



Inferencia espacial y predicción de la distribución de plantas: un estudio a diferentes escalas

Spatial inference and prediction of plant species distribution: a multiscale study

Nora Pérez García

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Barcelona, septiembre de 2013



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A mis padres y mi hermano

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INTRODUCCIÓN GENERAL

1. Introducción general

1.1. La conservación de la biodiversidad y los modelos de distribución de especies.

Desde la Conferencia de Naciones Unidas sobre medio ambiente y desarrollo sostenible celebrada en Río de Janeiro en 1992, la biodiversidad ha recibido cada vez más atención por parte de los científicos, los gobiernos y la opinión pública mundial. Sin embargo, a pesar de los esfuerzos realizados, existen pruebas claras de que estamos ante una gran crisis de la biodiversidad (Loreau *et al.* 2006), en la que prácticamente todos sus aspectos están en declive. Esta pérdida de biodiversidad se ha acentuado en los últimos años debido a numerosas amenazas que incluyen la destrucción y degradación del hábitat, el cambio climático, la propagación de especies invasoras y la sobreexplotación (véanse Pimm & Raven 2000; Sax & Gaines 2008). Sin embargo, mientras fenómenos como el calentamiento global, la contaminación y los cambios en los usos del suelo operan en áreas muy grandes o durante largos períodos de tiempo, los datos de campo que caracterizan la investigación ecológica se recogen normalmente en áreas relativamente pequeñas durante estudios de corta duración (Miller *et al.* 2004). Por tanto, los científicos necesitan cada vez más la utilización de medidas y datos locales para evaluar estos cambios a escala paisajística, regional y global, y modelos o simulaciones estadísticas para extrapolar estos datos ambientales al espacio geográfico (Miller *et al.* 2004; Peters *et al.* 2004). Los modelos de distribución de especies (MDE) son sólo un tipo dentro de estos modelos o simulaciones, pero son un ejemplo de creciente importancia. En las últimas décadas se ha producido un progresivo interés en el modelado de la distribución de especies, que resulta de la confluencia entre la creciente necesidad de información sobre la distribución geográfica de la biodiversidad y el desarrollo de nuevas y mejoradas técnicas de modelado (Franklin 2009).

Los MDE extrapolan datos de la distribución de las especies en el espacio y el tiempo, generalmente en base a modelos estadísticos. El propósito de los MDE y, en particular, de los mapas predictivos resultantes, es proporcionar información espacialmente explícita, es decir asociada a una ubicación en el espacio geográfico, sobre las especies y otros elementos de la biodiversidad para muy diversas aplicaciones, tales como el desarrollo de planes de conservación, evaluación de riesgos y gestión de recursos (Franklin 2009).

1.2. La escala geográfica

Una característica de los sistemas biológicos es que se rigen por procesos complejos que actúan a diferentes escalas espaciales y temporales. En el estudio de la distribución de las especies y comunidades vegetales, la resolución y la extensión determinan la escala geográfica del trabajo e influyen en la aplicabilidad de los resultados (Willis & Whittaker 2002; Elith & Leathwick 2009). La escala geográfica refleja, por lo general, el propósito del análisis. Por ejemplo, los estudios sobre cambios macro-ecológicos y globales tienden a ser a escala continental de alcance mundial (Araujo & New 2007), mientras que estudios dirigidos a la comprensión ecológica detallada o la planificación de la conservación tienden a una escala local para extensiones regionales (Fleishman *et al.* 2001; Ferrier *et al.* 2002). La resolución no sólo describe las propiedades de las variables ambientales, tamaño de celda o polígono del mapa digital, sino también la precisión espacial de la información referente a la distribución de las especies (Dungan *et al.* 2002; Tobalske 2002). La resolución debe ser coherente con el contenido informativo de los datos, ya que cambios en la resolución implican cambios en la percepción de los fenómenos, como patrones de presencia o abundancia (Guisan *et al.* 2007). Sin embargo, en la práctica esto no siempre es posible y, en ocasiones, las capas explicativas tienen que ser definidas a resoluciones más finas que los datos originales.

Por otro lado, aunque conceptualmente no existe una escala natural única en la que se deben estudiar los patrones ecológicos (Levin 1992), para una eficacia en la conservación de la biodiversidad es necesario su estudio bajo diferentes escalas geográficas. En esta Tesis se abordó el análisis de la diversidad vegetal empleando distintas escalas geográficas y niveles de organización de las plantas, en función de los objetivos planteados, las propiedades del sistema y los datos disponibles (Tabla 1).

Escala geográfica	Nivel de organización de plantas	Determinantes ambientales	Referencia
Regional (10km)	Floras	Clima	<i>Capítulo 1</i>
Paisajística (1km)	Comunidades vegetales	Clima, topografía, sustrato	<i>Capítulo 2</i>
Local (200m)	Especies individuales a nivel de detalle	Sustrato, interacciones bióticas	<i>Capítulo 3</i>

Tabla 1. Escalas estudiadas para el modelado eficaz en la conservación de la diversidad vegetal.

1.3. Aspectos conceptuales y teóricos

Un modelo es una construcción conceptual que describe de forma simplificada un sistema físico que existe en el mundo real y que nos ayuda a entender su funcionamiento (Benito 2009). En este contexto, un MDE es una construcción numérica que define en el espacio ecológico las relaciones existentes entre las presencias de una especie o comunidad vegetal y los valores de las variables ambientales con influencia en su distribución, ayudándonos a mejorar nuestra interpretación y comprensión de la distribución de las especies (Franklin 2009) y comunidades.

El área de distribución de una especie es el conjunto de lugares del espacio geográfico en los que puede detectarse su presencia (Soberón 2007), y refleja la ecología e historia evolutiva de la misma (Brown 1995). Este área de distribución está determinada por la interacción dinámica de diversos factores (bióticos, abióticos, potencial dispersivo y evolutivos) que operan con diferente intensidad y a distintas escalas (Gaston 2003; Pearson & Dawson 2003) tanto espaciales como temporales.

Los modelos de distribución de especies se basan generalmente en hipótesis biogeográficas (Box 1981), en el análisis de los gradientes ecológicos (Whittaker 1960; Whittaker *et al.* 1973) y en cómo los factores ambientales controlan la distribución de las especies y comunidades (Guisan & Zimmermann 2000), teniendo sus raíces en la teoría del nicho ecológico.

La primera definición formal del nicho ecológico se debe a Grinnell (1917), cuyo interés se centraba en los factores que determinan dónde puede encontrarse una especie. Su concepto se basa en la importancia de las condiciones ambientales definidas a una escala geográfica relativamente grosera. Una década más tarde, Elton (1927) define el nicho como el rol funcional de una especie en la comunidad biótica, afirmando que cada especie tiene un rol exclusivo en el ecosistema. Elton centra su definición de nicho en términos de interacciones entre especies y disponibilidad de recursos. En 1987, Hutchinson redefine el concepto de nicho como *un hipervolumen en el espacio ecológico multidimensional, determinado por los requerimientos de la especie para reproducirse y sobrevivir*. Más concretamente, Hutchinson distingue el nicho *fundamental* (fisiológico o potencial), definido como la respuesta de las especies al ambiente en ausencia de interacciones bióticas (competencia, depredación, mutualismo), del nicho *realizado* (ecológico o real) definido como las dimensiones

ambientales en las cuales la especie puede sobrevivir y reproducirse, incluyendo los efectos de las interacciones bióticas (Austin & Smith 1989; Austin 2002; Chase & Leibold 2003) (ver Figura 1). Finalmente, Pulliam (2000) propuso que el concepto de nicho de Hutchinson (1987) junto con la teoría de metapoblaciones (Hanski 1999) y la teoría de fuente-sumidero (Pulliam 1988) podrían ayudar a explicar las relaciones existentes entre la distribución de las especies y su hábitat idóneo.

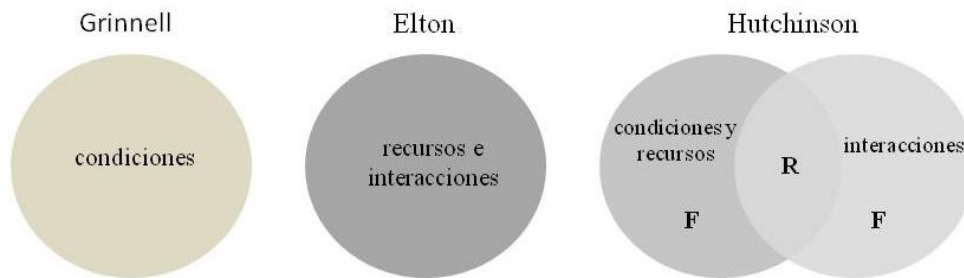


Figura 1. Conceptos de nicho ecológico de Ginnell, Elton y Hutchinson, donde **F** se refiere a nicho fundamental o potencial, y **R** a nicho realizado. Figura adaptada de Benito (2009).

Los MDE se apoyan fundamentalmente, aunque no exclusivamente, en el concepto de nicho que enfatiza los requerimientos de las especies, a través de representaciones de los factores abióticos que controlan su distribución.

1.4. Construcción de los MDE

La generación de un MDE es un proceso complejo, que necesita gran variedad de datos y el conocimiento exhaustivo de las distintas técnicas de modelado. Para garantizar la correcta construcción de un modelo predictivo, es imprescindible seguir un proceso que comprende nueve pasos fundamentales (Figura 2), los cuales se exponen a continuación y se repiten a lo largo del desarrollo de esta Tesis.

1.4.1. Modelo conceptual

La predicción de la distribución geográfica de una planta o una comunidad vegetal comienza con la formulación teórica del modelo basado en la teoría del nicho ecológico y bajo la premisa de que la distribución de la vegetación puede predecirse a partir de la distribución espacial de variables ambientales que están correlacionadas o controlan directamente la distribución de las plantas (Franklin 1995). Cuando se aplica el concepto de nicho en el modelado estático de la distribución de las especies, esto es, sin incluir elementos dinámicos, se asume que las especies están en (pseudo) equilibrio con

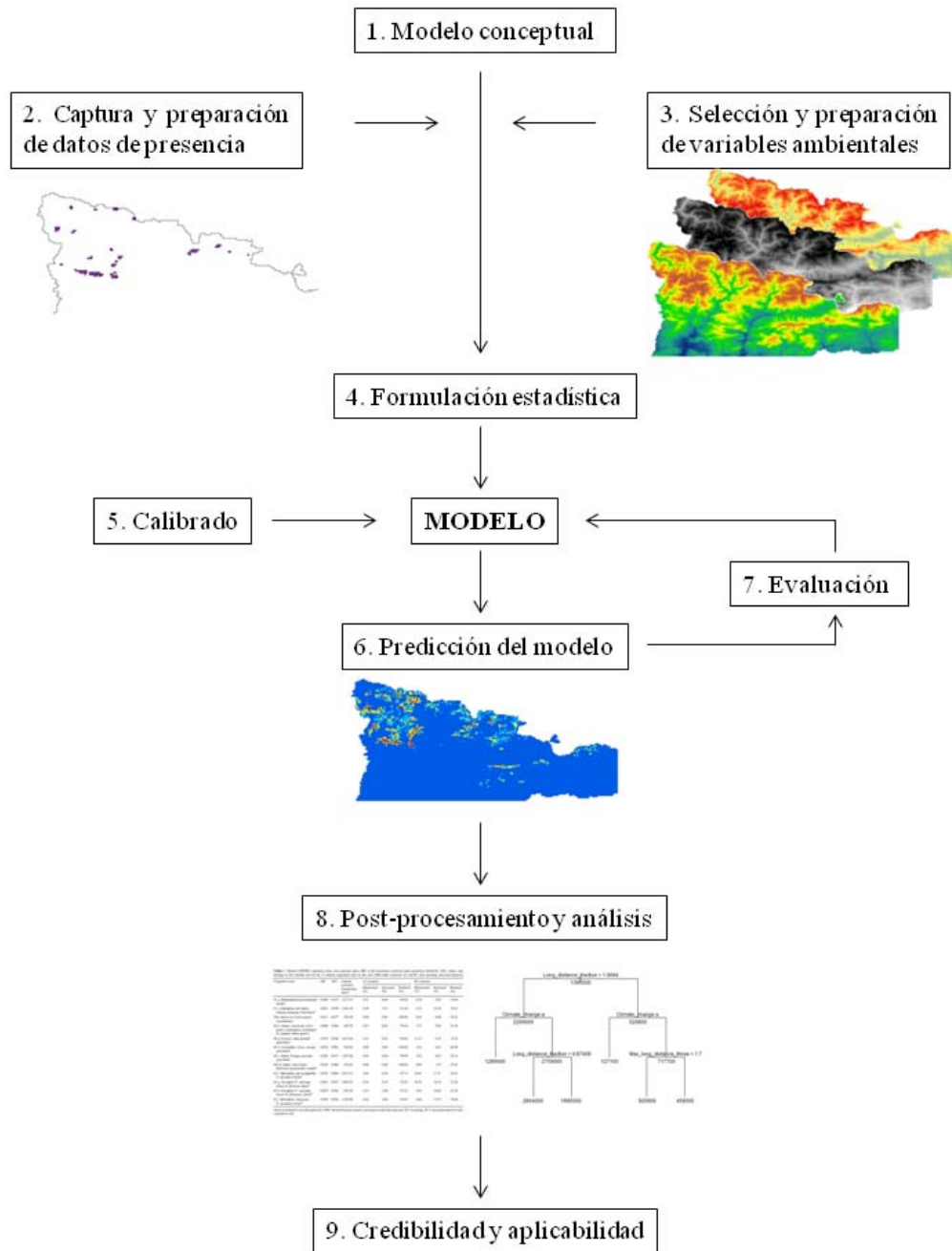


Figura 2. Visión general de los sucesivos pasos (de 1 a 9) necesarios para construir un modelo.

las condiciones ambientales actuales, y que las distribuciones y abundancias observadas son un indicador de sus tolerancias ambientales y requerimientos de recursos (Franklin 2009). Durante esta fase se deberían seleccionar los factores que afectan a la distribución de la especie o comunidad vegetal y que podrían ser incluidos en el modelo. La formulación teórica exige un conocimiento profundo de las técnicas de modelado, la biología del organismo estudiado y una definición clara de los objetivos (Benito 2009).

1.4.2. Captura y preparación de los datos de presencia

Los registros de presencia son imprescindibles para generar modelos de distribución. Estos registros de presencia se basan en pares de coordenadas que sitúan en el espacio geográfico localidades en las que se ha detectado la presencia de la especie o comunidad vegetal. Algunos algoritmos de modelado necesitan también registros de ausencia, sin embargo, estos datos de ausencia son difíciles de conseguir y generalmente están sujetos a gran incertidumbre. Organizaciones como la Infraestructura Mundial de Información en Biodiversidad (GBIF), el Sistema de Información de la Vegetación Ibérica y Macaronésica (SIVIM), el Banco de Datos de Biodiversidad de Cataluña (BDBC), entre muchos otros, están trabajando a distintas escalas para hacer los datos sobre biodiversidad accesibles vía internet, desarrollando protocolos para la compartición de datos. Estos proyectos proporcionan datos de incalculable valor que se utilizan para describir el área geográfica de las especies.

Una vez compilados los datos de presencia del objeto de estudio, es necesario procesarlos, filtrando errores (fundamentalmente de tipo taxonómico), analizando la presencia de sesgos en el muestreo y adaptando los registros de presencia al formato específico requerido para la aplicación del algoritmo de modelado.

1.4.3. Selección y preparación de variables ambientales

Una cuestión importante a la hora de modelar la distribución geográfica de las especies y comunidades es decidir que variables se deben utilizar para cumplir con nuestros objetivos. Debido a la complejidad del nicho ecológico, se hace prácticamente imposible trabajar con todas las variables que lo definen, por lo que para aumentar la precisión y poder predictivo del modelo, el número de variables descriptivas utilizadas debe reducirse a un número razonable (Harrell *et al.* 1996). Por otra parte, la selección

de variables descriptivas requiere considerar la jerarquía espacial a la que están sujetas las variables que controlan la distribución de las plantas (Neilson 1995; Huntley *et al.* 1995). Las variables climáticas controlan los patrones de distribución a extensiones amplias y resoluciones groseras, mientras que las variables topográficas y geológicas son fundamentales a pequeñas extensiones y altas resoluciones espaciales. Gracias al reciente desarrollo de modelos dinámicos, junto a estas variables habitualmente utilizadas en el modelado geográfico de las especies, es cada vez más frecuente el uso de elementos dinámicos tales como la capacidad dispersiva de las especies, los efectos de la competencia por los recursos disponibles en el medio así como variables demográficas, lo que permite aproximaciones cada vez más realistas.

1.4.4. *Formulación estadística*

Durante la formulación estadística, llamada verificación por algunos autores (por ejemplo, Rykiel 1996), se debe seleccionar un algoritmo apropiado con el fin de predecir un tipo de variable dependiente y estimar los coeficientes del modelo, así como una aproximación estadística óptima considerando el contexto del modelo (Guisan & Zimmermann 2000). Actualmente, se encuentran disponibles una gran variedad de técnicas específicamente diseñadas para modelar la distribución potencial de las especies y comunidades. Sin embargo, la mayoría de los modelos son específicos para un tipo particular de variable dependiente, pudiendo considerarse éste el primer condicionante a la hora de seleccionar el método de modelado a emplear (Guisan & Zimmermann 2000). Existen numerosos trabajos que comparan el funcionamiento práctico de distintos algoritmos (p.ej. Guisan *et al.* 1999; Pearce & Ferrier 2000; Thuiller *et al.* 2003; Elith *et al.* 2006). A continuación, se explican brevemente las principales técnicas de modelado empleadas en esta Tesis.

Modelo lineal generalizado (GLM, del inglés *Generalized linear models*). Los GLM son ampliamente utilizados en el modelado de la distribución de especies por su fuerte base estadística (Austin 2002). El modelo lineal generalizado es una extensión del modelo de regresión múltiple que utiliza una función *link* permitiendo otras distribuciones para la variable respuesta además de la gaussiana, como Poisson, Binomial o Gamma.

Modelo de regresión adaptativa multivariante (MARS, del inglés *Multivariate adaptive regression splines*). Este método ajusta una curva a los datos de entrada

mediante un análisis de regresión polinómica segmentada, de forma que calcula ecuaciones individuales para grupos de puntos, que posteriormente se agregan en una sola ecuación global (Friedman 1991; Leathwick *et al.* 2006b).

Máxima entropía. También conocido como Maxent (Phillips *et al.* 2006), es un método relativamente reciente, que de acuerdo con Elith *et al.* (2006) supera a otros métodos más establecidos, mostrando una precisión predictiva mayor que otras técnicas cuando se emplean sólo datos de presencia. Este método establece que la mejor aproximación de una distribución desconocida es una distribución de probabilidad con máxima entropía o la más uniforme (Phillips *et al.* 2006). Sus buenos resultados y facilidad de uso lo han extendido por la comunidad científica y desde su disponibilidad en el año 2004, ha sido ampliamente utilizado en el modelado de la distribución de las especies con diversos objetivos (Elith *et al.* 2011).

BioMove. La respuesta de las especies ante cambios ambientales dependerá, probablemente, de las interacciones entre las especies (Araújo & Luoto 2007), los procesos poblacionales (Maschinski *et al.* 2006) y las dinámicas paisajísticas (Wintle *et al.* 2005). Por tanto, las predicciones a cerca de la respuesta de las especies a cambios ambientales en base únicamente a los cambios proyectados en la disponibilidad de hábitat idóneo a partir de un MDE son, generalmente, incompletos. Estas predicciones podrían ser más precisas si se desarrollan modelos que incorporen las interacciones entre los cambios del hábitat, la estructura del paisaje y la dinámica demográfica de las especies. El programa Biomove (Midgley *et al.* 2010) fue diseñado para simular los cambios en el rango geográfico de especies de plantas en respuesta a cambios ambientales mediante la vinculación de un modelo dinámico de la vegetación (basado en tipos funcionales de plantas, PFT) con el modelo poblacional de la especie de estudio. Integrando la dinámica de la vegetación y modelos demográficos, BioMove puede abordar directamente el efecto de la competencia por los recursos.

1.4.5. *Calibrado del modelo*

Calibrar un modelo es estimar y ajustar sus parámetros y constantes para maximizar el ajuste entre los resultados del modelo y el conjunto de datos (Rykiel 1996). El resultado de la ejecución del algoritmo es un modelo de distribución de la especie definido en el espacio ecológico (Benito 2009).

1.4.6. Predicción del modelo

Una vez que la respuesta de la especie o comunidad vegetal es derivada a partir de las técnicas de modelado disponibles, su distribución potencial dentro del área estudiada puede ser proyectada (Guisan & Zimmermann 2000). Durante la proyección, el modelo definido en el espacio ecológico se transfiere (proyecta) al espacio geográfico (Benito 2009). Esta proyección puede realizarse en la misma o distinta región geográfica y/o en el mismo o distinto tiempo.

La mayoría de los estudios identifican una descripción del nicho realizado como la salida de los MDE (Austin 2002; Thuiller *et al.* 2004b; Guisan & Thuiller 2005). Otros prefieren el término modelo de hábitat o modelo de distribución para MDE correlativos (Jiménez-Valverde *et al.* 2008), y reservan el término modelo de nicho para análisis mecanicistas (Kearney 2006). Se ha sugerido que los modelos de cubiertas ambientales (del inglés *environmental envelope-type*) que utilizan datos sólo de presencia tienden a representar la distribución potencial (hábitat idóneo) y son más adecuados para la extrapolación, mientras modelos complejos que discriminan presencia y ausencia tienden a predecir distribuciones realizadas (hábitat ocupado), y son más adecuados para la interpolación (Jiménez-Valverde *et al.* 2008; Hirzel & Le Lay 2008). Alternativamente, Soberón y Peterson (2005) argumentan que los MDE basados en variables climáticas a escala grosera (modelado del nicho bioclimático) describe el nicho fundamental de las especies.

1.4.7. Evaluación

La evaluación es un paso fundamental en la elaboración de cualquier modelo de distribución. Al evaluar un MDE no se pone en cuestión su veracidad, ya que los modelos no pueden ser testados como verdaderos o falsos, sino su capacidad para proporcionar buenas hipótesis comparables (Levins 1966) y su precisión en la predicción de patrones biológicos (Guisan & Zimmermann 2000). Por tanto, lo que realmente se evalúa es el grado de ajuste del resultado a los datos reales. Sin embargo, hay algunos casos en los que los modelos no pueden ser evaluados ya que los sucesos que estudian aún no han tenido lugar. Es el caso de las predicciones sobre el efecto del cambio climático en la distribución de las especies y comunidades.

De acuerdo a Guisan y Zimmermann (2000) existen dos aproximaciones principales para evaluar el poder predictivo de un modelo. La primera aproximación se basa en utilizar un único conjunto de datos (registros de presencia) para calibrar el modelo y posteriormente evaluarlo mediante procedimientos como *bootstrap*, validación cruzada o *jack-knife*. La segunda aproximación consiste en utilizar dos conjuntos de datos independientes, uno para calibrar el modelo y el otro, obtenido de una fuente distinta o una prospección de campo, para evaluarlo mediante medidas como la aproximación ROC (del inglés *receiver operating characteristic*). Sin embargo, cuando se trata con datos procedentes de atlas o bases de datos, puede resultar difícil obtener conjuntos de datos independientes (Lobo 2008). En estos casos, una partición aleatoria de la muestra de presencia, separando los datos en un conjunto de calibrado y otro de evaluación, es a menudo la única solución disponible para evaluar el modelo.

1.4.8. Post-procesamiento y análisis

El resultado más común de un modelo de distribución de especies es un mapa georreferenciado cuyas celdas toman valores con significado de idoneidad de hábitat o probabilidad de presencia. La fase de post-procesamiento y análisis nos permite transformar el significado del MDE en información útil para responder a los objetivos del modelo. Para ello, será necesario emplear programas de análisis estadístico y sistemas de información geográfica (SIG). En este sentido, los SIG nos permiten visualizar la información proporcionada por los MDE en forma de mapas y los programas de análisis estadístico nos permiten obtener gráficas explicativas y tablas numéricas.

1.4.9. Credibilidad y aplicabilidad del modelo

Un modelo debe ser discutido únicamente en el contexto previamente definido de su aplicación. Dicha discusión es particularmente importante cuando los modelos se aplican en un contexto de gestión de la naturaleza (Guisan & Zimmermann 2000). De acuerdo a Rykiel (1996), la credibilidad de un modelo se basa en un intervalo de confianza subjetivo mientras que la aplicabilidad se basa en descubrir la región sobre la cual un modelo validado puede ser utilizado correctamente.

1.5. Aplicaciones de los MDE

Los modelos de distribución de especies nos permiten *entender*, en base a observaciones, las relaciones existentes entre las especies y su ambiente biótico y abiótico (Franklin 2009). Además del gran avance que han supuesto estos modelos en el estudio y evaluación de la biodiversidad, los MDE han ganado importancia como herramientas de investigación en numerosas aplicaciones. Mediante el uso de estas aplicaciones podemos mejorar nuestro nivel de conocimiento y ser más eficaces a la hora de conservar la biodiversidad. Algunas de estas aplicaciones se resumen aquí con el fin de proporcionar un sentido amplio de los distintos usos de esta metodología.

Mejorar los atlas faunísticos y florísticos

Los MDE son útiles en la cartografía automática de las especies al obtenerse buenos resultados con un volumen limitado de datos (Hausser 1995; von Wehrden *et al.* 2009), facilitando la localización de especies raras (Guisan *et al.* 2006a), así como la localización de nuevas poblaciones de especies (Guisan *et al.* 2006b; Williams *et al.* 2009). Por otro lado, el análisis de los patrones espaciales de la biodiversidad nos permiten detectar áreas con baja y alta riqueza de especies (véanse Murray-Smith *et al.* 2008; *Capítulo 1*) así como áreas pobremente recolectadas o prospectadas (*Capítulo 1*). La mejora de los atlas faunísticos y florísticos nos ayuda a una mejor planificación en la priorización de las estrategias de conservación.

Testar hipótesis ecológicas y/o biogeográficas

Los MDE nos ayudan a entender las relaciones existentes entre las especies y sus ambientes abiótico y biótico en base a observaciones con el propósito de testar hipótesis ecológicas y/o biogeográficas que anteriormente no podían serlo debido a limitaciones metodológicas (Mourelle & Ezcurra 1996; Leathwick 1998). Los recientes avances en los sistemas de información geográfica y la gran cantidad de datos disponibles en multitud de bases de datos de biodiversidad (véase Guisan & Thuiller 2005) permiten realizar análisis robustos del nicho ecológico de las especies (Chefaoui *et al.* 2005; Acevedo *et al.* 2007; Hortal *et al.* 2005). En este contexto, evaluar el papel del potencial dispersivo de las especies en paisajes cambiantes resulta de especial importancia a la hora de predecir su viabilidad en el tiempo (véanse Cabral *et al.* 2013; *Capítulo 3*).

Los modelos de distribución de especies son ampliamente utilizados para interpolar o extrapolar a partir de observaciones en el espacio. Los mapas de idoneidad de hábitat, o las distribuciones de especies resultantes, son útiles para testar hipótesis sobre las características del ámbito de distribución de las especies, particiones del nicho o conservadurismo del nicho (Martínez-Meyer *et al.* 2004).

Predecir los efectos del cambio climático

El cambio climático está alterando los patrones globales de biodiversidad al modificar la distribución geográfica de las especies (Brook *et al.* 2009). Los MDE se han utilizado en las últimas décadas para proyectar el efecto potencial del calentamiento global sobre la distribución geográfica de las especies y comunidades (Araújo & Rahbek 2006; *Capítulo 2*; *Capítulo 3*). Aunque la relación entre el clima y la distribución de las especies está bien establecida (Woodward 1987), el uso de MDE para predecir el impacto del cambio climático en la distribución de las especies requiere una serie de asunciones. Se tiene que asumir que la distribución actual de las especies tiende a estar en equilibrio con el clima actual (Lenihan 1993). Por otro lado, el enfoque estático de los MDE para modelar la respuesta geográfica de las especies al cambio climático, no tiene en cuenta la habilidad de las especies para moverse en el paisaje (dispersión o migración), o lo hace de manera simple, normalmente asumiendo una dispersión de "todo o nada" (Araújo *et al.* 2006; Midgley *et al.* 2006; Thuiller *et al.* 2006). Ya en 2005, Guisan y Thuiller apuntaban que únicamente mediante el desarrollo de modelos dinámicos, que incorporen procesos poblacionales y de dispersión, así como procesos ecológicos que influyen en la idoneidad de hábitat (por ejemplo perturbaciones), podremos ir más allá de la simple simulación de los cambios potenciales en el área de distribución de las especies. Las aplicaciones de esta metodología para predecir los impactos del calentamiento global está en continuo avance y desarrollo. Aún así, son pocos los trabajos que aplican modelos dinámicos al estudio de la biodiversidad (Renton *et al.* 2012; Cabral *et al.* 2013; Conlisk *et al.* 2013; *Capítulo 3*).

Diseño de reservas y planes de conservación

Las áreas protegidas pueden priorizarse en base a los patrones de ocurrencia de las especies mediante mapas de distribución de especies o de idoneidad de hábitat (*Capítulo 1*). Los MDE nos permiten a su vez evaluar las amenazas de estas áreas así

como localizar áreas de persistencia potencial de las especies e identificar corredores migratorios. Algunos de los ejemplos más representativos de esta aplicación los encontramos en los trabajos propuestos por Araújo *et al.* (2002), Cabeza *et al.* (2004), Ferrier (2002), Papes & Gaubert (2007) y en el *Capítulo 3* de la presente Tesis.

Otras aplicaciones no evaluadas en esta Tesis son: la evaluación del riesgo de invasión por especies exóticas, en la que los MDE se han utilizado a menudo para localizar áreas, a escala continental o regional, climáticamente similares a la extensión geográfica actual de especies exóticas y, que por tanto, serían susceptibles de una colonización exitosa en el caso de una introducción (Guisan & Thuiller 2005); evaluar el efecto de las posibles alteraciones del hábitat (Benito & Peñas 2008); o la reconstrucción de distribuciones en el pasado (Benito-Garzón *et al.* 2007; Rodríguez-Sánchez & Arroyo 2008).

1.6. Limitaciones

El mundo real es complejo y multidimensional, por lo que no es razonable esperar que toda la complejidad y heterogeneidad de la naturaleza sea reflejada con elevada precisión por un simple modelo (Guisan & Zimmermann 2000). Muchas de estas limitaciones son inherentes al proceso de modelado y, por tanto, difícilmente salvables, mientras que otras están siendo objeto de investigaciones en la actualidad (Pearson & Dawson 2004), como por ejemplo el efecto de la escala, las interacciones bióticas, o las capacidades dispersivas de las especies. En la literatura se encuentran numerosos trabajos sobre las limitaciones asociadas a estos modelos (Guisan & Zimmermann 2000; Hampe 2004; Pearson & Dawson 2004; Guisan & Thuiller 2005; Soberón & Peterson 2005; Pearson *et al.* 2006; Zurell *et al.* 2009). A continuación describiremos brevemente algunas de las limitaciones más destacadas en la literatura.

Al construir un modelo se asume que la especie o comunidad vegetal está en (pseudo) equilibrio con las condiciones ambientales (Araújo & Pearson 2005). Esto supone que la distribución de la especie o comunidad es estable en el tiempo y el espacio, algo que generalmente se desconoce (Mateo *et al.* 2011). Sin embargo, esta limitación resulta menos restrictiva para especies o comunidades con alta persistencia o que reaccionan lentamente a la variabilidad ambiental (Benito 2009).

Por otro lado, la distribución de las especies responde a procesos complejos donde las relaciones bióticas tienen gran importancia. La mayoría de los trabajos que emplean modelos de distribución de especies no tienen en consideración factores como la competencia (Davis *et al.* 1998; Fitzpatrick *et al.* 2007), la facilitación, herbivoría, depredación (Sánchez-Cordero & Martínez-Meyer 2000), simbiosis o el mutualismo (Gutiérrez *et al.* 2005).

Por último cabe destacar, que la mayoría de estudios de modelado de especies no incorporan el efecto de fenómenos como la dispersión de las especies. Por lo que estudios sobre el efecto del cambio climático en la distribución de las especies que ignoren el potencial dispersivo de las especies pueden diferir en gran medida de las distribuciones reales futuras debido a limitaciones para su dispersión (Pearson & Dawson 2003).

