Noss 2001). Including marginal populations could be a measure conserve more species per unit area than nature reserves near the center of the species' distributions (Araújo & Williams, 2001) and some conservation programmes have included marginal sites for re-introduction and/or to search undiscovered populations (Channell & Lomolino, 2000; Lomolino & Channell, 1995). Since resources available for conservation are limited (Araújo & Williams, 2001; Channell, 2004), to know whether the species' populations are located at the margin of their optimal ecological niche would be of great importance before spend these scarce resources and start conservation programs. Our framework could be useful as a preliminary tool to address this issue (especially for widely distributed taxa) and to assess the distribution patterns of species' populations (e.g. threatened populations) in a spatially explicit fashion, with the potential to optimize evaluation efforts in the field. Besides of the knowledge of the target organism and/or of the study area, it only requires the species occurrence data (especially important when only occurrence data are available) and environmental predictors (as occurrence data, normally are available in public databases) which can exert direct or indirect effects on species. It has simple calculation, is effective for large regions and it is based on ecological foundations.

We are aware that our modelling framework has some limitations. Firstly, this approach is a correlative, static method which associates the species occurrence with a particular state of the environment, thus it does not capture the dynamic nature of populations' fluctuations through time (Botkin et al., 2007; Yañez-Arenas et al., 2012). Also, model-based predictions tend to overlook the specific fine scale features habitat and jointly with spatial autocorrelation may overestimate the potential species distribution and inflate the model's predictive power (Chapman, 2010; Sinclair et al., 2010). It is especially true for high altitude plants which experience microclimatic environment completely different from atmospheric temperatures due complex relationships between its lifeform (biotype), topography, snow accumulation and phases of its life cycle (Körner & Hiltbrunner, 2017). Furthermore, our models were not capable to predict these small scale factors which are locally acting and leading the species' distribution in marginal populations (Normand et al., 2009). Finally, any representation of the ecological niche may be only partial, as in most instances, it is very difficult to consider all the axes of the multidimensional niche (Martínez-Gutiérrez, Martínez-Meyer, Palomares, & Fernández, 2018; Yañez-Arenas, Guevara, Martínez-Meyer, Mandujano, & Lobo, 2014).

In summary, the present work aims to be a theoretical basis on which to advance including other types of factors to achieve a better spatial approximation (e.g. biotic interactions, topography, human influence and populations’ fluctuations through time; Sinclair et al., 2010). This would allow a better understanding of the complex network of factors that occur in marginal species’ populations (Abeli et al., 2014).

We achieved to find climatic niche dissimilarities in 35 of 81 studied endemic European taxa. From these 35, 16 also presented differences between suitability values, these results could be a first step before to design conservation strategies. We proposed a standardized and effective framework which could be applicable for any target species in any study area. We think that our framework should be interesting for conservationist managers, since, it only requires the occurrence data and the relevant environmental data, besides of the previous knowledge about the target group and its calculation is simple.

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APPENDIX CHAPTER V

TABLE A1

List of studied taxa. Numbers in parentheses refer to species complexes which subsume species which distribution records cannot be unambiguously assigned in the available database (see footnotes for detailed explanations)

Taxa
AMPHIBIANS
Alytidae
Alytes cisternasii Boscá, 1879
Alytes dickhilleni Arntzen and García-París, 1995
Alytes obstetricans (Laurenti, 1768)
Discoglossus galganoi Capula, Nascetti, Lanza, Bullini and Crespo, 1985
Hylidae
Hyla intermedia Boulenger, 1882
Pelobatidae
Pelobates cultripes(Cuvier, 1829)
Pelodytidae
*Pelodytes*complex (1)
Plethodontidae
Speleomantes italicus (Dunn, 1923)
Ranidae
Pelophylax perezi (López-Seoane, 1885)
Rana graeca Boulenger, 1891
Rana iberica Boulenger, 1879
Rana italica Dubois, 1987
Rana latastei Boulenger, 1879
Salamandridae
Calotriton asper (Dugès, 1852)
Chioglossa lusitanica Bocage, 1864
Lissotriton boscai (Lataste in Tourneville, 1879)
Lissotriton helveticus (Razoumovsky, 1789)
Lissotriton italicus (Peracca, 1898)
Salamandra atra Laurenti, 1768
Speleomantes italicus (Dunn, 1923)
Triturus complex (2)
REPTILES
Blanidae
Blanus complex (3)
Colubridae
Elaphe quatuorlineata (Bonnaterre, 1790)
Hierophis gemonensis (Laurenti, 1768)
Hierophis viridiflavus (Lacépède, 1789)
Zamenis scalaris (Schinz, 1822)
Lacertidae
Algyroides moreoticus Bibron & Bory, 1833
Algyroides nigropunctatus (Duméril & Bibron, 1839)

Dalmatolacerta oxycephala (Schlegel, 1839)
Hellenolacerta graeca (Bedriaga, 1886)
Iberolacerta monticola (Boulenger, 1905)
Lacerta bilineata Daudin, 1802
Lacerta schreiberi Bedriaga, 1878
Podarcis bocagei (Seoane, 1885)
Podarcis carbonelli Perez Mellado, 1981
Podarcis erhardii (Bedriaga, 1882)
Podarcis melisellensis (Braun, 1877)
Podarcis peloponnesiacus (Bibron & Bory, 1833)
Podarcis siculus (Rafinesque-schmaltz, 1810)
Podarcis tiliguerta (Gmelin, 1789)
Podarcis waglerianus Gistel, 1868
Psammodromus hispanicus Fitzinger, 1826
Timon lepidus (Daudin, 1802)

Scincidae

Chalcides bedriagai (Bosca, 1880)
Chalcides striatus (Cuvier, 1829)

Testudinidae

Testudo hermanni Gmelin, 1789

Viperidae

Vipera aspis (Linnaeus, 1758)
Vipera seoanei Lataste, 1879

FLORA

Alismataceae

Alisma wahlenbergii (Holmb.) Juz.
Luronium natans (L.) Raf.

Amaryllidaceae

Allium stearnii Pastor & Valdés
Allium suaveolens Jacq.
Narcissus longispathus Degen & Hervier ex Pugsley
Narcissus triandrus L.

Apiaceae

Carum verticillatum (L.) W.D.J. Koch
Eryngium galioides Lam.

Brassicaceae

Diplotaxis ilorcitana (Sennen) Aedo, Mart.-Laborde & Muñoz Garm.
Lepidium villarsii Gren. & Godr.

Euphorbiaceae

Euphorbia nevadensis Boiss. & Reut.

Fabaceae

Astragalus arenarius L.

Hypericaceae

Hypericum elodes L.

Marsileaceae

Marsilea batardae Launert

Orchidaceae

Chamorchis alpina (L.) Rich.

Dactylorhiza lapponica (Laest. ex Hartm.) Soó

Dactylorhiza sambucina (L.) Soó

Epipactis leptochila (Godfery) Godfery

Epipactis muelleri Godfery

Epipactis phyllanthes G.E.Sm.

Epipactis purpurata Sm.

Gymnadenia odoratissima (L.) Rich.

Gymnadenia rhellicani (Teppner & E.Klein) Teppner & E.Klein

Ophrys bertolonii Moretti

Ophrys insectifera L.

Plantaginaceae

Callitriche cophocarpa Sendtn.

Callitriche platycarpa Kütz.

Poaceae

*Calamagrostis chalybaea*Fr.

Festuca summilusitana Franco & Rocha Afonso

Primulaceae

Soldanella villosa Darracq

Ranunculaceae

Pulsatilla grandis Wender.

Ranunculus peltatus Schrank

Rosaceae

Prunus ramburii Boiss.

Saxifragaceae

Saxifraga osloensis Knaben

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(1) *Pelodytes* complex includes records of *P. ibericus*, *P. punctatus*, and two undescribed candidate species of the Iberian Peninsula; which are not distinguished in the available databases.

(2) *Triturus* complex includes records of *T. marmoratus* and *T. pygmaeus* which are not distinguished in the available databases.

(3) *Blanus* complex includes records of *B. cinereus* and *B. mariae* which are not distinguished in the available databases.

TABLE A2

Total number of records of fauna species (10 × 10 km UTM squares). T (Total), C (Central) and M (Marginal) correspond to the record numbers per species of each dataset. AUC training and testing values for Maxent (mean 10 replicates) and AUC testing values for BIOCLIM and DOMAIN models

				AUC values											
Species	Number of records			Training			Testing								
				Maxent			Maxent			BIOCLIM			DOMAIN		
	T	C	M	T	C	M	T	C	M	T	C	M	T	C	M
AMPHIBIANS															
Alytidae															
Alytes cisternasii	1119	669	450	0.973	0.985	0.977	0.972	0.984	0.976	0.995	0.995	0.980	0.988	0.991	0.971
Alytes dickhilleni	169	94	75	0.996	0.998	0.996	0.996	0.997	0.996	0.994	0.914	0.828	0.993	0.992	0.992
Alytes obstetricans	3749	2074	1675	0.912	0.943	0.938	0.911	0.943	0.936	0.886	0.908	0.869	0.798	0.898	0.756
Discoglossus galganoi	1787	943	844	0.955	0.974	0.964	0.955	0.973	0.962	0.958	0.973	0.943	0.949	0.965	0.918
Hylidae															
Hyla intermedia	870	539	331	0.969	0.979	0.977	0.966	0.977	0.975	0.950	0.977	0.922	0.910	0.963	0.889
Pelobatidae															
Pelobates cultripes	2151	1323	828	0.946	0.945	0.963	0.945	0.946	0.963	0.958	0.986	0.961	0.970	0.977	0.954
Pelodytidae															
*Pelodytes*complex	2144	1300	844	0.939	0.942	0.954	0.939	0.942	0.951	0.902	0.936	0.921	0.913	0.944	0.917
Plethodontidae															
Speleomantes italicus	104	61	43	0.997	0.997	0.996	0.996	0.996	0.995	0.998	0.874	0.932	0.995	0.996	0.958
Ranidae															
Pelophylax perezi	5413	3061	2352	0.900	0.895	0.916	0.900	0.893	0.915	0.947	0.977	0.935	0.947	0.982	0.926
Rana graeca	204	138	66	0.988	0.989	0.983	0.985	0.988	0.977	0.930	0.955	0.835	0.928	0.959	0.929
Rana iberica	856	532	324	0.981	0.979	0.984	0.980	0.978	0.984	0.979	0.993	0.961	0.985	0.992	0.972
Rana italica	548	342	206	0.982	0.980	0.990	0.982	0.980	0.989	0.972	0.973	0.967	0.958	0.975	0.959
Rana latastei	220	137	83	0.994	0.993	0.996	0.994	0.992	0.996	0.931	0.968	0.872	0.990	0.995	0.981

				AUC values											
Species	Number of records			Training			Testing								
				Maxent			Maxent			BIOCLIM			DOMAIN		
	T	C	M	T	C	M	T	C	M	T	C	M	T	C	M
Salamandridae															
Calotriton asper	231	137	94	0.992	0.995	0.990	0.991	0.993	0.989	0.960	0.936	0.985	0.965	0.981	0.960
Chioglossa lusitanica	384	221	163	0.991	0.995	0.992	0.991	0.995	0.991	0.983	0.983	0.961	0.994	0.997	0.990
Lissotriton boscai	1514	870	644	0.967	0.966	0.972	0.965	0.965	0.971	0.967	0.981	0.962	0.971	0.989	0.956
Lissotriton helveticus	7602	5314	2288	0.895	0.916	0.900	0.894	0.915	0.899	0.939	0.982	0.908	0.921	0.972	0.907
Lissotriton italicus	257	153	104	0.991	0.991	0.991	0.989	0.990	0.990	0.963	0.992	0.918	0.979	0.985	0.977
Salamandra atra	662	452	210	0.982	0.982	0.988	0.980	0.981	0.985	0.956	0.949	0.951	0.973	0.978	0.976
Speleomantes italicus	104	61	43	0.997	0.997	0.996	0.996	0.996	0.995	0.998	0.874	0.932	0.995	0.996	0.958
Triturus complex	2089	1469	620	0.945	0.941	0.960	0.944	0.940	0.960	0.931	0.961	0.935	0.953	0.967	0.904
REPTILES															
Blanidae															
Blanus complex	1798	1090	708	0.959	0.975	0.968	0.959	0.974	0.965	0.979	0.984	0.949	0.976	0.989	0.963
Colubridae															
Elaphe quatuorlineata	891	489	402	0.976	0.982	0.983	0.975	0.980	0.982	0.945	0.960	0.954	0.932	0.956	0.938
Hierophis gemonensis	265	179	86	0.993	0.995	0.990	0.991	0.994	0.987	0.932	0.959	0.782	0.985	0.992	0.936
Hierophis viridiflavus	2742	1727	1015	0.926	0.950	0.946	0.927	0.949	0.944	0.888	0.906	0.898	0.850	0.868	0.895
Zamenis scalaris	3185	2010	1175	0.929	0.922	0.950	0.928	0.920	0.949	0.956	0.969	0.951	0.953	0.975	0.953
Lacertidae															
Algyroides moreoticus	132	81	51	0.998	0.999	0.999	0.998	0.998	0.998	0.977	0.999	0.854	0.993	0.992	0.999
Algyroides nigropunctatus	277	166	111	0.992	0.993	0.990	0.989	0.988	0.992	0.898	0.920	0.970	0.846	0.862	0.915
Dalmatolacerta oxycephala	92	60	32	0.994	0.998	0.993	0.992	0.997	0.984	0.796	0.733	0.843	0.973	0.991	0.896
Hellenolacerta graeca	137	85	52	0.998	0.999	0.998	0.998	0.999	0.996	0.996	0.940	0.886	0.998	0.997	0.989
Iberolacerta monticola	140	82	58	0.996	0.996	0.996	0.996	0.996	0.995	0.961	0.967	0.947	0.991	0.998	0.993
Lacerta bilineata	3336	2069	1267	0.909	0.912	0.940	0.908	0.911	0.938	0.871	0.885	0.920	0.849	0.875	0.925

