Modelos Predictivos: Aplicaciones para Optimizar la Conservación de la Biodiversidad Vegetal

Ricardo Enrique Hernández-Lambraño
B.Sc. Biología; M.Sc. Ciencias Ambientales

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MODELOS PREDICTIVOS: APLICACIONES PARA OPTIMIZAR LA CONSERVACIÓN DE LA BIODIVERSIDAD VEGETAL

PREDICTIVE MODELS: APPLICATIONS TO OPTIMIZE THE CONSERVATION OF PLANT BIODIVERSITY

Memoria presentada por el Graduado en Biología y Máster en Ciencias Ambientales RICARDO ENRIQUE HERNÁNDEZ LAMBRAÑO para optar al grado de Doctor en Biología de la Conservación y Biodiversidad por la Universidad de Salamanca

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La Comisión Académica del programa de Doctorado en Biología y Conservación de la Biodiversidad, **INFORMA FAVORABLEMENTE** sobre la Tesis Doctoral titulada *"Modelos predictivos: Aplicaciones para optimizar la conservación de la biodiversidad vegetal"*, presentada por D. Ricardo Enrique Hernández Lambraño para su tramitación en la modalidad de compendio de artículos/publicaciones (Comisión de Doctorado y Posgrado, 15 de febrero de 2013). D. Ricardo Enrique Hernández Lambraño presenta cinco artículos de primer autor de su Tesis Doctoral para el periodo 2017-2021 (dos artículos en revistas Q1, dos en revistas Q2 y uno en revista Q3), cumpliendo con los requisitos establecidos por la Escuela de Doctorado a través de la Comisión de Doctorado y Posgrado.

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FERNANDO -
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Dr. Fernando Silla Cortés
Coordinador del Programa de Doctorado en Biología y Conservación de la Biodiversidad.
Profesor Titular de Universidad
Facultad de Biología - Universidad de Salamanca
Email: fsilla@usal.es
Tfno: (+34) 677596025

La tesis titulada "*Modelos predictivos: aplicaciones para optimizar la conservación de la biodiversidad vegetal*", corresponde a un compendio de trabajos previamente publicados. Se incluyen 5 artículos.

1. Hernández Lambraño, R.E., R. Carbonell and J.A. Sánchez Agudo (2020). Making the most of scarce data: Mapping distribution range and variation in population abundance of a threatened narrow-range. Journal for Nature Conservation 57: 125889_1-9. https://doi.org/10.1016/j.jnc.2020.125889
2. Hernández-Lambraño, R.E; de la Cruz, DR, J.Á. Sánchez Agudo (2021). Effects of the climate change on peripheral populations of hydrophytes: A sensitivity analysis for European plant species based on climate preferences. Sustainability 13 (6): 3147. https://doi.org/10.3390/su13063147
3. Hernández-Lambraño, R.E., P González Moreno, J.Á. Sánchez Agudo (2017). Towards the top: niche expansion of Taraxacum officinale and Ulex europaeus in mountain regions of South America. Austral Ecology 42 (5), 577-589. https://doi.org/10.1111/aec.12476
4. Hernández-Lambraño, R.E., P González-Moreno, J.Á. Sánchez-Agudo (2018). Environmental factors associated with the spatial distribution of invasive plant pathogens in the Iberian Peninsula: The case of Phytophthora cinnamomi Rands. Forest Ecology and Management 419, 101-109. https://doi.org/10.1016/j.foreco.2018.03.026
5. Hernández-Lambraño, R.E., DR de la Cruz, J.Á. Sánchez-Agudo (2019). Spatial oak decline models to inform conservation planning in the Central-Western Iberian Peninsula. Forest Ecology and Management 441: 115-126. https://doi.org/10.1016/j.foreco.2019.03.028

Se expone a continuación el nombre y la afiliación completa actual de cada uno de los autores, por orden de aparición:

- Ricardo Enrique Hernández-Lambraño: ricardohl123@usal.es.
  Departamento de Botánica y Fisiología Vegetal, Facultad de Farmacia, Universidad de Salamanca.
  Avenida Licenciado Méndez Nieto s/n, 37007, Salamanca, España.
- Pablo González-Moreno: glezmoreno@gmail.com.
  Departamento de Ingeniería Forestal, Universidad de Córdoba,
  Campus de Rabanales, Crta. IV, km. 396, 14071 Córdoba, España.
- José Ángel Sánchez-Agudo: jasagudo@usal.es.
  Departamento de Botánica y Fisiología Vegetal, Facultad de Farmacia, Universidad de Salamanca.
  Avenida Licenciado Méndez Nieto s/n, 37007, Salamanca, España
- Roberto Carbonell: carbonel@bio.ucm.es.
  Servicio Territorial de Medio Ambiente de Salamanca, Junta de Castilla y León, 37071, Salamanca, España.
- David Rodríguez de la Cruz: droc@usal.es.
  Departamento de Botánica y Fisiología Vegetal, Facultad de Farmacia, Universidad de Salamanca.
  Avenida Licenciado Méndez Nieto s/n, 37007, Salamanca, España.

Dr. D. José Ángel Sánchez Agudo, Profesor Contratado Doctor del Departamento de Botánica y fisiología Vegetal de la Universidad de Salamanca,

CERTIFICA:

que la tesis doctoral titulada "*Modelos predictivos: aplicaciones para optimizar la conservación de la biodiversidad vegetal*", ha sido realizada por D. RICARDO ENRIQUE HERNÁNDEZ-LAMBRAÑO para optar al título de Doctor por la Universidad de Salamanca desarrollada en el marco del Programa de Doctorado en Biología y Conservación de la Biodiversidad bajo su dirección, por lo que autorizan su presentación, mediante compendio de publicaciones.

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Fdo.:
Dr. D. José Ángel Sánchez Agudo

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Enrique Hernández
Lambraño el día 19 de
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Ricardo.

Fdo.:
Doctorando D. Ricardo Enrique Hernández Lambraño

A mi familia,

Sully, Javier y …

CONTENIDO

CAPÍTULO 1

Fotos: Roberto Carbonell; Juan Antonio Sánchez Rodríguez; Sergio Pérez Gorjón; José Ángel Sánchez Agudo.

RESUMEN EXTENDIDO

La presente crisis global de biodiversidad -*i.e.*: rápida extinción de especies e intensa degradación de los ecosistemas- constituye sin duda alguna, la mayor amenaza a la que se enfrenta nuestra sociedad. Con el fin de tratar de revertir esta grave situación, desde hace décadas se están llevando a cabo, numerosas medidas dirigidas a salvaguardar los hábitats y sus especies que, en su mayoría, pueden agruparse en dos categorías/estrategias principales: elaboración de listas rojas y planes de conservación, y creación de parques y reservas naturales. Aunque los recursos invertidos en este sentido por parte de gobiernos e instituciones transnacionales han sido cuantiosos, las poblaciones de especies silvestres han continuado y continúan disminuyendo de forma alarmante en prácticamente todas las regiones biogeográficas (Almond et al., 2020). Sin duda se trata de un contexto desolador en el que, pese a que parece que poco más se puede hacer, por el contrario, debe actuar como agente revulsivo con el que, y apelando a la etimología de este término (del latín, *revulsum*), se produzca un gran cambio que induzca a personas, organismos e instituciones vinculadas a la conservación internacional, a desarrollar iniciativas todavía más eficaces e innovadoras. Estas, aun pudiendo ser rompedoras o iconoclastas, para garantizar su viabilidad y replicabilidad, deben ir siempre respaldadas por criterios científicos a través del uso de procesos sistemáticos (Margules and Pressey, 2000; Yemshanov et al., 2013). Este es el caso de los *modelos cuantitativos*, que precisamente suponen los sujetos de análisis en esta tesis doctoral. De forma sintética se pueden describir como herramientas ecoinformáticas de gran potencia analítica que, aplicadas sobre conjuntos de datos ambientales, permiten interpretar procesos biológicos complejos. Su utilidad práctica es clara en la toma de decisiones en la gestión de especies y hábitats, así como en el desarrollo de políticas de conservación derivadas de las mismas (García-Díaz et al., 2019). Ello se debe, sobre todo, a que:

- Proporcionan información fundamental sobre la dinámica de las especies objetivo y los sistemas ecológicos a conservar;
- Ofrecen una forma transparente, sistemática y repetible de evaluar, contrastar y proyectar la eficacia potencial de las soluciones de gestión de la conservación (Nicholson et al., 2019).

Son precisamente por estas razones, por las que decidimos que estos *modelos cuantitativos* constituyeran el eje vertebrador de este trabajo doctoral, puesto que en cada capítulo mostramos un ejemplo de su potencial aplicación en diversas cuestiones relacionadas con problemáticas de la conservación de la biodiversidad vegetal. La metodología es, por tanto, transversal, estando soportada conceptualmente por las teorías estadísticas y la biogeografía, y funcionalmente por las tecnologías de la información. Con esta aportación pretendemos llevar un poco más allá las posibilidades que nos brindan estos modelos, al proporcionar un marco metodológico replicable y cuyos resultados sirvan de apoyo a la gestión y la toma de decisiones para situaciones ambientales concretas, como son: 1) el estudio y seguimiento de *especies de plantas amenazadas*, 2) el estudio y seguimiento de *especies de plantas invasoras* y 3) la *gestión y análisis de riesgos* en ecosistemas forestales.

La estructura narrativa de esta propuesta doctoral se articula en torno a las 5 siguientes publicaciones científicas, de las que, a continuación, se ofrece un resumen:

- **Hernández Lambraño, R.E**., R. Carbonell and J.A. Sánchez Agudo (2020). Making the most of scarce data: Mapping distribution range and variation in population abundance of a threatened narrow-range. *Journal for Nature Conservation* 57: 125889_1-9. https://doi.org/10.1016/j.jnc.2020.125889
- **Hernández-Lambraño, R.E**; de la Cruz, DR, J.Á. Sánchez Agudo (2021). Effects of the climate change on peripheral populations of hydrophytes: A sensitivity analysis for European plant species based on climate preferences. *Sustainability* 13 (6): 3147. https://doi.org/10.3390/su13063147
- **Hernández-Lambraño, R.E.**, P González Moreno, J.Á. Sánchez Agudo (2017). Towards the top: niche expansion of *Taraxacum officinale* and *Ulex europaeus* in mountain regions of South America. *Austral Ecology* 42 (5), 577-589. https://doi.org/10.1111/aec.12476
- **Hernández-Lambraño, R.E**., P González-Moreno, J.Á. Sánchez-Agudo (2018). Environmental factors associated with the spatial distribution of invasive plant pathogens in the Iberian Peninsula: The case of *Phytophthora cinnamomi* Rands. *Forest Ecology and Management* 419, 101-109. https://doi.org/10.1016/j.foreco.2018.03.026
- **Hernández-Lambraño, R.E.**, DR de la Cruz, J.Á. Sánchez-Agudo (2019). Spatial oak decline models to inform conservation planning in the Central-Western Iberian Peninsula. *Forest Ecology and Management* 441: 115-126. https://doi.org/10.1016/j.foreco.2019.03.028

Resumen del primer artículo:

En el primer artículo de esta tesis (capítulo 2) utilizamos Modelos de Nicho Ecológico (MNE) para mapear el rango geográfico de distribución y la variación en la abundancia de las poblaciones de una planta endémica amenazada de rango estrecho (PE), *Antirrhinum lopesianum* Rothm. en la península ibérica. Las PEs amenazadas representan un desafío particular para los MNE, debido a sus distribuciones restringidas en forma de parches aislados con tamaños poblacionales pequeños. Con el calentamiento global en curso, estas especies son más susceptibles a presiones ambientales (Breggin, George y Pencak, 2003), un hecho que hace necesario la obtención de estimaciones confiables de su distribución y abundancia para diseñar estrategias fiables de conservación (Guisan et al., 2013). Los datos disponibles de estas distribuciones a menudo presentan sesgos importantes (esfuerzo de muestreo) de cara a su utilización en los programas de conservación. En este sentido, se plantea la siguiente hipótesis en el trabajo:

- Partiendo de escasos registros de presencia de una especie endémica de rango estrecho, ¿son capaces los MNE de estimar con precisión su área de distribución y las variaciones en su abundancia poblacional?

Para poder responder a esta interrogante, empleamos una base de datos con registros de presencia y abundancia para la especie analizada, un conjunto de variables ambientales de libre acceso y un enfoque metodológico basado en MNE (ver Figura 1).

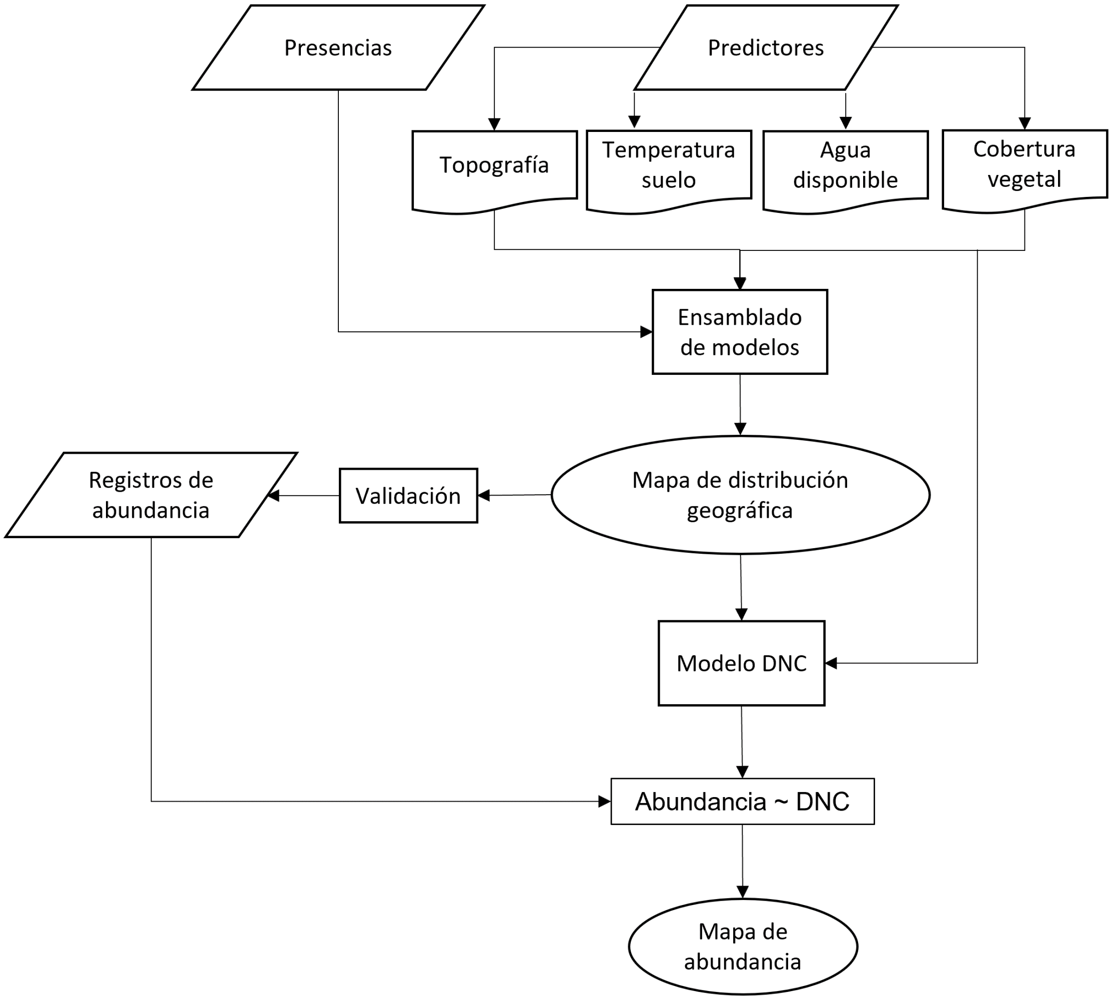

Figura 1. Esquema de trabajo utilizado en el artículo 1.

Se partió de una colección inicial de 28 registros de la especie, obtenidos a partir de la bibliografía y de la base de datos suministrada por el organismo gestor del Parque Natural Arribes del Duero. Los datos de abundancia fueron colectados por nuestro equipo de investigación mediante salidas de campo realizadas durante la primavera y el otoño de 2018. De esta forma se consiguió información de densidad poblacional de 35 localizaciones. Los datos ambientales utilizados para los análisis incluyeron variables relacionados con topografía, temperatura del suelo, disponibilidad de agua en el suelo y cobertura vegetal en el área de estudio. Estos datos fueron derivados a partir de imágenes satelitales (Landsat 8 OLI / TIRS) y sensores LiDAR. Con ellos simulamos la distribución geográfica de la especie utilizando un enfoque de ensamble de múltiples modelos (Máxima Entropía; MAXENT, regresión múltiple; GLM y árboles de regresión; GBM y RF), y mapeamos la distancia al centroide del nicho (DNC) de todas las celdas. Con este mapa de distancias extrajimos los valores de DNC de los 35 registros con datos de abundancia para la especie y evaluamos la relación entre la abundancia y su distancia al centroide del nicho utilizando un modelo lineal generalizado (GLM). El modelo resultante se utilizó para generar estimaciones espacialmente explícitas de la abundancia de la especie en todo su rango de distribución geográfica.

Los modelos DNC representan un enfoque novedoso para mapear patrones geográficos de abundancia basados en la teoría del nicho ecológico (Martínez-Meyer et al., 2013). Este enfoque asume que las condiciones óptimas para una especie se encuentran más próximas al centroide del nicho ecológico en un espacio multidimensional (Hutchinson, 1957; Maguire, 1973). En este sentido, una localidad cuyo ambiente este próximo al centroide del nicho *n*-dimensional albergará mejores condiciones para la especie y, como consecuencia, se esperará una mayor abundancia en estas localidades.

Nuestros modelos sugieren un claro efecto de la topografía y la cobertura vegetal en los patrones de distribución de los hábitats idóneos de la especie analizada. La mayoría de las áreas idóneas se ubican a lo largo de una estrecha franja a orillas de los ríos. El mapa incluye áreas con ambientes adecuados donde aún no se ha registrado la especie. Estas áreas se ubican en la parte sur y media de la Cuenca del río Sabor (Portugal), y otras en la parte sur y media del río Duero (España). El GLM mostró que la abundancia observada se asoció significativa y negativamente con la DNC. Como se esperaba, la abundancia observada cae cuando las condiciones ambientales se alejan de aquellas que se encuentran cerca del centroide del nicho ecológico de la especie. El mapa de abundancia resultante proyectó zonas con abundancias elevadas a lo largo de la Cuenca del Rio Sabor, principalmente en las partes sur y media, parte norte del río Maças, y otras en las zonas sur y media de la Cuenca del río Duero (Portugal-España).

El modelo espacialmente explícito presentado en este estudio proporciona una herramienta confiable para el manejo y conservación de *A. lopesianum* y un enfoque aplicable para otras PEs. Además, maximiza la explotación de información básica a través de recursos abiertos (*software* y variables ambientales), lo que lo hace de alto interés para instituciones con recursos limitados.

Resumen del segundo artículo:

En el segundo artículo de esta tesis (capítulo 3) aplicamos MNEs en un intento de evaluar explícitamente los efectos potenciales del cambio climático en los patrones de distribución de poblaciones amenazadas de plantas hidrófitas de ámbito europeo, en el margen sur (*i.e.,* borde trasero) de su rango de distribución (la península ibérica).

Las predicciones biogeográficas alertan de que deberían analizarse las retracciones generalizadas en los bordes traseros de los rangos de distribución de las especies en respuesta al cambio climático (Vilà-Cabrera et al., 2019). En efecto, el clima se considera el factor más importante que determina la distribución de especies de plantas, ya que la temperatura afecta a la disponibilidad de agua, especialmente en los bordes traseros de la distribución. Estas predicciones se basan en el hecho de que las poblaciones que habitan estas zonas a menudo se encuentran en el límite de tolerancia ecológica de la especie. Al ocupar hábitats menos favorables se espera que su rendimiento disminuya a medida que el calentamiento climático las empuja a la extirpación (Urban, 2015), no obstante, las evidencias empíricas en este sentido siguen siendo escasas (Pironon et al., 2015). El estudio de estas poblaciones marginales es de vital importancia para la conservación a largo plazo de la diversidad genética, el potencial evolutivo y la respuesta de las especies al cambio climático en curso. Por lo tanto, la identificación de su vulnerabilidad al cambio climático resulta crucial para orientar los esfuerzos de conservación (Stanton et al., 2015). Por todo ello, planteamos varias cuestiones en este estudio:

- Las poblaciones de plantas amenazadas que habitan el borde trasero de su rango de distribución, ¿se encuentran en los límites de tolerancia climática de la especie?
- ¿Pueden los MNE cuantificar los patrones geográficos de vulnerabilidad al cambio climático?
- ¿Podemos identificar de una manera espacialmente explícita, si las poblaciones de especies amenazadas que habitan en el borde trasero de su distribución se encuentran en hábitats vulnerables al cambio climático?

Para este trabajo se empleó una base de datos de registros de presencia de 5 especies de hidrófitos, un conjunto de variables ambientales de libre acceso y un enfoque metodológico basado en MNE (ver Figura 2).

Los datos de presencia de las especies analizadas proceden del Servicio de Información sobre Biodiversidad Global (GBIF; www.gbif.org). Los registros fueron procesados para garantizar que sólo se utilizarán los de mayor calidad en el análisis. Así, se conservaron los que cumplían las siguientes condiciones: (1) estar georreferenciados; (2) fecha del registro; (3) información sobre la localidad de muestreo; (4) coordenadas con resolución de un 1 × 1km y (5) registros dentro del área de distribución nativa conocida de la especie. Finalmente, eliminamos los registros fuera de los años 1979-2013 para alinearnos con la referencia temporal de las variables climáticas.

Las variables climáticas que describen el clima actual (representativas de 1973-2013) en la península ibérica se descargaron de “Climatologies at high resolution for the Earth’s land Surface áreas” (CHELSA; http://chelsa-climate.org/), con una resolución aproximada de 1 × 1km. Elegimos cuatro variables bioclimáticas (temperatura promedio anual, temperatura estacional, precipitación anual y precipitación estacional), para representar una amplia gama de patrones climáticos estacionales y anuales en todo el área de estudio. Para caracterizar las condiciones climáticas en el futuro (2050: promedio de 2041-2060), utilizamos los valores promedios de dos modelos climáticos globales (GCM): (1) Community Climate System Model (CCSM4; Gent et al., 2011) y 2) Hadley Global Environment Model (HadGEM2-ES; Martin et al., 2011). Para los análisis, utilizamos dos escenarios de emisiones de CO_2 (RCP): (1) RCP 4.5, que representa emisiones medias de CO_2; y (2) RCP 8.5, que representa elevadas emisiones de CO_2 (Harris et al., 2014). Los datos climáticos para el futuro fueron descargados de la base de datos del CHELSA, con una resolución aproximada de 1 × 1km.

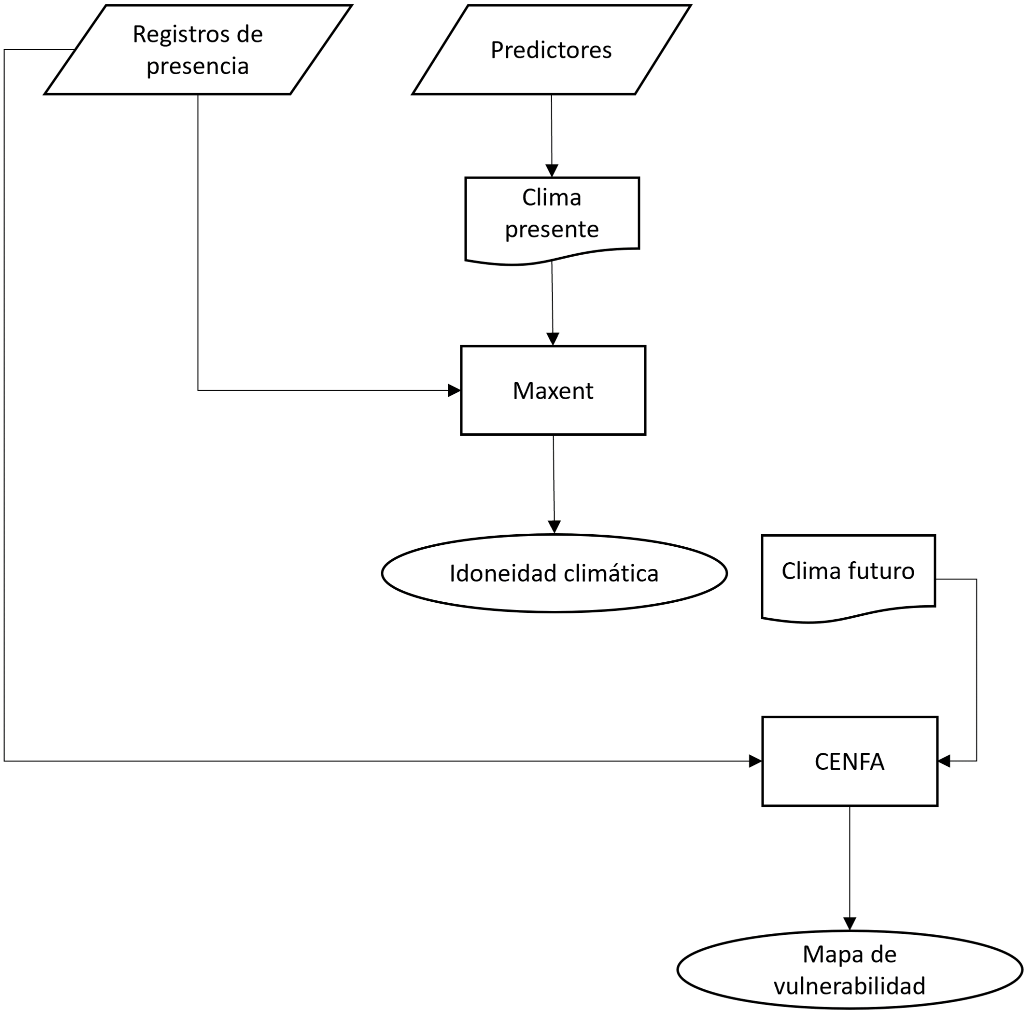

Figura 2. Esquema de trabajo utilizado en el artículo 2.

Con estos datos, en primer lugar y mediante el programa Maxent, calibramos el MNE para cuantificar la idoneidad climática de las localidades habitadas por las poblaciones amenazadas en la península ibérica. En esta ocasión, y con el objetivo de obtener las estimaciones más fiables de la idoneidad climática en el área de estudio, seguimos el enfoque de modelamiento propuesto por Cobos et al. (2019). Este enfoque permite seleccionar, entre los numerosos y complejos parámetros de calibración, aquellos que demuestran el mejor rendimiento en función de la significancia, la capacidad predictiva y el nivel de complejidad de los modelos calibrados. En segundo lugar, usando el paquete estadístico CNFA (Análisis de factores de nicho climático; Rinnan and Lawler, 2019) cuantificamos la vulnerabilidad de las poblaciones de las especies analizadas al cambio climático. Este enfoque proporciona una visión espacialmente explícita de los patrones geográficos de vulnerabilidad basado en datos espaciales fácilmente disponibles (*i.e.,* registros de solo presencia y datos climáticos). Para una descripción detallada del enfoque de modelamiento propuesto en este estudio, ver la sección "materiales y métodos" del capítulo 3.

Nuestros resultados mostraron que las poblaciones estudiadas habitan ambientes menos adecuados en la península ibérica en relación con los climas óptimos de cada una de las especies. Estos resultados sugieren una explicación plausible para el grado actual de estancamiento o regresión experimentado por estas poblaciones. Estas poblaciones, a su vez, mostraron alta sensibilidad y, por lo tanto, vulnerabilidad a los extremos térmicos y alta estacionalidad de la humedad y la temperatura. Las predicciones climáticas para 2050 muestran que la mayoría de las poblaciones tenderán a presentarse en situaciones de riesgo ambiental en la península ibérica. Nuestro enfoque de análisis de vulnerabilidad nos permitió detectar también áreas que podrían servir como refugio a estas plantas para escapar de las alteraciones climáticas esperadas para la península ibérica. Estas predicciones apuntan a que zonas del noreste de las cuencas hidrográficas del Duero y del Ebro, así como zonas adyacentes a las cuencas hidrográficas del Miño y en varias del País Vasco, pueden proporcionar refugios potenciales para las poblaciones analizadas frente al cambio climático.

El modelo espacialmente explícito propuesto en este estudio sugiere que acciones dirigidas a la conservación de estas poblaciones deben priorizarse en las zonas geográficas en las que la vulnerabilidad es mayor.

***Resumen del tercer artículo*:**

En el tercer artículo de esta tesis (capítulo 4) usamos dos especies de plantas ampliamente distribuidas a nivel mundial como modelos biológicos para probar la teoría de la conservación de nicho en las especies invasoras. Esta teoría establece que estas especies presentan características de nicho similares en sus rangos nativos e invadidos (Peterson, 2003). Sin embargo, esta teoría ha sido cuestionada recientemente por estudios que destacan la existencia de factores que pueden causar que las especies invasoras expandan su nicho más allá de sus requerimientos ambientales en el rango nativo (Broennimann et al., 2007). Evaluar si el nicho ecológico de una especie puede cambiar entre diferentes áreas geográficas es extremadamente importante para predecir la dispersión de especies invasoras en el actual contexto de rápido cambio global (Guisan et al., 2014). En este caso, planteamos las siguientes cuestiones:

- ¿*Taraxacum officinale* y *Ulex europaeus* experimentan cambio de nicho durante su invasión en Suramérica?
- ¿Cuáles son los principales factores que explican sus patrones de distribución en Sur América?

- ¿Es el clima el principal factor que explica los patrones de distribución de las especies invasoras a escala continental?
- ¿Resoluciones finas (descripción de los datos ambientales) mejoran nuestra comprensión de los patrones de distribución de las especies invasoras a escala continental?

Para llevar a cabo este estudio, empleamos una base de datos de registros de presencias para las especies analizadas en sus rangos de distribución (nativo e introducido), un conjunto de variables ambientales: climáticas y topográficas a diferentes resoluciones espaciales (cuadrículas de 1 × 1 y 20 × 20km) y un enfoque metodológico que combina el uso de análisis de componentes principales (PCA-env) y MNE recíprocos (ver Figura 3).

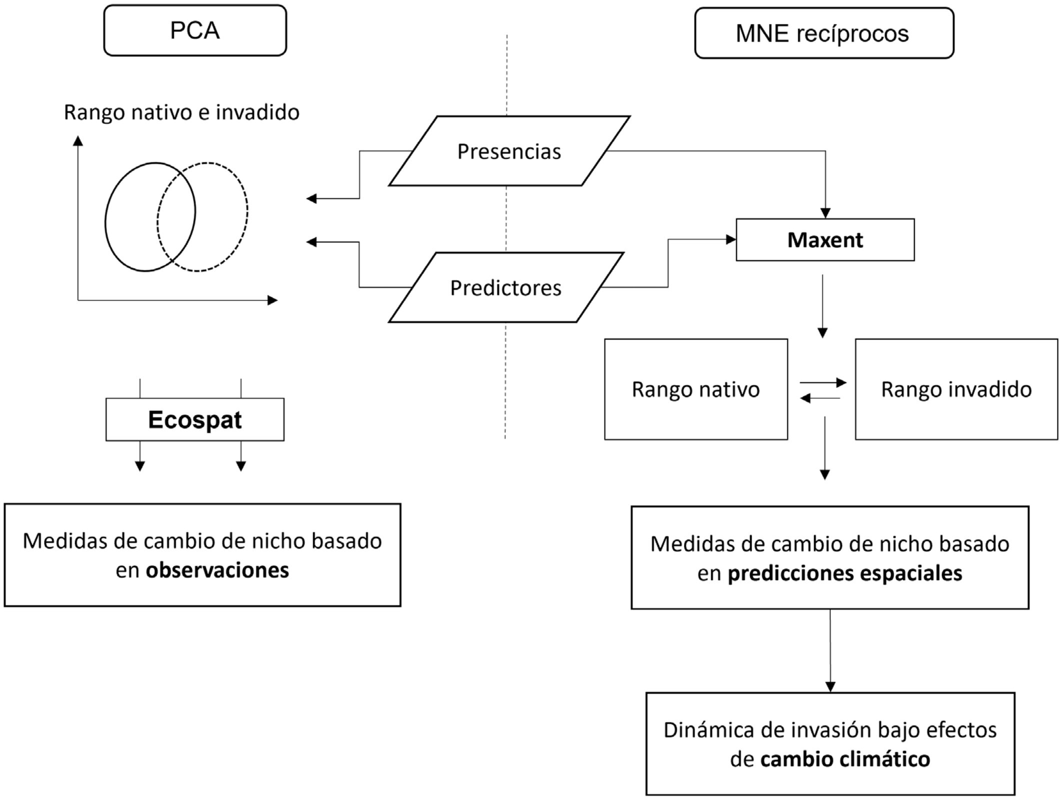

Figura 3. Esquema de trabajo utilizado en el artículo 3.

Los registros de presencias para la especie en sus rangos nativos se descargaron de las bases de datos de GBIF y del compendio de especies invasoras del Centre for Agriculture and Biosciences International (CABI; https://www.cabi.org/). Los registros fueron procesados (*i.e.,* eliminación de duplicados y agrupamiento espacial) teniendo en cuenta las dos resoluciones de estudio. Los registros de presencia para estas especies en Suramérica fueron descargadas de GBIF y CABI y fueron preparadas de la misma forma antes descrita. Los datos ambientales utilizadas para los análisis incluyen nueve variables climáticas disponibles en WorldClim database (https://www.worldclim.org/) a una resolución aproximada de 1 × 1 y 20 × 20km (T_AM, T_DR, T_WM, T_AR, T_WQ, P_A, P_WM, P_DM y P_S; ver capítulo 4 para los códigos de las variables) y dos variables no climáticas (topo_div y sun_l) derivadas de un modelo digital de elevación (MDT) disponible en el servicio geológico de los estados unidos (USGS; https://www.usgs.gov/). Para medir el cambio de nicho relacionado con factores climáticos y no climáticos (*i.e.,* radiación solar y topografía) para las especies analizadas entre sus rangos nativos e introducidos, usamos el enfoque metodológico de Broennimann et al. (2012). En este enfoque, un PCA-env es calibrado usando el conjunto de todas las condiciones ambientales en ambos rangos. Luego, las condiciones ambientales disponibles para la especie dentro del background estudiado son comparadas con aquellas condiciones en las áreas que son efectivamente ocupadas por la especie en cada uno de sus rangos (*i.e.,* nativo *vs.* introducido).

Para comparar los nichos ecológicos en el espacio geográfico, aplicamos Modelos de Máxima Entropía (Maxent) para generar mapas recíprocos (Peterson, 2003). En este enfoque, un modelo es calibrado sólo con los registros de presencia del área nativa y luego es proyectado al rango invadido. Este último es comparado con un modelo calibrado solo con los registros de presencia del área introducida. Este procedimiento es repetido, pero proyectando el modelo calibrado con los datos del rango introducido hacia el rango nativo y luego comparado de la misma forma antes descrita. Finalmente, investigamos la dinámica de invasión en un escenario de calentamiento global severo para el año 2050 (HadGEM2; RCP-8.5), con el objetivo de desentrañar el papel de los cambios de nicho en la distribución potencial de la especie en el futuro. Los modelos se calibraron con todos los registros de presencias (nativos más Suramérica) para tener en cuenta las posibles diferencias de nicho entre los rangos nativos e introducidos (Broennimann and Guisan, 2008).

Nuestros resultados indican una clara expansión de nicho para ambas especies en América del Sur hacia ubicaciones con temperaturas más altas y de mayor precipitación y radiación, en relación con sus rangos nativos. Por el contrario, era menos relevante el conjunto de condiciones ambientales que sólo ocupaban los rangos nativos (es decir, el nicho no cubierto = *anfilling*). La magnitud de los cambios de nicho no depende de la resolución de las variables. Los modelos calibrados con ocurrencias del rango nativo predijeron grandes áreas adecuadas en América del Sur (fuera del rango de los Andes) donde *T. officinale* y *U. europaeus* están actualmente ausentes. El nicho no cubierto (nicho *anfilling*) sugiere un alto potencial para invadir regiones adicionales en el futuro, lo cual es extremadamente relevante considerando el impacto actual de estas especies en el hemisferio sur. Además, ambas especies podrían aumentar sus distribuciones potenciales para 2050, principalmente en la parte sur del continente. Estos hallazgos confirman que las especies invasoras pueden ocupar nuevos nichos que no son predecibles a partir del conocimiento basado solo en variables climáticas o información del rango nativo.

***Resumen del cuarto artículo*:**

En el cuarto artículo de esta tesis (capítulo 5) usamos un hongo patógeno invasor ampliamente distribuido a nivel mundial como modelo biológico, y un enfoque de modelamiento basado en teorías de información en un intento de evaluar explícitamente los principales factores que determinan su distribución espacial en ecosistemas forestales de la península ibérica.

Los microorganismos patógenos del suelo son bien conocidos por sus importantes impactos ecológicos y socioeconómicos en los ecosistemas (Gómez-Aparicio et al., 2012). Entre los patógenos más importantes que causan grandes pérdidas económicas en la agricultura, y afectan la estabilidad de ecosistemas naturales en todo el mundo, se destaca *Phytophthora cinnamomi* Rands (Brasier, 1996). En Europa, su presencia ha provocado la devastación de importantes cultivos agrícolas y la reducción de grandes áreas forestales (de Sampaio e Paiva Camilo-Alves et al., 2013). Entender dónde y cuándo los patógenos del suelo como *Phytophthora* spp. tienen más probabilidades de causar grandes epidemias ha sido durante mucho tiempo un importante punto de estudio en las investigaciones agrícolas (Otten et al., 2004). Sin embargo, tenemos poco conocimiento sobre la complejidad de sus patrones de distribución espacial a gran escala, particularmente para hábitats naturales y seminaturales (Ettema and Wardle, 2002). En este sentido, varias cuestiones fueron planteadas en este artículo:

- ¿Cuál es el rol relativo de los factores ambientales y la influencia humana en la distribución de *Phytophthora cinnamomi* Rands, en ecosistemas mediterráneos?
- ¿Podemos estimar su posible distribución geográfica en la península ibérica como aproximación de su potencial impacto?

Para dar respuesta a estas cuestiones, en este estudio utilizamos una exhaustiva base de datos de registros de *P. cinnamomi* en la península ibérica, un conjunto de predictores ambientales reflejando condiciones abióticas (clima y suelo), condiciones bióticas (distribución potencial de los principales árboles hospederos susceptibles y cobertura vegetal basada en NDVI), la influencia humana (usos del suelo) y un robusto enfoque de modelamiento que incluye principios de teorías de información (ver Figura 4).

Los registros de presencia/ausencia de *P. cinnamomi* en el territorio analizado fueron obtenidos de diferentes fuentes datos (n = 295 registros de presencia/ausencia). Los registros fueron preparados a una resolución de cuadrícula de 1 × 1km para eliminar registros duplicados (es decir, solo un registro de ocurrencia por cuadrado de cuadrícula de 1 × 1 km). Este filtro redujo el número de registros de presencia/ausencia a 277 cuadrículas de 1 × 1km (presencia: n = 157; ausencias: n = 120).

Los potenciales predictores de la dispersión de *P. cinnamomi* en el área de estudio, obtenidos de diferentes bases de datos, fueron agrupados en tres grupos de variables; abióticas (clima y suelo), bióticas (plantas hospedadoras y cobertura vegetal), e influencia humana (usos del suelo). Para describir el clima en el área de estudio usamos la base de datos de WorldClim. Seleccionamos aspectos relevantes de la temperatura y las precipitaciones como son los rangos anuales y la temperatura media del cuatrimestre más húmedo. Las variaciones en las características físicas y químicas del suelo fueron descargados de la base de datos de suelos mundiales del ISRIC (https://soilgrids.org/). Las características relacionadas con la intervención humana en el paisaje fueron descargadas de la base de datos de usos del suelo del CORINE Land-cover (https://land.copernicus.eu/pan-european/corine-land-cover). Extrajimos el porcentaje de área ocupada con superficies artificiales (*i.e.,* tejido urbano continuo y discontinuo, unidades industriales y comerciales, minas, vertederos y construcción), áreas agrícolas (*i.e.,* tierras arables, cultivos permanentes, cultivos anuales, tierras agricolas con áreas significativas de vegetación natural y áreas forestales) y áreas de pastos (*i.e.,* tierras utilizadas para sustentar animales de pastoreo).

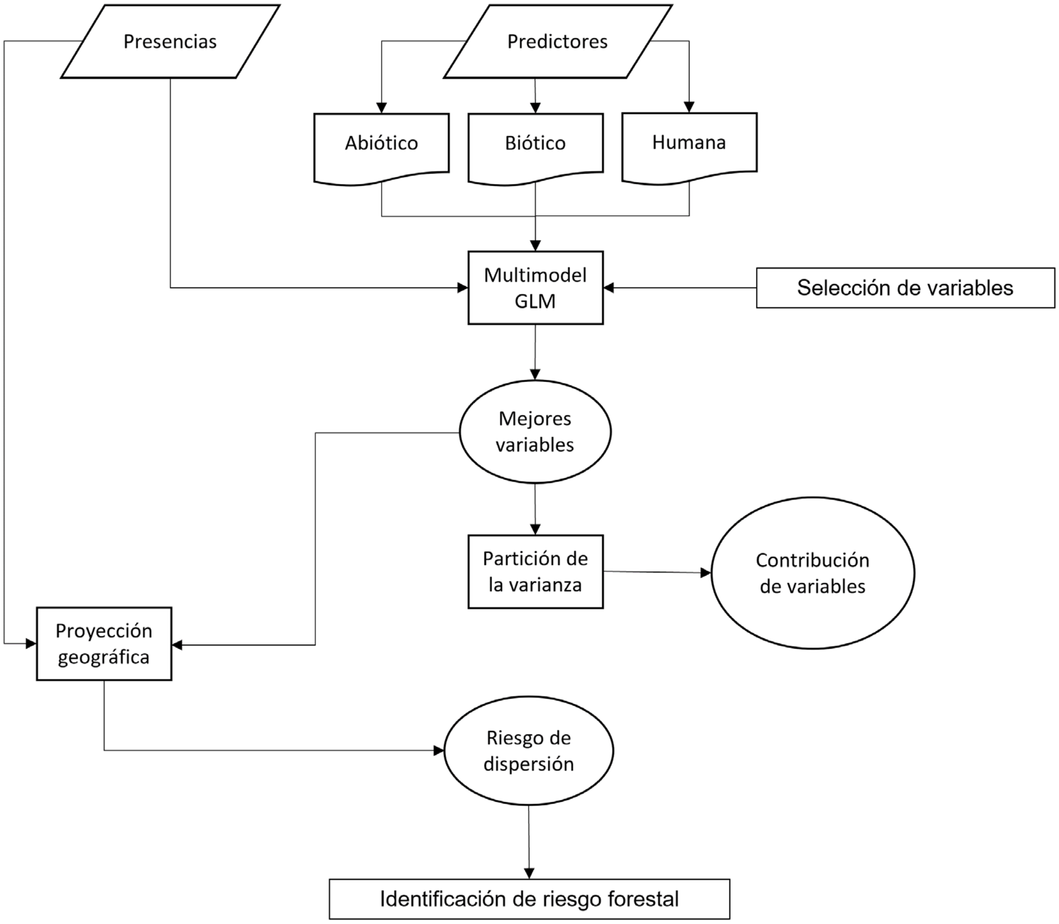

Figura 4. Esquema de trabajo utilizado en el artículo 4.

Con el fin de capturar la variación geográfica en la presencia de dos especies forestales hospederas susceptibles a *P. cinnamomi* en la península ibérica, creamos modelos de distribución geográfica para *Quercus ilex* y *Q. suber* utilizando modelos lineales generalizados (GLM). Finalmente, para representar el estado de la vegetación en el área de estudio, usamos un promedio anual del Índice de Vegetación de Diferencia Normalizada (NDVI; enero-diciembre de 2014) de la base de datos de la NASA-MODIS.

Con estos datos, aplicamos un enfoque de selección de modelos (multimodel inference; (Burnham and Anderson, 2002), basado en la selección del mejor modelo (GLM), que se ajuste a los datos existentes, a partir de un subconjunto de modelos utilizando el criterio de información de Akaike corregido para una gran cantidad de predictores (AICc). Luego, para cada modelo candidato en la selección final, calculamos su peso en el modelo (***Wi***) para clasificar los predictores en orden de importancia explicando la presencia de *P. cinnamomi* y sumamos los ***Wi*** de las variables para todos los modelos dentro de cuatro unidades de AICc del mejor modelo (González-Moreno et al., 2013). Para cuantificar el efecto individual o compartido de los conjuntos de variables (biótico, abiótico e influencia humana), utilizamos un enfoque de partición de la varianza. Finalmente, para ilustrar la distribución geográfica de *P. cinnamomi*, como una aproximación de su potencial impacto en toda la península ibérica, proyectamos el mejor modelo a todas las cuadrículas de 1 × 1km del área de estudio.

Los resultados obtenidos sugieren que la distribución de *P. cinnamomi* en la península ibérica es altamente dependiente de factores abióticos como las propiedades del suelo y la temperatura, seguidos de las variables de influencia humana (suelos agrícolas), y, finalmente, de factores bióticos, como la presencia de uno de sus principales hospederos susceptibles, *Q. suber*. Un hallazgo importante de este estudio es la asociación positiva entre la presencia de *P. cinnamomi* y la distribución de *Q. suber*. La presencia de *P. cinnamomi* y su virulencia pueden representar una amenaza importante para la estabilidad de los bosques mediterráneos de la península ibérica, dominados fundamentalmente por encinas, robles y alcornoques. Estos ecosistemas forestales son particularmente vulnerables a los procesos de declive principalmente debido al efecto combinado de condiciones climáticas extremas, alteraciones del suelo y distribución generalizada de patógenos exóticos (Brasier et al., 1993). Otro aspecto importante a considerar, es una asociación positiva y significativa de la presencia de *P. cinnamomi* con áreas agrícolas. Las actividades humanas, al promover el transporte de patógenos, han sido y serán factores importantes favoreciendo la propagación de patógenos transmitidos por el suelo (Anderson et al., 2004). Este hallazgo refuerza el importante efecto de las variables de influencia humana en la distribución de especies invasoras, y la importancia de realizar análisis de sensibilidad para cuantificar su verdadera relevancia (Gallardo et al., 2015). Las predicciones de la distribución potencial de *P. cinnamomi* en la península ibérica sugieren una posible expansión a lo largo del noreste (Cataluña), el sureste y la parte central de Portugal. Campañas de vigilancia y control deben estar centradas en la parte sur de la meseta central, donde la "dehesa" es el componente principal del paisaje y la economía local. Además, dada la dependencia de la actividad de *P. cinnamomi* de las propiedades del suelo, los esfuerzos de control deben concentrarse en el sureste de España (Andalucía) donde los altos contenidos de arcilla representan las condiciones adecuadas para su establecimiento y propagación. Dado el impacto significativo de este patógeno en los ecosistemas forestales, el modelado de su distribución geográfica en la península ibérica ofrece una importante herramienta de decisión para el monitoreo y restauración de los bosques mediterráneos de quercíneas en declive.

***Resumen del cuarto artículo*:**

El quinto artículo de esta tesis (capítulo 6), constituye un ejemplo más de simulación, aparte de otros ya publicados (ver anexos), de cómo los *modelos cuantitativos* pueden ser una valiosa herramienta para la planificación de objetivos de conservación. En este estudio usamos un enfoque combinado de modelos de Máxima Entropía y técnicas de partición de la varianza para desentrañar el efecto de factores ambientales que expliquen la distribución espacial de focos de declive de masas forestales de encinas en dehesas (SECA) y finalmente producir un modelo espacialmente explícito de riesgo de SECA, para asistir a los gestores de la conservación en la toma de decisiones.

En la península ibérica, la SECA se está convirtiendo en una seria y frecuente enfermedad en especies del género *Quercus* (*p.ej., Q. ilex*, *Q. faginea*, *Q. suber*, *Q. pyrenaica*), que son las que dominan los sistemas agrosilvopastoriles tradicionales llamados “dehesa” en España y “montado” en Portugal (de Sampaio e Paiva Camilo-Alves et al., 2013; Rodríguez-Calcerrada et al., 2017). Estos procesos de declive parecen involucrar múltiples factores bióticos y abióticos, los cuales se combinan para reducir el vigor de estas especies, a menudo causando su muerte (Thomas, 2008). Sin embargo, las causas exactas de su extensión son poco conocidas y, por lo tanto, dada la relevancia ecológica, económica y social de estas quercíneas en los países Mediterráneos (Olea and San Miguel-Ayanz, 2006), es crucial el desarrollo de herramientas que nos permitan anticipar su ocurrencia y por lo tanto reducir su expansión. En este sentido, este estudio plantea los siguientes interrogantes:

- ¿Podemos cuantificar el rol relativo de factores ambientales que afectan la distribución de focos de SECA en dehesas de la península ibérica?
- ¿Podemos crear un modelo espacialmente explícito de riesgo de SECA para respaldar a los gestores de la conservación en la toma de decisiones?

Con el fin de responder a estas cuestiones, usamos una base de datos de focos de SECA en dehesas de la provincia de Salamanca, tres grupos de variables descriptoras de aspectos relacionados con las características topográficas, condiciones de estrés abiótico, la influencia humana y un enfoque combinado de modelos de máxima entropía y partición de la varianza (ver figura 5).

Las localidades GPS de focos de SECA (n = 68) dentro del área de estudio se obtuvieron para el período 2015-2017, mediante el programa “*Metodología para el inventario y seguimiento de masas de encina afectadas por declive en la provincia de Salamanca*” del Instituto Hispano-Luso de Investigaciones Agrarias de la Universidad de Salamanca (CIALE).

Para caracterizar los factores relacionados con el declive de encinas y alcornoques en el área de estudio, utilizamos 13 variables como predictoras, relacionadas con (1) condiciones topográficas, (2) condiciones de estrés abiótico, y (3) usos del suelo. En primer lugar, las características topográficas fueron derivadas del Modelo Digital de Elevación (MDE) del Centro Nacional de Información Geográfica de España con una resolución espacial de 5 × 5m.