Finalmente, conociendo las limitaciones de los MDE, estaremos en una mejor posición para hacer un uso apropiado de sus resultados (Whittaker *et al.* 2005). Entender las limitaciones ambientales del modelado de la distribución de especies a través de estudios a distintas escalas, resulta fundamental a la hora de desarrollar aplicaciones útiles que puedan proporcionar predicciones fiables sobre la distribución de las especies.

2. General introduction

2.1. The conservation of biodiversity and species distribution models

Since the United Nations Conference on the environment and sustainable development held in Rio de Janeiro in 1992, biodiversity has received increasing attention from scientists, governments and the global public. However, despite the efforts made, there is clear evidence that we are facing a crisis of biodiversity (Loreau *et al.* 2006), of which practically all aspects are in decline. This loss of biodiversity has been accentuated in recent years due to numerous threats including the destruction and degradation of habitat, climate change, the spread of invasive species and over-exploitation (see Pimm & Raven 2000; Sax & Gaines 2008). However, while phenomena such as global warming, pollution and changes in land-use operate over very large areas or for long periods of time, the field data that characterize the ecological research is normally gathered in relatively small areas during studies of short duration (Miller *et al.* 2004). Scientists are therefore required to increasingly use local measurements and data to evaluate changes to the landscape of regional and global scales by using models or statistical simulations to extrapolate these environmental data to the geographical space (Miller *et al.* 2004; Peters *et al.* 2004).

Species distribution models (SDMs) are only one type of these models or simulations and are examples of models of growing importance. In recent decades there has been a growing interest in modelling the distribution of species resulting from the confluence between the growing need for information on the geographical distribution of biodiversity and the development of new and improved techniques for modelling (Franklin 2009). SDMs extrapolate distribution data of species in space and time, usually on the basis of statistical models. The purpose of SDMs and, in particular, of the resulting predictive maps, is to provide spatially-explicit information on the species and other elements of biodiversity associated with a location in geographical space for many different applications such as the development of conservation plans, risk assessment and resource management (Franklin 2009).

2.2. The geographical scale

A characteristic of biological systems is that they are governed by complex processes that act at different spatial and temporal scales. In the study of the distribution of species and plant communities, the resolution and the scope determine the

geographical scale of the work, and influence the applicability of the results (Willis & Whittaker 2002; Elith & Leathwick 2009). The geographical scale generally reflects the purpose of the analysis. For example, studies on macro-ecological and global changes tend to be at a continental scale and for worldwide scopes (Araujo & New 2007), while studies directed at detailed ecological understanding or conservation planning tend to be at a local scale for regional scopes (Fleishman *et al.* 2001; Ferrier *et al.* 2002). The resolution not only describes the properties of environmental variables, cell size or digital map polygon, but also describes the spatial accuracy of the information relating to the distribution of the species (Dungan *et al.* 2002; Tobalske 2002). The resolution needs to be consistent with the informational content of the data, as changes in resolution involve changes in the perception of phenomena such as patterns of presence or abundance (Guisan *et al.* 2007). In practice, however, this is not always possible and the explanatory layers sometimes need to be defined to resolutions that are finer than the original data.

On the other hand, although conceptually there is no unique natural scale to which to study ecological patterns (Levin, 1992), it is necessary to study at different geographical scales for efficiency in the conservation of biodiversity. This thesis addresses the analysis of plant biodiversity using different geographical scales and levels of organization of plants, according to the objectives set, the properties of the system and the available data (Table 1).

Geographic scale	Level of organization of plants	Environmental determinants	Reference
Regional (10km)	Flora	Climate	<i>Chapter 1.</i>
Landscape (1km)	Plant communities	Climate, topography, substrate	<i>Chapter 2.</i>
Local (200m)	Individual species-level detail	Substrate, biotic interactions	<i>Chapter 3.</i>

Table 1. Scales designed for effective modelling for the conservation of plant diversity.

2.3. Conceptual and theoretical aspects

A model is a conceptual construction that describes, in a simplified manner, a physical system that exists in the real world and that assists with the understanding of its operation (Benito 2009). In this context, an SDM is a numerical construction that defines, in ecological space, the relationships between the presence of a species or plant community and the values of environmental variables that influence their distribution,

assisting with the interpretation and understanding of the distribution of the species (Franklin 2009).

The area of distribution of a species is the set of locations of the geographical space in which its presence can be detected (Soberón 2007), and reflects the ecology and evolutionary history of the species (Brown 1995). This area is determined by the dynamic interaction of various factors (biotic, abiotic, dispersive and evolutionary potential) that operate with different intensity and at different spatial and temporal scales (Gaston 2003; Pearson & Dawson 2003).

Species distribution models are generally based on biogeographical hypotheses (Box 1981), on the analysis of ecological gradients (Whittaker 1960; Whittaker *et al.* 1973) and on how environmental factors control the distribution of species and communities (Guisan & Zimmermann 2000), having their roots in the ecological niche theory.

The first formal definition of an ecological niche is attributed to Grinnell (1917), whose interest focused on the factors that determine where a species can be found. The concept is based on the importance of environmental conditions defined at a relatively coarse geographical scale. A decade later, Elton (1927) defined the niche as the functional role of a species in the biotic community, stating that each species has a unique role in the ecosystem. Elton narrowed the definition of niche in terms of interactions between species and availability of resources. In 1987, Hutchinson redefines the concept of niche as *a hyper-volume in the multidimensional ecological space determined by the requirements of the species to reproduce and survive*. More specifically, Hutchinson differentiates the *fundamental* niche (physiological or potential), defined as the response of species to the environment in the absence of biotic interactions (predation, competition, mutualism), from the *realised* niche (organic or real), defined as the environmental dimensions in which the species can survive and reproduce, including the effects of biotic interactions (Austin & Smith 1989; Austin, 2002; Chase & Leibold 2003) (see Figure 1). Finally, Pulliam (2000) proposed that the concept of niche of Hutchinson (1987) along with the theory of meta-populations (Hanski 1999) and the source-sink theory (Pulliam 1988) could help to explain the relationships between the distribution of the species and its suitable habitat.

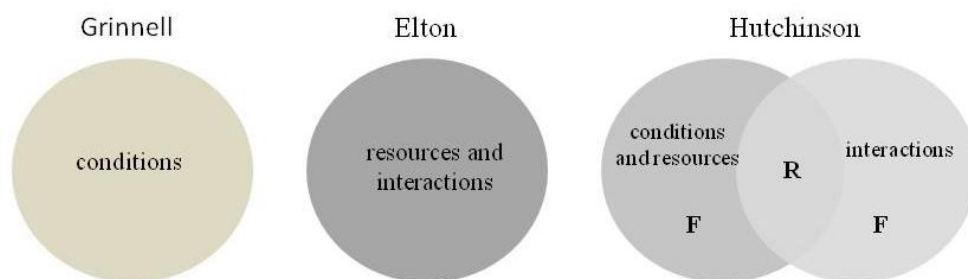


Figure 1. Concepts of ecological niche of Grinnell, Elton and Hutchinson, where **F** refers to the fundamental or potential niche and **R** to the realized niche. Figure adapted from Benito (2009).

SDMs rely primarily, although not exclusively, on the concept of the niche that emphasizes the requirements of the species, through representations of abiotic factors controlling their distribution.

2.4. Construction of SDMs

The generation of an SDM is a complex process which needs a large quantity of data and in-depth knowledge of the different modelling techniques. To ensure the correct construction of a predictive model, it is essential to follow a process that includes nine basic steps (Figure 2), which are explained below and are repeated throughout the development of this thesis.

2.4.1. Conceptual model

The prediction of the geographical distribution of a plant or a plant community begins with the theoretical formulation of the model. This is based on the theory of the ecological niche and under the premise that the distribution of the vegetation can be predicted from the spatial distribution of environmental variables that are correlated or that directly control the distribution of plants (Franklin 1995). When applying the concept of a niche in the static modelling of the distribution of the species, i.e. not including dynamic elements, it is assumed that species are in (pseudo) equilibrium with the current environmental conditions, and that the distributions and abundances observed are indicators of their environmental tolerances and resource requirements (Franklin 2009). During this phase, the factors that affect the distribution of the species or vegetal community and which could be included in the model should be selected. The theoretical formulation requires an in-depth knowledge of the modelling techniques, the biology of the studied organism and a clear definition of the objectives (Benito 2009).

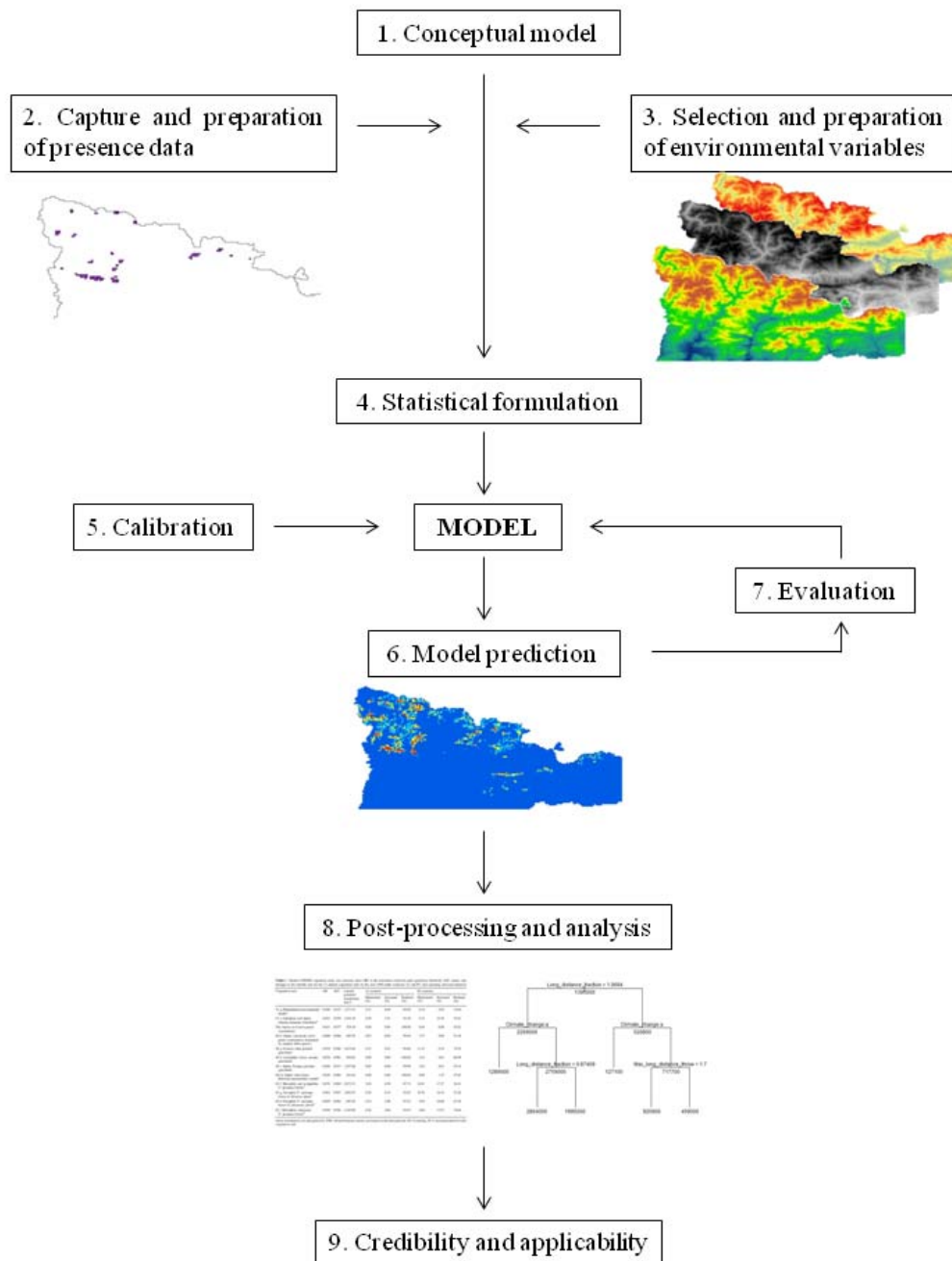


Figure 2. General view of the basic steps (1 to 9) needed to the correct construction of a predictive model.

2.4.2. Capture and preparation of presence data

Presence records are essential to generate distribution models. These presence records are based on pairs of coordinates that identify, in the geographic space, locations in which the presence of the species or plant community has been detected. Some modelling algorithms also need absence records; however, these absence data are difficult to obtain and are usually subject to great uncertainty. Organizations such as the Global Biodiversity Information Facility (GBIF), the Iberian and Macaronesian Vegetation Information System (SIVIM), the Biodiversity Data Bank of Catalonia (BDBC), among many others, are working on different scales to make biodiversity data accessible via the internet by developing protocols for data-sharing. These projects provide data of incalculable value that are used to describe the geographical area of the species.

Once data is compiled from the presence of the object of study, it is necessary to process them, filtering errors (mainly of taxonomic type), analysing the presence of bias in sampling and adapting presence records to the specific format required for the application of the algorithm of the modelling.

2.4.3. Selection and preparation of environmental variables

An important issue that pertains to modelling the geographical distribution of species and communities is to decide which variables should be used to meet the objectives. Due to the complexity of the ecological niche, it is virtually impossible to work with all the variables that define it. Therefore, to increase the accuracy and predictive power of the model, the number of descriptive variables used should be reduced to a reasonable number (Harrell *et al.* 1996). On the other hand, the selection of descriptive variables requires consideration of the spatial hierarchy which are subject to the variables that control the distribution of plants (Neilson 1995; Huntley *et al.* 1995). The climatic variables control the distribution patterns of large ranges and low resolutions, while geological and topographic variables are critical to small ranges and high spatial resolutions. Due to the recent development of dynamic models, which can add to the process of modelling elements such as demographic values, dispersive species capacity, and values on the effects of competition for the resources available in the environment, it is becoming more common to obtain more realistic approaches.

2.4.4. *Statistical formulation*

During the statistical formulation, referred to as verification by some authors (e.g. Rykiel 1996), an appropriate algorithm is required to be selected for the purpose of predicting a dependent variable type and to estimate the coefficients of the model, as well as an optimal statistical approach given the context of the model (Guisan & Zimmermann 2000). A variety of techniques specifically designed to model the potential distribution of species and communities is currently available. However, most of the models are specific to a particular type of dependent variable, being the first determining factor when selecting the method of modelling to be used (Guisan & Zimmermann 2000). There are numerous studies that compare the practical performance of different algorithms (e.g. Guisan *et al.* 1999; Pearce & Ferrier 2000; Thuiller 2003; Elith *et al.* 2006). Below the main modelling techniques used in this thesis are briefly described.

Generalized linear model (GLM). The GLM is widely used in modelling the distribution of species because of its strong statistical basis (Austin, 2002). The generalized linear model is an extension of the multiple regression model that uses a *link* function allowing other distributions for the response variable in addition to the Gaussian, such as Poisson, Binomial or Gamma.

Multivariate adaptive regression splines (MARS). This method fits a curve with input data using a segmented polynomial regression analysis, calculating individual equations for groups of points, which are subsequently added in a single global equation (Friedman 1991; Leathwick *et al.* 2006).

Maximum entropy. This model is also known as Maxent (Phillips *et al.* 2006) and is a relatively recent method, which, according to Elith *et al.* (2006), outperforms other more established methods, showing greater predictive accuracy than other techniques when presence-only data are used. This method establishes that the best approximation of an unknown distribution is a probability distribution with maximum entropy or the closest to uniform (Phillips *et al.* 2006). Its good performance and ease of use have extended its use by the scientific community. Since its introduction in 2004, it has been widely used in the modelling of the distribution of species with different objectives (Elith *et al.* 2011).

BioMove. The response of the species to environmental changes will likely depend on the interactions between the species (Araújo & Luoto 2007), population processes (Maschiski *et al.* 2006) and landscape dynamics (Wintle *et al.* 2005). Therefore, the predictions regarding the response of species to environmental changes based solely on projected changes in the availability of suitable habitat from an SDM are usually incomplete. These predictions may be more accurate if models that incorporate the interactions between the changes in habitat, the structure of the landscape and the population dynamics of the species are developed. The program BioMove (Midgley *et al.* 2010) was designed to simulate changes in the geographic range of plant species in response to environmental changes, by linking a dynamic vegetation model (based on plant functional types, PFT) with the population model of the species of study. Integrating demographic models and vegetation dynamics, BioMove can directly address the effect of competition for resources.

2.4.5. Calibration of the model

The calibration of a model involves the estimation and adjustment of its parameters and constants to maximize the fit between the results of the model and the data set (Rykiel 1996). The result of the execution of the algorithm is a species distribution model defined in the ecological space (Benito 2009).

2.4.6. Model prediction

Once the response of the species or vegetal community is derived from the modelling techniques available, their potential distribution within the studied area can be projected (Guisan & Zimmermann 2000). During the projection, the model defined in the ecological space is transferred (projected) to the geographical space (Benito 2009). This projection can be done in the same or a different geographical region or in the same or a different time.

Most studies identify a niche description as an output of the SDM (Austin 2002; Thuiller *et al.* 2004b; Guisan & Thuiller 2005). Others prefer the term “habitat model” or “distribution model” for correlative SDMs (Jiménez-Valverde *et al.* 2008), and reserve the term “niche model” for mechanistic analysis (Kearney 2006). It has been suggested that environmental envelope-type models that use presence-only data tend to represent the potential distribution (suitable habitat) and are more suitable for extrapolation, while complex models that discriminate presence and absence tend to

predict realised distributions (occupied habitat), and are more suitable for interpolation (Jiménez-Valverde *et al.* 2008; Hirzel & Le Lay 2008). Alternatively, Soberón and Peterson (2005) argue that SDMs based on climatic variables at a large scale (the bioclimatic niche modelling) describe the fundamental niche of the species.

2.4.7. Evaluation

Evaluation is a key step in the development of any distribution model. When evaluating a SDM its veracity is not in question as models cannot be tested as true or false; rather in question are its ability to provide good comparable hypotheses (Levins 1966) and its accuracy in the prediction of biological patterns (Guisan & Zimmermann 2000). What is actually evaluated is therefore the degree of adjustment of the results to the actual data. However, there are some cases in which models cannot be evaluated since the events being studied have not yet occurred. This is the case in predictions of the effect of climate change on the distribution of species and communities.

According to Guisan and Zimmermann (2000) there are two main approaches to assess the predictive power of a model. The first approach is based on using a single set of data (records of presence) to calibrate the model and then evaluate it through procedures such as bootstrap, cross validation or Jack-knife. The second approach is to use two independent datasets, one to calibrate the model and the other, from a different source or from a field survey, to evaluate it through measures such as the receiver operating characteristic (ROC) approach. However, when it comes with data coming from an atlas or from databases, it may be difficult to obtain independent datasets (Lobo 2008). In these cases, a random partition of the presence sample separating the data into a calibration set and another for assessment is often the only solution available to evaluate the model.

2.4.8. Post-processing and analysis

The most common result of a species distribution model is a georeferenced map whose cells take values with significance of habitat suitability or probability of presence. The post-processing and analysis phase allows us to transform the meaning of the SDM into useful information to respond to the objectives of the model. To do this, it will be necessary to employ statistical analysis and geographic information systems (GIS) programs. In this sense, GIS allows us to visualize the information provided by

the SDM in the form of maps and the statistical analysis programs allow us to obtain explanatory graphics and numerical tables.

2.4.9. Credibility and applicability of the model

A model should be discussed only in the previously defined context of its application. This discussion is particularly important when models are applied to a context of nature management (Guisan & Zimmermann 2000). According to Rykiel (1996), the credibility of a model is based on a subjective confidence interval while the applicability is based on discovering the region over which a validated model can be used correctly.

2.5 Application of the SDM

Species distribution models allow us to *understand*, based on observations, the relationships between species and their biotic and abiotic environments (Franklin 2009). In addition to the great progress these models have provided in the study and assessment of biodiversity, SDMs have gained importance as research tools in many applications. Through the use of these applications we can improve our level of knowledge and be more effective in conserving biodiversity. Some of these applications are summarized here in order to provide a broader sense of the different uses of this methodology.

Improvement of faunistic and floristic atlases

SDMs are useful in the automatic mapping of species, obtaining good results with a limited volume of data (Hausser 1995; von Wehrden *et al.* 2009), facilitating the location of rare species (Guisan *et al.* 2006) and the location of new populations of species (Guisan *et al.* 2006b; Williams *et al.* 2009). On the other hand, the analysis of the spatial patterns of biodiversity enable us to detect areas with high and low species richness (see Murray-Smith *et al.* 2008; *Chapter 1*) as well as areas poorly prospected or surveyed (*Chapter 1*). Improvement of the wildlife and floristic atlases helps us with better planning in the prioritization of conservation strategies.

Testing ecological or biogeographical hypotheses

SDMs assist in the understanding of the relationships between species and their abiotic and biotic environments based on observations, to test ecological and/or biogeographical hypotheses that previously could not be tested due to methodological

limitations (Mourell & Ezcurra 1996; Leathwick 1998). Recent advances in geographic information systems and the large amount of data available in a multitude of biodiversity databases (see Guisan & Thuiller 2005) allow robust analysis of the ecological niche of the species (Chefaoui *et al.* 2005; Acevedo *et al.* 2006; Hortal *et al.* 2005). In this context, to assess the role of the dispersal potential of the species in changing landscapes is of special importance in predicting its viability over time (see Cabral *et al.* 2013; *Chapter 3*).

Species distribution models are widely used to interpolate or extrapolate based on space observations. The habitat suitability maps, or the resulting species distributions, are useful to test hypotheses on the characteristics of the area of distribution of the species, partitions of the niche, or conservatism of the niche (Martinez-Meyer *et al.* 2004).

Predicting the effects of climate change

Climate change is altering the global biodiversity patterns by changing the geographical distribution of the species (Brook *et al.* 2009). SDMs have been used in recent decades to project the potential effect of global warming on the geographical distribution of species and communities (Araújo & Rahbek 2006; *Chapter 2*; *Chapter 3*). Although the relationship between the climate and the distribution of species is well established (Woodward 1987), the use of SDMs to predict the impact of climate change on the distribution of the species requires a number of assumptions. It is assumed that the current distribution of species tends to be in equilibrium with the current climate (Lenihan 1993). On the other hand, the static approach of SDMs to model species' geographical responses to climate change does not consider the ability of the species to move in the landscape (dispersal or migration), or it does so in a simplified manner, usually assuming a dispersal of "all or nothing" (Araújo *et al.* 2006; Midgley *et al.* 2006; Thuiller *et al.* 2006). As early as 2005, Guisan and Thuiller noted that only through the development of dynamic models that incorporate population and dispersal processes as well as ecological processes that influence the suitability of habitat (e.g. interference) can we go beyond simple simulation of potential changes in the area of distribution of the species. The applications of this methodology to predict the impacts of global warming are in continuous progress and development. Even so, few studies apply dynamic models to the study of biodiversity (Renton *et al.* 2012; Cabral *et al.* 2013; Conlisk *et al.* 2012; *Chapter 3*).

Design of reserves and conservation plans

Protected areas can be prioritized based on the patterns of occurrence of the species with distribution maps of species or suitability of habitat (*Chapter 1*). SDMs allow us in turn to evaluate the threats to these areas as well as to locate areas of potential persistence of the species and to identify migratory corridors. Some of the most representative examples of this application can be found in studies by Araújo *et al.* (2002), Cabeza *et al.* (2002), Ferrier (2002), Papes & Gaubert (2007) and in *Chapter 3* of this thesis.

Other applications not evaluated in this thesis are: the evaluation of the risk of invasion by exotic species, in which SDMs have often been used to locate areas, at a continental or regional scale, that are climatically similar to the current geographical spread of exotic species and, therefore, would be susceptible to a successful colonization in a case of an introduction (Guisan & Thuiller 2005); the evaluation of the effects of possible alterations of the habitat (Benito & Peñas 2007); or the reconstruction of distributions of the past (Benito-Garzón *et al.*, 2007; Rodríguez-Sánchez & Arroyo 2008).

2.6 Limitations

The real world is complex and multidimensional, therefore it is not reasonable to expect that all the complexity and heterogeneity of nature is reflected with high precision by a simple model (Guisan & Zimmermann 2000). Many of these limitations are inherent in the process of modelling and are therefore difficult to overcome, while others are currently under investigation (Pearson & Dawson 2004), for example, the effect of scale, biotic interactions or species dispersive capabilities. Numerous studies about the limitations associated with these models are in the literature (Guisan & Zimmermann 2000; Hampe 2004; Pearson & Dawson, 2004; Guisan & Thuiller 2005; Soberón & Peterson 2005; Pearson *et al.* 2006; Zurell *et al.* 2009). Below we describe briefly some of those most prominent in the literature.

When building a model it is assumed that the species or the plant community is in (pseudo) equilibrium with environmental conditions (Araújo & Pearson 2005), that is, that the distribution of the species or community is stable in time and space, something that is usually unknown (Matthew *et al.* 2011). However, this limitation is less

restrictive for species or communities with high persistence or that react slowly to environmental variability (Benito 2009).

On the other hand, the distribution of species responds to complex processes where the biotic relationships are of great importance. Most studies that use species distribution models do not take into account factors such as competition (Davis *et al.* 1998; Fitzpatrick *et al.* 2007), facilitation, herbivory, predation (Sánchez-Cordero & Martínez-Meyer 2000), symbiosis or mutualism (Gutiérrez *et al.* 2005).

It should finally be noted that most species-modelling studies do not include the effect of phenomena such as the dispersal of the species. Therefore, studies on the effect of climate change on the distribution of the species that ignore the dispersal potential of the species may differ greatly from actual future distributions due to limitations to its dispersal (Pearson & Dawson 2003).

Finally, by understanding the limitations of SDMs, we will be in a better position to make proper use of their results (Whittaker *et al.*, 2005). Understanding the environmental limitations of modelling the distribution of species through studies at different scales is essential to developing useful applications that can provide reliable predictions of the distribution of the species.

OBJETIVOS

1. Objetivos

1.1. Objetivos generales

La finalidad de esta Tesis doctoral es investigar la aplicabilidad del modelado de la distribución de especies al estudio de la diversidad vegetal, mediante el uso de distintas técnicas de modelado (MDE), escalas geográficas y niveles de organización de plantas. Es por tanto, una investigación aplicada que pretende mostrar la utilidad de nuevas herramientas de análisis espacial para la gestión y conservación de la diversidad vegetal. El estudio se ha realizado a través de diferentes aproximaciones, las cuales se enumeran a continuación:

a) Descripción de patrones de riqueza de plantas en Cataluña y detección de puntos calientes de biodiversidad en la región, mediante la utilización de tres técnicas distintas de modelado y en base a la distribución conocida de toda su flora (*Capítulo 1*).

b) Evaluación del efecto del cambio climático en las regiones alpinas y subalpinas del Pirineo Oriental, a través del estudio de la distribución potencial de unidades de vegetación (enfoque *top-down*) y valoración de su aplicabilidad en relación al modelado de especies (enfoque *bottom-up*) (*Capítulo 2*).

c) Construcción de un modelo dinámico para evaluar los efectos del cambio climático en la viabilidad a largo plazo de un taxón endémico y amenazado de la Península Ibérica, *Vella pseudocytisus* subsp. *pau* Gómez Campo. La generación de un modelo dinámico proporciona una aproximación más realista al incorporar la dinámica demográfica de la especie estudiada, y nos permite estimar su riesgo de extinción (*Capítulo 3*).

d) Selección e implementación de un algoritmo de modelado en línea en el servidor de datos Sistema de la Vegetación Ibérica y Macaronésica (SIVIM) (*Capítulo 4*).

1.2. Objetivos específicos

A continuación se detallan los objetivos específicos de cada uno de los capítulos:

Capítulo 1:

(i) Describir patrones de riqueza de especies de plantas en Cataluña a través de modelos de distribución de especies (MDE) y evaluar si estas técnicas de modelado son una metodología adecuada para mejorar los patrones de distribución proyectados por el

Banco de Datos de Biodiversidad de Cataluña (Banc de Dades de Biodiversitat de Catalunya, BDBC).

(ii) Identificar áreas de alta riqueza de especies vegetales.

(iii) Detectar zonas insuficientemente muestreadas en el territorio y estimar el número mínimo de especies esperadas en dichas áreas.

Capítulo 2:

(i) Evaluar, en términos de pérdidas de área, los posibles impactos del cambio climático en la distribución potencial de las principales unidades de vegetación alpinas y subalpinas del Pirineo Oriental a finales del siglo XXI. Concretamente, se estudiaron seis prados alpinos, dos matorrales subalpinos (y alpinos) y cuatro bosques subalpinos de *Pinus uncinata* L., empleando un algoritmo de máxima entropía (Maxent).

(ii) Estudiar la utilidad de las técnicas de modelado para predecir cambios futuros en la distribución de unidades de vegetación, a través de un enfoque *top-down*, en relación al modelado de especies (enfoque *bottom-up*).

Capítulo 3:

(i) Evaluar los efectos del cambio climático sobre la viabilidad futura de un taxón endémico y amenazado de la Península Ibérica, *Vella pseudocytisus* subsp. *pau* Gómez Campo, a partir de la construcción de un modelo dinámico (BioMove).

(ii) Estudiar la importancia del potencial dispersivo de la especie para su supervivencia, es decir, dilucidar si la dispersión es verdaderamente un factor limitante en la viabilidad a largo plazo de la especie.

(iii) Identificar áreas refugio que puedan albergar poblaciones viables en el futuro y apoyar así la planificación de políticas relacionadas con su conservación.

Capítulo 4:

(i) Seleccionar e implementar un algoritmo de modelado en el Sistema de Información Ibérica y Macaronésica (SIVIM).

2. Objectives

2.1. General objectives

The purpose of this doctoral thesis is to investigate the applicability of modelling the distribution of species on the study of plant diversity, through the use of various modelling techniques (SDM), geographic scales and levels of organization of plants. It is, therefore, an applied research that aims to show the utility of new tools of spatial analysis for the management and conservation of plant diversity. The study was conducted through different approaches, which are listed below:

a) Description of plant richness patterns in Catalonia and detection of biodiversity hotspots in the region through the use of three different modelling techniques and based on the known distribution of its entire flora (*Chapter 1*).

(b) Evaluation of the effect of climate change in the alpine and subalpine regions of the Oriental Pyrenees through the study of the potential distribution of vegetation units (top-down approach) and evaluation of their applicability in relation to species (bottom-up approach) modelling (*Chapter 2*).

(c) Construction of a dynamic model to assess the effects of climate change on the long-term viability of an endemic and threatened taxon of the Iberian Peninsula, *Vella pseudocytisus* subsp. *pau* Gómez Campo. The generation of a dynamic model provides a more realistic approach to incorporate the demographic dynamics of the studied species, and allows us to estimate its risk of extinction (*Chapter 3*).

(d) Selection and implementation of an online modelling algorithm on the server of the Iberian and Macaronesian Vegetation Information System (SIVIM) (*Chapter 4*).

2.2. Specific objectives

The objectives of each of the chapters are as follows:

Chapter 1:

(i) To describe plant species richness patterns in Catalonia based on species distribution models (SDMs) and assess whether these modelling techniques are an appropriate methodology to improve the distribution patterns designed by the Biodiversity Data Bank of Catalonia (Banc de Dades de Biodiversitat de Catalunya, BDBC).

Objectives

(ii) To identify areas of high plant species richness.

(iii) To identify areas insufficiently sampled in the territory and estimate the minimum number of species expected in those areas.

Chapter 2:

(i) To assess, in terms of losses of area, the potential impacts of climate change on the potential distribution of the main alpine and subalpine vegetation units of the Oriental Pyrenees at the end of the 21st century. In particular, we studied six alpine grasslands, two subalpine (and alpine) scrublands and four subalpine forests of *Pinus uncinata* L., using an algorithm of maximum entropy (Maxent).

(ii) To study the usefulness of modelling techniques to predict future changes in the distribution of vegetation units, through a top-down approach, in relation to the species modelling (bottom-up approach).

Chapter 3:

(i) To assess the effects of climate change on the future viability of an endemic and threatened taxon of the Iberian Peninsula, *Vella pseudocytisus* subsp. *pau* Gómez Campo, from the construction of a dynamic model (BioMove).

(ii) To study the importance of the dispersal potential of the species for its survival, i.e., whether dispersal is truly a limiting factor in the species' long-term viability.

(iii) To identify shelter areas that can accommodate viable populations in the future and thus support policy planning related to their conservation.