				AUC values											
Species	Number of records			Training			Testing								
				Maxent			Maxent			BIOCLIM			DOMAIN		
	T	C	M	T	C	M	T	C	M	T	C	M	T	C	M
Lacerta schreiberi	963	607	356	0.977	0.975	0.981	0.976	0.974	0.980	0.969	0.977	0.956	0.969	0.986	0.935
Podarcis bocagei	464	283	181	0.991	0.989	0.992	0.990	0.988	0.992	0.992	0.972	0.957	0.995	1.000	0.992
Podarcis carbonelli	115	84	31	0.997	0.997	0.997	0.997	0.996	0.996	0.886	0.885	0.995	0.995	0.998	0.993
Podarcis erhardii	595	449	146	0.991	0.997	0.989	0.991	0.997	0.984	0.960	0.996	0.893	0.976	0.971	0.926
Podarcis melisellensis	265	163	102	0.995	0.995	0.994	0.995	0.994	0.990	0.879	0.955	0.940	0.969	0.988	0.961
Podarcis peloponnesiacus	164	96	68	0.998	0.997	0.998	0.997	0.997	0.997	0.993	0.995	0.925	0.994	0.966	0.999
Podarcis siculus	1534	906	628	0.963	0.961	0.974	0.962	0.960	0.971	0.967	0.969	0.955	0.957	0.996	0.959
Podarcis tiliguerta	124	69	55	0.996	0.997	0.996	0.996	0.997	0.996	0.831	0.909	0.948	0.995	0.999	0.989
Podarcis waglerianus	135	79	56	0.997	0.997	0.998	0.997	0.996	0.998	0.978	0.965	0.888	0.999	0.997	1.000
Psammodromus hispanicus	1699	1149	550	0.955	0.950	0.971	0.953	0.951	0.970	0.956	0.982	0.964	0.974	0.980	0.952
Timon lepidus	4530	2866	1664	0.909	0.898	0.932	0.907	0.898	0.931	0.948	0.972	0.938	0.952	0.974	0.934
Scincidae															
Chalcides bedriagai	888	473	415	0.970	0.982	0.980	0.969	0.981	0.978	0.951	0.966	0.916	0.972	0.985	0.961
Chalcides striatus	1620	1102	518	0.954	0.969	0.971	0.953	0.969	0.972	0.942	0.967	0.913	0.940	0.958	0.945
Testudinidae															
Testudo hermanni	1722	1225	497	0.961	0.964	0.971	0.956	0.962	0.970	0.936	0.939	0.940	0.866	0.859	0.940
Viperidae															
Vipera aspis	2310	1514	796	0.924	0.924	0.950	0.922	0.923	0.947	0.877	0.860	0.911	0.809	0.807	0.896
Vipera seoanei	422	243	179	0.990	0.988	0.993	0.990	0.988	0.992	0.984	0.962	0.983	0.980	0.981	0.990

TABLE A3

Total number of records of flora species (10 × 10 km UTM squares). T (Total), C (Central) and M (Marginal) corresponds to the record numbers per species of each dataset. AUC training and testing values for Maxent (mean 10 replicates) and AUC testing values for BIOCLIM and DOMAIN models

Species	Number of records			AUC values											
				Training			Testing								
				Maxent			Maxent			BIOCLIM			DOMAIN		
	T	C	M	T	C	M	T	C	M	T	C	M	T	C	M
Alismataceae															
Alisma wahlenbergii	395	244	151	0.994	0.996	0.994	0.989	0.997	0.994	0.992	0.915	0.967	0.990	0.998	0.998
Luronium natans	2224	1434	790	0.944	0.959	0.943	0.944	0.958	0.939	0.948	0.972	0.892	0.915	0.980	0.904
Amaryllidaceae															
Allium stearnii	174	94	80	0.987	0.992	0.990	0.984	0.990	0.985	0.971	0.869	0.936	0.957	0.979	0.957
Allium suaveolens	291	238	53	0.993	0.996	0.989	0.992	0.996	0.981	0.985	0.998	0.999	0.976	0.995	0.989
Narcissus longispathus	161	111	50	0.997	0.997	0.996	0.995	0.997	0.991	0.965	0.931	0.997	0.990	0.994	0.986
Narcissus triandrus	719	506	213	0.978	0.978	0.976	0.976	0.977	0.975	0.940	0.978	0.902	0.956	0.966	0.958
Apiaceae															
Carum verticillatum	5750	3477	2273	0.918	0.951	0.934	0.916	0.950	0.933	0.926	0.964	0.922	0.918	0.954	0.908
Eryngium galioides	261	139	122	0.989	0.995	0.992	0.988	0.994	0.990	0.962	0.885	0.913	0.977	0.989	0.958
Brassicaceae															
Diplotaxis ilorcitana	300	222	78	0.995	0.998	0.994	0.995	0.998	0.993	0.986	0.988	0.964	0.993	0.999	0.988
Lepidium villarsii	131	81	50	0.988	0.991	0.994	0.986	0.990	0.982	0.828	0.908	0.954	0.855	0.960	0.928
Euphorbiaceae															
Euphorbia nevadensis	292	188	104	0.988	0.994	0.988	0.988	0.992	0.980	0.978	0.920	0.958	0.967	0.984	0.965
Fabaceae															
Astragalus arenarius	333	295	38	0.981	0.993	0.934	0.971	0.992	0.918	0.935	0.978	0.725	0.942	0.992	0.896
Hypericaceae															
Hypericum elodes	4264	3336	928	0.932	0.951	0.955	0.931	0.950	0.951	0.949	0.967	0.916	0.920	0.953	0.893

				AUC values											
Species	Number of records			Training			Testing								
				Maxent			Maxent			BIOCLIM			DOMAIN		
	T	C	M	T	C	M	T	C	M	T	C	M	T	C	M
Marsileaceae															
Marsilea batardae	166	105	61	0.995	0.996	0.995	0.994	0.995	0.993	0.976	0.952	0.996	0.990	0.997	0.994
Orchidaceae															
Chamorchis alpina	1670	1381	289	0.966	0.976	0.985	0.964	0.975	0.985	0.948	0.984	0.931	0.930	0.966	0.865
Dactylorhiza lapponica	1022	728	294	0.956	0.981	0.970	0.947	0.978	0.963	0.888	0.992	0.846	0.843	0.962	0.783
Dactylorhiza sambucina	3076	2451	625	0.935	0.967	0.958	0.931	0.968	0.956	0.934	0.969	0.928	0.912	0.950	0.912
Epipactis leptochila	598	323	275	0.963	0.982	0.966	0.961	0.982	0.965	0.953	0.962	0.938	0.910	0.956	0.874
Epipactis muelleri	1747	974	773	0.950	0.974	0.954	0.947	0.972	0.952	0.941	0.972	0.952	0.904	0.975	0.893
Epipactis phyllanthes	249	130	119	0.978	0.981	0.990	0.972	0.977	0.986	0.963	0.948	0.967	0.909	0.950	0.948
Epipactis purpurata	775	493	282	0.967	0.980	0.979	0.965	0.978	0.969	0.954	0.962	0.933	0.928	0.953	0.945
Gymnadenia odoratissima	1627	1313	314	0.946	0.962	0.954	0.943	0.962	0.942	0.890	0.933	0.870	0.750	0.861	0.774
Gymnadenia rhellicani	295	204	91	0.990	0.994	0.993	0.989	0.994	0.991	0.940	0.924	0.898	0.937	0.970	0.973
Ophrys bertolonii	397	250	147	0.983	0.984	0.984	0.979	0.983	0.980	0.954	0.931	0.849	0.933	0.956	0.907
Ophrys insectifera	6665	3469	3196	0.898	0.900	0.935	0.896	0.900	0.930	0.890	0.946	0.912	0.868	0.912	0.891
Plantaginaceae															
Callitriche cophocarpa	8086	5835	2251	0.875	0.937	0.880	0.873	0.936	0.881	0.911	0.977	0.815	0.871	0.953	0.742
Callitriche platycarpa	15479	10801	4678	0.890	0.953	0.866	0.889	0.953	0.867	0.976	0.996	0.948	0.946	0.986	0.924
Poaceae															
Calamagrostis chalybaea	765	493	272	0.987	0.993	0.987	0.986	0.991	0.983	0.976	0.992	0.973	0.973	0.988	0.962
Festuca summilusitana	171	91	80	0.996	0.998	0.995	0.996	0.998	0.994	0.996	0.940	0.990	0.998	0.993	0.988
Primulaceae															
Soldanella villosa	176	147	29	0.996	0.998	0.989	0.997	0.998	0.974	0.998	0.983	1.000	0.998	0.999	0.982
Ranunculaceae															
Pulsatilla grandis	269	193	76	0.987	0.987	0.987	0.980	0.987	0.982	0.988	0.987	0.960	0.988	1.000	0.952

				AUC values											
				Training			Testing								
Species	Number of records			Maxent			Maxent			BIOCLIM			DOMAIN		
	T	C	M	T	C	M	T	C	M	T	C	M	T	C	M
Ranunculus peltatus	1068	782	286	0.955	0.973	0.947	0.948	0.973	0.936	0.936	0.984	0.861	0.925	0.983	0.888
Rosaceae															
Prunus ramburii	304	206	98	0.999	0.999	0.998	0.998	0.998	0.998	1.000	0.988	0.974	0.999	0.986	1.000
Saxifragaceae															
Saxifraga osloensis	2097	706	1391	0.992	0.994	0.994	0.991	0.993	0.994	0.995	0.996	0.998	0.987	0.995	0.997

TABLE A4

List of climatic variables from WorldClim data (Fick & Hijmans, 2017; www.worldclim.org) used in BIOCLIM, DOMAIN and Maxent models. The seven variables used in all models are marked with an asterisk (*)

Code	Description
BIO1	Annual Mean Temperature
BIO2	Mean Diurnal Range*
BIO3	Isothermality
BIO4	Temperature Seasonality
BIO5	Max Temperature of Warmest Month*
BIO6	Min Temperature of Coldest Month*
BIO7	Temperature Annual Range
BIO8	Mean Temperature of Wettest Quarter*
BIO9	Mean Temperature of Driest Quarter
BIO10	Mean Temperature of Warmest Quarter
BIO11	Mean Temperature of Coldest Quarter
BIO12	Annual Precipitation
BIO13	Precipitation of Wettest Month
BIO14	Precipitation of Driest Month
BIO15	Precipitation Seasonality*
BIO16	Precipitation of Wettest Quarter
BIO17	Precipitation of Driest Quarter*
BIO18	Precipitation of Warmest Quarter*
BIO19	Precipitation of Coldest Quarter

TABLE A5

Pearson's correlation coefficients of the association among the variables used in models. Variables with cross-correlation coefficient values of r lower than 0.75were selected

Code	BIO1	BIO2	BIO3	BIO4	BIO5	BIO6	BIO7	BIO8	BIO9	BIO10	BIO11	BIO12	BIO13	BIO14	BIO15	BIO16	BIO17	BIO18	BIO19
BIO1	**1.000**																		
BIO2	0.376	**1.000**																	
BIO3	0.750	0.354	**1.000**																
BIO4	-0.587	0.179	-0.833	**1.000**															
BIO5	0.744	0.711	0.307	0.081	**1.000**														
BIO6	0.885	0.064	0.866	-0.886	0.365	**1.000**													
BIO7	-0.505	0.341	-0.737	0.981	0.190	-0.845	**1.000**												
BIO8	0.190	0.305	-0.290	0.456	0.554	-0.151	0.477	**1.000**											
BIO9	0.835	0.269	0.822	-0.708	0.486	0.863	-0.631	-0.216	**1.000**										
BIO10	0.841	0.596	0.377	-0.060	0.977	0.503	0.031	0.524	0.571	**1.000**									
BIO11	0.935	0.183	0.876	-0.834	0.475	0.989	-0.770	-0.078	0.883	0.600	**1.000**								
BIO12	0.153	-0.315	0.399	-0.567	-0.297	0.398	-0.590	-0.494	0.330	-0.202	0.344	**1.000**							
BIO13	0.141	-0.275	0.361	-0.517	-0.266	0.363	-0.535	-0.431	0.304	-0.183	0.314	0.950	**1.000**						
BIO14	0.107	-0.349	0.331	-0.516	-0.330	0.345	-0.554	-0.419	0.206	-0.232	0.287	0.860	0.710	**1.000**					
BIO15	-0.061	0.107	-0.054	0.091	0.036	-0.090	0.115	0.036	-0.016	-0.002	-0.079	-0.115	0.157	-0.510	**1.000**				
BIO16	0.133	-0.295	0.365	-0.526	-0.285	0.363	-0.546	-0.450	0.302	-0.199	0.312	0.964	0.993	0.728	0.133	**1.000**			
BIO17	0.153	-0.322	0.376	-0.550	-0.296	0.390	-0.581	-0.439	0.270	-0.197	0.335	0.895	0.749	0.986	-0.486	0.764	**1.000**		
BIO18	-0.283	-0.446	-0.137	-0.129	-0.524	-0.103	-0.193	-0.104	-0.313	-0.467	-0.157	0.638	0.615	0.684	-0.128	0.622	0.662	**1.000**	
BIO19	0.307	-0.204	0.532	-0.620	-0.129	0.522	-0.625	-0.544	0.541	-0.038	0.479	0.915	0.875	0.717	-0.056	0.889	0.763	0.304	**1.000**