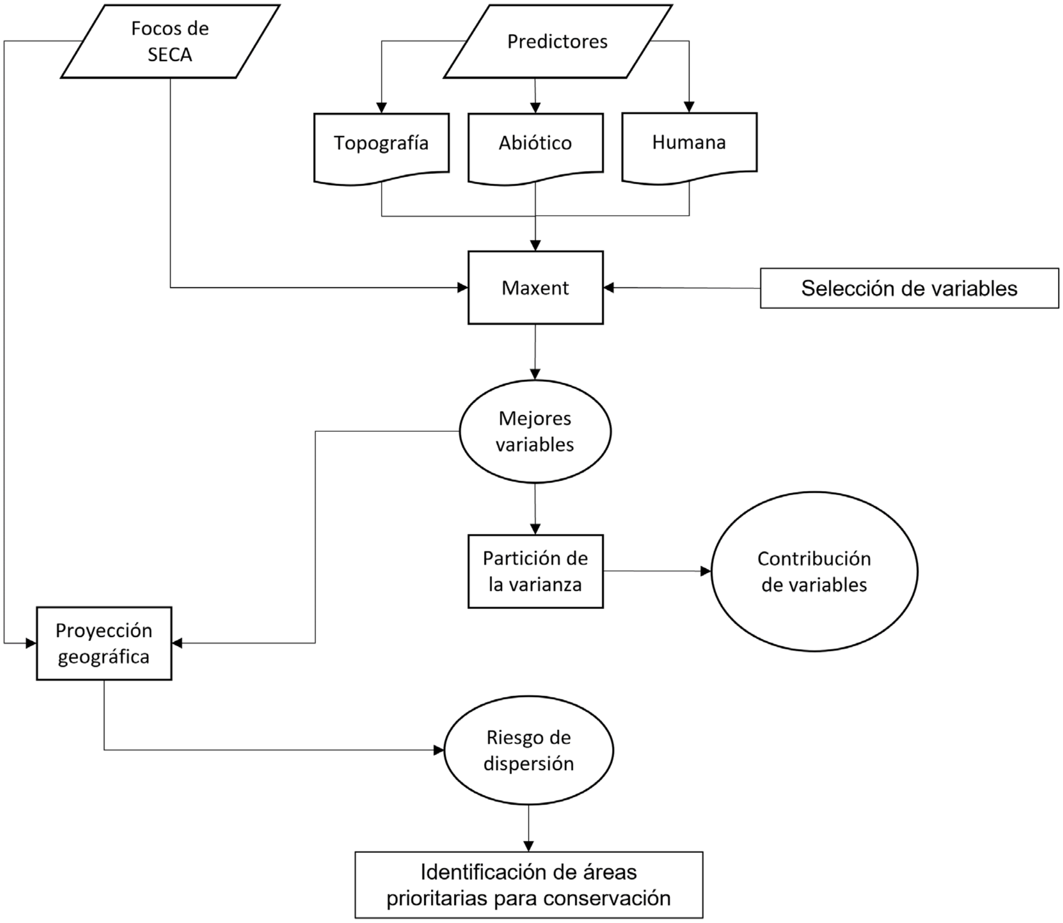

Figura 5. Esquema de trabajo utilizado en el artículo 5.

Condiciones relacionadas con el estrés abiótico fueron descritas mediante el uso de los índices NDII (Índice de Infrarrojos de Diferencia Normalizada) y NDVI (Índice de vegetación de diferencia normalizada). Estos índices aportan información directamente relacionada con la variabilidad de la disponibilidad de agua en los suelos (Sriwongsitanon et al., 2016) y el estado de la cobertura vegetal (Tucker, 1979). Estas variables fueron derivadas a partir de los datos del satélite Landsat 8 OLI/TIRS (https://www.usgs.gov/). Previo a los análisis, las imágenes satelitales fueron corregidas usando el enfoque Dark Object Subtraction (DOS) (Nazeer et al., 2014), implementado en QGIS (http://www.qgis.org). Para caracterizar la influencia humana, creamos una variable categórica describiendo los usos del suelo en el área de estudio. Para esto, usamos el mapa de uso del suelo 1:50000 del Tercer Inventario Forestal Nacional (IFN3) de España (MAGRAMA, 2007). Las clases consideradas en esta variable fueron: (1) superficies artificiales, (2) áreas agrícolas, (3) áreas agroforestales, (4) dehesas y (5) áreas forestales. Recientemente, Manzano et al., (2016) ha relacionado el declive y la mortalidad de quercíneas en el centro-oeste de España con la presencia de infraestructuras hidráulicas (*p.ej.*, estanques) resultantes de las actividades agrícolas. Estos cuerpos de agua, construidos aprovechando el relieve del terreno, suelen servir para abrevar al ganado y para el riego de cultivos forrajeros. Estas estructuras podrían inducir modificaciones importantes en el nivel freático en aquellas áreas con presencia de SECA. En este estudio, calculamos la proximidad a estos estanques como una aproximación de las modificaciones en el nivel freático del área de estudio. Para llevarlo a cabo, identificamos con precisión la ubicación de cada estanque mediante ortofotos de alta resolución (0,5 m) de la campaña fotogramétrica del Plan Nacional de Ortofotografía Aérea de 2014 (PNOA; http://centrodedescargas.cnig.es). Luego, calculamos la distancia (en metros) a los estanques usando la herramienta Distancia euclidiana de ArcGIS (ESRI, 2015).

Estos datos fueron procesados mediante Maxent y métodos de partición de la varianza para investigar los factores más importantes relacionados con los focos de SECA. En primer lugar, ejecutamos modelos con diferentes grupos de variables: topografía, estrés abiótico e influencia humana. Luego, calculamos el peso de cada variable usando el porcentaje de contribución, seleccionamos las mejores variables (valores de contribución más grande) para cada bloque de predictores y realizamos un modelo final combinando las mejores variables de cada grupo (modelo completo). En segundo lugar, aplicamos un procedimiento de partición jerárquica de la varianza (Borcard et al., 1992), para determinar la cantidad de información independiente y compartida contenida en los grupos de variables. Finalmente, con todos los focos disponibles de SECA calibramos el modelo combinando las mejores variables de cada grupo y proyectamos su distribución potencial a todas las cuadrículas de 30 × 30 m en el área de estudio. Luego, con el mapa de riesgo de SECA y los mapas de distribución de las especies objetivo en el área de estudio, elaboramos un mapa de áreas de manejo (como en Duque-Lazo et al., 2018). Las categorías de áreas propuestas fueron las siguientes: ***prevención***, para áreas con presencia de SECA identificada; ***protección***, para áreas donde actualmente no existe SECA, pero su ocurrencia se predice con alta probabilidad; y ***conservación***, para áreas donde la SECA está actualmente ausente, y su ocurrencia se predice con baja probabilidad. Para más detalles del enfoque propuesto, ver la sección “materiales y métodos” del artículo 5.

Nuestro estudio revela que es posible identificar los factores más influyentes que explican los patrones de distribución espacial de la SECA utilizando técnicas de máxima entropía y partición jerárquica de la varianza. Las variables con la mayor contribución en el modelo final mostraron que la distribución de esta afección es altamente dependiente del uso antrópico del suelo (dehesas), seguida de las condiciones de estrés abiótico y, por último, las características topográficas del área de estudio. Por otro lado, el análisis de partición de la varianza demostró que los diferentes grupos de variables ejercen una clara influencia sobre el riesgo de SECA. Nuestros resultados señalan que el componente compartido tuvo una proporción significativa de la variación, lo que indica una fuerte sinergia de los tres grupos de predictores que explican los patrones de distribución de la SECA en la citada provincia de Salamanca. Dada la actual presencia de SECA, las predicciones de su distribución potencial en la citada provincia sugieren que es posible que se dé una mayor expansión de este fenómeno a lo largo de la parte norte y central del territorio, donde la dehesa es el componente principal del paisaje y la economía local. En este sentido, las administraciones provinciales deben proponer e impulsar acciones de manejo frente a la SECA, enfocándose en las áreas de manejo, así como las medidas de conservación propuestas en este estudio (ver capítulo 6). Estas pautas deben establecerse con cautela y cada situación debe estudiarse y tratarse individualmente debido a la compleja etiología de esta afección.

Anexo

Finalmente, he incluido un último anexo con las portadas de varias publicaciones de las que soy autor principal o coautor y que han sido también desarrolladas durante mi periodo de formación predoctoral, en colaboración con otros miembros del equipo de investigación y con investigadores de otras universidades. Hemos decidido no incluir un artículo en el que soy autor principal como parte de la tesis, ya que consideramos que, por diversos motivos, no seguían la línea argumental que se estableció en el proyecto inicial y, por tanto, desvirtuarían la cohesión conceptual que genera la estructura de la tesis tal como se presenta. Se trata de aportaciones de gran valor científico, como atestiguan la calidad de las revistas en las que se han publicado.

CONCLUSIONES

Los *modelos cuantitativos*, pueden proporcionar una base replicable y confiable para optimizar los objetivos de las medidas de conservación (Nicholson et al., 2019). En esta tesis queda patente cómo la metodología empleada- *eje directriz*- proporciona o podría proporcionar soluciones prácticas que ayuden a los gestores a mejorar la eficiencia y alcance de su trabajo a la hora de tomar decisiones sobre conservación de la biodiversidad. Concretamente y en relación con el conjunto de casos de estudio analizados:

Especies amenazadas:

- El uso combinado de *Modelos de Nicho Ecológico* y *Modelos de Distancia al Centroide del Nicho* puede aplicarse para estimar con gran precisión la distribución y variación en abundancia de especies amenazadas de rango estrecho, facilitando la oportuna localización de áreas prioritarias para su gestión. Este enfoque metodológico maximiza la explotación de información básica a través de recursos abiertos (*software* y variables ambientales), lo que lo hace de gran interés para instituciones con recursos limitados.
- Los *Modelos de Nicho Ecológico* pueden usarse para cuantificar aspectos de exposición y vulnerabilidad al cambio climático de poblaciones amenazadas de hidrófitas. Predicciones climáticas para 2050 muestran que las poblaciones de estas especies que se encuentran distribuidas marginalmente en la península ibérica tenderán a presentarse en situaciones de riesgo ambiental. Los patrones de riesgo están perfectamente correlacionados con los incrementos térmicos y la mayor

estacionalidad de las precipitaciones y temperatura, vinculadas al calentamiento global.

Especies invasoras:

- *Las Técnicas de ordenación* y los *Modelos de Nicho Ecológico* pueden ser aplicados eficazmente para analizar la dinámica de los nichos de especies exóticas durante su invasión a nuevos territorios. La expansión del nicho observada durante la invasión de *Taraxacum officinale* y *Ulex europaeus* en América del Sur ejemplifica cómo las especies invasoras pueden ocupar nuevos nichos que no son predecibles a partir del conocimiento basado únicamente en factores climáticos o información del área de distribución nativa. La magnitud de los cambios de nicho observados no depende de la resolución de las variables (nivel de detalle de las variables).
- *Las técnicas de Inferencia Multimodelo*, *de Partición de la Varianza* y los *Modelos de Nicho Ecológico* pueden ser aplicados para cuantificar los factores ambientales asociados a la distribución espacial de patógenos edáficos en la península ibérica. La presencia de *Phytophthora cinnamomi* es favorecida principalmente por las características físicas del suelo y el clima, seguido de la presencia de suelos agrícolas y, por último, la presencia de sus principales especies forestales hospederas. Su distribución potencial sugiere un riesgo inminente de los ecosistemas forestales a lo largo del noreste y sureste de la península ibérica.

Gestión y riesgo de ecosistemas forestales

- *Modelos de Nicho Ecológico* y *Técnicas de Partición de la Varianza* pueden ser aplicados para cuantificar factores ambientales favoreciendo episodios de SECA y crear mapas de riesgos para una eficiente gestión del territorio. Las condiciones de estrés hídrico provocadas por el clima y topografía, y los cambios en el uso del suelo en la provincia de Salamanca representan los factores más importantes explicando la distribución de SECA. Una eficiente gestión de este fenómeno podría orientarse a la prevención de su expansión desde zonas con presencia, protección de zonas con alto riesgo y conservación de zonas de bajo riesgo. El enfoque metodológico propuesto puede aplicarse a la evaluación de riesgos para ecosistemas forestales en regiones en las que la dehesa es un componente fundamental de la economía.

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CAPÍTULO 2

Foto: Roberto Carbonell.

APROVECHANDO AL MÁXIMO LOS DATOS ESCASOS: MAPEO DEL RANGO DE DISTRIBUCIÓN Y LA VARIACIÓN EN LA ABUNDANCIA POBLACIONAL DE UNA PLANTA ENDÉMICA AMENAZADA DE RANGO ESTRECHO

AUTORES
Ricardo Enrique Hernández-Lambraño,
Roberto Carbonell,
José Ángel Sánchez-Agudo

RESUMEN

El diseño de estrategias eficaces para la conservación y el manejo de especies amenazadas de rango estrecho requiere conocimientos básicos sobre su distribución geográfica y abundancia. Cuando esta información es limitada, las técnicas de modelización pueden brindar la oportunidad de adquirir información básica e incorporarla inmediatamente a los programas de conservación. Este estudio utilizó modelos de nichos ecológicos para mapear el rango de distribución potencial y la variación en abundancia poblacional de una planta endémica amenazada de rango estrecho, *Antirrhinum lopesianum* Rothm. en la península ibérica. Simulamos la distribución geográfica potencial de la especie utilizando un enfoque de ensamblado de modelos basado 28 registros de presencia y un conjunto de datos ambientales fácilmente disponibles (Landsat 8 OLI / TIRS y LiDAR) y creamos un modelo espacial de la distancia al centroide del nicho. Probamos la relación entre la abundancia observada en campo y su distancia al centroide del nicho utilizando modelos de regresión generalizados, y el modelo resultante se utilizó para generar estimaciones espaciales de la abundancia de la especie en todo su rango de distribución potencial. El modelo de nicho ecológico de la especie analizada cubrió las áreas más adecuadas ubicadas a lo largo de una estrecha franja a orillas del río Duero y del río Sabor. Encontramos una relación robusta y negativa entre la abundancia observada para el taxón y la distancia al centroide del nicho. El modelo espacialmente explícito presentado aquí proporciona una herramienta confiable para el manejo y conservación de *A. lopesianum* y un enfoque aplicable para otras plantas endémicas de rango estrecho. Finalmente, este enfoque maximiza la explotación de información básica a través de recursos abiertos (software y variables ambientales), lo que la hace de alto interés para instituciones con recursos limitados.

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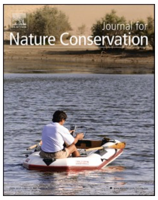

Making the most of scarce data: Mapping distribution range and variation in population abundance of a threatened narrow-range endemic plant

Ricardo Enrique Hernández-Lambraño [a,b,*], Roberto Carbonell [c,d], José Ángel Sánchez-Agudo [a,b]

[a] Departamento de Botánica y Fisiología Vegetal, Facultad de Farmacia, Universidad de Salamanca, Avenida Licenciado Méndez Nieto s/n, 37007, Salamanca, Spain
[b] Grupo de investigaciones en Biodiversidad, Diversidad humana y Biología de la Conservación, Departamento de Biología Animal, Ecología, Parasitología, Edafología y Química Agrícola, Universidad de Salamanca, Campus Miguel de Unamuno s/n., E-37007, Salamanca, Spain
[c] Departamento de Biodiversidad, Ecología y Evolución, Facultad de Ciencias Biológicas, Universidad Complutense de Madrid, C/José Antonio Novais, 2, E-28040, Madrid, Spain
[d] Servicio Territorial de Medio Ambiente de Salamanca, Junta de Castilla y León, 37071, Salamanca, Spain

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ABSTRACT

The design of effective strategies for the conservation and management of threatened narrow-range species requires basic knowledge on their geographic distribution and abundance. When such knowledge is lacking, modelling techniques can provide an opportunity to acquire basic information and incorporate it immediately into conservation programs. This study used ecological niche modelling to map the potential distribution range and rangewide variation in population abundance of a threatened narrow-range endemic plant, *Antirrhinum lopesianum* Rothm. in the Iberian Peninsula. We simulated the potential geographic distribution of the species using the Ensemble Modelling approach based on 28 species occurrences and a set of readily available environmental data (Landsat 8 OLI/TIRS and LiDAR) and created a spatial model of the distance to the niche centroid. We tested the relationships between 35 records with abundance data for the species and their distance to the niche centroid using generalized regression models, and the resulting model was used to predict spatial estimations of *A. lopesianum* abundance across its entire potential distribution range. The ecological niche model of *A. lopesianum* covered the most suitable areas located along a narrow strip on the banks of the River Duero and River Sabor. We found a robust and negative relationship between observed abundance for the taxon and distance to the niche centroid. The spatially explicit model presented here provides a reliable tool for regional/global management and conservation of *A. lopesianum* and an approach applicable for other narrow-range endemic plants. Finally, this approach maximization the exploitation of basic information through open resources (software and environmental variables), which makes it of high interest for institutions with limited resources.

1. Introduction

Narrow-range endemic plant species are of conservation concern and are a challenge for conservation agencies due to their rarity and uniqueness. The difficulty increases when these species occupy remote areas or those difficult to explore. With ongoing environmental global change, these species are more susceptible to different environmental pressures (Breggin, George, & Pencak, 2003) and hence, reliable estimates of their potential distribution and abundance are necessary both to evaluate its risk of extinction and design conservation strategies (Guisan et al., 2013; Rodríguez, Brotons, Bustamante, & Seoane, 2007). However, data on the current and/or historical distribution, biology, and ecology of many of these species is sparse, due to the fact that their populations, are, in many cases, present in small patches of difficult access (Gogol-Prokurat, 2011). Incomplete knowledge of this basic information makes its prioritisation for conservation an enormous challenge.

Species distribution models (SDMs) offer a practical solution to improving our knowledge of narrow-range endemic plant species (Peterson et al., 2011), thus locating and prioritising areas for conservation actions. SDMs use known occurrence locations and spatially-explicit data on the environmental conditions believed to control the geographic distribution of the target species to predict habitat suitability across the landscape (Soberón & Nakamura, 2009).

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* Corresponding author at: C/ General Margallo, 24, 1B izq, 28020, Madrid, Spain.
E-mail address: ricardohl123@usal.es (R.E. Hernández-Lambraño).

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However, endemic plant species with narrow-range distributions and specialised habitat requirements represent a particular challenge for SDMs for several reasons: 1) such species have both small distributions and small sample sizes, creating issues that may compromise model robustness (Pearson, Raxworthy, Nakamura, & Townsend Peterson, 2007); 2) sampling bias is inherent in occurrence data (Wisz et al., 2008); and 3) given that narrow-range species with specialised habitat requirements often have patchy distributions of occurrences, defining a general range becomes less useful from a management perspective compared to understanding habitat occupancy. This is a challenge for SDMs because they are meant to identify the overall extent of a species' range and may perform poorly if that range is heterogeneous or not well-sampled (McPherson & Jetz, 2007).

In recent years, a novel method to model geographic patterns of abundance based on the ecological niche theory, termed the Distance to the Niche Centroid (DNC) approach, was proposed by Martínez-Meyer, Díaz-Porras, Peterson, and Yáñez-Arenas (2013). This procedure is similar to those previously applied and based on orthogonal variables (Calenge, Darmon, Basille, Loison, & Jullien, 2008). This approach assumes that optimal conditions for a species are found towards the centroid of the ecological niche in a multidimensional space (Hutchinson, 1957; Maguire, 1973). Thus, a locality which environment is close to the centroid of the *n*-dimensional niche harbours better conditions for the species and, as a consequence, higher abundance would be expected at these localities (Yañez-Arenas, Guevara, Martínez-Meyer, Mandujano, & Lobo, 2014). The DNC approach fits a curve for the relationship between observed abundance across the species' geographic range and the distance to the ecological niche centroid that can be used to make range-wide estimates of the species' abundance. Based on this approach, different studies have successfully tested this hypothesis in different geographic contexts and at different scales (Manthey et al., 2015; Martínez-Gutiérrez, Martínez-Meyer, Palomares, & Fernández, 2018; Martínez-Meyer et al., 2013).

Expanding the use of the SDMs and DNC method to predict geographic patterns of distribution and abundances of narrowly endemic plants could be very helpful in designing management and conservation strategies. Here, we determined whether the distributional area of a narrow-range endemic plant, as well as variations in population abundance across its distribution range, can be accurately estimated at a fine scale using the SDMs and DNC method, based on very basic information of the species. We illustrate these approaches with the arribes snapdragon, *Antirrhinum lopesianum* Rothm., a threatened narrow-range endemic plant of the north-western Iberian Peninsula. Finally, the potential implications of the results for focussing future fieldwork and conservation efforts are discussed.

2. Materials and methods

2.1. Study area

We delimited the study area by generating a 15 km buffer around the current distribution range of *A. lopesianum* based on the IUCN distribution map (Amich-García, Bernardos-Hernández, González-Talaván, Caldas, & Alves, 2011). We assumed that this area reflects the geographic region that has been accessible to the species over relevant time periods (M in the BAM framework; Soberon & Peterson, 2005); Fig. 1).

This area is included in the Lusitan Duriensean biogeographical sector (Carpetan-Leonese subprovince) (Rivas-Martínez et al., 2002), with a Mediterranean pluviseasonal oceanic bioclimate, within the Mesomediterranean thermoclimatic belt, with two ombrotypes: dry and subhumid. The dominant rock is silicic, generally granite and quartz, which causes soils to be acidic (Bernardos, Crespi, Aguiar, Fernández, & Amich, 2004).

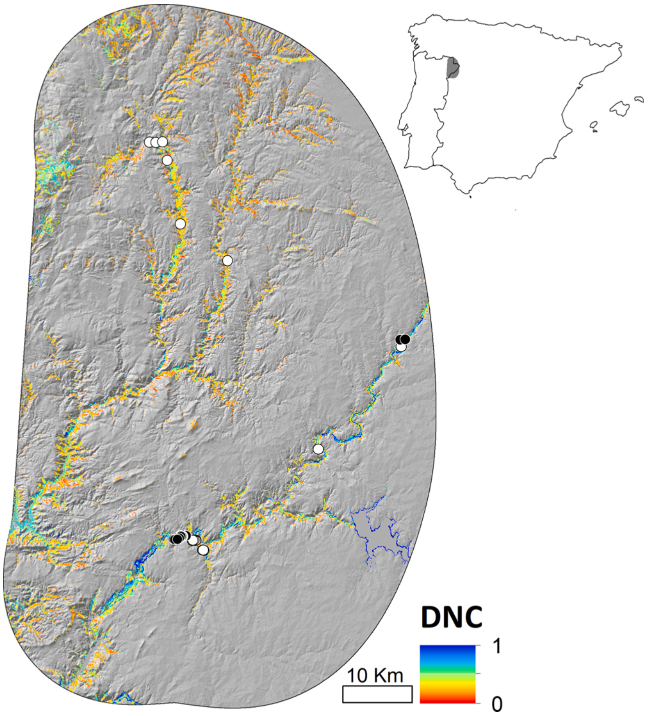

Fig. 1. Potential distribution range of *Antirrhinum lopesianum*: central western Iberian Peninsula. In colour, model of the ecological niche of *A. lopesianum* representing the distance to the niche centroid, with values from 0 (red) to 1 (blue). Absence prediction is represented in grey background. White dots indicate presence records ($n = 28$) and black dots abundance data ($n = 35$). The background image (digital elevation model) represents the complexity topographic of the study area (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article).

Fig. 2. The arribes snapdragon, *Antirrhinum lopesianum* Rothm. Photographed by R. Carbonell in Natural Park Arribes del Duero, Spain, June 2018.

2.2. Study species

The arribes snapdragon, *A. lopesianum* (Fig. 2), is a perennial chamaephyte with woody stems, very lanuginose leaves and flowers that are white with violet stripes (Bernardos et al., 2006).

Flowering occurs in spring (April-May) and fructification in summer (July-September), it is insect-pollinated, and seeds are dispersed by barochory/semachory. *A. lopesianum* grows on shaded cracks in calcareous substrates and has a discontinuous and highly fragmented distribution due to possibly stochastic and historical effects of both colonization (dispersion) and extinction. This taxon is listed as Endangered due to its current severely fragmented distribution, with a low area of occupancy, below 500 km^2 (Amich-García et al., 2011).

2.3. Presence data

Presence data across the current distribution range of the taxon were gathered from the literature (Gomes et al., 2013; Ramírez-Rodríguez & Amich, 2014) and the Arribes del Duero Natural Park. Presence records from the Global Biodiversity Information Facility (GBIF) were not used because the resolution at which they were uploaded into this database ($\geq 1 \times 1$ km grids) is coarser than the resolution of the environmental variables used in this study. We obtained a total of 28 presence records for *A. lopesianum* (Fig. 1).

2.4. Abundance data

Abundance data of the taxon were gathered across its potential distribution in the Duero Basin (Portugal and Spain) during the spring and autumn of 2018. Due to the geomorphological complexity of these “Arribes” territories (see Fig. A1), a motorboat was used to assist in our surveys. This allowed us to reach places that otherwise would have been impossible to explore. When the species was detected, we recorded geographical location (using a Garmin e-map GPS device) and abundance data (direct counting of all individuals as in Bernardos et al., 2006). A total of 35 records with abundance data for the taxon were gathered (Fig. 1).

2.5. Environmental variables

As potential predictors to characterize the species’ ecological niche, we used a set of variables related to topographic conditions, temperature, soil water availability and vegetation cover (Table 1). In areas with a rugged topography, the selection of variable resolution is a consequence of the availability and quality of data pertaining to the specific study area, which is typically the limiting factor in distribution studies (Zhang et al., 2016). Herein, predictor variables were derived by remote sensing data (Landsat 8 OLI/TIRS and LiDAR) and were chosen based on our knowledge of the species, and were assumed to be at least correlated with more proximal causal factors. Remote-sensing techniques have transformed ecological research by providing both spatial and temporal perspectives on ecological phenomena that would otherwise be difficult to study (He et al., 2015; Hernández-Lambraño, Rodríguez de la Cruz, & Sánchez-Agudo, 2019). A key advantage of these techniques is the capability to perform synoptic, spatially continuous and frequent observations of ecological indicators without interpolation or geographical biases at varying spatial and temporal resolutions (He et al., 2015), advantages that have huge potential when it improves the ability to predict the distribution at fine scale of a threatened narrow-range endemic plant. Other potentially important environmental variables such as edaphic, geological, phytocenotic and human influence variables, are not used due to the lack of a thematic cartography compatible with the resolution used in this study. To reduce multicollinearity between variables, we calculated the Variance Inflation Factor (VIF) using the VIF function of the “HH” package in R (Heiberger, Richard, & Holland, 2004). Variables with values of VIF > 5 were excluded (Table A1). All environmental data were standardised to Universal Transverse Mercator coordinates (Datum ETRS-89) at a spatial resolution of 30 × 30 m using ArcGIS ver. 10.3.1 (ESRI, 2015). See Appendix A1 for a more detailed description of the variables and estimation methods.

Table 1
Variables used as predictors of the Antirrhinum lopesianum presence in the study area. See Table A1 for variable descriptions and estimation methods.

Variables	Description	Range (min to max)
slope	Slope of the terrain (degrees)	0.119 to 55.92
LST_*avg*	Average of the land surface temperature in growing season (°C)	20.46 to 38.09
northness	South-north aspect	−1 to 1
SAVI_*avg*	Average of the Soil-Adjusted Vegetation Index in growing season	−0.063 to 0.608
eastness	West-East aspect	1 to −1
NDII_*avg*	Average of the soil water availability in growing season	−0.370 to 0.772
TPI	Topographic position index (m)	−13.19 to 9.984

2.6. Ecological niche-based distribution modelling

We modelled the ecological niche of *A. lopesianum* using Ensemble Modeling approach (EM). EM was built to reduce the biases and limitations inherent to the use of single SDM techniques (Araújo & New, 2007). We used BIOMOD2 version 3.3–7 (Thuiller, Georges, Engler, & Breiner, 2016) in R version 3.4.2 (R Core Team, 2017), to fit four modelling methods: Generalised Linear Models (GLM), Generalised Boosting Models (GBM), Maximum Entropy (MaxEnt) and Random Forest (RF). These models have shown good performance in other modelling exercises (Breiner, Guisan, Bergamini, & Nobis, 2015; Elith et al., 2006; Williams et al., 2009).

Models were calibrated with 28 presences of the specie and 10 000 random pseudo-absence points. Pseudo-absence data were limited to within 5 km from the known presence records (Williams et al., 2009). The Continuous Boyce Index (CBI) (Hirzel, Le Lay, Helfer, Randin, & Guisan, 2006), a metric specifically designed for presence only models and insensitive to pseudo-absences was used to evaluate the model performance. We considered models to be “wrong” when CBI values were below -0.5, “average to random” for values ranging from -0.5 to 0.5, and “good” for values above 0.5. For each model, we computed CBI by performing ten-fold split sampling (80 % training data and 20 % test data). We assembled all individual models into a single EM by weighting projections based on the individual CBI scores (CBI > 0.5). EM evaluation consisted of calculation of CIB using independent data. In this case, the abundance data gathered from field surveys were used as presence records for the EM validation. EM output was converted into a discrete binary map of presence/absence, using the minimum training presence (MTP) value. Finally, variable importance was calculated to assess the relevance of each predictor through all considered models and response curves were calculated to interrogate the relationship between the response (i.e., presence) and each explanatory variable (See Appendix A2 for a more detailed description of model implementation).

Here, we assume that the niche model is a good estimator/approximation of the fundamental niche of a plant with scarce knowledge about its biology, but we acknowledge that it is difficult to capture the true fundamental niche without an ecophysiological approach for the species (Peterson et al., 2011).

2.7. Distance to the niche centroid

Following Martínez-Gutiérrez et al. (2018), the niche centroid was calculated in the environmental space from potential distribution range. The niche centroid is located at the centre of the multidimensional envelope of the presence records in the environmental space. To obtain the DNC, we first extracted values of environmental variables for all grid cells where the species were predicted to be present according to the EM binary map, which represents a list of all unique environmental combinations along the potential geographic distribution of the species (Martínez-Gutiérrez et al., 2018). To avoid biases introduced by differences in scales among the 7 dimensions of the ecological niche, we converted them to a common scale (i.e., standardisation procedure, mean = 0 and standard deviation = 1). We calculated multidimensional Euclidean distance from each grid cell with a presence prediction to the niche centroid as follows:

$$DNC = \sqrt{\sum_{j} (P_{ij} - N_j)^2}$$

where DNC is distance to the niche centroid, N*j* is mean of variable *j* and P*ij* is value of the variable *j* in grid cell *i*.

Finally, we represented the DNC in a raster map (Fig. 1) using raster calculator in ArcGIS and rescaled the values between 0 and 1, with 0 representing the shortest DNC and 1 the largest distance to this centroid.

2.8. Relationship between the abundance and the Distance to the Niche Centroid, and abundance map

We analysed relationships between abundance data of *A. lopesianum* (i.e., response variable) to DNC measures (i.e., predictor variable) using a Generalized Linear Model (GLM). We modelled the error terms of the GLM using a negative binomial distribution (Abundance ~ DNC, family = negbin(link="log")), which is typically used for count data when overdispersion occurs (Gelman & Hill, 2007).

The fit model was evaluated using a randomly split 80/20 data for training/validation. We re-estimated the GLM model using the 80 % section of the data, and the resulting section was used to predict the abundance of the remaining 20 % data. The process of splitting the data was repeated ten times and the mean of R^2 (i.e., the squared correlation between the observed outcome values and the predicted values by the model) and its standard deviation were calculated as a performance metric for the fitted models. We used the R packages “tidyverse” ver. 1.2.1 (Wickham, 2017) and “caret” ver. 6.0–77 (Kuhn, Wing, & Weston, 2017) for the procedure of model evaluation. Since the specie’s presence can be given by historical and stochastic processes, we only validate DNC with those points where we have detected its presence.

The fitted GLM describing the relationship between abundance and DNC was used to generate an estimated abundance map of *A. lopesianum* across its entire potential distribution using the “predict” function of the R package “raster” ver. 3.0–7 (Hijmans, 2019) (see Table A2). We only showed spatial predictions for the observed range of abundances. Finally, we constructed correlograms and calculated global Moran’s I in ArcGIS using residuals from the GLM and evaluated it for evidence of autocorrelation. We did not detect strong spatial autocorrelation in the residuals of the GLM (see Fig. A2).

3. Results

3.1. Ecological niche-based distribution modelling

The CBI average values, ranging between 0.618 and 0.801, indicated that the single-algorithm model predictions exhibited a good discrimination capacity compared to the expected value (0.5) from a random prediction. Despite the initial good performance of the models, the EM outclassed the accuracy of their predictions with an CIB value of 0.818. The threshold value of consensus to produce the binary map of presence/absence was = 0.291. According to the resolution used, the potential habitat distribution covered an area of 273 km^2. Most suitable areas were located along a narrow strip on the banks of the rivers (Fig. 1). The binary map includes areas with suitable environments where the species has not yet been recorded. These predicted areas were located in the south and middle parts of the Sabor Basin (Portugal), and another in the south and middle parts of the Duero River (Portugal-Spain).

From the seven predictors considered for running the models, terrain slope (slope), land surface temperature (LST_*avg*), north-south aspect (northness) and soil-adjusted vegetation index (SAVI_*avg*) were the variables with the consistent highest contributions (Fig. 3).

These results identify variables related to landscape topographic features and land-cover as the most important to explain the potential distribution of the taxon. The model response curves in respect to these variables (Fig. 4), reveal that the most suitable areas for *A. lopesianum* are those that have steep slopes facing north with an average temperature for the growth season of approximately 21 °C. Moreover, they are areas with low vegetation cover and high humidity that are in relatively deeper valleys.

3.2. Relationship between observed abundance and distance to ecological centroid

The GLM showed that the observed abundance of *A. lopesianum* was significantly negatively associated with the DNC (regression coefficient of -26.09 ± 4.276 SE; $p < 0.001$) and the model for this species explained 0.598 of variation in abundance as a function solely of niche-centroid distance (Fig. 5). As expected, the observed abundance drops when the environmental conditions depart from those found near the species’ ecological niche centroid.

According to the validation procedure, GLM averaged an R^2 of 0.712 ± 0.274 ($p < 0.001$). Abundance estimates are within reasonable ranges (4–73 individuals) and coincide with our observed field data (1–65 individuals). Finally, spatial predictions of *A. lopesianum* abundance across its entire potential habitat distribution were estimated with the coefficients of the GLM (Fig. 6; Table A2). Areas with high estimated abundances are predicted along the Sabor Basin, mainly in the south and middle parts, north part of the Maças River, and another in the south and middle zones of the Duero Basin (Portugal-Spain).

4. Discussion

4.1. Potential distribution range of Antirrhinum lopesianum

Herein, we developed a spatially-explicit model to represent the potential habitat distribution of the threatened narrow-range endemic *A. lopesianum* across its entire distributional range. The value of performance (CIB) of our SDM indicates a high dependence on the occurrence data and the set of variables included in the analysis. This result, however, may be an artefact of the small sample size used for the model calibration (Yañez-Arenas et al., 2014). This effect has often been reported for species with restricted distributions, or when study area is extremely large compared to narrow species distribution (Lobo, Jiménez-Valverde, & Real, 2008). Our SDM indicates that the potential habitat distribution covered the most suitable areas located along a narrow strip on the banks of the River Duero (north-eastern Portugal and central western Spain) and River Sabor (north-eastern Portugal). These findings are congruent with known range limits described by Bernardos et al. (2006) but expand them considerably. Results from the analysis of predictor importance revealed that the distribution patterns of *A. lopesianum* appear to be mostly influenced by topographic features (i.e., slope, aspect) and land surface temperature. In fact, the taxon presents a special preference for spatially heterogeneous areas. In these environments, the species likely finds refuge on humid and shady slopes, which reduce insolation and maintain water balance in the dry season. In addition, the presence probability of the taxon responds positively to zones with high soil moisture. These environments facilitate vegetative propagation via the production of new shoots with many adventitious

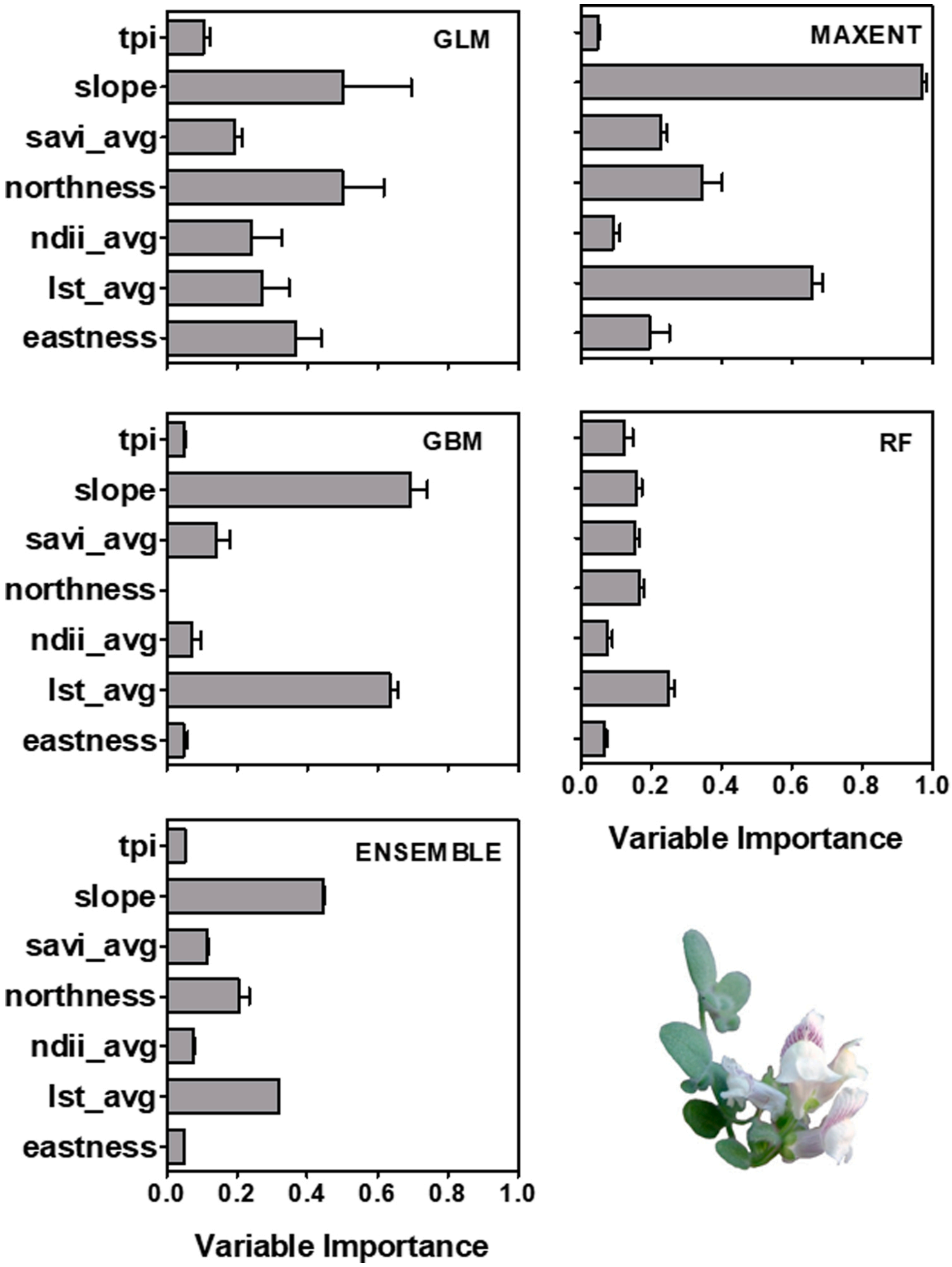

Fig. 3. Relative environmental variable importance derived from the single-algorithm models and ensemble model, with the error bars corresponding to standard deviation computed for each variable. See Table 1 for variable descriptions.

roots that are introduced in the fissures of the rock walls that colonises (Bernardos et al., 2006).

As we noted in the environmental variables section, our SDM has several limitations regarding other potentially important environmental variables that may influence the presence of *A. lopesianum*. Despite these limitations, the SDM-based distribution model represented the potential habitat patterns of the taxon fairly well and could serve as a first approximation for the species. Finally, any characterisation of the species' ecological niche will always be partial, inherent to the multidimensional niche (Martínez-Gutiérrez et al., 2018).

4.2. Relationship between observed abundance and distance to ecological centroids

We implemented the DNC approach to estimate the potential abundance of *A. lopesianum* across its entire potential distribution range. We found a significant, negative relationship between observed abundance for the taxon and DNC. Ecological theory has proposed that optimal conditions for species are found towards the centroid of their multidimensional ecological niche, thus abundance under such conditions should be maximal (Maguire, 1973). Our results provide empirical support for these ideas, as a strong inverse relationship was found between the distance to the centroid and observed values of abundance, indicating that the internal structure of the species' ecological niche contributes to population abundance Brown, Mehlman, and Stevens (1995)).

Our results were similar to those reported by Yañez-Arenas, Martínez-Meyer, Mandujano, and Rojas-Soto (2012); Ureña-Aranda et al. (2015) and Martínez-Gutiérrez et al. (2018), regarding the DNC–abundance relationship. These authors found that the abundance distribution followed a centralized pattern in the ecological space, where abundance tends to be highest toward the centre of these spaces and

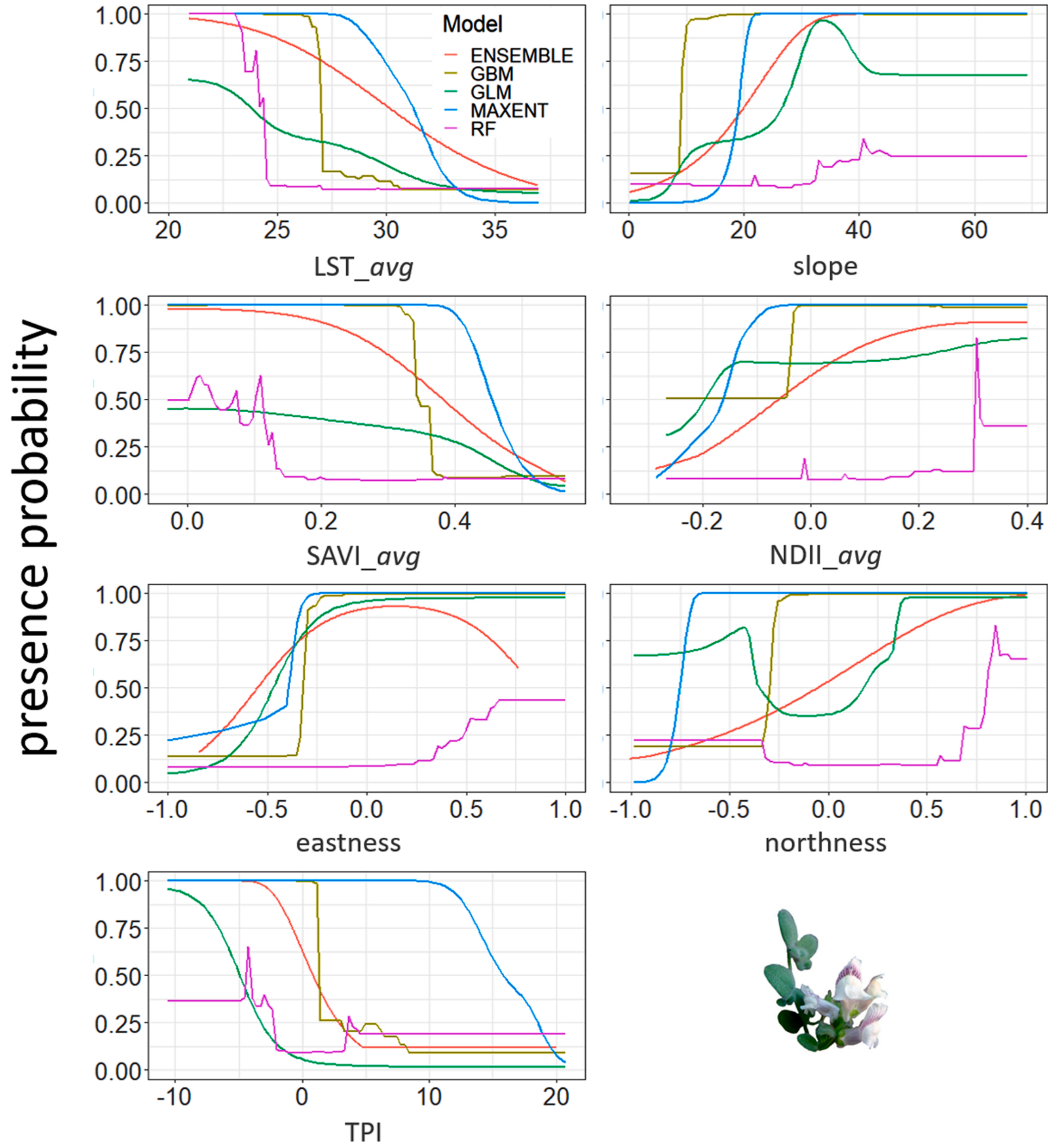

Fig. 4. Response curves: the panel represents the response curves of the environmental variables explaining the presence of *Antirrhinum lopesianum* derived from the single-algorithm models and ensemble model. Response curves were calculated for the models calibrated with all presence records ($n = 28$). See Table 1 for variable descriptions.

decrease toward the boundaries. On the other hand, the relationship that we found was not as strong as that reported for *Odocoileus virginianus* ($R^2 = 0.902$; Yañez-Arenas et al., 2012). If the hypothesis that the centroid of the ecological niche encompasses the optimal conditions for the species is correct, differences in the explanatory power of the model could be due to other factors that were not taken into account in characterising the species' niche (Brown et al., 1995; Osorio-Olvera, Soberón, & Falconi, 2019). For instance, *A. lopesianum* grows in vertical habitats, rocky cliffs, and on fissures in granitic walls with carbonate crusts (Bernardos et al., 2006). In addition, due to the habitat of *A. lopesianum*, rocky cliffs along riverbanks (Fig. A4), the majority of produced seeds may fall into the river, which could cause difficulties for new colonization and low population numbers in suitable habitats. Therefore, besides the abiotic variables considered in this study (i.e., climatic, topographic, and land cover), variables such as edaphic features, historic events, disturbances and biotic interactions are important factors that also drive species' distributions (Hernández-Lambraño, González-Moreno, & Sánchez-Agudo, 2018; Osorio-Olvera et al., 2019; Santini, Pironon, Maiorano, & Thuiller, 2019), and ultimately influence the presence and abundance of the species.

Recently Dallas, Decker, and Hastings (2017), performed a meta-analysis in which they suggest that distance-abundance relationships may be rare, difficult to detect, or are an oversimplification of the complex biogeographical forces that determine species spatial abundance patterns. However, the fact that the authors failed to detect significant relationships may result from methodological artefacts or ecological factors (Osorio-Olvera et al., 2019; Soberón, Peterson, & Osorio-Olvera, 2018), rather than to non-existence of such relationships. In fact, Dallas et al. (2017), limited their analyses to a given geographic area, irrespective of the range-wide distribution of the species considered, which can result in important biases in the estimate of distance from centre to edge, and in large under-estimation of species niches (Santini et al., 2019; Soberón et al., 2018).

The application of our abundance model must incorporate an

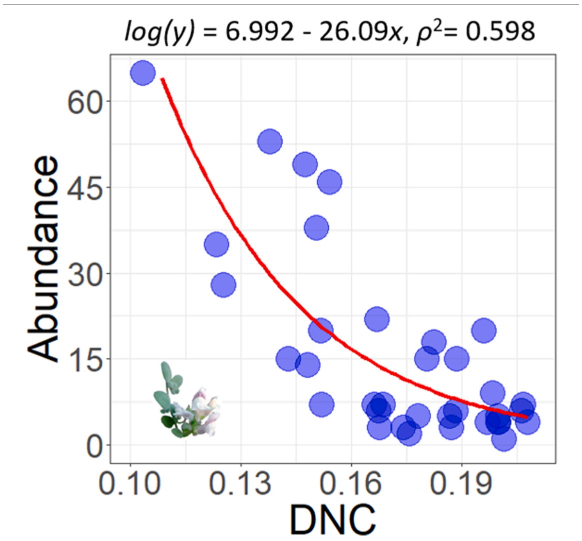

Fig. 5. Relationship between the observed abundance (individuals' number of *Antirrhinum lopesianum*) and the distance to the niche centroid.

understanding of potential biases. Performance of the DNC model is affected by sampling bias in the occurrence data and sample size (Yañez-Arenas et al., 2014); therefore, the accuracy of the estimates will depend on the quantity and quality of the data used. The DNC approach is a static method that does not capture the dynamic nature of population fluctuations over time (Yañez-Arenas et al., 2012). Also, the approach assumes that optimal conditions are always close to the mean values for all variables, and this may not necessarily hold true, due to the fact that for some variables optimal conditions may be closer to the extreme values (Yañez-Arenas et al., 2012). Despite these shortcomings, our results indicate that DNC is a good proxy for estimating *A. lopesianum* abundance across its potential distribution range (Fig. 6); therefore, mapping the distance to the centroid may be a useful approach for obtaining a spatial approximation of the potential abundance for other narrow-range endemic plants, in cases that such data are not available.

4.3. Management implications and future research

While we may be able to define rough range limits for these species at a landscape scale, conservation management actions require planning at the scale of habitat occupancy within the defined range (Margules & Pressey, 2000; Williams et al., 2009). At a conceptual level, range and habitat occupancy are fundamentally different concepts (Gaston, 2003) and SDMs have mostly been applied to predict species ranges. However, the better an SDM, the more it can distinguish between the characteristics of places where species occur and the surrounding background matrix where they are absent, i.e. a species' habitat occupancy (Williams et al., 2009). The modelling approach presented in this study is based on a solid ecological foundation (ecological niche theory; Hutchinson, 1957; Maguire, 1973), therefore facilitating the interpretation of results. The method is relatively simple, requiring only: 1) an occurrence dataset (presence-only or presence-absence) with or without associated abundance information, 2) a proper set of environment variables to characterise species' niche, 3) a reliable SDM and 4) a DNC calculation.

The fact that new occurrences of the taxon were discovered at locations where the binary map indicated favourable habitat suggests that our modelling approach can discriminate between the background matrix and potential habitat at fine scales. In this sense, the information provided by the binary map can support the identification of priority areas for population management such as, reinforcement, introductions

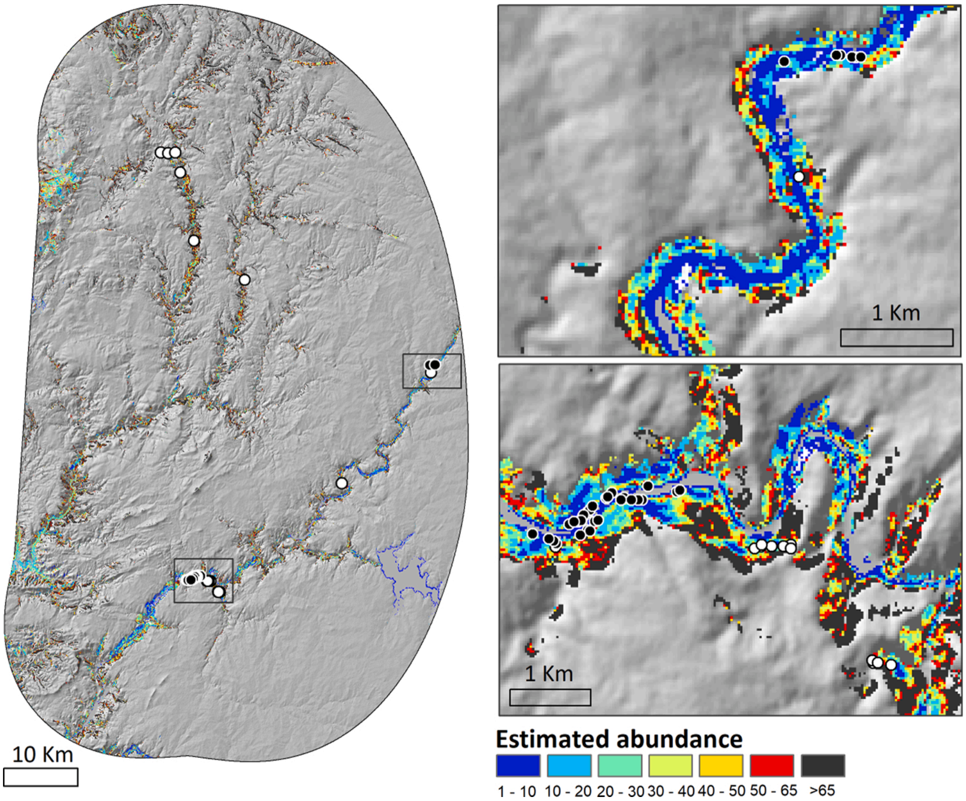

Fig. 6. Estimated abundance of *Antirrhinum lopesianum* along its potential distributional range based on the effect of distance to the niche centroid. We only showed spatial predictions for the observed rank of abundances; therefore, in black, we represent areas with an abundance prediction above the maximum observed. Absence prediction is represented in grey background. White dots indicate presence records and black dots abundance data.

and translocations (Borthakur et al., 2018; Guisan et al., 2006; IUCN/SSC, 2013).