Chapter 4:

(i) To select and implement a modelling algorithm within the Iberian and Macaronesian Vegetation Information System (SIVIM).

PUBLICACIONES

Chapter 1. Predicting vascular plant richness patterns in Catalonia (NE Spain) using species distribution models

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Predicting vascular plant richness patterns in Catalonia (NE Spain) using species distribution models

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Keywords

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Nomenclature

Bolòs *et al.*

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Abstract

Question: Given the current state of knowledge on plant species richness in Catalonia, how can we improve definition of sampled species richness patterns? We propose a concrete methodology that will highlight the most speciose areas and those areas that are insufficiently sampled.

Location: Catalonia, covering 31 980 km² in northeast Spain.

Methods: This study provides a quantitative assessment of plant richness using sampling units of 10 km × 10 km (n = 319). Generalized linear models (GLM), multivariate adaptive regression splines (MARS) and a maximum entropy model (Maxent) were used for all plant species contained in the Catalonia Database of Biodiversity (Banc de Dades de Biodiversitat de Catalunya, BDBC). The projected presence/absence maps were combined to create species richness maps based on distribution models for 2738 species.

Results: The modelling techniques were highly correlated, and we did not distinguish any differences in projections of geographic patterns of species richness among the modelling algorithms. However, MARS and Maxent achieved the best prediction success, whereas GLM tended to over-predict species number per quadrat. The MARS map gave the highest predictive performance based on both Kappa and the true skill statistic, and for the two components of disagreement (quantity and allocation disagreement). We were able to identify one previously known region of high diversity, the Pyrenees, and two additional areas, the coastal range and the pre-coastal mountain range.

Conclusions: We obtain improved distribution patterns for plant species in Catalonia over the previously sampled patterns, and, most importantly, we provide an estimate of the number of species present in those areas where sampling data are incomplete, with an expected 300 species. The model-predicted richness maps presented here can be used to detect zones with low and high species richness and to develop strategies for either restoring or protecting landscape biodiversity as part of national conservation plans.

Introduction

One of the major challenges for conservation biology is to stop the ongoing and accelerating decline of biodiversity (Pimm *et al.* 1995). One way to increase the efficiency of conservation is to focus efforts on species-rich sites or 'biodiversity hotspots' (Myers *et al.* 2000). Plant diversity hotspots are well identified on a global scale, but smaller, local hotspots must be identified within these regions to allow effective conservation of plants on both global and local scales (Murray-Smith *et al.* 2008). The estimation of geo-

graphical distribution of species richness is necessary to understand the ecological and evolutionary determinants of spatial patterns of biodiversity (Rosenzweig 1995; Ricklefs 2004). However, it is not easy to evaluate species richness distributions across heterogeneous regions where collecting efforts have not been sufficient or adequately planned (Hortal *et al.* 2007).

Recently, species distribution modelling (SDM) has emerged as a novel approach for generating distributions based on the relationship between species' presence or abundance records and environmental variables. Large

1. Introduction

One of the major challenges for conservation biology is to stop the ongoing and accelerating decline of biodiversity (Pimm *et al.* 1995). One way to increase the efficiency of conservation is to focus efforts on species-rich sites or “biodiversity hotspots” (Myers *et al.* 2000). Plant diversity hotspots are well-identified on a global scale, but smaller, local hotspots must be identified within these regions to allow effective conservation of plants on both global and local scales (Murray-Smith *et al.* 2008). The estimation of geographical distribution of species richness is necessary to understand the ecological and evolutionary determinants of spatial patterns of biodiversity (Rosenzweig 1995; Ricklefs 2004). However, it is not easy to evaluate species richness distributions across heterogeneous regions where collecting efforts have not been sufficient or adequately planned (Hortal *et al.* 2007).

Recently, species distribution modelling (SDM) has emerged as a novel approach for generating distributions based on the relationship between species’ presence or abundance records and environmental variables. Large amounts of distributional data are collected in biodiversity databases. Thanks to both the advances in geographic information systems (GIS) techniques and the availability of digital maps of environmental variables, a wide variety of modelling techniques specifically designed to model species distributions are currently available (see Guisan & Thuiller 2005). Thus, predictive models of single-species geographical distributions and species richness provide an attractive alternative to using incomplete or spatially biased survey data as a basis for conservation planning (Parviainen *et al.* 2009).

In addition to the fact that the Mediterranean area is considered a hotspot of biodiversity (Myers *et al.* 2000), mainly because of its plant richness, the existing transition between temperate and Mediterranean climates makes Catalonia (NE Spain) especially interesting from a biodiversity point of view (Pausas *et al.* 2003). Catalonia has an altitudinal range from sea level to 3143 m a.s.l, containing a large variety of floristic regions that shelter a broad diversity of plant species, ranging from Mediterranean flora to Medio-European (including Atlantic and Sub-Mediterranean) and Boreo-alpine elements (Ninot *et al.* 2007). A remarkable amount of progress has been made in describing the vegetation of this region, whose flora is perhaps better known than that of any other Mediterranean area of comparable size (Greuter 1999). However, some regions in Catalonia remain poorly surveyed. Furthermore, researchers

generally prefer to visit sites that are known to have high species richness rather than to survey new sites where species richness is unknown (Dennis & Tomas 2000).

The variety of existing SDM algorithms has the potential to estimate substantially different species distributions depending on the algorithm used (Carpenter *et al.* 1993; Loiselle *et al.* 2003). Because this difference could have serious consequences for the interpretation of the richness patterns in Catalonia, we used three different algorithms (GLM, MARS and Maxent) in this study. We aimed to identify richness areas based on the current distribution of all vascular plant species described in Catalonia using these three modelling techniques, which were applied to each plant species individually. We specifically focussed on (1) examining whether these modelling techniques provide an adequate methodology to improve the sampled species richness in Catalonia; (2) identifying areas of high plant species richness in Catalonian landscapes; and (3) detecting areas where sampling has probably been lacking to date.

2. Methods

2.1. Study area

Catalonia is a region on the northeast of the Iberian Peninsula (Fig. 1; 40° 30'-42° 40'N, 0° 15'-3° 20'E), covering an area of ca. 31 980 km². Catalonia presents a wide range of physiographic, biogeographic and orographic features, mainly due to the presence of the Pyrenees in the north and the Mediterranean Sea to the east. The majority of the area has a Mediterranean climate, with decreased rainfall from north to south and from the coast to the central plains. A continentality gradient is also present from the coast to the inland regions. The presence of numerous relief units results in highly variable climates (Pausas *et al.* 2003; Ninot *et al.* 2007).

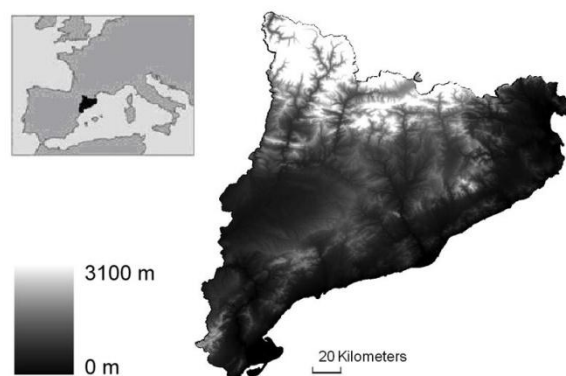


Figure 1. Location of the study area (Catalonia).

The basic spatial unit for this analysis was the universal transverse Mercator (UTM) 10 km x 10 km grid system (100-km² projected area) because this is the mapping grid used in plant recording schemes in the Catalonia Database of Biodiversity (Banc de Dades de Biodiversitat de Catalunya, BDBC). The area of study is composed of 319 such units, hereafter called “quadrats”, which were included in UTM zone 31T.

2.2. Plant species data

In this study, we used all georeferenced plant species occurrence records from the BDBC, which uses the taxonomy updated by Bolòs *et al.* (2005). The scientific literature and, secondarily, herbaria are the most important data sources for this database. Prior to modelling, we examined all of the records to identify and exclude any with errors in georeferencing, obvious misidentifications and duplicate species records for one quadrat. Additionally, a species had to be represented in at least five quadrats to be modelled (see Vargas *et al.* 2004; Pearson *et al.* 2007; Raes *et al.* 2009). In total, the species data for our study consisted of 2 543 274 records for 2738 species (of the 3415 species in the database).

2.3. Environmental data

Both the quality and the interpretability of models and the derived richness maps strongly depend on variable selection. Ninety-three variables were collected as predictive factors that influence the potential distribution of vascular plants (see Pausas *et al.* 2003). Each variable belonged to one of the following three types of environmental data: (1) geographical data, which included 14 variables; (2) climatic data, 72 variables; and (3) geological data, seven variables. These sets of explanatory variables have already been successfully used in both flora and fauna studies in Catalonia (e.g. Pausas & Sáez 2000; Pausas *et al.* 2003; Hawkins & Pausas 2004). The spatial resolution of the plant species data (10 km x 10 km) dictated the analysis resolution. We used ArcInfo workstation tools (ESRI 2009) to generate the environmental data.

Geographical set

The spatial patterns of biodiversity in Catalonia are strongly influenced by topographic features due to the heterogeneity of the territory (Pausas *et al.* 2003). Therefore, data on altitude, slope and orientation were obtained from a digital elevation model of Catalonia (resolution 20 m). We united the digital elevation model to a UTM

10-km x 10-km layer and calculated the maximum, minimum and average values of the altitude and slope data for each UTM quadrat. We also determined the percentage of every quadrat area oriented to each cardinal point (N, S, E, W, NE, NW, SE and SW).

Climatic set

Data on temperature, precipitation and radiation were derived from maps of the Digital Climatic Atlas of Catalonia (resolution 180 m; Ninyerola 2000). Seasonal data were chosen because in the Mediterranean climate seasons are easily distinguishable, making seasonal climatic factors the most important. Seasonal minimum temperature, maximum temperature, mean temperature, precipitation and radiation data were summarised as average, minimum and maximum values for each UTM quadrat.

Data on water deficit and potential evapotranspiration were obtained from the Climatic Atlas of Catalonia (<http://mediambient.gencat.cat/cat/inici/jsp>, ICC 1996). From this map, we first obtained the proportion of every quadrat area that corresponded to the following seven categories of water deficit: <0, 0-100, 100-200, 200-300, 300-400, 400-500 and >500 mm. Second, we obtained the percentage corresponding to each of the following five categories of potential evapotranspiration: 286-427, 427-572, 572-712, 712-855 and 855-997 mm.

Geological set

The different soil types present in the territory were obtained from the hydrogeological map of the Cartographic Institute of Catalonia (DPTOP & SGC 1992). The original 39 bedrock types on the map were grouped into the following seven main types per Pausas *et al.* (2003): gypsum, siliceous schist, siliceous granites, siliceous conglomerates, marls, limestones and Quaternary substrates. Due to the presence of different soil types in the same quadrat, we estimated the area occupied by each substrate in each quadrat.

2.4. Analyses

We modelled the potential distribution of 2738 plant species using three different methods. We applied a maximum entropy model (Maxent) that, according to Elith *et al.* (2006), consistently outperforms more established methods, including presence-only methods or presence-absence methods, particularly when sample sizes are low. We also applied a generalised linear model (GLM) and multivariate adaptive regression splines

(MARS) using the BIOMOD tool (Thuiller 2003), as implemented for R software (R Development Core Team 2009, Vienna, Austria).

A total of 93 variables for this study is a large number of factors that may be highly correlated. To avoid problems such as multi-collinearity, which can result in model over-fitting (Peterson *et al.* 2007), we reduced the number of predictors using a principal component analysis (PCA). We performed a PCA on the 93 observed predictors for the 319 quadrats of Catalonia. We selected the first 14 PCA axes as our environmental predictors (PCA01-14) because each of them separately explains more variance than would be expected by chance (1.07%) and they jointly explain 80.22% of the data variance.

Maxent model calibrations

We used the maximum entropy model (Maxent version 3.2.19, available at <http://www.cs.princeton.edu/~schapire/maxent>; Phillips *et al.* 2006), a presence-only algorithm that requires known species occurrence points and environmental variables. Maxent estimates the potential geographic distribution of the species by finding the probability distribution of maximum entropy, or closest to uniform distribution, subject to constraints derived from the occurrence data (Phillips *et al.* 2006). We automatically ran 2738 models (using the Maxent commands) with auto-features (Araújo & New 2007). For each run, a maximum number of 10 000 background quadrats were selected at random as pseudo-absences, the maximum number of iterations was 500, the convergence threshold was set to 10^{-5} and regularisation was set to the default value (Phillips *et al.* 2006). To evaluate the quality of predictions, we made a random partition of the occurrence localities for each species and divided the databases into two subsets: calibration and evaluation. The former, a random sample from 80% of the total database, was used to calibrate (train) the models, whereas the latter, comprising the remaining data, was used to evaluate (test) the model predictions (Fielding & Bell 1997).

Maxent model evaluation

We used receiver operating characteristic (ROC) analysis, which characterizes the species model performance at all possible thresholds with a single number that represents the area under the curve (AUC). This method does not require discrete presence/absence predictions and is therefore a measure that integrates many thresholds

(Pearce & Ferrier 2000; McPherson *et al.* 2004). Although the AUC has been recently criticized, this method has been extensively used in the species distribution modelling literature because it measures the ability of a model to discriminate between sites where a species is present and those where it is absent (Hanley & McNeil 1982).

Maxent richness map

To develop plant species richness maps, a threshold was set to convert the continuous SDM predictions to discrete presence/absence predictions. We selected the threshold using the criterion of “maximum training sensitivity plus specificity”, which has recently been shown to produce successful predictions (Liu *et al.* 2005; Jiménez-Valverde & Lobo 2007). Once the threshold was set, the plant species richness map was developed by combining the presence/absence maps for individual species by summing the predicted presences (Lehmann *et al.* 2002). Thus, distribution maps of the 2738 species were overlapped to obtain an estimation of the potential species richness for each quadrat (i.e. a species richness map).

BIOMOD model calibrations

The methods included in the analysis framework were generalised linear models (GLM) and multivariate adaptive regression splines (MARS). GLMs have been one of the most commonly used techniques in species distribution modelling and are able to predict current species distribution (Austin & Meyers 1996; Brito *et al.* 1999). The MARS model provides an alternative regression-based method for fitting non-linear responses using piecewise linear fits. Due to the lack of independent data for model evaluation, we used a random data splitting procedure, as in the Maxent model calibration. For each species, the following procedure was used.

(1) For GLM (McCullagh & Nelder 1989) with linear terms, we used a stepwise procedure to select the most parsimonious model and the most significant variables. The statistical criterion used for selecting models of increasing fit was the Akaike Information criterion (AIC) (Akaike 1974; MathSoft 1999).

(2) MARS (Friedman 1991) represents a relatively new technique that utilizes classical linear regression and was recently tested in an extensive study comparing 16 predictive techniques (Elith *et al.* 2006). We used the default values, in which the maximum interaction degree is equal to 1.

BIOMOD model evaluation

The accuracy of the species models was evaluated using the area under the relative operating characteristic curve, which considers many different thresholds to transform probability values from models into binary presence-absence form (Pearce & Ferrier 2000).

BIOMOD richness maps

To create species richness maps derived from GLM and MARS, we followed the same procedure as in Maxent.

Performance assessment of the richness maps

To be reliable, predictive modelling should always include a testing phase (Mac Nally 2000). Two measures of association, Kappa and the true skill statistic (TSS), were used to assess the predicted species composition of the three richness maps. Moreover, we calculated two components of disagreement between the richness maps in terms of the quantity and spatial allocation of the categories (related to our study species presences and absences). Otherwise, Pearson correlation (COR) was applied to assess the prediction performance of the predicted species richness.

For Kappa, we compared the predicted to the sampled local species composition for a set of 21 UTM quadrats (UTM assessment set) that had already been thoroughly studied by botanical experts and had floristic compositions that are considered to be very well known (Table 1). This UTM assessment set is representative of the environmental heterogeneity of the territory, containing coastal and inland areas as well as the Pyrenees (Fig. 2). We evaluated how well the different modelling approaches identified the sampled species composition in the UTM assessment set using Cohen's Kappa (κ) statistic (Cohen 1960). For this, we created a contingency matrix for each quadrat of the UTM assessment set, comparing the sampled and predicted species composition (Table 2). We built a total of sixty-three 2x2 contingency matrices corresponding to the three models and the 21 quadrats. Regarding the Kappa value, we used the following ranges for assessing the richness maps: $0.40 \leq K < 0.55$ was moderate, $0.55 \leq K < 0.70$ was good, $0.70 \leq K < 0.85$ was very good, $0.85 \leq K < 0.99$ was excellent and $0.99 \leq K \leq 1.00$ was perfect (Monserud & Leemans 1992). Nevertheless, we have to be aware that there is controversy about the universal standards of claims for high accuracy. As Pontius *et al.* (2007) and Pontius

UTM	Locality	Cited species	Predicted species by GLM (κ; TSS)	Predicted species by MARS (κ; TSS)	Predicted species by Maxent (κ; TSS)
31TEG07	Castelló d'Empúries	1098	1033 (0.712; 0.649)	1124 (0.787; 0.752)	1026 (0.755; 0.688)
31TDG84	Girona	1111	968 (0.751; 0.683)	1012 (0.788; 0.733)	1068 (0.781; 0.728)
31TDG99	Sant Climent Sescebes	1171	917 (0.543; 0.464)	1212 (0.674; 0.643)	1047 (0.719; 0.660)
31TCG36	Isona	804 *	648 (0.707; 0.431)	448 (0.776; 0.396)	435 (0.799; 0.404)
31TDG66	Santa Pau	886	997 (0.687; 0.602)	955 (0.732; 0.646)	1025 (0.743; 0.672)
31TBF89	Aitona	715	906 (0.737; 0.643)	788 (0.851; 0.770)	670 (0.895; 0.785)
31TBF99	Sarroca de Segrià	756	591 (0.814; 0.622)	622 (0.843; 0.680)	569 (0.833; 635)
31TDG08	Grèixer	1251	926 (0.651; 0.603)	1080 (0.727; 0.695)	1046 (0.697; 0.652)
31TCF79	La Llacuna	745	637 (0.785; 0.579)	567 (0.772; 0.547)	631 (0.738; 0.514)
31TCG46	Abella de la Conca	1054	919 (0.541; 0.440)	1049 (0.710; 0.650)	831 (0.650; 0.530)
31TCF34	Cambriis	535 ***	685 (0.803; 0.661)	735 (0.817; 0.726)	681 (0.851; 0.752)
31TBF81	Santa Bàrbara	861	1423 (0.553; 0.579)	1006 (0.841; 0.812)	883 (0.804; 0.712)
31TDG46	Vidrà	963	1082 (0.696; 0.637)	1069 (0.736; 0.682)	1064 (0.752; 0.691)
31TCH21	Boí	1046	1332 (0.692; 0.685)	1132 (0.845; 0.826)	1121 (0.795; 0.755)
31TCH41	Espot	1050	1270 (0.705; 0.687)	1131 (0.756; 0.718)	1139 (0.721; 0.669)
31TDG38	Riber de Freser	1265	1239 (0.569; 0.655)	1279 (0.712; 0.699)	1295 (0.672; 0.650)
31TCF27	Montsant	1106	724 (0.666; 0.553)	744 (0.694; 0.587)	952 (0.749; 0.673)
31TDG57	Olot	1136	1273 (0.574; 0.545)	1028 (0.725; 0.671)	1026 (0.703; 0.636)
31TDF28	Barcelona	1207	884 (0.599; 0.532)	903 (0.673; 0.611)	1042 (0.677; 0.620)
31TDG58	Beget	1078	965 (0.597; 0.513)	1132 (0.745; 0.706)	1036 (0.755; 0.692)
31TDG72	Maçanet de la Selva	1119	1277 (0.713; 0.694)	1201 (0.756; 0.730)	1162 (0.765; 0.726)

Table 1. UTM assessment set.

*The number of species used for statistical analysis in the 31T CG36 quadrat is 407. The number of records in this locality is not updated.

***The CF34 grid includes only 25% of emerged land.

(κ; TSS) Kappa and the true skill statistic values

& Millones (2011) point out, it makes no sense to have universal standards for accuracy in practical applications, because a universal standard is not related to any specific research question or study area (Foody 2008; Pontius *et al.* 2007; Pontius & Millones 2011). Moreover, in spite of its wide use, several studies have criticized the Kappa statistic for being inherently dependent on prevalence, and have claimed that this dependency introduces bias and statistical artefacts to estimates of accuracy (Cicchetti & Feinstein 1990; Byrt *et al.* 1993; Lantz & Nebenzahl 1996; McPherson *et al.* 2004; Pontius & Millones 2011). The TSS corrects for this dependency while still retaining all of the advantage of Kappa (Allouche *et al.* 2006). Regarding TSS, we proceeded in the same way as for Kappa, evaluating the prediction success of the different modelling approaches. For this, we created a contingency matrix for each quadrat of the UTM assessment set that compares the sampled and predicted species composition using TSS. Like Kappa, TSS takes into account both omission and commission errors, and success as a result of random guesses, and ranges from -1 to +1, where +1 indicates perfect agreement and values of zero or less indicate a performance no better than random (Allouche *et al.* 2006).

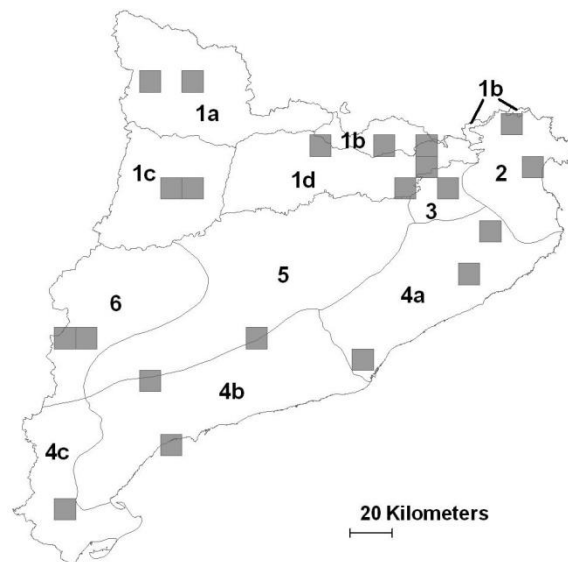


Figure 2. Location of the UTM assessment set within the Catalan physiogeographic territories, according to Bolòs (1975). The gray squares represent the UTM quadrats used for the UTM assessment set.

		Sampled species	
		present species	absent species
Predicted species by the model	present species	<i>a</i>	<i>b</i>
	absent species	<i>c</i>	<i>d</i>

Table 2. A contingency matrix used to evaluate the predicted species composition of the richness maps. *a*, number of species for which their presence in a quadrat were correctly predicted by the model; *b*, number of species for which their presence in a quadrat were not sampled but the model predicted their presence; *c*, number of species for which their presence in a quadrat were sampled but the model predicted their absence; *d*, number of species for which their absence in a quadrat were correctly predicted by the model.

Kappa analysis and its variants has become a standard component of almost every accuracy assessment (Congalton & Green 2009). However, Pontius & Millones (2011) found that Kappa and its variants (i.e. TSS) are flawed metrics. Thus, they recommend replacing these indices with a more useful and simpler approach by summarizing the contingency matrices in terms of quantity disagreement and allocation disagreement. Quantity disagreement is the amount of difference between the reference map (sampled species composition) and a comparison map (predicted species composition) that is due to the less than perfect match in the proportions of the categories. Allocation disagreement is the amount of difference between the reference map and a comparison map that is due to the less than optimal match in the spatial allocation of the categories, given the proportions of the categories in the reference and comparison maps (Pontius & Millones 2011). The disagreement analysis was based on the built contingency matrices for each quadrat of the UTM assessment set.

In order to observe the relationship between the sampled and predicted richness, we carried out a linear regression analysis. Then we calculated Pearson correlations (between the sampled and predicted richness) to evaluate the performance of the richness maps. These calculations take into account how much the predictions vary from the observations. In addition, the adequacy of the richness maps was assessed by detecting outliers that disproportionately influenced the fit of the maps, examining the standard errors of coefficients, plotting the residuals *vs* the fitted values, plotting the residuals in a normal probability plot, and examining the leverage of the observations. Alternatively, to identify the most poorly studied areas according to the results of the distribution richness maps, we analysed the standardised Pearson residuals to detect quadrats that show negative standard residuals lower than -1.95 (Lobo *et al.* 2004).

Finally, the autocorrelation of the residuals of the linear models was checked using generalised least squares; we did not find spatial autocorrelation. These analyses were performed using the R program.

3. Results

3.1. Prediction of plant species richness in Catalonia

The spatial pattern of plant diversity in Catalonia was well summarized with GLM, MARS and Maxent models. The predicted species richness maps produced a much smoother pattern than that found in the sampled species richness map (Fig. 3). Based on visual examination and statistical evaluation, there was little variation between modelling methods (i.e. the patterns of relative richness did not vary among models; Table 3). For the three models analysed, the stacked and summed predicted distributions of 2738 plant species indicate that areas with concentrations of the greatest species richness occur along the Pyrenees, the pre-coastal mountain range and the coastal range (Fig. 3). Ribes de Freser (quadrat 31T DG38) was the locality in which the highest number of both sampled and predicted species were concentrated, containing 1268 sampled species and 1279, 1239 and 1295 predicted species, as determined by MARS, GLM and Maxent, respectively. In contrast, low predicted richness values were common in inland areas. Central Catalonia, which includes the regions of Bages, southern Solsonès, southern Berguedà, Anoia and Segarra, was the least species-rich area, followed by the plain of Lleida, which includes the regions of Pla d'Urgell, Urgell, Segrià and Noguera.

3.2. Accuracy of species distribution models

We considered four classes of model accuracy. The low accuracy ($AUC < 0.7$) class included 173 species for GLM, 229 species for MARS and 1069 species for Maxent, representing 6.32%, 8.36% and 39.04% of the total data, respectively. The fair accuracy class ($0.7 < AUC < 0.8$) included 554 species for GLM (20.23%), 263 species for MARS (9.6%) and 435 species for Maxent (15.88%); this class included species with several occurrences (e.g. *Equisetum ramosissimum* and *Aristolochia rotunda*) as well as more scarce species (such as *Diplotaxis viminea* and *Berberis vulgaris*). Good accuracy status ($0.8 < AUC < 0.9$) was assigned to findings of 833 species (30.62%) for GLM, 850 species (31.05%) for MARS and 518 species (19%) for Maxent; this class also included both highly abundant species and more scarce species. The high accuracy

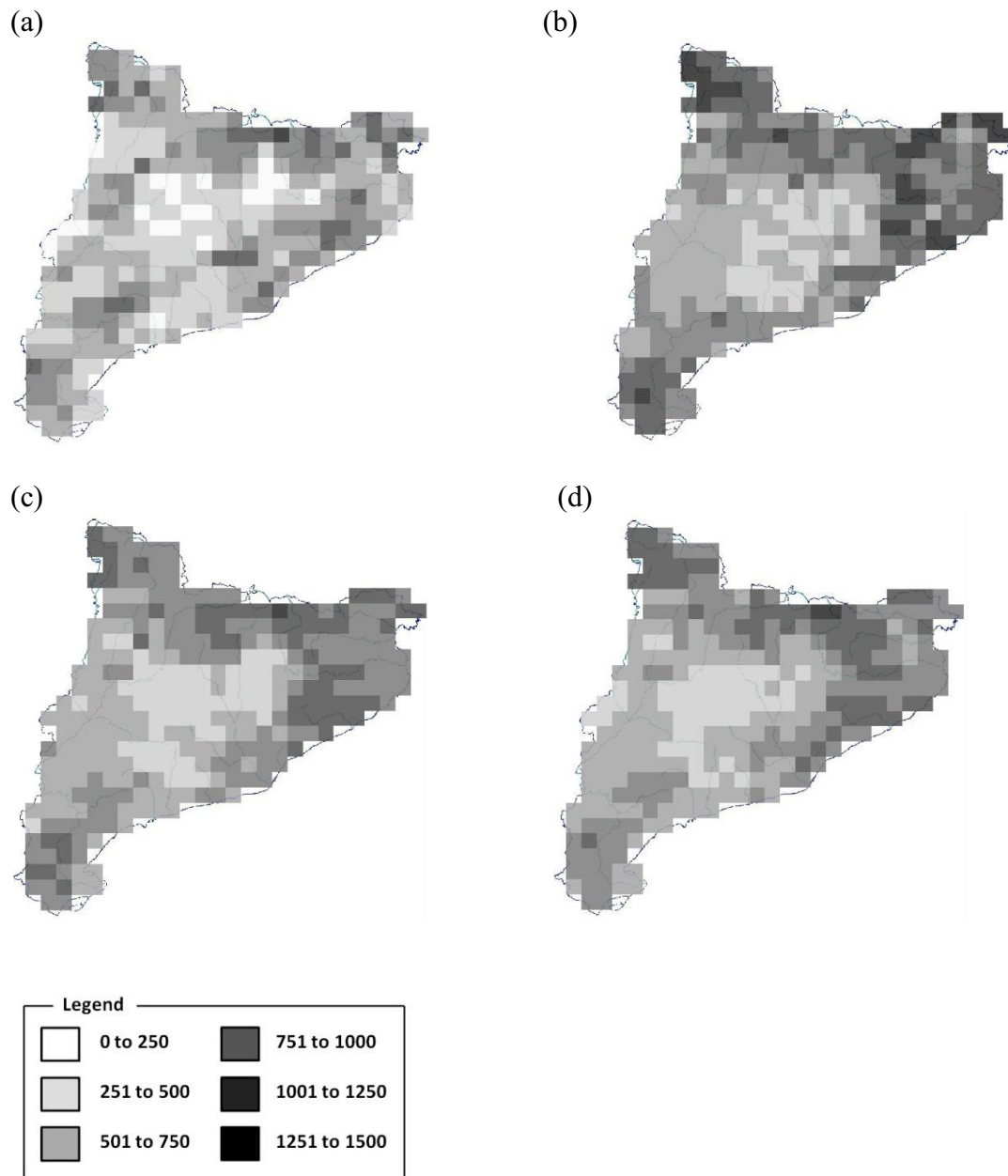


Figure 3. (a) Sampled species richness in Catalonia according to the BDBC, (b) predicted species richness according to GLM, (c) predicted species richness according to MARS and (d) predicted species richness according to Maxent in Catalonia.

	Observed	MARS	GLM
MARS	0.67		
GLM	0.49	0.89	
Maxent	0.72	0.92	0.82

Table 3. Pairwise correlation coefficient for the predicted richness among three modelling techniques and sampled richness based on the BDBC database.

class ($AUC > 0.9$) included 1195 species for GLM (43.66%), 1585 species for MARS (57.91%) and 715 species for Maxent (26.11%).

Finally, the results of the species distribution models evaluation indicate that MARS is the model that best predicts species actual distributions (Fig. 3c) (GLM: $AUC_m=0.865$, $SD=0.098$; MARS: $AUC_m=0.902$, $SD=0.085$; Maxent: $AUC_m=0.736$, $SD=0.187$).

3.3. Performance assessment of the richness maps

For the three statistical values (Kappa, TSS and COR) and the two components of disagreement, there is no obvious difference between the MARS and Maxent richness maps (Table 4), indicating that the overall prediction performance of these two richness maps is very close. In fact, the highest correlation coefficient for predicted richness was obtained between MARS and Maxent ($r = 0.918$). However, there is a difference between these maps and the GLM richness map, which showed the lowest values for the three statistics and the highest values for the two components of disagreement (Table 4).

Criteria	GLM	MARS	Maxent
Kappa	0.671	0.760	0.755
TSS	0.589	0.680	0.659
Quantity disagreement	6.952	4.095	3.428
Allocation disagreement	11.857	9.904	11.333
COR	0.492	0.671	0.717

Table 4. Statistical assessment criteria of prediction richness maps.