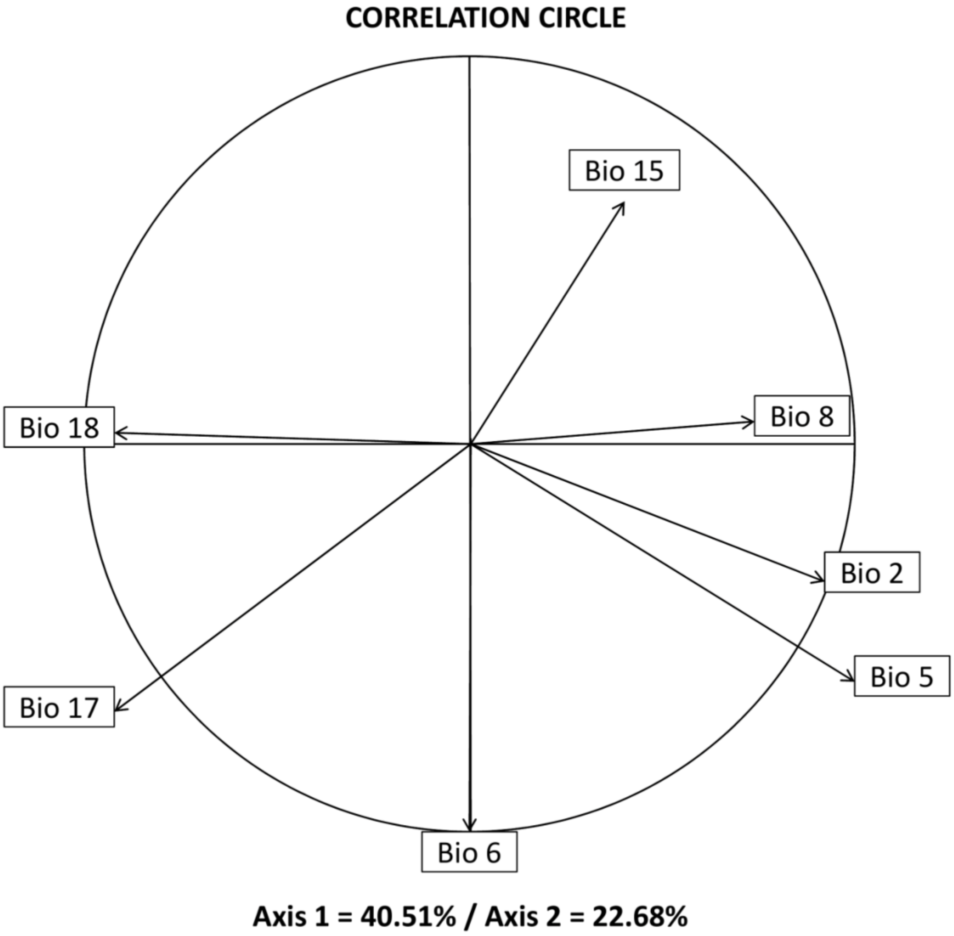


FIGURE A1 Seven climatic variables are distributed along the first two axes (axis 1: 40.51%, axis 2: 22.68%) of the principal components analysis

TABLE A6

Pairwise comparison of niches in climatic space (PCA) between the different datasets for fauna species. Comparisons (C) :Total-Central (T-C), Total-Marginal (T-M) and Central-Marginal (C-M). Niche shift metrics: Expansion (E), Stability (S) and Unfilling (U). Values range from 0 to 1, with 1 being total niche expansion or unfilling and 0 reflecting no change between ranges. Bold values in these columns indicate that the amount of expansion or unfilling was above 10%. Niche equivalency and similarity tests with 100 replication between datasets per species (T-C, T-M and C-M). Bold indicates significant values (*p* <0.05) in these columns

Species	C	E	S	U	D	P	Similarity 2 -> 1	Similarity 1 -> 2
AMPHIBIANS								
Alytidae								
Alytes cisternasii	T-C	**8.211E+09**	**1.000**	**0.136**	0.666	1.000	**0.020**	**0.010**
	T-M	0.020	**0.980**	0.001	0.581	1.000	0.059	**0.020**
	C-M	**0.362**	**0.638**	0.001	0.265	1.000	0.119	0.089
Alytes dickhilleni	T-C	0.000	**1.000**	**0.101**	0.738	0.872	**0.010**	**0.020**
	T-M	0.039	**0.961**	0.009	0.699	0.901	**0.020**	**0.020**
	C-M	**0.255**	**0.745**	0.007	0.459	0.990	**0.040**	**0.040**
Alytes obstetricans	T-C	0.000	**1.000**	0.056	0.727	1.000	**0.010**	**0.010**
	T-M	0.004	**0.996**	0.085	0.543	1.000	0.257	0.178
	C-M	**0.128**	**0.872**	**0.151**	0.281	1.000	**0.030**	**0.040**
Discoglossus galganoi	T-C	0.000	**1.000**	**0.211**	0.468	1.000	0.119	0.089
	T-M	0.007	**0.993**	0.003	0.717	1.000	**0.010**	**0.010**
	C-M	**0.441**	**0.559**	0.004	0.215	1.000	**0.020**	**0.020**
Hylidae								
Hyla intermedia	T-C	0.000	**1.000**	**0.162**	0.620	1.000	0.149	0.109
	T-M	0.010	**0.990**	0.020	0.394	1.000	0.079	0.079
	C-M	**0.398**	**0.602**	0.020	0.200	1.000	0.149	0.168
Pelobatidae								
Pelobates cultripes	T-C	0.000	**1.000**	**0.128**	0.493	1.000	0.079	0.059
	T-M	0.015	**0.985**	0.000	0.601	1.000	0.109	**0.040**
	C-M	**0.359**	**0.641**	**4.208E +09**	0.174	1.000	0.267	0.317
Pelodytidae								
Pelodytes complex	T-C	0.000	**1.000**	0.099	0.642	1.000	**0.010**	**0.010**
	T-M	0.008	**0.992**	0.062	0.489	1.000	0.119	0.109
	C-M	**0.264**	**0.736**	0.097	0.148	1.000	0.446	0.426
Plethodontidae								
Speleomantes italicus	T-C	0.000	**1.000**	**0.103**	0.769	0.743	**0.010**	**0.010**
	T-M	0.044	**0.956**	0.018	0.750	0.693	**0.020**	**0.010**
	C-M	**0.235**	**0.765**	0.020	0.543	1.000	**0.020**	**0.020**

Species	C	E	S	U	D	P	Similarity 2 -> 1	Similarity 1 -> 2
Ranidae								
Pelophylax perezi	T-C	0.000	**1.000**	0.081	0.613	1.000	**0.010**	0.059
	T-M	0.004	**0.996**	0.000	0.683	1.000	0.069	0.069
	C-M	**0.201**	**0.799**	0.000	0.316	1.000	0.119	0.109
Rana graeca	T-C	0.000	**1.000**	**0.275**	0.544	1.000	**0.010**	**0.010**
	T-M	0.055	**0.945**	0.066	0.504	1.000	**0.020**	**0.030**
	C-M	**0.697**	**0.303**	0.050	0.111	1.000	0.257	0.228
Rana iberica	T-C	0.000	**1.000**	0.081	0.732	1.000	**0.010**	**0.010**
	T-M	0.004	**0.996**	0.036	0.707	1.000	**0.030**	**0.030**
	C-M	**0.220**	**0.780**	0.042	0.466	1.000	**0.010**	**0.020**
Rana italica	T-C	0.000	**1.000**	**0.162**	0.739	0.812	**0.050**	**0.030**
	T-M	0.029	**0.971**	0.055	0.536	0.980	0.059	0.069
	C-M	**0.406**	**0.594**	0.069	0.395	1.000	0.168	0.089
Rana latastei	T-C	0.000	**1.000**	**0.170**	0.471	0.990	**0.040**	**0.030**
	T-M	0.030	**0.970**	0.036	0.607	0.178	**0.040**	**0.030**
	C-M	**0.415**	**0.585**	0.045	0.194	1.000	0.069	0.099
Salamandridae								
Calotriton asper	T-C	0.044	**0.956**	0.004	0.785	0.911	**0.010**	**0.010**
	T-M	0.004	**0.996**	**0.165**	0.607	1.000	**0.050**	**0.020**
	C-M	0.011	**0.989**	**0.288**	0.399	1.000	**0.020**	0.059
Chioglossa lusitanica	T-C	0.000	**1.000**	**0.163**	0.726	1.000	**0.010**	**0.010**
	T-M	0.035	**0.965**	0.011	0.712	1.000	**0.030**	**0.040**
	C-M	**0.394**	**0.606**	0.013	0.453	1.000	**0.020**	**0.030**
Lissotriton boscai	T-C	0.000	**1.000**	**0.146**	0.485	1.000	**0.030**	**0.030**
	T-M	0.017	**0.983**	0.014	0.496	1.000	0.079	**0.050**
	C-M	**0.376**	**0.624**	0.023	0.151	1.000	**0.050**	0.079
Lissotriton helveticus	T-C	0.000	**1.000**	**0.123**	0.613	1.000	**0.010**	**0.010**
	T-M	0.009	**0.991**	0.004	0.543	1.000	0.099	0.119
	C-M	**0.426**	**0.574**	0.005	0.188	1.000	0.089	0.158
Lissotriton italicus	T-C	0.000	**1.000**	**0.168**	0.639	0.614	**0.020**	**0.020**
	T-M	0.029	**0.971**	**0.120**	0.561	0.921	**0.030**	**0.050**
	C-M	**0.362**	**0.638**	**0.182**	0.298	0.970	0.109	0.129
Salamandra atra	T-C	0.000	**1.000**	0.035	0.818	0.990	**0.020**	**0.030**
	T-M	0.001	**0.999**	**0.107**	0.619	1.000	**0.050**	**0.040**
	C-M	**0.105**	**0.895**	**0.154**	0.443	1.000	**0.040**	**0.050**
Triturus marmoratus complex	T-C	0.001	**0.999**	0.047	0.486	1.000	0.089	0.129
	T-M	0.001	**0.999**	0.047	0.486	1.000	**0.050**	0.069
	C-M	0.001	**0.999**	0.047	0.486	1.000	0.149	0.109
REPTILES								
Blanidae								
Blanus complex	T-C	0.000	**1.000**	0.050	0.735	1.000	**0.010**	**0.010**
	T-M	0.009	**0.991**	0.013	0.509	1.000	0.089	0.079
	C-M	**0.144**	**0.856**	0.018	0.284	1.000	0.158	0.099

Species	**C**	**E**	**S**	**U**	**D**	**P**	**Similarity 2 -> 1**	**Similarity 1 -> 2**
Colubridae								
Elaphe quatuorlineata	T-C	0.000	**1.000**	**0.197**	0.210	1.000	0.376	0.426
	T-M	0.019	**0.981**	0.013	0.764	1.000	**0.020**	**0.010**
	C-M	**0.388**	**0.612**	0.012	0.098	1.000	0.129	0.109
Hierophis gemonensis	T-C	0.000	**1.000**	**0.218**	0.577	1.000	**0.010**	**0.010**
	T-M	0.029	**0.971**	**0.192**	0.705	1.000	**0.050**	0.069
	C-M	**0.605**	**0.395**	**0.185**	0.346	1.000	**0.050**	**0.040**
Hierophis viridiflavus	T-C	0.000	**1.000**	0.036	0.767	1.000	0.079	0.069
	T-M	0.002	**0.998**	0.028	0.577	1.000	**0.020**	**0.050**
	C-M	**0.104**	**0.896**	0.043	0.353	1.000	0.129	0.188
Zamenis scalaris	T-C	0.000	**1.000**	0.090	0.696	1.000	**0.030**	**0.010**
	T-M	0.008	**0.992**	0.001	0.528	1.000	0.089	0.129
	C-M	**0.262**	**0.738**	0.001	0.254	1.000	0.178	0.218
Lacertidae								
Algyroides moreoticus	T-C	0.012	**0.988**	0.007	0.839	0.149	**0.010**	**0.020**
	T-M	0.000	**1.000**	**0.294**	0.534	0.990	**0.010**	**0.020**
	C-M	0.013	**0.987**	**0.438**	0.416	1.000	**0.010**	**0.020**
Algyroides nigropunctatus	T-C	0.001	**0.999**	**0.229**	0.137	1.000	0.287	0.396
	T-M	0.051	**0.949**	**0.162**	0.837	0.872	**0.010**	**0.010**
	C-M	**0.500**	**0.500**	**0.239**	0.052	1.000	0.347	0.347
Dalmatolacerta oxycephala	T-C	0.003	**0.997**	0.097	0.829	0.158	**0.010**	**0.010**
	T-M	0.037	**0.963**	0.069	0.850	0.069	**0.010**	**0.010**
	C-M	**0.206**	**0.794**	**0.100**	0.689	0.584	**0.010**	**0.010**
Hellenolacerta graeca	T-C	0.000	**1.000**	**0.146**	0.630	1.000	**0.030**	**0.010**
	T-M	0.032	**0.968**	**0.267**	0.725	0.921	**0.010**	**0.010**
	C-M	**0.329**	**0.671**	**0.401**	0.362	1.000	**0.040**	**0.050**
Iberolacerta monticola	T-C	0.000	**1.000**	0.100	0.876	0.228	**0.010**	**0.010**
	T-M	0.045	**0.955**	0.000	0.849	0.287	**0.010**	**0.010**
	C-M	**0.217**	**0.783**	0.000	0.742	0.941	**0.010**	**0.010**
Lacerta bilineata	T-C	0.000	**1.000**	0.067	0.748	1.000	0.069	**0.050**
	T-M	0.001	**0.999**	0.043	0.581	1.000	0.168	0.198
	C-M	**0.173**	**0.827**	0.066	0.340	1.000	0.267	0.238
Lacerta schreiberi	T-C	0.000	**1.000**	**0.119**	0.638	1.000	**0.010**	**0.010**
	T-M	0.036	**0.964**	0.010	0.653	1.000	0.119	0.059
	C-M	**0.337**	**0.663**	0.011	0.303	1.000	**0.040**	**0.020**
Podarcis bocagei	T-C	0.001	**0.999**	0.082	0.837	1.000	**0.010**	**0.010**
	T-M	0.034	**0.966**	0.045	0.761	1.000	**0.030**	**0.010**
	C-M	**0.230**	**0.770**	0.069	0.603	1.000	**0.010**	0.198
Podarcis carbonelli	T-C	**0.727**	**0.273**	**0.456**	0.115	1.000	0.188	0.267
	T-M	**0.119**	**0.881**	**0.153**	0.609	0.475	**0.010**	**0.010**
	C-M	**0.119**	**0.881**	**0.153**	0.609	0.505	0.198	**0.030**