The validation of our DNC model (R^2 of 0.712) also suggests that the differential values of abundance estimated by the model might also be used to guide other types of conservation management decisions. These could include identifying potential restoration sites or scoring aggregate conservation values based on high densities of cells with high values of expected abundance for the taxon (Williams et al., 2009). On the other hand, our SDM can also support accurate forecasts of range dynamics under scenarios of climate change. Specifically, for our test species the model highlighted a high dependence on features of the temperature regime, which would support more accurate forecasts if climate change scenarios are applied (Sala et al., 2000).

Since there are still a lot of unanswered questions about the ecological processes involved in the persistence of the taxon, it is crucial to develop several research lines to provide an effective conservation plan in the long term. The DNC model can help to design new studies to address knowledge gaps, for example flowering phenology, plant size, and genetic and breeding systems of the species to assess the main factors affecting female reproductive success (Bernardos et al., 2006).

Authors' contributions

R.E.H-L and J.A.S-A. jointly conceived the ideas; R.E.H-L. developed the methodology, R.C, R.E.H-L and J.A.S-A collected and analysed the data and R.E.H-L led the writing of the manuscript. All authors contributed critically to the drafts and gave final approval for publication.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix A. Supplementary data

Supplementary material related to this article can be found, in the online version, at doi:https://doi.org/10.1016/j.jnc.2020.125889.

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INFORMACIÓN SUPLEMENTARIA

Table A1. Main variables considered for modelling the *Antirrhinum lopesianum* occurrence in the study area. Variables in bold were included in the final analysis to avoid collinearity

Name	**Description**	**Calculation**	**Ecological meaning**	**Variance Inflation Factor**
slope	Slope of the terrain (degrees)	$\arctan(\sqrt{([dz/dx]^2 + [dz/dy]^2)}) \times 57.29$	Solar radiation, stability, erosion, moisture (Meineri, Dahlberg, & Hylander, 2015)	1.167
eastness	East-west aspect	$\sin(aspect)$	Morning/afternoon solar radiation, wind, moisture (Bader & Ruijten, 2008)	1.049
northness	North-south aspect	$\cos(aspect)$	Summer/winter solar radiation, vegetation patterns (Bader & Ruijten, 2008)	1.055
TPI	Topographic position index (m)	$(z_0 - \bar{z}_D)^a$	Soil moisture, wind, erosion/deposition (Das, Nagendra, Anand, & Bunyan, 2015)	1.028
LST_*avg*	Average of the land surface temperature in growing season (ºC)	$T_B/(1 + (\lambda \times s + T_B/c2) \times \ln(\varepsilon))^b$	Vegetation patterns, evapotranspiration, soil Moisture (Kerr, Lagouarde, Nerry, & Ottlé, 2004)	1.904
NDII_*avg*	Average of the soil water availability in growing season	$(NIR - SWIR)/(NIR + SWIR)$	Vegetation patterns, soil nutrients (Sriwongsitanon, et al., 2016)	3.175
SAVI_*avg*	Average of the Soil-Adjusted Vegetation Index in growing season	$[(NIR - red)/(NIR + red + L)] \times (1 + L)^c$	Vegetation patterns, biomass productivity (Huete, 1988)	2.130

[a] $D = 3$. D is the specified neighbourhood.

[b] Thermal constants are provided in the metadata file of the Landsat 8 images.

[c] $L = 0.5$. L is a canopy brightness correction factor (Huete, 1988)

Appendix A1

Detailed description of topographical variables and their estimation methods.

As potential predictors to characterise the species' ecological niche, we used 8 variables related to topographic conditions, land surface temperature, soil water availability and vegetation cover (Table A1).

Topographic features were derived from a Digital Elevation Model (DEM) obtained from the LiDAR data at a 5 × 5 m spatial resolution (CNIG, 2018). These variables include both primary and secondary (or compound) parameters. Primary parameters are directly calculated from DEM and include variables such as aspect and terrain slope. Secondary parameters involve combinations of the primary parameters and are indices that characterise the spatial variability of specific processes occurring in the landscape, such as moisture gradients, temperature and the effects of solar radiation acting upon vegetation (Moore, Grayson, & Ladson, 1991). We calculated slope using the Spatial Analyst Tool in ArcGIS ver.10.3.1. (ESRI, 2015). Aspect (eastness and northness), the topographic position index (TPI) was calculated using the Geomorphometry and Gradient Metrics toolbox v.237 (Evans, Oakleaf, Cushman, & Theobald, 2014) for ArcGIS.

We estimated Normalized Difference Infrared Index (NDII) (Sriwongsitanon, et al., 2016), as a proxy for variability of soil moisture storage in the study area using Landsat 8 OLI/TIRS satellite image data at 30 × 30 m spatial resolution (see https://lta.cr.usgs.gov/L8). Images were acquired from the United States Geological Service's Earth Explorer (USGS; https://earthexplorer.usgs.gov/), for the growing season (April-September) from 2013 to 2018. The NDII was calculated for each of the satellite images (see equation in Table A1), and an average of the NDII was calculated for the growing season (2013 to 2018). Rare endemic plants are often associated with vegetation communities (Gogol-Prokurat, 2011). We used Soil-Adjusted vegetation index (SAVI, see Table S1) (Ren & Feng, 2015) to capture fine-scale information on land cover, such as vegetation density and/or amount of exposed soil. The SAVI was averaged for the growing season (2013 to 2018). Finally, we calculated land surface temperature (LST) as a proxy of the temporal and spatial variations of water balance in the study area (Kerr, et al., 2004). The LST in degree Celsius was calculated from thermal band 10 (Cristóbal, et al., 2018), using the Semi-Automatic Classification Plugin tool (SCP) (Congedo, 2016), in QGIS ver.2.18. (http://www.qgis.org). The LST was averaged for the growing season (2013 to 2018). Prior to analyses, atmospheric correction of the satellite images was carried out using the Dark Object Subtraction (DOS) approach (Nazeer, Nichol, & Yung, 2014), implemented in SCP for QGIS.

To reduce multicollinearity between variables, we calculated the Variance Inflation Factor (VIF). Variables with values of VIF > 5 were excluded (Table S1) (Heiberger, Richard, & Holland 2004). All environmental data were standardised to Universal Transverse Mercator coordinate (Datum ETRS-89) at a spatial resolution of 30 × 30 m using ArcGIS ver.10.3.1.

Appendix A2

Ecological niche-based distribution modelling

We modelled the ecological niche of *A. lopesianum* using Ensemble Modeling approach (EM). EM was built to reduce the biases and limitations inherent to the use of single SDM techniques (Araújo & New, 2007). We used the BIOMOD2 version 3.3-7. (W. Thuiller, Georges, Engler, & Breiner, 2016) in R program version 3.4.2 (R Core Team, 2017), to fit four modelling methods: Generalised Linear Models (GLM), Generalised Boosting Models (GBM), Maximum Entropy (MaxEnt) and Random Forest (RF).

Models were calibrated with presence data (n = 28) and 10 000 random background points. Background data were limited to within 5 km from the known presence records (Williams, et al., 2009). Background and presence points were weighted equally in the models (Wilfried Thuiller, Lafourcade, Engler, & Araújo, 2009). The Continuous Boyce Index (CBI) (Hirzel et al., 2006), a metric specifically designed for presence only models and insensitive to pseudo-absences was used to evaluate the model performances. We considered models to be “wrong” when CBI values were below -0.5, “average to random” for values ranging from -0.5 to 0.5, and good for values above 0.5. For each model, we computed CIB by performing ten-fold split sampling (80% training data and 20% test data). We assembled all individual models into a single EM by weighting projections based on the individual CIB scores. A CIB of 0.5 was established as a cut-off value, and only projections from those models with CIB above that value were considered. We selected this approach to maximise the informative character of the results. EM evaluation consisted of calculation of CIB using independent data. In this case, the abundance data gathered in field were used as presence records for the EM validation. To transform the EM into discrete binary map of presence/absence, the minimum training presence (MTP) value was used. The MTP is a conservative method used for identifying unknown distribution areas (Pearson, Raxworthy, Nakamura, & Townsend Peterson, 2007).

To assess the relevance of each predictor through all considered models, we used values of variable importance to calculate their mean value. With a permutation procedure, BIOMOD2 provides a measure of the relative importance of each variable which is independent of the modelling technique used (for details see BIOMOD2 package documentation; BIOMOD2 package is available at http://r-forge.r-project.org/projects/biomod/). Variable importance is determined as one minus the correlation score between the original prediction and the prediction made with a permuted variable (Wilfried Thuiller, et al., 2009). This procedure was repeated ten times and mean, and standard deviation were calculated for each variable. Finally, response curves were calculated to interrogate the relationship between the response (i.e., presence) and each explanatory variable. These show how a given explanatory variable influences the response variable while keeping all other predictors at their average (Wilfried Thuiller, et al., 2009).

Figure A1. Natural Park Arribes del Duero

Table A2. Generalised Linear model results for the relationship between the observed abundance (individuals' number of *Antirrhinum lopesianum*) and the distance to niche centroid (DNC) (*n* = 35).

glm.nb(formula = Abundance ~ DNC, data, init.theta, link = log)

Coefficients	Coefficients	Std. Error	z value	Pr(>|z|)
(Intercept)	6.9922	0.7319	9.553	<2e-16***
DNC	-26.0958	4.2757	-6.103	1.04e-09 ***

Signif. codes: 0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1

Spatial autocorrelation across the geographic space is an inherent property of most ecological data and may break the assumption of independence of the data modelled (Legendre, 1993). We calculated global Moran's index and we constructed the Moran's*I* correlogram of residuals for the Generalised Liner Model relating the observed abundance (individuals' number of *Antirrhinum lopesianum*) and the distance to the species´ niche centroid. We calculated *p* values for Moran's *I* values at each lag distance using a Monte Carlo randomisation procedure (999 permutations).

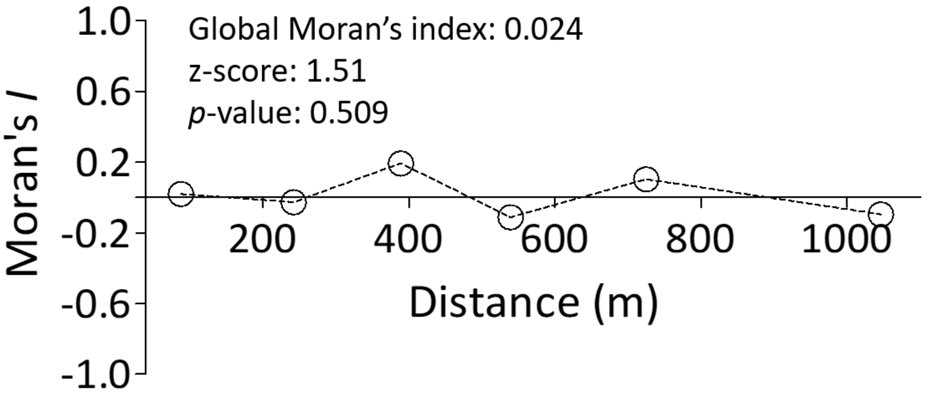

Figure A2. Correlograms of Residuals and calculated global Moran's index for the Generalised Liner Model. Significant lags are indicated by a black circle.

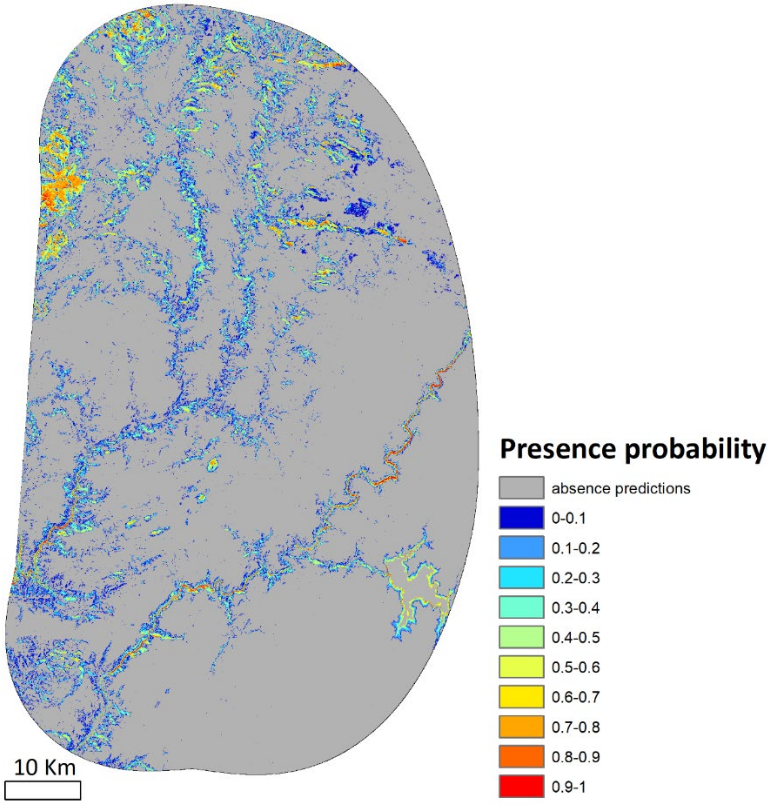

Figure A3. Presence probability map (ensemble model) for *Antirrhinum lopesianum* across its entire distribution range

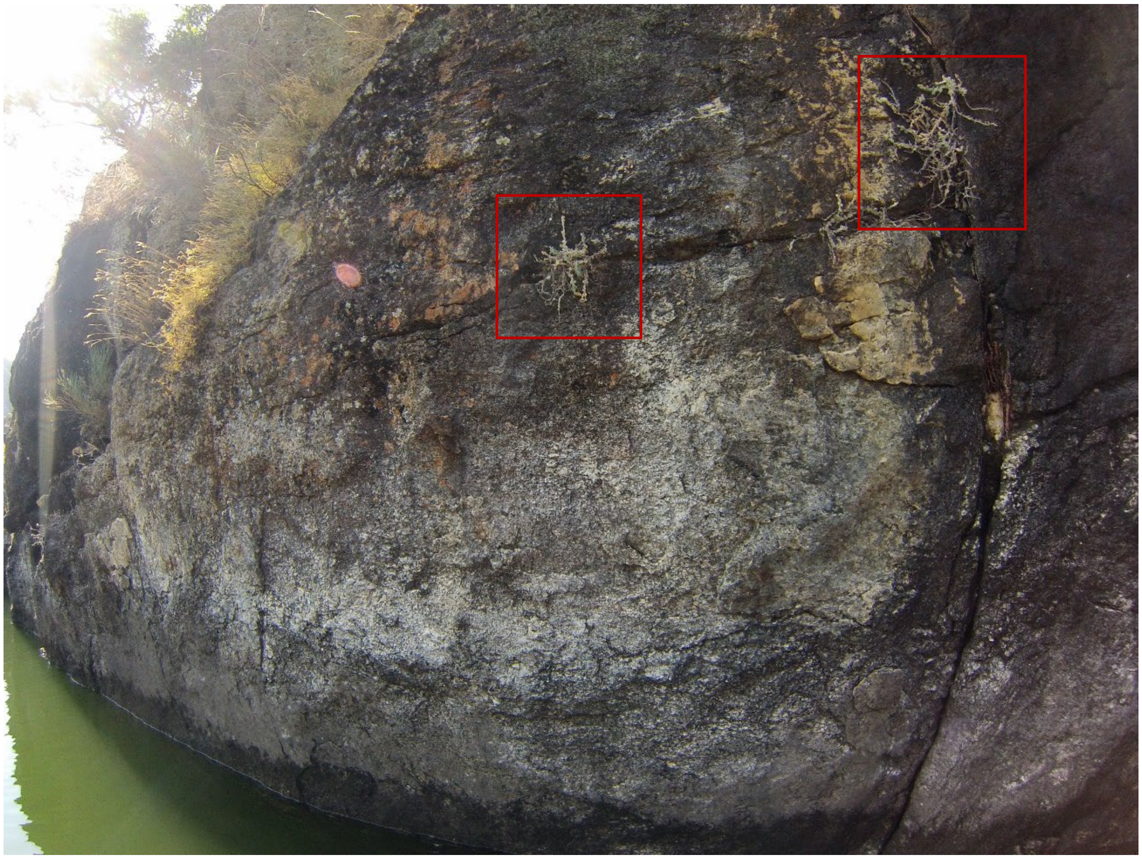

Figure A4. Landscape features of the main habitats of *A. lopesianum* in the Duero Basin (España-Portugal)

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CAPÍTULO 3

Foto: Juan Antonio Sánchez Rodríguez.

EFECTOS DEL CAMBIO CLIMÁTICO EN POBLACIONES PERIFÉRICAS DE HIDRÓFITOS: UN ANÁLISIS DE SENSIBILIDAD PARA ESPECIES DE PLANTAS EUROPEAS BASADO EN PREFERENCIAS CLIMÁTICAS

AUTORES
Ricardo Enrique Hernández-Lambraño,
David Rodríguez de la Cruz,
José Ángel Sánchez-Agudo

RESUMEN

Las predicciones biogeográficas indican que se esperan retracciones generalizadas de las zonas más al sur del rango de distribución de las especies (i.e., borde trasero) debido al cambio climático antropogénico. Estos cambios serán más acusados en poblaciones vinculadas a hábitats frágiles, como aquellas que habitan los márgenes traseros que dependen estrechamente de las condiciones específicas del agua. Este artículo estudia los efectos potenciales del cambio climático sobre los patrones de distribución de poblaciones amenazadas de especies que habitan en los márgenes posteriores de sus rangos de distribución geográfica (península ibérica). Nosotros exploramos (i) si estas poblaciones se encuentran en el límite de tolerancia climática de la especie, (ii) cuantificamos sus patrones geográficos de vulnerabilidad al cambio climático y, además, (iii) identificamos de manera espacialmente explícita si las poblaciones de estas especies amenazadas se encuentran en entornos vulnerables al cambio climático. Para hacer esto, simulamos el nicho climático de cinco especies de hidrófitos utilizando un MDE basado en registros de presencias y un conjunto de datos climáticos fácilmente disponibles. Nuestros resultados muestran que las poblaciones ibéricas estudiadas ocupan ambientes menos adecuados en relación con los climas óptimos de cada una de las especies. Estos resultados sugieren una explicación plausible para el grado actual de estancamiento o regresión experimentado por estas poblaciones que a su vez mostraron alta sensibilidad y, por lo tanto, vulnerabilidad a los extremos térmicos y alta estacionalidad de la humedad y la temperatura. Las predicciones climáticas para 2050 muestran que la mayoría de las poblaciones analizadas experimentaran situaciones de riesgo ambiental en la península ibérica. Por lo tanto, acciones dirigidas a la conservación de estas poblaciones deben priorizarse en las ubicaciones geográficas en las que la vulnerabilidad es mayor.

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Article

Effects of the Climate Change on Peripheral Populations of Hydrophytes: A Sensitivity Analysis for European Plant Species Based on Climate Preferences

Ricardo Enrique Hernández-Lambraño [1,2,*], **David Rodríguez de la Cruz** [1,2] **and José Ángel Sánchez Agudo** [1,2]

[1] Grupo de Investigación en Biodiversidad, Diversidad humana y Biología de la Conservación, Campus Miguel de Unamuno, Universidad de Salamanca, s/n, E-37007 Salamanca, Spain; droc@usal.es (D.R.d.l.C.); jasagudo@usal.es (J.Á.S.A.)
[2] Departamento de Botánica y Fisiología Vegetal, Área de Botánica, Campus Miguel de Unamuno, Universidad de Salamanca, s/n, E-37007 Salamanca, Spain
* Correspondence: ricardohl123@usal.es

Abstract: Biogeographical theory suggests that widespread retractions of species' rear edges are expected due to anthropogenic climate change, affecting in a particularly intense way those linked to fragile habitats, such as species' rear edges closely dependent on specific water conditions. In this way, this paper studies the potential effects of anthropogenic climate change on distribution patterns of threatened rear edge populations of five European hydrophyte plants distributed in the Iberian Peninsula. We explored (i) whether these populations occur at the limit of the species' climatic tolerance, (ii) we quantified their geographic patterns of vulnerability to climate change, and in addition, (iii) we identified in a spatially explicit way whether these threatened populations occur in vulnerable environments to climate change. To do this, we simulated the climatic niche of five hydrophyte species using an ecological modelling approach based on occurrences and a set of readily available climatic data. Our results show that the Iberian populations studied tended to occur in less suitable environments relative to each of the species' optimal climates. This result suggests a plausible explanation for the current degree of stagnancy or regression experienced by these populations which showed high sensitivity and thus vulnerability to thermal extremes and high seasonality of wet and temperature. Climatic predictions for 2050 displayed that most of the examined populations will tend to occur in situations of environmental risk in the Iberian Peninsula. This result suggests that the actions aimed at the conservation of these populations should be prioritized in the geographic locations in which vulnerability is greatest.

Keywords: sensitivity; vulnerability; threatened species; hydrophyte plants; species' rear edges; climatic change; MaxEnt; CENFA

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1. Introduction

Biodiversity of freshwater habitats, especially in relation to wetland plants, is of conservation concern world-wide [1,2]. These species are threatened by multiple factors. Climate and land use changes are standing out and are the most important factors [3,4]. Risk of extinction due to anthropogenic climate change is a significant threat for these species [2], especially those populations inhabiting at the rear range edge [5].

Biogeographical theory suggests that widespread retractions of species' rear edges should be seen in response to anthropogenic climate change [5,6]. Indeed, climate is considered the most important driver of plant species distribution, with temperature mostly affecting the upper elevation/latitude edges and water availability the low elevation/latitude edges [7]. In this way, it is reasonable to expect that population loss and range retractions should be seen in the most drought-prone areas of a species' distribution [8]. This prediction is based on the fact that rear edge populations often occur at the limit of the species' ecological tolerance. Thus, they habitually occupy less favourable habitats [9,10] and are expected to decline in performance as climate warming pushes them to extirpation [5,11], although empirical evidence remains rare [12]. The study of these populations are critically important for the long-term conservation of genetic diversity, phylogenetic history, evolutionary potential, and species' response to ongoing climate change [6]. In this sense, identifying the vulnerability of threatened rear edge populations to climate change is vital for guiding effective conservation efforts [13].

Williams et al. [14] describe three fundamental aspects of the vulnerability of a species or individuals to climate change: (i) sensitivity, as the degree to which the species' persistence ability is determined by the climatic conditions of its habitat; (ii) exposure, as the degree to which the species will experience climate change across its distribution range; and finally (iii) adaptive capacity, as the ability to adapt to changes in climate, through dispersal, evolutionary responses, and phenotypic plasticity [15]. Under this scenario, climate-niche models based on ecological niche theory [16] may offer a spatially-explicit insight into geographic patterns of species vulnerability (e.g., sensitivity and exposure) to climate change. This approach uses known occurrence locations and spatially-explicit data on the environmental conditions believed to restrict the geographic distribution of the target species to predict habitat suitability across the landscape [17]. In recent years, a novel approach to model the species' climate niche based on Hutchinson's concepts, termed Climate-Niche Factor Analysis (CNFA), was proposed by Rinnan and Lawler [15]. CNFA quantifies species marginality and the specialization relative to the global distribution [18] and provides a spatially-explicit insight into geographic patterns of species vulnerability to climate change [15].

A particularly interesting situation for the study of the effects of the anthropogenic climate change on the persistence ability of threatened species populations living in the rear edge range concerns the hydrophytic flora of the Iberian Peninsula, where many Central European species occur at their northern range limits, often in peripheral isolates [19]. This pattern is closely associated with the climatic and geological history of the region with an important role of migratory processes caused by glacial and interglacial periods [20]. For this study we selected hydrophyte plants since it is known that aquatic and wetland habitats are among the most threatened worldwide mainly due to hydrological system alterations, especially those derived from global warming, pollution, and invasive species [21,22]. Moreover, many of these taxa are very scarce in the Iberian Peninsula and therefore have been included in the Red List of the Vascular Flora of Spain and Portugal [23–25]. Based on a comparative analysis of such species (n = 5), the aims of this paper are threefold: (i) we test whether threatened populations living on the rear range edge occur at the limit of the species' climatic tolerance; (ii) we quantify the geographic patterns of vulnerability to climate change; (iii) we attempt to identify in a spatially explicit way whether threatened rear edge populations occur in vulnerable habitats to climate change.

2. Materials and Methods

2.1. Study Species

Five hydrophyte plant species of the European Flora were selected to carry out this study (Table 1). 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 [19]. Moreover, due to the species' rarity within the Iberian territory, they are included in the Red List of the Vascular Flora [23–25]. We based our selection on listed species because their distribution is solidly documented [19] and also because of their conservation significance.

2.2. Study Area and Dataset

The study area covers most of Continental Europe including the British Islands. The limits used are according to those defined by Flora Europaea [27], excluding Iceland, Faroe Islands, Svalbard, and Novaya Zemlya (Figure 1). Partial territories in the Russian Federation west of the Urals were also included [9]. The Iberian Peninsula was established a priori as a geographical marginal territory due to its latitude, orographical and climatic characteristics. In addition, this territory has historically been one of the major Mediterranean refugia for Central European species [20].

Table 1. List of studied species, their biological features, and species' threat category.

Species	Flowering Month	Biological Type	Iberian Threat Category	IUCN Global Category
Callitriche platycarpa Kütz. in Rchb.	Early-summer	Hydrophyte	VU	LC
Eleocharis austriaca Hayek (=*Eleocharis mamillata* subsp. *austriaca* (Hayek) Strandh.)	Late-spring	Hydrophyte, Geophyte	CR	LC
Luronium natans (L.) Raf.	Mid-summer	Hydrophyte, Herb	EN	LC
Nymphoides peltata (S.G. Gmel.) O. Kuntze	Mid-summer	Hydrophyte, Herb	CR, EN	LC
Rumex hydrolapathum Huds.	Late-spring	Hydrophyte, Herb	CR	LC

Note: Iberian red list category according to the Spanish and Portuguese legislations (EN, endangered; CR, critically endangered; VU, vulnerable) [23–25] and to the IUCN global red list category (LC, least concern) [26].

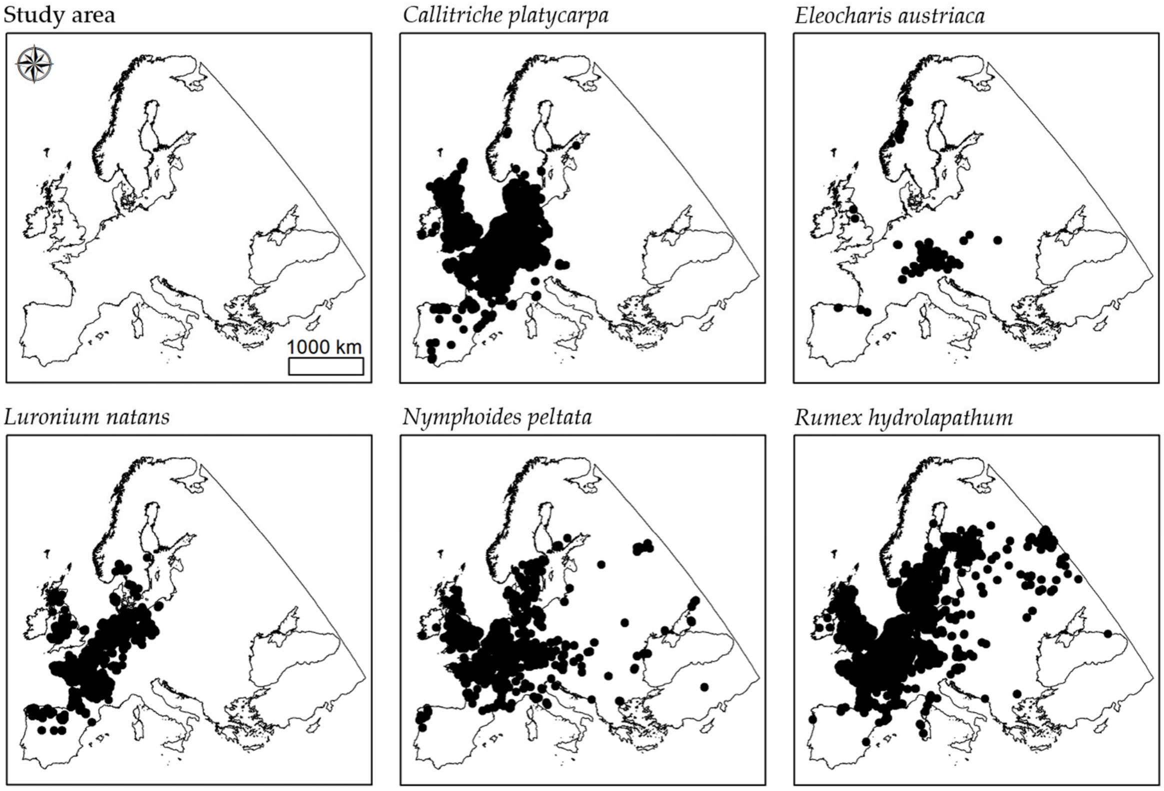

Figure 1. Occurrence records per analyzed species in the study area.

Data on the geographical distributions of the study species (Figure 1) were compiled from the Global Biodiversity Information Facility (GBIF; www.gbif.org (accessed on 3 June 2019)). The dataset was cleaned manually so that only high-quality records were used in the analysis; records conforming to these sets of conditions were retained: (i) georeferenced; (ii) with year of record; (iii) with "county" or "municipality" locality data; (iv) inland coordinates; (v) and inside the known native range of the species, as depicted by species range maps of Figure 1. We used a grid resolution of 1 × 1 km to remove duplicate records (i.e., only one occurrence record per grid square of 1 × 1 km), thereby reducing clustering (spatial bias; [28]). We omit occurrence data outside the years 1979–2013 to align with the temporal reference of the climatic variables (described below).

For our analysis, climatic variables of the current climate (representative of 1973–2013) were downloaded from the climatologies at high resolution for the Earth's land surface areas (CHELSA; http://chelsa-climate.org/ (accessed on 3 June 2019)) database at a 30 arc-second resolution (~900 m). This dataset provides improved climatic estimates in landscapes with complex topography [29]. We chose four bioclimate variables (Table 2 and Figure A2) to represent a broad range of seasonal and annual climatic patterns across the study area while minimizing redundancy (Figure A1). These variables were chosen because of their strong link with important ecological processes in plant species, such as distribution, reproduction, and phenology [30]. Furthermore, these variables are enough to explain most of the climatic variation, and other important variables (e.g., winter and summer temperatures) are strongly related to linear combinations of the four variables considered. Climate data were aggregated by averaging to 1 × 1 km to match the species data grid. All spatial information processing was handled using ArcGIS 10.3 [31].

Table 2. Bioclimatic variables used for this study, obtained from the CHELSA database [29], and calculated from monthly air temperature means and precipitation sums.

Variable	Calculation	Unit	Source
Annual mean temperature	$\left(\frac{\sum_{i=1}^{12} t_i}{12}\right)$	°C	CHELSA [29]
Temperature seasonality	$\left(\sqrt{\frac{1}{11}\sum_{i=1}^{12}\left(t_i-\left(\sum_{i=1}^{12}\frac{t_1}{12}\right)\right)^2}\right)$	SD	
Annual precipitation	$\sum_{i=1}^{12} p_i$	mm	
Precipitation seasonality	$\left(\sqrt{\frac{1}{11}\sum_{i=1}^{12}\left(p_i-\left(\sum_{i=1}^{12}\frac{p_i}{12}\right)\right)^2}\right)/\left(\frac{\sum_{i=1}^{12} p_i}{12}\right)$	CV	

t_i = monthly temperature, p_i = monthly precipitation, SD = standard deviation and CV = coefficient of variation.

For future climate (2050: average of 2041–2060), we used an ensemble method of two global climate models (GCMs) due to climate uncertainty [32,33]. The two GCMs used were the Community Climate System Model (CCSM4) [34] and the Hadley Global Environment Model (HadGEM2-ES) [35]. Both models have been used extensively in addressing the effects of climate change on species distributions [36]. For the future climate ensembles, we used two representative concentration pathways (RCPs) for the prescribed greenhouse gas emissions: (i) RCP 4.5, which represents medium CO_2 emissions; (ii) and RCP 8.5, which represents high CO_2 emissions [37]. The future climate data were downloaded from the CHELSA dataset at a 30 arc-second resolution and were aggregated by averaging to 1 × 1 km to match the species data grid (Figure A2).

In relation to projections of the effects of future climate change for European regions, the Iberian Peninsula has been identified as one of the areas that is most vulnerable to the predicted changes [38,39] and is expected to experience greater increases in temperature and aridity than other regions. In this sense, we evaluated spatial changes in the Iberian Peninsula climate characteristics through the differences between the future climate and the current climate.

2.3. Modelling Climatic Suitability

To assay whether threatened populations living on the Iberian Peninsula occur at the limit of the species' climatic tolerance we used the ecological-niche model. This approach uses known occurrence locations and spatially-explicit data on the environmental conditions (herein climatic variables) believed to restrict the geographic distribution of the target species to predict climatic suitability across the landscape [17]. To do it, we used the maximum entropy (MaxEnt) modeling [40]. MaxEnt is a machine-learning process that uses presence-only data and environmental covariates to estimate the relative suitability of one place vs. another [41]. MaxEnt has been described as especially efficient to handle complex interactions between response and covariates [41,42], and to be little sensitive to small sample sizes [43]. We used this method because it has been demonstrated to perform well in a diverse set of modeling scenarios in ecology, biogeography, and conservation, besides being widely used to fit models across many different taxa, geographical areas, and time periods [44,45].

To build the climatic-niche models for each of the species, we used the kuenm package in R [46]. This tool allows detailed calibrations of ecological-niche models in Maxent, helping to select among the complex and numerous sets of parameters those that demonstrate best performance based on significance, predictive ability, and complexity level [46]. In this study, for each species, we created 493 candidate models by combining 1 set of climatic predictors, 17 values of the regularization multiplier (0.1–1.0 at intervals of 0.1, 2–6 at intervals of 1, 8, and 10), and all 29 possible combinations of the 5 feature classes (linear = l, quadratic = q, product = p, threshold = t, and hinge = h). We evaluated the candidate model performance based on significance (partial ROC, with 500 iterations and 50% of the data for bootstrapping), omission rates (E = 5%), and model complexity (AICc). Best models for each species were selected according to the following criteria: (i) significant models with (ii) omission rates $\leq$5%. Then, from among this model set, models with delta AICc values of $\leq$2 were chosen as final models. The candidate model creation was performed using the "kuenm_cal" function and the candidate model evaluation and the best model selection was done using the "kuenm_ceval" function.

We created final models (i.e., the best fitted model for each species) using the full set of occurrences and the selected parameterizations (Table 2). We produced 10 replicates by bootstrap with logistic outputs. The final model evaluations consisted of calculations of partial ROC, omission rates, and AICc using an independent dataset. Final models were performed with the "kuenm_mod" function. Finally, we extracted habitat suitability values from the final model for the threatened species populations inhabiting the Iberian Peninsula.

2.4. Modelling Vulnerability to Climate Change

Species' vulnerability can be interpreted as a function of both extrinsic (exposure) and intrinsic (sensitivity and adaptability) traits [14,47]. Exposure is the degree to which the species will experience climate change across its distribution range [14]. Sensitivity is the degree to which the species' persistence ability is determined by the climatic conditions of its habitat, while adaptability is the ability to adapt to changes in climate through dispersal, evolutionary responses, and phenotypic plasticity [14,15]. In this study adaptability was not considered, as climatic niche evolution of species is slower than the rate of climate change [48].

We used the CNFA approach [15] to quantify vulnerability to climate change of five species of hydrophyte plants with threatened populations living on the Iberian Peninsula. This approach expands on the earlier ecological-niche factor analysis [18,49], provides spatially-explicit insight into geographic patterns of vulnerability, relies only on readily-available spatial data, and is suitable for a wide range of species and habitats [15]. One of the strengths of this approach is the ability to identify and describe aspects of climate vulnerability to climate change with relatively little information about the species itself [15]. Thus, this enables us to more proactively identify species of highest climate vulnerability and species in need of immediate conservation actions. We used this approach because it has been demonstrated to perform well in different taxa and geographical areas [15,50–52].

To quantify CNFA models we compared the species distribution in the ecological space with the global distribution of available environmental conditions [15]. We quantified two aspects of a species' niche: (i) the marginality axis (m), which is a measurement capturing the difference between the conditions used by the species and the conditions available in the global distribution and (ii) specialization axis (p), which is the ratio of size of the species niche to that of the global distribution [15]. To define the global distribution in our study, we used the combined range of the five hydrophyte species in Europe as N cells. For the distribution of each species with N cells, we used occurrence records. For the multi-dimensional ecological space composed of bioclimatic variables with C dimensions, the components of marginality and specialization are defined as the marginality factors (m_j) and the specialization factors ($p_{j1},\ p_{j2}, \ldots,\ p_{jC-1}$), respectively. Based on the first factor, we extracted the marginality values for the threatened populations of each species in order to identify how far the climatic conditions used for such populations are from the optimal climatic conditions for the global distribution.

Following Rinnan and Lawler [15], we measured the following metrics: sensitivity (s), exposure (e), and vulnerability (v) of each species to climate change. We obtained the sensitivity factor through the marginality and specialization axis for each bioclimatic variable. We first normalized the vector ($m_j,\ p_{j1},\ p_{j2}, \ldots,\ p_{jC-1}$) to ($w_{j1},\ w_{j2}, \ldots,\ w_{jC}$). We then calculated the sensitivity factor s_j corresponding to each bioclimatic variable j as $\sum_{k=1}^{C} w_{jk}\rho_k$, where ρ_1 is the amount of specialization on the marginality axis, and $\rho_k(k > 1)$ is the amount of specialization expressed on the specialization axis. The s metric quantifies the average species specialization in each climatic variable. Thus, if a species only tolerates a narrow range of climatic conditions, we may reasonably expect it to be more sensitive to the effects of climate change. The overall sensitivity $s = \sqrt{1/C \sum_{j=1}^{C} s_j}$, can then be used to compare the sensitivity between different species.

The e metric quantifies the differences between current and future conditions (departure) inside the species range. In this sense, this metric reflects the amount of climate change a species might experience if it remains in place. The departure factor is $d_j = \sum_{i=1}^{N} p_j |\delta_{ij} - z_{ij}|$, where δ_{ij} and z_{ij} represents the value of current and future bioclimatic variable j at location i, respectively, and p_i is the habitat utilization at location i. Then, the overall exposure is $e = \sqrt{\sum_{j=1}^{C} d_j^2}$.

Finally, to calculate the species vulnerability to climate change, we combined sensitivity and exposure. To do this, we calculated the vulnerability factor v_j for each bioclimatic variable j as $\sqrt{(1 + d_j)s_j}$, and the predicted vulnerability of cell i for the global distribution as $v_{Gi} = \sqrt{\sigma_{Gi}\varepsilon_{Gi}}$. Thus, the overall vulnerability is $v = \sqrt{1/C \sum_{j=1}^{C} v_j}$. The v metric reflects the interaction between s and e to climate change. Larger values of s and e indicate higher climate sensitivity and exposure, which result in larger v values, indicating higher vulnerability in the climatic variable. See [15] for more thorough details on the CNFA process.

We implemented the CNFA method with the "cnfa" function of the package CENFA [15] in the R program [53]. We also used the "predict" function in the CENFA package to evaluate the spatial vulnerability within a potential habitat used by the threatened populations living on the Iberian Peninsula. To select the potential habitat, we used the minimum convex polygon (convex hull) produced by the full set of presence records for each species in the Iberian Peninsula. Maps of spatial vulnerability were generated with ArcGIS [31].

3. Results

3.1. Projected Changes in the Iberian Peninsula Climate Characteristics

Analysis of projected changes in the climate variables used in this study showed that the Iberian Peninsula is very likely to undergo warmer and drought events (Figure 2). These changes present similar spatial patterns for the near future (2050) under the scenarios RCPs 4.5 and 8.5. On the one hand, annual patterns of temperature are projected to increase overall on the peninsula, especially in the mountain zones. On the other hand, for the annual patterns of precipitation a decrease over the entire peninsula is projected, especially in the north and northwest. Finally, seasonal patterns of temperature and precipitation are projected to increase throughout the peninsula.

3.2. Climatic Suitability

The final best models for each species performed well in throughout the study area according to the external validations (Table 3).

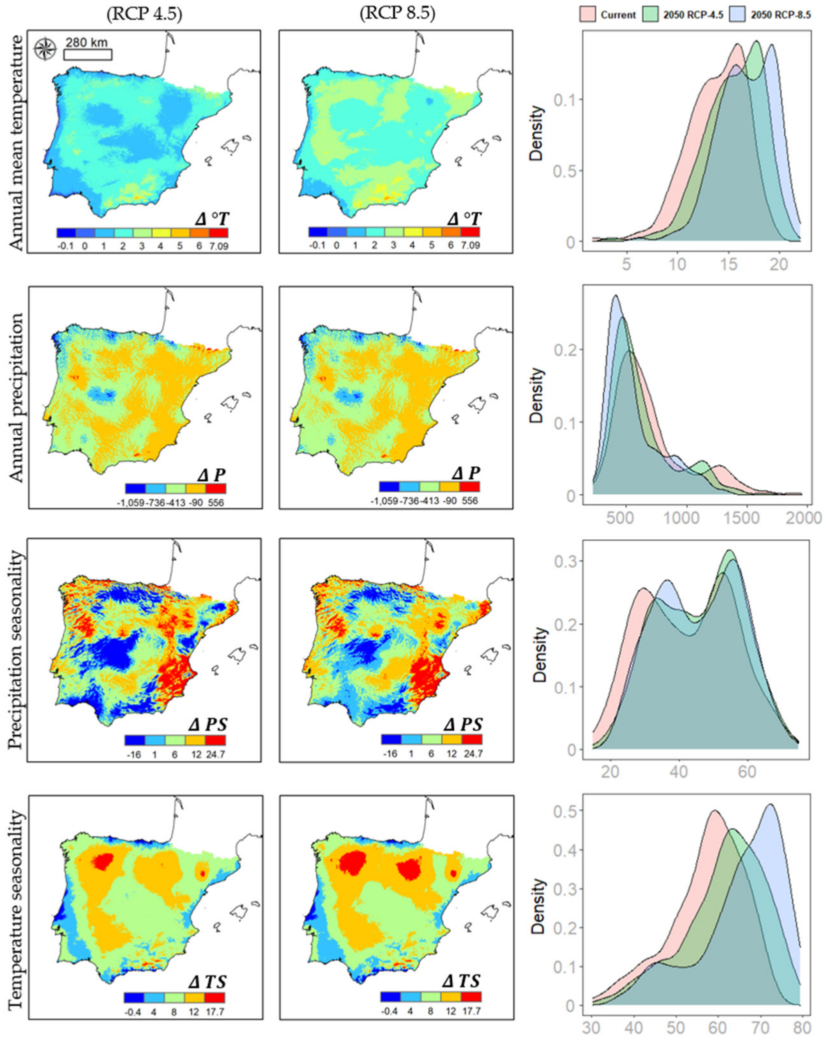

Figure 2. The first two columns are spatial differences between Iberian Peninsula climate variables for the future period (2050: average of 2041–2060) and the current period (average of 1973–2013). The third column is the distribution of climate variables throughout the Iberian Peninsula. The future climate scenario was estimated from an ensemble of two global climate models projections under the representative concentration pathways (RCPs) 4.5 and 8.5. **TS** and **PS**: temperature and precipitation seasonality, respectively.

Table 3. Final models performance for each species under optimal parameters. Feature classes (linear = l, quadratic = q, product = p, threshold = t, and hinge = h).

Species	Regularization Multiplier	Feature Classes	Mean AUC Ratio	Partial ROC	Omission Rate (5%)	AICc
Luronium natans	0.5	lqp	1.15	0.01	0.045	346.46
Rumex hydrolapathum	2	lqph	1.28	0.00	0.030	985.65
Nymphoides peltata	0.1	lqp	1.22	0.02	0.049	458.27
Callitriche platycarpa	0.1	lqp	1.19	0.01	0.023	248.13
Eleocharis austriaca	0.7	lq	1.16	0.02	0.041	148.13

These results indicate high dependence on the occurrence data and the set of climatic variables included in the analysis. In relation to the optimal climates of the analyzed species, the threatened populations of all species tend to occur in less climatic suitable habitats on the Iberian Peninsula (Figure 3).

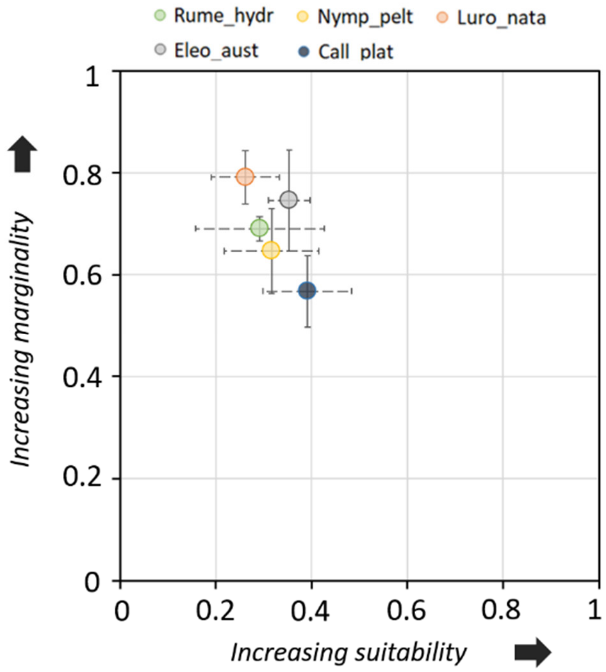

Figure 3. Mean suitability vs. mean marginality for all species. The grey bars are standard errors reflecting variation for marginality and grey dashed bars are standard errors reflecting variation for habitat suitability. Rume_hydr, *Rumex hydrolapathum*; Nymp_pelt, *Nymphoides peltate*; Luro_nata, *Luronium natans*; Eleo_aust, *Eleocharis austriaca*; Call_plat, *Callitriche platycarpa*.

3.3. Vulnerability to Climate Change

Application of the CNFA method to the calibration set indicated that only two axes (i.e., the axis of marginality and the first axis of specialization) accounted for most of the information for all species studied. The five species have high overall marginality indexes (Table 4). These results show that the niche of the species differs clearly from the mean conditions in their global distributions.

Table 4. Overall marginality (*m*), sensitivity (*s*), exposure (*e*), and vulnerability (*v*) of five hydrophyte species in the study area under future climate for the year 2050. The future climate scenarios were estimated from ensembles of two global climate models projections under the representative concentration pathways (RCPs) 4.5 and 8.5.

Species	*m*	*s*	*e* (RCP 4.5)	*e* (RCP 8.5)	*v* (RCP 4.5)	*v* (RCP 8.5)
Luronium natans	2.16	3.81	0.43	0.74	2.00	2.07
Rumex hydrolapathum	1.98	3.36	0.43	0.73	1.91	1.97
Nymphoides peltata	2.08	2.95	0.44	0.75	1.79	1.85
Callitriche platycarpa	2.06	2.86	0.43	0.68	1.74	1.79
Eleocharis austriaca	2.12	1.92	0.37	1.08	1.44	1.53

Marginality coefficients point out that species are essentially linked to wets and less seasonality environments (see *m* factor in Figure 4). Climatic conditions of the populations living on the Iberian Peninsula were rather different from the mean available conditions (Figure 3), indicating that these marginal populations tended to occur in less suitable climatic environments relative to each of the species' optimal climates.

The factor account for specialization (see *p* factor in Figure 4), mostly regarding annual mean temperature and precipitation seasonality, indicates some species' sensitivity to shift away from the optimal values of these variables. In fact, the overall sensitivity index (Table 4) shows that the ranges of species' tolerable climate conditions are quite restricted, with the greatest sensitivity to hot temperature extremes and high fluctuations in precipitation (i.e., high seasonality) (see *s* factor in Figure 4).

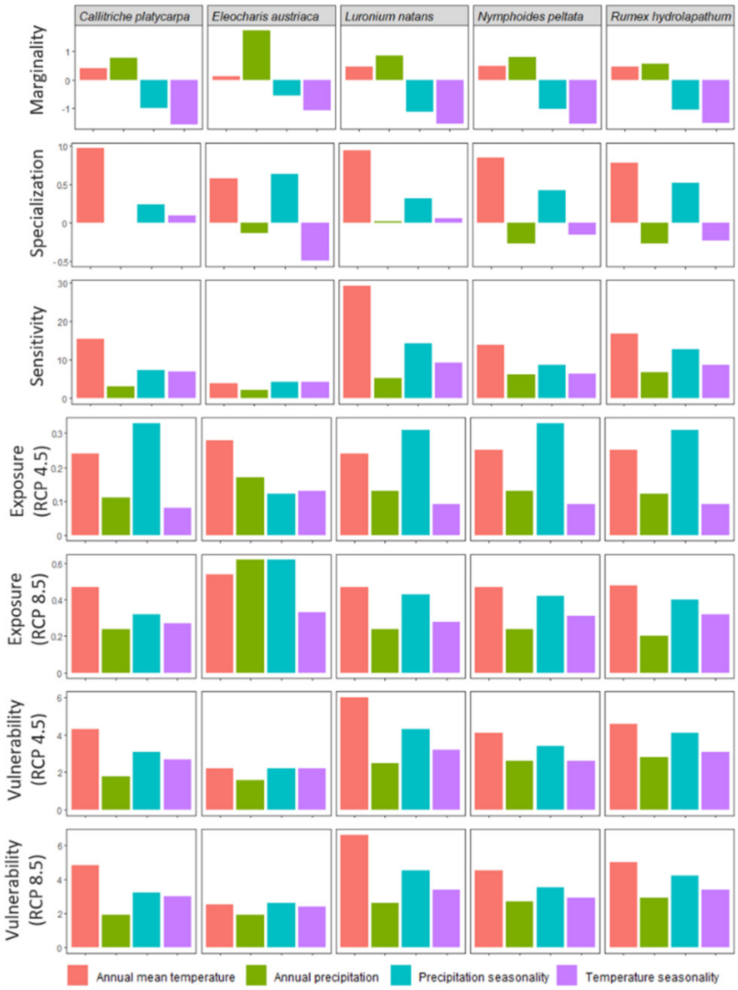

Figure 4. The marginality factor, specialization factor, sensitivity factor, exposure factor, and vulnerability factor of five hydrophytes species for four bioclimatic variables calculated under future climate for the year 2050 as estimated from an ensemble of two global climate models projections under the representative concentration pathways (RCPs) 4.5 and 8.5.

The RCP 8.5 scenario had greater departure than the RCP 4.5 scenario in almost every variable, reflecting the expected increase in climate change associated with the concentration of greenhouse gas emissions. The five species had high departure indexes, hence, this led to high overall vulnerability indexes (Table 4). In general, the species studied demonstrated high vulnerability to thermal extremes and high seasonality of precipitation and temperature (see *v* factor in Figure 4).