Based on both Kappa statistics and TSS, the MARS map achieved the highest success ($\kappa_{mean} = 0.760 \pm 0.055$, $TSS_{mean} = 0.680 \pm 0.094$) in predicting the sampled species composition in the assessment data (21 UTMs with floristic composition thoroughly studied) (Table 4 and Fig. 4). Kappa and TSS values obtained for the maximum entropy algorithm ($\kappa_{mean} = 0.755 \pm 0.061$, $TSS_{mean} = 0.659 \pm 0.088$) allow us to conclude that the predictive power of Maxent in identifying plant species richness is “very good”. Moreover, the richness maps derived from MARS and Maxent produced a baseline with an average of 4.1% ($\pm 3.0\%$) and 3.4% ($\pm 2.2\%$) quantity disagreement and an average of 9.9% ($\pm 3.6\%$) and 11.3% ($\pm 2.9\%$) allocation disagreement respectively (Fig. 5). The maps produced by MARS and Maxent produced a baseline with 85.76% and 85.14% of agreement, respectively, which highlights that the species

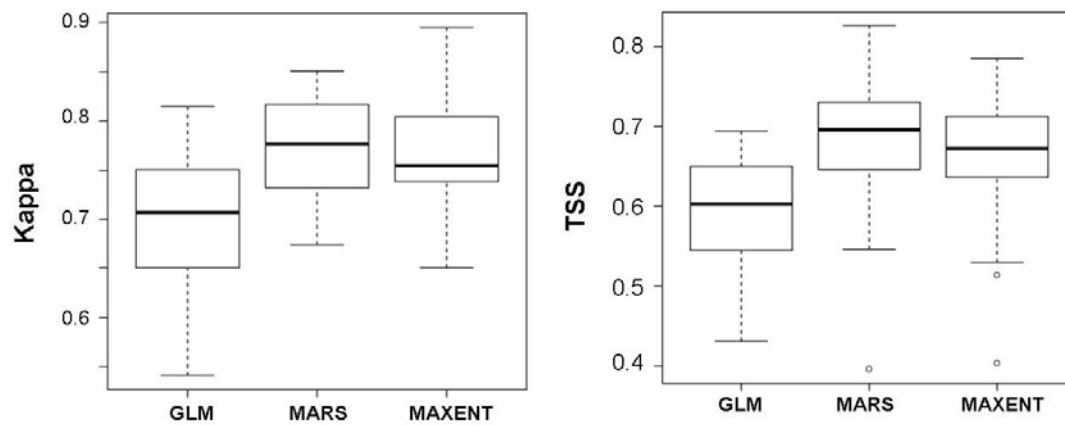


Figure 4. Results of the richness maps' assessment of the 21 Kappa and TSS values computed for each model. The boxes represent the interquartile range, and the median is marked as a bold line within these bars; the line extensions from each box are the largest and the smallest values and the circles represent the outliers.

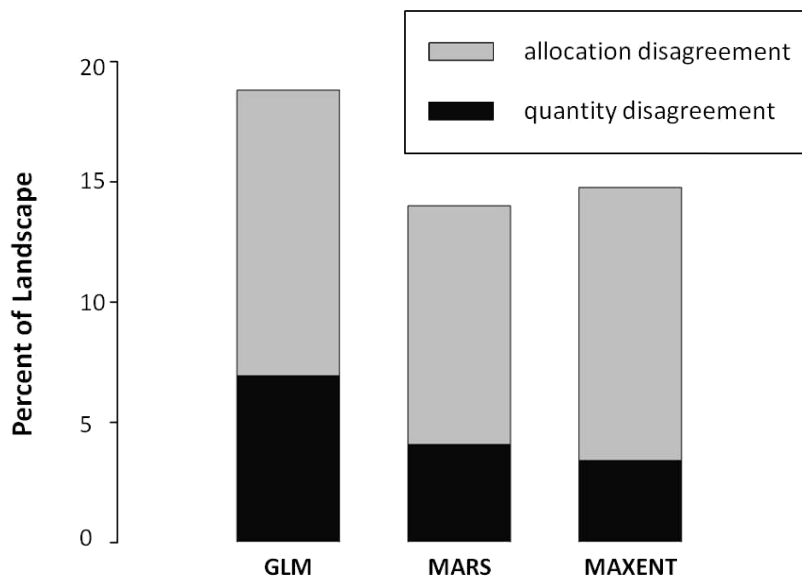


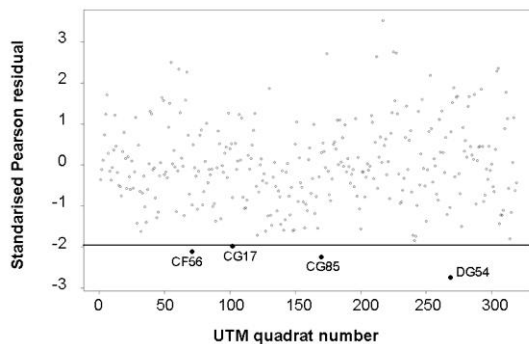
Figure 5. Quantity disagreement and allocation disagreement for each matrix of the UTM assessment set.

richness distribution in the landscape derived from the models is “very good”. Furthermore, the component of quantity disagreement for these two algorithms reflects a prediction of more than the reference quantity of presence for ten and seven quadrats respectively, of the UTM assessment set (Table 1). This highlights a potential improvement in richness patterns over prior knowledge of the plant species richness in

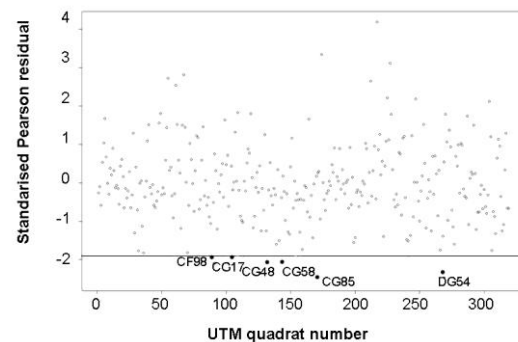
these quadrats. The Kappa, TSS and COR values obtained for the GLM analysis ($\kappa_{\text{mean}} = 0.671 \pm 0.086$, $\text{TSS}_{\text{mean}} = 0.589 \pm 0.081$) could indicate that its ability to predict plant species richness for Catalonia is “moderate”. However, the separation of the overall disagreement into components of quantity ($6.9\% \pm 4.5$) and allocation ($11.8\% \pm 5.0$) shows that most of the error is allocation error, revealing that this map is actually more useful for our particular purpose (produces good quality plant species richness maps) than implied by the reported measures of association (Kappa and TSS), which tend to focus more on the allocation error than on the quantity error. This evaluation of the predictive richness maps based on both Kappa and TSS statistics and on the analysis of the two components of disagreement agrees with the results obtained from the Pearson correlation analysis (Table 4), confirming that the MARS and Maxent algorithms have higher accuracy in measurements than GLM as predictors of plant species richness for Catalonia.

Neither the examination of residuals nor that of spatial autocorrelation showed especially aberrant features. These results suggest that the models predict reasonably well the plant species richness in the more poorly sampled quadrats. However, 12 quadrats showed negative standard residuals below -1.95 (fitted values higher than observed; Fig. 6). These 12 quadrats contain fewer species than predicted by the explanatory variables, probably because the number of database records for each quadrat may not always reflect a comparable sampling effort. The results of the three modelling techniques indicate that these quadrats are the most poorly studied areas and are, therefore, the areas that should be focused on in future flora studies (31TCG85, 31TCG58, 31TDG54, 31TCG48, 31TCG17, 31TEG02, 31TCF56, 31TCF98, 31TCH51, 31TCG55, 31TCH52 and 31TDG65).

(a)



(b)



(c)

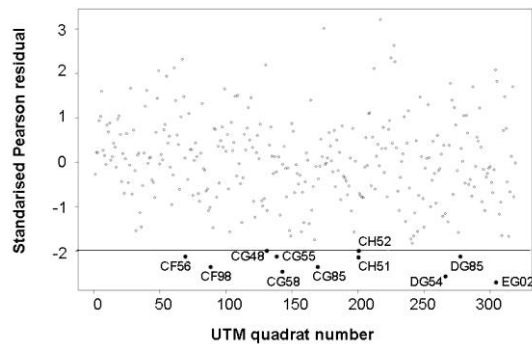


Figure 6. Standardised Pearson residual scores for (a) the GLM, (b) the MARS and (c) Maxent. Lines delimit the UTM quadrats with negative residuals less than -1.95.

4. Discussion

Most studies describe species richness patterns based on a small group of indicator species, genera or families (Mac Nally & Fleishman 2004; Murray-Smith *et al.* 2008; Schouten *et al.* 2009). Hence, this study can be considered of great importance in plant species diversity assessment because 2738 species were modelled of a total of 3415 species in Catalonia (ca. 80% of the total flora of Catalonia).

When considering the accuracy of maps produced through a modelling system, it is important to note that high scores of global performance measures do not necessarily imply that maps will be better suited to management applications. Although the predictive performance of Maxent for species distribution, based on the AUC values, was fair, both the richness map produced by this model and the map produced by MARS were best supported by the performance analysis based on Kappa and TSS statistics, the two components of disagreement, Pearson correlations and by known plant species richness. Moreover, the highest correlation coefficient for predicted richness was obtained between MARS and Maxent, indicating that these models provided reasonably similar predictions of species richness. The GLM tends to over-predict the species richness in Catalonia, reaching values of ca. 1400 species in the richest quadrats. According to Pausas *et al.* (2003), this value is too large and does not represent the true species richness of these areas.

The use of distribution modelling methods allows us to produce a geographical representation of the plant species richness distribution over the territory. As shown in the results, the spatial patterns of species richness in Catalonia are neither uniformly nor

randomly distributed across the landscape. Generally, high species richness areas are predicted to occur along the Pyrenees, the pre-coastal mountain range and the coastal range, which are ancient geomorphological features that have high environmental heterogeneity. One of the most important variables determining vegetation composition at a coarse scale in Catalonia was quadrat heterogeneity, which showed a positive relationship to plant species richness in the quadrats (Pausas *et al.* 2003). Spatial heterogeneity is a surrogate for niche diversity, and it follows that highly heterogeneous areas should support more species than areas of lower heterogeneity (Rosenzweig 1995). The high plant species richness node observed in Barcelona (possibly due to the nearby presence of numerous universities and research centres) was predicted to be moderately rich, whereas the northern Catalan coast and the Ebro delta were predicted to have a higher richness than has been sampled. Regions of relatively low richness occur mainly in the central areas, possibly due to both the low environmental heterogeneity and the role of the agricultural activities in these areas, which we did not explore in this paper.

According to Pausas *et al.* (2003), the weighted mean, the minimum and the maximum number of species per quadrat in Catalonia were 620, 120 and 1222, respectively. The weighted mean, the minimum and the maximum number of species per quadrat predicted by MARS were 767, 313 and 1279, respectively, and with Maxent, these values were 764, 305 and 1295, respectively. It is important to point out that the two algorithms raised the minimum number to at least 300 species (i.e. the predicted richness in the poorest areas predicted by the SDMs was higher than estimated in Pausas *et al.* 2003). Therefore, the two models increased the expected number of species present in the least sampled regions. Our results highlight that we have improved upon the patterns of species richness developed by Pausas *et al.* (2003), increasing the weighted mean and the minimum number of species per quadrat and obtaining potentially valuable distribution richness maps, especially in the most poorly sampled quadrats. Furthermore, the maximum number of expected species predicted by MARS and Maxent coincides closely with the prediction made by Pausas *et al.* (2003). Hence, from a botanical point of view, we believe that our results fit the reality of vascular plant richness in Catalonia.

In addition, analysis of the standardised Pearson residuals has allowed us to identify the most poorly studied areas, i.e. the quadrats that had the highest differences

between sampled and predicted species number; these quadrats should be the focus of future sampling efforts. Once the modelling was completed, the Generalitat of Catalonia organized the “1-4 June 2010 Catalonia Bioprospecting campaign”, during which we conducted a survey in the two taxonomically poorest quadrats of the region. Thanks to this survey we increased the number of species encountered in the two quadrats from 76 and 83, to 417 and 361, respectively. So, these sampled values reached the minimum number of expected species predicted by the modelling algorithms. Moreover, MARS and Maxent predicted, for each quadrat, an actual number of species close to the surveyed number for the two quadrats (respectively, 337 and 347 with MARS; 419 and 425 with Maxent). Consequently, the results indicate that these two modelling algorithms are useful techniques to estimate plant species richness in Catalonia.

As stated above, we found some variation in modelling success between the different modelling techniques. This confirms that it is worthwhile to consider prediction outputs from multiple models when making assessments of species richness trends (Thuiller 2003; Elith *et al.* 2006). Our results confirm that modelling species distributions separately for each species and summing the predicted presences can be a useful strategy for assessing spatial variation in species richness, particularly for poorly sampled regions (Pineda & Lobo 2009). The model-predicted richness maps presented here can be used to detect zones with low and high species richness and to derive strategies for either restoring or protecting landscape biodiversity as part of national conservation plans. Although we are confident that the modelled maps reflect the actual richness pattern, we must stress that areas with lower values for the three models are not necessarily less important for conservation.

5. Main Conclusions

The species distribution models used in this study provided improved distribution patterns of plant species richness in Catalonia over the previously sampled patterns, and, most importantly, provided an estimate of the number of species present in those insufficiently sampled areas. Therefore, with this approach, we have developed patterns of species richness that are more reliable than those expounded in Pausas *et al.* (2003), thus providing a useful alternative to classical richness approximations for Catalonia.

Of the three modelling techniques used in this work, MARS and Maxent were the two methodologies that provided more accurate species richness maps than GLM.

Finally, this study has shown that is possible to generate indices of plant richness in Catalonia using species distribution models. These indices are of potential value for management institutions, as they can be used as tools to identify target areas that require more survey and conservation efforts.

Acknowledgements

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Chapter 2. Drastic reduction in the potential habitats for alpine and subalpine vegetation in the Pyrenees due to twenty-first-century climate change

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ORIGINAL ARTICLE

Drastic reduction in the potential habitats for alpine and subalpine vegetation in the Pyrenees due to twenty-first-century climate change

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Abstract Recent climate change is already affecting both ecosystems and the organisms that inhabit them, with mountains and their associated biota being particularly vulnerable. Due to the high conservation value of mountain ecosystems, reliable science-based information is needed to implement additional conservation efforts in order to ensure their future. This paper examines how climate change might impact on the distribution of the main alpine and subalpine vegetation in terms of losses of suitable area in the Oriental Pyrenees. The algorithm of maximum entropy (Maxent) was used to relate current environmental conditions (climate, topography, geological properties) to present data for the studied vegetation units, and time and space projections were subsequently carried out considering climate change predictions for the years 2020, 2050 and 2080. All models predicted rising altitude trends for all studied vegetation units. Moreover, the analysis of future trends under different climate scenarios for 2080 suggests an average loss in potential ranges of 92.3–99.9 % for alpine grasslands, 76.8–98.4 % for subalpine (and alpine) scrublands and 68.8–96.1 % for subalpine forest. The

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drastic reduction in the potential distribution areas for alpine grasslands, subalpine scrublands and *Pinus uncinata* forests highlights the potential severity of the effects of climate change on vegetation in the highest regions of the Pyrenees. Thus, alpine grasslands can be expected to become relegated to refuge areas (summit areas), with their current range being taken over by subalpine scrublands. Furthermore, subalpine forest units will probably become displaced and will occupy areas that currently present subalpine scrub vegetation.

Keywords Alpine grasslands · Climate change · Maxent · *Pinus uncinata* forest · Pyrenees · Subalpine shrubs

Introductio

Recent climate change is already affecting both ecosystems and the organisms that inhabit them (Walther *et al.* 2002; Parmesan 2006; Rosenzweig *et al.* 2008), with mountains and their associated biota being particularly vulnerable to climate change (Beniston *et al.* 1996; Theurillat and Guisan 2001). In fact, it has been noted that plants of alpine and subalpine areas appear to be especially sensitive to global warming (Shaw *et al.* 2000; Erschbamer 2001; Pauli *et al.* 2001). Moreover, it is likely that such effects are more intense in mountain systems under extreme and climatically marginal conditions (Beniston 2000), such as in many alpine areas with a Mediterranean climate influence, in which most of the orophilous species are relicts from glacial periods and are considered at the limit of their climatic tolerance range (Sanz-Elorza *et al.* 2003). Furthermore, impacts on flora from regions projected to undergo increased warming accompanied by decreased precipitation, such as the Pyrenees, will likely be greater than those on flora in regions

1. Introduction

Recent climate change is already affecting both ecosystems and the organisms that inhabit them (Walther *et al.* 2002; Parmesan 2006; Rosenzweig *et al.* 2008), with mountains and their associated biota being particularly vulnerable to climate change (Beniston *et al.* 1996; Theurillat and Guisan 2001). In fact, it has been noted that plants of alpine and subalpine areas appear to be especially sensitive to global warming (Shaw *et al.* 2000; Erschbamer 2001; Pauli *et al.* 2001). Moreover, it is likely that such effects are more intense in mountain systems under extreme and climatically marginal conditions (Beniston 2000), such as in many alpine areas with a Mediterranean climate influence, in which most of the orophilous species are relicts from glacial periods and are considered at the limit of their climatic tolerance range (Sanz-Elorza *et al.* 2003). Furthermore, impacts on flora from regions projected to undergo increased warming accompanied by decreased precipitation, such as the Pyrenees, will likely be greater than those on flora in regions where the increase in temperature is less pronounced and rainfall increases concomitantly (Engler *et al.* 2011).

In the last two decades, species- and community-based models have been increasingly used in conservation planning, and more recently, they have become important tools to evaluate the potential impacts of climate change on biodiversity (Guisan and Zimmermann 2000; Thomas *et al.* 2004; Guisan and Thuiller 2005; Ferrier and Guisan 2006). Concerning the former, species distribution models (SDMs) generate species' potential distributions in landscapes based on the relationship between species observations (presence/absence or abundance) and environmental variables. Regarding community-based models, two major approaches currently prevail (Guisan & Rahbek 2011). The first approach focuses directly on realized properties of species assemblages and uses macroecological modelling. The second approach focuses on aggregate properties of individual constituent species, used to reveal the properties of assemblage, and applies SDMs to a spatial stack of species (S-SDMs). Many studies have modelled the potential areas of species in the future under climate change scenarios of the Intergovernmental Panel on Climate Change (IPCC), but the work carried out by Thomas *et al.* (2004) was one of the first studies to apply SDMs to the problematic of climate

change impact on organism geographic distribution for a large number of species. In Europe, the greatest modelling effort was carried out by Engler *et al.* (2011), who assessed the possible effects of climate change on the potential distributions of 2,632 plant species by the end of the twenty-first century in all major European mountain ranges at a fine spatial resolution (100 m; 1 km for the Spanish Pyrenees). However, most studies in Europe have focused on modelling species presence at the continental scale at a resolution of 50 x 50 km (Bakkenes *et al.* 2002; Thuiller *et al.* 2005) using input data taken from the Atlas Florae Europaeae (Jalas and Suominen 1972-1996). Other regional approaches have been applied for the Swiss Alps (Bolliger *et al.* 2000; Dirnböck *et al.* 2003, Walther *et al.* 2005; Pauli *et al.* 2007) and for 20 tree species on the Iberian Peninsula (Benito Garzón *et al.* 2008). Effects of ongoing climate warming on alpine plant species distribution have already been detected in several Iberian mountain ranges (Peñuelas and Boada 2003; Sanz-Elorza *et al.* 2003; Benito *et al.* 2011). Specially, Benito *et al.* (2011) pointed out that the suitable areas for species inhabiting the summits of Sierra Nevada (SE Iberian Peninsula) may disappear before the middle of the century. Thus, according to these studies, the alpine and subalpine vegetation in the Pyrenees can be expected to suffer similar trends as a consequence of the projected climate change. Hence, we expected that the vegetation belts in the Pyrenees will suffer an upwards shift, being, thus, the alpine belts the most affected by the climate change (see Benito *et al.* 2011; Engler *et al.* 2011).

In this study, we chose to model the potential distribution of entire vegetation units (as defined in CORINE; Vigo *et al.* ed. 2006) rather than individual species for the following reasons: first, although vegetation units are not as sharply and objectively defined biological entities as species, for all of the vegetation units studied in this work, the mapping at our disposal, which is based on detailed orthophotomaps and intense field work, provides continuous layers of current distributions with a planimetric accuracy much greater than what is achieved in the case of species. Furthermore, the studied vegetation units are mainly defined by the presence of the dominant or key species. The behaviour of the key species will determine the survival of many accompanying species, given that the former act as a nurse plant for the latter, creating appropriate micro-niches (Castro *et al.* 2004). Thus, investigation of the distribution of these vegetation units is

consistent with investigation of the distribution of their dominant or key species. What is more, the reduction in the area that is climatically suitable for a particular vegetation unit determines the magnitude of the extinction risk for species belonging to it (Thomas *et al.* 2004). Moreover, to our knowledge, no detailed study has been conducted that assesses the future of the alpine and subalpine vegetation in the Pyrenees with such planimetric accuracy (resolution of approximately 0.6 km²) under future climatic conditions. Finally, it is important to note that the studied units have a high conservation value because seven of them are habitats of community interest and two are habitats of priority interest under the ‘Habitats’ Directive 97/62/UE (Council Directive 97/62/UE of 27 October 1997 adapting Directive 92/43/EEC to technical and scientific progress on the conservation of natural habitats and wild fauna and flora).

In this study, we assess the impacts of climate change on the potential distribution of six alpine grasslands, two subalpine (and alpine) scrublands and four subalpine forests of *Pinus uncinata* in the Oriental Pyrenees by the end of the twenty-first century using 700 x 900 m habitat samples and data expressing two IPCC-based climate change scenarios for the years 2020, 2050 and 2080.

2. Methodology

2.1. Study area

The study area covers a total area of 9,894 km², including the subalpine and alpine belts in the eastern half of the Spanish Pyrenees and Andorra (Fig. 1). Detailed vegetation mapping (Carreras *et al.* ed. 2003; Vigo *et al.* ed. 2006) and field surveys carried out mainly by Spanish botanists have provided excellent knowledge regarding the vegetation and flora in this area. In the Pyrenees, there is essentially one tree species that inhabits the upper subalpine area: mountain pine (*P. uncinata*). At the treeline ecotone, open woods give way to a patchy area with small areas of dwarf scrub, grassland, tree islands and isolated trees. The vegetation above the forest limit, in the alpine zone, forms a small-scale mosaic of structurally and floristically distinct plant communities, including short grasslands clearly dominated by *Festuca eskia*, *Festuca airoides* or *Carex curvula* (on acidic substrata) and grasslands of *Kobresia myosuroides* or *Festuca gautieri* (in carbonated soils), dwarf scrub (formed by, e.g., *Rhododendron ferrugineum*, *Genista*

balansae, *Vaccinium uliginosum* ssp. *microphyllum*), and sparse vegetation on rocky substrata and scree (Braun-Blanquet 1948; Carrillo and Ninot 1992). *Rhododendron* and *Genista balansae* dwarf scrub are placed on north- and south-facing slopes, respectively, and both can be either primary or secondary vegetation communities in alpine and subalpine areas severally. Traditional logging and bush burning for pasture are the main causes that explain their presence in subalpine areas as secondary vegetation communities.

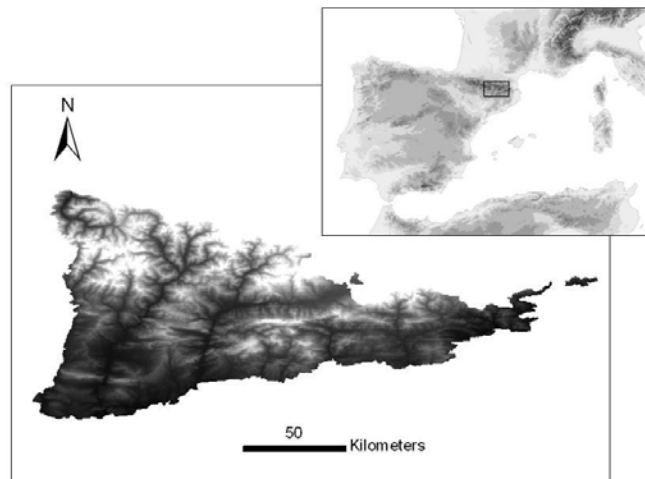


Figure 1 Map showing the location of the study area in the Oriental Pyrenees (NE Spain and Andorra)

2.2. Distribution data

In the Oriental Pyrenees 57 CORINE vegetation units (legend units of the interpretation manual; Vigo *et al.* ed. 2006) appear covering the surface of the alpine and subalpine belts (see Vigo *et al.* ed. 2006 for further details). According to criteria such as occupation area, representativeness, and ecological importance, we selected 12 of these units (Table 1) which comprise the Pyrenees' main alpine and subalpine landscapes: subalpine forest of *P. uncinata* and subalpine (and alpine) scrublands, and grasslands distributed mainly in the alpine belt. The geo-referenced distribution data for the 12 studied vegetation units were obtained from both Catalonia habitats mapping (scale 1:50,000 with a minimum area of representation of 150 x 150 m, approximately 2.25 ha),

a scientific project conducted during the period 1998-2003 (Vigo *et al.* ed. 2006), and Andorra habitats mapping (scale 1:25,000 and 1.6 ha resolution; Carreras *et al.* ed. 2003).

However, due to the spatial accuracy of the climate maps, the study was conducted at a resolution of approximately 0.6 km², that is, the spatial accuracy of the climate maps dictated the resolution at which spatial projection and analyses were carried out for the study area. Hence, the habitats mapping were rasterized to a 700 x 900 m grid using ArcGis 9.3 analysis tools (ESRI 2009). Lastly, these rasterized maps were converted into points which were positioned at the centers of all cells that they represent for modelling using ArcGis 9.3 conversion tools (ESRI 2009).

2.3. Environmental data

Environmental data included 36 climate layers, five layers describing geological materials and 11 topographic layers. We represented the current climate using monthly minimum temperature (Tmin), monthly maximum temperature (Tmax) and monthly precipitation (Ptotal) data layers provided by the WorldClim database. These data layers are generated through the interpolation of mean monthly climate data (averaging the period corresponding to 1950-2000) from climate stations onto a 0.6 km² resolution grid (Hijmans *et al.* 2005).

The spatial biodiversity patterns in the Pyrenees are strongly influenced by topography and geological properties (Pausas *et al.* 2003). Based on geological maps of Catalonia (scale 1:250,000) from the Cartographic Institute of Catalonia (ICC 1996), we carried out a simplification to obtain five geological variables (carbonate materials, silicon materials, substrates with sulphate, Quaternary deposits and water bodies). Then, these geological data were adapted to the reference grid, and we calculated the percentage of each cell containing each type of geological material. Additionally, topographic data were obtained from a digital elevation model of Catalonia (DEM; with a resolution of 20 x 20 m) developed from the topographic database of Catalonia at a 1:50,000 scale (ICC 2010). From this map, we calculated the maximum, minimum and average for both the altitude and the slope for each cell of the study area. Moreover, we obtained the percentages of each cell facing north, south, east, west and plane surfaces from the DEM.

Vegetation unit	OR	AUC	A2 scenario			B2 scenario			
			Current potential distribution (km ²)	Maintained (%)	Increased (%)	Reduced (%)	Maintained (%)	Increased (%)	Reduced (%)
31g <i>Rhododendron ferrugineum</i> heaths ^a	0.048	0.935	1377.23	0.31	0.48	98.90	8.34	6.94	74.84
31u Subalpine and alpine <i>Genista balansae</i> formations ^a	0.051	0.950	1102.29	0.59	3.43	95.38	9.23	19.28	55.62
36a Alpine acid snow-patch communities	0.031	0.977	529.10	0.00	0.00	100.00	0.65	0.00	92.82
36b Alpine calcareous snow-patch communities dominated by espalier <i>Salix</i> species	0.000	0.986	682.59	0.03	0.00	99.94	2.27	0.00	92.38
36g <i>Festuca eskia</i> garland-grasslands	0.034	0.906	1615.64	0.15	0.03	99.66	11.32	0.24	74.76
36h Acidiphile <i>Carex curvula</i> grasslands	0.026	0.981	404.85	0.00	0.00	100.00	3.25	0.61	86.98
36i Alpine <i>Festuca airoides</i> grasslands	0.049	0.973	1247.68	0.05	0.00	99.90	1.03	0.01	95.14
36m Alpine calcicolous <i>Kobresia myosuroides</i> swards ^a	0.049	0.986	363.64	0.00	0.00	100.00	0.09	1.35	97.05
42f Mesophile and acidophilous <i>Pinus uncinata</i> forests ^a	0.076	0.888	2072.51	2.64	6.99	87.72	24.01	17.27	26.41
42g Xerophile <i>Pinus uncinata</i> forest of siliceous adrets ^a	0.062	0.907	1862.03	0.56	6.24	92.65	18.76	18.16	52.28
42h Xerophile <i>Pinus uncinata</i> forest of calcareous adrets ^b	0.059	0.964	887.85	0.14	2.08	97.63	9.54	18.68	67.38
42i Mesophile calcareous <i>Pinus uncinata</i> forests ^b	0.050	0.956	1105.09	0.36	4.80	94.47	8.80	17.97	74.64

Table 1 Studied CORINE vegetation units; test omission rates (OR) at the maximum sensitivity plus specificity threshold; AUC values; and changes in the suitable area for the 12 studied vegetation units by the year 2080 under scenarios A2 and B2, and assuming universal dispersal. Areas maintained, lost and gained by 2080. All performance metrics are based on the data partition (80% training, 20% test) generated for each vegetation unit

^a Habitats of Community interest under the Habitats Directive

^b Habitats of Priority interest under the Habitats Directive

Finally, these data were adapted to a resolution of 700 x 900 m, allowing them to be overlaid with climate data.

To avoid multi-collinearity problems, which can result in model over-fitting (Peterson *et al.* 2007), we reduced the number of environmental predictors using a principal component analysis (PCA) in the software Ginkgo (version 1.7, <http://biodiver.bio.ub.es/vegana/>). We selected the first ten PCA axes as our environmental predictors (PCA01-10; Table S1 in Online Resources) because each of these axes separately explains more variance than would be expected by chance (1.78 %), and they jointly explain 97 % of the variance in the data.

2.4. Climate change scenarios

To simulate the distribution of the investigated vegetation units under possible future climate conditions, we used global climate model data from the IPCC third assessment report provided by the WorldClim database (<http://www.worldclim.org/futdown.htm>).

We used two different climate projections for the 1990-2080 time period developed by the UK Hadley Center for Climate Prediction and Research (Mitchell *et al.* 2004; Mitchell and Jones 2005). These were derived from a global circulation model (HadCM3; Carson 1999) and are based on two different socioeconomic scenarios proposed by the IPCC (Nakicenovic and Swart 2000): A2FI and B2FI (hereafter referred to as A2 and B2, respectively). The A2 scenario storyline describes a very heterogeneous world with a continuously increasing global population and regionally oriented economic growth that is more fragmented and slower than in other scenarios. The B2 scenario describes a world in which the emphasis is on local solutions to economic, social and environmental sustainability, with a continuously increasing population (lower than A2) and intermediate economic development.

With projected average warming of +4.99 °C over our study area by 2080, the A2 projection represents the most severe climate change scenario that we considered, while B2 was the mildest (+3.58 °C). Greenhouse gas emissions from the two scenarios will affect global climate change in different ways, with A2 having a more drastic effect on

vegetation compared to B2. The future climatic condition trends in the study area are shown in Fig. 2 as changes in air temperature and precipitation.