Species	**C**	**E**	**S**	**U**	**D**	**P**	**Similarity 2 -> 1**	**Similarity 1 -> 2**
Podarcis erhardii	T-C	0.000	**1.000**	**0.340**	0.574	1.000	**0.010**	**0.010**
	T-M	0.027	**0.973**	**0.283**	0.589	1.000	**0.010**	**0.010**
	C-M	**0.892**	**0.108**	**0.255**	0.365	1.000	**0.010**	**0.010**
Podarcis melisellensis	T-C	0.005	**0.995**	**0.234**	0.098	1.000	0.416	0.228
	T-M	0.045	**0.955**	0.023	0.792	0.525	**0.010**	**0.010**
	C-M	**0.476**	**0.524**	0.025	0.030	1.000	0.485	0.446
Podarcis peloponnesiacus	T-C	0.011	**0.989**	0.071	0.529	1.000	**0.030**	0.059
	T-M	0.007	**0.993**	**0.169**	0.802	0.564	**0.010**	**0.010**
	C-M	**0.165**	**0.835**	**0.257**	0.338	1.000	**0.050**	0.059
Podarcis siculus	T-C	0.000	**1.000**	0.070	0.603	1.000	**0.020**	**0.050**
	T-M	0.007	**0.993**	0.021	0.556	1.000	**0.050**	0.139
	C-M	**0.188**	**0.812**	0.031	0.168	1.000	0.337	0.337
Podarcis tiliguerta	T-C	0.000	**1.000**	**0.208**	0.659	1.000	**0.010**	**0.010**
	T-M	0.080	**0.920**	0.022	0.758	0.951	**0.010**	**0.010**
	C-M	**0.421**	**0.579**	0.024	0.437	1.000	**0.010**	**0.010**
Podarcis waglerianus	T-C	0.019	**0.981**	0.021	0.712	0.980	**0.010**	**0.040**
	T-M	0.000	**1.000**	**0.241**	0.656	0.951	**0.010**	**0.010**
	C-M	0.027	**0.973**	**0.356**	0.454	1.000	**0.010**	**0.010**
Psammodromus hispanicus	T-C	0.000	**1.000**	0.098	0.673	1.000	**0.010**	**0.010**
	T-M	0.016	**0.984**	0.002	0.509	1.000	0.089	0.089
	C-M	**0.319**	**0.681**	0.002	0.255	1.000	0.139	0.188
Timon lepidus	T-C	0.000	**1.000**	0.072	0.665	1.000	**0.050**	0.059
	T-M	0.006	**0.994**	0.000	0.605	1.000	0.099	0.079
	C-M	**0.210**	**0.790**	**8.343E+09**	0.283	1.000	0.277	0.188
Scincidae								
Chalcides bedriagai	T-C	0.000	**1.000**	0.051	0.658	1.000	0.059	**0.040**
	T-M	0.000	**1.000**	0.029	0.637	1.000	**0.040**	**0.040**
	C-M	**0.107**	**0.893**	0.039	0.372	1.000	0.109	0.069
Chalcides striatus	T-C	0.000	**1.000**	0.054	0.534	1.000	0.059	**0.040**
	T-M	0.008	**0.992**	0.021	0.685	1.000	**0.020**	**0.020**
	C-M	**0.185**	**0.815**	0.028	0.262	1.000	0.208	0.238
Testudinidae								
Testudo hermanni	T-C	0.000	**1.000**	0.032	0.642	1.000	0.069	0.069
	T-M	0.007	**0.993**	0.056	0.546	1.000	0.208	0.119
	C-M	**0.114**	**0.886**	0.072	0.224	1.000	0.257	0.287
Viperidae								
Vipera aspis	T-C	0.097	**0.903**	0.091	0.390	0.851	0.079	0.099
	T-M	0.097	**0.903**	0.091	0.390	1.000	0.257	0.188
	C-M	0.097	**0.903**	0.091	0.390	1.000	0.446	0.376
Vipera seoanei	T-C	0.000	**1.000**	0.034	0.816	1.000	0.416	0.337
	T-M	0.001	**0.999**	0.060	0.554	1.000	0.386	0.337
	C-M	0.097	**0.903**	0.091	0.390	1.000	0.426	0.525

TABLE A7

Pairwise comparison of niches in climatic space (PCA) between the different datasets for flora species. Comparisons (C): Total-Central (T-C), Total-Marginal (T-M) and Central-Marginal (C-M). Niche shift metrics: Expansion (E), Stability (S) and Unfilling (U). Values range from 0 to 1, with 1 being total niche expansion or unfilling and 0 reflecting no change between ranges. Bold values in these columns indicate that the amount of expansion or unfilling was above 10%. Niche equivalency and similarity tests with 100 replication between datasets per species (T-C, T-M and C-M). Bold indicates significant values (*p* <0.05) in these columns

Species	**C**	**E**	**S**	**U**	**D**	**P**	**Similarity 2 -> 1**	**Similarity 1 -> 2**
Alismataceae								
Alisma wahlenbergii	T-C	0.000	**1.000**	**0.522**	0.351	1.000	**0.010**	**0.010**
	T-M	0.002	**0.998**	**0.423**	0.353	1.000	**0.030**	**0.010**
	C-M	**0.915**	0.085	**0.619**	0.015	1.000	0.178	0.178
Luronium natans	T-C	0.000	**1.000**	**0.196**	0.500	1.000	**0.010**	**0.010**
	T-M	0.026	**0.974**	**6.896E+08**	0.625	1.000	0.059	**0.040**
	C-M	**0.542**	**0.458**	0.000	0.162	1.000	0.099	0.099
Amaryllidaceae								
Allium stearnii	T-C	0.000	**1.000**	**0.310**	0.227	1.000	0.119	0.129
	T-M	0.057	**0.943**	0.018	0.644	0.960	**0.020**	**0.020**
	C-M	**0.584**	**0.416**	0.013	0.072	1.000	0.297	0.208
Allium suaveolens	T-C	0.000	**1.000**	0.066	0.894	0.356	**0.010**	**0.010**
	T-M	0.050	**0.950**	**0.156**	0.495	1.000	0.059	**0.030**
	C-M	**0.335**	**0.665**	**0.184**	0.399	1.000	**0.050**	0.059
Narcissus longispathus	T-C	0.000	**1.000**	**0.174**	0.587	1.000	**0.010**	**0.010**
	T-M	0.019	**0.981**	**0.248**	0.664	0.624	**0.010**	**0.010**
	C-M	**0.436**	**0.564**	**0.323**	0.310	1.000	**0.040**	**0.030**
Narcissus triandrus	T-C	0.000	**1.000**	0.096	0.439	1.000	0.158	0.158
	T-M	0.017	**0.983**	0.060	0.606	1.000	**0.030**	0.059
	C-M	**0.287**	**0.713**	0.073	0.118	1.000	0.297	0.347
Apiaceae								
Carum verticillatum	T-C	0.000	**1.000**	**0.217**	0.525	1.000	0.079	**0.050**
	T-M	0.014	**0.986**	0.001	0.604	1.000	0.238	0.119
	C-M	**0.556**	**0.444**	0.001	0.180	1.000	0.277	0.178
Eryngium galioides	T-C	0.000	**1.000**	**0.235**	0.361	1.000	0.139	0.139
	T-M	0.041	**0.959**	0.007	0.608	0.951	**0.010**	**0.030**
	C-M	**0.483**	**0.517**	0.006	0.096	1.000	0.129	0.069
Brassicaceae								
Diplotaxis ilorcitana	T-C	0.000	**1.000**	**0.188**	0.637	1.000	**0.010**	**0.010**
	T-M	**0.129**	**0.871**	0.059	0.283	1.000	0.069	0.139
	C-M	**0.691**	**0.309**	0.058	0.094	1.000	0.089	0.119
Lepidium villarsii	T-C	0.000	**1.000**	**0.329**	0.201	1.000	0.356	0.317
	T-M	0.006	**0.994**	**0.164**	0.556	0.084	0.178	0.139
	C-M	**0.598**	**0.402**	**0.231**	0.070	1.000	0.525	0.604

Euphorbiaceae								
Euphorbia nevadensis	T-C	0.000	**1.000**	**0.223**	0.422	1.000	**0.040**	**0.040**
	T-M	0.070	**0.930**	0.000	0.529	0.941	0.059	0.099
	C-M	**0.570**	**0.430**	0.000	0.116	1.000	0.198	0.149
Fabaceae								
Astragalus arenarius	T-C	0.000	**1.000**	0.081	0.870	1.000	**0.010**	**0.010**
	T-M	**0.335**	**0.665**	0.046	0.322	1.000	0.119	0.069
	C-M	**0.715**	**0.285**	0.035	0.232	1.000	0.099	**0.050**
Hypericaceae								
Hypericum elodes	T-C	0.000	**1.000**	0.099	0.629	1.000	**0.010**	**0.010**
	T-M	0.050	**0.950**	0.000	0.422	1.000	0.257	0.228
	C-M	**0.467**	**0.533**	0.000	0.133	1.000	0.158	0.109
Marsileaceae								
Marsilea batardae	T-C	0.000	**1.000**	**0.291**	0.495	1.000	**0.020**	**0.010**
	T-M	0.046	**0.954**	0.024	0.537	1.000	**0.010**	**0.040**
	C-M	**0.704**	**0.296**	0.005	0.107	1.000	0.069	0.119
Orchidaceae								
Chamorchis alpina	T-C	0.000	**1.000**	0.066	0.756	1.000	**0.030**	**0.010**
	T-M	0.021	**0.979**	0.046	0.422	1.000	0.168	0.129
	C-M	**0.366**	**0.634**	0.048	0.290	1.000	0.158	0.119
Dactylorhiza lapponica	T-C	0.000	**1.000**	**0.140**	0.660	1.000	0.059	**0.050**
	T-M	0.000	**1.000**	**0.140**	0.660	1.000	**0.050**	0.089
	C-M	**0.439**	**0.561**	0.020	0.323	1.000	0.119	0.129
Dactylorhiza sambucina	T-C	0.000	**1.000**	0.083	0.716	1.000	**0.010**	**0.010**
	T-M	0.020	**0.980**	0.002	0.491	1.000	**0.020**	**0.030**
	C-M	**0.403**	**0.597**	0.001	0.229	1.000	0.069	**0.050**
Epipactis leptochila	T-C	0.000	**1.000**	**0.102**	0.849	0.673	**0.010**	**0.010**
	T-M	0.000	**1.000**	**0.157**	0.243	1.000	0.257	0.158
	C-M	**0.194**	**0.806**	**0.280**	0.128	1.000	0.317	0.436
Epipactis muelleri	T-C	0.000	**1.000**	0.074	0.783	1.000	**0.010**	**0.010**
	T-M	0.006	**0.994**	0.053	0.497	1.000	**0.030**	**0.040**
	C-M	**0.167**	**0.833**	0.094	0.287	1.000	0.109	0.119
Epipactis phyllanthes	T-C	0.000	**1.000**	**0.368**	0.527	1.000	**0.010**	**0.010**
	T-M	0.002	**0.998**	**0.300**	0.582	1.000	0.059	0.089
	C-M	**0.731**	**0.269**	**0.563**	0.142	1.000	0.079	0.139
Epipactis purpurata	T-C	0.000	**1.000**	0.030	0.775	1.000	**0.010**	**0.010**
	T-M	0.011	**0.989**	0.020	0.706	1.000	**0.010**	**0.020**
	C-M	0.078	**0.922**	0.027	0.499	1.000	**0.020**	**0.040**
Gymnadenia odoratissima	T-C	**2.692E+09**	**1.000**	0.016	0.949	**0.010**	**0.010**	**0.010**
	T-M	0.007	**0.993**	0.064	0.503	1.000	0.188	0.198
	C-M	0.085	**0.915**	0.078	0.459	1.000	0.267	0.248
Gymnadenia rhellicani	T-C	0.001	**0.999**	0.071	0.815	0.881	0.693	**0.030**
	T-M	0.011	**0.989**	**0.115**	0.732	0.822	**0.020**	**0.030**
	C-M	**0.211**	**0.789**	**0.159**	0.557	1.000	**0.010**	**0.010**

Ophrys bertolonii	T-C	0.000	**1.000**	**0.128**	0.588	1.000	**0.030**	**0.040**
	T-M	0.020	**0.980**	0.032	0.681	0.941	0.079	0.089
	C-M	**0.305**	**0.695**	0.033	0.335	1.000	0.218	0.188
Ophrys insectifera	T-C	**4.423E+09**	**1.000**	0.089	0.543	1.000	**0.050**	**0.020**
	T-M	0.001	**0.999**	0.014	0.614	1.000	**0.040**	**0.030**
	C-M	**0.190**	**0.810**	0.025	0.176	1.000	0.317	0.356
Plantaginaceae								
Callitriche cophocarpa	T-C	**7.980E+08**	**1.000**	0.060	0.700	1.000	**0.010**	**0.010**
	T-M	0.017	**0.983**	**5.571E+07**	0.610	1.000	**0.020**	**0.020**
	C-M	**0.246**	**0.754**	0.000	0.324	1.000	**0.030**	**0.030**
Callitriche platycarpa	T-C	0.000	**1.000**	**0.106**	0.625	1.000	**0.010**	**0.010**
	T-M	0.004	**0.996**	0.000	0.582	1.000	**0.020**	**0.010**
	C-M	**0.368**	**0.632**	0.000	0.229	1.000	**0.030**	**0.040**
Poaceae								
Calamagrostis chalybaea	T-C	0.000	**1.000**	0.066	0.743	1.000	**0.010**	**0.010**
	T-M	0.045	**0.955**	0.003	0.558	1.000	**0.040**	**0.030**
	C-M	**0.236**	**0.764**	0.003	0.315	1.000	**0.020**	**0.010**
Festuca summilusitana	T-C	0.000	**1.000**	**0.205**	0.642	1.000	**0.010**	**0.010**
	T-M	0.014	**0.986**	0.053	0.731	0.980	**0.010**	**0.020**
	C-M	**0.341**	**0.659**	0.072	0.405	1.000	**0.040**	**0.010**
Primulaceae								
Soldanella villosa	T-C	0.000	**1.000**	**0.107**	0.835	0.842	**0.010**	**0.010**
	T-M	**0.227**	**0.773**	**0.191**	0.352	1.000	0.069	**0.010**
	C-M	**0.574**	**0.426**	**0.209**	0.295	1.000	**0.040**	**0.030**
Ranunculaceae								
Pulsatilla grandis	T-C	0.000	**1.000**	**0.729**	0.045	1.000	**0.010**	**0.010**
	T-M	**0.166**	**0.834**	**0.141**	0.329	1.000	**0.030**	**0.030**
	C-M	**0.995**	0.005	0.000	0.002	1.000	0.089	**0.040**
Ranunculus peltatus	T-C	0.000	**1.000**	**0.219**	0.533	1.000	**0.020**	**0.010**
	T-M	0.090	**0.910**	0.006	0.506	1.000	0.208	0.129
	C-M	**0.729**	**0.271**	0.006	0.100	1.000	**0.040**	0.089
Rosaceae								
Prunus ramburii	T-C	0.000	**1.000**	0.025	0.806	1.000	**0.010**	**0.010**
	T-M	0.000	**1.000**	**0.196**	0.691	1.000	**0.020**	**0.010**
	C-M	0.056	**0.944**	**0.278**	0.502	1.000	**0.010**	**0.010**
Saxifragaceae								
Saxifraga osloensis	T-C	0.000	**1.000**	**0.424**	0.212	1.000	**0.020**	**0.010**
	T-M	0.001	**0.999**	**0.266**	0.817	1.000	**0.010**	**0.010**
	C-M	**0.623**	**0.377**	**0.838**	0.040	1.000	0.119	0.089