For the five species, the overall vulnerability index under RCP 8.5 is higher than those under RCP 4.5 (Table 4). Compared with the other hydrophyte species, *L. natans* and *R. hydrolapathum* have the highest overall vulnerability to climate change, followed by *N. peltata*, *C. platycarpa*, while *E. austriaca* shows the least overall vulnerability (Table 4). The different CO_2 emission scenarios do not change the vulnerability ranking for the five hydrophyte species.

The most vulnerable current environments for the hydrophyte threatened populations taking into account future climatic projections for the Iberian Peninsula are shown in the Figures 5 and A3. Overall, most of the examined populations occur in environments that will undergo significant climatic changes (Figures 5 and A3). The spatial patterns of climatic vulnerability under RCP 4.5 show a similar pattern for RCP 8.5 (Figures 5 and A3). However, the high CO_2 emission increases the climatic vulnerability for the studied populations (Figure 5). These results also allow us to detect areas that can serve as a refuge from climatic disturbances. Thus, the predictions suggest that the northeast zones of both hydrographic basins of the Duero and Ebro may provide potential suitable refuges from climate change for *R. hydrolapathum*, *L. natans* and *C. platycarpa*. For *N. peltata* and *E. austriaca*, climate refuges could be located in zones adjacent to the hydrographic basins of the Miño and Pais Vasco, respectively.

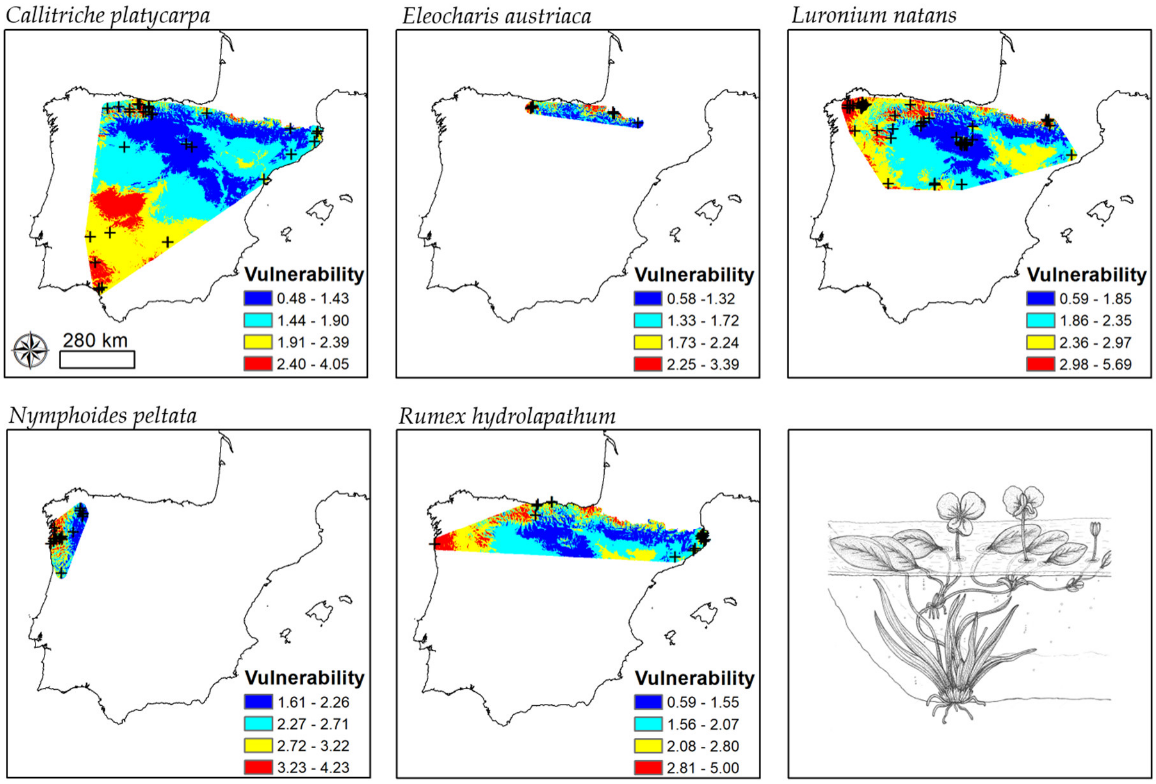

Figure 5. Predicted vulnerability across the potential habitat used by the threatened populations living on the Iberian Peninsula. The future climate scenario was estimated from an ensemble of two global climate model projections under the representative concentration pathway (RCP) 8.5 (year 2050). Predicted vulnerability for RCP 4.5, see Figure A3.

4. Discussion

4.1. Vulnerability to Climatic Change

In this study, we apply a niche-based ecological model in an attempt to explicitly assess the potential effects of the climate change on the distribution patterns of species' rear edges. In this case, hydrophytic plants were ideal due to their specific ecological requirements. In recent years, niche-based ecological models have become a strong approach for addressing this conservation issues at large scales [9,15]. This approach can provide useful information in order to lead priority conservation plans to endangered populations in a timely manner, when there is a lack of updated data about the real degree of threat for these populations, and the available resources for practical conservation actions are scarce [9].

In this study, we have found a correspondence between ecological (i.e., climatic) and geographical marginality for threatened rear edge populations of some European hydrophytes on the Iberian Peninsula. These results would support the hypothesis that marginality within the set of habitable conditions (i.e., climate niche) could represent an outstanding factor on the performance and thus persistence of isolated plant populations. Less availability of suitable environments at their rear edge distribution ranges could be translated into lower survival potential for these populations [5]. The optimal climatic habitats for our target species are associated with colder, wetter, and less seasonal environments and, for the Iberian Peninsula, these conditions 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 are particularly highlighted. Numerous studies provide empirical evidence of an important rear edge population decline. For example, Allen et al. [54] report range retractions and population decline (i.e., mortality) associated with elevated drought stress at species' rear edges in forest ecosystems across the globe. However, this rear edge population decline has been often questioned by empirical data [55]. These mismatches can occur, for instance, if peripheral populations are genetically isolated and adapted to conditions in border areas [56], their ecological optima are not properly established [57], their original patterns have been altered by anthropogenic land use changes [5], or their distribution patterns occur in suitable environmental conditions (i.e., microrefugium) surrounded by inhospitable regional climate [9]. On the other hand, many of the threatened populations of the analyzed species are distributed in a scattered way with few populations throughout the Iberian Peninsula. Some of them are also associated with anthropogenic activities that would make them especially vulnerable. In fact, in the Iberian territory, the distribution areas of these populations are subject to a strong anthropogenic pressure due to the conditioning of river banks, the construction of river walks, the transformation of water courses, the drainage of the water table, and livestock [24]. These factors may increase fragmentation and isolation, which can result in a significant population decline [6].

Our results indicate that the studied species have narrower climate niches, suggesting that they may be very sensitive to climate change. In fact, the two largest components of the species sensitivity factor are all associated with colder, wetter, and less seasonal environments. Analysis of projected changes in the climate variables used in this study showed that the Iberian Peninsula is very likely to undergo significant climatic changes. These changes display similar spatial patterns for the near future (2050) with increase of the temperatures and droughts in the Iberian Peninsula under scenarios RCPs 4.5 and 8.5. This climatic panorama might exacerbate the rapid decline in performance of the current threatened populations as climate warming pushes them to extirpation. Recent cases of local extinction of populations of hydrophytes in the Iberian Peninsula have already been documented [24,58]. Among the recently extinct species are *Sagittaria sagittifolia* L. and *Oenanthe aquatica* (L.) Poir., hydrophytes formerly distributed in the north of the Iberian Peninsula. The causes of their extinction are mainly associated with the loss/deterioration of their suitable habitats due to extreme climatic events such as drought and to the strong anthropogenic pressure to which the distribution areas of these species in the Iberian Peninsula are subjected [58].

It is important to note, that by neglecting other ecological processes that shape the habitat, the approach present here entails some of the issues common to niche-based ecological models [59]. For instance, our results are based on an analysis of the species' climate niches. Non-climatic constraints, such as biotic interactions, dispersal ability, and land uses are important factors that also drive the species' distribution [60,61]. Another issue is that the CNFA approach is a static method that does not capture the dynamic nature of population fluctuations over time. In addition, we must realize that the spatial scale of our approach may reduce the range of some drivers (regional/local, topographic, and microclimatic landscape features) and their effects on the study patterns [62]. However, we think that this approach is a suitable tool for a first-pass assessment of distribution patterns of species vulnerability to climate change in a spatially explicit fashion, with the potential to optimize the conservation efforts of the most vulnerable populations.

4.2. Management Implications

Climate change will have far-reaching impacts on biodiversity, including increasing extinction rates [63]. Despite that increasing impacts are expected for the future, only a few studies have aimed for a general understanding of the vulnerability of rear edge populations to climate change [38]. Herein we regard the present approach as a first step towards identifying the rear edge populations that could be potentially affected by the ongoing climate change.

Depending on each species' capacity to adapt to climate change via dispersal, rapid evolution, or other processes [63], recommended actions aimed at the conservation of these populations involve monitoring and supporting adaptive responses, prioritizing the geographic locations in which vulnerability is greatest (Figure 5). On the other hand, feasible in situ conservation measures (e.g., reduce or remove threats, maximize habitat quality, reinforcement, seed collection, translocations, enhance habitat heterogeneity, improvement of landscape connectivity [6,64]) for these populations should be concentrated in those parts that are expected to have low vulnerability to climate change. In addition, areas with low vulnerability should be considered as potential suitable climate refuges from anthropogenic climate change when planning the creation of new micro-reserves or enlarging the existing ones. Climate refugia may reduce the local extirpation risk for organisms [65].

Since there are still a lot of unanswered questions about the ecological processes involved in the persistence of these populations, it is crucial to develop several research lines to provide an effective conservation plan in the long term. The vulnerability map can help to design new studies to address knowledge gaps, for example, flowering phenology, and genetic and breeding systems of the species to assess the main factors affecting female reproductive success.

5. Conclusions

Climate change vulnerability assessments are an important tool for understanding the threat that the anthropogenic climate change poses to species and populations. In this sense, the results of our study to this methodological field show that some threatened hydrophyte populations in the Iberian Peninsula tended to occur in less suitable environments relative to each of the species' optimal climates. This result suggests a plausible explanation to the current degree of stagnancy or regression experienced by these populations. Populations of the five species showed high sensitivity and thus vulnerability to thermal extremes and droughts. Climatic predictions for 2050 displayed that most of the examined populations will tend to occur in situations of environmental risk in the Iberian Peninsula. Therefore, actions aimed at the conservation of these populations should be prioritized in the geographic locations in which vulnerability is greatest.

Author Contributions: Conceptualization, R.E.H.-L. and J.Á.S.A.; methodology, R.E.H.-L.; software, R.E.H.-L.; validation, D.R.d.l.C. and J.Á.S.A.; formal analysis, R.E.H.-L.; investigation, R.E.H.-L.; writing—original draft preparation, R.E.H.-L.; writing—review and editing, R.E.H.-L., J.Á.S.A. and D.R.d.l.C.; visualization, R.E.H.-L.; supervision, J.Á.S.A. All authors have read and agreed to the published version of the manuscript.

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Conflicts of Interest: The authors declare no conflict of interest.

Appendix A

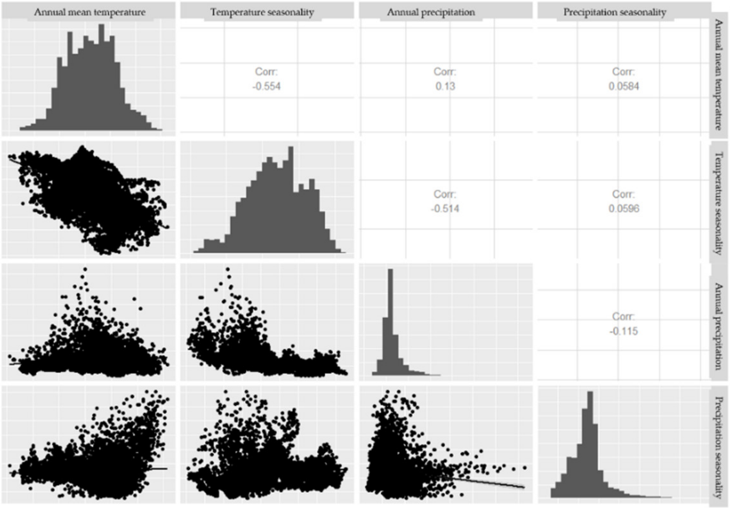

Figure A1. Pearson's correlation coefficients among the variables used to calibrate the MaxEnt and CNFA models.

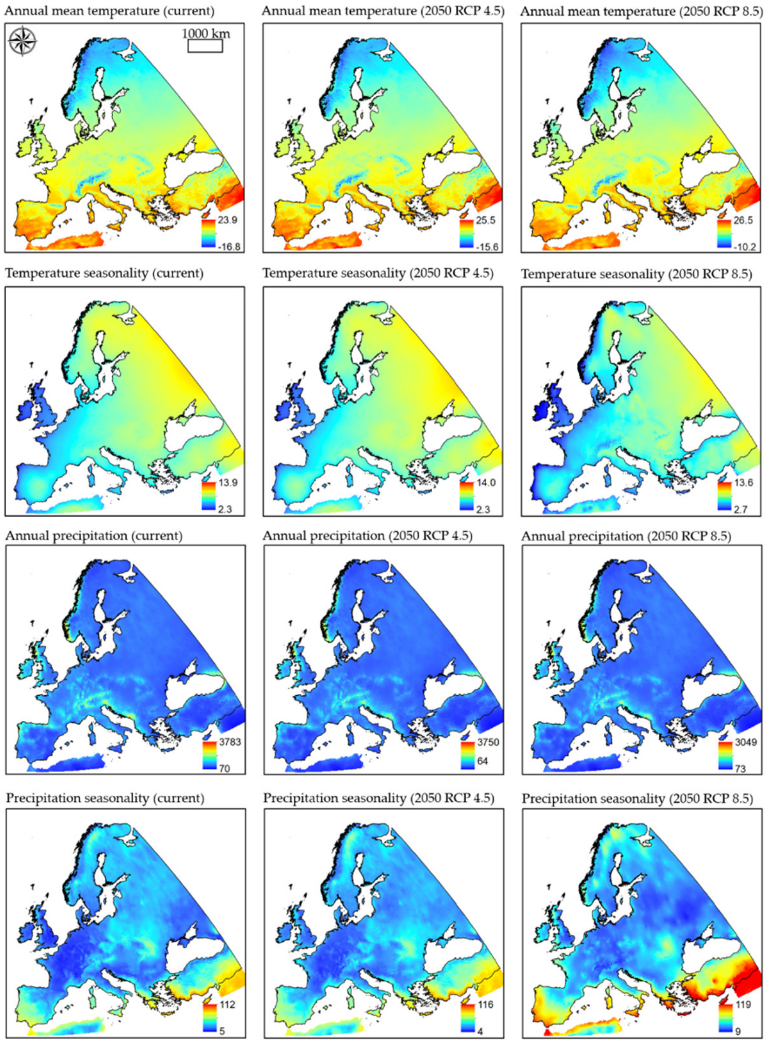

Figure A2. Spatial distribution of the climatic dataset in the study area. The future climate data were estimated from an ensemble of two global climate model projections under the representative concentration pathway (RCP) 4.5 (year 2050).

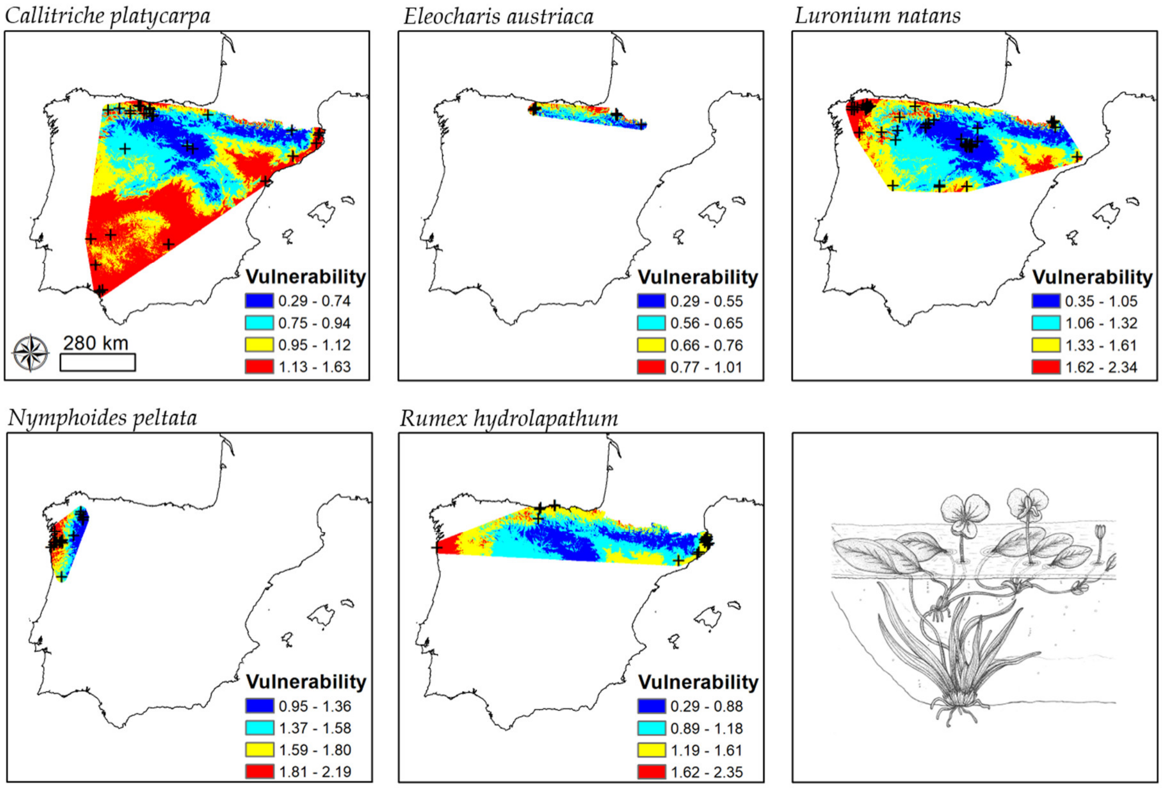

Figure A3. Predicted vulnerability across the potential habitat used by the threatened populations living on the Iberian Peninsula. The future climate scenario was estimated from an ensemble of two global climate model projections under the representative concentration pathway (RCP) 4.5 (year 2050).

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CAPÍTULO 4

Fotos: Juan Antonio Sánchez Rodríguez.

HACIA LA CIMA: EXPANSIÓN DE NICHO DE *Taraxacum officinale* y *Ulex europaeus* EN REGIONES MONTAÑOSAS DE AMÉRICA DEL SUR

AUTORES
Ricardo Enrique Hernández-Lambraño,
Pablo González-Moreno,
José Ángel Sánchez-Agudo

RESUMEN

En el contexto actual del cambio global en curso, la comprensión de cómo los nichos de las especies invasoras pueden cambiar entre diferentes áreas geográficas o períodos de tiempo es extremadamente importante para la detección temprana y el control de futuras invasiones. Para ello, evaluamos el efecto de las variables climáticas y no climáticas y la sensibilidad a varias resoluciones espaciales (es decir, 1 y 20 km) sobre los cambios de nicho durante la invasión de *Taraxacum officinale* y *Ulex europaeus* en América del Sur, y estimamos cambios de nicho realizado utilizando una combinación de métodos: 1) análisis de componentes principales (PCA) y 2) Modelos de nicho ecológico recíprocos (rENM). Además, investigamos la dinámica de invasión en un escenario de calentamiento severo para el año 2050 con el objetivo de desentrañar el papel de los cambios de nicho en la distribución potencial de la especie en el futuro. En nuestros resultados observamos una clara expansión de nicho para ambas especies en América del Sur hacia temperaturas más altas, precipitación y radiación en relación con sus rangos nativos. Por el contrario, el conjunto de condiciones ambientales que solo ocupaban los rangos nativos (es decir, el nicho no cubierto = anfilling) era menos relevante. La magnitud de los cambios de nicho no depende de la resolución de las variables. Los modelos calibrados con ocurrencias del rango nativo predijeron grandes áreas adecuadas en América del Sur (fuera del rango de los Andes) donde *T. officinale* y *U. europaeus* están actualmente ausentes. Además, ambas especies podrían aumentar sus distribuciones potenciales para 2050, principalmente en la parte sur del continente. Además, el nicho no cubierto (nicho anfilling) sugiere un alto potencial para invadir regiones adicionales en el futuro, lo cual es extremadamente relevante considerando el impacto actual de estas especies en el hemisferio sur. Estos hallazgos confirman que las especies invasoras pueden ocupar nuevos nichos que no son predecibles a partir del conocimiento basado solo en variables climáticas o información del rango nativo.

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Towards the top: niche expansion of *Taraxacum officinale* and *Ulex europaeus* in mountain regions of South America

RICARDO ENRIQUE HERNÁNDEZ-LAMBRAÑO,[1]* PABLO GONZÁLEZ-MORENO[2,3]
AND JOSÉ ÁNGEL SÁNCHEZ-AGUDO[1]
[1]*Instituto Hispano-Luso de Investigaciones Agraria (CIALE) Universidad de Salamanca, Parque Científico, C/ Del Duero, 12; 37185 Villamayor, Salamanca, España (Email: ricardohl123@usal.es),* [2]*Estación Biológica de Doñana, Consejo Superior de Investigaciones Científicas (EBD-CSIC), Isla de la Cartuja, Sevilla, Spain, and* [3]*CABI, Bakeham Lane, Egham, UK*

Abstract In the current context of ongoing global change, the understanding of how the niches of invasive species may change between different geographical areas or time periods is extremely important for the early detection and control of future invasions. We evaluated the effect of climate and non-climate variables and the sensitivity to various spatial resolutions (i.e. 1 and 20 km) on niche changes during the invasion of *Taraxacum officinale* and *Ulex europaeus* in South America. We estimated niche changes using a combination of principal components analyses (PCA) and reciprocal Ecological Niche Modelling (rENM). We further investigated future invasion dynamics under a severe warming scenario for 2050 to unravel the role of niche shifts in the future potential distribution of the species. We observed a clear niche expansion for both species in South America towards higher temperature, precipitation and radiation relative to their native ranges. In contrast, the set of environmental conditions only occupied in the native ranges (i.e. niche unfilling) were less relevant. The magnitude of the niche shifts did not depend on the resolution of the variables. Models calibrated with occurrences from native range predicted large suitable areas in South America (outside of the Andes range) where *T. officinale* and *U. europaeus* are currently absent. Additionally, both species could increase their potential distributions by 2050, mostly in the southern part of the continent. In addition, the niche unfilling suggests high potential to invade additional regions in the future, which is extremely relevant considering the current impact of these species in the Southern Hemisphere. These findings confirm that invasive species can occupy new niches that are not predictable from knowledge based only on climate variables or information from the native range.

Key words: biological invasion, ecological niche models, Niche shift, *Taraxacum officinale*, *Ulex europaeus*.

INTRODUCTION

Globalization (i.e. expansion of transport and global trade) has led to an increase in the geographical scope and impact of biological invasions (Mack *et al.* 2000). In fact, along with changes in atmospheric chemistry and climate, biological invasions have been added to the list of important drivers of global change with significant effects on biodiversity and ecosystem functioning (Kriticos *et al.* 2003). Despite the growing knowledge on biological invasions, we still lack a thorough understanding of the processes driving the distribution of invasive species and the changes that might occur between the native and introduced ranges (Guisan *et al.* 2014).

The environmental requirements of an invasive species (i.e. ecological niche) (Peterson & Vieglais 2001; Peterson 2003; Santana *et al.* 2008) define the boundaries of its potential distribution in both native and introduced regions. Identifying these key factors is useful to prioritize areas for the detection and control of early invasions (Peterson & Vieglais 2001; Peterson 2003; Franklin 2010; Elith 2013). A common approach is to make predictions about the potential introduced ranges using the data about the species distribution in either the native or the introduced range (Peterson 2003; Herborg *et al.* 2007; Franklin 2010). This approach is based on the assumption that invasive species have similar niche characteristics in native and introduced ranges (i.e. niche conservatism) (Peterson & Vieglais 2001; Peterson 2003; Carlos-Júnior *et al.* 2015). However, this approach has been questioned by recent studies highlighting the existence of factors that can cause invasive species to expand beyond their native environmental envelope (Guisan & Zimmermann 2000; Broennimann *et al.* 2007; Tingley *et al.* 2014; González-Moreno *et al.* 2015; Parravicini *et al.* 2015). Niche differentiation may result from different biotic factors such as the absence of competitors and/or pathogens, evolutionary changes through genetic

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*Corresponding author.

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drift or selection in the introduced range (Müller-Schärer *et al.* 2004; Hierro *et al.* 2005; Richardson *et al.* 2010).

Having a clear understanding of whether ecological niches are similar in the native and introduced range is important for two main reasons: i) anticipation is the most effective management strategy to predict species occurrences in new areas and ii) detecting significant deviations from niche conservatism may highlight invasive species that are characterized by ecological or evolutionary changes during invasions, helping us to understand when such changes are likely to occur (Broennimann & Guisan 2008; Alexander & Edwards 2010; Petitpierre *et al.* 2012). For example, observed shifts into novel climates in the introduced range that are not occupied in the native range (i.e. expansion) suggest that changes in biotic interactions or rapid evolution may have extended the species climatic tolerances (Petitpierre *et al.* 2012; Guisan *et al.* 2014). Furthermore, the presence of suitable climates in the introduced range not yet occupied by the species (i.e. unfilling) is critically important because it suggests the likelihood of invading additional geographical regions in the future (Petitpierre *et al.* 2012; Guisan *et al.* 2014).

Niche conservatism in invasive species is usually studied with regard to climate variables (Broennimann *et al.* 2007; Rödder & Lötters 2009; Gallagher *et al.* 2010; Petitpierre *et al.* 2012; Parravicini *et al.* 2015). These studies assume that climate variables at coarse spatial resolution (e.g. 10, 20 and 50 km) are the leading factors of the distribution of invasive species (Austin & Van Niel 2011b; Guisan *et al.* 2014). This assumption ignores the importance of local environmental heterogeneity in shaping species distribution (Austin & Van Niel 2011b). For example, a species might occur under conditions in specialized habitats (e.g. mountains or stream banks) that could generally be characterized at a finer spatial grain (e.g. 1 km) (Bertrand *et al.* 2012).

However, niche changes may be observed when non-climate variables are included in the analyses (Bertrand *et al.* 2012; Guisan *et al.* 2014; González-Moreno *et al.* 2015). For example, solar radiation has long been known to influence plant distribution based on known biophysical processes such as chlorophyll inhibition or resistance to ultraviolet radiation (Tranquillini 1964; Austin & Van Niel 2011b). Furthermore, topographic diversity as a proxy of available soil moisture and nutrients has been shown to determine a significant part in the distribution of the plants (Austin & Van Niel 2011a). Although previous studies pinpoint the climate at large scales as the main factor driving species distributions and niche shifts for invasive species, the role of non-climate components or microclimates is largely unknown, despite the fact that they could provide important insights into the understanding of niche shifts for invasive species.

We carried out a large biogeographical study on *Taraxacum officinale* G. H. Weber ex Wiggers. (Asteraceae) and *Ulex europaeus* L. (Fabaceae). Both species are native to Eurasia and Europe, respectively, but are largely invading temperate areas worldwide with a significant impact. Thus, these species are ideal for testing the existence of niche shifts associated with biological invasions. We used occurrence data fully covering the large environmental gradients in their native and introduced ranges, to examine a) the effect of climate and non-climate variables (solar radiation and topographic diversity) and b) sensitivity to various spatial resolutions (i.e. 1 and 20 km) in the niche changes during the invasion of these species. We further investigated future invasion dynamics under a severe warming scenario for 2050 (HadGEM2; RCP-8.5) to unravel the role of niche shifts in their future distribution. This study represents the first assessment of niche dynamics for *T. officinale* and *U. europaeus* in South America and can provide insights into climatic influences driving species range expansions and potential adaptive physiological shifts now and into the future.

METHODS

Study species

Taraxacum officinale (dandelion) is a perennial herb from Eurasia that has spread worldwide. It is believed that it originated in Greece or perhaps Asia and spread across temperate areas to Europe and Asia Minor (Holm *et al.* 1997; CABI 2001; Stewart-Wade *et al.* 2002). This species has a fossil record that goes back to glacial and interglacial times in Europe, and it is thought to have colonized the Americas post-Pleistocene via Beringia (Holm *et al.* 1997; CABI 2001; Stewart-Wade *et al.* 2002; Molina-Montenegro & Cavieres 2010). *Taraxacum officinale* has apomictic reproduction and in its introduced range can be found growing in sites with contrasting climates and disturbance regimes and shows a wide range of adaptability to light, being able to grow vigorously in full sunlight, or in diffused light in the shade of trees or buildings (Stewart-Wade *et al.* 2002; Molina-Montenegro & Cavieres 2010).

Ulex europaeus (gorse) is a fast-growing woody legume of the family Fabaceae, native to the western coastal area of Europe and the British Isles including Ireland where it is an important component of native heathland vegetation (Gaynor & MacCarter 1981; Holm *et al.* 1997; Rees & Hill 2001; Hill *et al.* 2007; ILDIS 2007). *Ulex europaeus* has been introduced worldwide as a hedge plant to contain grazing animals, as fodder, and even to assuage the nostalgia of European colonists (CABI 2001). It has become naturalized elsewhere in Europe, North Africa and the Middle East (Holm *et al.* 1997; Bojnanský & Fargašová 2007; Hill *et al.* 2007). Its status as native to Italy and other countries of central Europe, and in localized montane districts of

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North Africa, remains uncertain (CABI 2001; ILDIS 2007). The species is considered as invasive in many parts of the world at different latitudes, including New Zealand, Australia, South and North America (Chile, Colombia, California, Oregon, etc.) and tropical islands (Hawaii, Reunion), in altitudes that vary from 0 to 4000 m (Lowe *et al.* 2000; Hornoy *et al.* 2011).

Occurrence datasets

Data on the native distributions of *T. officinale* (Eurasia) ($n = 7887$) and *U. europaeus* (Europe) ($n = 5541$) were compiled from the Global Biodiversity Information Facility (GBIF; www.gbif.org) and Invasive Species Compendium from the Centre for Agriculture and Biosciences International (CABI; www.cabi.org).

To assess the effect of spatial resolution on the significance of the climate and in combination with non-climate variables in measuring the niche shift, we used two grid resolutions of 30 arc-seconds and 10 arc-minute to remove duplicate records (i.e. only one occurrence record per grid square of 1 km and 20 km, respectively) thereby reducing clustering (spatial bias). This filtering decreased the number of records for *T. officinale* to 423 grids of 1 km and 398 of 20 km and for *U. europaeus* to 333 and 301 grids, respectively. Occurrence data points for these species from the South American introduced ranges were collated from GBIF and CABI (*T. officinale* $n = 199$ and *U. europaeus* $n = 53$) and were prepared in the same way with the procedure described above (*T. officinale:* 199 grids of 1 km and 156 grids of 20 km; *U. europaeus:* 53 and 38 grids, respectively). The compiled database is the result of an extensive search of the occurrence of the species in the study area. Nevertheless, we acknowledge that this database may not represent the full range of environmental conditions in which the species can be found (e.g. other introduced areas) as in other studies elsewhere (e.g. Petitpierre *et al.* 2012).

Environmental variables

Our initial variable set was composed of 19 bioclimatic variables, solar radiation and topographic diversity. Bioclimatic variables were available from WorldClim climate database at 30 arc-seconds and 10 arc-minute spatial resolutions (about 1 and 20 km at the equator) (Hijmans *et al.* 2005). Solar radiation was calculated using the Area solar tool from program ArcGIS 10.0 (ESRI 2015), which calculates clear-sky insolation across a Digital Elevation Model (DEM) at 1-km spatial resolution (US Geological Surveys; www.usgs.gov) accounting for aspect, slope and topographic shading. Topographic diversity was calculated using the Neighborhood toolset in ArcGIS 10.0. For each DEM grid cell, it calculates the diversity of elevation values considering all surrounding cells within a 3-km radius. Both layers were resampled to 20 km. Future climate projections under a severe warming scenario for 2050 (HadGEM2-RCP-8.5 at 1 km) (Martin *et al.* 2011) were also downloaded from the WorldClim climate database.

In order to avoid the cross-correlation within the selected environmental variables, a multi-collinearity test was conducted using Pearson's correlation coefficient. Variables with cross-correlation coefficient values of $r > \pm 0.7$ were excluded. The final explanatory variables selected were annual mean temperature (T_AM), mean diurnal range (T_DR), maximum temperature of warmest month (T_WM), temperature annual range (T_AR), mean temperature of wettest quarter (T_WQ), annual precipitation (P_A), precipitation of wettest month (P_WM), precipitation of driest month (P_DM), precipitation seasonality (P_S), topographic diversity (topo_div) and solar radiation (sun_l) (Appendix S1). All spatial information processing was handled using the Spatial Analyst Tool from ESRI ArcGIS 10.0 (ESRI 2015).

Measuring Niche Shifts

We used the Broennimann *et al.* (2012) and Petitpierre *et al.* (2012) approach to measure the niche shift related to climate and non-climate factors (i.e. radiation and topography) for *T. officinale* and *U. europaeus* between the native and introduced ranges. In this approach, a PCA is calibrated using the set of all environmental conditions in both ranges. Then, the available environmental conditions for the species within the full studied background are compared to those conditions in areas that are effectively occupied by the species in each of its ranges (native *vs.* introduced). First, we extracted the environmental conditions for both native and introduced ranges at two spatial resolutions (i.e. 1 and 20 km). Based on these data, we performed a PCA for each spatial resolution and used its first two axes to characterize the environmental space within which we could compare the native and introduced niches. We then divided this environmental space into a grid of 100 × 100 cells, as in Broennimann *et al.* (2012). Next, we used a kernel density function to convert occurrences of *T. officinale* and *U. europaeus*, and the available environments in each range into densities in order to correct for sampling bias and environmental availability, respectively, and to ensure that the results were independent of the grid resolution (Broennimann *et al.* 2012). Later, for each species and spatial resolution, we assessed the niche overlap between native and introduced ranges using Schoener's D metric which expresses an overall fit between niches over the full environmental space and determines whether we can infer the characteristics of the introduced niche from the native niche. This metric varies from 0 (totally dissimilar) to 1 (complete overlap) (Warren *et al.* 2008; Broennimann *et al.* 2012). Following Petitpierre *et al.* (2012), we also measured the proportion of the native niche non-overlapping with the introduced niche (i.e. unfilled), and the proportion of the introduced niche non-overlapping with the native niche (i.e. expansion), considering either the common environmental space for native and introduced ranges or the whole environmental space. These metrics were calculated using the 75th percentile of environments available in each range to avoid bias due to artefacts of the density function. Finally, we calculated the median of the distribution density and the median of the available environmental space in both ranges in order to

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assess the overall direction of the shifts (Broennimann *et al.* 2012; Petitpierre *et al.* 2012; González-Moreno *et al.* 2015). All analyses were run using ecospat packages in R 3.1.3 (R Core Team 2015).

Fitting reciprocal Ecological Niche Modelling, future prediction and evaluation

To explore niche conservatism across ranges of *T. officinale* and *U. europaeus*, we generated reciprocal Ecological Niche Models (Broennimann *et al.* 2007; Medley 2010; González-Moreno *et al.* 2015) using the Maxent program (Phillips *et al.* 2006). The Maxent model is a maximum entropy-based machine learning programme that estimates the potential distribution for a species based on the environmental constraints (Phillips *et al.* 2006). To generate reciprocal models, first we made distribution models of potential suitable habitats with the same occurrence points and environmental variables that were used in our PCA analyses for the two species and for each of the ranges at two spatial resolutions. Then, we projected native models into introduced ranges and visually compared them with models calibrated with data occurrence in the introduced range. We then repeated this step but projected the introduced models into the native range and then compared them in the same way.

In fitting these models, we used 75% of the data for calibration and the other 25% for evaluation, a convergence threshold of 10^{-5}, the selection of feature classes (autofeature), regularization multiplier value of 1, a maximum of 5000 iterations and 10000 background points. To select the background points or pseudo-absences, we generated a Kernel Density map to draw background points at random in Maxent. This limits the background points to areas that we assume were surveyed for the species, which provides Maxent with a background file with the same bias as the present locations (Elith *et al.* 2011). We measured variable importance by comparing jackknife of training gain values when models were made with individual variables. To avoid projections into environments outside which the models were trained upon, we used the 'fade-by-clamping' option in Maxent, which removes heavily clamped pixels from the final predictions (Phillips *et al.* 2006). The outputs generated by Maxent were converted into binary maps using the 10th percentile training presence threshold to define suitable or unsuitable habitats for both species.

Predictive performance of each model was assessed using 15-fold cross-validation and the area under a receiver operating characteristic curve (AUC), which measures a model's ability to discriminate presence from background records (0.5 = random, 1 = perfect). We also calculated binary omission rates as the proportion of evaluation points that were not predicted by the models (Medley 2010).

Finally, the climate models for each species were projected into future climate scenarios to generate species distribution maps of the introduced range under a severe warming scenario for 2050 (HadGEM2; RCP-8.5). Models were calibrated with all the occurrence data points (native plus South America) to account for potential niche differences between native and introduced ranges (Broennimann & Guisan 2008; Jiménez-Valverde *et al.* 2011; González-Moreno *et al.* 2015).

RESULTS

Environmental niche shift

A niche shift of *T. officinale* and *U. europaeus* between native and introduced ranges was observed at different spatial resolutions of environmental variables and using both climate and climate-plus non-climate variables as predictors. Niche shifts metrics mostly varied with respect to the variables included in the analyses (i.e. higher shifts when considering both groups of variables). Nevertheless, shift metrics were rather constant across spatial resolutions (Table 1).

For both species, the change in the mean niche position between the native and introduced ranges was similar to the change in the background climate (continuous and dashed arrows, respectively, Figs 1 and 2, Appendices S10 and S11). For both species, the niche overlap between the native and introduced environmental spaces was lower when climate-plus non-climate variables were considered (*D*, Table 1). For *T. officinale*, the introduced niche exhibits a proportion outside of its native niche, occupying wetter and warmer environments with higher solar radiation relative to its native range (Fig. 1, Appendices S10 and S12). However, the analysis showed a small proportion of suitable environments in the introduced range not yet occupied by the species (unfilling) when climate-plus non-climate variables were considered and in opposite direction to the niche expansion (Fig. 1c and Table 1).

Similarly, the introduced niche of *U. europaeus* was expanded to areas with higher temperature, solar radiation and precipitation during the driest months relative to its native range (Fig. 2, Appendices S11 and S13). Furthermore, when climate-plus non-climate variables were considered, the species niche showed unfilling in areas of very low solar radiation and high temperature seasonality (Fig. 2c and Table 1).

However, when we considered only the common environmental space between the native and introduced ranges, expansion and unfilling were reduced for both species (Table 1). However, niche expansion was still relevant when considering climatic and non-climatic variables together (>11%).

Reciprocal ecological niche modelling

Climate-only and climate-plus non-climate models at different spatial resolutions for both species were all significantly better than random with high AUC (>0.83) and relatively low omission values (<22%), indicating that for each species, the most suitable habitats predicted were highly correlated with the

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Table 1. Niche metrics from PCA analysis for each species, resolution and variable included in the analysis. D = Schoener's D statistic of niche overlap. Environmental space indicates what quantile of the environmental density used to remove marginal climates was retained to calculate niche expansion and unfilling metrics; full indicates analysis was performed on the whole environmental extent native and invaded, and ∩ indicates analysis was performed at the intersection between native and invaded range

Species	Resolution	Variables	D	Environmental space	Expansion %	Unfilling %
Taraxacum officinale	1 km	Climate	0.351	Full	21.1	0
				∩	9.10	0
		Climate-plus non-climate	0.075	Full	48.2	12.2
				∩	39.3	0.22
	20 km	Climate	0.402	Full	19.8	0
				∩	6.61	0
		Climate-plus non-climate	0.081	Full	39.8	11.5
				∩	28.9	0.10
Ulex europaeus	1 km	Climate	0.264	Full	45.3	0
				∩	5.10	0
		Climate-plus non-climate	0.061	Full	71.1	19.2
				∩	48.2	0
	20 km	Climate	0.263	Full	52.0	0
				∩	6.90	0
		Climate-plus non-climate	0.070	Full	70.4	17.5
				∩	11.0	0

actual occurrences of the species (Table 2). AUC and omission values were rather constant across spatial resolutions and both groups of variables selected.

Temperature annual range was the most important variable for both species in their native ranges (Appendices S2–S9). While in the introduced range solar radiation, annual precipitation, maximum temperature of warmest month and mean temperature of wettest quarter were the most important variables for both species (Appendices S2–S9).

The native model for *T. officinale* projected onto South America identified part of Ecuador, northern Peru, a small isolated area in northern Brazil, southern Brazil and Paraguay, Uruguay and southern Argentina and Chile, as potentially suitable areas. The native model failed to predict the known occurrences along the Andes Mountain Range in Colombia, Peru and Bolivia (Fig. 3a and b; Appendices S13, S16 and S18). The introduced model for *T. officinale* predicted a portion of the native distribution mostly in the Mediterranean region, north of India and south of China, but failed to predict nearly all actual occurrences in northern Europe (Fig. 3c and d; Appendices S13, S16 and S18).

The native model for *U. europaeus* predicted a broad distribution across central South America; however, its current distribution also covers the southern Andes (Fig. 4a and b; Appendices S15, S17 and S19). Finally, when we projected the introduced model for *U. europaeus* into the native range, it predicted a very small portion of the native distribution to the north-west of France, Alps and south-west of England with areas in the eastern Europe beyond the native distribution of the species (Fig. 4c and d; Appendices S15, S17 and S19).

Predicting future potential distribution

The best models calibrated with pooled data from all ranges (native plus South America) at 1-km resolution performed slightly better than those calibrated only with reciprocal models for both *T. officinale* (AUC: 0.95 ± 0.05, % omission 13.2 ± 0.01) and *U. europaeus* (AUC: 0.96 ± 0.03, % omission 11.2 ± 0.12). When we projected these models into the introduced range for 2050, the habitats along the northern Andes remained stable for both species (Fig. 5a and b). For *T. Officinale*, the model predicted an increase in a wide range of areas in the southern part of the continent (Fig. 5a). In contrast, for *U. Europaeus*, models predicted an increase of the range along the central Andes, south-eastern Brazil and southern Argentina (Fig. 5b).

DISCUSSION

Assessing whether the environmental niche of a species may change between different geographical areas or time periods is extremely important for predicting the spread of invasive species in the context of ongoing global change (Alexander & Edwards 2010; Guisan *et al.* 2014; González-Moreno *et al.* 2015). Adding new relevant variables to characterize the niche-space of invasive species offers an important

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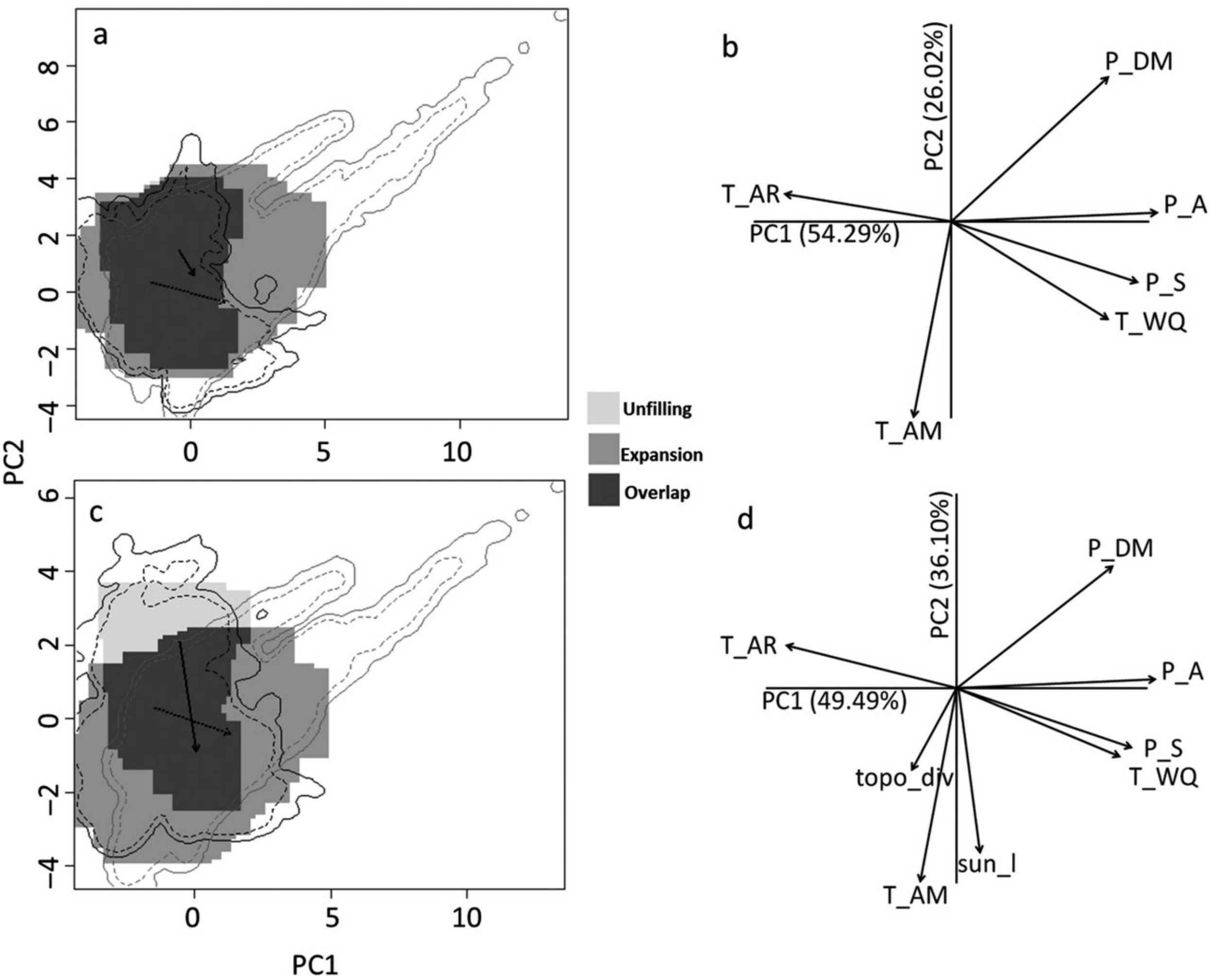

Fig. 1. Niche overlap between the native and introduced ranges of *Taraxacum officinale* using a grid resolution of 1 km. (a) Composed niche overlap of both ranges only using climate variables. (b) The contribution of the climate variables on the two axes of the PCA. (c) Composed niche overlap of both ranges considering climate-plus non-climate variables. (d) The contribution of the climate-plus non-climate variables on the two axes of the PCA. For each PCA axis in (b) and (d), the percentage of inertia explained is shown. The solid and the dashed contour lines in (a) and (c) correspond to 100% and 75%, respectively, of the available (background) environment for each range of *T. officinale* considered in the analyses. Shaded areas represent the portion of these conditions actually occupied by *T. officinale*: medium grey for niche expansion (presence only in the introduced range), light grey for niche unfilling (presence only in the native range) and dark grey for the conditions that are occupied in both ranges. The continuous black arrow shows the environmental distance between the median of the distribution density for each range. The dashed black arrow shows the environmental distance between the median of the available environmental space in each range. See *Materials and Methods* for variable descriptions.

opportunity to study the complexity of niche dynamics and to explore how the niches change after an introduction to novel environments (Guisan *et al.* 2014; González-Moreno *et al.* 2015). Here, although some of the invading populations still grow under similar climatic conditions as the native populations, we demonstrated that adding solar radiation and topographic diversity to climatic variables resulted in a substantial change in the measure of niche shift metrics of *T. officinale* and *U. europaeus*. These observations highlight the importance of defining species niches more broadly than simply by climate because other factors may have important effects on niche shifts (Bertrand *et al.* 2012; González-Moreno *et al.* 2015). Thus, both for *T. officinale* and *U. europaeus*, considering only climatic factors might underestimate their potential to invade new regions.

Although most studies of niche shifts consider environmental variables at coarse spatial resolution, data at a finer grain (e.g. 1 km) might provide complementary answers to questions on climatic niche changes and improve our ability to predict and anticipate invasions (Guisan *et al.* 2014). However, we found similar niche changes and model

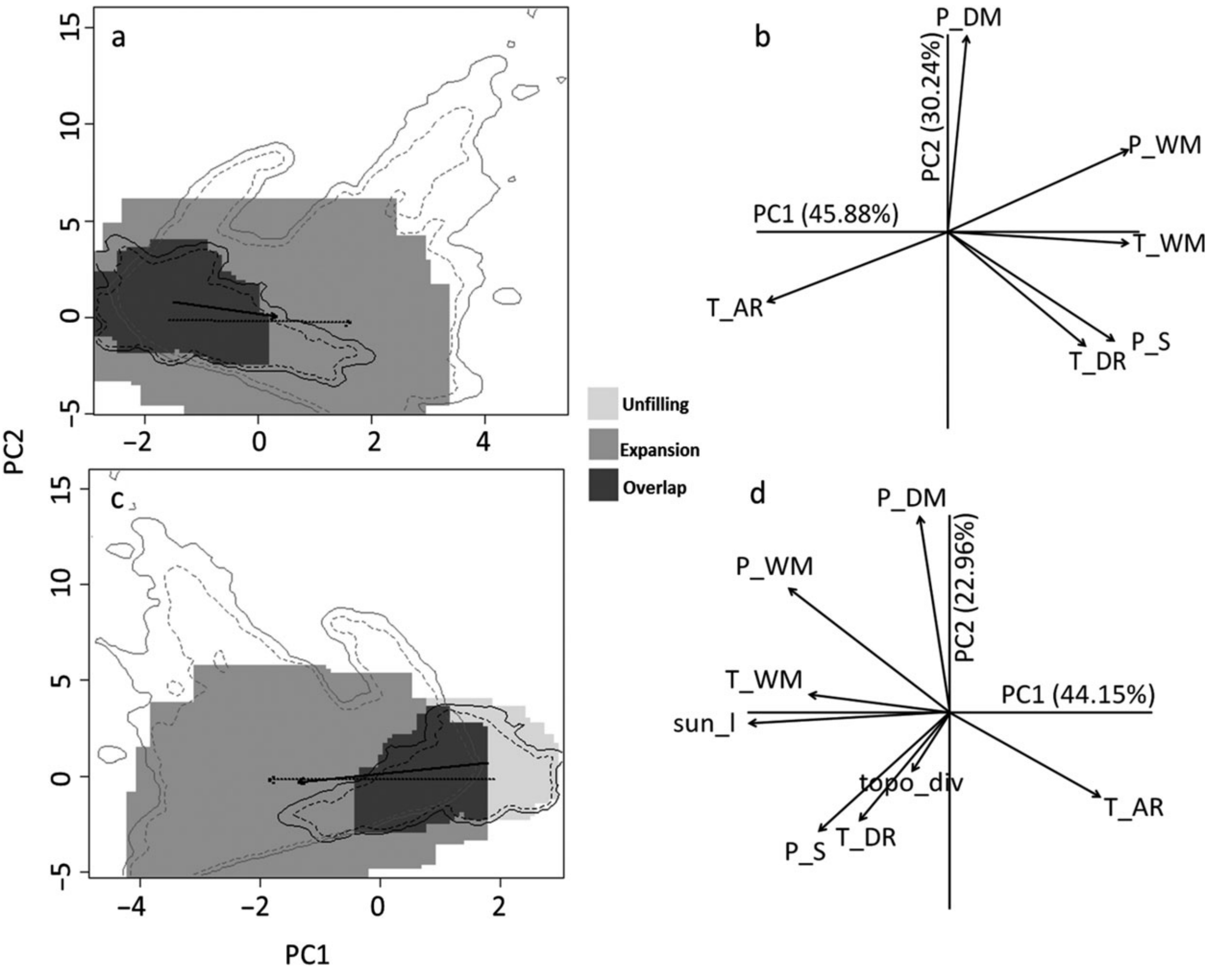

Fig. 2. Niche overlap between the native and introduced ranges of *Ulex europaeus* using a grid resolution of 1 km. (a) Composed niche overlap of both ranges only using climate variables. (b) The contribution of the climate variables on the two axes of the PCA and the percentage of inertia explained by the two axes. (c) Composed niche overlap of both ranges considering climate-plus non-climate variables. (d) The contribution of the climate-plus non-climate variables on the two axes of the PCA and the percentage of inertia explained by the two axes. The solid and the dashed contour lines in (a) and (c) correspond to 100% and 75%, respectively, of the available (background) environment for each range of *U. europaeus* considered in the analyses. Shaded areas represent the portion of these conditions actually occupied by *U. europaeus*: medium grey for niche expansion (presence only in the introduced range), light grey for niche unfilling (presence only in the native range) and dark grey for the conditions that are occupied in both ranges. The continuous black arrow shows the environmental distance between the median of the distribution density for each range. The dashed black arrow shows the environmental distance between the median of the available environmental space in each range. See *Materials and Methods* for variable descriptions.

fitness across the two resolutions tested (i.e. 1 and 20 km). These findings suggest that at a continental scale, broad resolutions (>20 km) can fairly represent the climatic niche of invasive plants with broad geographical range. In fact, as invasion success in plants and birds is related to broad climate tolerances (Vazquez 2006; Hayes & Barry 2008), we expect similar patterns for a wide range of invasive species.