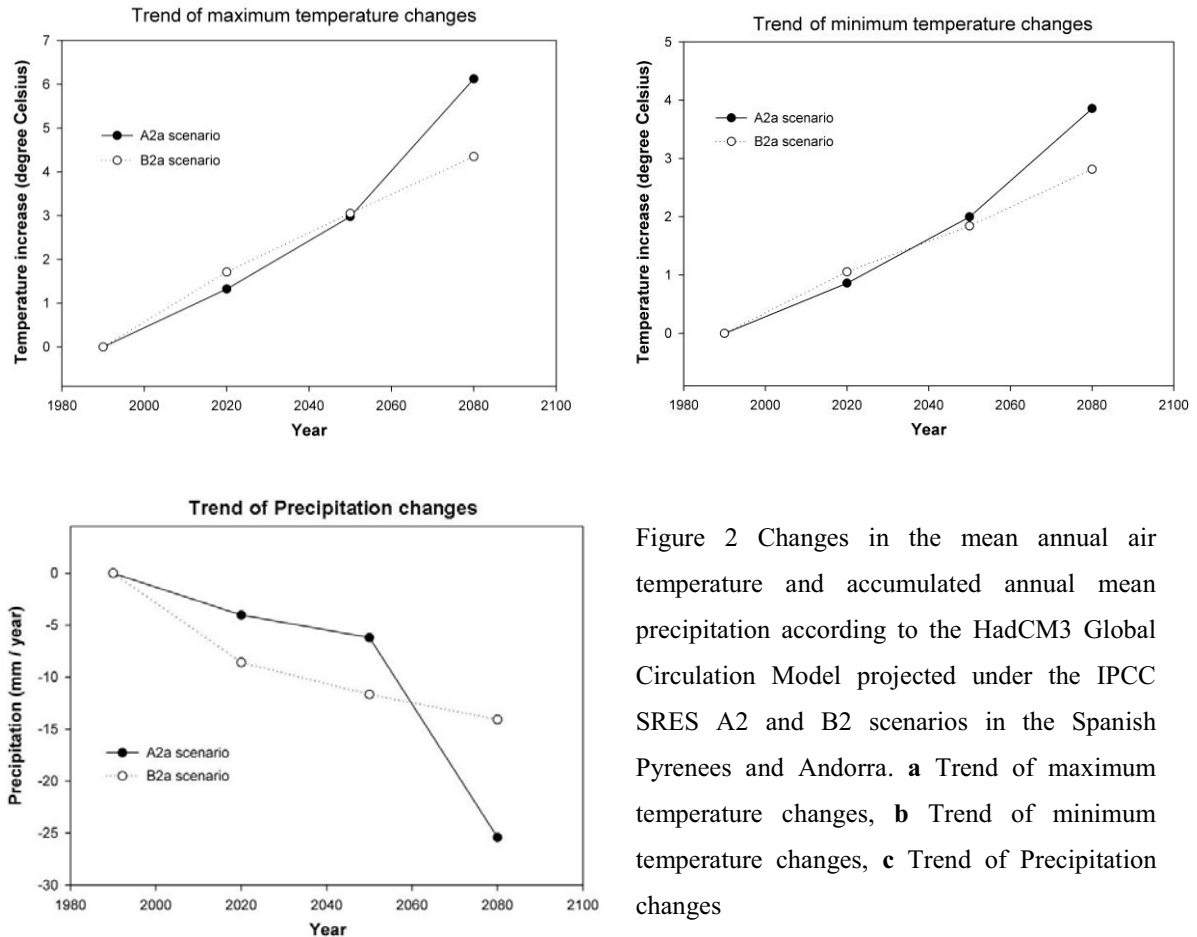


Figure 2 Changes in the mean annual air temperature and accumulated annual mean precipitation according to the HadCM3 Global Circulation Model projected under the IPCC SRES A2 and B2 scenarios in the Spanish Pyrenees and Andorra. **a** Trend of maximum temperature changes, **b** Trend of minimum temperature changes, **c** Trend of Precipitation changes

2.5. Vegetation units distribution modelling

We used Maxent (Phillips *et al.* 2006) version 3.3.1 to relate current environmental conditions to vegetation occurrence data (i.e., points of vegetation units' presences derived from CORINE habitats mapping) and subsequently carried out spatial and temporal projections for the two possible future climate scenarios. Maxent estimates the potential geographic distribution of studied vegetation units by finding the probability distribution of maximum entropy, or closest to uniform, subject to constraints derived from occurrence data (Phillips *et al.* 2006). Maxent has been found to represent a

promising and robust approach for modelling species distributions in both current (Elith *et al.* 2006; Hernandez *et al.* 2006) and future environments (Hijmans and Graham 2006).

Occurrence data often exhibit a spatial bias in survey efforts, which will impact the quality of predictions (Phillips *et al.* 2009). However, the coverage of the vegetation units across the Oriental Pyrenees is continuous, consistent and has a good planimetric resolution, so one of the advantages of modelling these types of data over their associated species occurrences is that the sampling distribution for these vegetation units in the study region is exactly known (with much greater precision than the climate data). Before projecting the model, we applied a mask representing rocky areas to avoid projections at locations that are unsuitable, regardless of climate, topography and geological properties.

We employed recommended default parameters for this version of the model, including regularization multiplier=1, maximum iterations=500, convergence threshold=0.00001 and a maximum of 10,000 background points. To evaluate the quality of the predictions under current climatic conditions, we carried out a random partitioning of the occurrence localities for each vegetation unit and divided the databases into two subsets: calibration and evaluation. The former subset, a random sample from 80% of the total database, was used to calibrate (train) the models, whereas the latter subsample, comprising the remaining data, was used to evaluate (test) the model's predictions (Fielding and Bell 1997).

The results provided by Maxent were evaluated from the evaluation dataset (20 % of total data), employing the area under the receiver operating curve (AUC, ROC) method (Manel *et al.* 2001). The ROC curve characterizes the model's performance at all possible thresholds using a single number that represents the area under the curve (AUC). This procedure has been extensively used to evaluate models (Hanley and McNeil 1982; Fielding and Bell 1997). For models found to have a good predictive performance (test AUC > 80 %), we projected the model from the present (1990) to each interval of 30 years until the year 2080.

Before performing migration simulations (described below), the model results were imported into ArcGis 9.3 (ESRI 2009) to produce maps of potentially suitable areas. We reclassified the probabilistic projections of each Maxent model into binary values

(presence-absence grids) representing either suitable or unsuitable areas. This conversion required the selection of a threshold above which a pixel was reclassified as potentially suitable, whereas it was unsuitable below the threshold. We tested the threshold that maximizes sensitivity plus specificity under the current climate (see Liu *et al.* 2005; Jiménez-Valverde and Lobo 2007; Fitzpatrick *et al.* 2008).

2.6. Dispersal scenarios

We used three simple dispersal scenarios, universal, zero or limited dispersal, to estimate the percentage gain or loss of the geographic range for each vegetation unit. The universal dispersal scenario assumes that vegetation can track their shifting climate envelopes, and the future distribution of vegetation will mirror the future spatial extent and location of those environments that are suitable for them. Therefore, we are assuming that all pixels projected to become potentially suitable as a result of climate change will be occupied by the vegetation units. This assumption might be conservative (i.e., optimistic), but it has been shown to provide good estimates of species loss levels for mountain areas (Engler *et al.* 2009). The zero dispersal scenario assumes that vegetation will persist only in areas where the modelled current and future geographic ranges overlap. In cases where there is no overlap, vegetation units are assumed to become extinct. However, historical constraints will cause realized species ranges to fill only limited proportions of the fundamental range, which is defined as the range that would be achieved should all dispersal constraints be overcome (Gaston 2003). Thus, using the limited dispersal scenario, we quantify the extent to which vegetation units fill their current modelled climatic potential range in the study area (i.e., the capacity to occupy their full suitable area). For this objective, we computed the current realized/potential range size ratio (R/P) (Gaston 2003) across the study area, where P is the number of climatically suitable pixels defined by the Maxent model maps, and R is the number of climatically suitable pixels within the occupied distribution maps of the vegetation units. Thus, we obtained an indicator of the amount of the suitable area that was actually occupied (dispersal ability simulator). We assumed that maintained areas remain constant, and we applied this indicator to expansion areas after assuming universal

dispersal. This scenario represents an intermediate dispersal scenario. We thus obtained the percentage of area lost, but we do not know where that loss occurs.

The spatial overlap between the modelled current and future vegetation presence/absence grids was calculated using ArcGis 9.3 tools (ESRI 2009) for each climate scenario and time period, producing cell counts of current and future distributions.

2.7. Changes in vegetation units' distribution

Using the predictions for each vegetation unit, the maintenance, expansion or reduction in their ranges with respect to their current potential distribution was quantified for each scenario. The maintained distribution area was predicted from the area occupied at the present time that was also expected to be occupied in the future (year 2080). Expansion was defined as the area not occupied at present that was likely to be occupied by the vegetation unit in the future. Reduction was calculated from the area occupied at present that will most likely not be occupied in the future.

Finally, we calculated both the altitudinal shifts and the potential area loss of the modelled vegetation units for the year 2080 as follows:

$$[(Area_{2080} * 100) / Area_{current}] - 100$$

A unit is expected to become extinct when it is predicted to lose 100 % of its suitable area. However, because the link between area losses and extinction formally requires a population viability analysis in addition to predictions of spatial distribution analysis (Botkin *et al.* 2007), we only discuss our projections in terms of suitable area losses, that is, the percentage change in the size of the area.

3. Results

3.1. Algorithm performance

The models developed using Maxent had good to excellent predictive ability, as measured by the AUC values (Table 1). The AUC ranged from 0.888 to 0.986. The relatively high AUC values indicate that the distributions of the vegetation units are well described by the climate, topography and geological properties of the study area.

Additionally, for the chosen threshold, all models showed low omission rates, indicating that only a small percentage of test points fell outside the area predicted as suitable (Table 1).

3.2. Projected distribution by 2080

Our models predict that climate change will have a substantial impact on the geographic ranges of the 12 studied vegetation units (Table 1), with the climate change severity scenario and dispersal scenario influencing the magnitude of the modelled range change responses. An increase in climate change severity (A2 scenario) increases the risk of loss of potential areas for all modelled vegetation units. Considering our results, the following trends are apparent (Table S2, and Figures S1 and S2 in Online Resource).

Alpine grasslands (vegetation units 36 in Table 1). By 2080, the size of the area occupied by alpine grasslands was significantly reduced under the two climate scenarios, losing 99.9 % (± 0.1 standard deviation) of the area of occupation on average under the conditions of the A2 scenario and 92.3 % (± 7.5 standard deviation) under the conditions of the B2 scenario. For the six studied alpine grassland, assuming universal dispersal, the modelled geographic ranges decline with increasing climate change severity. When incorporating the current R/P range size ratio, or if zero dispersal is assumed, the same trends in direction occur, but declines in the modelled range size are more severe. Therefore, these vegetation units were predicted to suffer an intense and rapid reduction in their ranges (Table 1; Fig. 3a), with particularly strong effects being seen for the snow-patch communities of acid soils (36a; Figure S1c and Figure S2c in Online Resource), the grasslands of *Carex curvula* (36h; Fig. 4; Figure S1f and Figure S2f in Online Resource) and the swards of *Kobresia myosuroides* (36m; Figure S1h and Figure S2h in Online Resource); these are formations that appear at higher elevations and seem to show a low capacity to maintain or expand their ranges, which could lead to their extinction by the year 2080.

Regarding changes in altitudinal trends, it is expected that the studied group of alpine grasslands (group 36 in the legend for CORINE habitat mapping of Catalonia and Andorra) will rise between 310 and 415 m by the year 2080, reaching a mean altitude of 2,733 m under the A2 scenario and 2,627 m under the conditions of the B2 scenario.

Subalpine (and alpine) scrublands (vegetation units 31 in Table 1). Our models predict a great reduction in the modelled geographic ranges of the two high mountain scrub formations by 2080, with this potential area loss being greater with increasing

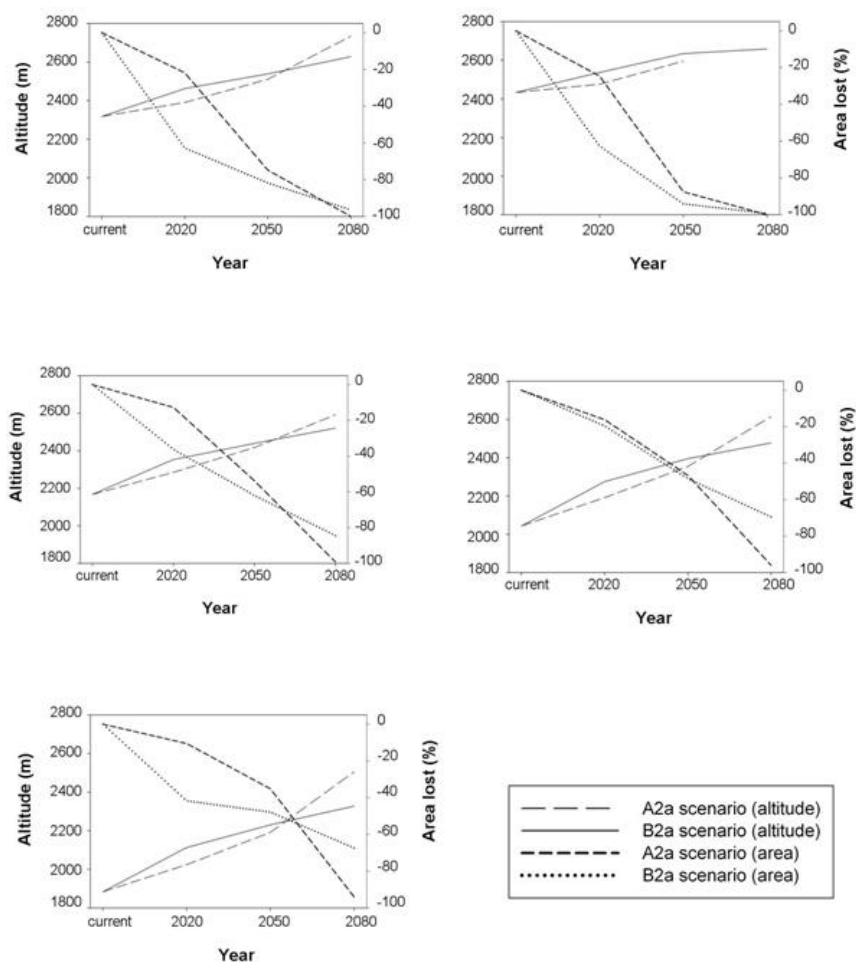


Fig. 3 Quantifying the change trends expressed as losses in the potential range and as an increase in the mean altitude for the two change scenarios assuming universal dispersal: **a** alpine grasslands (units of group 36); **b** alpine acid snow-patch communities (unit 36a); **c** *Rhododendron ferrugineum* heaths (unit 31g); **d** *Genista balansae* scrublands (unit 31u); and **e** subalpine *P. uncinata* forests (units of group 42)

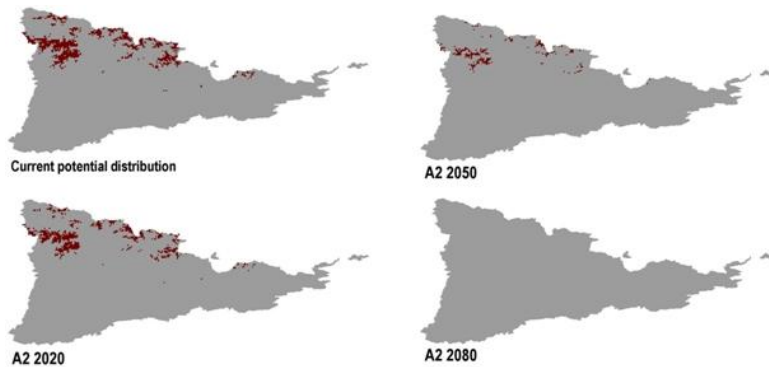


Fig. 4 Potential distribution of acidophile *Carex curvula* grassland (unit 36h) in the present and under the climate projections of scenario A2 (2020, 2050 and 2080) assuming universal dispersal

climate change severity and decreasing dispersal rates. For the *Rhododendron ferrugineum* heaths (31g), the modelled geographic range declines by 98.9 % under the more severe scenario (A2) assuming universal dispersal and by 74.8 % under the B2 scenario with universal dispersal. When zero dispersal is assumed, the modelled range size for this formation decreases more dramatically, losing 99.7 % of its potential area under the A2 scenario and 91.6 % under B2. Finally, when incorporating the R/P ratio, we observe an intermediate situation, in which the loss of suitable area is 99.2 % under the conditions of the A2 scenario and 78.6 % under the less severe scenario (B2). The *Genista balansae* formations (31u) are predicted to suffer a slightly less drastic decline, losing 95.4 % of their area by 2080 under the A2 scenario and 55.6 % under the B2 scenario assuming universal dispersal. When zero dispersal is assumed, this subalpine scrubland shows a reduction in its potential area of 99.4-90.8 % (scenarios A2 and B2, respectively). Figure 3c, d show the general trends of reduction in the ranges of these subalpine scrubs.

Regarding the changes in altitudinal trends, our results show an altitudinal increase for these subalpine scrublands of between 394 and 498 m by the year 2080, reaching an average altitude of 2,603 m under the A2 scenario and 2,500 m under the B2 scenario.

Pinus uncinata subalpine forest (vegetation units 42 in Table 1). In general terms, our results suggest that by the year 2080, these vegetation units will present suitable occupation areas at higher altitudes than today (Fig. 3e), reaching an average altitude of 2,505 m under the A2 scenario and 2,327 m under the B2 scenario, shifting scrublands

and alpine grasslands in part. These subalpine forests were generally predicted to undergo a less drastic reduction in the area occupied than any other vegetation unit analyzed in this study (Table 1), losing 96.1 % (± 3.8 standard deviation) of their potential range on average by the year 2080 under the A2 scenario and 68.8 % (± 21.2 standard deviation) under the B2 scenario. Specifically, when assuming universal dispersal, their average area lost is 93.1 % under the conditions of the A2 scenario and approximately 55 % under the B2 scenario. When assuming zero dispersal, the modelled range size decreases, losing 99 % of the suitable area under the A2 scenario and 84.7 % under B2. When incorporating the current R/P range size ratio, the projected potential area lost by the models varied between 96 and 66 % (scenarios A2 and B2, respectively).

This is the group of vegetation units for which we found the greatest differences in potential area loss based on the climate change scenario employed.

3.3. Vegetation unit extinction by 2080

Among the group of 12 vegetation units investigated, the percentage of units going extinct in the study area (100 % threshold) varied from 0 % (universal dispersal under B2) to 25 % (under A2). The percentage of vegetation units going quasi-extinct (i.e., units with over a 90 % decrease in distribution) varied from 91.6 % (universal dispersal under A2) to 100 % (zero dispersal under A2) and was never below 33 % (universal dispersal under B2). Extinctions are expected to occur between 2050 and 2080.

4. Discussion and conclusions

Credible scientific predictions of future impacts on biodiversity will be required to guide conservation planning and adaptation. Engler *et al.* (2011) suggest that changes in precipitation, in addition to warming, play an important role in determining the potential impacts of climate change on vegetation. Furthermore, in high mountains, the effects of global warming with regard to the biota are amplified (Benito *et al.* 2011). This is especially true in the Pyrenees, which are strongly influenced by the Mediterranean climate, because Mediterranean climate regions are projected to be among the most significantly affected by anthropogenic climate changes and show the highest levels of confidence in projected changes in rainfall (IPCC 2007). Models that forecast species

distributions based on climatic scenarios for the twenty-first century predict a dramatic increase in these climatic trends, resulting in a massive reduction in mountain plant diversity. This is a matter of concern, as mountain ecosystems represent invaluable resources, both in terms of biodiversity and the ecosystem services they provide (Körner 2003; Viviroli and Weingarther 2004). Here, we used fine mapping scale data to assess climate change impacts on the potential distribution of alpine and subalpine vegetation units in the Oriental Pyrenees, and our results point to severe changes in the occupation area. Our models projected that many of the vegetation units analyzed in this study may be threatened by climate change. For all of the analyzed vegetation units, the projected impacts of climate change on the modelled geographic ranges differed mainly in the magnitude rather than the direction of the response across climate change severity and dispersal scenarios, with all vegetation unit ranges being projected to decline. Specifically, the trend shown in our analysis was that higher elevation vegetation is more vulnerable to area losses due to climate change than vegetation at lower elevations. The altitudinal extension of the Pyrenees allows scrublands and forest with a subalpine habitat suitability to move upward as the climate becomes warmer and drier. However, the alpine vegetation belt of the Pyrenees is restricted by altitude (there is no more space available at higher altitudes), which would lead to dramatic losses in appropriate areas for different vegetation units. With the rise in altitude, the area of available habitat diminishes, the topography becomes more hostile (higher slopes) and the soil loses the power to sustain shrub and tree species (Benito *et al.* 2011). Therefore, as we expected and as our results show, the impact of climate change will mainly affect alpine vegetation units. Moreover, carbonated soils in the study area are limited to altitudes approximately below 2,700 m (ICC 1996); hence, calcareous vegetation units would also lack of suitable surfaces with the projected rise in altitude. As a consequence, we should be mindful of the risks calcareous alpine vegetation would face in the future.

This study confirmed a general trend found in studies based on species data conducted for Europe (Engler *et al.* 2011) and on regional scales (Dirnböck *et al.* 2003; Benito Garzón *et al.* 2008; Benito *et al.* 2011). As the climate becomes warmer and drier for the Oriental Pyrenees, alpine vegetation units can be expected to become relegated to summits, with their current range being taken over mainly by subalpine vegetation.

Several works across the world have reported a force response in the altitudinal migration of plant species in New Zeland (Wardle and Coleman 1992) and in northern Europe (Kullman 2002), or in Alps, where resampling of vegetation in some areas has shown a significant increase in the number of shrub and herbaceous species in alpine ecosystems (Grabherr *et al.* 1994). More specifically, in the Mediterranean mountains, some studies have suggested that changes in temperature and precipitation would lead to a shift toward vegetation types currently found under drier conditions in Mediterranean mountains (Gritti *et al.* 2005). In a study performed in the Spanish Central Range, Sanz-Elorza *et al.* (2003) reported a replacement in high mountains grassland communities dominated by *Festuca aragonensis* by shrub patches of *Juniperus communis* and *Genista balansae* from lower altitudes. Furthermore, this altitudinal shift means that there will be increasingly restricted availability of potentially suitable areas for the analyzed alpine grassland units because, as mentioned above, the higher the altitude, the less the available surface area, being calcareous alpine grasslands more vulnerable due to the lack of carbonated soils above 2,700 m in the study area. This trend for alpine grasslands has also been observed in the Alps (Dirnböck *et al.* 2003), where similarly to the Oriental Pyrenees, alpine plant species show more limited availability of potentially suitable areas above the timberline over the years, so they will likely experience severe fragmentation and loss of suitable areas as a result of climate change. However, in alpine and subalpine environments, where the timberline is often maintained artificially at low altitudes by human activities, preservation of traditional land uses, such as pasturing, can decrease area losses for open vegetation that would become excluded through upward shifts of trees and reforestation of areas that are already suitable for forests under current climatic conditions (Theurillat and Guisan 2001; Dirnböck *et al.* 2003; Dirnböck *et al.* 2011; Engler *et al.* 2011). Thus, a real challenge lies in the preservation of biodiversity of the mountain summits, since the species living there lack areas of expansion and will be subjected to great pressure, both by the degradation of the conditions appropriate to each species and by the arrival of new competitive species from lower altitudes (Benito *et al.* 2011).

A relatively recent study on the distribution of Iberian tree species is also noteworthy (Benito Garzón *et al.* 2008), in which the investigators used the *random forest* algorithm (RF) and projected losses in the size of the potential distribution area of

P. uncinata on the Iberian Peninsula of approximately 92 % by the year 2080 under the conditions of the A2 scenario. This coincides with our results, which forecast a very similar percentage of 95 % of area lost (lost area based on the weighted average of each unit in group 42, *P. uncinata* forests) by 2080 under the same climate scenario. However, despite the loss of current area, these vegetation units are expected to be capable of altitudinal displacement and will therefore survive if they can colonize similar areas created by climate change. The extinction of some of the alpine and subalpine species would lead to a reduction in genetic diversity on the Iberian Peninsula, although it may be expected to survive in other European areas (Benito Garzón *et al.* 2008). A study performed regarding the future of the Alps also suggests that this species will survive at high altitudes (Theurillat and Guisan 2001).

A fine spatial resolution study in Europe (Engler *et al.* 2011) projects that an average of ~20 % of the plant species of European mountains areas could lose their entire suitable area by 2070-2100 under the A2 climate change scenario. This coincides with our results, which forecast a similar degree of threat to high mountain Pyrenees vegetation, with an average of 25 % of vegetation units projected to lose their entire suitable area by 2080 under this climate change scenario. Specifically, Engler *et al.* (2011) forecast that a maximum of 100 % of alpine species and 56 % of subalpine species will lose their entire suitable area in the Spanish Pyrenees by 2070-2100 under the A2 scenario. In contrast, our results forecast a much lower degree of threat to alpine and subalpine vegetation, with maximum levels of 50 % and 0 % of alpine and subalpine units, respectively, projected to lose their entire suitable area by 2080 under this climate change scenario. The difference between these results is likely due to the different planimetric precision of the two studies, with the accuracy of CORINE vegetation units usually being much higher than that achieved in the case of species. Furthermore, we should note that this value of 100% of alpine species that are projected to lose their entire suitable area by 2070-2100 in Engler *et al.* (2011) is based on only four species, so the actual average for all alpine species in the Pyrenees would be certainly lower, as found in this study. Nevertheless, our results coincide with the direction of the risks of predictions made by Engler *et al.* (2011) for the Spanish Pyrenees.

Hence, we note that models that predict future changes in the distribution of vegetation units can be as useful as those used in previous studies for species with the aim of obtaining better tools for policy planning related to biodiversity conservation. This study emphasizes that the investigated units could be potentially affected by climate change, and if we consider their high conservation value (as more than a half of the studied vegetation are of community interest under the ‘Habitats’ Directive 97/62/UE), we should consider implementing additional conservation efforts to ensure the future of these vegetation units. Moreover, these units shelter both endemic (e.g., *Dianthus vigoi*, *Festuca bordevei*, *Festuca yvesii*, *Arneria muelleri*) and threatened species (*Oxytropis lapponica*, *Pedicularis tuberosa*, *Vaccinium vitis-idaea*), for which conservation either in situ or ex situ is essential.

Finally, we should note some intrinsic limitations of the methodology used in this study that should be considered when interpreting our results. The first of these limitations derives from the assumption that the climate forecast performed by the third IPCC working Group for the next 70 years is correct. If the expected climatic patterns we used in this study do not match the future patterns exactly, such as a less pronounced increase in temperature occurring, the trends of altitudinal and range size changes predicted in this study may differ substantially. Another limitation to consider is related to the implementation of the limited dispersal scenario. For this, we used a statistical approach by applying a dispersal ability simulator of the vegetation units in the study area to their modelled future projections. However, the conditions that have led to the current range filling of the vegetation units might not exist in the future. Typically, the climate change scenario forecast changes in climate that are much faster than what happened in the past, and plants might not be able to migrate fast enough to keep up with the change. This means that the limited dispersal scenario used in this study probably overestimate the dispersal capacity of the vegetation units. The latter limitation to consider is that our models consider only the potential distribution of vegetation units as defined by bioclimatic envelopes (i.e., estimate the potential future distribution of vegetation based solely on environmental conditions) and therefore do not consider either competition phenomena or the ability of species to resist severe climatic conditions that are not lethal for their survival. Therefore, in light of these methodological limitations, the actual loss

of area of occupancy of the studied vegetation units by 2080 could be considerably lower than predicted based on the results of this work. Nevertheless, our predictions provide important information about trends in the range sizes (occupation areas) of the studied vegetation formations.

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Online Resource

Table S1 Variable loadings for the first ten PCA axes selected as our environmental predictors.

Table S2 Percentage of area losses for the studied vegetation units by the year 2080.

Figure S1 Projected decrease in vegetation unit distributions under A2 scenario.

Figure S2 Projected decrease in vegetation unit distributions under B2 scenario.

Chapter 3. Climate vulnerability assessment of an edaphic endemic plant (*Vella pseudocytisus* subsp. *pau*) by using a spatially explicit demographic dispersal model

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Climate vulnerability assessment of an edaphic endemic plant (*Vella pseudocytisus* subsp. *pau*) by using a spatially explicit demographic dispersal model

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Abstract

Predicting accurate species responses to climate change in fragmented landscapes is a challenging task in conservation biogeography, for which we need to move beyond static species distribution model (SDM) predictions to incorporate key dynamic processes determining species distributions. In this study, we linked time series of habitat suitability with spatially explicit population models to predict the climate-induced range dynamic of threatened *Vella pseudocytisus* subsp. *pau*, an edaphic endemic plant in the Iberian Peninsula, and explore factors that influence its viability under stable and changing climate scenarios. Using the dynamic model BioMove we enhanced current understanding of climate change impacts on a species for which both life-history and ecological requirements are well understood. Whereas long-distance dispersal ability is generally assumed to be critical for the long-term persistence of plant species in fragmented landscapes, we found this edaphic endemic shrub would benefit most from low, but not long dispersal capacity. Results indicate that complex interactions between habitat availability and demographic processes mediate the species' extinction risk, with differences in population size by the middle of the 21st century being more impacted by dispersal traits than by climate change scenarios. Moreover, our study points out a high dispersal-related mortality for the species when distances between patches of suitable habitat are larger than 2km, and enables to hypothesize that this high cost of dispersal has caused selection toward low dispersal ability. BioMove has successfully performed the population processes, allowing for a more complete and direct evaluation of future vulnerability than do static SDM approaches, and will

eventually support development of more effective conservation strategies to mitigate population losses due to climate change.

Keywords: BioMove; conservation management; edaphic endemism; habitat suitability; hybrid models; landscape models; linked model; risk assessment; semi-arid species

1. Introduction

Climate change is already affecting species worldwide (Brook *et al.*, 2009). Nonetheless the future of species will not only depend on the severity of climate-warming but also on species demographic traits (Morin *et al.*, 2008; Schurr *et al.*, 2007; Jeltsch *et al.*, 2008; Keith *et al.*, 2008; Anderson *et al.*, 2009; Pagel & Schurr, 2012). Minimizing negative climatic-warming impacts on biodiversity requires conservation strategies that will enhance species' opportunities to adapt to climate change, especially as their capacity for natural adaptation very likely will be exceeded this century (Parry *et al.*, 2007). Hence, one of the core needs in conservation biology is the assessment of the long-term viability of species' populations under a range of possible management interventions and environmental changes (Midgley *et al.*, 2010). For this approach, robust predictive models of species and community responses to climate change are essential to inform policy and management (Barnard & Thuiller, 2008).

To-date, species distribution models (SDMs) have been the principal approach used to project potential species' distribution changes resulting from climate change (Midgley *et al.*, 2002; Araújo & Guisan, 2006; Thuiller *et al.*, 2006; Huntley *et al.*, 2008). These models extrapolate species location data in space based on correlations of species occurrence with environmental variables thought to influence habitat suitability (Franklin, 2010). Nonetheless, SDMs are static, correlative models that rely on the assumptions that species location data used for modeling are representative of their true distribution, that observed species distributions are in equilibrium with environmental factors that limit those distributions, and that the correct environmental predictors have been involved in the model (Guisan & Zimmermann, 2000; Guisan & Thuiller, 2005). SDMs are also strongly criticized for being limited in their ability to project species patterns over time and space into 'non-analog' environments, that is, novel combinations of environmental factors (Pearson *et al.*, 2006), especially because the models are correlative and do not incorporate dynamic ecological processes. Indeed, there are several shortcomings of SDMs. Firstly, they do not realistically account for population-level processes. Demographic processes affect species' abilities to achieve range expansions from source populations and to persist under less favorable climatic conditions. SDMs do not consider population phenomena such as persistence in sub-optimal climate conditions, or the mechanisms for dispersal and establishment of populations in new geographic ranges that may affect extinction risk (Harte *et al.*,

2004). Second, they do not account for community interactions and processes such as inter- and intra-specific competition (Davis *et al.*, 1998). Therefore, SDMs produce valuable, first-order assessments of potential climatic change impacts on biodiversity. However, their limitations, together with the urgent need to provide more robust information to policy-makers and conservation practitioners, demand the development of integrated models (Huntley *et al.*, 2010). Only by developing dynamic models of species' potential range shifts, that incorporate population and dispersal processes, as well as ecological processes that influence habitat suitability (e.g. disturbance), can we move beyond simply simulating species' potential range changes (Guisan & Thuiller, 2005). Many authors have urged that to meet the needs of conservation biogeography, we need to move beyond static SDM predictions to incorporate key dynamic processes determining species distributions (Guisan & Thuiller, 2005; Araújo & Guisan, 2006; Heikkinen *et al.*, 2006; Thuiller *et al.*, 2008; Franklin, 2009). The use of a hybrid approach, combining the advantages of population viability analysis (PVA) approaches, landscape models and habitat suitability models, would permit more realistic estimates of potential population change rates (e.g. Cabral *et al.*, 2013; Conlisk *et al.*, 2013; McRae *et al.* 2008).

Modeling software BioMove has recently been developed that incorporates a grid-based landscape simulation model of plant community disturbance and succession (Midgley *et al.*, 2010). BioMove was designed to simulate plant species range shifts in response to environmental change and community structure on annual time steps by linking a model of vegetation dynamics (based on plant functional types, PFTs) to a population model for a focal species that is grid-based, age-structured and uses Kernel seed dispersal. In BioMove, species population dynamics are simulated through matrix modeling. Thus, this approach integrates species habitat suitability and population-level demographic rates with simulations of landscape-level processes (Midgley *et al.*, 2010). SDMs for both the PFTs that represent the vegetation landscape, and the target species are developed externally and then linked to BioMove. These models are then used to scale the demographic processes, mortality, recruitment and fecundity and have the effect of excluding recruitment of the target species and PFTs in unsuitable habitats (Keith *et al.*, 2008). Hence, this approach has the potential to make the PFTs and focal species effectively variable with regard to environmental conditions. Finally, BioMove

permits a competitive interaction between the target species and adjoining PFTs, based on strata and competition for light (Midgley *et al.* 2010).