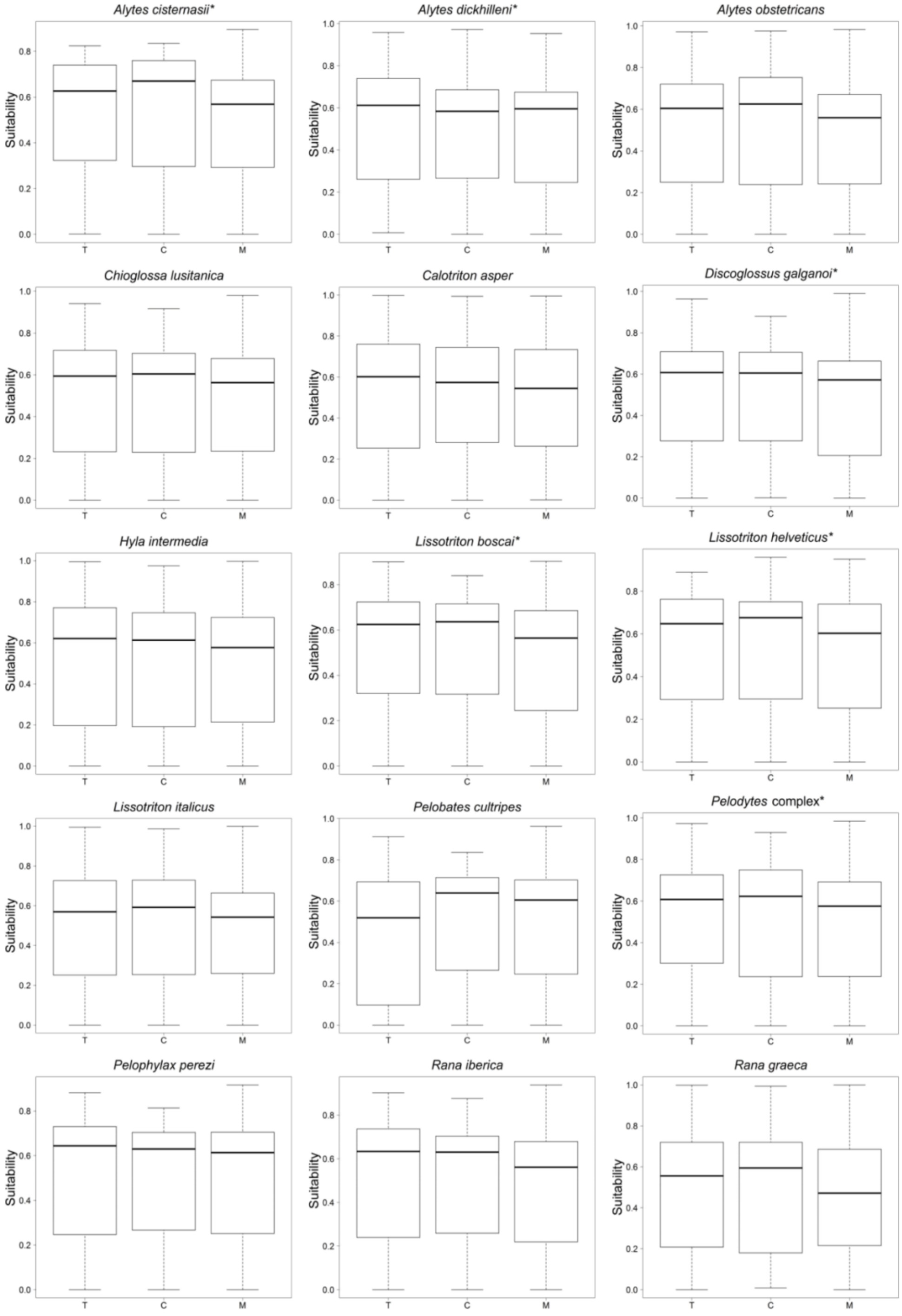


FIGURE A2 Boxplot of mean predicted suitability values for amphibians species. Taxa with significant differences are marked with an asterisk (*)

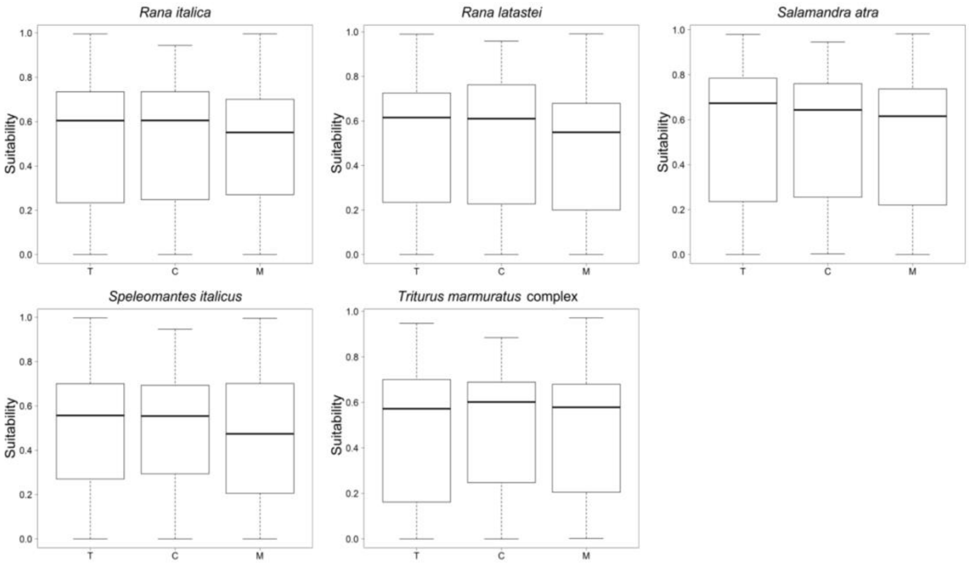


FIGURE A3 Boxplot of mean predicted suitability values for amphibians species. Taxa with significant differences are marked with an asterisk (*)

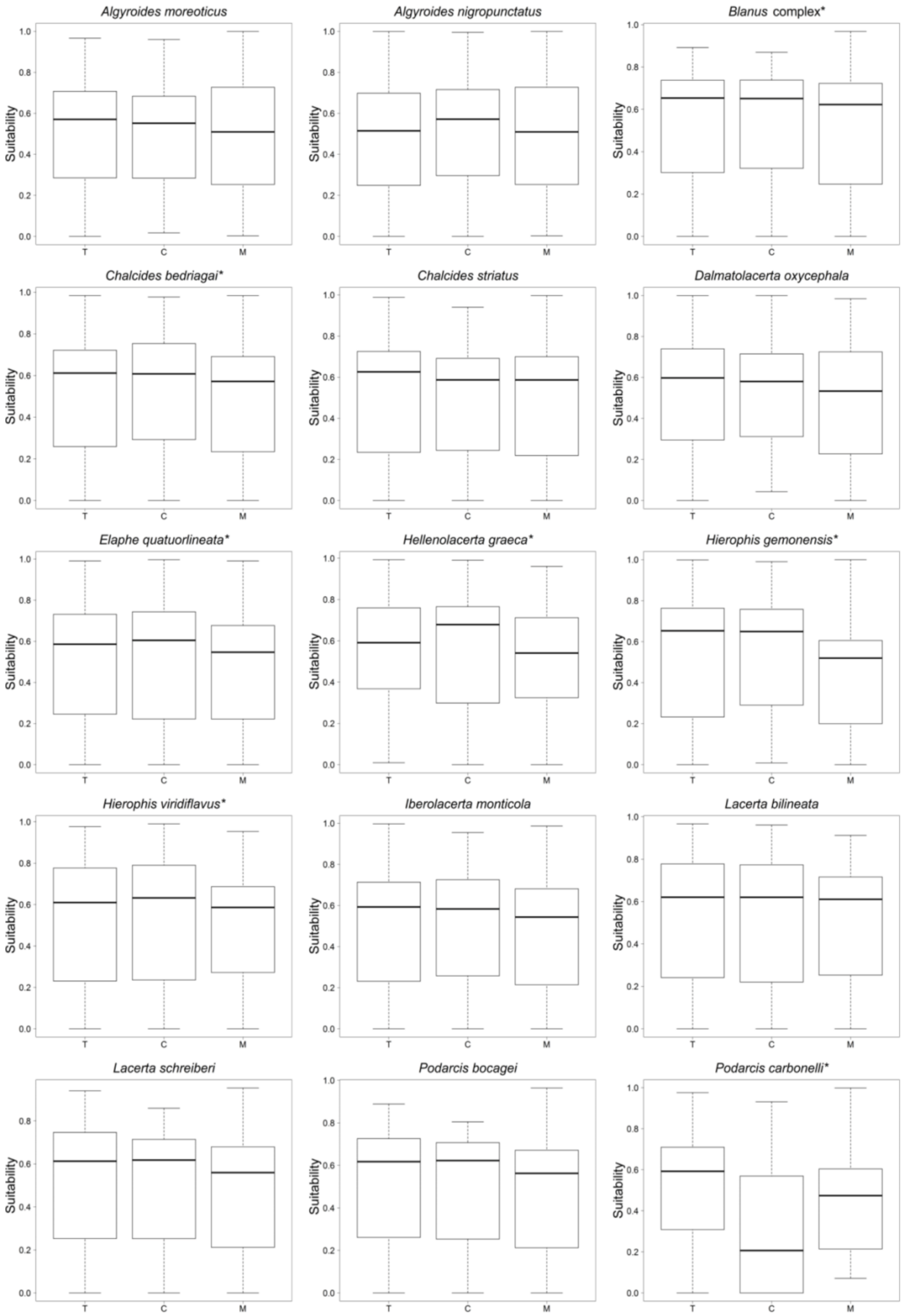


FIGURE A4 Boxplot of mean predicted suitability values for reptiles species. Taxa with significant differences are marked with an asterisk (*)