Both species showed niche expansion in South America (>11%) towards higher temperature, precipitation and solar radiation in relation to their native range. Previous studies from a variety of invasive species have also reported niche shifts during different stages of biological invasions (Broennimann *et al.* 2007; González-Moreno *et al.* 2015; Parravicini *et al.* 2015). Although a recent review of studies from various taxonomic groups suggested that only about 50% of 180 species showed niche shifts (Guisan *et al.* 2014), comparative analyses of niche conservatism are difficult because of the varied ways (e.g. variables types, species characteristics and methods used) in which niche changes have been quantified (Guisan *et al.* 2014).

For *T. officinale* and *U. europaeus*, the fact that the realized niche differs between native and introduced ranges suggests that both species have the ability to

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Table 2. Model accuracy results on evaluation dataset (25% independent data) using area under the curve (AUC) and binary tests of omission for each species, resolution and variables included in the analyses. A significant binomial test indicates that the predicted omission rate was less than a random prediction. *P*-values for all omission tests were <0.001

Species	Resolution	Variables	Calibration	Projection	AUC	Omission %
Taraxacum officinale	1 km	Climate	Native	Introduced	0.89 ± 1.01	16.4 ± 0.10
			Introduced	Native	0.93 ± 0.12	15.4 ± 0.29
		Climate-plus non-climate	Native	Introduced	0.84 ± 0.41	14.5 ± 0.10
			Introduced	Native	0.94 ± 0.72	15.1 ± 0.39
	20 km	Climate	Native	Introduced	0.87 ± 0.08	16.2 ± 0.05
			Introduced	Native	0.91 ± 0.82	14.1 ± 0.17
		Climate-plus non-climate	Native	Introduced	0.88 ± 0.21	15.6 ± 1.04
			Introduced	Native	0.93 ± 0.43	20.1 ± 0.18
Ulex europaeus	1 km	Climate	Native	Introduced	0.83 ± 0.01	12.0 ± 0.03
			Introduced	Native	0.95 ± 0.02	16.7 ± 0.10
		Climate-plus non-climate	Native	Introduced	0.84 ± 0.02	12.5 ± 0.06
			Introduced	Native	0.95 ± 0.03	13.3 ± 0.11
	20 km	Climate	Native	Introduced	0.85 ± 0.02	12.5 ± 0.03
			Introduced	Native	0.94 ± 0.04	16.7 ± 0.12
		Climate-plus non-climate	Native	Introduced	0.85 ± 0.01	13.5 ± 0.04
			Introduced	Native	0.95 ± 0.04	22.0 ± 0.16

Data of AUC and omission rate are expressed as mean ± SD.

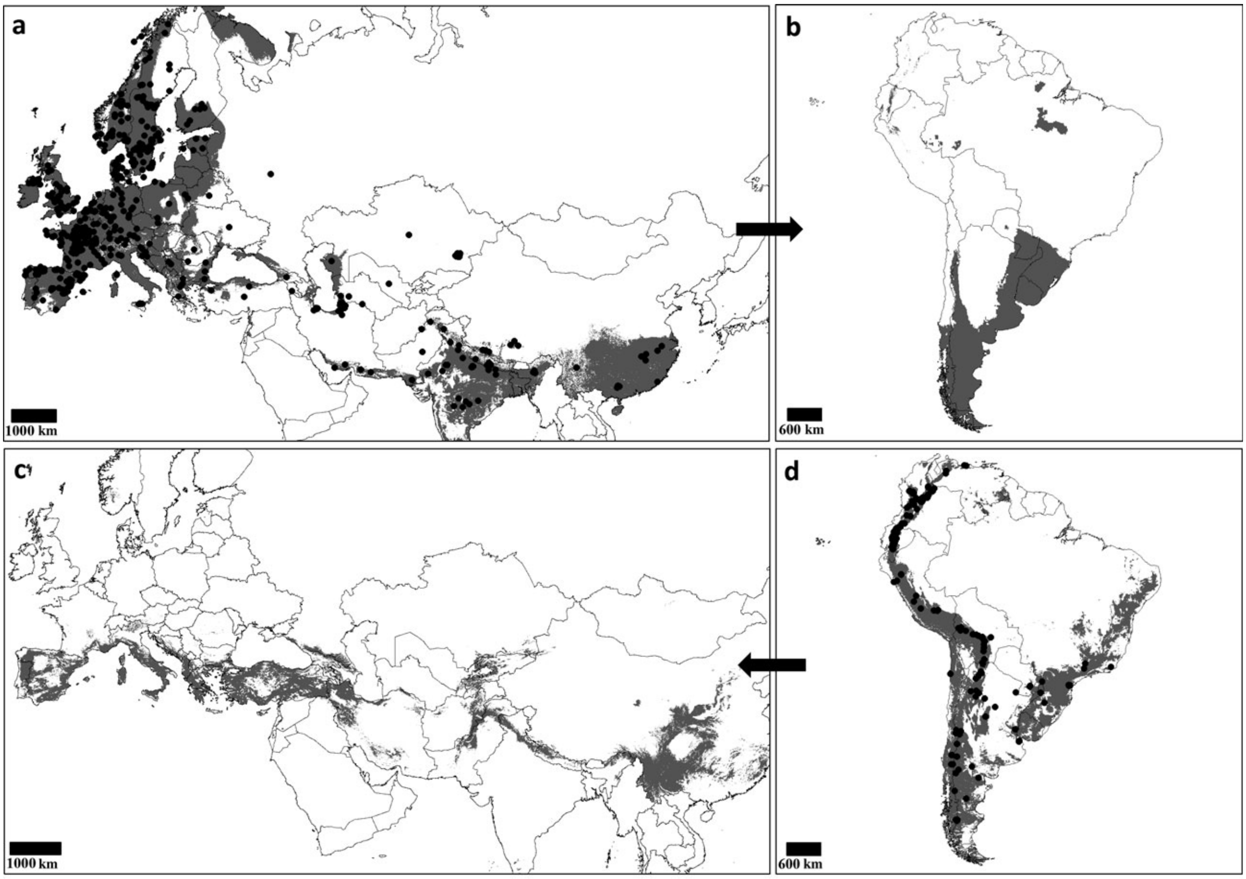

Fig. 3. Predictions of the potential distributions of *Taraxacum officinale* with maximum entropy model (Maxent) using a grid resolution of 1 km and considering climate-plus non-climate variables. The grey shaded area represents areas suitable for *T. officinale*, (a) model calibrated with occurrences points from native range, (b) native model projected onto introduced range, (c) introduced model projected onto Eurasia, (d) model calibrated with occurrences points from South America. Arrows indicate the direction of model projections. Black points represent the observed distribution of *T. officinale* in the study area.

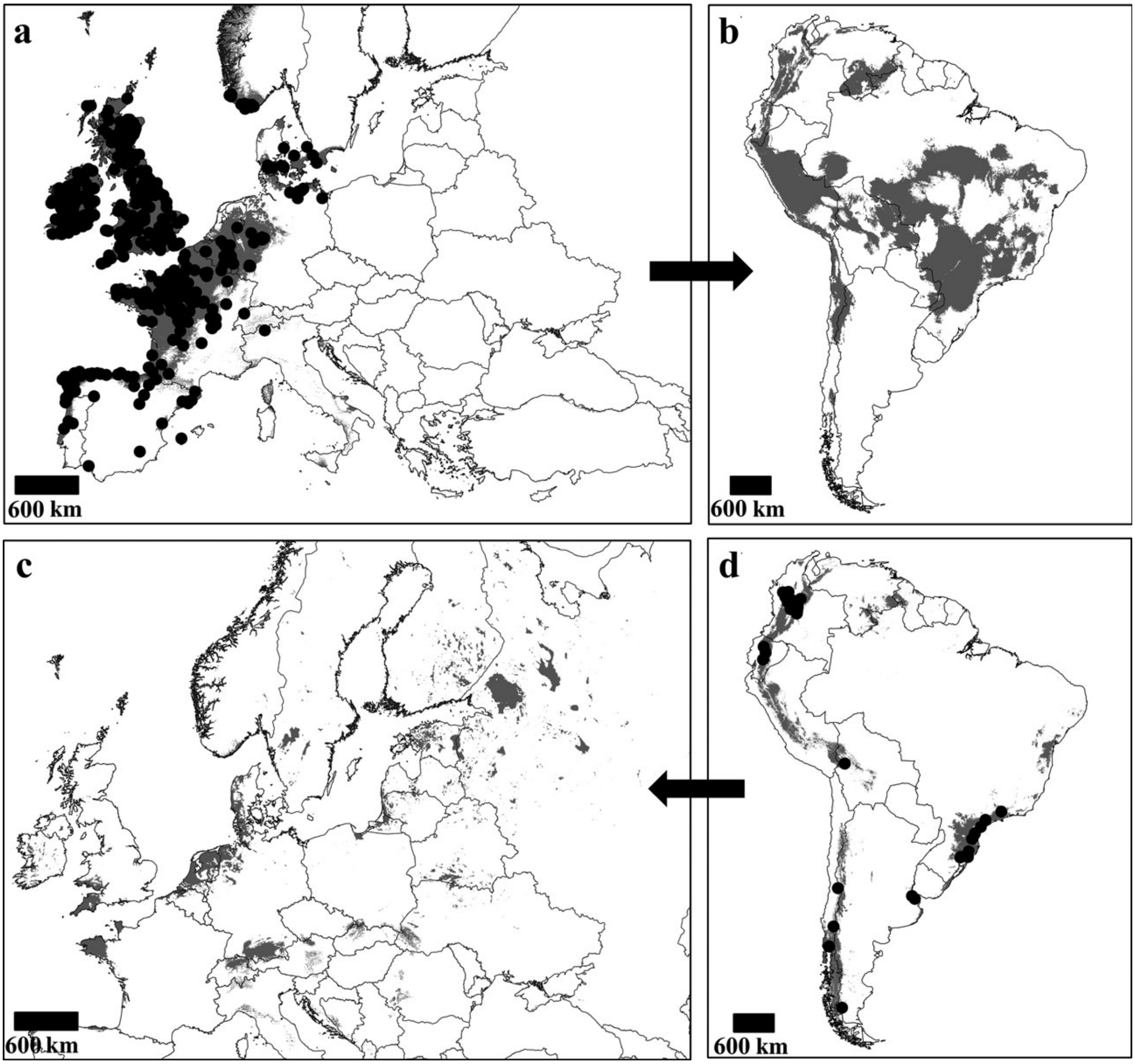

Fig. 4. Predictions of the potential distributions of *Ulex europaeus*. with maximum entropy model (Maxent). The grey shaded area represents areas suitable for *U. europaeus* using a grid resolution of 1 km and considering climate-plus non-climate variables. The grey shaded area represents areas suitable for *U. europaeus*, (a) model calibrated with occurrences points from native range, (b) native model projected onto introduced range, (c) introduced model projected onto Europa, (d) model calibrated with occurrences points from South America. Arrows indicate the direction of model projections. Black points represent the observed distribution of *U. europaeus* in the study area.

establish and spread in broad environmental conditions. The presence of these characteristics in several invasive plant species is called the 'Jack-of-all-trades scenario' and 'Master-of-some scenario' (Richards *et al.* 2006) and could be the result of several non-exclusive factors such as phenotypic plasticity, genetic adaptation or biological interactions. For instance, Molina-Montenegro and Cavieres (2010) described for *T. officinale* a higher amount of pigments involved in the xanthophyll cycle in two populations growing in an altitudinal gradient in the Andes of central Chile (2600 and 3600 m). This characteristic is probably its main asset to avoid photoinhibition and to expand its niche into the areas of high solar radiation of the introduced range (i.e. higher altitude). We cannot discount that the species was already pre-adapted to these conditions in the native range, reflecting just the expression of phenotypic plasticity. However, two common garden experiments carried out with both seedlings and adults of *T. officinale* from its native and introduced ranges suggested that the functional response of the introduced individuals to stressful habitats is the result of local adaptation and less likely due to plasticity (Molina-Montenegro *et al.* 2011).

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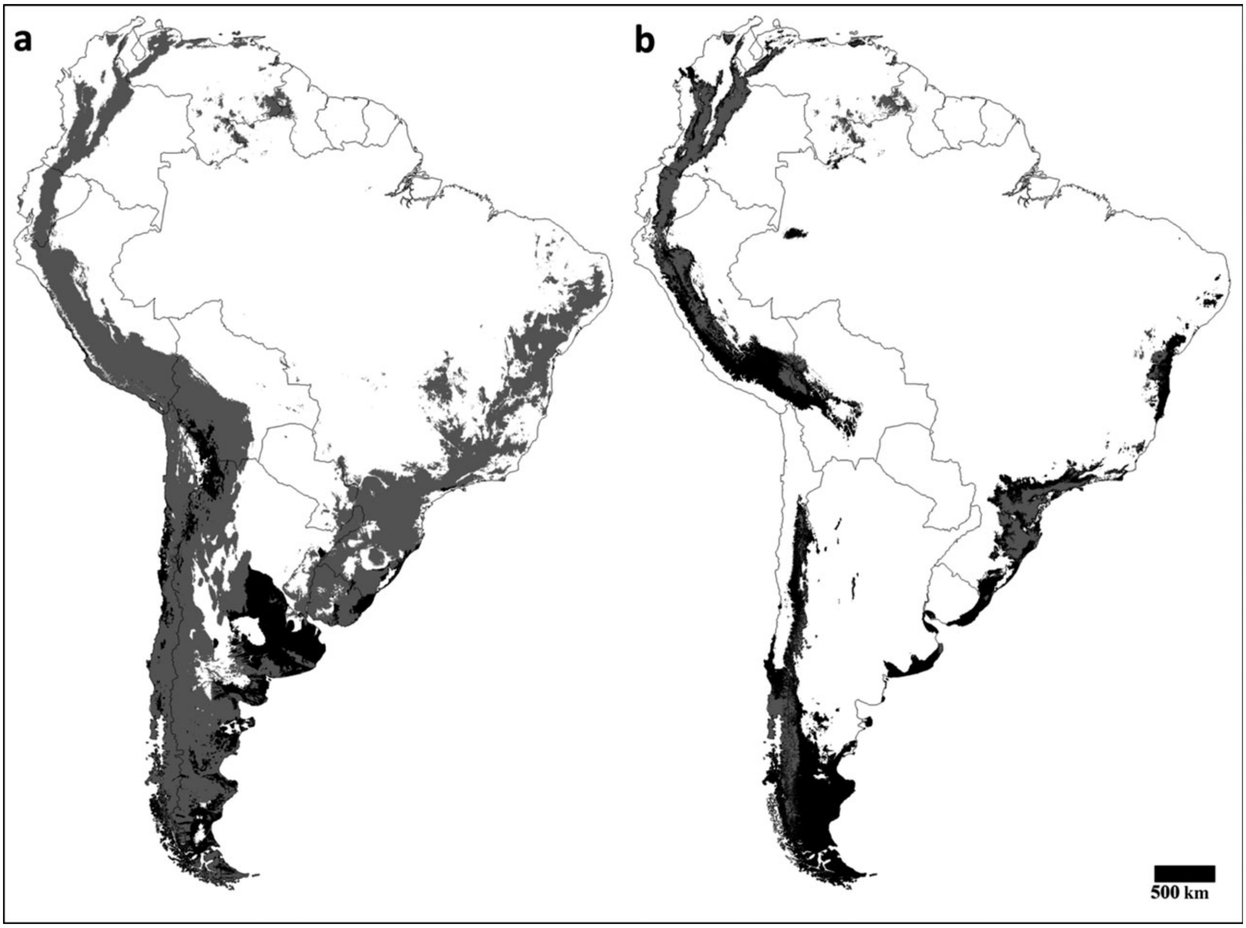

Fig. 5. Predicted future potential distribution for (a) *Taraxacum officinale* and (b) *Ulex europaeus*. In grey, area suitable/stable and in black area gained. Future predictions are based on HadGEM2 global circulation models for 2050 (RCP-8.5A emission scenario).

The observed niche shift could also be a consequence of a different biotic environment in the introduced range (e.g. positive or negative interactions) (Richardson *et al.* 2000; Callaway *et al.* 2002; Lenz & Facelli 2003; Rodriguez 2006; Tecco *et al.* 2006). Indeed, it has been proposed that mutualisms between invasive plants and native organisms (plants and animals) favour the establishment of the former species, ultimately leading to successful spread (Richardson *et al.* 2000; Rodriguez 2006). For example, recent studies have demonstrated a positive association between native cushion plant *Azorella monantha* Clos and *T. officinale* in stressful habitats such as alpine environments in South America (Cavieres *et al.* 2005, 2008; Badano *et al.* 2007). Native cushion plants provide microhabitats with milder temperatures, higher water availability, optimum nutrient availability and less sun radiation (Cavieres *et al.* 2008), facilitating the establishment of exotic species adapted to more mesic conditions.

Furthermore, several hypotheses that attempt to explain invasive processes are based on missing biotic interactions, such as the introduction without natural enemies (e.g. pathogens, parasites or herbivores) (Hornoy *et al.* 2011). Among the most influential, the Evolution of Increased Competitive Ability hypothesis (EICA) states that, in the absence of enemies, exotic plants evolve a shift in resource assignation from defence to reproduction or growth (Blossey & Notzold 1995). This increase in vegetative growth and/or reproductive effort would result in a better competitive ability of the invasive species in the introduced ranges (Hornoy *et al.* 2011). However, genetic constraints on life-history traits (i.e. genetic correlations resulting from previous correlational selection) strongly influence the invasion dynamics and the range limits of introduced species (Sinervo & Svensson 2002; Alexander & Edwards 2010; Colautti *et al.* 2010). From this perspective, Hornoy *et al.* (2011) investigated changes in both trait means and trait correlations of *U. europaeus* from native and introduced regions in a common garden experiment, in order to explore the joint evolution of life-history traits (i.e. flowering onset, pod density and plant height) and susceptibility to seed predation. Their observations demonstrated lower correlations between life-history traits and infestation rate in the introduced range relative to the native range. These findings suggest an independent evolution of these key traits, potentially facilitating local adaptation of *U. europaeus* to a wide variety of environmental conditions in the introduced range (Hornoy *et al.* 2011).

In addition to niche expansion, we detected for both species suitable environments in South America not yet occupied by either species (unfilling). This pattern is likely due to dispersal limitation or because it represents areas where both species have never yet been introduced. The existence of unfilling could reflect an ongoing colonization, indicating that both species might invade additional geographical regions in the future (Petitpierre *et al.* 2012), primarily in the central part of the South American continent. On top of this incipient spread, climate change could alter the future spatial distribution of the species. A severe warming scenario could increase the invasion potential of both species for 2050 towards the southern part of South America. This increase could be limited by the dispersal capacity of the species and its ability to colonize natural habitats. In contrast, the new invasion scenario could also be exacerbated by modifications in their ecophysiological traits, and thus, enhance their ecological niche breadth and ability to persist under a global change scenario (Schweitzer & Larson 1999; Richards *et al.* 2006).

In the current context of ongoing global changes, the niche expansion observed during the biological invasion of *T. officinale* and *U. europaeus* in South America exemplifies how invasive species can occupy new niches that are not predictable from knowledge based only on climates factors or information from the native range. Our results indicate that neither species is fully occupying suitable environments that mirror its native range and that the observed niche expansion is towards areas with higher solar radiation and with warmer and wetter climates. Despite most of this expansion being outside the climate available in the native region, recent studies support local adaptation and enemy release as the main factors driving the shift (Hornoy *et al.* 2011; Molina-Montenegro *et al.* 2011). These evolutionary processes will certainly affect the future distribution of the species and their potential impact in the Southern Hemisphere.

Finally, while biological invasions provide a fascinating insight into species distribution limits and a unique opportunity to investigate mechanisms underlying ecological and evolutionary processes (Guisan *et al.* 2014; Tingley *et al.* 2014), understanding these basic processes also has important implications for effective management decisions under future climate change.

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AUTHOR CONTRIBUTIONS

All authors contributed to the formulation of ideas and the writing of the manuscript.

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SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article at the publisher's web-site:

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Appendix S3. Maxent models using a grid resolution of 1 km: Climate-plus non-climate Model for *T. officinale*.

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Appendix S18. Predictions of the potential distributions of *Taraxacum officinale* with Maxent model, with 20 km grid resolution, including climate plus non-climate variables.

Appendix S19. Predictions of the potential distributions of *Ulex europaeus* with Maxent model, with 20 km grid resolution, including climate plus non-climate variables.

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Appendix S1. Pearson's correlation coefficients of the association among the variables used in the analyses for each species. Variables with cross-correlation coefficient values of $r > \pm 0.7$ were excluded

	Taraxacum officinale								*Ulex europaeus*							
	T_AM	T_AR	T_WQ	P_A	P_DM	P_S 15	top_div	sun_l	T_DR	T_WM	T_AR	P_WM	P_DM	P_S	top_div	sun_l
T_AM	**1**								**1**							
T_AR	-0.474	**1**							0.560	**1**						
T_WQ	0.565	0.000	**1**						0.171	0.502	**1**					
P_A	0.215	-0.497	-0.040	**1**					0.169	-0.066	-0.652	**1**				
P_DM	-0.021	-0.220	-0.186	0.696	**1**				-0.243	-0.257	-0.419	0.596	**1**			
P_S	0.208	-0.122	0.178	-0.008	-0.594	**1**			0.334	-0.013	-0.426	0.616	-0.125	**1**		
top_div	0.324	-0.466	0.003	0.318	-0.074	0.477	**1**		0.305	-0.060	-0.312	0.513	0.168	0.511	**1**	
sun_l	0.360	-0.649	0.123	0.274	-0.243	0.664	0.662	**1**	0.533	-0.082	-0.629	0.611	0.137	0.583	0.496	**1**

T_AM. Annual Mean Temperature; T_DR. Mean Diurnal Range (Mean of monthly (max temp - min temp)); T_WM. Max Temperature of Warmest Month; T_AR. Temperature Annual Range; T_WQ. Mean Temperature of Wettest Quarter; P_A. Annual Precipitation; P_WM. Precipitation of Wettest Month; P_DM. Precipitation of Driest Month; P_S. Precipitation Seasonality (Coefficient of Variation); topo_div. Topographic diversity and sun_l. Sun radiation.

Percentage variable contribution to Maxent models using a grid resolution of 1 km

Appendix S2.

Variable		Climate-only Model for T. officinale	
		Native	Introduced
		Percentage Contribution	Percentage Contribution
T_AR	Temperature Annual Range	59.9±0.35	10.2±1.20
P_S	Precipitation Seasonality	29.7±1.01	8.40±0.58
T_WQ	Mean Temperature of Wettest Quarter	5.30±2.51	47.5±1.82
T_AM	Annual Mean Temperature	2.80±1.75	17.7±4.56
P_DM	Precipitation of Driest Month	2.30±1.31	0.90±0.12
P_A	Annual Precipitation	0.10±0.35	15.3±1.25

Appendix S3.

Variable		Climate-plus non-climate Model for T. officinale	
		Native	Introduced
		Percentage Contribution	Percentage Contribution
T_AR	Temperature Annual Range	67.1±0.02	9.00±2.85
P_S	Precipitation Seasonality	20.5± 0.37	11.6±0.08
P_DM	Precipitation of Driest Month	2.20±2.03	7.30±0.37
T_WQ	Mean Temperature of Wettest Quarter	5.40±0.78	15.1±5.39
T_AM	Annual Mean Temperature	5.94±1.20	5.60±6.32
topo_dive	Topographic diversity	1.70± 0.01	5.1±2.10
sun_l	Sun radiation	1.10 ±2.31	32.4±2.98
P_A	Annual Precipitation	0.50± 1.53	19.9±2.30

Appendix S4.

Variable		Climate-only Model for U. europaeus	
		Native	Introduced
		Percentage Contribution	Percentage Contribution
T_AR	Temperature Annual Range	80.8±1.05	1.80±1.34
P_DM	Precipitation of Driest Month	6.10±2.66	1.50±2.66
P_WM	Precipitation of Wettest Month	5.50±0.33	11.8±1.77
T_WM	Max Temperature of Warmest Month	2.00±1.84	69.3±1.23
T_DR	Mean Diurnal Range	4.90±0.21	1.50±1.26
P_S	Precipitation Seasonality	0.70±1.92	14.2±2.85

Appendix S5.

Variable		Climate-plus non-climate Model for U. europaeus	
		Native	Introduced
		Percentage Contribution	Percentage Contribution
T_AR	Temperature Annual Range	77.3±1.01	0.20±0.08
T_DR	Mean Diurnal Range	6.20±1.56	5.70±0.17
P_DM	Precipitation of Driest Month	3.50±0.49	13.9±0.84
P_WM	Precipitation of Wettest Month	4.80±1.43	2.80±1.53
sun_l	Sun radiation	2.51±1.75	41.5±2.18
topo_dive	Topographic diversity	2.39±0.39	1.80±1.12
P_S	Precipitation Seasonality	2.10±0.34	7.00±1.37
T_WM	Max Temperature of Warmest Month	1.20±1.31	27.2±1.57

Percentage variable contribution to Maxent models using a grid resolution of 20×20 km

Appendix S6.

Variable		Climate-only Model for T. officinale	
		Native	Introduced
		Percentage Contribution	Percentage Contribution
T_AR	Temperature Annual Range	59.8±0.25	10.2±1.30
P_S	Precipitation Seasonality	29.8±1.11	8.30±1.48
T_WQ	Mean Temperature of Wettest Quarter	5.20±2.31	47.6±1.92
T_AM	Annual Mean Temperature	2.90±2.75	17.6±3.16
P_DM	Precipitation of Driest Month	2.20±1.14	1.10±1.42
P_A	Annual Precipitation	0.15±1.35	15.2±1.02

Appendix S7.

Variable		Climate-plus non-climate Model for T. officinale	
		Native	Introduced
		Percentage Contribution	Percentage Contribution
T_AR	Temperature Annual Range	66.1±0.12	9.00±2.75
P_S	Precipitation Seasonality	21.5± 0.77	13.9±0.48
P_DM	Precipitation of Driest Month	2.30±1.04	7.30±1.37
T_WQ	Mean Temperature of Wettest Quarter	5.30±2.48	11.6±3.39
T_AM	Annual Mean Temperature	5.74±0.29	5.60±4.32
topo_dive	Topographic diversity	1.90± 1.31	5.1±2.14
sun_l	Sun radiation	1.00 ±1.51	32.4±4.98
P_A	Annual Precipitation	0.60± 1.73	15.1±1.30

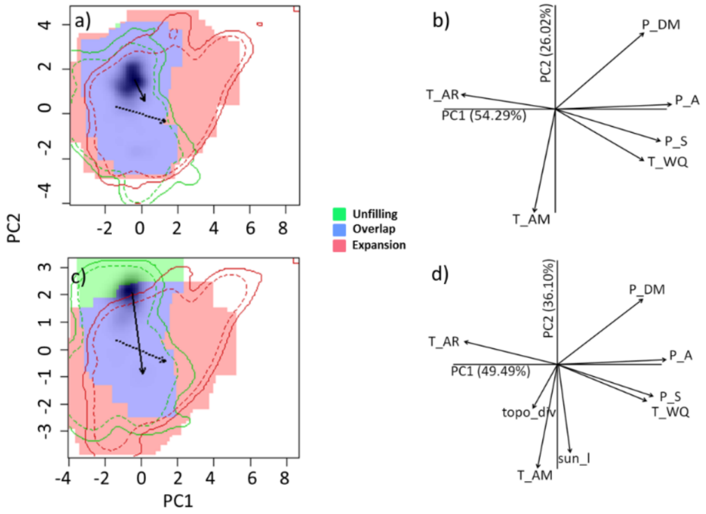
Appendix S8.

Variable		Climate-only Model for U. europaeus	
		Native	Introduced
		Percentage Contribution	Percentage Contribution
T_AR	Temperature Annual Range	80.0±1.01	1.81±0.34
P_DM	Precipitation of Driest Month	6.90±2.62	1.52±2.56
P_WM	Precipitation of Wettest Month	5.70±0.35	11.5±1.47
T_DR	Mean Diurnal Range	4.70±0.28	1.53±1.26
T_WM	Max Temperature of Warmest Month	2.05±0.84	69.0±1.03
P_S	Precipitation Seasonality	0.65±1.02	14.2±0.81

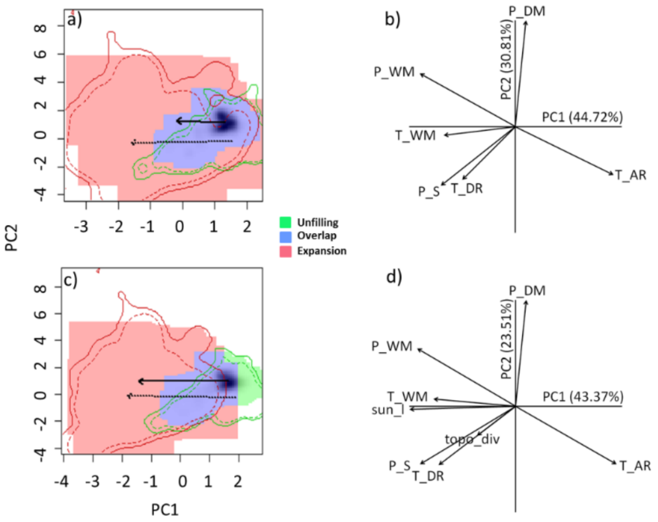
Appendix S9.

Variable		Climate-plus non-climate Model for U. europaeus	
		Native	Introduced
		Percentage Contribution	Percentage Contribution
T_AR	Temperature Annual Range	75.3±0.01	0.50±1.08
T_DR	Mean Diurnal Range	8.20±1.51	5.40±0.18
P_DM	Precipitation of Driest Month	3.60±0.49	13.7±0.44
P_WM	Precipitation of Wettest Month	4.70±1.23	3.00±1.13
sun_l	Sun radiation	2.52±1.85	40.5±3.18
topo_dive	Topographic diversity	2.38±1.39	2.80±1.11
P_S	Precipitation Seasonality	2.00±0.44	6.00±1.34
T_WM	Max Temperature of Warmest Month	1.30±1.30	28.2±1.17

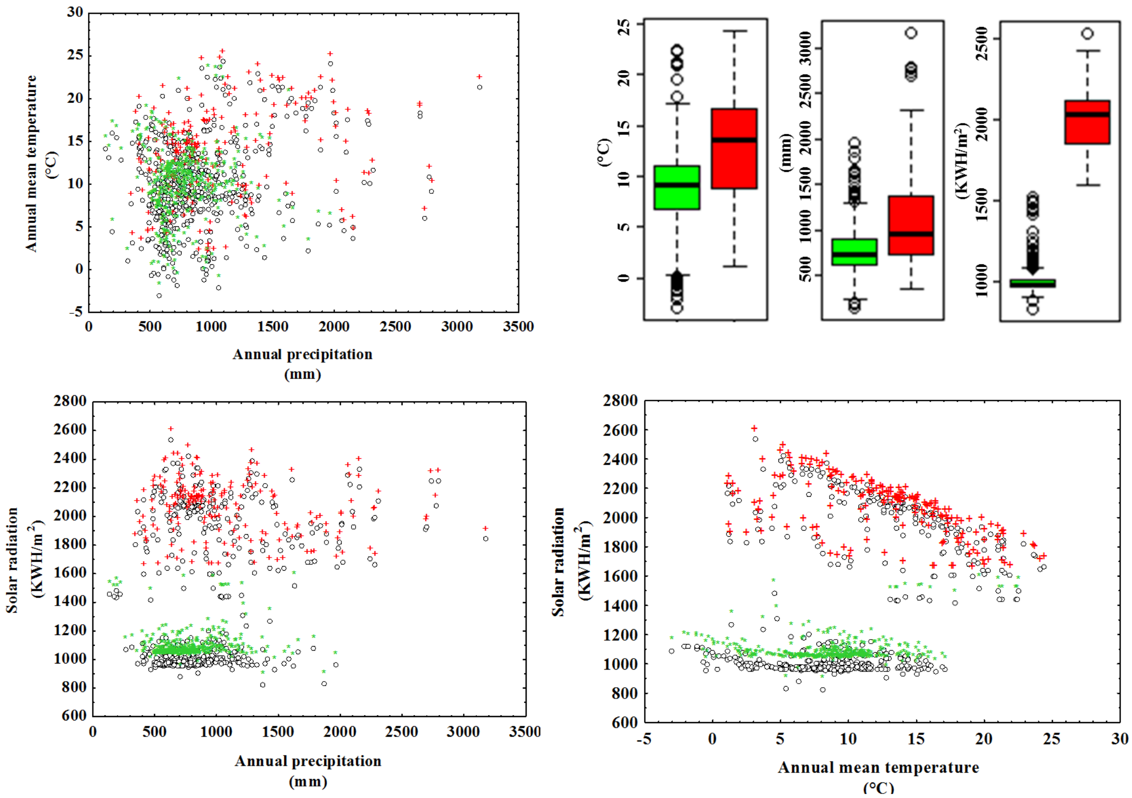
Niche overlap between the native and introduced ranges of the study species using a grid resolution of 20 km. a) Composed niche overlap of both ranges considering climate variables. b) The contribution of the climate variables on the two axes of the PCA and the percentage of inertia explained by the two axes. c) Composed niche overlap of both ranges considering climate-plus non-climate variables. d) The contribution of the climate-plus non-climate variables on the two axes of the PCA. For each PCA axis in b) and d) the percentage of inertia explained is shown. The solid and the dashed contour lines in (a) and (c) correspond to 100% and 75%, respectively, of the available (background) environment for each range considered in the analysis. Shaded areas represent the portion of these conditions actually occupied by both species: red for niche expansion (presence only in the introduced range), green for niche unfilling (presence only in the native range) and blue for the conditions that are occupied in both ranges. The continuous black arrow shows the environmental distance between the median of the distribution density for each range. The dashed black arrow shows the environmental distance between the median of the available climatic space in each range.



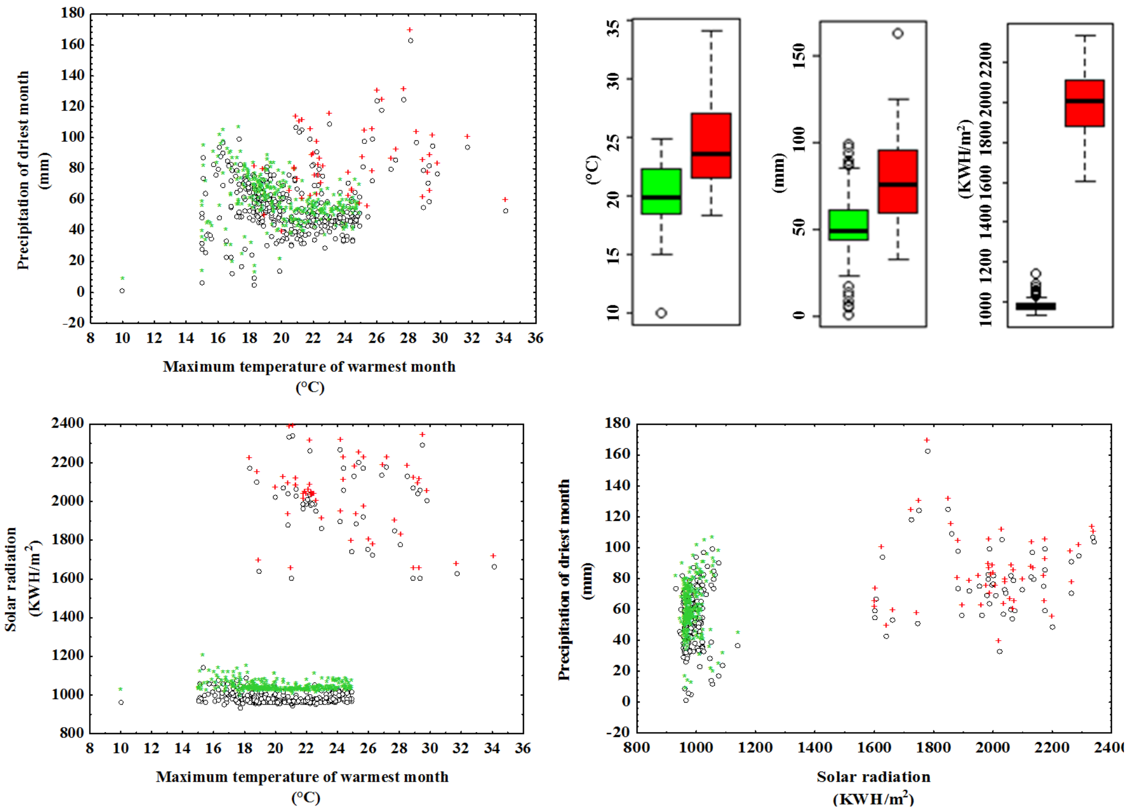
Appendix S10. Niche overlap between the native and introduced ranges of *Taraxacum officinale*.



Appendix S11. Niche overlap between the native and introduced ranges of *Ulex europaeus*.

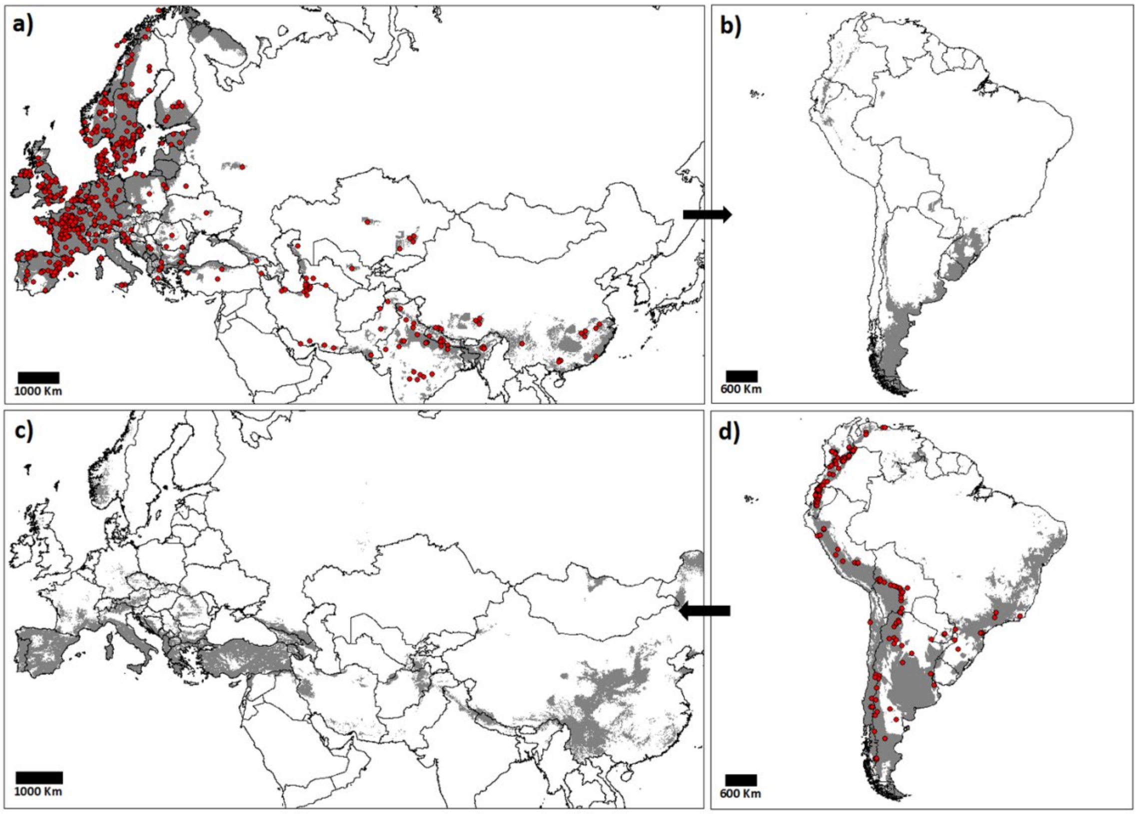


Appendix S12. Projections of the native (green points) and introduced (red points) ranges of *T. officinale* considering the most important variables describing the species' niche. The figures illustrate how that adding the non-climate variables in the analyses resulted in a substantial change in the measure of niche shift metrics of *T. officinale*.

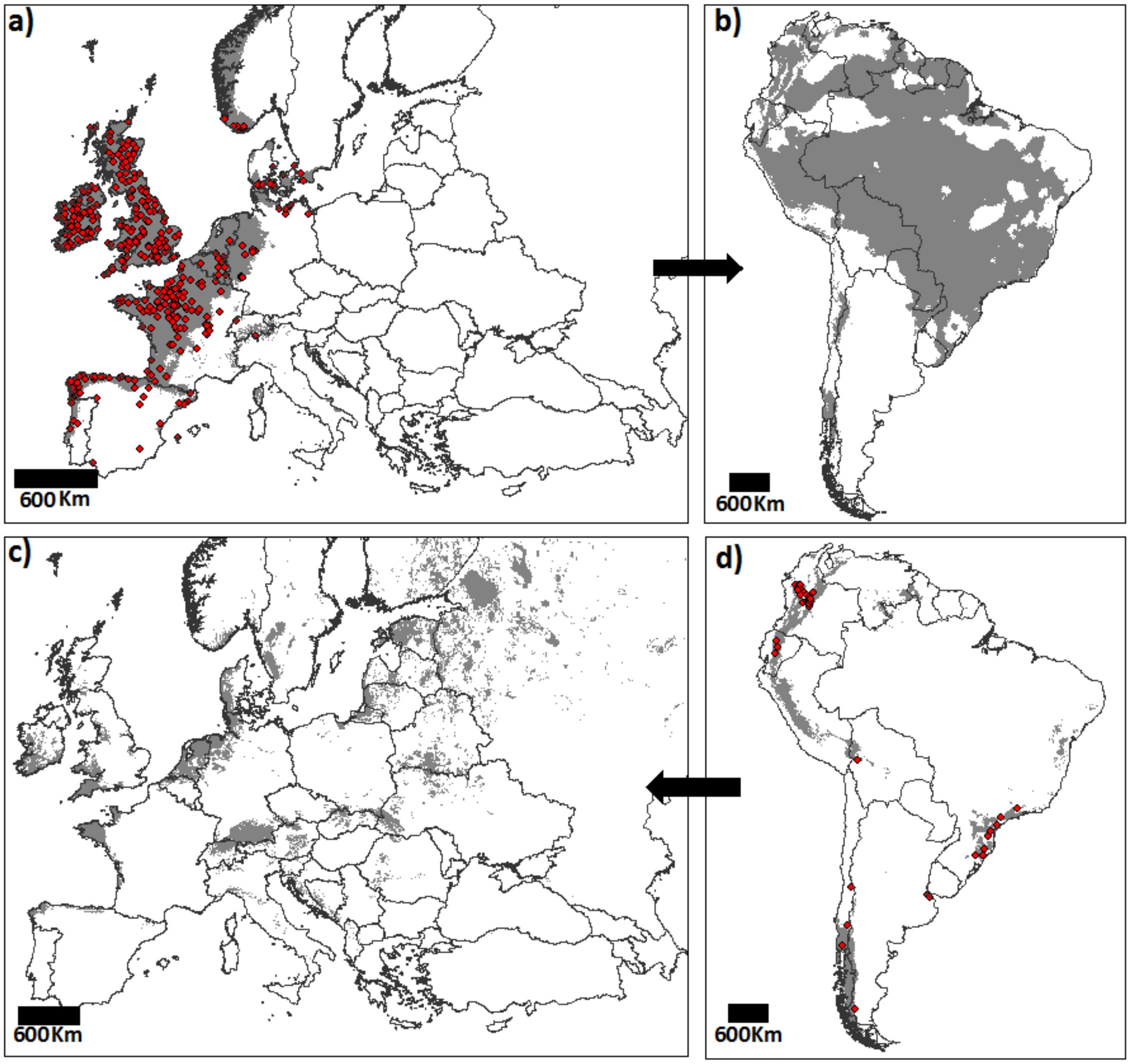


Appendix S13. Projections of the native (green points) and introduced (red points) ranges of *U. europaeus* considering the most important variables describing the species' niche. The figures illustrate how that adding the non-climate variables in the analyses resulted in a substantial change in the measure of niche shift metrics of *U. europaeus*.

Predictions of the potential distributions of the study species with maximum entropy model (Maxent) using a grid resolution of 1 km and considering only climate variables. The grey shaded area represents areas suitable, a) models calibrated with occurrences points from native range, b) native models projected onto South American, c) introduced models projected onto native range, d) model calibrated with occurrences points from South America. Arrows indicate the direction of model projections:

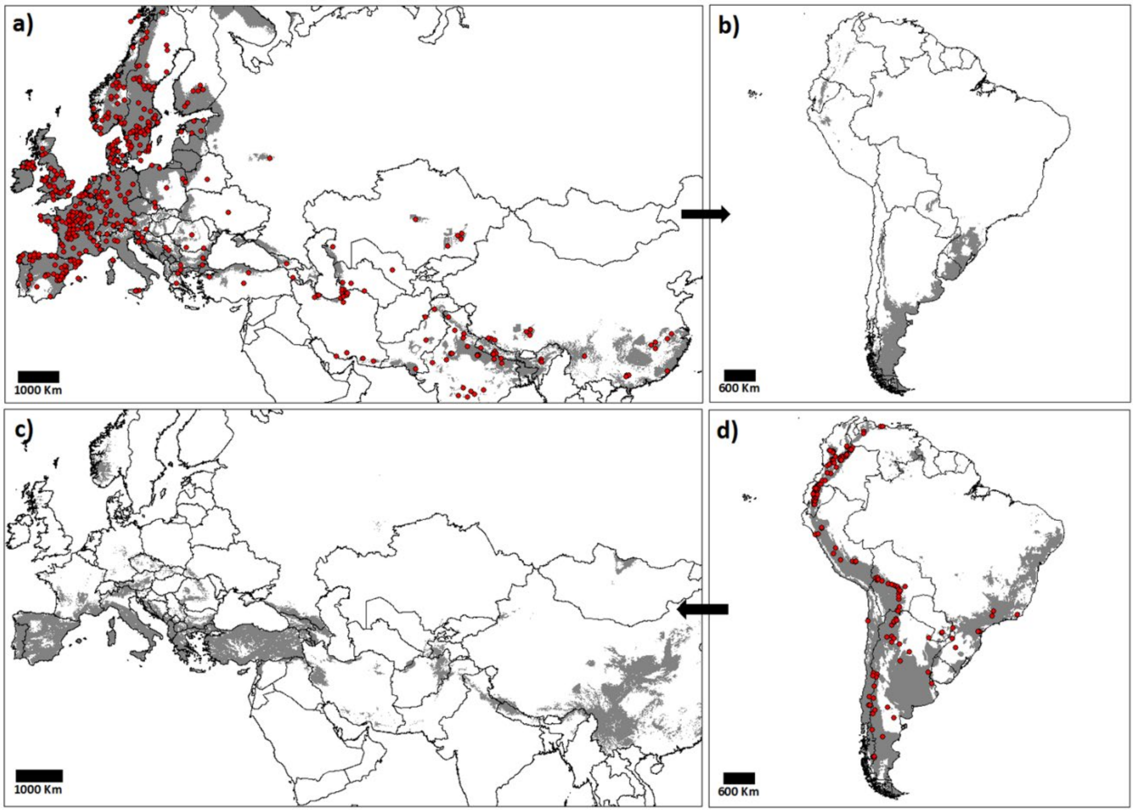


Appendix S14. Predictions of the potential distributions of *Taraxacum officinale* with maximum entropy model (Maxent). Red points represent the observed distribution of *T. officinale* in the study area.

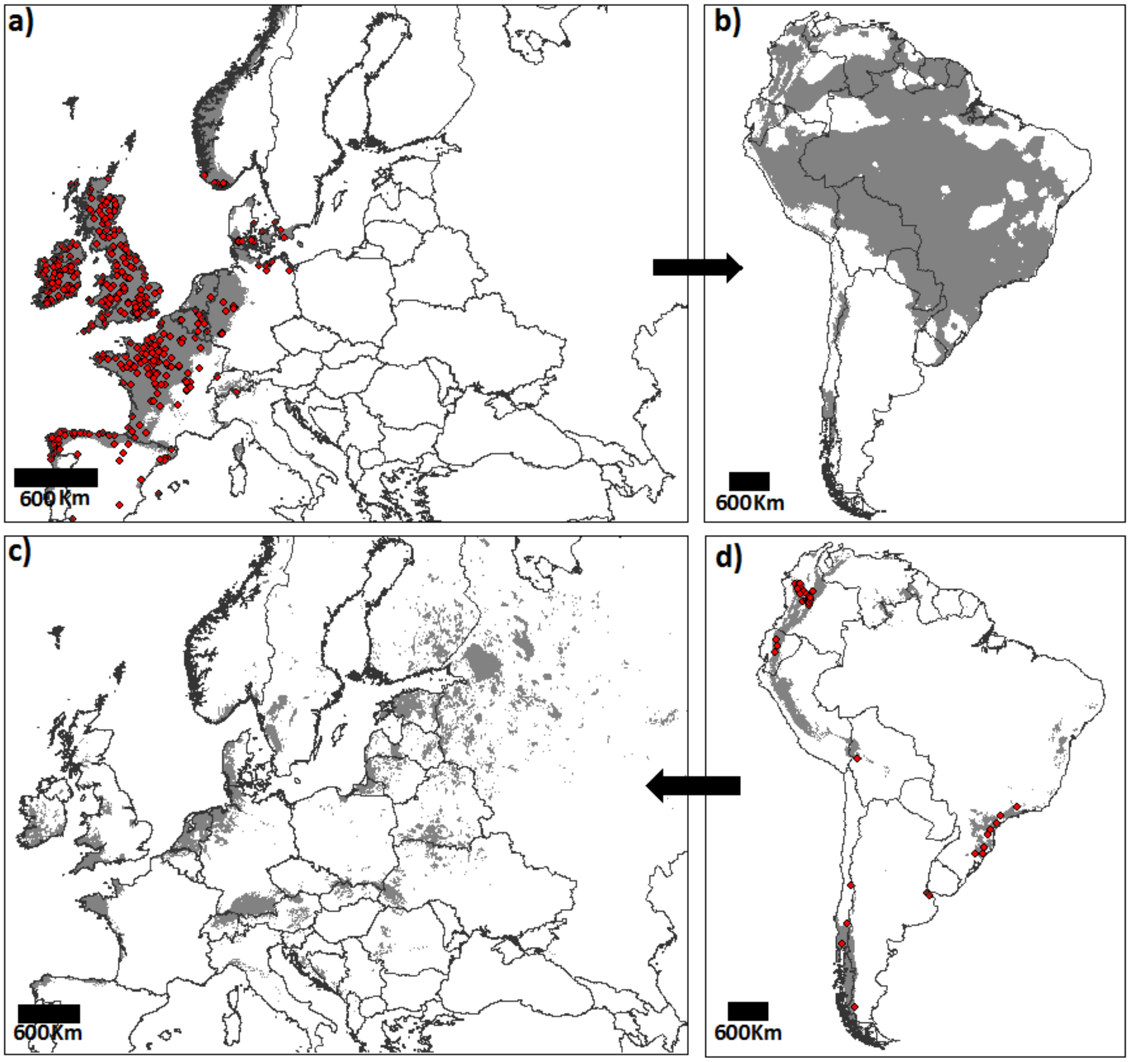


Appendix S15. Predictions of the potential distributions of *Ulex europaeus* with maximum entropy model (Maxent). Red points represent the observed distribution of *U. europaeus* in the study area.