We coupled landscape and population modeling to predict climate change impacts on the viability of a narrowly-distributed endemic and threatened taxon in the Iberian Peninsula, *Vella pseudocytisus* subsp. *pau* Gómez Campo, using BioMove. This approach provided a robust simulation of the demographic and community processes that affect persistence and recruitment in a newly available range for this endangered species. Furthermore, we assessed the importance of dispersal traits for regional survival of the species, investigating whether dispersion is a truly limiting factor for the species' long-term viability.

2. Methods

2.1. Studied species

Vella pseudocytisus subsp. *pau* (Cruciferae; hereafter called “*Vella*”) is a woody shrub endemic to the Iberian Peninsula living in the plateau of East Central Spain, found between 860 and 980m elevation. The plant grows in a highly fragmented and human driven landscape. As a consequence of human disturbance, the species has been a conservation target since near the inception of Spanish plant conservation. It is protected by regional law since 1995 (Aragon Endangered Species Catalog), and an official Recovery Plan was enacted in 2003 (Domínguez-Lozano & Moreno 2008). There are two isolated and independent natural populations of *Vella*, which are separated by a few kilometers. Moreover, in 2003 two more populations were reintroduced in the region, as part of the official Recovery Plan, motivated by a limited natural dispersion of known populations and as a precaution against possible disasters (Guzmán & Sanz, 2011). *Vella* forms part of a steppe vegetation community on dry gypsum substrate. The gypsum-tolerant vegetation patches are surrounded by widespread limestone vegetation dominated by *Rosmarinus officinalis* L., and *Genista scorpius* (L.) DC. These two species were selected to represent the shrub community accompanying *Vella* (hereafter referred to as the shrub PFT). Furthermore, two hemicryptophytic or perennial grasses, *Bracypodium retusum* (Pers.) Beauv. and *Koeleria vallesiana* (Honckeny) Gaud., were selected to represent the grass community (grass PFT) competing with *Vella* for resources and contending its recruitment.

2.2. Distribution data

The geo-referenced distribution data for *Vella* was obtained from the species' mapping provided by the Aragon Government. This mapping was based on orthophoto maps with a scale 1:10 000 and intense field work conducted in 2005, providing accurate continuous layers of current distribution (Goñi, 2005; Gartzia & Sanz, 2009; Sanz & Cervantes, 2010). Due to computational limitation the study was conducted at a resolution of $4 \cdot 10^4$ m². Hence, the mapping for *Vella* was rasterized to a 200x200 m grid using ArcGis 10 analysis tools (ESRI, 2011). Lastly, this rasterized map was converted into points which were positioned at the centers of all cells that present *Vella* individuals for modeling using ArcGis 10 conversion tools (ESRI, 2011).

Furthermore, the geo-referenced occurrence data for the species characterizing the PFTs were obtained from the Iberian and Macaronesian Vegetation Information System (SIVIM, www.sivim.info). The scientific literature and, secondly, herbaria are the most important data sources for this database. Prior to modeling, we examined all the records to identify and exclude any with errors in geo-referencing.

2.3. Environmental variables

The models were run with four explanatory variables, including three climate layers and one describing geological substrate. We represented the current climate for the study area surface using annual minimum temperature, annual maximum temperature and annual precipitation data layers. These data are generated through the interpolation of mean monthly climate data (averaging the period corresponding to 1950-2000) from climate stations onto a 100x100 m resolution grid and were provided by the Aragon Government. These climate data were average for the annual maximum and minimum temperature and annual precipitation and adapted to a resolution of 200x200 m using ArcGis 10 tools (ESRI, 2011). Geological properties have a large impact on plant distributions and persistence (Keitt *et al.*, 2001) and are important in delimiting distributions of the species. Geologic data were provided by the Aragon Government and adapted to a resolution of 200x200m. Climate input for 2020-2100 were derived from one atmosphere-ocean general circulation model (CGCM2, Flato & Boer, 2001) driven with the SRES A2 scenario. This climate scenario is described below.

2.4. Climatic-warming scenario

In order to generate future climate maps we used one climate projection for the 2011-2100 time period developed by the Canadian Centre for Climate Modelling and Analysis, since it contained the time series desired. This was derived from a global circulation model, CGCM2 (Flato & Boer, 2001), and for this study, is based on the socio-economic scenario A2 of the IPCC (International Panel on Climate Change; Nakicenovic & Swart 2000). These data were provided by the Spanish National Climate authority (AEMET, *Agencia Estatal de Meteorología*), and come from the regionalization technique of the INM Analogos, based on empiric methods, and where current observational and future projected records are presented diary. These climate change projections, in the form of 50x60 km grid records from 44 thermometric stations around Aragon, were used to calculate annual maximum and minimum temperature and precipitation anomalies for our study area between the standard period of 1961-1990 and nine ten-year periods from 2020 to 2100. To build high-spatial-resolution maps for the climatic-warming scenario, these anomalies were then downscaled to 200m grid resolution using bilinear interpolation and added to the current climates provided by the Aragon Government (annual precipitation and temperatures) using ArcGis 10 tools (ESRI, 2011) (absolute sum for temperatures and precipitation).

With a projected average warming of +5.3°C and a decrease of 113 mm in precipitation over the study area by the year 2100, the climate scenario considered in this study would have drastic effects on the environment where *Vella* is located. The future climate condition trends considered in this study are air temperature and precipitation (Figure 1).

2.5. Species distribution modeling

Single-models for *Vella* and for both the shrub PFT, represented by *Rosmarinus officinalis* and *Genista scorpius*, and the grass PFT, represented by *Brachypodium retusum* and *Koeleria vallesiana*, are developed externally and then linked to BioMove.

We used Maxent software version 3.3.3k (Phillips *et al.*, 2006), a statistical learning method based on the principles of maximum entropy modeling, to predict current habitat suitability for the organisms of interest (Phillips *et al.*, 2006; Phillips & Dudík, 2008) and subsequently carried out spatial and temporal projections for the possible future climatic scenario. Maxent estimates the probability of distribution for

species' occurrence based on environmental constraints (Phillips *et al.*, 2006). Occurrence records and the four environmental predictors previously described were used to model habitat suitability for *Vella* and the PFTs. Before fitting the model we applied a mask representing rocky areas, water bodies and human infrastructure to avoid projections at locations that are unsuitable, regardless of climate and geological properties.

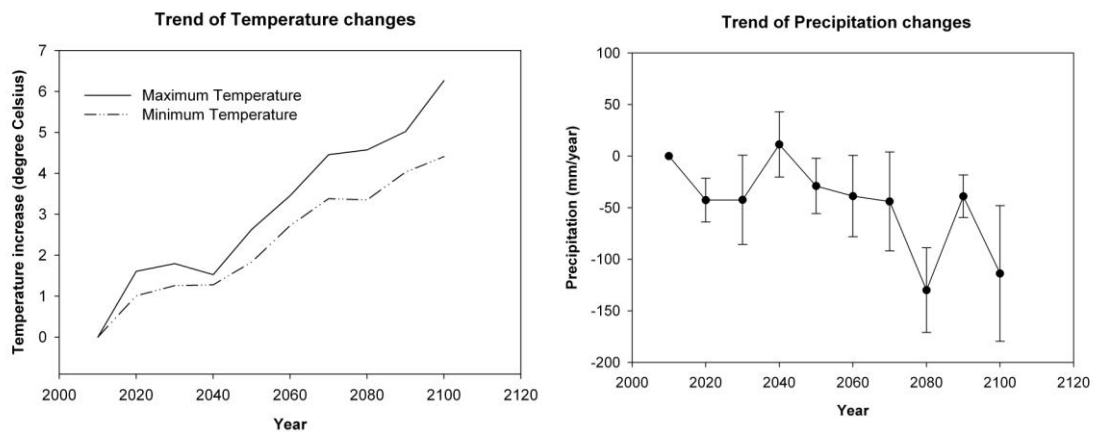


Figure 1 Changes in the mean annual air temperature and accumulated annual mean precipitation according to the CGCM2 Global Circulation Model projected under the IPCC SRES A2 scenario in the study area.

We ran the model for each species with default options, including regularization multiplier=1, maximum iterations=500, coverage threshold=0.00001 and a maximum of 10 000 background points. We used the logistic output of the model that indicates relative environmental suitability of each pixel in relation to background for the studied area (Phillips *et al.*, 2006; Phillips & Dudík, 2008). When dealing with data from atlas databases, randomly partitioning occurrence data into training and test sets is often the only solution available to calibrate and test the model. To evaluate the quality of our predictors under current climate conditions, we carried out a random partitioning of the occurrence localities for each species and divided the database into two subsets: calibration and evaluation. We selected 70% data for training and the rest 30% for testing. We evaluated model performance based on AUC (area under the curve of the receiver-operating characteristic plot) values.

Finally, the results obtained from Maxent for *Brachypodium retusum* and *Koeleria vallesiana* on the one hand, and for *Rosmarinus officinalis* and *Genista scorpius* on the other, were combined using ArcGis 10 Spatial Analyst Tools (ESRI, 2011) to get the habitat suitability envelopes for the PFTs considered in this study.

2.6. BioMove

BioMove simulates plant species' geographic range shifts in response to climate and community structure at annual time steps by integrating species habitat suitability and population-level demographic rates with simulations of landscape-level processes (Midgley *et al.*, 2010). Habitat suitability envelopes for each PFT and *Vella* were performed in Maxent (explained above) for the studied area and imported into BioMove to scale the demographic processes, mortality, recruitment and fecundity.

Vella parameterization. The target species, *Vella pseudocytisus* subsp. *pau*, was parameterized based on exhaustive field measures and several sources in literature. Yearly monitoring effort for the species started in 2001 under the "Atlas de la Flora Amenazada" project of the Spanish Environment Ministry. We used demographic monitoring data for ten years (corresponding to the period from 2001 to 2011) to describe the specie's natural demographic dynamics. Populations were structured in six classes and we employed matrix model analysis to explicitly define life history characteristics for each stratum (Table 1) (Domínguez *et al.*, 2005; Domínguez *et al.*, 2011). *Vella* is a long-lived species with high seedling mortality and low adult mortality. Thanks to previous studies (Domínguez *et al.*, 2005; Dominguez *et al.*, 2011) and consecutive field observations, we know that *Vella* first-year seedling mortality is approximately 84% per year under natural field conditions, mortality for second-year seedlings declines to 50% per year; juvenile and adult mortality are found to be in the range of 7.5-2.3% and 0.5-0.3% per year respectively. Based on previous studies in the natural populations, the maximum abundance was chosen to produce a realistic density of reproductive individuals per cell comparable to dense *Vella* stands, using a maximum abundance of 10 000 individuals per cell (Goñi & Campo-Borau, 2011). This corresponds to a reproductive shrub density of approximately one individual every 4 meters (Table 1; for further details on the demographic dynamic see Domínguez *et al.*, 2005, Domínguez *et al.*, 2011). Moreover, *Vella* has a passive ballistic dispersal mechanism by which, based on the dispersal experiments performed by Dominguez *et al.* (2005), seeds are rarely dispersed beyond 4m and most of the seeds fall in the range

of 1.0-1.5m. Furthermore, based on our knowledge of the species and field observations, we set the maximum long-distance dispersal to 2km and the fraction of seeds dispersed through a long-distance dispersal event to 0.1% (Dominguez *et al.*, 2011). Seeds are dispersed randomly into the neighborhood of the parent grid cell according to an exponentially-weighted probability function. Finally, the effect of envelope values on mortality for the different age classes is based on the factors that are expected to control the current distribution of the species. Domínguez *et al.*, (2011) highlighted that adult survivorship produces the highest sensitivity values for the structured population, indicating that changes in this life-history stage are the most contributing to the overall population dynamic changes. Hence, the mortality of adults is affected by the habitat suitability envelope with a logarithmic type function; such that low envelope values are strongly affected by the envelope and high envelope values are less affected. Furthermore, the effect of climate on seedlings is likely to be scarce. Likewise, the envelope has a subtle effect on fecundity (Table 1).

	S1	S2	J1	J2	A1	A2
Age range (years)	1-2	2-5				
Annual mortality (%)	84	50	7.54	2.28	0.55	0.27
Effect of envelope	week exp=0.5		strong exp=1.0		strong exp=1.0	
Effective Fecundity (seeds/year)	0	0	8	70	528	7200
Physical stratum	0	0	1	1	1	1
Maximum cell population	10,000 (sum of all age classes)					

Table 1 Summarizes the key demographic and physical parameters used in the BioMove model of *Vella pseudocytisus* subsp. *pau*. S1) 1st-year seedlings; S2) 2nd-year seedlings; J) juvenile; A) adults.

PFTs parametrization. The PFTs are chosen based on their relevance to the ecosystem studied. BioMove requires semi-quantitative parameters to simulate the PFTs, including their competitive ability and different life stages, their dispersal ability and their mortality in the study area. This information was derived from literature, herbaria specimens and field work conducted in the study area during the year 2012.

Competition was modeled with two plant functional types. A shrub PFT whose distribution was controlled by the combined envelopes for *Genista scorpius* and *Rosmarinus officinalis* as modeled in Maxent; and a grass PFT whose distribution was

controlled by the combined envelopes for *Koeleria vallesiana* and *Brachypodium retusum* as modeled in Maxent. These were selected to represent accompanying community of *Vella* in the study area based on previous studies (Domínguez *et al.*, 2011) and several Braun-Blanquet surveys carried out in the study area during the year 2012. Inter-specific competition in BioMove is accomplished by specifying the slope and inflexion of a light response curve in addition to the allocation of different age classes to different strata. *Vella* is not thought to have much competition for light, although there might be competition for water after rain. However, the main possible interaction between *Vella* and the PFTs used is that the PFTs restrict the recruitment of new individuals of the species.

Simulation. We ran a 500-year simulation using current habitat suitability data (based on current climate conditions) derived from Maxent for *Vella* and the PFTs to bring the species distributions to equilibrium. The results were used as the initial conditions for the subsequent model runs. First, a 120-year simulation using only the current habitat suitability envelopes (derived from Maxent) for the target and plant functional types was run based on the demographic and dispersal parameters explained above. Ten replicate simulations were obtained as the model contains stochastic processes. One more simulation using the climatic-warming scenario was run, which reloaded new bioclimatic envelopes (derived from Maxent) every ten years for the years between present (2000) and 2100 for both *Vella* and the PFTs. The simulation ran for an additional 20 years using the 2100 scenario. Ten replicate simulations were obtained to examine the sensitivity of outputs to changes in model inputs.

To estimate uncertainty and explore the importance of dispersal traits and climate change, i.e. to assess which parameter interactions are the most critical in determining variation in output (number of individuals), we performed a Monte Carlo analysis in BioMove. First, 50 Monte Carlo simulations using only the current habitat suitability envelopes were run for 120 years up to 2120. Then, 50 Monte Carlo simulations using the climate-warming scenario were run, applying the decadal bioclimatic envelopes between present and 2100. These simulations ran for an additional 20 years using the 2100 scenario, so that time periods were equivalent. For both scenarios, every simulation was run ten times to examine the variability of outputs to the random starting conditions selected by BioMove. In total, 1000 Monte Carlo simulations were run and, subsequently, examined by a Regression tree analysis (explained below).

2.7. Regression tree analysis

A regression tree analysis was used to assess the effect of climate change and dispersal traits on *Vella* long-term viability, as measured by the number of individuals under different permutations of climate and dispersal capacity. Regression trees provide an alternative to regression techniques (e.g. Thuiller *et al.*, 2003) as they do not rely on a priori hypothesis about the relation between independent and dependent variables.

Regression trees are a robust non-parametric alternative to regression for exploring and describing patterns between a response variable (in our study number of individuals) and multiple predictor variables (dispersal traits and climate change). Regression trees are constructed via binary recursive partitioning, a process in which the data are progressively split into a dichotomous branching tree. Each additional split increases the overall explanatory power of the tree, as measure by total deviance (Murray, 2010). However, greater numbers of branches also increase the degree of over-fitting and complexity. Thus, an approach based on a pruned regression tree was applied. The pruned regression tree is based on reducing a fully grown tree, with the extent of the reduction based on the minimal cost-complexity criterion (Venables & Ripley, 2002).

All calculations and analysis were performed in the statistical programming environment R 2.15.3 (R Development Core Team, 2013).

3. Results

3.1. Species distribution models performance

The model developed for *Vella* using Maxent had excellent predictive ability, as measured by the AUC value (AUC=0.953). This high AUC value indicates that the distribution of *Vella* is well described by the climate and geological properties of the study area. Additionally, the models developed for the shrub PFT using Maxent had good predictive ability (*Rosmarinus officinalis* AUC=0.756; *Genista scorpius* AUC=0.712); while the models for the grass PFT had moderate predictive ability (*Brachypodium retusum* AUC=0.678; *Koeleria vallesiana* AUC=0.668) indicating that these distributions are just partially described by the climate and geological properties of the study area.

3.2. BioMove

The simulations developed in the absence of climate change suggest that *Vella* would remain on the territory through the year 2120 under current bioclimatic conditions (Figure 2). When *Vella* was assigned low long-distance dispersal capacity, BioMove indicated that the species would persist on the landscape with no meaningful lost of individuals (Figure 3), showing the maintenance of the species in its natural range. However, moderate long-distance dispersal capacity may prove to be an important constraint for the species. When *Vella* was assigned moderate long-distance dispersal capacity, BioMove showed that the species would only persist in the southern part of its range (Figure 4) and, hence, the populations would lose a significant number of individuals. Additionally, these results suggest that the reintroduced populations will become extinct from the landscape by the year 2050.

The models outputs suggest that climate change will have a drastic impact on the long-term viability of *Vella*, increasing the risk of extinction by the year 2070 for the species (Figure 2). We also found that long-distance dispersal capacity is tightly tight to the level of *Vella's* response to climate change. In general terms, the results suggest that by the year 2050, if low long-distance dispersal capacity is assigned to *Vella*, the species would still retain important populations in the northern part of its natural range (Figure 5a), going extinct by 2070. However, when *Vella* was assigned moderate long-distance dispersal capacity, the models predict the quasi-extinction of the species by the year 2050 (Figure 5b) maintaining few individuals out of its current distributional range.

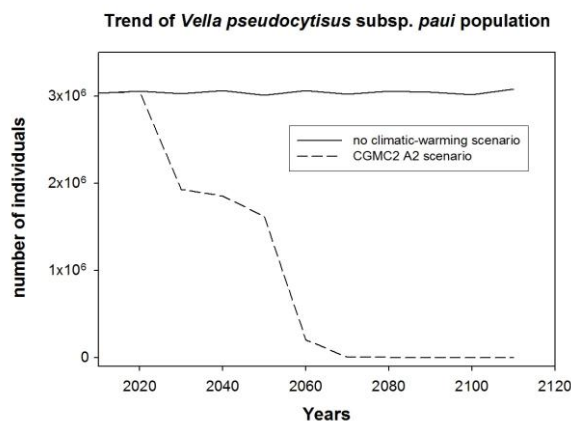


Figure 2 Change trends in the number of individuals of *Vella* under current and climatic-warming conditions assuming long-distance dispersal capacity (2km, 0.1%, and 1.5m mean dispersal).

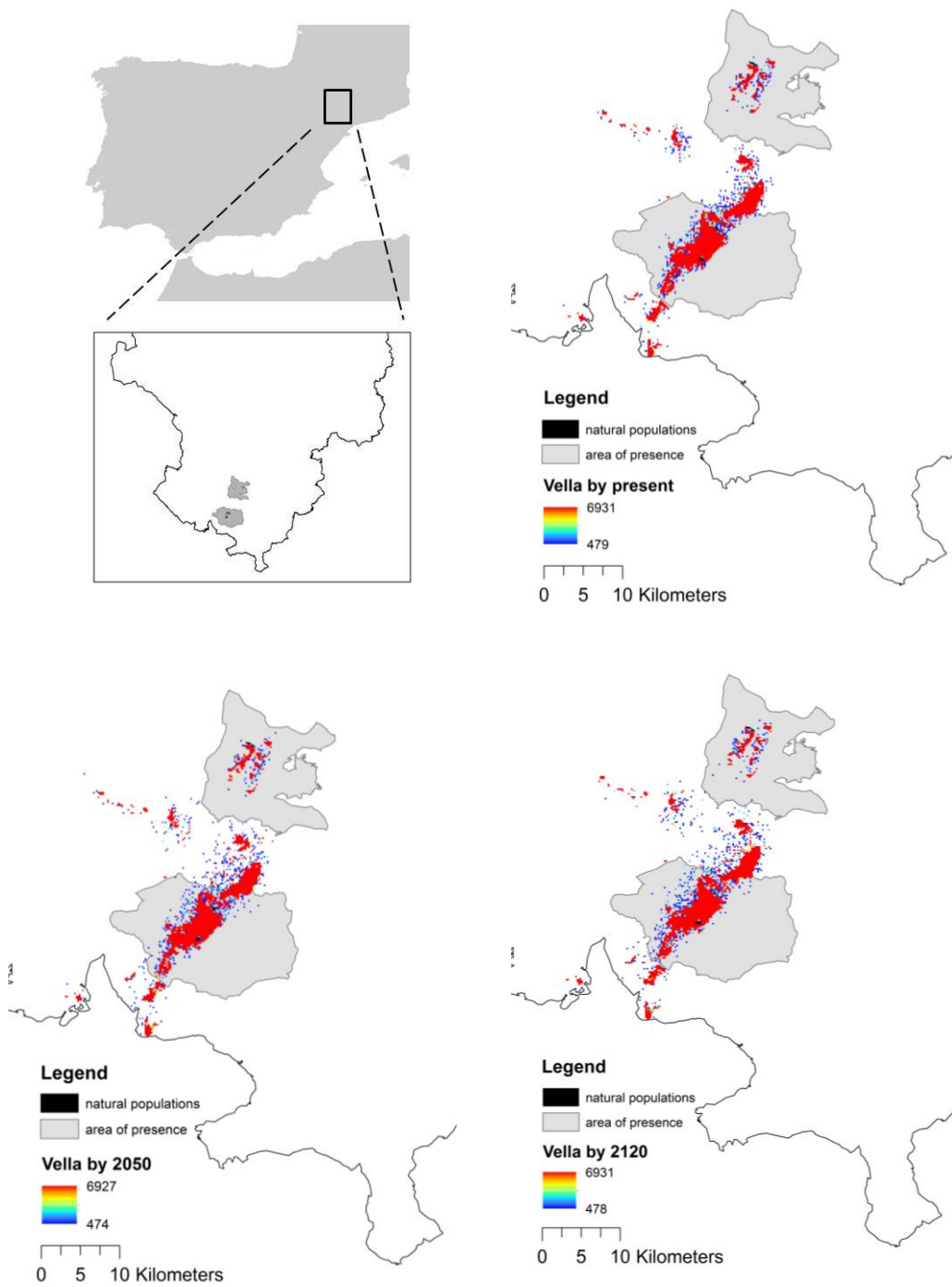


Figure 3 a) map showing the location of the study area in the Iberian Peninsula; BioMove results for *Vella* using current distribution data (no climate change and with low long-distance dispersal capacity (3km, 0.15% long-distance dispersal) by b) present; and the years c) 2050; d)2120. The color ramp refers to the number of individuals of *Vella*.

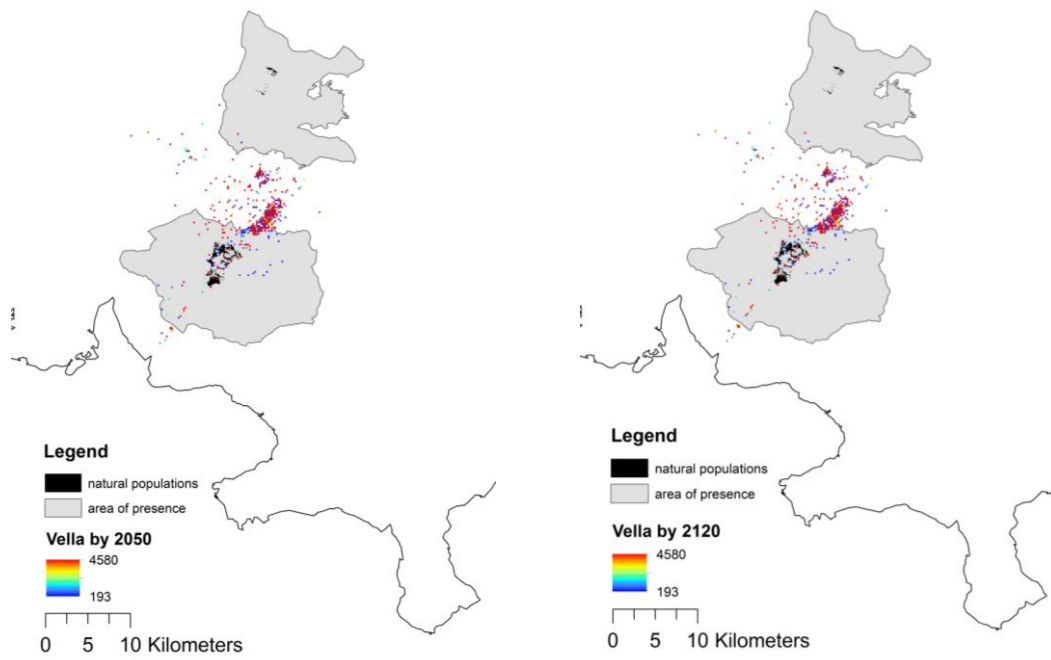


Figure 4 BioMove results for *Vella* using current distribution data (no climate change) and with moderate long-distance dispersal capacity (7.2km, 2.41% (> 1%) long-distance dispersal) by the years a) 2050; b)2120.

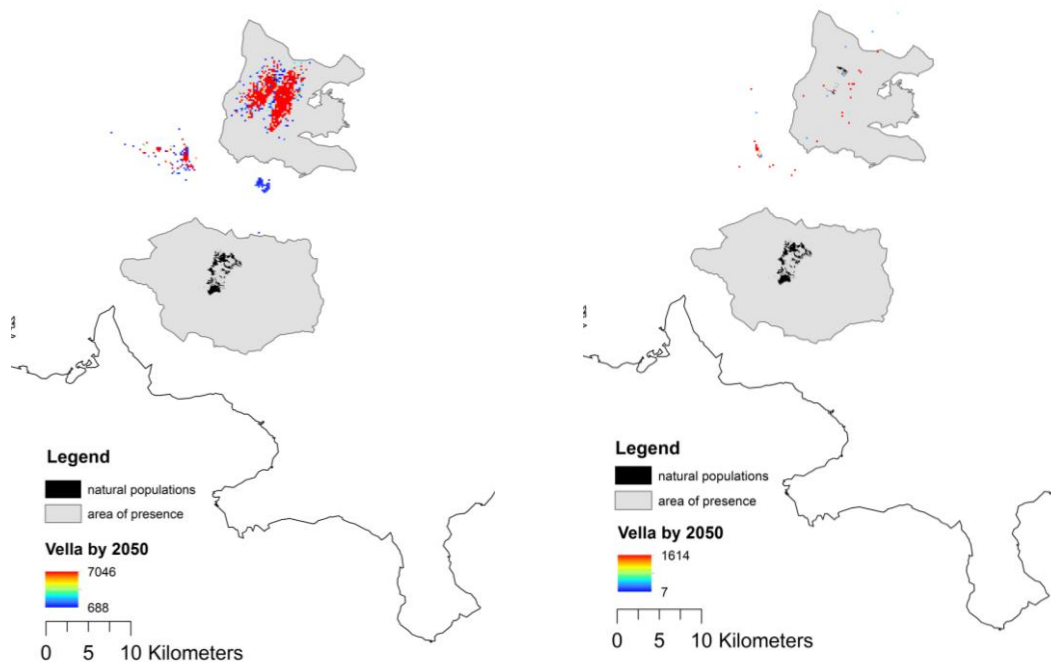


Figure 5 BioMove results for *Vella* using CGCM2 A2 climatic-warming scenario by the year 2050 with a) low long-distance dispersal capacity (2km, 0.3% long-distance dispersal); and b) moderate long-distance dispersal capacity (7.2km, 2.41% (< 1%) long-distance dispersal).

3.3. Regression tree analysis

Considering that the extinction of *Vella* is predicted to occur by the year 2070, we performed regression tree analysis for the year 2050.

The regression tree model for the number of individuals by the year 2050 indicated that the fraction of long-distance dispersed seed, followed by climate change, were consistently the strongest explanatory variables of the individuals' number in the future (Figure 6a). Specifically, the fraction of long-distance dispersed seed was the most important variable determining number of individuals by 2050, with simulations that dispersed more than 1% of the seeds through long-distance dispersal events achieving lower number of individuals by the year 2050 than those that did not (Figure 6a). Moreover, in all simulations the existence of climate change was the second most important determinant of the number of individuals in the future, with simulations that face the climate-warming scenario showing lower number of individuals. In addition, the most important variable for simulations that were not impacted by climate change and dispersed more than 1% of the seeds through long-distance, was maximum long dispersal distance. Interestingly, low long-dispersal distances (in this study less than 2km) are associated with higher numbers of individuals (Figure 6a). The best fit regression tree model explained roughly 97% of the simulations variability using the four variables (three dispersal traits and the presence or absence of climate change). Finally, evidence to select a pruned tree was ambiguous, with a tree from three to five leaves receiving support (Figure 6b). Based on the 1-SE rule a five-leave tree should be selected.

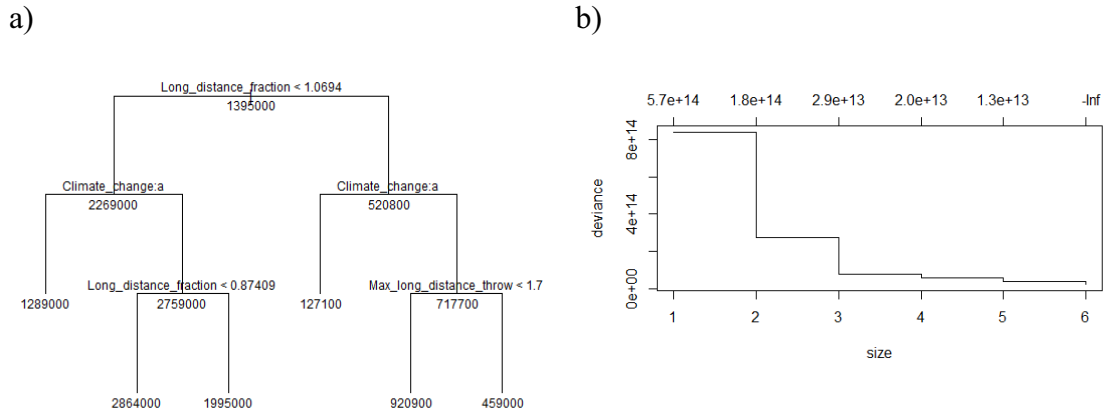


Figure 6 Regression tree analysis; a) Full tree for the four dependent variables (maximum long-dispersal distance, fraction of seeds dispersed through long-dispersal distance, mean short-dispersal distance, and climate change scenario). All observations that satisfy the criterion at a given split fall to the left-hand daughter node while those not meeting the criterion continue to the right. The labels indicate the variable on which the tree split and the numbers and letters indicate the values and category (respectively) on the left split. The numbers at the bottom of each branch are the mean number of individuals at that node by 2050, which is equal to the model estimate; b) reduction in deviance with number of terminal nodes. *a: CGCM2 A2 scenario.

4. Discussion

Robust predictive models of species and community responses to climate change are essential to guide conservation planning (Barnard & Thuiller, 2008). This study coupled landscape and population modeling to predict climate-induced range dynamics of threatened *Vella pseudocytisus* subsp. *pau* endemic in the Iberian Peninsula and evaluated the importance of dispersal traits for regional survival of the species.