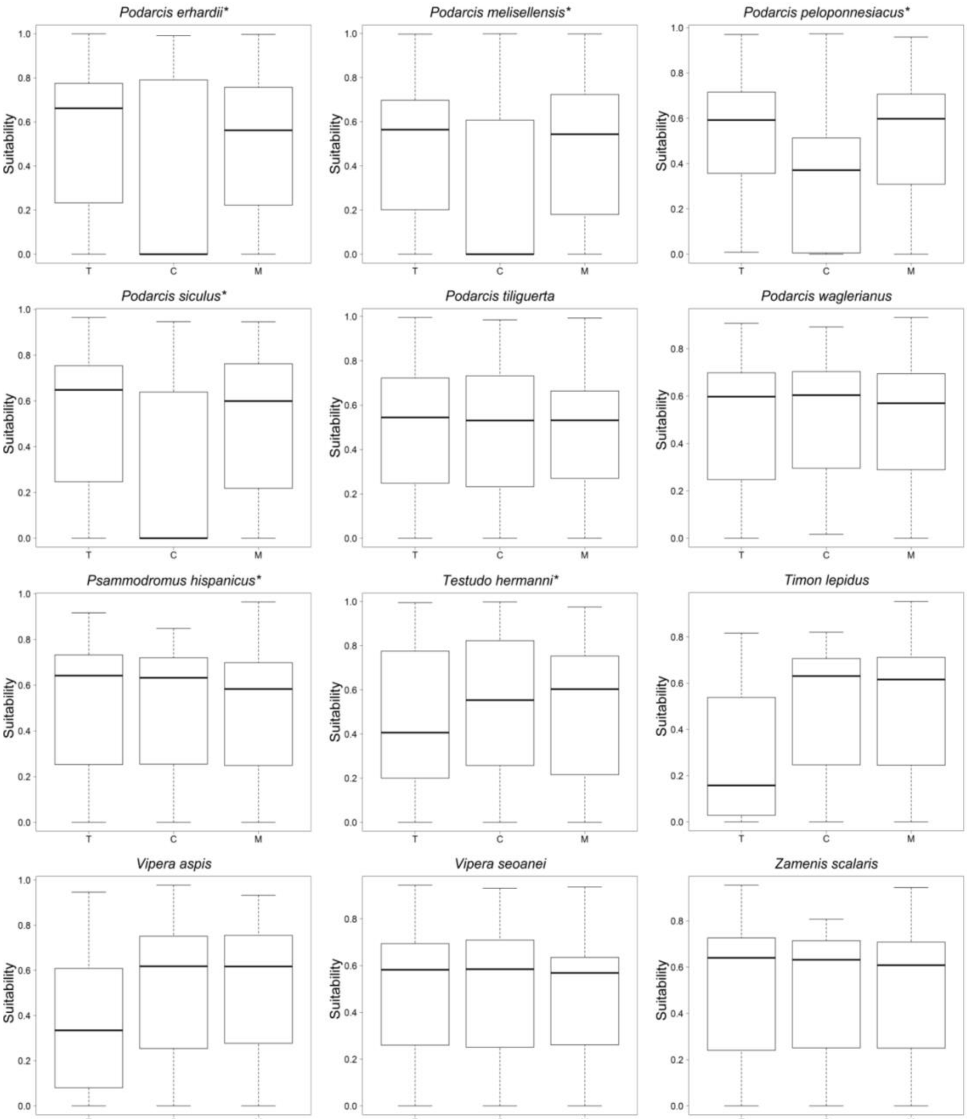
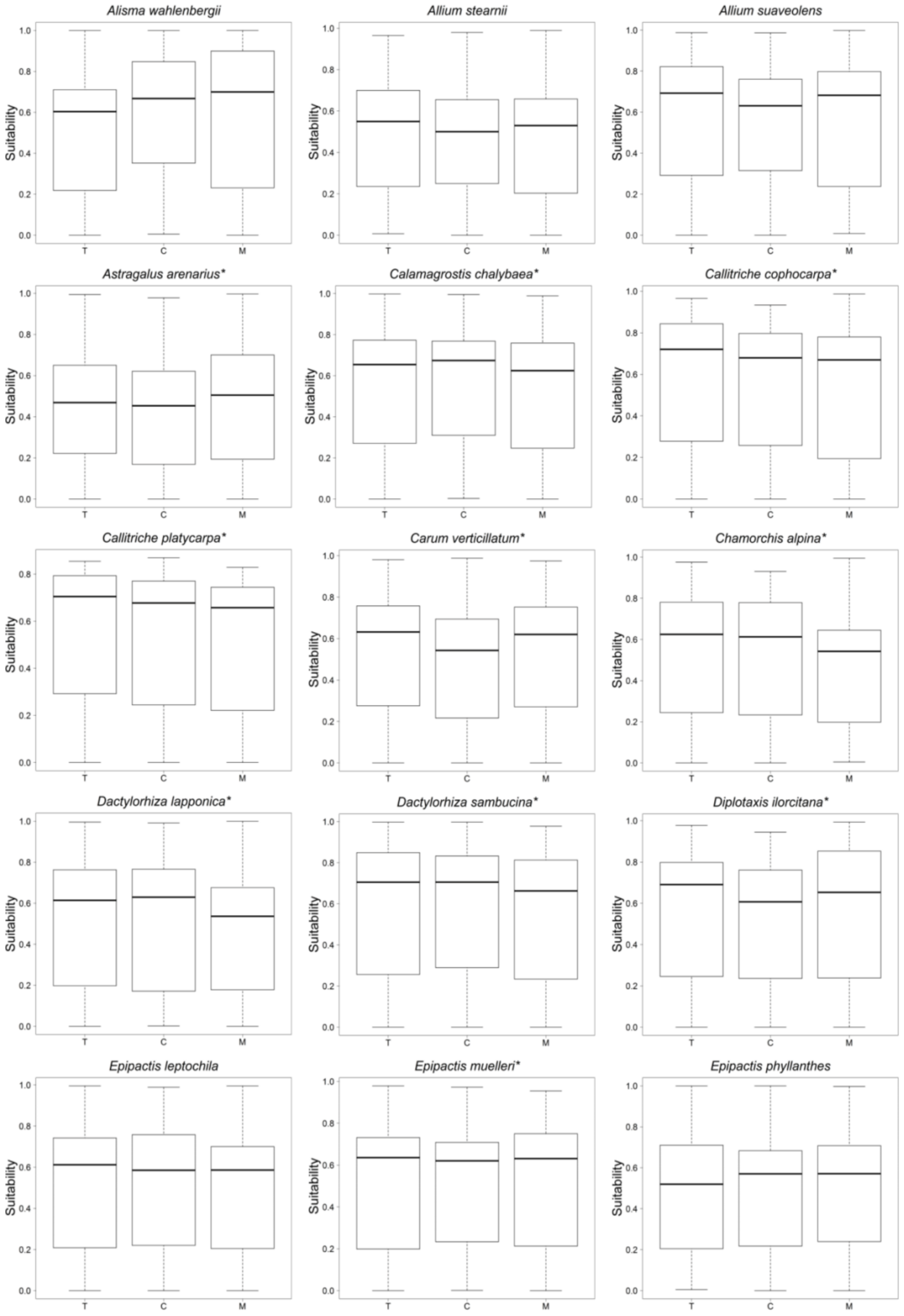


FIGURE A5 Boxplot of mean predicted suitability values for reptiles species. Taxa with significant differences are marked with an asterisk (*)



Alisma wahlenbergii

Allium stearnii

Allium suaveolens

Astragalus arenarius*

Calamagrostis chalybaea*

Callitriche cophocarpa*

Callitriche platycarpa*

Carum verticillatum*

Chamorchis alpina*

Dactylorhiza lapponica*

Dactylorhiza sambucina*

Diplotaxis ilorcitana*

Epipactis leptochila

Epipactis muelleri*

Epipactis phyllanthes

FIGURE A6 Boxplot of mean predicted suitability values for flora species. Taxa with significant differences are marked with an asterisk (*)

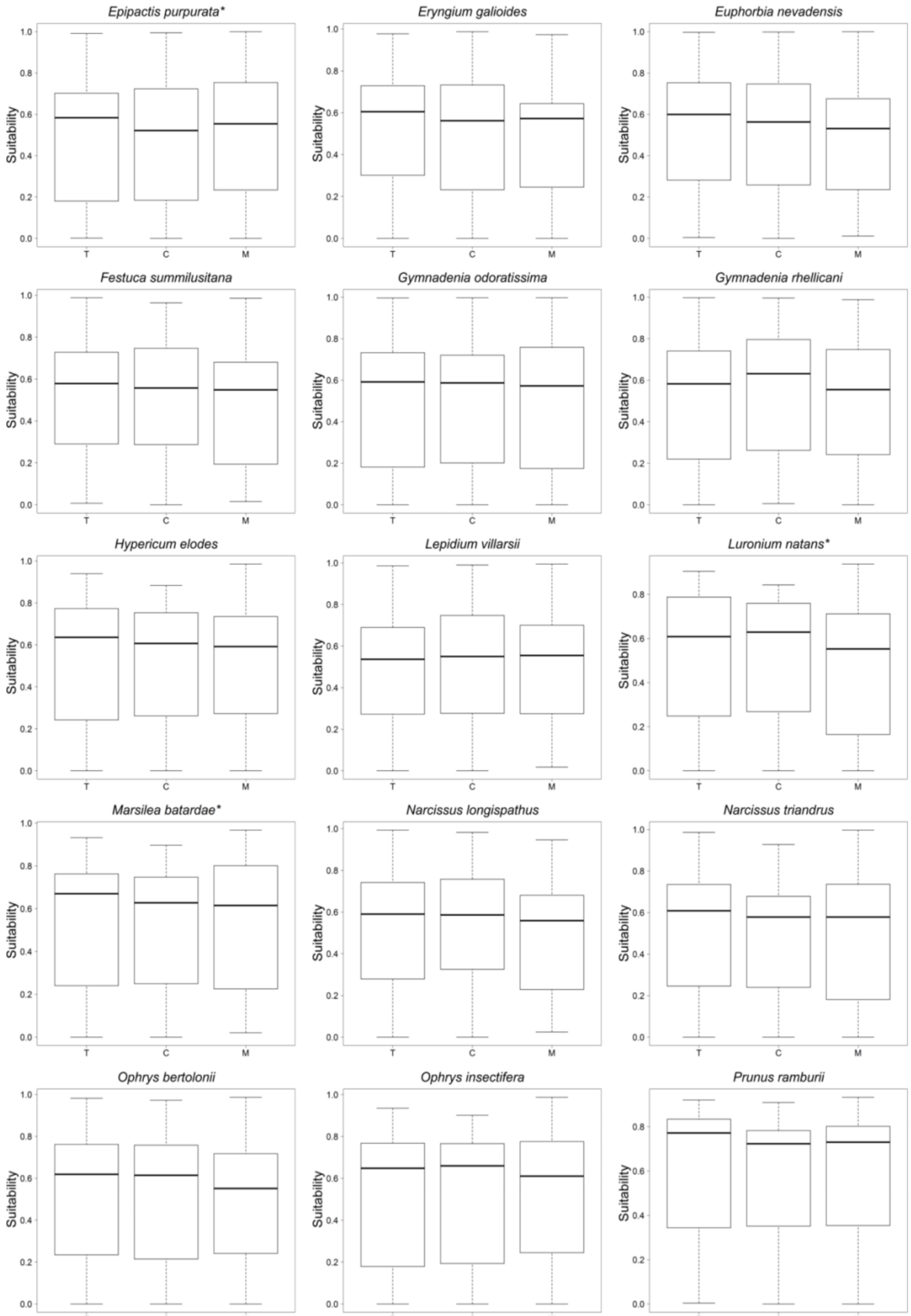


FIGURE A7 Boxplot of mean predicted suitability values for flora species. Taxa with significant differences are marked with an asterisk (*)

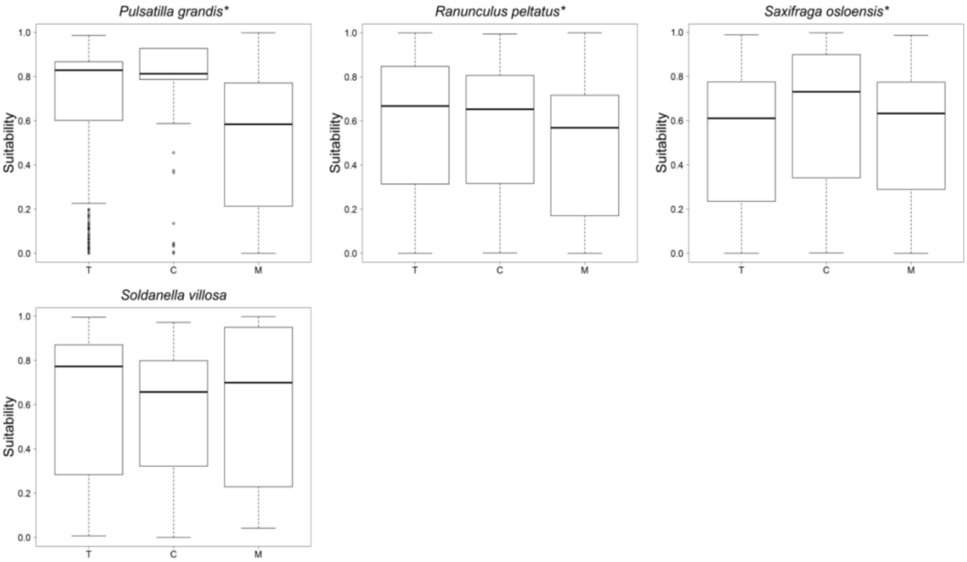
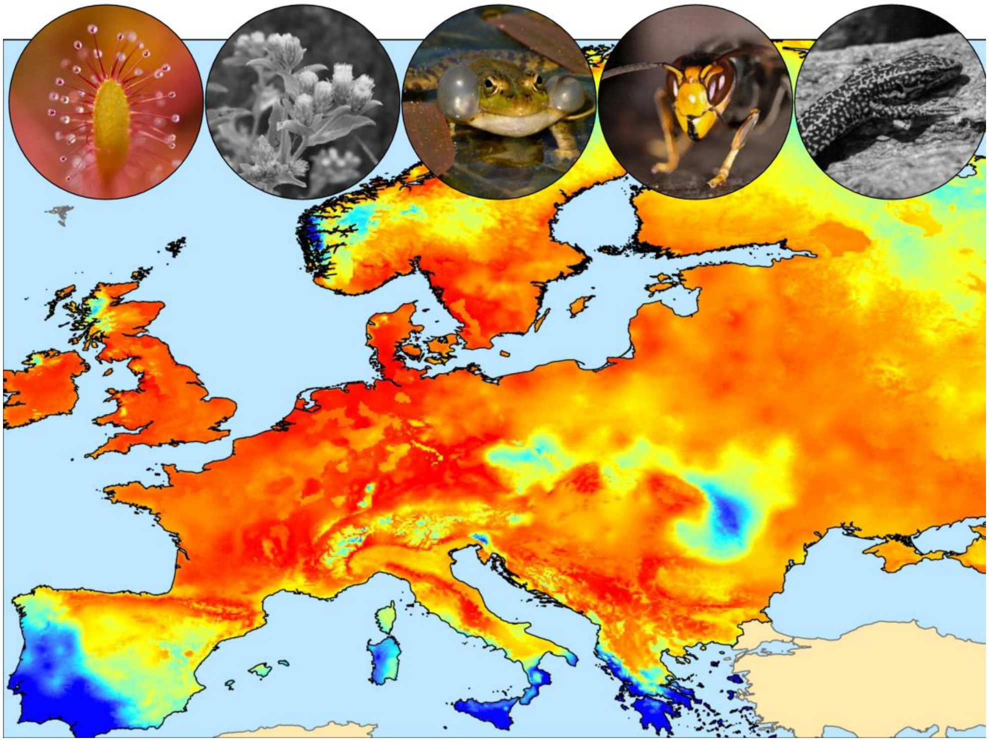


FIGURE A8 Boxplot of mean predicted suitability values for flora species. Taxa with significant differences are marked with an asterisk (*)

CAPÍTULO VI



Fotos animales: Cristina Mimbrañes y Juan Ramón Peralta Rincón

VI. CONCLUSIONES

-Los Modelos de Nicho Ecológico en combinación con los Sistemas de Información Geográfica constituyen el hilo conductor metodológico de la presente memoria doctoral, habiendo sido aplicados con éxito en tres situaciones/hipótesis de trabajo vinculadas a problemáticas y cuestiones relevantes de la Biología de la Conservación, que son: los patrones de distribución de una especie invasora, la determinación de variables de distribución temporal de una especie migradora, y la comprobación de la hipótesis centro-periferia en poblaciones marginales de especies de interés, ibéricas y europeas.

-Los MNE pueden ser aplicados eficazmente para comparar bases de datos biológicos georreferenciados procedentes de fuentes diferentes, en concreto para determinar la fiabilidad de los registros de presencia de una especie invasora tomados por no especialistas, lo que puede ser de gran ayuda a la hora de diseñar sistemas de alerta temprana de invasiones biológicas. Para el caso de la avispa asiática hemos demostrado que hay coincidencia entre los mapas de idoneidad generados a partir de registros procedentes de no especialistas con los obtenidos de datos de entomólogos y técnicos ambientales.