Predictions of the potential distributions of the study species with maximum entropy model (Maxent) using a grid resolution of 20 km and considering only climate variables. The grey shaded area represents areas suitable, a) models calibrated with occurrences points from native range, b) native models projected onto South American, c) introduced models projected onto native range, d) model calibrated with occurrences points from South America. Arrows indicate the direction of model projections:

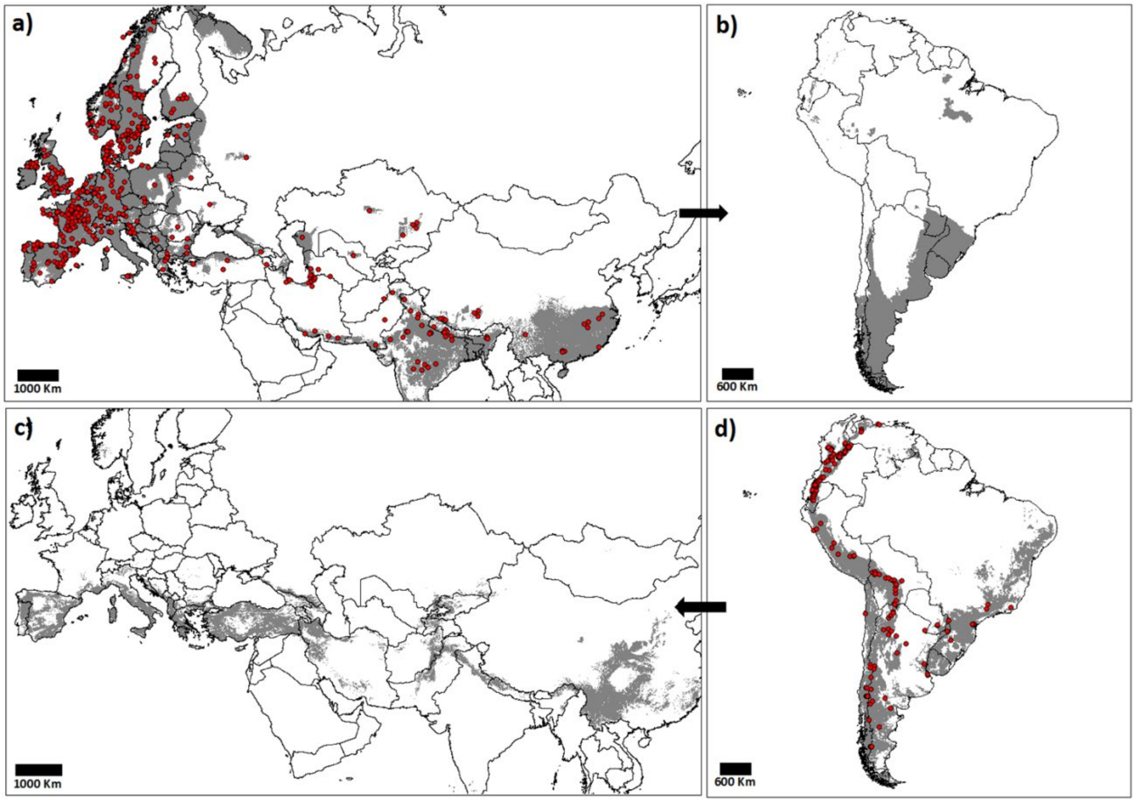


Appendix S16. Predictions of the potential distributions of *Taraxacum officinale* with maximum entropy model (Maxent). Red points represent the observed distribution of *T. officinale* in the study area.

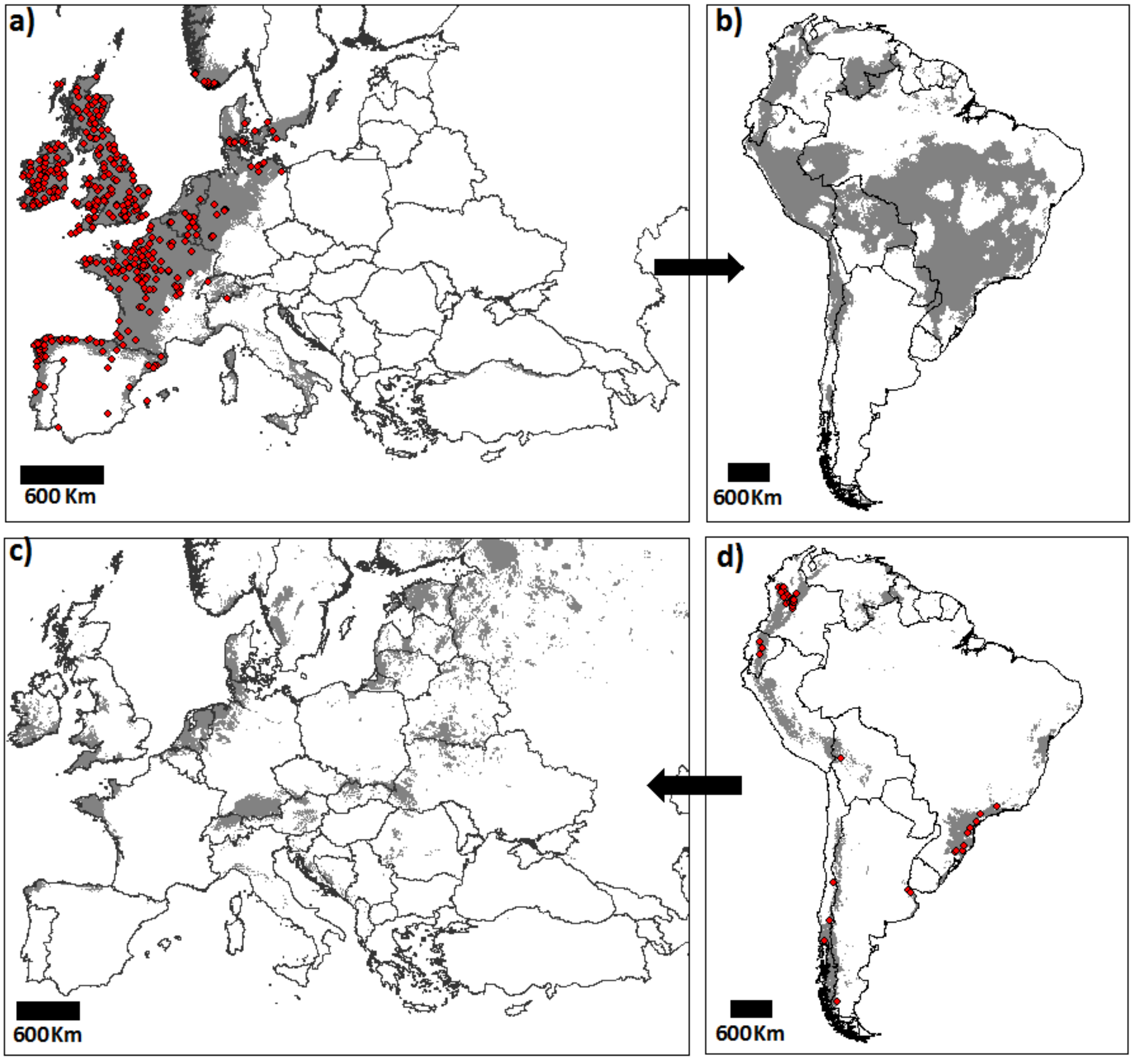


Appendix S17. Predictions of the potential distributions of *Ulex europaeus* with maximum entropy model (Maxent). Red points represent the observed distribution of *U. europaeus* in the study area.

Predictions of the potential distributions of the study species with maximum entropy model (Maxent) using a grid resolution of 20 km and considering climate-plus non-climate variables. The grey shaded area represents areas suitable, a) models calibrated with occurrences points from native range, b) native models projected onto South American, c) introduced models projected onto native range, d) model calibrated with occurrences points from South America. Arrows indicate the direction of model projections:



Appendix S18. Predictions of the potential distributions of *Taraxacum officinale* with maximum entropy model (Maxent). Red points represent the observed distribution of *T. officinale* in the study area.



Appendix S19. Predictions of the potential distributions of *Ulex europaeus* with maximum entropy model (Maxent). Red points represent the observed distribution of *U. europaeus* in the study area.

CAPÍTULO 5

Fotos: Juan Antonio Sánchez Rodríguez; Sergio Pérez Gorjón.

FACTORES AMBIENTALES ASOCIADOS CON LA DISTRIBUCIÓN ESPACIAL DE PATÓGENOS DE PLANTAS EN LA PENÍNSULA IBÉRICA: EL CASO DE *Phytophthora cinnamomi* RANDS

AUTORES
Ricardo Enrique Hernández-Lambraño,
Pablo González-Moreno,
José Ángel Sánchez-Agudo

RESUMEN

Aunque la variabilidad espacial en la distribución de los organismos del suelo a menudo se considera aleatoria, recientes estudios han encontrado una estructura espacial significativa a varias escalas espaciales. Comprender los factores que impulsan esta variabilidad a gran escala podría ayudar a evaluar los impactos ecológicos y socioeconómicos de los organismos del suelo en los ecosistemas. En el presente estudio, nuestro objetivo es (i) comprender el papel relativo de los factores ambientales y la influencia humana en la distribución de uno de los patógenos de plantas más destructivos e invasivos del mundo, *Phytophthora cinnamomi* Rands, y (ii) estimar su posible distribución geográfica en la península ibérica como proxy de su potencial impacto. Para ello, utilizamos un total de 277 registros de *P. cinnamomi* (presencia: $n = 157$; ausencias: $n = 120$) en la península ibérica y tres conjuntos de variables explicativas que reflejan las condiciones abióticas (clima y suelo), condiciones bióticas (distribución potencial de los principales árboles hospederos susceptibles y cubierta vegetal basado en NDVI) y la influencia humana. La distribución actual de *P. cinnamomi* en la península ibérica parece estar influenciada principalmente por la textura fina del suelo y el clima, seguido del uso del suelo y, por último, la presencia de una de sus principales especies de árbol hospedero. Su distribución potencial en este territorio sugiere un potencial para una futura expansión a lo largo del noreste y sureste de España y el centro de Portugal. Dado el impacto significativo de este patógeno en los ecosistemas forestales, el modelado de su distribución en la península ibérica ofrece una importante herramienta de decisión para el monitoreo y restauración de los bosques de roble mediterráneo en declive.

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Environmental factors associated with the spatial distribution of invasive plant pathogens in the Iberian Peninsula: The case of *Phytophthora cinnamomi* Rands

Ricardo Enrique Hernández-Lambraño[a,*], Pablo González-Moreno[b,c], José Ángel Sánchez-Agudo[a]

[a] *Instituto Hispano-Luso de Investigaciones Agraria (CIALE) Universidad de Salamanca, Parque Científico, C/ Del Duero, 12; 37185 Villamayor, Salamanca, Spain*
[b] *Estación Biológica de Doñana, Consejo Superior de Investigaciones Científicas (EBD-CSIC), Av. Américo Vespucio S/N, Isla de la Cartuja, 41092 Sevilla, Spain*
[c] *CABI, Bakeham Lane, Egham TW20 9TY, UK*

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ABSTRACT

Although spatial variability in the distribution of soil organisms is often regarded as random, recent attempts have found significant spatial structure at several scales. Understanding the drivers of this variability at large scale could help to evaluate the ecological and socio-economic impacts of soil organisms in the ecosystems. In the present study we aim to (i) understand the relative role of environmental factors and human influence on the distribution of one of the World's most destructive and invasive plant pathogens, *Phytophthora cinnamomi* Rands, and (ii) to estimate its potential geographic distribution in the Iberian Peninsula as a proxy of its potential impact. For this purpose, we used a total of 277 records of *P. cinnamomi* (presence: $n = 157$; absences: $n = 120$) in the Iberian Peninsula and three sets of explanatory variables reflecting abiotic conditions (climate and soil), biotic conditions (main susceptible host tress distribution and vegetation cover based on NDVI) and human influence. The current distribution of *P. cinnamomi* in the Iberian Peninsula seems to be influenced principally by fine texture soil and climate, following the land use and lastly the presence of its main host forest species. Its potential distribution across the Iberian Peninsula suggests potential for further expansion along the northeast and southeast of Spain and central Portugal. Given the significant impact of this pathogen on forest ecosystems, the modelling of its distribution in the Iberian Peninsula offers an important decision tool for the monitoring and restoration of declining Mediterranean oak forests.

1. Introduction

Nowadays, soil pathogens are well recognized for their significant ecological and socio-economic impacts on the ecosystems (Ettema and Wardle, 2002; Gómez-Aparicio et al., 2012). Among the most important soil pathogens, the oomycete *Phytophthora cinnamomi* Rands, causes extensive economic losses in agriculture, horticulture and forestry and is a major threat to natural ecosystems and biodiversity around the world (Brasier, 1996; Brasier et al., 1993; Hardham, 2005; Weste and Marks, 1987). In Europe, its occurrence has been recorded since early 19th century (Brasier, 1996; Brasier et al., 1993; de Sampaio e Paiva Camilo-Alves et al., 2013; Jung et al., 2015; Zentmyer, 1988) but it only experienced a rapid spread during the last decades, leading to devastation of important agricultural crops and reduction of large woodland areas (de Sampaio e Paiva Camilo-Alves et al., 2013; Hardham, 2005; Jung et al., 2015). Understanding where and when soil pathogens like *Phytophthora* spp. are more likely to cause great epidemics has long been an important point of study in agricultural research (Otten et al., 2004). However, we have little knowledge about the complexity of their distribution patterns at large scales, particularly for natural and semi-natural habitats (Ettema and Wardle, 2002; Reinhart and Clay, 2009).

The abundance and diversity of phytopathogenic fungi in soil are not usually randomly distributed (Ettema and Wardle, 2002). These exhibit spatially predictable patterns influenced by a variety of environmental factors (Agrios, 2005; Ettema and Wardle, 2002). For instance, abiotic factors such as high temperature, high soil water content and its dynamics are key in the establishment, spread and longevity of *Phytophthora* spp. (Corcobado et al., 2013a, 2013b; Hardham, 2005; Weste and Marks, 1987). Soil textures ranging from loamy to silty or clayey have been associated with the occurrence of *Phytophthora* spp., as these soil factors favour moist conditions and sporulation (Corcobado et al., 2013b; Jönsson et al., 2005; Jung et al., 2000). Furthermore, *Phytophthora* spp. require nutrient rich soils with $pH_{(H_2O)}$ values

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[*] Corresponding author at: C/ General Margallo, 24, 1B izq, 28020 Madrid, Spain.
E-mail address: ricardohl123@usal.es (R.E. Hernández-Lambraño).

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between 4.0 and 4.8 to stimulate sporangia production (Jönsson et al., 2005; Jung et al., 2000). On the other hand, biotic factors such as vegetation is a major determinant of the spatial distribution of soil pathogens (Ettema and Wardle, 2002). Host plant species can affect pathogen abundance in the forest soil directly by providing living host tissue, or indirectly by generating environmental conditions that affect their reproductive activity (Augspurger, 1990; Saetre, 1999). Other factors that could be associated with the spreading of introduced plant pathogens are related to human influence such as, cropland and grazing, built up areas or transportation infrastructures (Corcobado et al., 2013b). These human-altered areas are a common reservoir of soil pathogens and may increase the risk of dispersal into natural or semi-natural areas.

P. cinnamomi is well adapted to the climate of the Iberian Peninsula and it is recognized as the main biotic factor of oak decline in the Mediterranean forests in Spain and Portugal (Corcobado et al., 2013a, 2013b; Moreira and Martins, 2005; Sánchez et al., 2002). These ecosystems, dominated by evergreen cork oaks (*Quercus suber* L.) and holm oaks (*Q. ilex* L.), are among the most representative Iberian Mediterranean landscapes and have considerable conservational and socioeconomical value. In this study, we try to elucidate the influence of environmental factors and human influence on the distribution of *P. cinnamomi* in the Iberian Peninsula. Specifically, we considered the following questions: (i) which is the relative importance of environmental factors (biotic and abiotic) and the degree of human influence for explaining the distribution of *P. cinnamomi*? and (ii) considering the most important drivers of *P. cinnamomi* occurrence, which is its current potential distribution in the Iberian Peninsula? We discuss the findings in relation to the dynamics and restoration of the declining Mediterranean oak forests.

2. Material and methods

2.1. Study area

Our study area is the entire Iberian Peninsula (Portugal and Spain; Fig. 1). This extends over a surface of 582,925 km^2 from latitude 43° 47′ N to 36° 01′ N and longitude 9° 30′ W to 3° 19′ E, encompassing several mountain ranges (the Pyrenees, the Cantabrian Mountains, the Northwest ranges, the Central Range, the Iberian Range and the Betic Range) (Oliva et al., 2016). The climate of the area is divided by two major climate zones: (i) the Atlantic climate characterized by mild summers and cold, rainy winters and (ii) the Mediterranean climate with mild winters and hot, dry summers (Dasari et al., 2014). The main vegetation types vary from semi-desertic flora, Mediterranean oak forests, steppeland areas and evergreen pine forests, to deciduous vegetation and subalpine and alpine vegetation (Pascual et al., 2011). Due to these characteristics, the Iberian Peninsula currently stands out as hosting almost 50% of European plants and terrestrial vertebrate species and with > 30% of endemic species (Araujo et al., 2007).

2.2. The modelled species

P. cinnamomi, a soil-borne fungus, is one of the world's most destructive and invasive plant pathogen (Brasier, 1996; de Sampaio e Paiva Camilo-Alves et al., 2013; Hardham, 2005). *P. cinnamomi* is thought to be native to Southeast Asia, but it is now present in most temperate and tropical regions and is responsible for severe crop losses and strong disturbances in natural ecosystems (Brasier, 1996; Zentmyer, 1988). It was first recorded in Europe in the 19th century, most likely linked to contaminated nursery stock and other plant material (Hardham, 2005). In susceptible hosts, *P. cinnamomi* colonizes the roots causing necrosis, loss of fine roots, root rot and ultimately death (Corcobado et al., 2013a; Hardham, 2005; Ruiz Gómez et al., 2015; Sánchez et al., 2002). *P. cinnamomi* may persist in soil or infected plants as chlamydospores, and when conditions favouring mycelium growth predominate, the pathogen enters the asexual sporulation cycle (de Sampaio e Paiva Camilo-Alves et al., 2013; Hardham, 2005). This asexual cycle of reproduction may be repeated many times, and thus rapidly amplifying the inoculum potential in infected areas (Hardham, 2005).

2.3. Key susceptible hosts in the Iberian Peninsula

A large part of forests in the Iberian Peninsula are currently dominated by evergreen oak species susceptible to *P. cinnamomi* such as cork (*Q. suber* L.) and holm oak (*Q. ilex* L.). These woodlands are of high conservation and socioeconomic value within their areas of geographic distribution around the Mediterranean basin (de Sampaio e Paiva Camilo-Alves et al., 2013). In Western Iberia, holm and cork oaks occupy large extensions forming traditional agrosilvopastoral systems called "dehesa" in Spain and "montado" in Portugal (de Sampaio e Paiva Camilo-Alves et al., 2013; Gea-Izquierdo et al., 2006). This multifunctional system is characterized by offering a diversity of products such as forage, acorn, wood, and cork, and its long-term ecological sustainability derives from the sub optimization of the resources and continued management (de Sampaio e Paiva Camilo-Alves et al., 2013).

2.4. Phytophthora cinnamomi dataset

To analyse the patterns of distribution of *P. cinnamomi* in the study area, we gathered a total of 295 presence/absence records (presence: $n = 175$; absences: $n = 120$; Fig. 1) in the Iberian Peninsula from four different datasets: Corcobado et al. (2013b), Moreira and Martins (2005), Red SEDA (2015) and Romelaro-Tapia (2008). In all of these cases, data was obtained from soil sampled in forest surveys (details in: Appendix A – Table A2). We used a grid resolution of 1 × 1 km to remove duplicate records (i.e. only one occurrence record per grid square of 1 × 1 km). This filtering decreased the number of presence/absence records for *P. cinnamomi* in the Iberian Peninsula to 277 grids of 1 × 1 km (presence: $n = 157$; absences: $n = 120$).

This compiled database is the result of an extensive search of the occurrence of *P. cinnamomi* in the study area. The spatial independence of these datasets is an important underlying assumption of this study as it allows an accurate representation of the observed occurrence of the species in the study area. However, we acknowledge that this database 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 distribution of the species.

2.5. Explanatory variables

Modelling success depends on using appropriate variables linked to relevant ecological processes. Herein, to characterize the most important habitat heterogeneity and environmental conditions for the establishment and spread of *P. cinnamomi* in the study area, we used 15 broad-scale variables as predictors, related to abiotic conditions (climate and soil), biotic conditions (susceptible host plants and vegetation cover) and human influence (Table 1). These variables were chosen based on our knowledge of the species' ecology (Corcobado et al., 2013b; de Sampaio e Paiva Camilo-Alves et al., 2013; Hardham, 2005; Moreira and Martins, 2005; Weste and Marks, 1987), and were assumed to be at least correlated with more proximal causal factors.

Climatic variables were available from WorldClim climate database at 1 km resolution (Hijmans et al., 2005). We selected relevant aspects of temperature and rainfall such as annual ranges and mean temperature of wettest quarter in the Iberian Peninsula (Table 1). Soil texture (content of clay and sand) and soil pH at 1 km resolutions were downloaded from ISRIC-World Soil Information SoilGrids database (Hengl et al., 2014). Soil water content was downloaded from CGIAR-

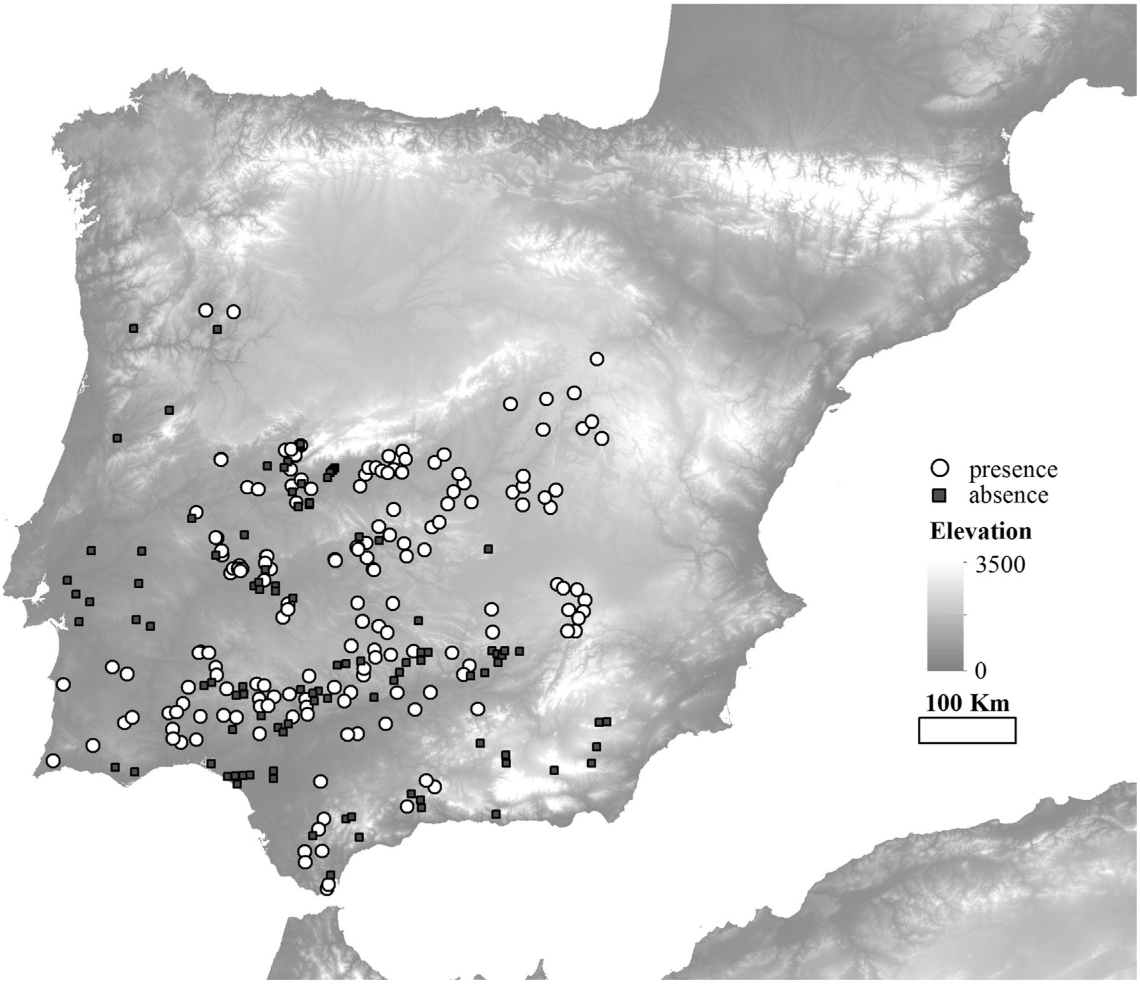

Fig. 1. Observed distribution of *Phytophthora cinnamomi* Rands in the Iberian Peninsula (presence: $n = 157$; absences: $n = 120$).

Table 1

Variables used as predictors of the *P. cinnamomi* presence in the Iberian Peninsula.

Variable	Descriptions	Source	VIF
Abiotic factors			
TEMP	Mean annual temperature (°C)	WorldClim	11.26
TEMP_R	Temperature annual range (°C)		**3.332**
TEMP_W	Mean temperature of wettest quarter (°C)		**2.250**
RAIN	Annual precipitation (mm)		68.71
RAIN_S	Precipitation Seasonality		18.76
RAIN_W	Precipitation of wettest quarter (mm)		83.93
pH	Soil pH in water suspension (10^{-1})	ISRIC	**3.517**
Clay	Clay content in soil (%)		**1.193**
Sand	Sand content in soil (%)		**1.169**
Silt	Silt content in soil (%)		15.90
SWater	Water content in soil (mm)	CGIAR-CSI	**3.649**
Biotic factors			
QIlex	Suitable habitats for the occurrence of *Quercus ilex*	Model (App. 1)	**2.162**
QSuber	Suitable habitats for the occurrence of *Quercus suber*		**7.559**
NDVI	Vegetation cover: annual average Normalized Difference Vegetation Index	NASA-MODIS	**1.464**
Human influence			
Artificial	Percentage of artificial surfaces (continuous and discontinuous urban fabric, industrial and commercial units, mines, dumps, and construction)	Modified from CORINE	**1.350**
Agricultural	Percentage of agricultural areas (arable land, permanent crops, annual crops, land principally occupied by agriculture with significant areas of natural vegetation and agro-forestry areas)		**1.160**
Pasture	Percentage of pasture areas (land used to support grazing animals)		**1.312**
Road	Minimum distance to roads (km)	OpenStreetMap	**1.214**

Variables in bold were included in the final analysis to avoid collinearity.

CSI at 1 km resolution (Trabucco and Zomer, 2010). To characterize human influence at landscape scale, we extracted the percentage area of the following land cover at 100 m grid from the CORINE Land-cover Map 2006 (European Environment Agency; http://www.eea.europa.eu/); artificial surfaces (i.e. continuous and discontinuous urban fabric, industrial and commercial units, mines, dumps, and construction), agricultural areas (i.e. arable land, permanent crops, annual crops, land principally occupied by agriculture with significant areas of natural vegetation and agro-forestry areas) and pasture areas (i.e. land used to support grazing animals). Finally, we calculated the minimum distance to roads from the centre of each 1 km grid based on the road network of the global community-owned OpenStreetMap project (Neis et al., 2012), using the Euclidean distance (in km) by ArcGis program version 10.3.1. (ESRI, 2015).

In order to capture the geographical variation in the presence of two key host forest species susceptible to *P. cinnamomi* in the Iberian Peninsula, we built species distribution models for *Q. ilex* and *Q. suber* using Generalized Linear Models (GLMs) (see in Appendix A – A1). We used all available occurrence records for each susceptible host from the Third National Forest Inventory (MAGRAMA, 2007) and GBIF (www.gbif.org) and a set of environmental variables describing climate, topographic and soil texture of the study area based on the species' ecology (Barbero et al., 1992; Magri et al., 2007; Serra-Diaz et al., 2013). The final results are raster grids at 1 km resolution in which values range from 0 to 1 (Fig. 2), where higher values indicate more suitable habitats for the occurrence of the species. Several studies have shown that the values of these grids also correlate with species abundance, where localities with higher values have greater abundance values for the species being studied (Oliver et al., 2012; Tôrres et al., 2012). We used the R package "dismo" to build the models (Hijmans et al., 2013).

Finally, to represent the status of vegetation in the study area, we used an annual average from the Normalized Difference Vegetation Index (NDVI; January-December 2014) from the NASA-MODIS/Terra dataset at 250 m resolution (Justice et al., 1998). This vegetation index has been used successfully to calibrate species distribution models in other studies (Benito et al., 2013). All data were re-sampled to 1 km spatial resolution using an interpolation bilinear re-sampling technique (ESRI, 2015). Prior to analyses all variables were checked for collinearity using the Variance Inflation Factor (VIF). All variables with VIF > 10 were discarded for further analyses (Barea-Azcón et al., 2014; Zuur et al., 2010).

2.6. Statistical analyses

2.6.1. Multimodel inference

Multimodel inference is a model selection method frequently employed to identify the model that is best supported by the data (i.e. best model) from among the candidate sets and it also allows the measurement of the importance (i.e. weight of evidence) of each independent variable to explain the response variable (Burnham and Anderson, 2002; González-Moreno et al., 2013; Thuiller et al., 2007). Herein, we performed multimodel inference based on the all-subsets selection of Generalized Linear Models (GLMs) using Akaike's information criterion corrected for a large number of predictors (AICc). GLMs using a binomial distribution and a logistic link function were fitted using presence/absence of *P. cinnamomi* as the response variable and the sets of variables as predictors. The response variable considered was first related separately to either a linear or quadratic function of each variable in order to take possible curvilinear relationships into account (Lobo et al., 2006). The best function for each variable (i.e. lowest AICc) was then used in the rest of the modelling procedure. Then, for each candidate model in the final selection, we calculated the weight of evidence (***Wi***) to rank the predictors in order of importance explaining the presence of *P. cinnamomi*. We summed the model AICs weights for all models within four AICc units from the best model in which each predictor appeared (González-Moreno et al., 2013). However, the ***Wi*** values are relative and not absolute because they will be > 0, even if the predictor has no explanatory importance (Brook et al., 2006; Burnham and Anderson, 2002; Thuiller et al., 2007). To avoid this problem, we used a stratified permutation test to calculate the absolute weight of evidence (**Δ*Wi***) (Brook et al., 2006; Thuiller et al., 2007). We randomized the data for each predictor separately within the data set, then re-calculated ***Wi*** and repeated this procedure 100 times for each predictor. The **Δ*Wi*** was then calculated by subtracting the median value of the 100 randomized ***Wi*** from the original ***Wi***. Only predictors with **Δ*Wi*** > 0 have true explanatory power on the occurrence of *P. cinnamomi* in the Iberian Peninsula.

We also used multimodel inference to calculate regression coefficients and their confident intervals (with the adjusted standard error) within the best models subset (ΔAICc < 4). We calculated the coefficient for a given predictor as the sum across all possible models where the predictor was present, of the predictor's coefficient multiplied by the ***Wi*** as in Burnham and Anderson (2002).

Finally, spatial autocorrelation across the geographic space is an inherent property of most ecological data and it might break the assumption of independence of the data modelled (Legendre, 1993). For

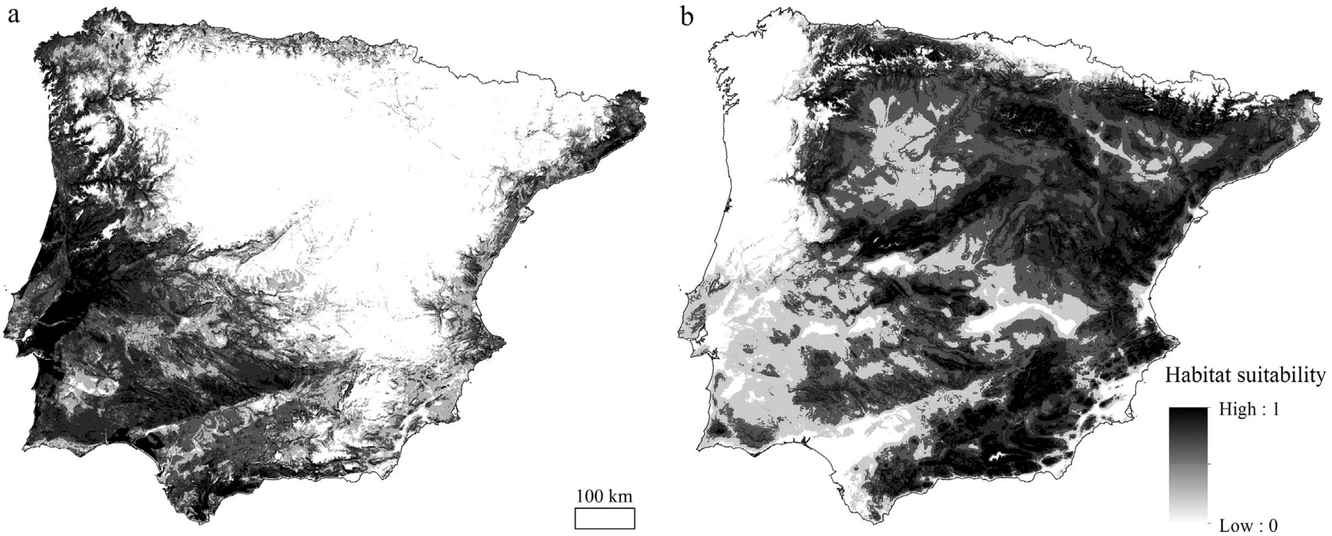

Fig. 2. Predicted potential distribution of two key hosts forest species susceptible to *P. cinnamomi* in the Iberian Peninsula. (a) *Q. suber* and (b) *Q. ilex*.

each GLM in the multimodel inference procedure we tested the spatial autocorrelation in the model's residuals by the Moran's index. We did not detect significant spatial autocorrelation in the residuals of the subset of models within four AICc units from the best model (see in Appendix A – Table A5).

2.6.2. Deviance partitioning

Assuming that the deviance is a good measure of the variability explained by a model (Borcard et al., 1992; Carrete et al., 2007), we performed a hierarchical partitioning procedure to specify how much of the variation of the GLMs were explained by the pure effect of each set of explanatory variables (i.e. abiotic, biotic and human influence factors) and which proportion was attributable to their shared effects (González-Moreno et al., 2013; Muñoz et al., 2005). We set up GLMs including a different subset of non-collinear variables: only abiotic, only biotic, only human influence and the combination of the three. The deviance explained by each model was then used to identify the single and shared effects on the occurrence of *P. cinnamomi* by simple equation systems.

2.6.3. Prediction of the potential distribution of *P. cinnamomi* in the Iberian Peninsula

Potential distribution is defined as the geographic area in which the environment of the modelled species is suitable at a given time (Rodríguez et al., 2015). To predict the potential distribution of *P. cinnamomi* across the entire Iberian Peninsula, we divided the presence/absence data randomly from the study area into training (80%) and testing (20%) datasets for calibrating and testing the accuracy of the best model (smallest AICc) obtained by multimodel inference. We performed a 10-fold cross-validation, calibrating the best model with the training dataset and projecting it into the testing dataset. We evaluated the predictive performance of the model using two statistics, the area under the Receiver Operating Characteristic curve (AUC) and correlation (COR) (Elith et al., 2006). AUC measures the ability of a model to discriminate between sites where a species is present, versus those where it is absent. The AUC ranges from 0 to 1 (0.5 = random, 1 = perfect). COR measures how far the prediction varies from the observation (Elith et al., 2006). AUC and COR values were computed by *k*-fold validation (ten groups). Finally, we used all available occurrences of *P. cinnamomi* to calibrate the best model and we projected its final potential distribution to all of the Iberian Peninsula's 1 × 1 km grids.

All analyses were performed with the R-CRAN software version 3.3.3. (R Core Team, 2015). We used the R package "MuMin" for the procedures of the multimodel inference method, the R package "VEGAN" as the base code for deviance-partition, the R package "ncf" and "spdep" for spatial autocorrelation analysis, the R package "dismo" to estimate the potential distribution and finally we used the function "evaluate" from the R package "dismo" to evaluate the predictive performance of the models (Hijmans et al., 2013).

3. Results

3.1. Factors influencing the distribution of *P. cinnamomi* in the Iberian Peninsula

The presence of *P. cinnamomi* in the study area was significantly associated with soil properties (Table 2). Soil clay content showed a positive effect, while the association with sand content and pH was negative. Temperature annual range and mean temperature of wettest quarter had a significant effect. On the other hand, the presence of *P. cinnamomi* was significantly associated with lands principally occupied by agriculture, as well as with the presence of one of its susceptible host species (*Q. suber*) and high NDVI.

The deviance partition analysis revealed that 42% of the variability in *P. cinnamomi* was explained by the best model (Fig. 3 and Appendix A – Table A4). The decomposition of the variation showed that purely abiotic factors were able to explain most of the variation while human activity and biotic factors showed little single effect. A large proportion of the variation was explained simultaneously by abiotic and biotic variables independently of human activity.

3.2. Potential distribution of *P. cinnamomi* in the Iberian Peninsula

The average of AUC and COR values for a set of 10-replicate of the best model ranged between 0.82 and 0.88 (mean AUC = 0.85 ± 0.01) and 0.53–0.66 (mean COR = 0.61 ± 0.01) respectively. These values indicated overall good ability to predict the potential geographical distribution of *P. cinnamomi* in the Iberian Peninsula.

The current suitable habitats for *P. cinnamomi* were predicted in the South West of the Iberian Peninsula with patches in the North-Northeast. Furthermore, the model suggests the existence of areas with suitable environments where records of *P. cinnamomi* were not found. These predicted areas were located in the North East of Cataluña, the South East of Spain and central Portugal (Fig. 4).

4. Discussion

4.1. The important role of abiotic and biotic factors and human influence in the distribution of *P. cinnamomi*

We identified the most influential variables explaining the distribution of *P. cinnamomi* using multimodel inference of GLMs and variance-partition techniques. The variables retained by regression models as statistically significant revealed that *P. cinnamomi* distribution is highly dependent on abiotic factors such as soil properties and temperature, followed by human influence variables and lastly biotic factors such as the presence of one of its main susceptible host. According to Soberon and Peterson (2005), biotic, historical and human factors contribute together to control the distribution and abundance of species. Mapped representations of these factors are often used as explanatory variables to predict species distribution (Guisan and Thuiller, 2005). However, biotic interactions and human influence are usually disregarded in large-scale analyses as effective variables determining the distributions of the modelled species, because they are assumed to characterize only local effects (Dirnböck et al., 2003; Soberón and Nakamura, 2009). In contrast to these criticisms, our findings demonstrate the important additional information that biotic variables (susceptible host and NDVI index) and human influence (agricultural lands) contribute to explain the distribution of *P. cinnamomi* in the Iberian Peninsula. These results are consistent with those found by other studies, which indicate a significant effect of these variables in the explanatory power of species distribution models at macroscales and particularly for invasive species (Gallardo et al., 2015; Heikkinen et al., 2007; Jetz et al., 2007).

Fine textured soil seems to favour the occurrence of pathogen more than coarse textured soils, presumably as a result of the direct influence on water availability. In coarse textured soils, water depletes quickly, which is detrimental for the production of sporangia and release of zoospores, while in fine textured soils, water retention strongly benefits the activity of the pathogen and provides conditions for inoculum increase (Corcobado et al., 2013b; Gómez-Aparicio et al., 2012; Hardham, 2005; Jönsson et al., 2005; Jung et al., 2000). These results support previous findings by Gómez-Aparicio et al. (2012) and Corcobado et al. (2013b), who suggest that the presence of *P. cinnamomi* is significantly constrained to soils with high clay content and low sand content. In addition, in this study, soil pH was associated negatively with the presence of the pathogen. Based on lab studies *Phytophthora* spp. show reduced activity at pH values below 4.0 (Jung et al., 2000). Increases in soil pH have been shown to inhibit mycelial growth, as well as sporangial formation and germination (Jönsson, 2006).

Climatic variables were also important to explain the distribution of

Table 2
Multimodel inference results: non-corrected and unbiased weight of evidence, averaged and standardized coefficient estimates (β) and confidence intervals (95% CI) of abiotic, biotic and human influence predictors for *P. cinnamomi* presence in the Iberian Peninsula.

Variable	Type	Weight	Unbiased weight	β Averaged	Adjusted SE	Lower CI	Upper CI
Intercept				**−11.34**	3.404	−18.36	−3.479
TEMP_R	Abiotic	1.000	0.815	**0.405**	0.066	0.265	0.525
Clay	Abiotic	1.000	0.800	**0.084**	0.029	0.026	0.141
Sand	Abiotic	1.000	0.798	**−0.053**	0.019	−0.092	−0.015
TEMP_W	Abiotic	1.000	0.788	**13.42**	4.929	3.362	22.73
TEMP_W^2	Abiotic			**−13.27**	4.989	–23.01	−3.410
Agricultural	Human influence	1.000	0.779	**0.052**	0.017	0.018	0.086
NDVI	Biotic	0.984	0.771	**3.671**	1.517	0.609	6.710
QSuber	Biotic	0.946	0.732	**2.952**	1.143	0.530	5.417
pH	Abiotic	0.925	0.719	**−0.564**	0.261	−1.175	−0.068
SWater	Abiotic	0.407	0.176	−0.713	1.282	−4.167	0.930
QIlex	Biotic	0.358	0.141	2.185	1.841	−1.380	6.199
Pasture	Human influence	0.340	0.093	−1.747	1.337	−5.362	1.599
Road	Human influence	0.197	−0.026	−2.893	6.043	−14.981	9.127
Artificial	Human influence	0.175	−0.057	−0.004	0.011	−0.028	0.018

Predictors are sorted by importance according to the unbiased weight of evidence. Significant averaged coefficients are shown in bold. See Table 1 for a complete description of variables.

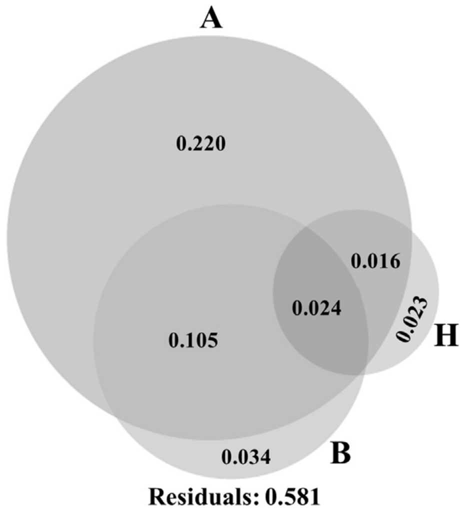

Fig. 3. Variation partitioning of the presence of *P. cinnamomi* in the Iberian Peninsula. Each circle corresponds to a group of variables. (A) abiotic, (B) biotic and (H) human influence. The numbers within the circles are the proportion of deviance explained by each set of predictors alone (non-overlapped part of circles) or shared (overlapped part of circles). Residuals indicate the non-explained deviance by the models.

this pathogen and its potential impact en Mediterranean oak forests. The probability of *P. cinnamomi* occurrence was positively associated with very seasonal climates while the relation with temperature in the wettest quarter showed a hump shape with optimum at 18 °C in the study area. This result is consistent with our knowledge of the species, as warmer soils, particularly combined with moist conditions, are optimum for its development and virulence (Brasier, 1992; Brasier et al., 1993; Shearer, 2014). The important effect of climate conditions on the development and virulence of *P. cinnamomi* has also been investigated with respect to possible effects of global warming on its distribution and impact. Martín-García et al., (2015) establish a clear effect of temperature on the survival of germinating holm oak acorns. High temperatures in infested soils with *P. cinnamomi* caused rot on embryos and necrosis on emerging acorn radicles (Martín-García et al., 2015). From a conservation point of view, seed germination and radicle elongation represents a crucial step in the processes of natural forest regeneration. Any limitations of the radicle during germination may have a significant impact on the plant's ability to tolerate extreme climatic events (e.g. drought) (Cubera et al., 2012). On the other hand, analysis of scenarios with increasing temperature predicts that global warming could result in a increase in the incidence of periods favouring the growth of this pathogen and thus, increase its range towards areas in the northeast of the European continent (Bergot et al., 2004; Brasier, 1996). However, these predictions are based solely on the effects of temperature on the habitat suitability for the pathogen. Predicting the impacts of climate change on the distribution *P. cinnamomi* must also consider the host-pathogen interactions, human influence and changes in rainfall patterns, particularly in Mediterranean regions (Yáñez-López et al., 2012).

One important finding of this study is the positive association between the presence of *P. cinnamomi* and the distribution of one of susceptible host species (*Q. suber*). The presence of *P. cinnamomi* and their virulence may represent an important threat to the stability of Mediterranean forests in the Iberian Peninsula which are dominated by evergreen holm and cork oaks. These forest ecosystems are particularly vulnerable to oak decline processes mainly because of the combined effect of extreme weather conditions such as warmer climates, water stress, soil disturbances and widespread distribution of exotic pathogens (Brasier et al., 1993). In fact, an extensive mortality and decline of oaks, principally *Q. suber*, has occurred in parts of southern Spain and Portugal in recent decades and *P. cinnamomi* has been cited as the main biotic factor of oak decline being responsible for multiple fine-root infections followed by substantial root girdling and death (de Sampaio e Paiva Camilo-Alves et al., 2013; Gómez-Aparicio et al., 2012; Moreira and Martins, 2005). Another important aspect to consider is the positive association between the presence of *P. cinnamomi* and high NDVI. Higher vegetation index represents areas of higher tree density, where we expect higher competition for resources among neighbouring plants. These negative interactions will be exacerbated by extreme climatic events (e.g. drought) increasing the susceptibility of the less competitive plants to infections by *P. cinnamomi* (Corcobado et al., 2014). In the current scenario for the Iberian Peninsula of low-intensity forest management and increasing biomass, this competition process might exacerbate the spread the pathogen to large areas of oak forests across its suitable abiotic area.

Our results suggest a significant association of the presence of *P. cinnamomi* with an increasing area occupied by agriculture. Recently, Manzano et al., (2016) relate decline and *P. cinnamomi*-induced mortality of corn and holm oaks to the presence of hydraulic infrastructures (e.g. ponds) resulting from agricultural activities. Fine texture soils, moist conditions and the abundance of suitable hosts in crops could not only increase the inoculum potential (see above) but also derive in

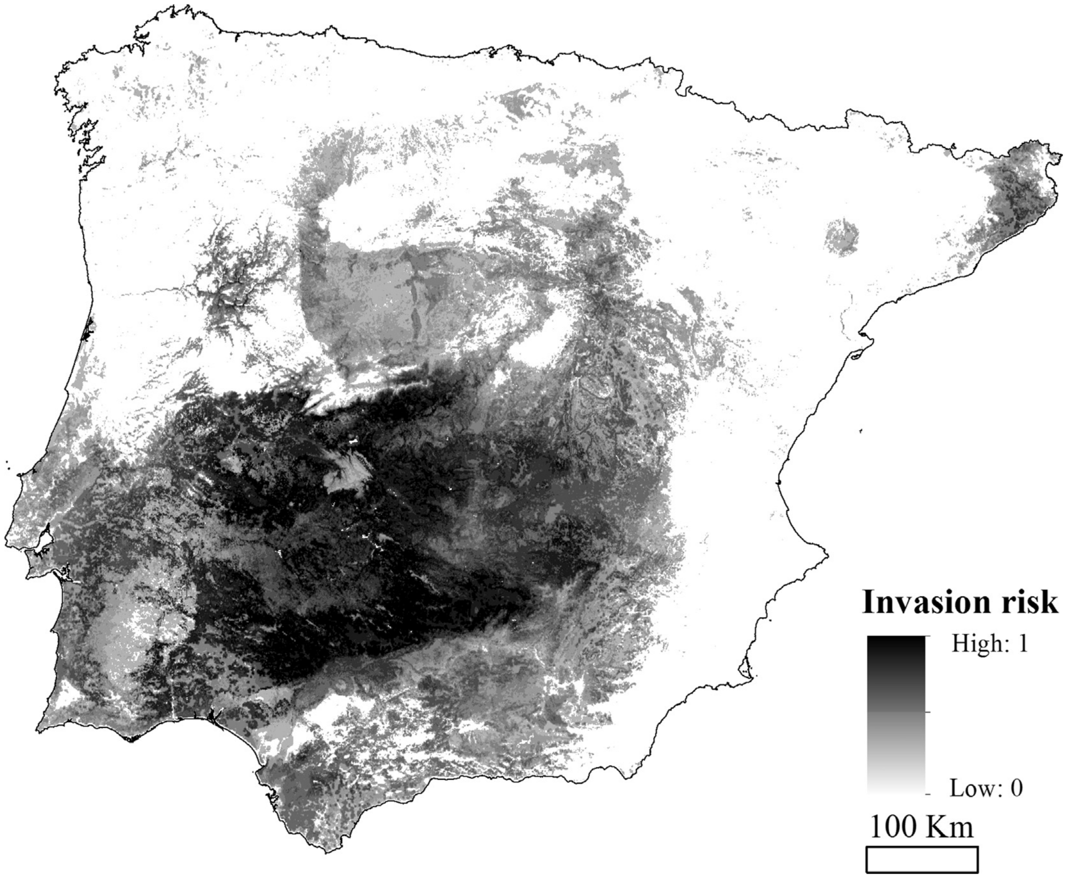

Fig. 4. Potential distribution of *P. cinnamomi* invasion risk (0–1 scale) in the Iberian Peninsula using the best GLM model obtained by multimodel inference.

important implications for hygiene management, as clayey soils would more easily adhere to passing humans and vehicles, and thus increase risk of pathogen dispersal. Human activities, by promoting parasite transport, have been and will be major factors potentially favouring the spread of soil-borne pathogens (Anderson et al., 2004). This finding reinforces the important effect of human influence variables on invasive species distribution, and the importance of performing sensitivity analyses to quantify its true relevance (Gallardo et al., 2015).