A relatively recent study on the climate change impacts on the Spanish biodiversity (Felicísimo *et al.*, 2011) using the algorithm Maxent proposes that *Vella* would not be threatened by climate change, projecting a 25% of spatial overlap between the modeled current and future (year 2100) potential distribution areas under the CGCM2 A2 scenario. In contrast, our results forecast a much higher degree of threat. Specifically, our results predict that while populations are expected to remain more or less unchanged until the middle of the century, in the second half of the century abrupt losses to populations are likely to occur. Indeed, our results forecasted the extinction of the species by the year 2070 under this climate-warming scenario. The use of a non-dynamic approach that focuses on climate change alone produced valuable, first-order assessments of potential climate warming impacts on *Vella*, but may lead to

underestimation of its extinction risks because important interactions between life history traits and habitat suitability were ignored. Our results suggest that extinction risk cannot be estimated only from expected changes in the locations of suitable habitat (Akçakaya *et al.*, 2006; Keith *et al.*, 2008; Brook *et al.*, 2009). Indeed, the expected population trend by the middle of the 21st century (year 2050) results from the interaction between available habitat and demographic processes, with differences in population size being more impacted by dispersal traits than by climate change scenarios.

The ability of plants to migrate and keep pace with the shift of their suitable habitats is likely to be of prime importance for plant species survival (Davis & Shaw, 2001; Jump & Peñuelas, 2005). The frequency of long-distance dispersal events plays an important role in determining regional survival of *Vella* by the year 2050. However, the results showed that higher number of long-distance dispersal events reduced regional survival for *Vella*, with a cutoff at about 1% of overall seed production

At the landscape scale, dispersal success, and therefore colonizing of new suitable habitats, will not only depend on species' ability to disperse but also on the distances between patches of suitable habitat and the configuration of the surrounding landscape (Eriksson *et al.*, 2002). The results highlighted an optimal long-distance dispersal for the species up to 2km. In other words, with unassisted migration as part of a recovery plan, distances between patches of suitable habitat for *Vella* should not be greater than 2km to ensure its survival. Because the model results suggest that moderate to high long-distance dispersal capacity could be a disadvantage for the long-term viability of *Vella* an increasingly fragmented landscape, with great distances between habitat fragments, would suggest an increase in its dispersal-related mortality.

According to Midgley *et al.* (2002) and Cabral *et al.* (2013), alternative conservation actions are likely to be needed for species with low migration ability that are likely to experience strong range shifts. In particular, assisted migration is a hotly debated conservation measure for species highly threatened by climate change (McLachlan *et al.*, 2007; Hoegh-Guldberg *et al.*, 2008; Hunter, 2007; Ricciardi & Simberloff, 2009; Sax *et al.*, 2009). Further analysis to evaluate the degree of fragmentation of the landscape should be performed, since a further challenge to *Vella* migration may prove to be the human-driven habitat fragmentation by clearing, mostly, for agriculture.

Moreover, the efficacy of restoration techniques needs to be understood for effective and strategic implementation (Williams *et al.*, 2005). In 2003 two populations were planted in the region (approximately 150km apart from the natural populations), as part of the official Recovery Plan motivated by a limited natural dispersion of known populations and as a precaution against possible disasters (Guzmán & Sanz, 2011). However, our results highlighted that natural recolonization of these planted populations seems very unlikely, since every simulation predicted the future extinction of the planted populations even with the simulations that excluded climate change.

In summary, the application of BioMove, an integrated bioclimate-population approach, to our studied species has so far confirmed the feasibility of linking spatial and demographic dynamics to evaluate viability of species facing climate change (Keith *et al.*, 2008, Anderson *et al.*, 2009, Brook *et al.*, 2009). Moreover, it is highly relevant to investigate extinction risk of *Vella pseudocytisus* subsp. *pau* using this multi-modeling framework, since previous attempts have ignored biotic interactions and population dynamics. Data-driven models integrating demography can serve to better identify refugia expected to sustain viable populations (Cabral *et al.*, 2013). The multi-modeling framework presented here using BioMove provides a powerful method for performing robust and comprehensive projections of how *Vella pseudocytisus* subsp. *pau* populations will respond to changing environments. Besides enhancing current understanding of this steppe vegetation system, the results obtained here are outstandingly interesting and likely generalizable to other specialist species (like edaphic endemics) or long-lived shrubs on fragmented landscapes, where distances between patches of suitable habitat could mean a large dispersal-related mortality and, therefore, long-distance dispersal capacity may play a negative role for their survival. As suggested by Büchi & Vuilleumier (2012), our results support that the probability for the specialists' seeds to disperse beyond suitable habitats is high, which may increase dispersal-related mortality and favor a reduction of dispersal capacity for these species.

The absence of the demographic data required to parameterize the processes may limit the application of BioMove to other species. However, even in such situations, the use of spatially explicit demographic dispersal models can be helpful, because they can be used as a sort of sensitivity analysis, to help identify the relative importance of different components of species/environment interactions (Hannah *et al.* 2012). In this

case, a low dispersal distance edaphic endemic shrub was found to benefit most from low, but not moderate long dispersal capacity.

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Chapter 4. The Iberian and Macaronesian Vegetation Information System (SIVIM, www.sivim.info), five years of online vegetation's data publishing

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The Iberian and Macaronesian Vegetation Information System (SIVIM, www.sivim.info), five years of online vegetation's data publishing

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Abstract

The SIVIM website was born six years ago. After a first stage of fast growing, the number of queries to its database has currently surpassed 100,000 per year. SIVIM offers its users the opportunity to access to large datasets facilitating phytosociological reviews, plant conservation management and taxonomic chorological studies, amongst others. Therefore, the number of scientific papers and books as well as other websites that cite our website is enlarged everyday. New data have been constantly brought into the project, which means that more than 130,000 phytosociological relevés are currently accessible, storing more than two million specific floristic observations. According to the Global Index of Vegetation-Plot Databases (GIVD), and taking into account the number of computerized relevés, SIVIM is the fourth largest database in the world.

New analysis tools have been developed during this year, among them the on line calculation of species and syntaxa's fidelity values, and a new remarkable tool to model the potential distribution of taxa and syntaxa (based on the maximum entropy algorithm), and their future trends in response to climate change (projections for the years 2020, 2050, and 2080). We should also emphasize *ZamiaDroid*, the latest integration within the project, which allows querying SIVIM by mobile devices (smartphones and tablets). With respect to programming, we implemented a new system so that users can report errors directly to SIVIM administrators.

Concerning future actions, we aim to develop an online expert system in order to survey and classify vegetation communities and to open SIVIM to participative projects, especially those related to photography of plants and vegetation types. The SIVIM project has been funded by two research projects, CGL2006-13421-C04 (2007-2009) and CGL2009-13317-C03 (2010-2012), consecutively.

Keywords: analysis tools, database, relevés,

Introduction

The importance of having large biodiversity databases has been highlighted in several international forums, as well as in the recent national report on the climate change impacts (Moreno, 2005). Databases of plant species occurrence in conjunction with environmental data can be a powerful tool to understand ecological relations or predict the effect of external drivers on ecological processes and species reactions (Chytrý & Rafajová, 2003; Smart *et al.*, 2003; Lenoir *et al.*, 2008; Schaminée *et al.*, 2009). Descriptive studies on vegetation using phytosociological methods include, in most cases, data as relevé tables and constitute an important source of phytosociological, ecological and floristic information.

The great number of publications currently available within the Iberian Peninsula and the Macaronesian archipelagos (nearly 1,700 references are already compiled in SIVIM) give rise to a large number of accessible relevés. We estimate there are approximately 175,000 relevés available for the concerned area (Font *et al.*, 2009). These data are scattered in numerous publications (either national or international), and in a great

number of unpublished works (PhDs, Master theses, reports, and so on). The difficulty in finding some of these works, along with the large diversity detected on the information sources, frequently causes some data to go easily unnoticed even to expert users, being for non-specialists almost impossible to work with all the data from an extensive territory.

Moreover, the knowledge of the composition and distribution of plant communities is becoming increasingly necessary, partially as a consequence of surveying the habitats enclosed in the Habitats Directive 92/43/CE (the legend of which is mostly based on phytosociological vegetation units). However, not only is the knowledge of the distribution and occurrence of vegetation types important for phytosociological studies, but also for the assessment of decision making on land planning and management and for ecological research in general.

We can find a substantial number of independent projects aiming to computerize vegetation data all over the world. The Global Index of Vegetation-Plot Databases (GIVD, <http://www.givd.info>) has recorded 184 databases hosting 2,838,550 vegetation plots worldwide. The first initiative to relate these databases is being

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institutional, scientific and technological obstacles that should be overcome are still important. Among the scientific challenges of computerizing information on plants, we could point out the taxonomic and nomenclatural ones (Jansen & Dengler, 2010), which can be partially solved by using nomenclatural web services like that suggested by the EuroSL project (Dengler *et al.*, 2012).

A standard exchange for plot-based vegetation data (Veg-X) that allows for observations of vegetation at both individual and aggregated observation levels, and makes them available to the entire ecological community has been created (Wiser *et al.*, 2011). The access to large biodiversity data banks is leading to the emergence of new research lines on this topic, and to methodological possibilities unthinkable until now (Ozinga *et al.*, 2005; Bekker *et al.*, 2007).

2. SIVIM project

SIVIM was born in the frame of a nationally funded research project of the Global Change, Earth Sciences and Biodiversity Program (CGL2006-13421-C04) with the involvement of several Spanish universities (University of Barcelona, University of the Basque Country, University of Castilla-La Mancha and University of León). The project was refunded in 2010 for the next 3 years (CGL2009-13317-C03). The direct precursor of SIVIM was the BDBC project (Biodiversity Database of Catalonia, <http://biodiver.bio.ub.es/biocat/>), funded by the Generalitat (regional government) of Catalonia, which begun 17 years ago and currently hosts 21,765 relevés from Catalonia and neighboring areas (Font & Ninot, 1995). Secondly, SIVIM also includes data from the BIOVEG project (Vegetation-Plot Database of the University of Basque Country, <http://www.givd.info/>) which hosts 20,172 relevés (Biurrun *et al.*, 2012). Most of the characteristics applied in SIVIM are based on those already implemented and tested in the BDBC. SIVIM is conceived as a vegetation information system designed for capturing, hosting, editing, analyzing and outputting georeferenced vegetation data. It was created with the aim of being a helpful tool, both in scientific research and in assessment of decision making on land planning and management. Since SIVIM has been developed to record phytosociological relevés, these data (the coverage of all species present in a relevé, regardless of their frequency and taxonomic status) are an important complement to the distributional data from herbarium collections and the floristic literature, both of which are preferentially focused on relatively uncommon species and taxonomically difficult groups and lack the information about species co-

occurrence. In this context, it is remarkable that SIVIM holds the largest number of floristic data records in the national information system on phytodiversity. SIVIM currently stores almost 130,066 phytosociological relevés derived from 1,570 bibliographic references, mainly from the Iberian Peninsula and the Canary Islands. According to the *Global Index of Vegetation-Plot Databases* (GIVD), and taking into account the number of computerized relevés, SIVIM is the fourth largest database in the world. These relevés contain 2,141,254 floristic records (16.5 species per relevé in average), summing altogether 6,637 species. The individual floristic records contained in SIVIM are now available for consultation also in the national (<http://www.gbif.es>) and international (<http://www.gbif.org>) GBIF nodes.

SIVIM uses a taxonomic thesaurus following the proposals of the Anthos project (<http://www.anthos.es>) of the Royal Botanical Garden of Madrid for the Iberian flora, complemented by other floristic repertories from northwest Africa and the Macaronesian archipelagos and the periodic updating derived from the project *Flora iberica*. With regards to syntaxonomical nomenclature, SIVIM follows the checklist of Rivas-Martínez *et al.* (2001, 2002, 2011), but the database structure includes separated fields for the original name (verbatim, unchangeable) and for the corrected or updated name of each relevé. The syntaxonomical thesaurus solves synonymies and allows users to address queries at different levels of the hierarchical classification of vegetation.



Figure 1. The SIVIM Homepage.

3. Website

The SIVIM website (<http://www.sivim.info>, Fig. 1) was presented at the XXI Conference of the Spanish Phytosociological Association in Madrid more than five years ago. In contrast to other vegetation databases, SIVIM offers free online access to

relevés, tables, and floristic observations by versatile queries. Currently, the SIVIM portal allows the following query options: relevés of a specific syntaxon, distribution area (map) of a selected syntaxon, syntaxa or relevés in one or more (up to 6) selected UTM 10x10 km grid cells, syntaxa or relevés present in one or more selected localities, syntaxa or relevés including one or more selected species, taxa (and their frequencies) present in a selected syntaxon, and literature references containing relevés of a selected syntaxon. Data of both relevés and tables are downloaded in B-VegAna XML format. In general, scientists and conservation managers agree that all information on biodiversity should be public and easily available as a way to improve knowledge and prevent and halt impacts on and losses of biodiversity. The only limitation concerns the public accessibility to data containing accurate locations of threatened or protected species. These data in particular should not be finer than 10x10 or 1x1 km grid cell to avoid undesirable risks. Accurate locations of these species should only be facilitated upon request and previous justification of their use for research or conservation purposes.

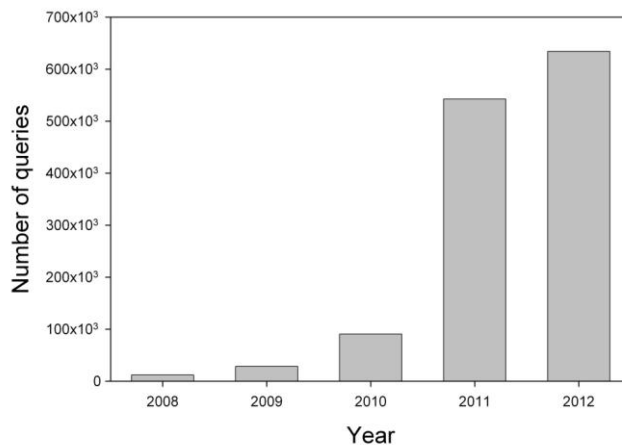


Figure 2. Number of queries to the SIVIM website through time (2008-2012).

4. Web statistics of SIVIM usage

The number of queries to the SIVIM web portal has been rising since the very beginning of the project (Fig. 2), when the website was opened. During the year 2011 the increase in the number of queries was extremely high, achieving more than 500,000 queries, a rate maintained during 2012. This increase is mostly due to GoogleBot, the Google's tracker robot, which has queried all the options of the website several times, and has indexed all the SIVIM database contents. Almost a 70% of the current queries

follow this path. Thanks to all this, the contents of SIVIM are also directly accessible using the Google searcher.

If we look to the origin of the queries, most of them come from Spain and are focused in academic institutions and research centers.

5. Relevés survey through time

Although the SIGMA trip in Catalonia promoted by J. Braun-Blanquet and P. Font-Quer during the year 1934 is usually considered the beginning of the phytosociology in the Iberian Peninsula, the relevés obtained from this famous expedition, which were published one year later (Braun-Blanquet *et al.*, 1935) were not the first relevés sampled at the Iberian Peninsula. This merit goes to the Scandinavian botanist J. Frodin (1926) who published 55 relevés of the central Pyrenees, using a similar recording method to the current phytosociological approach. Nearly ninety years have passed since these first surveys, and we estimate that about 175,000 relevés have been surveyed in the territory in this period (Font *et al.*, 2009, 2010). However, the surveying intensity has not been the same across time (Fig. 3), and the following four periods can be distinguished:

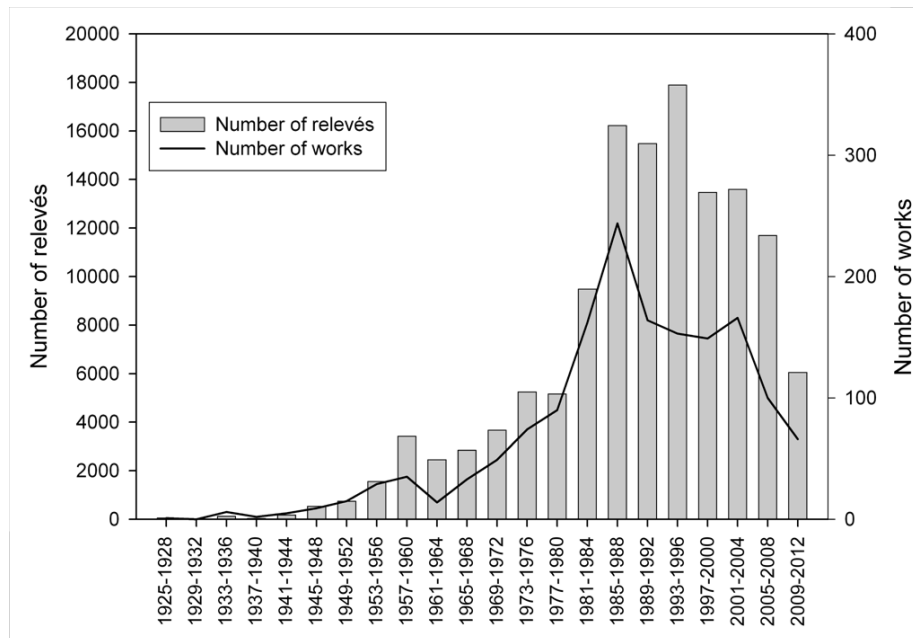


Figure 3. Number of relevés surveyed through 4-year periods, and number of works from which these relevés come from.

1926-1947 - Besides the mentioned precedents and the works carried out by Susplugas in Vallespir (Catalonia), there are few works to be highlighted for this initial

period, which comprises more than 20 years. Furthermore, these works are scarce (a total of 19), and contribute few data (500 relevés).

1948-1980 - In 1948 Braun-Blanquet published his monograph dealing with Alpine vegetation of the Pyrenees (Braun-Blanquet, 1948) and from then on new phytosociological data were annually published at increasingly higher rates. In this period numerous local researchers, some of them already deceased like O. de Bolòs and S. Rivas Goday, constantly contributed with new relevés. Besides the aforementioned researchers, we should stand out S. Rivas-Martínez, J. Vigo and G. Lapraz, who published a substantial number of relevés. During this 33-year period, 343 works storing 25,000 relevés were published. Thus, during this period there was a constant gain of researchers and, consequently, of published relevés.

1981-2004 - During this 24-year period, the phytosociology experienced an authentic boom, thanks to hundreds of committed researchers who published 1,038 works (more than 43 publications per year in average) hosting more than 86,000 relevés. Throughout this period this botanical discipline was taught in almost every University in Spain, and numerous PhDs were disserted. Among them, the study performed by Sardinero (2004), storing 1,554 relevés, holds the record of published relevés within one work.

2005-2012 - Lately, the number of publications has gradually been decelerating (20 works per year in average) due to the ageing of the researchers interested on vegetation survey (in some cases due to their retirement), to the extinction of their chairs due to the current economical crisis and also to some kind of competitiveness penalty to researchers devoted to descriptive studies on vegetation. Moreover, we should not forget the effect that changes in educational plans have had on this discipline, causing in many cases the disappearance of lectures related to phytosociology and vegetation science (Jansen & Dengler, 2010). Thus, the number of PhDs dealing with this discipline has decreased abruptly in the last years. This is the reason why we expect that the current deceleration in the volume of works will continue until reaching the levels registered during the 60s.

6. Relevés survey through the space

The 130,066 relevés contained in SIVIM are not evenly distributed through the territory, being mountain areas clearly better surveyed (Fig. 4). Among the

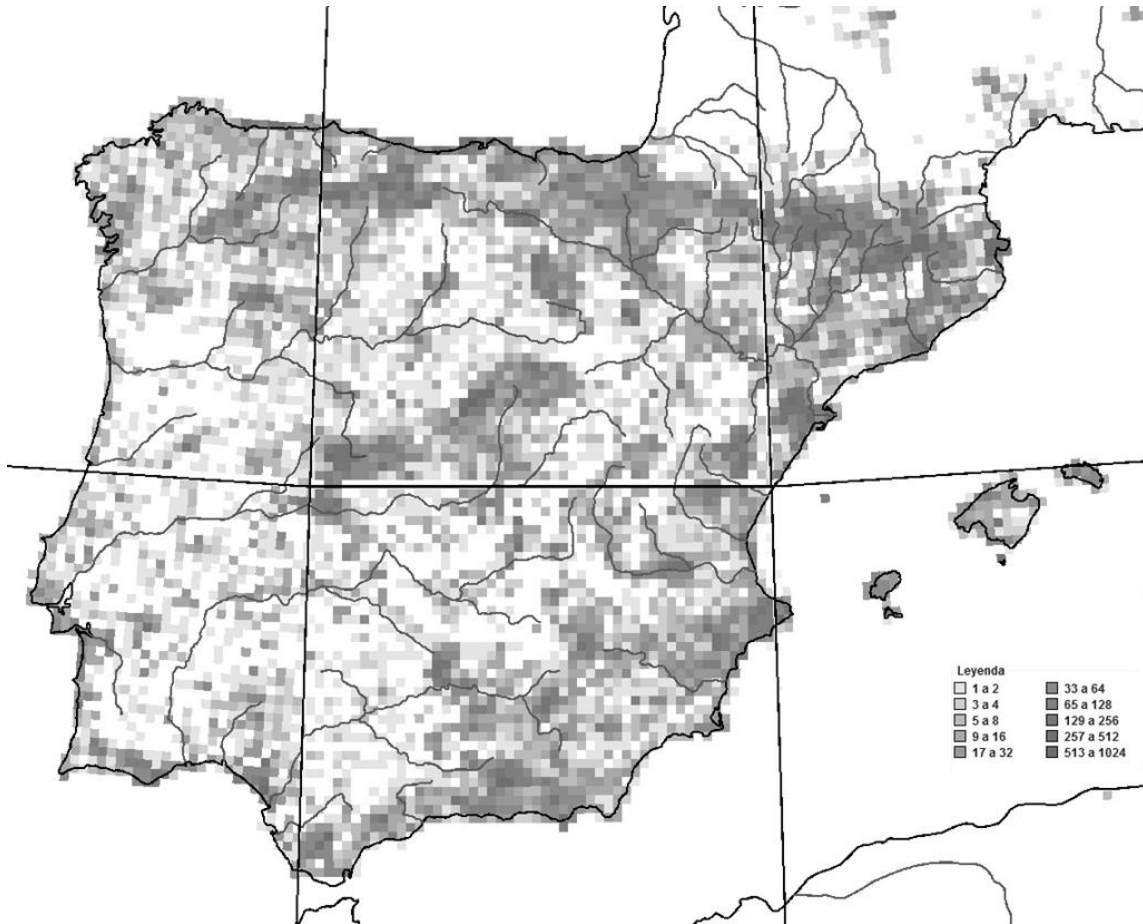


Figure 4. Geographic distribution of the relevés computerized in SIVIM.

computerized relevés accessible at the SIVIM website, 108,694 were carried out in the Spanish peninsular territory (21,765 in Catalonia; 20,172 in Basque Country and bordering territories), 2,774 correspond to relevés performed in the Macaronesian archipelagos, 1,917 to the Balearic Islands, 7,550 come from continental Portugal, 4,776 from Southern France, and 35 from Northern Africa. The remaining 4,325 relevés are not properly georeferenced. However, there are still nearly 1,500 UTM quadrats (10 x 10 km grid size) where no phytosociological relevés have been surveyed up to date, while on the other hand the UTM quadrat 31TBH52, in the Pyrenean Ordesa valley, where 893 relevés have been performed, holds the record of phytosociological surveys.

7. News of 2012

Plenty of innovations have been programmed during the year 2012 in order to improve the SIVIM website. Among the analysis capabilities developed this year, we should highlight the implementation of a potential distribution modeling tool for taxa and syntaxa stored on the database, which is based on the maximum entropy (MaxEnt)

algorithm (Phillips *et al.*, 2006). Figure 5 shows two examples of the generated maps. This tool also provides the resulting ROC curves, which evaluate the model performance. Additionally, nowadays it is possible to calculate the fidelity values for both species and syntaxa online. This allows users to find out the fidelity of a particular taxon to the associations in the database, as well as the opposite option (i.e. to select a particular association and see which are its faithful species). Moreover, it is worth to mention the recent integration of SIVIM in mobile devices, smartphones, and tablets, with an Android operating system. The new app ZamiaDroid (<http://biodiver.bio.ub.es/zamiaDroid>) lets the user enter georeferenced data at the field (floristic observations, and relevés), and address data query to the SIVIM is also possible. Finally, a new system has been implemented by which users can easily report errors detected in the data: nomenclatural adjustments, syntaxonomical ascriptions, georeferencing, discrepancies with respect to original sources, and so on.

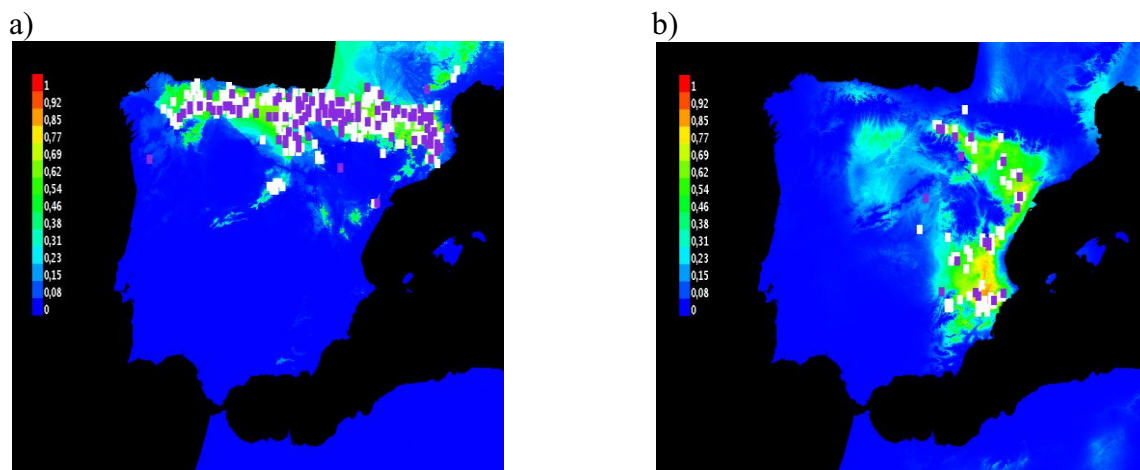


Fig. 5. Generated maps based on the maximum entropy algorithm: a) potential distribution of *Fagus sylvatica*; b) potential distribution of *Rhamno lycioidis-Quercetum cocciferae* Br.-Bl. et O. Bolòs 1958.

8. Conclusions and future issues

SIVIM is conceived to offer free online access to vegetation relevés from the Iberian Peninsula, the Balearic and Macaronesian archipelagos, and the bordering territories. It includes some basic tools for data analysis among which are worth to mention the taxa and syntaxa's potential distribution mapping and the quantitative estimation of fidelity (Phi and Ochiai) of taxa to plant communities. These characteristics, together with the large amount of compiled relevés, make this Project unique among the currently available vegetation databases. The SIVIM Project

represents a small contribution to the task of opening up and spreading basic biodiversity data for their extensive use in research and applied issues.

Moreover, several improvements are ongoing. Regarding the data, we are working on data quality control and we are collecting more data from Portugal and the South of France, areas from where the number of available sources at our web portal is still small. The quality control will require an additional reviewing effort and an update of the taxonomic and syntaxonomic files (thesaurus) for which new regional experts' contributions will be needed. The application of automatic filters to detect probabilistic models-based errors would be helpful. Regarding the improvement of the analysis tools, all of them based on software enhancement, we should point out the possibility of using climate change models (ECHAM5, Roeckner *et al.*, 2003) in order to project the taxa and syntaxa's potential distribution for the future (years 2020, 2050, and 2080); and a web service for automatic determination of vegetation relevés as well. Araucaria (De Cáceres *et al.*, 2009), an early experimental version of this web service, is already implemented in the BDBC. We are currently working on a second version based on probabilities, which will be gradually implemented in SIVIM over the next three years. We also consider very important to encourage the participation of users, so we have developed an application to report errors and we are working on a new application to share images of plants and their communities at SIVIM.

Finally, the linkage to other national or local databases, in a similar way to EVA (European Vegetation Archive) or others initiatives, is a key task for the immediate future.

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RESUMEN DE LAS PUBLICACIONES

1. Patrones de riqueza de plantas vasculares en Cataluña (NE de España) a partir de modelos de distribución de especies

1.1. Introducción y objetivos

Uno de los principales retos de la biología de la conservación es detener el continuo y acelerado declive de la biodiversidad (Pimm *et al.* 1995). Para ello, es preciso aumentar la eficiencia de las políticas en conservación, por ejemplo, realizando mayores esfuerzos en la detección de puntos calientes o *hotspots* de biodiversidad (Myers *et al.* 2000). Estos puntos calientes de diversidad vegetal están bien identificados a escala global, sin embargo, la identificación de puntos calientes de biodiversidad locales es necesaria para una conservación efectiva de plantas tanto a escala global como local (Murray-Smith *et al.* 2008). Así mismo, la estimación de la distribución geográfica de la riqueza de especies es imprescindible para entender los determinantes ecológicos y evolutivos de los patrones espaciales de la biodiversidad (Rosenzweig 1995; Ricklefs 2004). No obstante, evaluar los patrones de riqueza específica a lo largo de regiones heterogéneas, donde los esfuerzos de recolección no han sido suficientes o adecuadamente planeados, no es una tarea fácil (Hortal *et al.* 2007).

Recientemente, los modelos de distribución de especies (MDE) se han revelado como una novedosa aproximación en la predicción de la distribución geográfica de las especies, basados en las relaciones existentes entre sus presencias (o sus registros de abundancia) y los valores de las variables ambientales con influencia en su distribución. Actualmente, existe una gran variedad de técnicas específicamente diseñadas para modelar la distribución potencial de las especies. Esto ha sido posible gracias tanto a los avances en los sistemas de información geográfica (SIG) y, por tanto, a la disponibilidad de mapas digitales de variables ambientales, como a la gran cantidad de datos de distribución de especies georeferenciados que en la actualidad se encuentran disponibles en multitud de bases de datos de biodiversidad (véase Guisan & Thuiller 2005). Por tanto, los MDE pueden ser empleados como base para una correcta planificación de la conservación vegetal mediante su utilización en la predicción de la distribución geográfica de las especies y/o de la riqueza específica de los territorios, proporcionando

una atractiva alternativa a la utilización de datos procedentes de muestreos incompletos o sesgados espacialmente (Parviainen *et al.* 2009).

El área mediterránea se considera un punto caliente de biodiversidad (Myers *et al.* 2000), principalmente debido a su riqueza específica. Este hecho, unido a la transición existente en Cataluña (noreste de España) entre los climas templado y mediterráneo, hace que la zona de estudio sea especialmente interesante desde el punto de vista de la biodiversidad (Pausas *et al.* 2003). Cataluña presenta una gran variedad de regiones florísticas que albergan una gran diversidad de especies vegetales, incluyendo desde elementos propios de la flora mediterránea a elementos medioeuropeos y boreo-alpinos (Ninot *et al.* 2007). Gracias al trabajo realizado durante las últimas décadas, se ha logrado un notable avance en la descripción de la flora y vegetación de esta región, cuyo estado de conocimiento es quizás mayor que el de cualquier otra región del Mediterráneo de tamaño comparable (Greuter 1999). Sin embargo, algunas regiones de Cataluña siguen estando poco estudiadas. Los investigadores generalmente prefieren visitar lugares que se sabe presentan una alta riqueza de especies en lugar de examinar nuevas áreas donde se desconoce la riqueza específica (Dennis & Tomas 2000).

Teniendo en cuenta el estado de conocimiento actual sobre la riqueza florística en Cataluña, se pretenden identificar áreas de riqueza en base a la distribución conocida de toda su flora mediante la utilización de tres técnicas distintas de modelado. Más concretamente, este estudio se centra en (1) examinar si estas técnicas de modelado son una metodología adecuada para describir los patrones de riqueza de especies en Cataluña, (2) identificar áreas de alta riqueza de especies vegetales en los paisajes catalanes y (3) detectar zonas insuficientemente muestreadas en el territorio.

1.2. Material y métodos

La unidad espacial básica para este análisis es la cuadrícula UTM (Universal Transverse Mercator) de 10 km de lado, ya que se trata de la unidad cartográfica utilizada en el Banco de Datos de Biodiversidad de Cataluña (Banc de Dades de Biodiversitat de Catalunya, BDBC). La información referente a la distribución de especies de plantas, proporcionada por el BDBC, se analizó en búsqueda de errores taxonómicos y/o de georreferenciación. Posteriormente, del total de 3.415 especies vegetales citadas en el

BDBC, se seleccionaron para su análisis aquellas que estaban presentes en al menos cinco cuadrículas UTM (véase Vargas *et al.* 2004; Pearson *et al.* 2007; Raes *et al.* 2009).