-Hemos aplicado los MNE en combinación con los SIG para determinar las variables predictoras que condicionan la distribución estacional de una especie migradora. Es una de las primeras aproximaciones metodológicas de los MNE en la que se introduce el marco temporal, puesto que la principal limitación de los modelos es su visión estática de la realidad de una especie, que habitualmente es dinámica. En concreto hemos analizado la presencia invernal de poblaciones de milano real, una especie migradora en claro declive que posee en el oeste de Castilla y León sus principales efectivos. La disponibilidad trófica de roedores (topillo, conejo) y la presencia de muladares y vertederos parece ser, según nuestros resultados, el principal condicionante que atrae a esta especie a esta región ibérica, lo que debe ser tenido en cuenta de cara a establecer estrategias para su conservación (control de plaguicidas, venenos y contaminantes).

-Hemos desarrollado un flujo de trabajo específico para determinar la existencia de marginalidad ecológica en poblaciones ubicadas en los límites de sus rangos de distribución. En concreto lo hemos aplicado en un primer momento a cuatro especies de flora de interés de Castilla y León: *Artemisia umbelliformis*, *Drosera longifolia*, *Empetrum nigrum*, *Inula bifrons*. Los resultados indican que las poblaciones localizadas en el margen de su distribución de tres de las cuatro especies están localizadas en hábitats menos idóneos en comparación con sus poblaciones centrales. Este hecho soportaría la idea de que la marginalidad puede representar un factor determinante para el desarrollo de las poblaciones marginales.

-A fin de seguir testando y optimizando la metodología previamente desarrollada en relación al análisis de marginalidad, hemos incorporado de forma experimental el paquete de análisis en R, “ecospat”, y lo hemos aplicado al, estudio de la hipótesis centro-periferia en 81 endemismos europeos correspondientes a varios grupos de organismos, plantas, anfibios y reptiles. Los resultados muestran diferencias entre los nichos de las poblaciones centrales y marginales en más del 66% de las especies analizadas, mayoritariamente plantas, lo que en principio era esperable dada su menor movilidad.

-En resumen, aportamos cuatro nuevas aproximaciones metodológicas de los Modelos de Nicho Ecológico en el ámbito de la Biología de la Conservación, demostrando el gran potencial que aún tienen para abordar situaciones concretas que afectan a la biodiversidad.

RESUMEN EXPANDIDO

Fotos animales: Ricardo Córdoba Cámara y Thomas Lahlafi

VII. RESUMEN EXPANDIDO

¿Qué tan fiable es el ojo inexperto en la identificación de una especie invasora? El caso de la avispa asiática en la Península Ibérica

Debido a sus estrategias reproductivas y de dispersión, los insectos sociales (p.ej. hormigas, abejas y avispas) son considerados los invasores más exitosos alrededor del mundo (Moller, 1996; Villemant et al., 2011). *Vespa velutina* Lepeletier, 1836, después de su introducción y establecimiento en Francia, se convirtió en el primer Vespidae exótico que logró una invasión exitosa en Europa (Beggs et al., 2001; Villemant et al., 2011). De forma similar a otras invasiones causadas por otras especies de Vespidae, la invasión de *V. velutina* genera una serie de impactos ecológicos, económicos y sociales (Beggs et al., 2001).

Usando como modelo esta especie invasora, en el **Capítulo 2**, nos planteamos la siguiente pregunta: "¿los registros de ocurrencia (alertas de presencia) de la avispa asiática (*V. velutina*), procedentes de personas no expertas, ¿son igual de fiables que los que son tomados por técnicos especialistas? Es una cuestión que tiene relevancia desde el punto de vista de las estrategias necesarias para su control, ya que los avisos de aparición de este tipo de organismos en un nuevo territorio, por la alarma social que generan, suelen proceder con más frecuencia de personas no expertas, por lo que es crucial evaluar correctamente su grado de verosimilitud. Es evidente que este tipo de análisis deberá ser específico de cada especie analizada y los resultados variarán en función de numerosas circunstancias; en este caso tiene gran peso el hecho de que esta avispa invasora tenga especies autóctonas muy parecidas morfológicamente.

Para realizar este análisis, utilizamos una metodología que implica calcular los nichos realizados (*sensu* Sillero, 2011) de ese insecto, utilizando dos conjuntos de datos independientes: por un lado los procedentes de personal experto (p.ej. personal técnico e investigadores de instituciones científicas ambientales) y por otro, datos tomados por voluntarios no expertos (p.ej., naturalistas, aficionados, apicultores). Los datos *Oficiales* españoles proceden del Ministerio de Agricultura, Pesca, Alimentación y Medio Ambiente (MAPAMA; previamente denominado MAGRAMA) y los datos de Portugal fueron facilitados por "Instituto da Conservação da Natureza e das Florestas (ICNF)" disponibles en la plataforma en línea “SOS Vespa” (www.sosvespa.pt). El conjunto de datos *Oficial* final está compuesto por 5627 registros. Los datos de la *Web* está compuesto por los datos disponibles en la página del *“Instituto Vasco de Investigación y Desarrollo Agrario”* (NEIKER-Tecnalia; www.avisosneiker.com) y del “mapa de seguimiento del avispón asiático por Europa” creado y gestionado por la página “Mel de Selva” (hasta diciembre de 2016). Esta última es una plataforma abierta y colaborativa que recompila todas las notificaciones en toda Europa (sin validación o supervisión de expertos). El conjunto de datos *Web* final se compone por 2619 registros. Para reducir los problemas de autocorrelación espacial, se ha realizado un proceso de filtrado que redujo el número de registros de presencia del conjunto de datos *Oficial* a 314 y del *Web* a 630 (ver detalles en Zohner, Benito, Fridley, Svenning, & Renner, 2017). Las variables ambientales utilizadas para los modelos son seis variables disponibles en WorldClim (Bio4, Bio6, Bio12 y Bio14; ver texto principal para los códigos de las variables), además de diversidad topográfica, huella humana y coberturas del suelo. Para reducir la multicolinealidad entre variables, aplicamos un análisis de clúster jerárquico seguido de un análisis VIF (ver detalles en Benito et al., 2017). Los modelos fueron evaluados mediante 10 repeticiones del tipo *boostrap* (80% de los datos para la calibración y 20% para la evaluación) y AUC (Liu, Berry, Dawson, & Pearson, 2005). La importancia de las variables se evaluó con un test de tipo *jackknife*. Finalmente, para el cálculo del tamaño de áreas predichas, se convirtió en binaria cada una de las réplicas de cada uno de los conjuntos de modelos. Para evaluar el nivel de similitud entre modelos (*Oficial* y *Web*), primeramente realizamos una comparación global utilizando el coeficiente de correlación rho de Spearman (como recomendado por Parolo, Rossi, & Ferrarini, 2008). A continuación, utilizamos el programa ENMTools (http://purl.oclc.org/enmtools/; Warren, Glor, & Turelli, 2010) para medir la superposición entre nichos y, en consecuencia, el nivel de similitud entre ambos. ENMTools utiliza pruebas estadísticas y métricas comparativas de similitudes (la "D" Schoener y la distancia Hellinger o "I"). Ambas métricas varían entre 0 y 1 dentro del espacio geográfico (mayor valor significa mayor superposición de nicho) (Warren, Glor, & Turelli, 2008).

Nuestros resultados indicaron un alto valor de correlación entre modelos (*rho* de Spearman=0.973) y un solapamiento de nichos por encima del 75% (D=0.785; I=0.956). Además las áreas de distribución potencial arrojadas por ambos modelos tenían un patrón muy similar a los encontrados por estudios previos (Barbet-Massin et al., 2013; Bessa, Carvalho, Gomes, & Santarém, 2016; Ibáñez-Justicia & Loomans, 2011; Villemant et al., 2011). Las variables más importantes fueron temperatura mínima del mes más frio, estacionalidad de las temperaturas, y precipitación anual para ambos modelos.

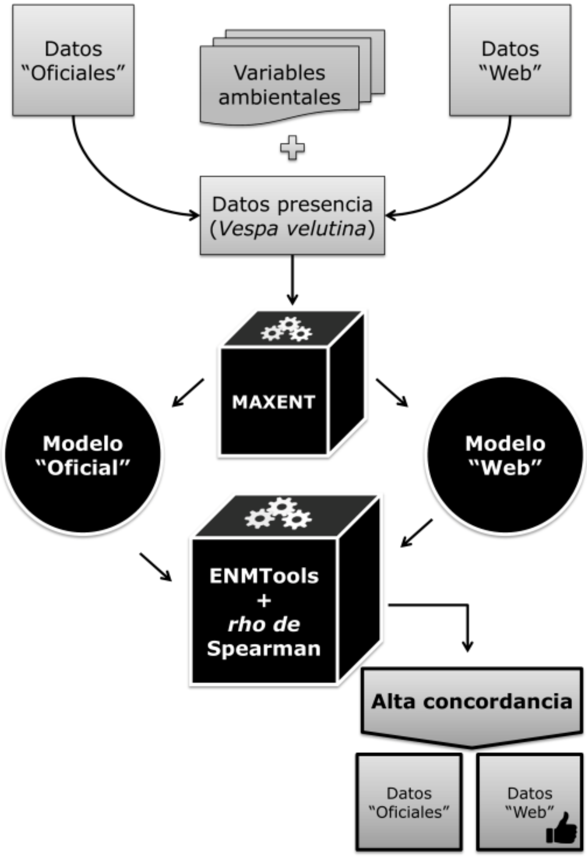


FIGURA 1 Esquema de trabajo utilizado en el Capítulo 2

Por todo ello pudimos concluir que los datos del "ojo inexperto" son fiables a la hora de crear estrategias de manejo (alertas tempranas), al menos para esta especie. A pesar de ello, puesto que los modelos generados con los "datos oficiales" tuvieron un mejor desempeño, se hace preciso mantener precaución a la hora de interpretar resultados derivados solamente de esta fuente de datos, siendo lo ideal el utilizar toda la información disponible, de expertos e inexpertos, en su totalidad. Los hallazgos de este trabajo son especialmente importantes para la especie analizada, ya que la avispa asiática continua desplegando su agresivo potencial invasor (ya ha invadido ocho países europeos entre 2004-2017; Barbet-Massin, Rome, Villemant, & Courchamp, 2018), generando graves problemas ecológicos (depreda numerosos polinizadores importantes, como abejorros), económicos (se alimenta también de la abeja de miel (*Apis mellifera*; Keeling, Franklin, Datta, Brown, & Budge, 2017) y sociales (sus nidos pueden aparecer en zonas pobladas y son especialmente violentas, llegando a atacar al hombre[14].), A estas circunstancias se suma el daño provocado a su congénere autóctona *V. cabro*, especie amenazada en algunos países europeos, cuyas colonias son confundidas y destruidas. Por todo ello se justifica un trabajo como el que se ha presentado en esta tesis, que añade una nueva herramienta para poder controlar el avance de esta especie.

Factores comportamentales, ecológicos y humanos explican la distribución invernal del milano real (*Milvus milvus* Linnaeus, 1758) en la Península Ibérica: consecuencias y oportunidades para la conservación de las rapaces europeas

El milano real (*M. milvus*) es una de las aves europeas más vulnerables al cambio climático (Wormworth & Mallon, 2007), que actualmente está experimentando un rápido declive demográfico (BirdLife International, 2016, 2017). Se trata de una especie que presenta poblaciones centroeuropeas migradoras que durante el invierno se concentran en el oeste de Castilla y León junto con otras poblaciones ibéricas residentes, constituyendo esta región su principal reducto de presencia durante ese periodo, siendo por tanto de importancia clave para su conservación (Viñuela, 2017). Es precisamente en este territorio de uso temporal invernal donde se sospecha que se concentran las principales amenazas que son responsables de ese declive (BirdLife International, 2017; Carter, 2001; Mougeot, Garcia, & Viñuela, 2011).

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[14] https://www.lavozdegalicia.es/noticia/galicia/2017/11/15/muere-hombre-54-anos-atacado-velutinas-porrino/0003_201711G15P6991.htm

Es por ello que en el **Capítulo 3** de esta tesis abordamos el análisis de los requerimientos ambientales de estas zonas de invernada del milano real, aplicando técnicas de modelado que ya habían sido aplicadas para diseñar estrategias de conservación para esta especie, pero centradas en su distribución durante el periodo reproductor (Viñuela, 2017).

Los datos de ocurrencia de los dormideros fueron extraídos de los censos nacionales de la población invernal más recientes; en España realizados entre 2013-2015 (*n* = 431 dormideros; Molina, 2015) y en Portugal durante el invierno 2014-(*n* = 12 dormideros; Leitão et al., 2015). El conjunto de datos final está compuesto por 443 registros de dormideros (solo un registro por cuadrícula de 5km x 5km). Se utilizaron las 10 variables que más podían estar relacionadas con la distribución de esta especie en la Península Ibérica durante el invierno (p.ej. usos del suelo, clima, topografía, recursos tróficos; ver texto principal), y que fueron seleccionadas utilizando el mismo procedimiento del capítulo anterior (ver texto principal y Benito et al., 2017), juntamente con un proceso de simplificación paso a paso (ver texto principal y Elith, Leathwick, & Hastie, 2008). Los modelos *Boosted Regression Trees* (BRT) fueron calibrados de acuerdo con las recomendaciones de Elith et al. (2008). El grado en que los valores ajustados discriminan entre los resultados observados se midió utilizando el AUC y el coeficiente de correlación mediante un procedimiento de 5 repeticiones cruzadas (*k-fold*). Se calibraron dos modelos: (i) con todas las presencias y (ii) quitando todas las presencias de la subpoblación de la meseta norte. Consideramos que, al calibrar el modelo sin los datos de la mayor área de invernada, se obtendría una mejor comprensión del porqué esta especie se concentra durante el invierno en esa región, es decir: hasta qué punto el uso de su hábitat está sesgado por el recurso trófico generado por las habituales plagas de topillos (el censo español está realizado durante un inverno con topillos), y dejando fuera esa variable, cuáles son sus otros requerimientos de hábitat.