4.2. Predicting the potential distribution of P. cinnamomi

We developed a conservative predictive model to represent the potential distribution of one of the most widely distributed and destructive forest pathogens in the Iberian Peninsula. The strength of our model relies on the availability of high quality records of *P. cinnamomi* (presence/absence) for the study area and a robust and biologically relevant selection of explanatory variables. The high values of performance (AUC and COR) of our model in predicting the potential distribution of *P. cinnamomi* in the Iberian Peninsula indicates a high dependence of the occurrences data and the set of variables included in the analysis (Roura-Pascual et al., 2009). Given the observed occurrence of *P. cinnamomi*, predictions of its potential distribution across the Iberian Peninsula suggest that a further expansion of this soil pathogen is possible along the northeast of Spain (Cataluña), the southeast of Spain and central part of Portugal. Special attention in scrutiny efforts should focus on the southern part of the central plateau of Spain, where the “dehesa” is the main component of the landscape and the local economy. Furthermore, given the dependence of *P. cinnamomi* activity on soil properties, control efforts should focus along South-eastern Spain (Andalusia) where the high clay contents represent suitable conditions to its establishment and spread.

5. Conclusion

This study provides new insights into the highly complex spatial distribution of soil-borne pathogens and reveals the degree to which abiotic and biotic factors and human influence can explain pathogen distributions at large scales. *P. cinnamomi* distribution seems to be influenced principally by fine texture soil, seasonal and warm climates, followed by abundance of agriculture area and by the presence of its susceptible host forest species in the Iberian Peninsula. The higher likelihood of occurrence of *P. cinnamomi* in forest areas embedded in an agricultural matrix suggests that adequate management farming practices involving manipulations of the soil, equipment transport and drainage should be implemented to limit the expansion of this soil pathogen into forest areas. Finally, given the significant impact of this pathogen on forest ecosystems, the modelling of its potential distribution in the Iberian Peninsula provides an important decision tool for the monitoring and restoration of declining Mediterranean oak forests, highlighting areas of potential further expansion, especially along Southeast Spain and central Portugal.

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Conflict of interest

We declare that we have no conflict of interest.

Author contributions

All authors contributed to the formulation of ideas and the writing of the manuscript.

Appendix A. Supplementary material

Supplementary data associated with this article can be found, in the online version, at http://dx.doi.org/10.1016/j.foreco.2018.03.026.

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INFORMACIÓN SUPLEMENTARIA

Appendix A

A1: *Modelling the current distribution of the main hots forest species susceptible to Phytophthora cinnamomi in the Iberian Peninsula*

In order to capture geographical variation in the presence of two key host forest species susceptible to Phytophthora cinnamomi in the study area, two maps representing the potential distribution of *Quercus suber* and *Q. ilex* were built using Generalized Linear Models (GLMs). All available records were gathered from Third National Forest Inventory (MAGRAMA, 2007) and Global Biodiversity Information Facility (GBIF; www.gbif.org) (*Q. ilex* n = 59105 and *Q. suber* n = 10385) and were filtered in the same way than P. cinnamomi records (see main text for details*; Q. ilex* n = 4650 and *Q. suber* n = 1272). These records can be considered a fairly accurate approximation of the real distribution of the species of cork and holm oaks in the Iberian Peninsula. We disregarded records of other species of *Quercus* in this study, because they were not reported as important hosts susceptible to *P. cinnamomi* in the Iberian Peninsula. To summarize the environmental space potentially available for both species in the study area, we used 9 non-collinear predictors (VIF < 10), related to climate, topographic and soil conditions (Table A1). These variables were chosen based on our knowledge of the species' ecology (Barbero et al., 1992; Magri et al., 2007; Serra-Diaz et al., 2013)

GLMs habitually are calibrated with presence/absence data. However, it can be applied to presence-only records by using pseudo-absence selected randomly in the study area as in other studies elsewhere (Barbet-Massin et al., 2012; Roura-Pascual et al., 2009; Serra-Diaz et al., 2013). Herein, to calibrate the models for both species, we generated an equal number of pseudo-absences as presences by selecting a random subset of pixels from the overall study area. Then we divided presence/pseudo-absence data randomly from study area into training (80%) and testing (20%) datasets for calibrating and testing the accuracy of models respectively. With the training data and a set of environmental variables, we developed models for both species in the Iberian Peninsula using GLM. To evaluate the predictive performance of the models, we performed a 10-fold cross-validation calibrating the models with the training dataset and projecting into the testing dataset. We applied two statistics, the area under the Receiver Operating Characteristic curve (AUC) and correlation (COR) (Elith et al., 2006). Finally, we used all available occurrences of each species to produce their final distributions.

GLM models for both species were all better than random with AUC (0.74±0.01 for *Q. suber* and 0.64 ± 0.01 for *Q. ilex*) and COR values (0.42 ± 0.03 for *Q. suber* and 0.35 ± 0.02 for *Q. ilex*), indicating that for each species, the most suitable habitats predicted were highly correlated with the actual occurrences of the species. High suitability areas predicted by the GLM models for both species coincide with their current distribution ranges (Barbero et al., 1992; Magri et al., 2007; Serra-Diaz et al., 2013). GLM models for *Q. suber* identified as suitable areas in the Western Iberian Peninsula, while for *Q. ilex* GLM models identified a wide distribution of the suitable areas across the central part of the Iberian Peninsula.

Table A1

Variables used as predictors of the presence of host species susceptible to *P. cinnamomi* (*Q. suber* and *Q. ilex*) in the Iberian Peninsula. Variables in bold were included in the final analysis to avoid collinearity.

Variable	Descriptions	Source	VIF
TEMP	Mean annual temperature (°C)	WorldClim	**1.257**
RAIN	Annual precipitation (mm)		**8.709**
SUN_R	Mean annual solar radiation (WH/m^2)*	DEM	**9.658**
T_Div	Topographic diversity*		**4.365**
pH	Soil pH in water suspension (10^{-1})	ISRIC	**7.517**
Clay	Clay content in soil (%)		**9.345**
Silt	Silt content in soil (%)		19.23
Sand	Sand content in soil (%)		**6.369**
Organic	Organic content in soil (tonnes/ha)		**5.871**
SWater	Water content in soil (mm)	CGIAR-CSI	**6.849**

* Solar radiation was calculated using the Area solar tool from program ArcGIS 10.3.1. (ESRI, 2015), which calculates clear-sky insolation across a Digital Elevation Model (DEM) at 1 km spatial resolution (US Geological Surveys; www.usgs.gov) accounting for aspect, slope and topographic shading.

* Topographic diversity was calculated using the Neighborhood toolset in ArcGIS, which calculate for each DEM grid cell the diversity of elevation values considering all surrounding cells within a 3-km radius.

Table A2

Location and sampling strategies of the presence of *Phytophthora cinnamomi* in Iberian Peninsula.

Location	**Sampling strategies**	**Records of presence/absence**	**Source**
Spain	Soil samples for *P. cinnamomi* determination were extracted from forest surveys in Andalusian (*Q. ilex* and *Q. suber* trees). The soil was sampled at the vertexes of 8 × 8 km grids. The vertexes were located on the ground using a hand-held GPS with a spatial accuracy of 10 m. The samples were analysed at the Agroforestry Pathology Department (University of Córdoba).	50/45	Red SEDA (2015)
Spain	Soil and root samples were extracted from forest surveys in Extremadura (*Q. ilex* trees). The soil was dug to allow sampling using a hydraulic backhoe with a 40 cm-wide scoop. The maximum soil depth dug was 1.5 m. Samples of soil and root of *Q. ilex* were collected at three depths (0.5, 1.0 and 1.5 m, when possible). The samples were analysed at the University of Extremadura.	50/46	Corcobado et al. (2013)
Spain	Field surveys were carried out in oak sites (*Quercus* spp.) located in 5 regions of province of Castilla la Mancha. In each site, the presence of *P. cinnamomi* was determinate in soil and root samples of asymptomatic trees.	48/0	Romelaro-Tapia (2008)
Portugal	Sampling for *P. cinnamomi* was carried out in 56 cork and holm oak sites located in four regions of Portugal. Some of these sites were typical Iberian ecosystems known as 'montado', where several shrub species co-exist with the two main tree species *Q. suber* and *Q. ilex*. In each site the presence of *P. cinnamomi* was determinate in soil and root samples of nearby asymptomatic individuals of other shrub and tree species were collected.	27/29	Moreira and Martins (2005)

Table A3

Selection of best models considering AICc criteria (Delta<4: all models within 4 AICc units from the best model) for *P. cinnamomi* presence considering abiotic, biotic and human influence as predictors. In bold the best model.

Component models:	df	logLik	AICc	delta	weight
1+2+3+7+9+poly(10,2)+12+13	10	-133.92	288.54	0	0.11
1+2+3+6+7+9+poly(10,2)+12+13	11	-133.06	288.95	0.42	0.09
1+2+3+7+9+poly(10,2)+11+12+13	11	-133.39	289.61	1.07	0.06
1+2+3+7+8+9+poly(10,2)+12+13	11	-133.44	289.71	1.18	0.06
1+2+3+6+7+9+poly(10,2)+11+12+13	12	-132.45	289.89	1.35	0.06
1+2+3+6+7+8+9+poly(10,2)+12+13	12	-132.53	290.06	1.52	0.05
1+2+3+4+7+9+poly(10,2)+12+13	11	-133.81	290.46	1.92	0.04
1+2+3+7+8+9+poly(10,2)+11+12+13	12	-132.77	290.53	2	0.04
1+2+3+5+7+9+poly(10,2)+12+13	11	-133.86	290.55	2.02	0.04
1+2+3+6+7+8+9+poly(10,2)+11+12+13	13	-131.77	290.71	2.17	0.04
1+2+3+7+poly(10,2)+12+13	9	-136.08	290.73	2.19	0.04
1+2+3+4+6+7+9+poly(10,2)+12+13	12	-132.96	290.92	2.38	0.03
1+2+3+5+6+7+9+poly(10,2)+12+13	12	-132.98	290.96	2.42	0.03
1+2+3+6+7+poly(10,2)+12+13	10	-135.4	291.49	2.96	0.03
1+2+3+4+7+9+poly(10,2)+11+12+13	12	-133.27	291.54	3	0.02
1+2+3+4+7+8+9+poly(10,2)+12+13	12	-133.32	291.64	3.1	0.02
1+2+3+5+7+9+poly(10,2)+11+12+13	12	-133.35	291.69	3.15	0.02
1+2+3+5+7+8+9+poly(10,2)+12+13	12	-133.38	291.75	3.21	0.02
1+2+3+4+6+7+9+poly(10,2)+11+12+13	13	-132.35	291.86	3.32	0.02
1+2+3+7+9+poly(10,2)+11+13	10	-135.62	291.93	3.39	0.02
1+2+3+5+6+7+9+poly(10,2)+11+12+13	13	-132.4	291.96	3.42	0.02
1+2+3+4+6+7+8+9+poly(10,2)+12+13	13	-132.43	292.03	3.49	0.02
1+2+3+5+6+7+8+9+poly(10,2)+12+13	13	-132.46	292.08	3.54	0.02
1+2+3+7+8+9+poly(10,2)+11+13	11	-134.67	292.18	3.64	0.02
1+2+3+4+5+7+9+poly(10,2)+12+13	12	-133.64	292.28	3.74	0.02
1+2+3+4+7+8+9+poly(10,2)+11+12+13	13	-132.64	292.45	3.91	0.02
1+2+3+8+9+poly(10,2)+11+13	10	-135.89	292.47	3.93	0.02
1+2+3+7+8+poly(10,2)+12+13	10	-135.9	292.51	3.97	0.02

1: Agricultural, 2: Temperature annual range, 3: clay, 4: Road distance, 5: Artificial, 6: Soil water content, 7: NDVI, 8: Pasture, 9: pH, 10: Mean temperature of wettest quarter, 11: *Quercus ilex*, 12: *Quercus suber*, 13: sand.

Table A4

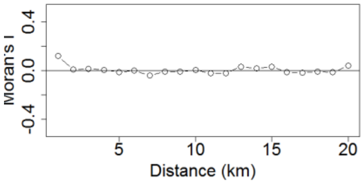
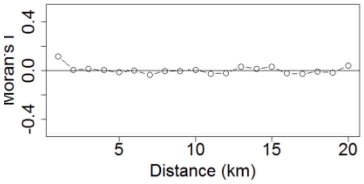
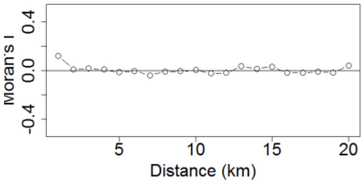
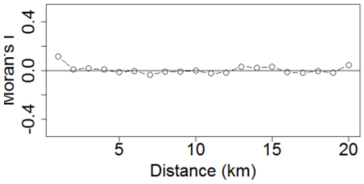
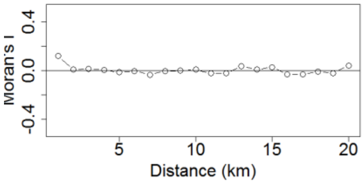
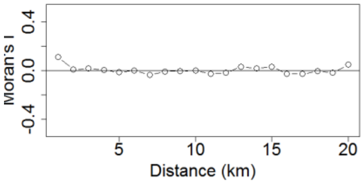
Coefficient estimates for best model from the multimodel inference selection for *P. cinnamomi* presence in the Iberian Peninsula.

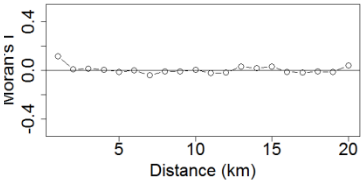
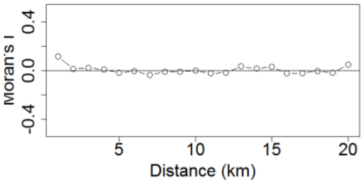
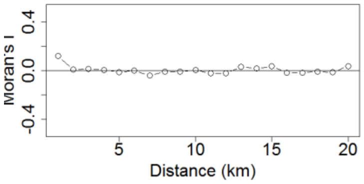
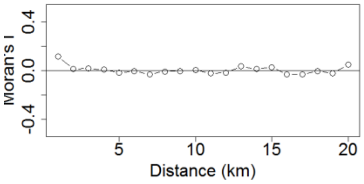
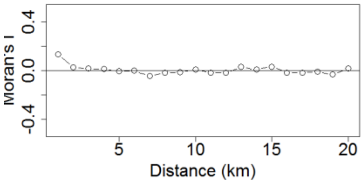
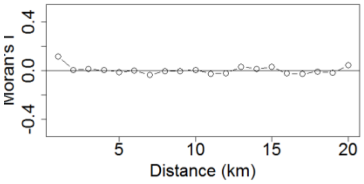
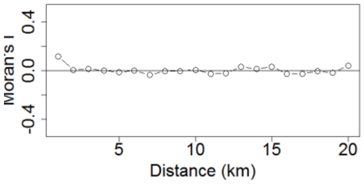
Coefficients	Estimate	Std. Error	z value	Pr(>|z|)	
Intercept	-12.6078	2.78706	-4.524	6.08E-06	***
Agricultural	0.05103	0.01689	3.021	0.00252	**
TEM_R	0.42578	0.06158	6.914	4.70E-12	***
Clay	0.08565	0.02878	2.976	0.00292	**
NDVI	3.65741	1.40198	2.609	0.00909	**
pH	-0.48796	0.2361	-2.067	0.03876	*
TEMP_W	14.59281	4.54234	3.213	0.00132	**
TEMP_W ^{2}	-12.8154	4.8729	-2.63	0.00854	**
QSuber	2.87668	0.9293	3.096	0.00196	**
Sand	-0.05252	0.01922	-2.732	0.00629	**

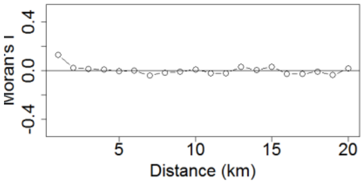
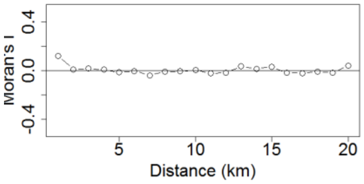
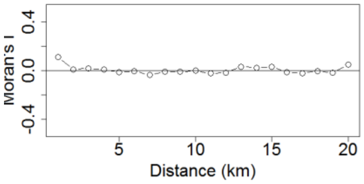
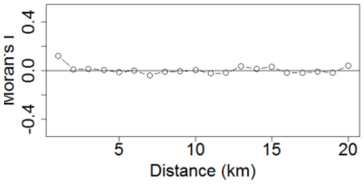
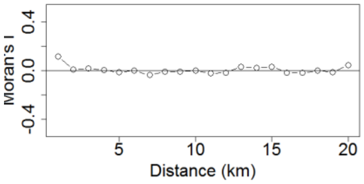
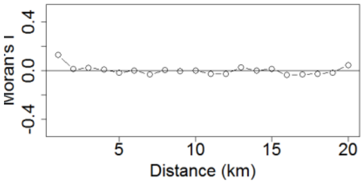
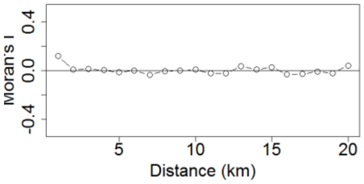
Significance: 0 ***, 0.001 **, 0.01 *, 0.05 ·

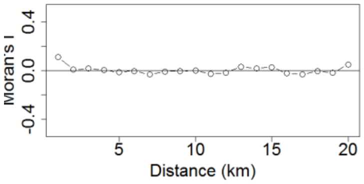
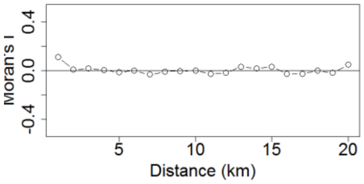
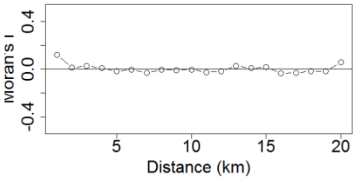
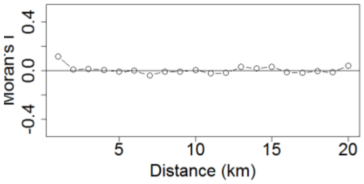
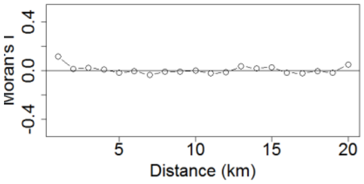
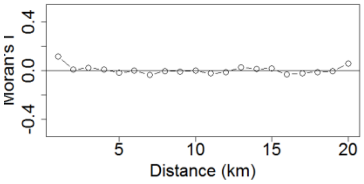
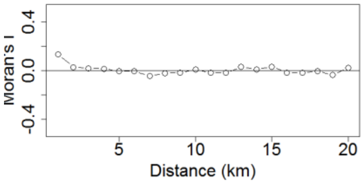
Table A5

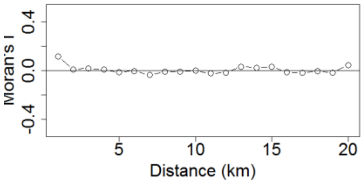
Results of spatial autocorrelation in the residuals of the models within four AICc units from the best model (global Moran’s I and correlograms plot). In bold the best model.

GLM Models	Moran’s *I*	*p*-value	Correlogram plot
1+2+3+7+9+poly(10,2)+12+13	-3.1473e-03	0.6945	
1+2+3+6+7+9+poly(10,2)+12+13	-3.1741e-03	0.7313	
1+2+3+7+9+poly(10,2)+11+12+13	-3.1233e-03	0.6598	
1+2+3+7+8+9+poly(10,2)+12+13	-3.1433e-03	0.6889	
1+2+3+6+7+9+poly(10,2)+11+12+13	-3.1420e-03	0.6871	
1+2+3+6+7+8+9+poly(10,2)+12+13	-3.1716e-03	0.7281	

1+2+3+4+7+9+poly(10,2)+12+13	-3.1543e-03	0.7043	
1+2+3+7+8+9+poly(10,2)+11+12+13	-3.1150e-03	0.6475	
1+2+3+5+7+9+poly(10,2)+12+13	-3.1381e-03	0.6814	
1+2+3+6+7+8+9+poly(10,2)+11+12+13	-3.1342e-03	0.6758	
1+2+3+7+poly(10,2)+12+13	-3.0656e-03	0.5712	
1+2+3+4+6+7+9+poly(10,2)+12+13	-3.1799e-03	0.7391	
1+2+3+5+6+7+9+poly(10,2)+12+13	-3.1639e-03	0.7177	

1+2+3+6+7+poly(10,2)+12+13	-3.0781e-03	0.5909	
1+2+3+4+7+9+poly(10,2)+11+12+13	-3.1293e-03	0.6687	
1+2+3+4+7+8+9+poly(10,2)+12+13	-3.1506e-03	0.6993	
1+2+3+5+7+9+poly(10,2)+11+12+13	-3.1165e-03	0.6497	
1+2+3+5+7+8+9+poly(10,2)+12+13	-3.1341e-03	0.6757	
1+2+3+4+6+7+9+poly(10,2)+11+12+13	-3.1468e-03	0.6939	
1+2+3+7+9+poly(10,2)+11+13	-3.2067e-03	0.7728	

1+2+3+5+6+7+9+poly(10,2)+11+12+13	-3.1347e-03	0.6766	
1+2+3+4+6+7+8+9+poly(10,2)+12+13	-3.1778e-03	0.7363	
1+2+3+5+6+7+8+9+poly(10,2)+12+13	-3.1613e-03	0.7141	
1+2+3+7+8+9+poly(10,2)+11+13	-3.1816e-03	0.7413	
1+2+3+4+5+7+9+poly(10,2)+12+13	-3.1403e-03	0.6846	
1+2+3+4+7+8+9+poly(10,2)+11+12+13	-3.1212e-03	0.6567	
1+2+3+8+9+poly(10,2)+11+13	-3.1763e-03	0.7342	

1+2+3+7+8+poly(10,2)+12+13	-3.0607e-03	0.5634	

1: Agricultural, 2: Temperature annual range, 3: clay, 4: Road distance, 5: Artificial, 6: Soil water content, 7: NDVI, 8: Pasture, 9: pH, 10: Mean temperature of wettest quarter, 11: *Quercus ilex*, 12: *Quercus suber*, 13: sand.

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CAPÍTULO 6

Fotos: José Ángel Sánchez Agudo.

MODELO ESPACIAL DEL DECLIVE DEL ROBLE (SECA) PARA APOYAR LA PLANIFICACIÓN DE LA CONSERVACIÓN EN EL CENTRO-OCCIDENTE DE LA PENÍNSULA IBÉRICA

AUTORES
Ricardo Enrique Hernández-Lambraño,
David Rodríguez de la Cruz,
José Ángel Sánchez-Agudo

RESUMEN

En la península ibérica, el declive de especies del género Quercus (en adelante, OD) se está convirtiendo en una seria y frecuente enfermedad en los bosques mediterráneos. Los procesos de declive parecen involucrar múltiples factores bióticos y abióticos, los cuales se combinan para reducir el vigor de estas especies, a menudo causando su muerte. Sin embargo, las causas exactas de su extensión son poco conocidas y, por lo tanto, dada la relevancia, ecológica, económica y social de las quercíneas en los países Mediterráneos es crucial el desarrollo de herramientas que nos permitan anticipar su ocurrencia y por lo tanto reducir su expansión. En este sentido, el presente estudio tiene como objetivos (i) revelar el rol relativo de factores ambientales explicando la distribución de uno de los fenómenos más importante que amenaza la biodiversidad de las especies ibéricas del género Quercus, y (ii) producir un modelo espacialmente explícito de riesgo de OD, para apoyar a los gestores de la conservación que lidian con este fenómeno. Para hacer esto, usamos una base de datos de focos de OD registrada durante el periodo 2015-2017 en el sureste de Castilla y León" (esta región está comenzando a sufrir los daños de esta enfermedad). En total, 68 localidades fueron usadas para evaluar la relación con factores ambientales (topografía, estrés abiótico e influencia humana) usando Modelos de Máxima Entropía (en adelante, MaxEnt) y técnicas de partición de la varianza. OD distribución parece ser influenciada principalmente por los usos del suelo (principalmente dehesas), seguida de áreas secas con pendientes suaves orientadas al sur o suroeste. El modelo resultante ha sido usado para producir un detallado mapa de riesgo de OD en la parte centro occidente de España. Nuestro enfoque de modelamiento puede contribuir a informar planificación de la conservación y a establecer adecuadas políticas de manejo para las dehesas ibéricas, al ayudar a identificar regiones donde el riesgo de OD es alto.

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Spatial oak decline models to inform conservation planning in the Central-Western Iberian Peninsula

Ricardo Enrique Hernández-Lambraño*, David Rodríguez de la Cruz, José Ángel Sánchez-Agudo

Departamento de Botánica y Fisiología Vegetal, Facultad de Farmacia, Universidad de Salamanca, Avenida Licenciado Méndez Nieto s/n, 37007 Salamanca, Spain
Instituto Hispano-Luso de Investigaciones Agraria (CIALE), Universidad de Salamanca, Parque Científico, C/ Del Duero, 12, 37185 Villamayor, Salamanca, Spain

A R T I C L E I N F O

Keywords:
Oak decline
Dehesa
Species distribution models
Maxent
Variation partitioning
NDII
NDVI

A B S T R A C T

In the Iberian Peninsula, Oak Decline (hereafter, **OD**) is becoming a serious and frequently occurring disease in Mediterranean oaks. Decline processes seem to involve multiple biotic and abiotic factors, which combine to reduce the vigour of oak trees often causing death. However, the exact causes of its extension are still unknown and therefore, given the ecological, economic and social relevance of these trees in Mediterranean countries it is crucial to develop tools that allow us to anticipate its occurrence and to reduce its expansion. In this sense, the present work aims to (i) unravel the relative role of environmental factors on the distribution of one of the most important phenomena that threat the biodiversity of the Iberian oaks, and (ii) to produce a spatially explicit model of **OD** risk, to assist conservation managers dealing with this phenomenon. To this, we have used a dataset of **OD** foci gathered during the period 2015–2017 by the program “Methodology for the inventory and monitoring of oak masses affected by the decline of oak in the southwest of Castilla y Leon” (this region is beginning to suffer the damages of this disease). In total, 68 locations were used to assess relationships with environmental factors (topographic conditions, abiotic stress conditions and human influence) using maximum entropy models (hereafter, MaxEnt) and variance-partitioning. **OD** distribution seems to be principally influenced by land-use (mainly *dehesas*), followed by dryer areas and areas with low slope gradients facing south or southeast. The resulting model has been used to produce a detailed **OD** risk map in central-western Spain. Our modelling approach may contribute to inform conservation planning and to establish the adequate management policy for Iberian oak *dehesas*, by helping to identify regions where the risk of **OD** is high.

1. Introduction

Since the beginning of the twentieth century, **OD** has been a serious and frequently occurring disease in oaks world-wide (Brasier, 1992; Thomas et al., 2002; Haavik et al., 2015; Rodríguez-Calcerrada et al., 2017a, 2017b). Being a phenomenon of local and/or regional importance in the past, **OD** in its current phase has been devastating the oaks (major die-offs of trees at the genus or species level) since the beginning of the 1980s in the southwest of the Iberian Peninsula (Brasier et al., 1993; Sánchez et al., 2002; Moreira and Martins, 2005; Corcobado et al., 2013). **OD** symptoms are very unspecific and consist of wilting and leaf chlorosis, loss of foliage, branch lesions, epicormic shoots, tarry exudations, root rot and the sudden death of the trees (Brasier, 1992; Gallego et al., 1999; Jung et al., 2000; Thomas, 2008). In oak trees in the Mediterranean basin, **OD** is considered of paramount importance because this phenomenon involves oak species of the *Quercus* genus (e.g., *Q. ilex*, *Q. faginea*, *Q. suber*, *Q. pyrenaica*) which dominate the traditional agrosilvopastoral systems called “*dehesa*” in Spain and “*montado*” in Portugal (de Sampaio e Paiva Camilo-Alves et al., 2013). Oak trees are a major element in these systems and maintain ecosystem functions and services such as soil protection, enhancing diversity, provision of resources (e.g., forage, acorn, wood, cork, charcoal) and cultural services (Gea-Izquierdo et al., 2006; Olea and San Miguel-Ayanz, 2006; Kim et al., 2017). In this sense, their high socioeconomic and environmental values in the regions of the Mediterranean basin highlights the need to understand the main drives of their decline. The causes underlying this phenomenon are complex and uncertain, but it is believed that they are frequently associated with one or more global change drivers.

OD occurrence in Mediterranean ecosystems is considered a complex multifactorial phenomenon involving the combination of primary or predisposing factors (warmer climates, water stress, air pollutants, soil features, land use disturbance, leaf defoliators and bark beetles) and secondary or opportunistic factors (invasive pests and pathogens)

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* Corresponding author at: Ricardo Enrique Hernández-Lambraño, C/ General Margallo, 24, 1B izq, 28020 Madrid, Spain.
E-mail address: ricardohl123@usal.es (R.E. Hernández-Lambraño).

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(Thomas, 2008; Rodríguez-Calcerrada et al., 2017a, 2017b), operating at tree, stand, and landscape scales. In most cases, none of these factors act alone. The simultaneous interaction of at least two stress agents—where one of them comprises an extreme climatic event (e.g., drought)— has triggered important outbreaks of decline (Rodríguez-Calcerrada et al., 2017a, 2017b). Although Mediterranean oak species exhibit morphological and physiological adaptations that enable them to increase water deficit tolerance, changes in rainfall patterns- which may include a severe or prolonged drought- can initiate decline events by compromising the physiological capacity of mature oaks (Allen et al., 2010; Haavik et al., 2015; Rodríguez-Calcerrada et al., 2017a, 2017b). Also, physical landscape attributes such as topography (e.g., slope aspect, curvature) and land-use disturbances (silvicultural mismanagement) can induce highly variable moisture conditions with different impacts on the trees, thereby leading to the sudden death of affected trees or gradual decline until their death (Thomas, 2008). Secondary biotic agents, often termed contributing factors, include root pathogens of the genus *Phytophthora* (Haavik et al., 2015). Although several *Phytophthora* species have been isolated in soils from declining oak trees (Jung et al., 2015), *P. cinnamomi* is by far the most aggressive and has been recognized as a main biotic factor of oak mortality in the Iberian oaks (Hernández-Lambraño et al., 2018). This pathogen is not commonly capable of killing healthy oaks, but it can kill oaks weakened by some other primary factor such as drought (Thomas et al., 2002; Haavik et al., 2015). It is challenging to identify a cause that overcomes others, either because it may be related to other factors or because the proximate cause of death may mask the primary one (de Sampaio e Paiva Camilo-Alves et al., 2013). Despite the perception of an increasingly visible damage on Iberian oaks, the main causes and functional basis influencing the spatial distribution patterns of **OD** at landscape level remain unclear. To our knowledge few studies have investigated spatial patterns of **OD** in Iberian oaks (Costa et al., 2010; Serrano et al., 2016; Duque-Lazo et al 2016; Duque-Lazo et al 2018). This lack of evidence is primarily due to the inherent difficulties of surveying **OD** foci, monitoring and estimating the primary factors causing the decline in great extensions of oaks. Therefore, the description of the spatial patterns of **OD** could provide a better understanding of the possible primary causes that trigger this phenomenon as well as to evaluate its ecological and socio-economic impacts in the Mediterranean basin ecosystems, where reducing the rate of biodiversity loss has become a key target.

Successful strategies to prevent this phenomenon include adequate forestry practices such as forest harvesting to improve the vigour of adult oak trees in open field and sanitation measures to minimize pathogen spread (de Sampaio e Paiva Camilo-Alves et al., 2013; Rodríguez-Calcerrada et al., 2017a, 2017b). However, the resources available for the adequate implementation of actions against **OD** are frequently limited. In this sense, there is an urgent need for the efficient allocation of such scarce resources to maximize the efficiency of these actions (Keane et al., 2008). The identification of the primary or predisposing factors behind the **OD**, as well as identifying areas with most risk, would greatly facilitate the basis for where, when, how often, and what management alternatives should be used. In fact, the use of risk maps and model visualization has been widely used as a powerful tool in effective management of natural resources (Margules and Pressey, 2000; Yemshanov et al., 2013).

Nowadays, the use of systematic processes to optimize conservation plans based on scientific criteria has increased (Franklin, 2010; Yemshanov et al., 2013). Highlighted among these processes is the development of predictive models, specifically the Species Distribution Models (SDMs); an innovative GIS-based method used to produce predictive maps of where species are likely or not to occur across a landscape (Soberón and Nakamura, 2009). This approach is currently expanding its scope and is being applied not only to predict species occurrence probabilities, but as a set of processes that are closely tied to conservation biology (Mateo-Tomás et al., 2012; Santos et al., 2013; Silva et al., 2014; Yañez-Arenas et al., 2014; Garrote et al., 2018). In this way, SDMs offer a possible solution for the identification of the predisposing factors behind the **OD** and even the identification of areas of highest risk, by combining **OD** foci data with environmental factors considered to influence its occurrence.

This study aims to make a relevant contribution in conservation biology by employing a new approach using SDMs. To do this, we took advantage of an intensive monitoring programme about **OD** in central-western Spain conducted from 2015 until 2017, (i) to try to elucidate the influence of environmental factors on spatial patterns of OD in Iberian oaks and (ii) to produce a spatially explicit model of OD risk, to assist conservation managers dealing with this phenomenon. Given the changes in land-use patterns and frequent changes in highly variable rainfall patterns in the Mediterranean basin, we hypothesize land-use and drought to be important predictors for explaining the OD distribution patterns in central-western Spain.

2. Material and methods

2.1. Study area

The study was conducted in central-western Spain within the Mediterranean ecological region in the province of Salamanca, between 40°50′ N and 6°00′ O, with a total area of 12 349 km^2 (Fig. 1). The study area consists of wide flat or gently undulating plains in the north-east part with an average elevation of 800 m a.s.l. The main geographical features are the southern mountain ranges (Sierras de Gata, Béjar and Francia), which reach almost 2000 m a.s.l. and the deep river valleys of the north-west part (Arribes) with heights of 150 m a.s.l. The climate is mostly Mediterranean continental with an average annual temperature of 12 °C, mean annual rainfall of 400 mm, and an acute summer drought during two-three months, between June and September, when there is no risk of frost (Peris et al., 1992). The most widespread soils, classified by the WRB-FAO, are Dystric or Eutric Cambisols and Regosols on slates and granites, and Haplic Luvisols and Eutric Cambisols on sediments (Martín-Sanz et al., 2015). The zone is representative of oak trees in Spain, populated mainly by holm-oaks (*Q. ilex*) and other *Quercus* species (*Q. faginea*, *Q. suber*, *Q. pyrenaica*), with a total area of 4844 km^2 and managed as a traditional agro-sylvo-pastoral system mainly for livestock (*dehesa*), with grazing areas intercropped with pasture areas of grasslands and legumes (Regato-Pajares et al., 2005). Other semi-natural forests (pinewoods and chestnut groves) are present in the south of the province.

2.2. Data acquisition

GPS locations of **OD** foci ($n = 68$, see Fig. 1) within the study area were obtained for the period of 2015–2017 by the program “Methodology for the inventory and monitoring of oak masses affected by oak decline in the province of Salamanca” from the Hispano-Luso Institute of Agrarian Research of the Salamanca University (**CIALE** Spanish acronym). This program has surveyed trees within the *dehesa* and oak forest areas across the study area. Living oak trees (diameter at breast height > 7 cm) were inspected visually for the following decline symptoms: death, chlorosis, cankers or defoliation without an apparent causal agent. Other semi-natural forests (pinewoods and chestnut groves) are only present in the south of the province and were not the object of this study.

To characterize the most important predisposition factors to **OD** in the study area, we used 13 variables as predictors, related to (1) topographic conditions, (2) abiotic stress conditions and (3) land-use (Table 1). These variables were chosen based on our knowledge of the **OD** phenomenon (Rodríguez-Calcerrada et al., 2017a, 2017b), and were assumed to be at least correlated with more proximal causal factors.

Variations in topographic features can cause differences in edaphic

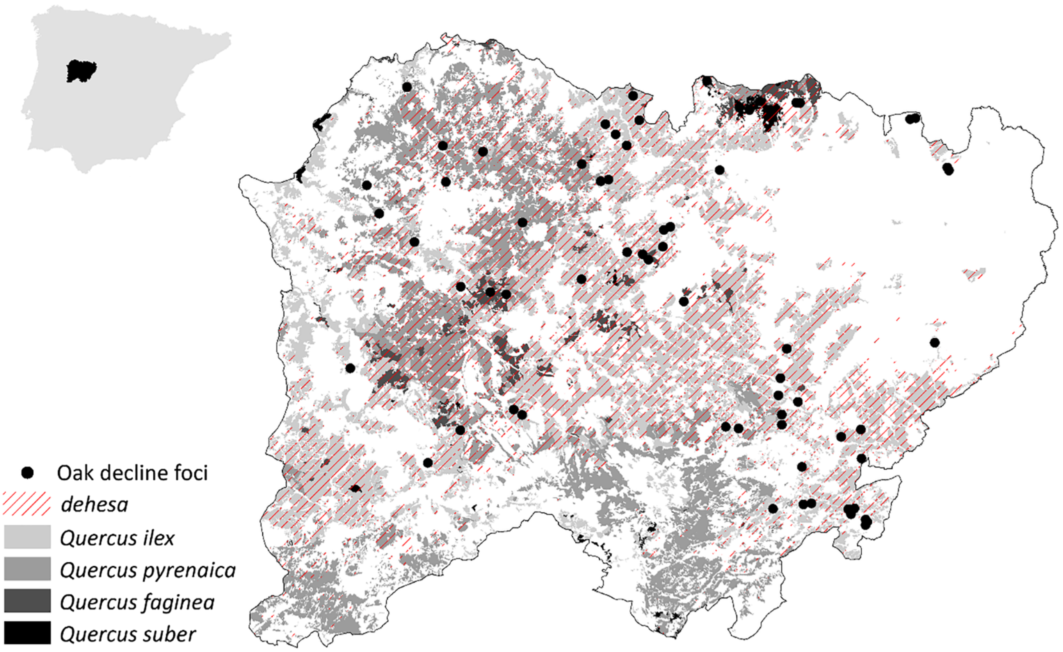

Fig. 1. Location of the study area and the occurrence of Oak Decline foci against the background of the *Quercus* spp. distribution and the *dehesa.*

factors, such as moisture and availability of nutrients with different impacts on the trees, thereby leading to the sudden death of affected trees or gradual decline until their death (Esselink and van Gils 1994; Thomas, 2008; de Sampaio e Paiva Camilo-Alves et al., 2013). Herein, the topographic features of the study area were derived from a Digital Elevation Model (**DEM**) by National Center for Geographic Information of Spain at 5 m spatial resolution (**CNIG** Spanish acronym; http://centrodedescargas.cnig.es). We calculated slope and aspect using the Spatial Analyst Tool in ArcGIS v.10.3.1 (ESRI, 2015), to account for gravitational processes and effects of potential solar radiation. Terrain surface curvature (**curvature**), was calculated using Spatial Analyst Tool in ArcGIS to account for soil erosion patterns as well as the distribution of water on study area (Zevenbergen and Thorne, 1987). The curvature can be positive (indicating peaks), negative (indicating valleys) or zero (indicating flat surface). The topographic position index (**TPI**), was calculated using the Slope Position tool in Geomorphometry and Gradient Metrics toolbox v.2 (Evans et al., 2014) for ArcGIS. **TPI** compares the elevation of each cell in a **DEM** to the mean elevation of a specified neighbourhood (3 × 3 pixels) around that cell (De Reu et al., 2013). Positive **TPI** values indicate that the central point is located higher than its average surroundings, while negative values indicate a position lower than the average. **TPI** can be used as a proxy of available soil moisture in the study area (Das et al., 2015). Finally, we estimated a Heat load index (**HLI**) using the HLI tool in Geomorphometry and Gradient Metrics toolbox for ArcGIS. **HLI** shows that a south facing slope should have warmer temperatures than a north facing slope, even though the amount of solar radiation they receive is equivalent (McCune and Keon, 2002). Values range from 0 to 1, where higher

Table 1
Main variables considered for modelling the oak decline occurrence in the study area. Those variables finally used to run the models after reducing multicollinearity (i.e. high correlation between variables, $r_s > |0.7|$) are shown in bold.

Name	Description	Range
(1) Topographic features		
Slope	Slope of the terrain (degrees)	0–41.4
Aspect	The terrain slope direction. Eight aspect classes were considered: east (E), southeast (SE), south (S), southwest (SW), west (W), northwest (NW), north (N) and northeast (NE)	NA
HLI	Heat load index	0.67–0.88
Curvature	Terrain surface curvature	−1.64 to 3.01
TPI	Topographic position index (m)	−4.05 to 8.31
LST_*w*	Land surface temperature in winter (°C)	4.82–15.5
LST_*s*	Land surface temperature in summer (°C)	19.2–38.2
LST_*sd*	Variability of the land surface temperature between 2015 and 2017 (°C)	1.64–6.43
(2) Abiotic stress conditions		
NDII_*w*	Soil water availability in winter	0–0.51
NDII_*s*	Soil water availability in summer	0–0.42
NDII_*sd*	Variability of the soil water availability between 2015 and 2017	0–0.26
NDVI_*w*	Winter average of the Normalized Difference Vegetation Index	0–061
NDVI_*s*	Summer average of the Normalized Difference Vegetation Index	0–0.57
NDVI_*sd*	Variability of the Normalized Difference Vegetation Index between 2015 and 2017	0–0.19
(3) Human influence		
Land-use	Land-use composition classes. Five land-use classes were considered: (1) artificial surfaces, (2) agricultural areas, (3) agro-forestry areas, (4) *dehesas* and (5) forestry areas	NA
Pond	Minimum distance to ponds (km)	0.08–23.7

NA = categoric variable.

values indicate slopes with warmer temperatures.

In European Mediterranean regions, successive droughts have been a recent climatic feature of most areas with **OD** presence, and thus have frequently been proposed as the primary factor in these declines. Herein, we estimated Normalized Difference Infrared Index (**NDII**) as a proxy for variability of the water availability in the study area (Sriwongsitanon et al., 2016), using Landsat 8 OLI/TIRS satellite data (for more details see https://lta.cr.usgs.gov/L8). **NDII** has be effectively used to detect canopy stress (Emmerik et al., 2015), according to the property of shortwave infrared reflectance, which is negatively related to leaf water content due to the large absorption by the leaf (Sriwongsitanon et al., 2016). Landsat 8 OLI/TIRS satellite images were acquired from the United States Geological Service's Earth Explorer (USGS; https://earthexplorer.usgs.gov/) for the summer and winter periods from 2015 to 2017. The **NDII** was calculated for each of the satellite images using near infrared reflectance (NIR; band 5) and shortwave infrared reflectance (SWIR; band 6) of the Landsat images as shown in the following equation: $(\rho NIR - \rho SWIR)/(\rho NIR + \rho SWIR)$. The **NDII** was averaged for each of the periods (winter and summer). Also, as a measure of seasonal variation of water availability in the study area, we calculated standard deviation (**SD**) of **NDII** for the period between 2015 and 2017. In addition to **NDII**, we calculated the Normalized Difference Vegetation Index (**NDVI**) (Tucker, 1979), as a proxy of the shifts in plants' performance in response to environmental changes. The **NDVI** has been effectively used to monitor and investigate the health of Mediterranean forests (Jucker Riva et al., 2017; Recanatesi et al., 2018). The **NDVI** was calculated using near infrared reflectance (NIR; band 5) and red reflectance (RED; band 4) as shown in the following equation: $(\rho NIR - \rho RED)/(\rho NIR + \rho RED)$. The **NDVI** was averaged for each of the periods (winter and summer) and the **SD** for the period between 2015 and 2017 was calculated. Finally, we calculated land surface temperature (**LST**) as a proxy of the temporal and spatial variations of water balance in the study area. The **LST** is widely used in a variety of fields including evapotranspiration, climate change, hydrological cycle and vegetation monitoring, among others (Ottlé et al., 2004). The **LST** in degrees Celsius was calculated from thermal band 10 (Cristóbal et al., 2018), using the Semi-Automatic Classification Plugin tool (**SCP**) (Congedo, 2016), for QGIS open-source software version 2.18 (http://www.qgis.org). The **LST** was averaged for each of the periods (winter and summer) and the **SD** for the period between 2015 and 2017 was calculated. Prior to analyses, atmospheric correction of the Landsat 8 OLI/TIRS images was carried out using the Dark Object Subtraction (**DOS**) approach (Nazeer et al., 2014), implemented in **SCP** for QGIS.

Change in land-use patterns in the Mediterranean basin, such as overgrazing and the neglect of traditionally maintained oak pasture systems have been a recent land feature of most areas with **OD** presence. In the 1960s, due to the emergence of swine fever, there was a marked reduction in the use of pasture for this type of livestock activity. At the same time, as a consequence of the common agricultural policies in the European Union, an intensification of the agricultural use in the pasture was favoured. All this led to a depreciation of the value of the acorn and consequently, less interest in maintaining the forest cover that traditionally forms part of this habitat (Esselink and van Gils 1994). However, from the 1990s to present day, the revaluation of meat products from the pasture has led to a significant livestock overload on many farms. This radical change in use has frequently been proposed as an important factor in these declines (Brasier, 1996; Rodríguez-Calcerrada et al., 2017a, 2017b). To characterize human influence in the study area, a land-use variable was constructed with a 30 m spatial resolution, based on a 1:50 000 land-use map from Third National Forest Inventory (**IFN3** Spanish acronym) of Spain (MAGRAMA, 2007). Five land-use classes were considered in this study: artificial surfaces (i.e. urban areas, roads and construction), agricultural areas (i.e. permanent crops and annual crops), agro-forestry areas (i.e. land principally occupied by tree cultures, mainly olive groves and fruit trees), *dehesas* (i.e. agro-sylvo-pastoral systems for livestock, populated mainly by *Q. ilex* and other *Quercus* species such as *Q. suber*, *Q. faginea* and *Q. pyrenaica*) and forestry areas (i.e., coniferous and broadleaf forests). Recently, Manzano et al. (2016) related decline and mortality of cork and holm oaks in central-western Spain to the presence of hydraulic infrastructures (e.g., ponds) resulting from agricultural activities. These water bodies- built taking advantage of the terrain relief- is usually for the use of water by livestock and irrigation of forage crops. Therefore, this could induce important modifications in the water table in those area with **OD** presence. Herein, we calculated proximity to ponds as a proxy of the modifications in the water table in the study area. To do this, each pond was accurately checked for location using high resolution orthophotos (0.5 m) from the photogrammetric campaign of the National Plan for Aerial Orthophotography in 2014 (**PNOA** Spanish acronym: http://centrodedescargas.cnig.es). Then, we calculated the distance (in meters) to ponds using the Euclidean distance tool by ArcGIS.

All environmental data were standardized to Universal Transverse Mercator coordinate (Datum ETRS-89) at a spatial resolution of 30 × 30 m. Finally, to reduce multicollinearity between variables, we calculated the Spearman's correlation coefficients (r_s). Variables with values of $r_s > |0.7|$ were excluded (Hernández-Lambraño et al., 2017).

2.3. Model development

OD in the study area was modelled using MaxEnt version 3.4.1, a machine-learning process that uses presence-only data (Phillips et al., 2006). MaxEnt gives insight about what predictors are important and estimates the relative suitability of one place vs. another, as well as the probability of occurrence (Elith et al., 2011). This approach has been demonstrated to perform well in a diverse set of modelling scenarios and is widely used in a great number of studies in ecology, biogeography and conservation (Elith and Leathwick, 2009; Franklin, 2010; Duque-Lazo et al., 2016; Duque-Lazo et al., 2018).

To investigate the most important factors associated with **OD**, we carried out MaxEnt models including a different subset of non-collinear variables: only topographic conditions, only abiotic stress conditions and only human influence. For each MaxEnt model, we calculated the relative contribution values ($\boldsymbol{R_c}$) to rank the variables in order of importance in relation to **OD**. The $\boldsymbol{R_c}$ value is calculated based on how much the variable contributed to the model depending on the path selected by Maxent for a particular model run (Phillips et al., 2006). We selected the best variables (largest $\boldsymbol{R_c}$) for each block of non-collinear predictors and performed a final model; combining the best variables of each block (full model). We performed 10 replications using a bootstrap procedure in which we divided our dataset using 80% of data for model calibration and retaining 20% of the data to evaluate models. For the test values, we reported the mean and standard deviation of the area under the curve of the receiver operating characteristic (**AUC**) for the 10 runs. **AUC** measures the ability of a model to discriminate between sites with **OD** occurrence, versus those where it is absent. The AUC ranges from 0 to 1 (0.5 = random, 1 = perfect). Runs used herein were conducted using the MaxEnt default parameters (Phillips et al., 2006). Background points were randomly chosen within the area enclosed by a minimum convex polygon comprising all **OD** foci (Elith et al., 2011). Response curves were calculated to interrogate the relationship between the response (i.e., **OD** risk) and each explanatory variable. These show how a given explanatory variable influences the response variable while keeping all other predictors at their average (Phillips et al., 2006).

2.4. Deviance partitioning

Assuming that the deviance is a good measure of the variability explained by a model (Borcard et al., 1992), we performed a hierarchical partitioning procedure to determine the amount of independent and shared information contained in the topographic, abiotic stress and human influence variables. We fitted generalized linear models (**GLMs**) with presence and background data as the response variables and using a different subset of the best predictors selected in the above section: only the topographic variables (topography), only the abiotic stress variables (abiotic stress), only human influence (land-use). The deviance explained by each model was then used to identify the single and shared effects on the occurrence of **OD** by simple equation systems. We used R v.3.4.2 (R Core Team, 2017), in all analyses and the *varpart* function of the R package "vegan" v.2.4-6 (Oksanen et al., 2018), for variance partitioning procedures. For the **GLM**, we selected 10 000 random background points from throughout the sampling region, as suggested by Barbet-Massin et al., (2012)

2.5. Oak decline risk map and identification of priority areas for management interventions

We used all available occurrences of **OD** to calibrate the model combining the best variables of each block (i.e., topographic, abiotic stress and human influence) and we projected its final potential distribution to all the 30 × 30 m grids in the study area. We classified probability categories for the **OD** risk map using the threshold that represents the value that maximizes the sum of sensitivity and specificity (Liu et al., 2005). This was selected to favour oak conservation versus its threatened status due to the **OD** occurrence. The **OD** risk map and the associated distribution maps of oaks in the study area were used to assess the priority areas for management interventions (Duque-Lazo et al., 2018). Oak maps were obtained from **IFN3**. We proposed the following areas: prevention, for areas with identified **OD** occurrence; protection, for areas where **OD** is currently absent, but its occurrence is predicted with high probability; and conservation, for areas where **OD** is currently absent, and its occurrence is predicted with low probability. The recommended management strategies for the proposed areas are summarized in the Table 3.

3. Results

3.1. Oak decline risk models

The MaxEnt models including a different subset of non-collinear variables (i.e., topography, abiotic stress and human influence) exhibited a good discrimination capacity, with average **AUC** values ranging between 0.64 and 0.82. Despite the initial good performance of the models, the combination of the best variables in a final model (i.e., full model) resulted in higher mean **AUC** values (0.93 ± 0.03, $F_{3,39} = 108.2$, $P < 0.0001$; see Fig. 2).