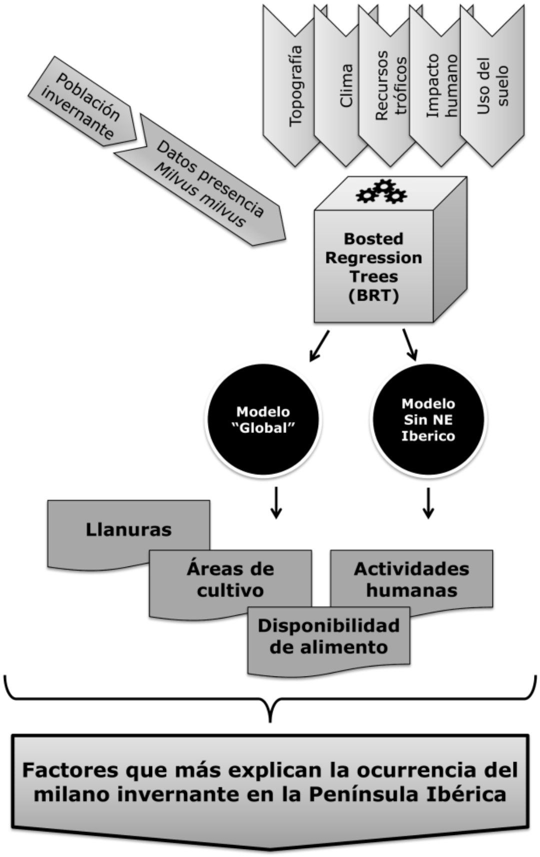

FIGURA 2 Esquema de trabajo utilizado en el Capítulo 3

Nuestros resultados muestran que los hábitats más idóneos son las regiones asociadas a áreas de laderas planas o suaves ocupadas por tierras extensivamente cultivadas y agroforestales y con un cierto grado de uso humano. Este hecho corrobora la idea de que las poblaciones centroeuropeas de esta especie llegan en el inverno a la Península Ibérica, debido principalmente a la cantidad de recursos tróficos disponibles durante ese periodo (Molina, 2015; Viñuela, Martí, & Ruiz, 1999), como son los pequeños mamíferos, especialmente el topillo común (*Microtus arvalis*), que ocasionalmente constituye plagas, el conejo común (*Oryctolagus cuniculus*), y también por los vertedores y los muladares existentes. Como hemos dicho antes, parte de la estrategia de investigación consistió en excluir de los modelos los registros de presencia de esta especie en Castilla y León (los más numerosos), para evaluar cómo influía el peso de las variables de ese territorio en el resto de su distribución, lo que provocó que la variable con mayor poder explicativo se trasladara a la disponibilidad de ganado muerto, en cualquier caso, otro recurso trófico. Toda esta información obtenida a partir de nuestros modelos es de gran relevancia por su potencial aplicabilidad a las estrategias de conservación que son necesario tomar para garantizar la supervivencia de esta especie.

Viviendo al límite: ¿la idoneidad del hábitat difiere entre las poblaciones centrales y marginales de plantas?

Las poblaciones de una especie que se encuentran localizadas en los límites de su rango de distribución (marginales o climáticamente relictas en la biogeografía clásica) pueden diferir sustancialmente en términos de viabilidad, de las poblaciones ubicadas en el centro/núcleo (Abeli, Gentili, Mondoni, Orsenigo, & Rossi, 2014; Hampe & Jump, 2011). Estas poblaciones periféricas pueden tener un alto potencial evolutivo o, por el contrario, ser más propensas a la extinción, pero los procesos que impulsan cada uno de estos dos patrones aún no están claros (Abeli et al., 2014). Por ambos motivos las poblaciones marginales tienen un gran interés el ámbito de conservación y han sido objeto de numerosos estudios y revisiones, estando la mayoría enfocados hacia su composición genética (Abeli et al., 2014).

Por ello, en el **Capítulo 4**¸ hemos propuesto un flujo de trabajo que nos ha permitido calcular nichos ecológicos realizados (*sensu* Sillero, 2011) y estimar la distancia entre los de las poblaciones marginales y centrales. Como una primera aproximación, hemos seleccionado cuatro especies de plantas (*Artemisia umbelliformis*, *Drosera longifolia*, *Empetrum nigrum* e *Inula brifrons*) incluidas en la Lista Roja de flora vascular española (Moreno, 2008) y en el Catálogo de flora amenazada de Castilla y León (BOCYL, 2007), siendo este último territorio mencionado, el margen occidental de su rango de distribución. Fueron utilizadas ocho variables climáticas (Bio4, Bio1, Bio2, Bio5, Bio8, Bio15, Bio16, Bio17 y Bio18); ver texto principal para los códigos de las variables) – disponibles en CHELSA; http://chelsa-climate.org/ – que alcanzaron un coeficiente de correlación de Pearson menor que 0.7. Los modelos fueron evaluados mediante 10 repeticiones del tipo *boostrap* (80% de los datos para la calibración y 20% para la evaluación) y AUC (Liu et al., 2005). Se convirtieron a formato binario las salidas de los modelos de Maxent, utilizando el valor conservador de umbral del 10º percentil (Bosso, Rebelo, Garonna, & Russo, 2013; Rebelo & Jones, 2010). Para estimar las distancias de los espacios ambientales de cada población al centroide de nicho de la especie, seguimos a Yáñez-Arenas et al. (2012). Brevemente, extrajimos los valores de las variables ambientales para todos los píxeles donde se predijeron que las especies estarían presentes de acuerdo con las salidas binarias de Maxent. Para evitar los sesgos introducidos por las diferencias de escala entre las dimensiones ecológicas (por ejemplo, °C para la temperatura y mm para la precipitación), estandarizamos cada dimensión (media=0, varianza=1). De esta forma, el centroide del nicho multidimensional es el punto donde los valores de todas las variables son 0, y los cálculos de las distancias de los espacios ambientales de cada población al centroide de la especie se convierten en simples descomposiciones de distancias euclidianas (Yañez-Arenas et al., 2012).

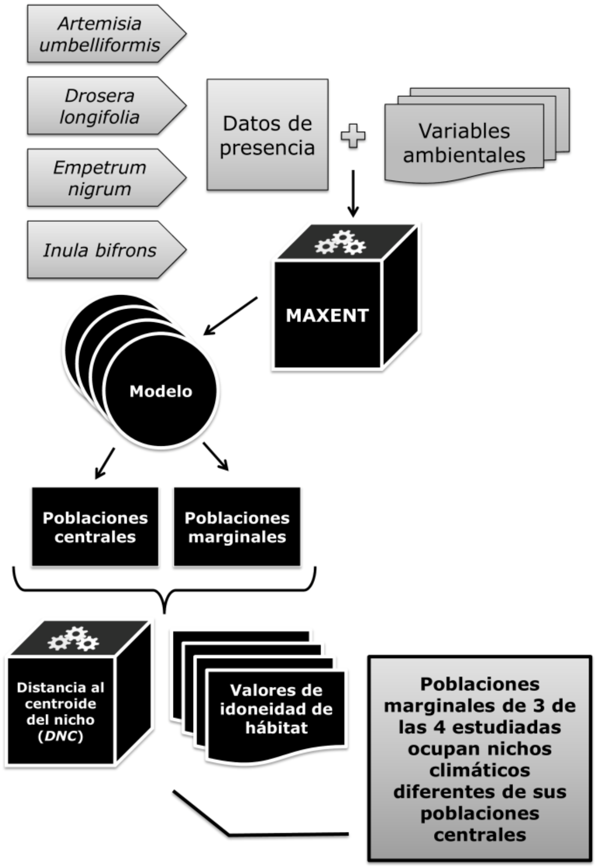

FIGURA 3 Esquema de trabajo utilizado en el Capítulo 4

Los resultados muestran que en tres de las cuatro especies analizadas (*D. longifolia*, *E. nigrum* y *I. brifrons*) sus poblaciones periféricas estarían experimentando ambientes aparentemente menos idóneos que los que experimentan las de sus núcleos de distribución. Por ello consideramos que a la hora de diseñar estrategias de conservación además de tener en cuenta las habituales amenazas a las que suelen estar sometidas las poblaciones silvestre, también deberían tenerse en cuenta estas “fragilidades” endógenas detectadas de estas poblaciones marginales derivadas de su ubicación subóptima, que se verán agravadas por la situación actual de cambio climático (Tylianakis, Didham, Bascompte, & Wardle, 2008). Asumimos, no obstante una de las principales críticas a este planteamiento y es el hecho probable de que muchas de las poblaciones marginales ponen de manifiesto la existencia de nichos especiales – microrefugios –, de gran importancia ecológica y que les confieren una alta viabilidad, que es ajena a las características adversas del medio que les rodea (Ashcroft, Gollan, Warton, & Ramp, 2012).

Evaluación de las similitudes de nicho entre poblaciones centrales y marginales de especies endémicas europeas

Siguiendo la línea metodológica y conceptual desarrollada en el capítulo previo, en el **Capítulo 5**, se ha revisado y testado una vez más la hipótesis de centro-periferia (“*Centre–Periphery Hypothesis*”; *sensu* Pironon et al., 2017). En esta ocasión el objetivo es generar un proceso metodológico estandarizado que pueda ser aplicado eficazmente a cualquier taxón, de cualquier ámbito geográfico con el fin de evaluar si hay correspondencia entre la distancia geográfica y la distancia ecológica de sus poblaciones. Aunque hay algunos trabajos que muestran que para algunas especies no siempre hay concordancia (Abeli et al., 2014; Channell & Lomolino, 2000; Mandák, Bímová, Plačková, Mahelka, & Chrtek, 2005; Pironon, Villellas, Morris, Doak, & García, 2015; Sagarin & Gaines, 2002; Sagarin, Gaines, & Gaylord, 2006), en nuestra aproximación metodológica hemos querido ir un paso más allá empleando una metodología más precisa (la unión MNE y análisis multivariados) y aplicándola a un mayor número de especies, en concreto a 81 endemismos europeos, que además corresponden a varios grupos de organismos de ecologías, hábitos y comportamientos muy diversos.

Para realizar este análisis, calculamos los nichos realizados (*sensu* Sillero, 2011) utilizando tres diferentes técnicas de modelado: Bioclim, Domain y Maxent. El grado en que los valores ajustados discriminan entre los resultados observados se midió utilizando AUC (Liu et al., 2005). Además, calculamos un conjunto de 100 modelos nulos para cada método de modelado, siguiendo la metodología de Raes y Steege (2007). Como el área de estudio es la misma para todas las especies, calculamos los mismos modelos nulos para cada método de modelado, independientemente de la especie. Por lo tanto, se compararon las AUC entre un método de modelado específico y su correspondiente modelo nulo, mezclando todos los valores de AUC. Las estimaciones del nicho realizado por la especie para los diferentes conjuntos de datos se compararon siguiendo el enfoque de Broennimann et al. (2012) y Petitpierre et al. (2012) aplicando los procedimientos implementados en el paquete de R 'ecospat' (Broennimann, Di Cola, & Guisan, 2016). Ecospat cuantifica la superposición de nicho entre dos entidades, ya sean especies o poblaciones (por ejemplo, nativa versus invasiva o dos intervalos parciales como en este caso). El paquete funciona en tres pasos (Warren et al., 2008): (i) extrae los valores ambientales de los registros del par de especies (usando las mismas variables de los cálculos del MNE), transforma estos valores en densidades por parámetros kernel, y los representa a lo largo de los ejes ambientales de una PCA; (ii) mide la superposición de nicho a lo largo de los gradientes de la PCA; y (3) aplica pruebas estadísticas de equivalencia de nicho y similitud (Carretero & Sillero, 2016). Finalmente, extrajimos todos los valores de idoneidad por especie y por conjunto de datos para los tres métodos de modelado. Luego, se compararon los valores de idoneidad entre conjuntos de datos, mezclando todos los valores de idoneidad.

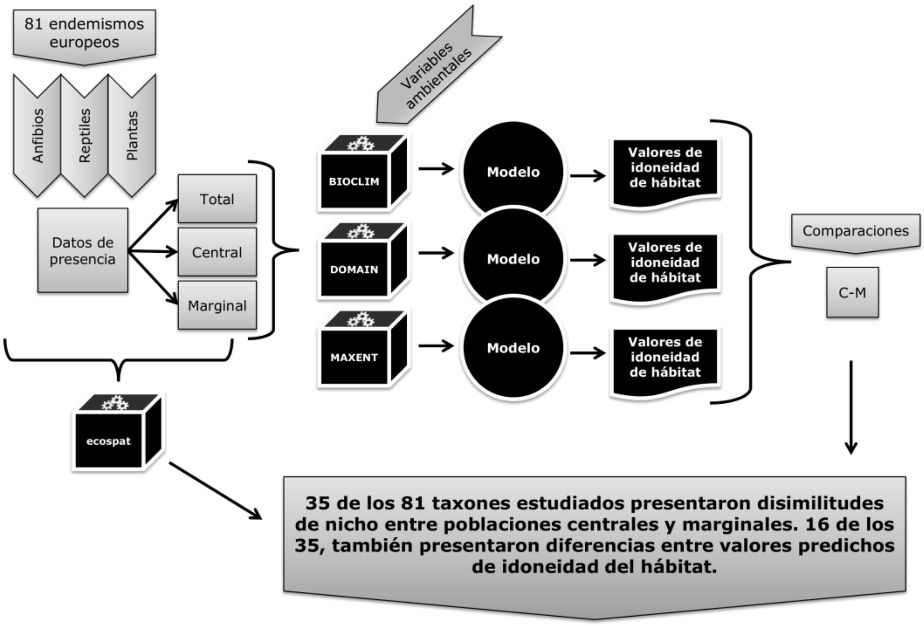

FIGURA 4 Esquema de trabajo utilizado en el Capítulo 5

Nuestros resultados muestran un buen desempeño de las técnicas aplicadas para las especies estudiadas, eminentemente sésiles (plantas) o de escasa movilidad (reptiles y anfibios), pero esperamos que se mantenga su eficacia con cualquier otro grupo de organismos, ya que a una escala amplia como la empleada, las variables clima y topografía son las que habitualmente gobiernan la distribución de las especies (Hortal, Roura-Pascual, Sanders, & Rahbek, 2010; Pearson & Dawson, 2003; Thuiller, Araújo, & Lavorel, 2004).