3.2. Factors influencing the distribution of oak decline in central-western Spain

The variables that contributed most highly to the **OD** models are presented in Table 2.

The model developed with best variables showed that the likelihood of **OD** risk in the study area was higher in *dehesas* than in other land-uses (see Fig. 3). Moreover, areas with ponds located at less than 2.5 km from **OD** foci were associated with an increase **OD** risk. The probability of **OD** occurrence was negatively associated with abiotic stress conditions (i.e., **NDII** and **NDVI**). The lower these indices the higher the probability of **OD** occurrence. Additionally, areas with lower variation values (**SD**) presented by these indices were associated with the high probability of **OD** occurrence. These low values suggest repeated and protracted drought periods in the affected areas. Concerning topographic features, higher **OD** risk was predicted for flat slopes (< 5%) and for south and south-easterly facing slopes. Moreover, the probability of **OD** risk was associated positively with land surface temperature (i.e., **LST**). The higher land surface temperature the higher the risk of **OD** occurrence.

The results of the variation partitioning are shown in Fig. 4. Human influences explain most of the variation, followed by influence of abiotic stress variables, whereas topography accounts for a smaller proportion of the variation. The magnitude of the shared effect represents the proportion of the model variation that is attributable to the combined effect of the three sets of variables. In our case, the shared component had a large proportion of the variation, indicating strong

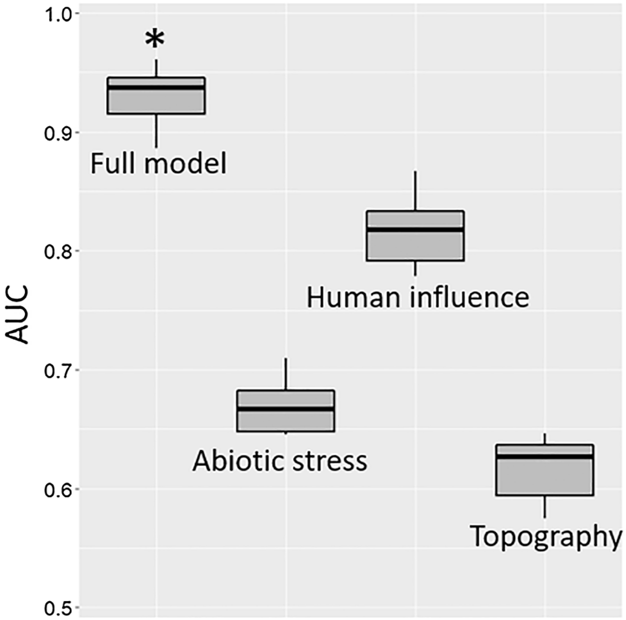

Fig. 2. The boxplots of AUC values obtained by 10-replications (bootstrap procedure) for each of the models using a different subset of non-collinear variables: just the topographic variables (topography), just the abiotic stress variables (abiotic stress), just human influence variables (human influence), and the combination of the best predictors (largest ***Rc***) of each subset of variables (full model). Asterisk (*) on top of box indicates significant difference when compared to full model, Bonferroni's Multiple Comparison Test $P < 0.05$.

Table 2
Mean values of the relative contributions (%) of the predictor variables for the MaxEnt models. Mean values were calculated from the 10-replications of the models. The R_c1 column indicates contribution values of the predictor variables for the models developed with each block of non-collinear predictors (i.e., topography, biotic stress and human influence) and the R_c2 column indicates contribution values of the predictor variables for the final model (full model) developed with best variables (largest R_c1) of each block. See Table 1 for variable descriptions.

Variables	R_c1	R_c2
Human influence		
Land-use	59.2	46.8
Pond	40.8	32.6
Abiotic stress conditions		
NDII_*s*	30.5	4.10
NDVI_*sd*	24.0	3.90
NDVI_*s*	23.7	0.30
NDII_*sd*	15.0	2.00
NDVI_*w*	6.20	–
NDII_*w*	0.60	–
Topographic features		
Aspect	28.6	8.20
LST_*s*	26.9	1.80
Slope	21.1	0.30
LST_*w*	14.8	–
LST_*sd*	8.60	–

Table 3
Summary of recommended forestry practices according to the identification of presence and predicted probability of occurrence of oak decline.

Area	Occurrence		Policy	Forestry practices	Reference
	Identified	Prediction			
Prevention	yes	high	Control, mitigation	Selective thinnings of suppressed stems, girdling selected stems in multi-stems trees, inoculation of endophytes or chemical cocktails, prevention of the spread of xylophage insects and fungal pathogens, good planning of the grazing activities	(Rodríguez-Calcerrada et al., 2011; de Sampaio e Paiva Camilo-Alves et al., 2013; Oberhuber et al., 2017; Rodríguez-Calcerrada et al., 2017a, 2017b)
Protection	No	high	Monitoring	Selective cut of smaller trees from the midstory and thinning of forest by removing some of the mature trees	(Clatterbuck and Kauffman, 2006; Wang et al., 2013)
Conservation	No	low	Monitoring	Increase sexual regeneration through sowing/planting, preservation of marginal oak populations	(Clatterbuck and Kauffman, 2006; Rodríguez-Calcerrada et al., 2017a, 2017b)

dependent contributions of the three sets of predictors, explaining distribution patterns of **OD** in the study area.

3.3. Risk map of the potential distribution of oak decline in central-western Spain: analysis of current protection and conservation

Considering the value that maximizes the sum of sensitivity and specificity as a threshold (i.e., 0.35), the area predicted by the full model with high risk of OD (i.e., risk probability above the considered threshold) was 80% of the total area populated by oak trees in the study area, while the remaining 20% was predicted with low risk (Fig. 5). In agreement with our observations, the map showed an **OD** risk scattered throughout oak areas with higher probabilities in the northern and central part of the study area, while the northwest and southern part showed lower probabilities of occurrence. These areas coincide broadly with holm-oak pastures, although **OD** foci were also found in *Q. faginea dehesas*.

According to the identification of **OD** foci and its predicted risk probabilities in the study area, several sites were proposed as potential areas for management interventions (Fig. 6). All sites where **OD** was present were dominated by oaks (*Q. ilex*, *Q. faginea* or *Q. pyrenaica*). With the aim of mitigating the extent of decline at the sites with **OD** foci, the following strategies have been recommended: harvesting practices to improve the vigour of trees, application of biological treatments to stimulate the defence mechanisms of the fine roots of the oak stands suffering decline, sanitation measures to minimize pathogen spread and control over the population densities of the xylophage insects (Cerambyx complex) (see Table 3) (de Sampaio e Paiva Camilo-Alves et al., 2013; Rodríguez-Calcerrada et al., 2017a, 2017b).

4. Discussion

4.1. The important role of predisposing factors influencing the spatial distribution patterns of oak decline in central-western Spain

Our study reveals that it is possible to identify the most influential variables explaining the spatial distribution patterns of **OD** using maximum entropy modelling and variance-partition techniques. This approach was found to be capable of capturing the relationship between risk probability of **OD** and predisposing factors on oaks in central-western Spain. The variables with the largest $\boldsymbol{R_c}$ revealed that **OD** distribution seems highly dependent on land-use, followed by abiotic stress conditions and lastly topographic features.

Land-use was an important predictor, explaining the **OD** distribution patterns. In fact, in the study area, most of the **OD** foci were found in *dehesas* land-use with abundant understorey shrubs (encroached). This is in agreement with observations made in regions with similar topographic features, where the shrub encroachment dominated by shrub gum rockrose (*Cistus ladanifer*) as a consequence of land-use changes was considered to be a decisive factor in tree decline (Cubera and Moreno, 2007; Costa et al., 2010). This negative effect could be related to a significant increase in competition for soil water (Moreno and Pulido, 2009; Caldeira et al., 2015) and frequent changes in the soil nutrient content (Esselink and van Gils, 1994). The high density of shrubs in invaded stands with their dense shallow rooting system can promote the drying out of the surface soil layers and thus a decreased deep soil moisture recharge, contributing to the lower recovery and resilience of the oak trees in the invaded stands (Rolo and Moreno, 2011). However, in areas with no water limitations or with other shrub species (*Retama sphaerocarpa*), competition may be absent (Rolo and Moreno, 2011). Therefore, the effect of the understory in the ecophysiological status of trees in the Iberian oak *dehesas* could depend on the shrub species that are involved and on water availability, which, in turn, may depend on other characteristics like topography (Rolo and Moreno, 2011; de Sampaio e Paiva Camilo-Alves et al., 2013). On the other hand, the high density of evergreen shrubs in the invaded stands

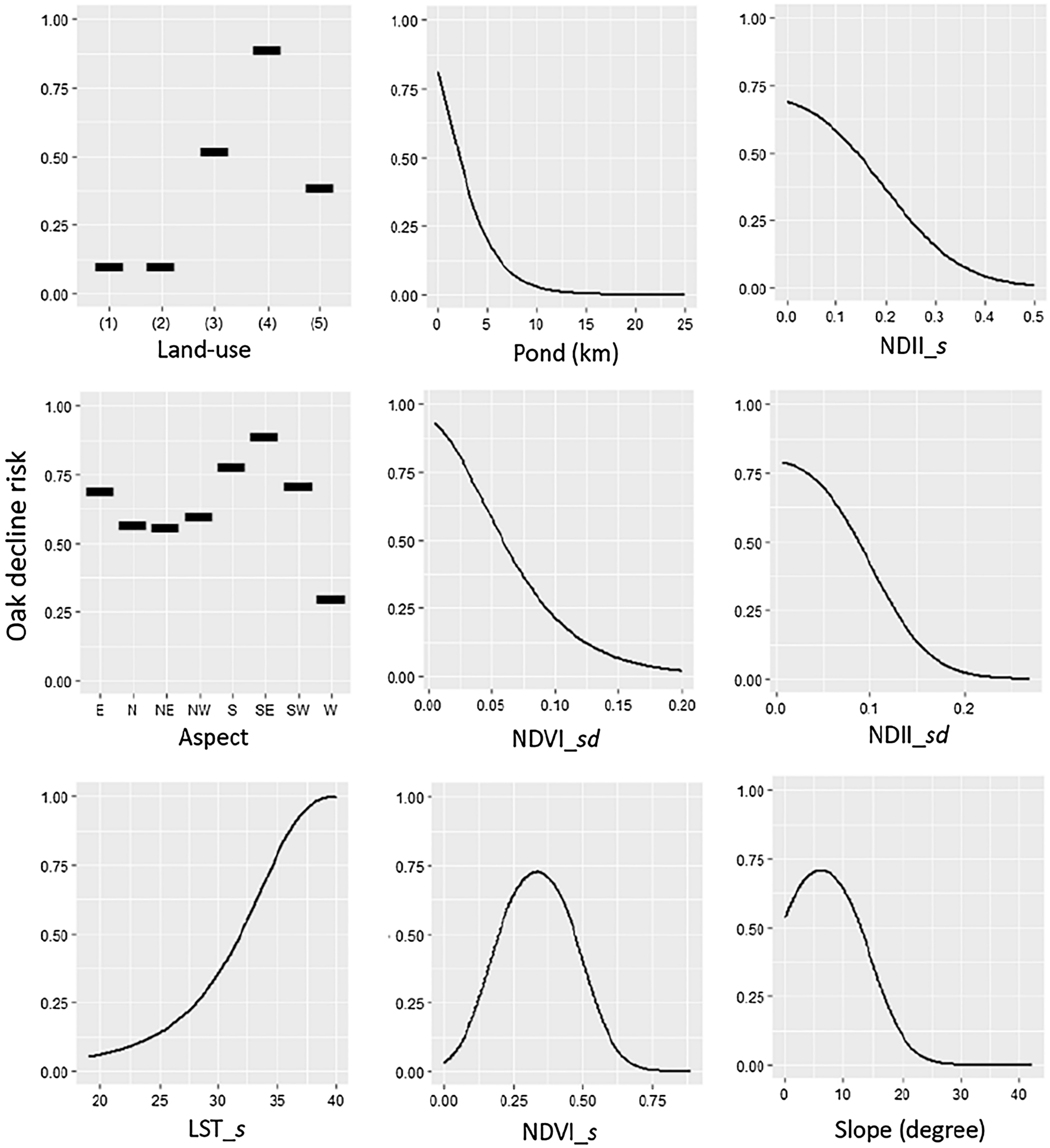

Fig. 3. Response curves of the variables most related to oak decline risk. Response curves were calculated for the full model calibrated with all oak decline foci in the study area. See Table 1 for variable descriptions.

can promote P deficiency in the soil, due to a competitive advantage of shrubs on these soils by their higher efficiency of nutrient use (Esselink and van Gils, 1994). This might therefore contribute to the lower recovery of the affected trees in the invaded stands.

Oak trees experiencing decline in Spain have been influenced by some extent by human activities. Oak trees forming *dehesas*, have been managed to obtain multiple products and benefits. The continued exploitation of these stands has been intensified in response to new socioeconomic circumstances, which lead, in most cases, to an inappropriate use of the forests, causing damages over the system and in particular over the natural regeneration of the tree layer (González-Alonso, 2008). For instance, *dehesas* where livestock are feeding directly on the acorns from the trees, usually lose stability and suffer damages when the carrying capacity is exceeded. The creation of closed areas with fences in order to keep the animals from gaining weight in a particular portion of the *dehesa*, often cause problems such as compression of the soil, contamination of soils by an excessive accumulation of excrements, dust accumulation over the leaves and numerous mechanical damages on trees (e.g., debarking of the base of trunks) (González-Alonso, 2008). These problems can result in a loss of tree vigour and in a decrease of natural regeneration due to lack of viable seeds on the site.

The existence of water bodies (i.e., ponds) near the areas affected by decline were associated with an increase in OD risk probabilities. This

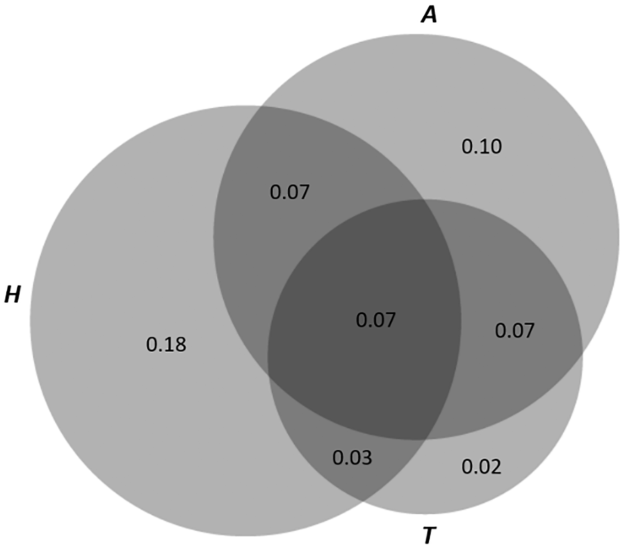

Fig. 4. Variation partitioning of the occurrence of oak decline in study area. Each circle corresponds to a group of variables. (*H*) human influence, (*A*) abiotic stress and (*T*) topographic conditions. The numbers within the circles are the proportion of deviance explained by each set of predictors alone (non-overlapped part of circles) or shared (overlapped part of circles). R^2 unexplained = 0.46.

finding is considered interesting from the point of view of the soil waterlogging in the study area. These water bodies are usually built for the use of water by livestock and irrigation of forage crops. Thus, repeated and/or protracted rain periods could increase the waterlogging around affected trees. In European oak forests, waterlogging can affect the health of trees due to a deficient soil aeration (Gaertig et al., 2002). Moreover, high water content favours root infection by pathogenic fungi (Hernández-Lambraño et al., 2018). In fact, Duque-Lazo et al., (2016) and Duque-Lazo et al., (2018) report distance to water bodies (i.e., rivers) and water retention capacity of the soil as powerful predictors of OD caused by *P. cinnamomi*. Water is known as the natural dispersal medium of *P. cinnamomi*. In this sense, ponds in affected stands by *P. cinnamomi*, are likely to be able to maintain the humidity for longer periods and/or free running water in the soil, this, together with the presence of root of the host, can allow for colonization of new trees (Duque-Lazo et al., 2018).

Unsurprisingly, soil water availability significantly influenced the presence of **OD**, with dryer areas (i.e., low **NDII** index) associated with affected sites. Similarly, dryer areas were associated with low **NDVI** indices. These findings can be used to inform management both in terms of species choice when planting new areas, but also the choice of site preparation and silvicultural systems employed. In European Mediterranean regions, successive droughts have been a recent climatic feature of most areas with **OD** presence, and thus has frequently been proposed as the primary factor in these declines (Allen et al., 2015). Repeated and protracted drought periods in unmanaged stands can affect the health of oak trees via two distinct pathways: (i) carbon starvation, which is a gradual process that occurs when stomata close, restricting transpiration and limiting photosynthesis; and (ii) xylem embolisms, this hydraulic failure can result in a substantial impairment of xylem transport (Bréda et al., 2006; Rodríguez-Calcerrada et al., 2017a, 2017b). In this manner, the trees can be predisposed for the impact of additional stressors; or can suffer severe damages due to an inefficiency in regeneration processes if they are already weakened by the action of other stress factors (Thomas, 2008). Indeed, General Circulation Models forecast an increase in drought frequency, duration, and intensity, which might decrease the distribution areas suitable for oak trees (Acácio et al., 2017) and enhance the performance of oak-related pests (Duque-Lazo et al., 2018). Oak trees will probably undergo substantially stronger water limitations by the end of the 21st century (Ruffault et al., 2014), phenomenon recently observed in the south of France during the four last decades and which raises the question of oak forests' vulnerability in the future (Ruffault et al., 2013). On the other

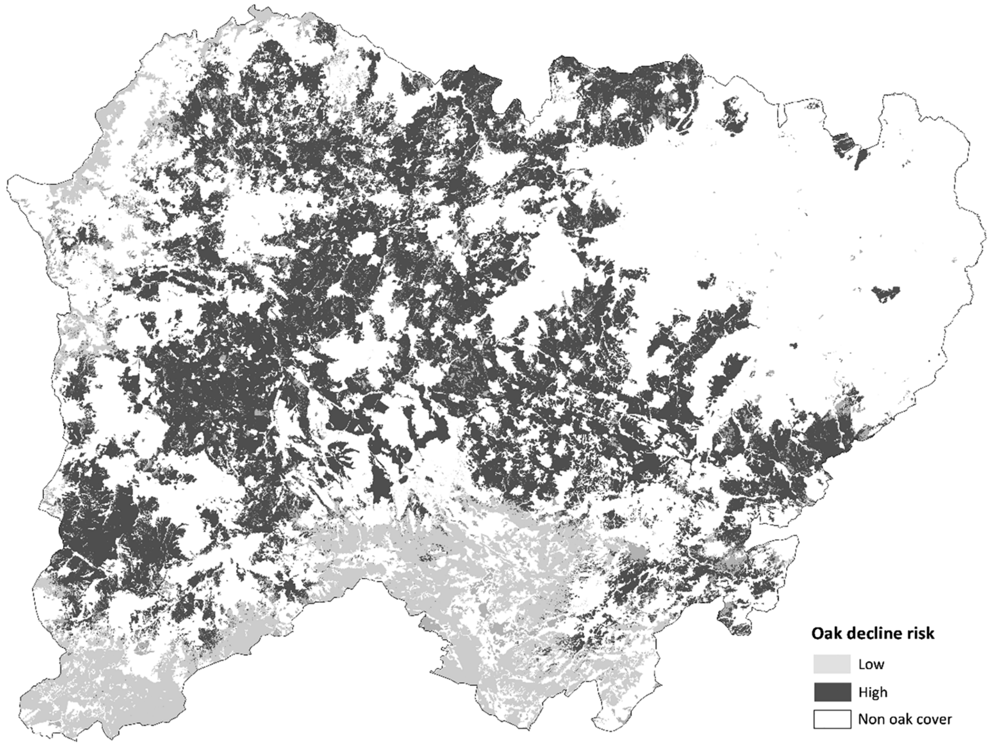

Fig. 5. Current probability of oak decline using MaxEnt modelling. Colour range indicates the probability of OD occurrence in central-western Spain oaks. We classified probability categories for the OD risk map according to occurrence probability as < 0.35 (low) and ≥0.35 (high).

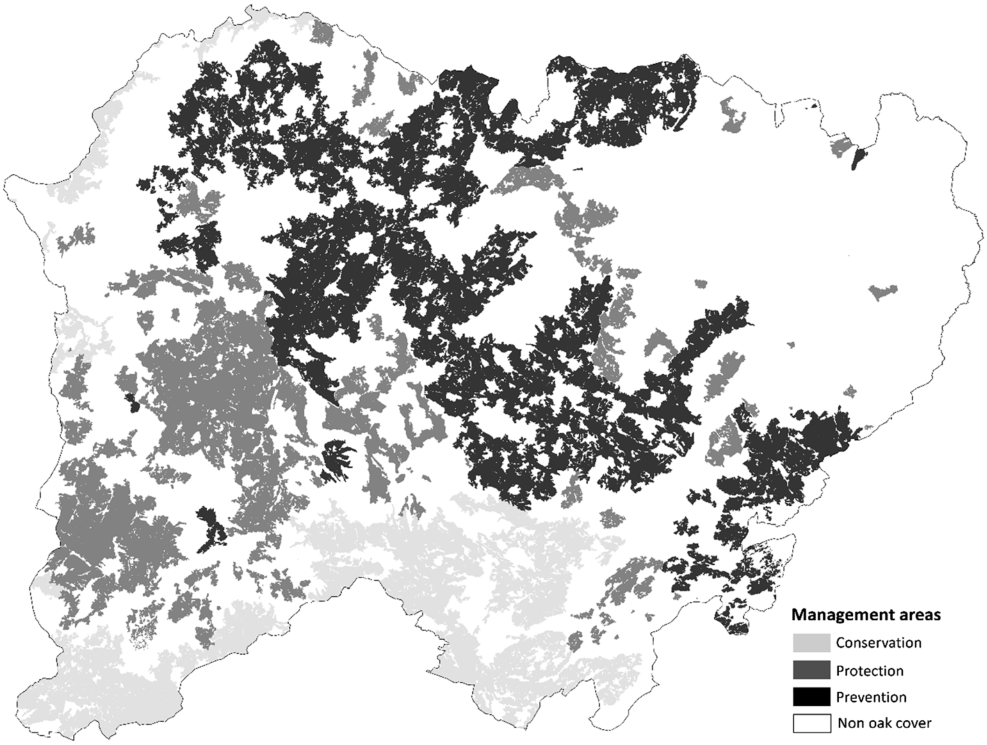

Fig. 6. Proposed areas for management interventions focused to reduce the negative impact of Oak Decline in central-western Spain oaks. Prevention (black), for areas with identified **OD** occurrence; protection (dark grey), for areas where **OD** is currently absent, but its occurrence is predicted with high probability; and conservation (light grey), for areas where **OD** is currently absent, and its occurrence is predicted with low probability.

hand, future predictions of OD caused by *P. cinnamomi* in southern Spain suggest an expansion of the pathogen distribution in response to climate change scenarios (Duque-Lazo et al., 2018). This therefore, could increase the incidence of periods favouring the growth of this pathogen and, thus increase its negative impact on the oaks in central-western Spain.

Concerning topographic features, low slope gradients with south or southeast facing orientation were associated with higher **OD** risk. In such geomorphic conditions the enhanced water stress may be caused by a more intense solar radiation. Similar trends were also registered by Costa et al. (2010) for cork oaks in south-western Portugal. In North America, Kabrick et al. (2008) also reported that decline in deciduous oak was more severe in southernly or south-westerly slopes. Moreover, the probability of **OD** risk was associated positively with soil temperature (i.e., **LST**): the higher soil temperature, the higher the risk of **OD** occurrence. In fact, as has been shown in Haldimann et al. (2008) an increase in temperature could affect tree performance by limiting photosynthesis. This negative effect could be exacerbated by a long-lasting combination of drought and high solar irradiance in Iberian Mediterranean regions, leading to the sudden death of affected trees or gradual decline until their death (Leininger, 1998; Haldimann et al., 2008).

In this study, variance-partitioning demonstrated that the different categories of variables exerted a clear influence on **OD** risk. In our case, it is important to note that the shared component had a significant proportion of the variation, indicating strong dependent contributions of the three sets of predictors explaining distribution patterns of **OD** in central-western Spain. In fact, **OD** occurrence in Iberian oaks is considered a complex multifactorial phenomenon, involving the combination of predisposing factors operating at tree, stand, and landscape scales (Rodríguez-Calcerrada et al., 2017a, 2017b). In most cases, none of these factors have acted alone (de Sampaio e Paiva Camilo-Alves et al., 2013). The simultaneous interaction of at least two stress agents–where one of them comprises an extreme climatic event (e.g., drought)–has triggered important outbreaks of decline (Rodríguez-Calcerrada et al., 2017a, 2017b).

4.2. Potential distribution of oak decline and insights for prioritising target areas and measures for intervention

We developed a spatially explicit model to represent the potential distribution of **OD** in central-western Spain. The strength of our model relies on the availability of high-quality records of **OD** foci for the study area, a robust dataset of explanatory variables (Land-use and Remote-sensing derivate variables) and a biologically relevant selection of the most important variables explaining the **OD** risk. Remote-sensing techniques (space-borne and air-borne remote-sensing instruments) have transformed ecological research by providing both spatial and temporal perspectives on ecological phenomena that would otherwise be difficult to study (He et al., 2015; Vogeler and Cohen, 2016). A key advantage of these techniques is the capability to perform synoptic, spatially continuous and frequent observations of ecological indicators without interpolation or geographical biases at varying spatial and temporal resolutions (He et al., 2015), advantages that have huge potential when it comes to improving the ability to predict one of the most important phenomenon that threat the biodiversity of the forest ecosystems in the Iberian Peninsula.

Despite the MaxEnt models each being calibrated with distinct non-colinear variables (i.e., topography, abiotic stress and human influence) they exhibited a good discrimination capacity, the combination of the best variables in the final model resulted in the increase in mean AUC. This increase is likely to be caused by a reduction of commission errors, suggesting that the combination of the best variables narrows model predictions to areas that have high risks of OD. This supports earlier findings that OD is considered a complex multifactorial phenomenon, involving the combination of predisposing factors operating at tree, stand, and landscape scale (Rodríguez-Calcerrada et al., 2017a, 2017b; Duque-Lazo et al., 2018). Given the observed occurrence of **OD**, predictions of its potential distribution across the study area suggest that a further expansion of this phenomenon is possible along the northern and central part of the study area, where the *dehesa* is the main component of the landscape and the local economy. Moreover, special attention in monitory efforts should focus on the northwest and southern part of the Salamanca province. These zones dominated by oak forests have been included in the European lists of priority habitats for conservation, (Annex I of Council Directive 92/43/EEC) which provide a wide variety of environmental benefits: structural and biological diversity, environmental stability (erosion, climate, nutrient and water cycles, fire), tourism, cultural heritage, among others.

According to the identification of **OD** foci and predicted risk probability, management strategies are required to prevent a possible expansion into target areas with high socioeconomical and environmental values. However, the implementation of a general management strategy that satisfies the requirements of the proposed areas for management interventions (see Fig. 5), is a complex task (Duque-Lazo et al., 2018). Each site might need a specific study to assess the combinations of factors related to the **OD** and, consequently, a customised management strategy (Sena et al., 2018). Forestry practices have been widely recognized as the main management strategy to alleviate oak decline (Rodríguez-Calcerrada et al., 2017a, 2017b). For areas with identified **OD** occurrence (i.e., prevention area), we propose the following measures (Table 3): Selective thinnings of suppressed stems to increase irradiance and the availability of soil water and nutrients for residual trees (Rodríguez-Calcerrada et al., 2011). This increase in resources availability is reflected in a better physiological status of residual trees (Rodríguez-Calcerrada et al., 2017a, 2017b; Cabon et al., 2018). In addition, other studies developed in the Iberian Peninsula found a relationship between oak cover and the presence of *P.cinnamomi* (Duque-Lazo et al., 2018). Girdling selected stems in multi-stems trees. This practice could favour the accumulation of nonstructural carbohydrates above the girdled zone and produce more acorns (Oberhuber et al., 2017; Rodríguez-Calcerrada et al., 2017a, 2017b). The inoculation of endophytes or chemical cocktails could be a promising practice to recover the vigour of weakened trees, particularly those with a significant cultural value. However, its use on a forest-wide basis is likely to be unadvised (Clatterbuck and Kauffman, 2006; Rodríguez-Calcerrada et al., 2017a, 2017b). **OD** has mainly been related to biotic factor such as *Phytophthora* sp. and xylophage insects (Cerambyx complex). Thus, the prevention of the spread of *Phytophthora* sp. together with control over the population densities of the beetles should be implemented to limit the expansion of **OD** into areas with high socioeconomical and environmental values (for more details about these management strategies see Duque-Lazo and Navarro-Cerrillo, 2017; Duque-Lazo et al., 2018). Regarding *dehesas* where livestock graze, a good planning of the grazing activities is crucial. Recommendations lead to avoid grazing at the end of summer and beginning of autumn, mainly for decreasing damages caused by the animals on the natural regeneration of the oak trees (González-Alonso, 2008). Postponed grazing plans are more appropriate to be sustainable when oak decline is already taking place.

For the protection areas (Table 3), we recommend improving the existing trees by selectively cutting smaller trees from the midstory and thinning the trees by removing some of the larger trees to develop oak seedlings and saplings (Clatterbuck and Kauffman, 2006). These practices also reduce the number of less desirable competitors. (Rodríguez-Calcerrada et al., 2017a, 2017b) In conservation areas (Table 3), the sowing of acorns and planting of young seedlings are viable strategies to assist sexual regeneration (Rodríguez-Calcerrada et al., 2017a, 2017b). For initial seedling growth and survival, the selection of microsites of sowing/planting is important. In general, sowing/planting should be conducted in forest understories and gaps where canopy cover is enough to moderate solar radiation and improve soil physicochemical properties (Rey Benayas et al., 2005). Likewise, these sites should not provide excessive shade or competition for availability of soil water and nutrients (Rey Benayas et al., 2005; Dickie et al., 2007). The optimal light availability ranges from 20 to 50% of full sunlight among species and populations (Gardiner et al., 2001). One factor that is being given increasing consideration in sowing/planting practices is the use of plant material from species with higher genetic tolerance to drought (Aitken and Bemmels, 2016). Finally, the preservation of marginal oak populations could therefore be crucial to species' conservation (Rodríguez-Calcerrada et al., 2017a, 2017b).

The application of these forestry practices could reduce the expansion and strength of the OD disease. However, an important factor to guarantee the success of these recommendations is for different collectives to address the issue. Therefore, support from the government is crucial in these cases. Specifically, in Spain, if a Quercus' *dehesa* becomes unproductive, the owners will be unlikely to apply treatments for the recovery of the trees unless they can be sure that these practices will actually work in the short term and that they will be able to obtain benefits again. In this sense, it is of upmost importance that the government economically supports these recommendations for mitigating the negative impact of the decline process.

5. Conclusions

This study provides new insights into the complex spatial distribution of **OD** and reveals the degree to which predisposing factors can explain its distribution in central-western Spain. **OD** distribution seems to be principally influenced by land-use, followed by dryer areas and areas with low slope gradients facing south or southeast. Given the higher likelihood of occurrence of OD in oak areas embedded in a *dehesa* matrix, the government of Salamanca should propose and encourage management actions against OD, focusing on prevention of expansion of this phenomenon from current presence zones, protection of suitable zones and conservation of unsuitable zones. Guidelines should be put in place carefully and each site must be studied and treated individually due to the complex etiology of the OD. Finally, our modelling approach provides an important decision tool for the control, monitoring and restoration of declining Iberian oaks.

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Conflict of interest statement

We declare that we have no conflict of interest.

Author contributions

All authors contributed to the formulation of ideas and the writing of the manuscript.

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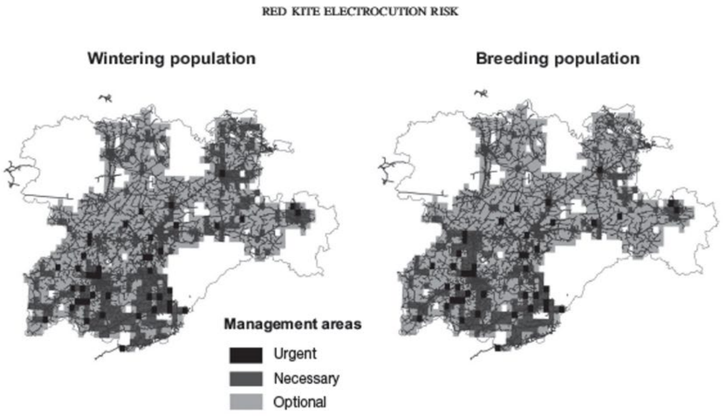
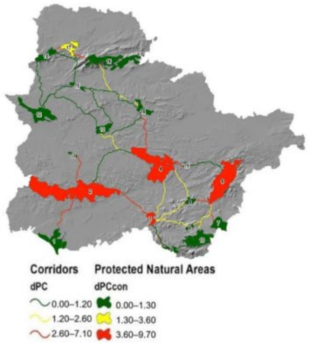
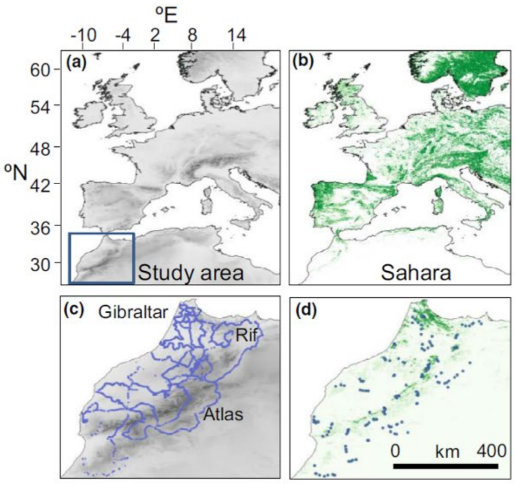
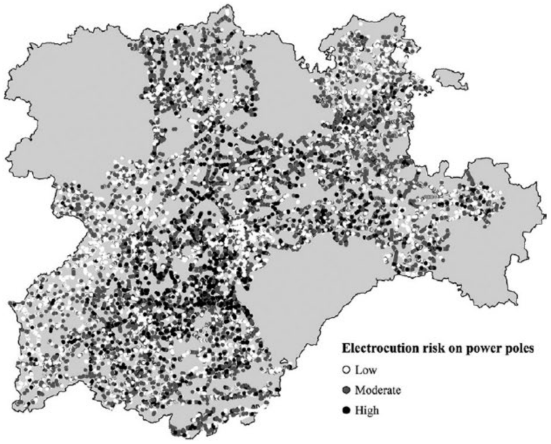
ANEXOS









Fotos: Gabriela Crespo Luengo; Iván Barbero Bermejo; José Luis-Tellería; Ricardo Enrique Hernandez-Lambraño.

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RESEARCH ARTICLE

Ecological and geographical marginality in rear edge populations of Palaearctic forest birds

José Luis Tellería[1] | **Ricardo Enrique Hernández-Lambraño**[2] | **Roberto Carbonell**[1]

[1]Department of Biodiversity, Ecology and Evolution, Universidad Complutense, Madrid, Spain

[2]Departamento de Botánica y Fisiología Vegetal, Facultad de Farmacia, Universidad de Salamanca, Avenida Licenciado Méndez Nieto s/n, Salamanca, Spain

Correspondence
José Luis Tellería, Department of Biodiversity, Ecology and Evolution. Universidad Complutense, 28040 Madrid, Spain.
Email: telleria@bio.ucm.es

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Abstract

Aim: The centre–periphery hypothesis predicts that habitat suitability will decrease at the edge of a species' range, a pattern often questioned by empirical data. Here we explore if habitat suitability decreases southwards and shapes the abundance distribution of rear edge populations of forest birds within the restricted geographical setting of the south-western Palaearctic. We also test if birds endemic to the area fit more poorly to the latitudinal decrease in habitat suitability due to the putative effect of adaptations to regional conditions.

Location: North-western Africa (Morocco).

Taxon: Passerines (11 species).

Methods: Bird occurrences were used to model species distribution and line transects were used to estimate bird abundance. Occurrence probabilities provided by species distribution models were used to display the spatial patterning of habitat suitability. Habitat suitability was employed to predict abundance after controlling for the effect of the distance to some regional source areas of forest birds (tree covered large areas). The species were classified as North African endemic according to an updated review of their taxonomic status.

Results: Habitat suitability decreased southwards, supporting the predicted relationship between ecological and geographical marginality in most species. Abundance was positively correlated with habitat suitability and negatively correlated with distance to source areas. The taxonomic status of birds did not affect the patterns.

Main conclusions: The southward decrease in habitat suitability predicted by the centre–periphery hypothesis shapes the distribution of rear edge populations of forest birds within the south-western Palaearctic. As most of these populations are endemic, the results suggest that they track the gradients in isolation within the geographical setting of north-western Africa. These results support the vulnerability of these isolated, peripheral populations of forest birds to large-scale environmental changes in a region under the effect of increasing drought and temperature.

KEYWORDS

centre–periphery hypothesis, habitat suitability, refuge areas, species distribution, stepping stone effect, taxonomic differentiation

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RESEARCH ARTICLE

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Where to start? Development of a spatial tool to prioritise retrofitting of power line poles that are dangerous to raptors

Ricardo Enrique Hernández-Lambraño[1,2] | **José Ángel Sánchez-Agudo**[1,2] | **Roberto Carbonell**[3]

[1]Grupo de investigaciones en Biodiversidad, Diversidad humana y Biología de la Conservación, Departamento de Biología Animal, Ecología, Parasitología, Edafología y Química Agrícola, Universidad de Salamanca, Salamanca, Spain

[2]Instituto Hispano-Luso de Investigaciones Agraria (CIALE), Universidad de Salamanca, Salamanca, Spain

[3]Departamento de Zoología y Antropología Física, Facultad de Ciencias Biológicas, Universidad Complutense de Madrid, Madrid, Spain

Correspondence
Ricardo Enrique Hernández-Lambraño, C/General Margallo, 24, 1B izq, 28020 Madrid, Spain.
Email: ricardohl123@usal.es

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Abstract

1. Avian electrocution on power lines is a major conservation issue on a global scale. Electrocution risk models have recently been proposed as an effective alternative to prioritising high-risk pole retrofitting activities at a large scale. However, existing models ignore the specific features of the power poles (hereafter, poles) supporting the power distribution lines and make the tenuous assumption that pole density and power line length are key factors to assessing the electrocution risk at a large scale. This assumption may be violated in areas with high variations in pole configuration.
2. In this study, we used data on raptors electrocuted on poles to develop a predictive model of raptor electrocution risk throughout an extensive geographical area in north-western Spain, using boosted regression trees. With the best-fitting model, we predicted the hazard of a set of 188,741 poles and validated the model predictions with new data collected from the study area.
3. Our model highlights the relevance of combining both habitat and technical features to identify the most dangerous poles for raptors on a large geographical scale. A 9.86% of the total poles evaluated were characterised as high risk for raptors. The model showed good performance in external validation. The new electrocution events were registered at poles with high-risk values.
4. *Synthesis and applications*. In this study, we improved the accuracy of the predictive models of raptor electrocution risk for large geographical areas. By incorporating the technical characteristics of the power poles into the models, we achieved a high level of prediction at the power pole level, which is the ultimate correction unit. This will allow electric companies and wildlife managers to specify retrofitting activities of high-risk power poles for raptors in large geographical areas, thus maximising the effect of investment in the correction of dangerous power poles and conservation of the raptor populations.

KEYWORDS

boosted regression trees, electrocution risk map, high-risk power poles, Iberian Peninsula, power line poles, predictive modelling, raptor electrocution, retrofitting activities

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

Cristian Madeira de Medeiros · **Ricardo Enrique Hernández-Lambraño** · **Karoline Aparecida Felix Ribeiro** · **José Ángel Sánchez Agudo**

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Abstract The performance of populations at the edge of 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 and/or they are restricted to microrefugia with ecological conditions very different from those around them. 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.

Keywords Iberian Peninsula · Ecological niche models · Spatial distribution · Endangered plant species · Marginal populations · Microrefugia · Plant conservation

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 et al. 2014). The distribution limits of a species are mainly established by its adaptive strategies to abiotic and biotic conditions and their interactions (Sexton et al. 2009; Wiens 2011). To explain their large-scale biogeographical patterns, it is necessary to

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C. M. de Medeiros (✉) · R. E. Hernández-Lambraño · J. Á. Sánchez Agudo
Departamento de Botánica y Fisiología Vegetal, Facultad de Farmacia, Universidad de Salamanca, Avenida Licenciado Méndez Nieto s/n, 37007 Salamanca, Spain
e-mail: medeiros@usal.es

K. A. F. Ribeiro · J. Á. Sánchez Agudo
CIALE (Instituto Hispanoluso de Investigaciones Agrarias), Universidad de Salamanca, Campus de Villamayor, Calle Del Duero n° 12, Villamayor, 37185 Salamanca, Spain

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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[1]

C. M. de Medeiros[a, *], **R. E. Hernández-Lambraño**[a, **], **and J. Á. Sánchez Agudo**[a, ***]

[a] *Instituto Hispanoluso de Investigaciones Agrarias (CIALE), Universidad de Salamanca, Campus de Villamayor, Villamayor, Salamanca, 37185 España*

**e-mail: medeiros@usal.es*

***e-mail: ricardohl123@usal.es*

****e-mail: jasagudo@usal.es*

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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. Here, we used the Species Distribution Models approach to compare two independent datasets for the invasive alien species the Yellow-legged hornet 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. Our results showed a high degree of concordance and similarity between models. Thus, both datasets would have the same reliability to be used in management strategies for this species.

Keywords: datasets, invasive alien species, Maxent, Species Distribution Models (SDM), *Vespa velutina*

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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 known yet, some aspects raised concerns on population: the predation of domestic honeybees (*Apis mellifera* Linnaeus, 1758) 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 (Beggs et al., 2001; Villemant et al., 2011). 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* Thomson, 1869 or *Dolichovespula* Rohwer, 1916). 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 et al., 2011; Monceau et al., 2014; Robinet et al., 2017; Rome et al., 2011; Villemant et al., 2010, 2011).

At present, there are over 200 million records of biodiversity data available online to researchers worldwide (Jiménez-Valverde et al., 2010). Data coming

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[1] The article is published in the original.

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ANALYSIS OF SPATIO-TEMPORAL PATTERNS OF RED KITE *MILVUS MILVUS* ELECTROCUTION

ANÁLISIS DE LOS PATRONES ESPACIO-TEMPORALES DE ELECTROCUCIÓN DEL MILANO REAL *MILVUS MILVUS*

Gabriela Crespo-Luengo[1] *, Ricardo Enrique Hernández-Lambraño[1],
Iván Barbero-Bermejo[1] and José Ángel Sánchez-Agudo[1]

Summary.—The Spanish Castilla y León region is one of the most important wintering areas in Europe for the Red Kite *Milvus milvus*. At the same time, the steepest population declines of Red Kite have been recorded there, electrocution by power lines being one of the main causes. Thus, knowledge about the annual spatio-temporal ecology of this raptor, and its relationship to electrocution events, is necessary to develop effective conservation measures. Distribution models for the breeding and wintering populations of the Red Kite in Castilla y León were developed, considering climate, topography and land uses, to analyse the potential spatial variation between them. Models for electrocution risk also considered the technical characteristics of the power poles to determine their impact on electrocution events in both seasons. Our results show two different areas are used seasonally: 1) an important wintering area in the centre of the region, characterised by crop zones, moderate temperatures, rubbish dump sites and human presence, and 2) a nesting area in the south of the region, in which the availability of livestock carcasses, low levels of precipitation, distance from landfills and gentle relief were the most influential variables. The electrocution risk model indicates that the most suitable areas for Red Kite reproduction are also those that are most risky, including power poles of the most dangerous types; those with straight or vaulted cross-arms. Finally, the theoretical approach presented here provides a framework for the design of management and control measures aimed at minimising Red Kite electrocutions in the northern half of the Iberian Peninsula.—Crespo-Luengo, G., Hernández-Lambraño, R.E., Barbero-Bermejo, I. & Sánchez-Agudo, J.A. (2020). Analysis of spatio-temporal patterns of Red Kite *Milvus milvus* electrocution. *Ardeola*, 67: 247-268.

Key words: breeding population, distribution models, MaxEnt, mitigation measures, power poles, raptors, risk prediction, wintering population.

Resumen.—El territorio de Castilla y León constituye una de las áreas de invernada más importantes de Europa para el milano real *Milvus milvus* y es, a la vez, una zona donde se está registrando un fuerte declive de su población, siendo la electrocución en líneas eléctricas una de las principales causas de mortalidad. Es por ello que, para poder plantear medidas eficaces de conservación para esta

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[1] Grupo de Investigación en Biodiversidad, Diversidad Humana y Biología Animal; Ecología, Parasitología, Edafología y Química Agrícola, Universidad de Salamanca, Campus Miguel de Unamuno s/n., E-37007-Salamanca, Spain.

* Corresponding author: gabrielacl94@usal.es

sustainability

Article

Analysis of the Adaptative Strategy of *Cirsium vulgare* (Savi) Ten. in the Colonization of New Territories

Jhony Fernando Cruz Román [1], Ricardo Enrique Hernández-Lambraño [1,2], David Rodríguez de la Cruz [1,2] and José Ángel Sánchez Agudo [1,2,*]

[1] Departamento de Botánica y Fisiología Vegetal, Área de Botánica, Universidad de Salamanca, Campus Miguel de Unamuno s/n, E-37007 Salamanca, Spain; jhonycruz@usal.es (J.F.C.R.); ricardohl123@usal.es (R.E.H.-L.); droc@usal.es (D.R.d.l.C.)

[2] Grupo de Investigación en Biodiversidad, Diversidad Humana y Biología de la Conservación, Universidad de Salamanca, Campus Miguel de Unamuno s/n, E-37007 Salamanca, Spain

* Correspondence: jasagudo@usal.es

Abstract: The current situation of global environmental degradation as a result of anthropogenic activities makes it necessary to open new research lines focused on the causes and effects of the main alterations caused in the ecosystems. One of the most relevant is how the niche dynamics of invasive species change between different geographical areas, since its understanding is key to the early detection and control of future invasions. In this regard, we analyzed the distribution pattern of *Cirsium vulgare* (Savi) Ten., a plant of the Asteraceae family originally from the Eurasian region that currently invades wide areas of the world. We estimated its niche shifts between continents using a combination of principal components analysis (PCA) and Ecological Niche Modelling (ENM) on an extensive set of data on global presences of its native and invaded ranges from Global Biodiversity Information Facility (GBIF). A set of bioclimatic variables and the Human Footprint (HFP) with a resolution of 10 km were selected for this purpose. Our results showed that the species has a marked global trend to expand toward warmer climates with less seasonality, although in some regions its invasiveness appears to be less than in others. The models had a good statistical performance and high coherence in relation to the known distribution of the species and allowed us to establish the relative weight of the contribution of each variable used, with the annual temperature and seasonality being the determining factors in the establishment of the species. Likewise, the use of non-climatic variable HFP has provided relevant information to explain the colonizing behavior of the species. The combination of this methodology with an adequate selection of predictor variables represents a very useful tool when focusing efforts and resources for the management of invasive species.

Keywords: ecological niche dynamics; MaxEnt; reciprocal niche models; biological invasions

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1. Introduction

Globalization, with its intense commercial activity of nations around the world, implies a massive flow of transportation of goods, people, and others from one territory to another. All the processes carried out in these movements involve strong environmental consequences such as the emission of pollutants, global warming, changes in land use, destruction of habitat, and landscape fragmentation [1–3]. No less important is the spread of some species with high colonizing capacity that give rise to biological invasions, which is considered to be one of the phenomena responsible for the planet's loss of biodiversity [4,5]. Although a large number of species can be transported voluntarily or involuntarily from their natural habitats to other territories [6], the majority do not survive because they do not adapt to new ecological conditions. Some of them become naturalized, coexisting in harmony with the native species, but a few are able to overcome adaptive barriers and become invasive, displacing native species and causing serious damage to the balance of the ecosystem [7–9]. Despite having more information available on biological invasions,

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Article

Natural Protected Areas as Providers of Ecological Connectivity in the Landscape: The Case of the Iberian Lynx

Iván Barbero-Bermejo [1,2,*], Gabriela Crespo-Luengo [1,2], Ricardo Enrique Hernández-Lambraño [1,2], David Rodríguez de la Cruz [1,2] and José Ángel Sánchez-Agudo [1,2,*]

[1] Grupo de Investigación en Biodiversidad, Diversidad humana y Biología de la Conservación, Campus Miguel de Unamuno s/n, Universidad de Salamanca, E-37007 Salamanca, Spain; gabrielacl94@usal.es (G.C.-L.); ricardohl123@usal.es (R.E.H.-L.); droc@usal.es (D.R.d.l.C.)

[2] Departamento de Botánica y Fisiología Vegetal, Área de Botánica, Campus Miguel de Unamuno s/n, Universidad de Salamanca, E-37007 Salamanca, Spain

* Correspondence: ivanbarbero@usal.es (I.B.-B.); jasagudo@usal.es (J.A.S.-A.)

Abstract: The design of conservation plans for the improvement of habitats of threatened species constitutes one of the most plausible possibilities of intervention in the structure and composition of the landscape of a large territory. In this work we focus on the Iberian lynx in order to establish potential ecological corridors using ecoinformatic tools from the GIS environment to improve connectivity between the existing natural spaces within the scope of its historical distribution. We processed 669 records of the presence of the lynx and six predictor variables linked to the habitat of the species. With this, corridors have been generated between natural areas. The determination of possible bottlenecks or dangerous areas (e.g., hitches on highways) allows for focusing efforts on their conservation. This type of approach seeks to improve efficiency in the design of measures aimed at expanding the territory's capacity to host its populations, improving both its viability and that of all the other species that are linked to it. The proposals for action on the specific areas defined by the models elaborated in this work would imply interventions on the land uses and existing vegetation types in order to improve connectivity throughout the territory and increase the resilience of its ecosystems.

Keywords: landscape; GIS; Corridor Designer; MaxEnt; species distribution models; ecological corridors

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Citation: Barbero-Bermejo, I.; Crespo-Luengo, G.; Hernández-Lambraño, R.E.; Rodríguez de la Cruz, D.; Sánchez-Agudo, J.Á. Natural Protected Areas as Providers of Ecological Connectivity in the Landscape: The Case of the Iberian Lynx. *Sustainability* **2021**, *13*, 41. https://doi.org/10.3390/su13010041

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1. Introduction

Human activities shape and transform territories on a global scale through the modification of the forms and properties of the surface and subsoil; being, therefore, a dominant factor in the evolution of the landscape in this current period [1,2]. As a consequence of this transformation, severe alterations in ecosystem dynamics are generated, resulting in population and species reductions and extinctions. In this context, the fragmentation of habitats and populations appears as one of the main factors responsible for the serious and rapid loss of biodiversity [3,4].

Habitat fragmentation results in a loss of connectivity in the landscape. The preservation and restoration of connectivity has become one of the main conservation objectives [5]. Understanding the ecological processes which depend on connectivity and taking effective planning measures requires an understanding of how landscape features can affect it. Taylor et al. [6] define connectivity as the level of facilitation or resistance to the movement of organisms between patches of habitat with resources. This resistance is determined by a landscape matrix which can present different levels of alterations and is able to modulate connectivity between patches or provide resources to species. In this way, a well-preserved matrix with a low degree of alteration can act as a buffer zone for habitat patches and mitigate the isolation of these. In addition, the matrix between these patches is characterized


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