Se modeló, de manera individual, la distribución potencial de 2.738 especies vegetales a partir de sus datos de presencia georreferenciados, mediante tres técnicas de modelado deferentes: Maxent, Modelo Lineal Generalizado (GLM) y Modelo de regresión adaptativa multivariante (MARS). Maxent (Phillips *et al.* 2006) es un modelo basado en un algoritmo de máxima entropía que de acuerdo con Elith *et al.* (2006) supera a otros métodos más establecidos, principalmente cuando los tamaños de muestra son pequeños. El modelo lineal generalizado y el modelo de regresión MARS se ejecutaron mediante la herramienta BIOMOD (Thuiller 2003), implementada en el programa estadístico R (R Development Core Team 2009).

Finalmente, los mapas de riqueza específica se generaron mediante la combinación de los mapas de presencia/ausencia proyectados por cada uno de los modelos para todas las especies estudiadas. Para ello, se sumaron las presencias predichas en cada unidad de muestreo (Lehmann *et al.* 2002), obteniendo así una estimación de la riqueza potencial de especies para cada cuadrícula UTM y tres mapas de riqueza específica, uno por cada técnica de modelado.

1.3. Resultados

Los MDE empleados en este estudio (MARS, GLM y Maxent) proporcionaron una buena descripción del patrón espacial de diversidad vegetal en Cataluña. Los mapas de riqueza florística obtenidos a partir de este trabajo muestran un patrón mucho más suave que el que se observa en el mapa de riqueza proyectado a partir de los datos recogidos por el BDBC (Figura 3, pág. 54).

A partir de estas técnicas hemos sido capaces de identificar una región de una gran riqueza de especies previamente conocida, los Pirineos, y dos áreas adicionales, la cordillera Litoral y la cordillera Prelitoral (Figura 3, pág. 54). Ribes de Freser (cuadrícula 31T DG38) es la localidad en la que se concentra el mayor número de especies de plantas tanto observadas, presentando 1.268 especies registradas, como predichas por los modelos con 1.279, 1.239 y 1.295 especies determinadas por MARS, GLM y Maxent, respectivamente. Por contra, valores bajos de riqueza se predicen principalmente en

zonas del interior. La Cataluña Central es la zona más pobre en especies vegetales, seguida de la Plana de Lleida.

Los resultados muestran que las técnicas de modelado utilizadas en este estudio están altamente correlacionadas, no detectándose una variación significativa en las proyecciones de los patrones geográficos de riqueza específica entre los algoritmos de modelado (Tabla 3, pág. 54). Sin embargo, MARS y Maxent lograron un mayor éxito predictivo, mientras GLM tiende a sobreestimar la predicción del número de especies por cuadrícula UTM. El mapa obtenido a través de MARS mostró el rendimiento predictivo más alto basándose en los estadísticos Kappa y TSS, así como basándose en dos componentes de error, cantidad de error y asignación del error (Tabla 4, pág. 55).

1.4. Discusión y conclusiones

La mayoría de los estudios que describen patrones de riqueza de especies lo hacen en base a un pequeño grupo de especies, géneros o familias indicadoras (Mac Nally & Fleishman 2004; Murray-Smith *et al.* 2008; Schouten *et al.* 2009). Por lo tanto, este estudio puede considerarse de gran importancia para la diversidad de especies de plantas ya que 2.738 especies fueron modeladas de un total de 3.415 especies descritas en Cataluña (aproximadamente el 80% de la flora total de Cataluña).

Con este trabajo, se han mejorado los patrones de distribución de especies de plantas para Cataluña frente a los patrones previamente proyectados en base a los datos recogidos por el BDBC y, lo que es más importante, ofrecemos una estimación del número mínimo de especies presentes en las zonas donde los datos son aún incompletos, con un número mínimo previsto de 300 especies por cuadrícula UTM de 10x10. Los mapas de riqueza florística que se presentan en este trabajo se pueden utilizar para detectar zonas con baja y alta riqueza de especies para una mejor planificación en las estrategias de conservación, ya sea para restaurar o proteger la biodiversidad a través de planes de conservación.

2. Reducción drástica de los hábitats potenciales para la vegetación alpina y subalpina en Pirineos debido al cambio climático del siglo XXI

2.1 Introducción y objetivos

El actual cambio climático afecta tanto a los ecosistemas como a los organismos que los habitan (Walther *et al.* 2002; Parmesan 2006; Rosenzweig *et al.* 2008), siendo particularmente vulnerable la biota de los sistemas montañosos (Beniston *et al.* 1996; Theurillat & Guisan 2001). Recientemente se ha constatado que las especies de áreas alpinas y subalpinas son especialmente sensibles al calentamiento global (Shaw *et al.* 2000; Erschbamer 2001; Pauli *et al.* 2001). Debido al alto valor de conservación de los ecosistemas de montaña, se necesita información de base científica fiable para implementar las acciones de conservación adicionales necesarias con el fin de asegurar el futuro de dichos ecosistemas.

En las últimas décadas, los modelos de distribución de especies y comunidades han experimentado un uso creciente en la planificación de la conservación y, más recientemente, se han convertido en herramientas importantes para evaluar los impactos potenciales del cambio climático sobre la biodiversidad (Guisan & Zimmermann 2000; Thomas *et al.* 2004; Guisan & Thuiller 2005; Ferrier & Guisan 2006). Entre los estudios basados en comunidades prevalecen aquellos que estudian las propiedades globales de las especies individuales que constituyen una comunidad para explicar las propiedades del conjunto de dicha unidad vegetal. Este enfoque superpone modelos de distribución de especies (MDE) a un conjunto de especies (S-MDE) y se conoce como enfoque *bottom-up*.

En este estudio, elegimos modelar la distribución potencial de unidades de vegetación (tal como se definen en CORINE; Vigo *et al.* eds. 2006) en lugar de especies individuales por varias razones. En primer lugar, los modelos de distribución de unidades de vegetación han sido relativamente poco explorados hasta la fecha, lo que nos motivó a estudiar su utilidad. Por otro lado, aunque las unidades de vegetación no son entidades biológicas tan nítidas y objetivables como la especies, para todas las unidades estudiadas en este trabajo, la cartografía a nuestra disposición basada en detallados ortofotomapas e intenso trabajo de campo, ofrece capas continuas de distribuciones actuales con una

exactitud planimétrica mucho mayor que lo que se consigue en el caso de las especies. Por otra parte, las unidades de vegetación estudiadas en este trabajo se definen principalmente por la presencia de una especie clave y/o dominante. Lo que es más, la reducción del área climáticamente idónea para una unidad de vegetación particular determina la magnitud del riesgo de extinción de las especies que pertenecen de manera casi exclusiva a la misma (Thomas *et al.* 2004). Lo que es más, hasta donde sabemos, no se ha realizado ningún estudio detallado en el que se evalúe el futuro de la vegetación alpina y subalpina de Pirineos con tanta precisión planimétrica (resolución de aproximadamente 0,6 km²) bajo posibles condiciones climáticas futuras. Por último, es importante tener en cuenta que las unidades estudiadas tienen un alto valor de conservación, ya que siete de ellas son hábitats de interés comunitario y dos son hábitats de interés prioritario por la Directiva Hábitats 97/62/UE (Directiva 97/62 / UE de 27 de octubre de 1997, Directiva 92/43/CEE adaptada al progreso técnico y científico sobre la conservación de los hábitats naturales y de la fauna y flora silvestres).

En este estudio se evalúa, en términos de pérdida de área, los impactos del cambio climático en la distribución potencial de seis tipos de prados alpinos, dos matorrales subalpinos (y alpinos) y cuatro bosques subalpinos de *Pinus uncinata* en el Pirineo Oriental a finales del siglo XXI.

2.2. Material y métodos

El área de estudio comprende el Pirineo Oriental, sistema de relieve acusado, con un amplio intervalo altitudinal y una alta heterogeneidad de sustratos. La elevada variedad ambiental resultante conlleva una gran diversidad de unidades de vegetación. Este trabajo se realizó a una resolución de aproximadamente 0,6 km² (cuadrados de 700 x 900 m de lado) y sobre una superficie total de 9.894 km². La resolución de este estudio queda definida por la resolución de los datos climáticos disponibles.

Para simular la distribución de las unidades de vegetación estudiadas bajo posibles condiciones climáticas futuras, se utilizaron los datos del tercer informe de evaluación del Panel Internacional por el Cambio Climático (IPCC) proporcionados por la base de datos WorldClim (<http://www.worldclim.org/futdown.htm>). Más concretamente, se utilizaron dos proyecciones climáticas diferentes para los años 2020, 2050 y 2080, elaboradas por el

Centro Hadley para la Predicción e Investigación del Clima de Reino Unido (Mitchell *et al.* 2004; Mitchell & Jones 2005). Estas proyecciones se derivan de un modelo de circulación global (HadCM3, Carson 1999) y se basan en dos escenarios socio-económicos diferentes propuestos por el IPCC (Nakicenovic & Swart 2000): A2FI y B2FI (llamados en adelante, A2 y B2, respectivamente).

Empleamos el algoritmo de máxima entropía Maxent (version 3.3.1) con el objetivo de relacionar las condiciones ambientales actuales con los datos de presencia de las unidades de vegetación estudiadas y posteriormente realizar proyecciones espaciales y temporales para los dos escenarios climáticos futuros considerados. Maxent estima el área de distribución geográfica potencial de las unidades de vegetación estudiadas mediante la búsqueda de la distribución de probabilidad de máxima entropía, o más cercana a la uniforme, sujeto a las limitaciones derivadas de los datos de presencia (Phillips *et al.* 2006). Los resultados proporcionados por Maxent se evaluaron a partir de un conjunto de datos de evaluación (que suponen el 20% del total de datos), mediante el método del área bajo la curva ROC (AUC) (Manel *et al.* 2001).

Posteriormente, con el objetivo de estimar el porcentaje de ganancia o pérdida de área en la distribución geográfica de cada unidad de vegetación se utilizaron tres escenarios de dispersión: dispersión universal, dispersión nula y dispersión limitada. El escenario de dispersión universal, asume que la vegetación tiene una capacidad de migración ilimitada, por lo que en un futuro ocupará todas aquellas áreas proyectadas como potencialmente idóneas como consecuencia del cambio climático. El escenario de dispersión nula asume que la vegetación se mantendrá sólo en aquellas áreas donde los límites geográficos actuales y futuros se superpongan. En los casos en los que no hay solapamiento, se asume que dichas unidades de vegetación se extinguirán. Sin embargo, las especies ocupan áreas limitadas de su rango fundamental, el cual puede definirse como el área de distribución que se lograría si se superasen todas las limitaciones a la dispersión (Gaston 2003). Con el objetivo de reflejar esta situación en nuestro estudio, se calculó la proporción actual entre el tamaño del área potencial o fundamental y el área realizada u ocupada (R / P) (Gaston 2003) para las unidades de vegetación en la zona de estudio, donde P es el número de píxeles climáticamente adecuados a partir de los mapas modelados en Maxent y R es el número de píxeles adecuados según la cartografía de

estas unidades de vegetación. De esta manera se obtiene un indicador de la cantidad de área idónea que realmente es ocupada por las distintas unidades de vegetación estudiadas. Para este escenario de dispersión limitada asumimos que las áreas mantenidas en el futuro permanecen constantes y se aplica este indicador (R/P) a las zonas de expansión que resultan de asumir un escenario de dispersión universal. Este escenario representa un escenario de dispersión intermedio que nos permite obtener un porcentaje de área perdida, sin embargo, no sabemos donde se produce esa pérdida.

2.3. Resultados

Los modelos desarrollados por Maxent presentaron una capacidad predictiva de buena a excelente, tal y como muestran los valores de AUC que oscilaron entre 0,888 y 0,986 (Tabla 1, pág. 76). Estos valores de AUC relativamente elevados indican que la distribución actual de las unidades de vegetación estudiadas se encuentra bien descrita por el clima, la topografía y las características geológicas de la zona de estudio.

Los resultados obtenidos muestran como el cambio climático tendrá un impacto sustancial en la distribución geográfica de las 12 unidades de vegetación estudiadas (Tabla 1, pág. 76), influyendo en la magnitud de la respuesta la severidad de los escenarios de cambio climático y dispersión. Un incremento en la severidad climática (escenario A2) aumentará el riesgo de pérdida de áreas potenciales para todas las unidades modeladas. Lo que es más, todos los modelos predicen un aumento en la altitud media de las áreas de ocupación potencial para todas las unidades de vegetación estudiadas.

Prados alpinos (unidades de vegetación 36 en la Tabla 1, pág. 76)

Para el año 2080 nuestros resultados muestran una reducción drástica en el tamaño de la área ocupada por los prados de alta montaña bajo los dos escenarios climáticos analizados, perdiendo de media el 99,9% ($\pm 0,1$ desviación estándar) de su área de ocupación actual bajo las condiciones del escenario A2 y el 92,3% ($\pm 7,5$ desviación estándar) bajo el escenario B2. Se prevé que los prados alpinos sufran una intensa y rápida reducción en sus áreas de distribución (Tabla 1, pág. 76; Figura 3a, pág. 83), siendo especialmente afectados los neveros de terrenos ácidos, los prados de *Carex curvula* y los prados de *Kobresia myosuroides* (unidades 36a, 36h y 36m

respectivamente), los cuales aparecen, en general, a mayor altitud y parecen mostrar poca capacidad para mantener o expandir sus áreas de distribución, lo que podría conducir a su extinción para el año 2080. Por otro lado, en cuanto a los cambios en las tendencias altitudinales, se espera que estas unidades de vegetación asciendan entre 310 y 415 m para el año 2080, alcanzando una altitud media de 2.733 m bajo el escenario A2 y de 2.627 m bajo las condiciones del escenario B2.

Matorrales subalpinos (y alpinos) (unidades de vegetación 31 en la Tabla 1, pág. 76)

Los modelos predicen una importante reducción para el año 2080 en el área modelada de las dos formaciones de matorral subalpino, siendo mayor esta pérdida de área potencial al aumentar la intensidad del cambio climático. Nuestros resultados indican una pérdida media de área del 98,9% y del 74,8% para los matorrales de *Rhododendron ferrugineum* bajo los escenarios A2 y B2 respectivamente. Las formaciones de *Genista balansae* sufrirán una pérdida de área menos drástica, perdiendo de media el 95,4% de su área de distribución para el año 2080 bajo el escenario A2 y el 55,6% bajo el escenario B2, asumiendo dispersión universal. En cuanto a los cambios altitudinales, nuestros resultados muestran un aumento de altitud en las áreas de ocupación de estas unidades de vegetación de entre 394 y 498 m para el año 2080.

Bosques subalpinos de Pinus uncinata (unidades de vegetación 42 en la Tabla 1, pág. 76)

En términos generales, nuestros resultados sugieren que, para el año 2080, estas unidades de vegetación presentarán áreas de ocupación idóneas a altitudes superiores a las observadas actualmente, alcanzando los 2.505 m de altitud media bajo el escenario A2 y los 2.327 m bajo el escenario B2, y desplazando, en parte, a los matorrales y prados alpinos montaña arriba. Por otro lado, estos bosques subalpinos sufrirán, en general, una reducción en el área ocupada menos drástica que cualquier otra unidad de vegetación analizada en este estudio (Tabla 1), mostrando una pérdida media para el año 2080 del 96,1% ($\pm 3,8$ desviación estándar) de su área potencial bajo el escenario A2 y del 68,8% ($21,2 \pm$ desviación estándar) bajo el escenario B2.

2.4. Discusión y conclusiones

La drástica reducción de las áreas de distribución potencial de los prados de alta montaña y de los matorrales y bosques subalpinos de *Pinus uncinata*, pone de manifiesto la potencial gravedad del efecto del cambio climático sobre la vegetación de Pirineos. A la luz de nuestros resultados es esperable que los prados de alta montaña sean relegados a zonas refugio (culminícolas), y que su área de distribución actual sea ocupada por matorrales subalpinos que en la actualidad tienen su óptimo en niveles altitudinales inferiores. Por otra parte, las unidades forestales subalpinas serán probablemente desplazadas y ocuparán áreas que actualmente son propias de la vegetación de matorral subalpino. Estos resultados coinciden ampliamente con los obtenidos en estudios previos realizados tanto a escala continental europea (Engler *et al.* 2011) como a escala regional (Dirnböck *et al.* 2003; Benito Garzón *et al.* 2008; Benito *et al.* 2011) en base a registros de especies y confirman la tendencia general de declive de la vegetación alpina frente al cambio climático.

Finalmente, nuestros resultados muestran que los modelos que predicen cambios futuros en la distribución de las unidades de vegetación (enfoque *top-down*) pueden ser tan útiles como los utilizados en estudios previos para especies (Benito Garzón *et al.* 2008; Engler *et al.* 2011), con el objetivo de obtener mejores herramientas para la planificación de políticas relacionadas con la conservación de la biodiversidad.

3. Evaluación de la vulnerabilidad climática de un endemismo edáfico (*Vella pseudocytisus* subsp. *pau*) mediante un modelo de dispersión demográfica espacialmente explícito

3.1. Introducción y objetivos

El cambio climático está alterando los patrones globales de biodiversidad al modificar la distribución geográfica de las especies (Brook *et al.* 2009). No obstante, el futuro de las especies no sólo dependerá de la severidad del cambio climático, sino también de las características demográficas de éstas (Morin *et al.* 2008; Schurr *et al.* 2007; Jeltsch *et al.* 2008; Keith *et al.* 2008; Anderson *et al.* 2009; Pagel & Schurr 2012). Reducir los impactos negativos del calentamiento global sobre la biodiversidad requiere

de estrategias de conservación eficaces que mejoren las oportunidades de las especies para adaptarse al cambio climático (Parry *et al.* 2007). Por tanto, para una mayor eficacia en la gestión y conservación de la biodiversidad, es esencial el desarrollo de modelos predictivos robustos de la respuesta de las especies y comunidades vegetales al cambio climático (Barnard & Thuiller 2008). El uso de un enfoque híbrido que combine las ventajas de los análisis de viabilidad poblacional (AVP), con modelos paisajísticos y de idoneidad de hábitat (MDE), permitiría estimaciones más realistas de las posibles tasas de cambio en las poblaciones ante el calentamiento global (véase por ejemplo, Cabral *et al.* 2013; Conlisk *et al.* 2013).

El programa Biomove (Midgley *et al.* 2010), fue diseñado para simular los cambios en la distribución geográfica de las especies de plantas en respuesta a cambios ambientales mediante la vinculación de un modelo dinámico de la vegetación (basado en tipos funcionales de plantas, PFT) con el modelo poblacional de la especie de estudio. Los mapas de idoneidad de hábitat (MDE) tanto para la especie objeto de estudio como para los tipos funcionales de plantas que componen la comunidad vegetal, son desarrollados externamente y posteriormente vinculados a Biomove. Integrando la dinámica de la vegetación y modelos demográficos, BioMove puede abordar directamente el efecto de la competencia por los recursos. Sin embargo, hasta donde sabemos, ninguna investigación utilizando BioMove ha sido aún publicada.

En el presente estudio, combinamos modelos poblacionales, de paisaje y MDE, mediante la aplicación BioMove, para predecir los efectos del cambio climático sobre la viabilidad futura de un taxón endémico y amenazado de la Península Ibérica, *Vella pseudocytisus* subsp. *pau* Gómez Campo. A su vez, se evaluó la importancia de las características de dispersión para la supervivencia de la especie, es decir, se investigó si la dispersión es un factor verdaderamente limitante para la viabilidad a largo plazo de la especie.

3.2. Material y métodos

BioMove simula los cambios en el rango geográfico de las especies en respuesta al clima y a la estructura de la comunidad en pasos anuales. Este enfoque integra la idoneidad del hábitat de las especies (MDE) y las tasas demográficas a nivel poblacional

con simulaciones de los procesos paisajísticos (Midgley *et al.* 2010). Los modelos de idoneidad de hábitat para las PFT y *Vella pseudocytisus* subsp. *pau*i en el área de estudio se desarrollaron en Maxent y posteriormente se importaron a BioMove. Estos modelos fueron posteriormente utilizados para escalar los procesos demográficos, mortalidad, reclutamiento y fecundidad y tienen el efecto de excluir el reclutamiento de la especie de estudio y PFT en hábitats inadecuados (Keith *et al.* 2008). Esto permite que tanto las PFT como la especie de estudio sean realmente variables con respecto a las condiciones ambientales. Por otra parte, la dinámica poblacional de la especie de estudio se simula mediante modelos matriciales y una función Kernel simula la dispersión de la población.

Para estimar el grado de incertidumbre y explorar la importancia de la dispersión y el cambio climático, es decir, para evaluar qué interacciones entre las variables son las más importantes en la determinación de la variación en el tamaño poblacional (número de individuos), se realizó un análisis de Monte Carlo en Biomove. En primer lugar, se llevaron a cabo 50 simulaciones Monte Carlo utilizando sólo los mapas de idoneidad actuales durante 120 años hasta el año 2120. Se obtuvieron diez réplicas de cada simulación. Por otra parte, se realizaron 50 simulaciones Monte Carlo utilizando los mapas de idoneidad de hábitat decenales entre el presente y 2100 a partir del escenario de cambio climático seleccionado. La simulación se ejecutó durante 20 años más utilizando el escenario obtenido para el año 2100. Se obtuvieron diez réplicas de las simulaciones para examinar la sensibilidad de los resultados a los cambios en las condiciones iniciales generadas en BioMove. En total, se ejecutaron 1.000 simulaciones Monte Carlo que, posteriormente, se examinaron mediante un análisis de árboles de regresión realizado en el programa R 2.15.3 (R Development Core Team 2013).

3.3. Resultados

Las simulaciones desarrolladas en ausencia del cambio climático sugieren que *Vella pseudocytisus* subsp. *pau*i permanecerá en el territorio al menos hasta el año 2120 bajo las condiciones bioclimáticas actuales. Sin embargo, los modelos predicen que el cambio climático tendrá un impacto drástico en la viabilidad a largo plazo de *Vella pseudocytisus* subsp. *pau*i, aumentando el riesgo de extinción de la especie (Figura 2, pág. 113).

Por otro lado, la capacidad de dispersión a larga distancia puede matizar la magnitud de la respuesta de la especie frente al cambio climático. Aún así, nuestros modelos predicen la extinción de la especie para el año 2070 en todas las simulaciones de calentamiento global analizadas en este estudio.

Los resultados obtenidos a partir del árbol de regresión indican que la fracción de semillas dispersadas mediante un mecanismo a larga distancia es la variable más importante en determinar el número de individuos para el año 2050 (Figura 6, pág. 117), con las simulaciones que dispersaron menos de un 1% de las semillas a través de un mecanismo de larga distancia alcanzando mayores números de individuos para el año 2050 que aquellas simulaciones que dispersaban un porcentaje de semillas mayor.

3.4. Discusión y conclusiones

Un estudio relativamente reciente sobre los impactos del cambio climático en la biodiversidad española (Felicísimo *et al.* 2011), mediante el uso del algoritmo Maxent, sugiere que *Vella* no estaría amenazada como consecuencia del calentamiento global, al predecir una superposición espacial del 25% entre las áreas de distribución potencial actual y futura (año 2100, bajo el escenario de cambio climático CGCM2 A2). Por el contrario, nuestros resultados pronostican que mientras las poblaciones permanecerán más o menos inalteradas durante la primera mitad del siglo XXI, en la segunda mitad del siglo se producirá una pérdida abrupta de individuos. De hecho, nuestros resultados estiman la extinción de la especie para el año 2070 bajo este mismo escenario de cambio climático (CGCM2 A2). El uso de un enfoque no híbrido para predecir el efecto del cambio climático sobre *Vella* proporciona aproximaciones valiosas de primer orden, sin embargo, puede dar lugar a subestimaciones en los riesgos de extinción, debido a que pueden ser ignoradas interacciones importantes entre las características vitales e idoneidad de hábitat.

Los modelos que integren las características demográficas de las especies pueden servir para una mejor identificación de áreas refugio que alberguen poblaciones viables en el futuro (Cabral *et al.* 2013). De esta manera, el uso de modelos de dispersión demográficamente explícitos puede ser de gran utilidad, permitiéndonos determinar la importancia relativa de los diferentes componentes en las interacciones especie-ambiente.

4. El Sistema de Información de la Vegetación Ibérica y Macaronésica (SIVIM, www.sivim.info), implementación de un MDE en línea

Organizaciones como la Infraestructura Mundial de Información en Biodiversidad (GBIF), el Sistema de Información de la Vegetación Ibérica y Macaronésica (SIVIM) o el Banco de Datos de Biodiversidad de Cataluña (BDBC), entre otros, están trabajando en hacer los datos sobre biodiversidad accesibles vía internet, mediante el desarrollo de protocolos para la compartición de información. Estos proyectos proporcionan datos de incalculable valor que se utilizan en la descripción del área geográfica de las especies y comunidades.

La importancia de contar con grandes bases de datos sobre biodiversidad ha sido destacada en varios foros internacionales (Moreno 2005). Los datos de presencia de especies de plantas almacenados en bases de datos junto con variables ambientales, pueden ser una herramienta importante para entender las relaciones ecológicas de las especies, o predecir el efecto de factores externos sobre los procesos ecológicos y en la respuesta de las especies (Chytrý & Rafajová 2003; Smart *et al* 2003; Lenoir *et al.* 2008; Schaminee *et al.* 2009).

El Sistema de la Vegetación Ibérica y Macaronésica (SIVIM) es uno de los portales de referencia sobre la diversidad vegetal en la Península Ibérica y tiene por objetivo la compilación de todas las citas florísticas, incluyendo su información taxonómica, topográfica y ecológica, y todos los inventarios de vegetación reunidos en la bibliografía especializada. SIVIM se concibe como un sistema de información sobre la vegetación diseñado para capturar, guardar, editar, analizar y publicar datos de vegetación georreferenciados. Es una herramienta útil tanto en la investigación científica como en la evaluación de la toma de decisiones para la gestión de la biodiversidad. Esta base de datos se creó 2006 en el marco de un proyecto de investigación financiado a nivel nacional (CGL2006-13421-C04) con la participación de varias universidades españolas (Universidad de Barcelona, Universidad del País Vasco, Universidad de Castilla-La Mancha y la Universidad de León).

La mayoría de los estudios descriptivos sobre vegetación que utilizan métodos fitosociológicos incluyen los datos en tablas de inventarios y constituyen una fuente

importante tanto de información florística como de datos ecológicos. Por otro lado, y dado que SIVIM fue desarrollado para registrar inventarios fitosociológicos, los datos de cobertura de todas las especies presentes en un inventario, independientemente de su frecuencia y estado taxonómico, son un complemento importante a los datos de distribución procedentes de colecciones de herbario y de la literatura florística, los cuales se centran preferentemente en especies raras y grupos taxonómicamente complejos. En este contexto, hay que destacar que SIVIM posee el mayor número de registros florísticos de la Península Ibérica. SIVIM almacena actualmente casi 137.763 inventarios fitosociológicos derivados de 1.680 referencias bibliográficas, principalmente de la Península Ibérica y las Islas Canarias.

La base de datos SIVIM es una fuente importante de datos de presencia de especies vegetales (2.260.359), donde los registros biológicos están disponibles en forma de registros de presencia. El deseo de maximizar la utilidad de este tipo de recursos ha permitido el desarrollo de diversos métodos (MDE) para el modelado de datos de presencia, es decir, pares de coordenadas que sitúan en el espacio geográfico localidades en las que se ha detectado la presencia de una especie o comunidad vegetal.

En el año 2012, con el objetivo de mejorar el portal de SIVIM se implementó una aplicación para el modelado de la distribución geográfica de los taxones y sintaxones almacenados en la bases de datos, la cual se basa en el algoritmo de máxima entropía Maxent (Phillips *et al.* 2006). Maxent es un algoritmo diseñado para modelar la distribución geográfica de las especies (Phillips *et al.* 2006; Phillips & Dudík 2008), basado en inteligencia artificial y en una distribución de máxima entropía (Jaynes 1957), que proporciona resultados precisos (Elith *et al.* 2006). Maxent calcula los modelos de distribución de las especies, en base a la búsqueda de la ecuación de máxima entropía (o más cercana a la uniforme) que explica las relaciones entre los registros de presencia de las especies y los valores de las variables ambientales que determinan su distribución. La ecuación resultante se proyecta geográficamente como un mapa de idoneidad de hábitat (Phillips & Dudík 2008).

Phillips y colaboradores (2006) apuntan algunas de las ventajas en el uso de Maxent en comparación con una amplia gama de modelos de distribución de especies,

que fundamentan la selección e implementación de este algoritmo de modelado en la base de datos SIVIM. Maxent sólo requiere datos de presencia e información ambiental del área de estudio para el modelado de la distribución de especies y comunidades vegetales y sus resultados son precisos y fácilmente interpretables. Por otro lado, Maxent tiene propiedades que le hacen muy robusto ante pequeñas muestras de presencia para calibrar el modelo.

En el portal de SIVIM se encuentran a disposición del usuario una serie de variables bioclimáticas obtenidas de la base de datos climáticos WorldClim, generadas con una resolución de aproximadamente 0,6 km² mediante la interpolación de datos climáticos mensuales. Estas variables caracterizan el clima actual y se corresponden con registros de temperatura mínima media mensual, temperatura máxima media mensual, temperatura media mensual y precipitación media mensual. Las variables bioclimáticas se obtienen a partir de los valores de temperatura y precipitación mensual con el objetivo de generar variables biológicamente más significativas (Hijmans *et al.* 2005) para el modelado de la distribución de especies y comunidades vegetales. El modelo generado por el algoritmo Maxent se transfiere al espacio geográfico, obteniéndose el mapa de idoneidad de hábitat para el taxón o sintaxón seleccionado. Esta proyección puede realizarse en el mismo o distinto periodo temporal, por ejemplo, a futuras condiciones simuladas. Este enfoque ha sido evaluado (Hijmans & Graham 2006) y aplicado (Fitzpatrick *et al.* 2008) satisfactoriamente para especies de plantas.

Las proyecciones climáticas para los años 2020, 2050 y 2080, obtenidas a partir de la base de datos climáticos WorldClim correspondientes al escenario climático SRES A1B están disponibles en SIVIM. Este escenario climático presupone un mundo futuro con un rápido crecimiento económico, un lento crecimiento de la población mundial y una rápida introducción de nuevas y más eficientes tecnologías, por lo que se corresponde con una visión futura medianamente optimista. Se seleccionaron las proyecciones climáticas desarrolladas por el Instituto Max Planck de Meteorología, que emplea los datos procedentes del modelo de circulación general ECHAM5, ya que ha proporcionado buenos resultados a nivel europeo.

Con la implementación de una herramienta para el modelado del área geográfica de las especies y comunidades vegetales en la base de datos SIVIM, pretendemos acercar estas metodologías a la comunidad científica menos familiarizada con ellas. Además, mediante esta aplicación se puede obtener información útil para una primera exploración y predicción de la distribución geográfica de especies y comunidades vegetales para su posterior estudio detallado, así como para apoyar y mejorar la planificación de políticas relacionadas con la conservación de la diversidad vegetal.

DISCUSIÓN GENERAL

1. Discusión general

En este apartado se exponen y discuten los resultados más significativos obtenidos en la presente Tesis doctoral.

1.1. Mejoras metodológicas

Los sistemas biológicos se rigen por procesos complejos que actúan a diferentes escalas espaciales y temporales. En el estudio de la distribución de las especies y comunidades vegetales, la resolución y la extensión determinan la escala geográfica del trabajo e influyen en la aplicabilidad de los resultados (Elith & Leathwick 2009).

En esta Tesis se abordó el análisis de la diversidad vegetal empleando distintas escalas geográficas (local, paisajística y regional) y niveles de organización de las plantas (especies, comunidades y floras), con el objetivo de desarrollar modelos de distribución útiles para la biología de la conservación, proporcionando predicciones fiables de la distribución de las especies (*Capítulos 1 y 3*) y comunidades vegetales (*Capítulo 2*).

Durante el modelado de la distribución geográfica de las especies y comunidades se debe considerar la relevancia ecológica de las variables que determinan el espacio ambiental (espacio conceptual definido por las variables ambientales a las que responde la especie o comunidad) con respecto a los objetivos del estudio (Elith & Leathwick 2009). La capacidad para modelar las relaciones existentes entre las especies y su ambiente generalmente se pierde en estudios a gran escala, dando lugar a modelos más relacionados con los límites del rango climático general de las especies (Franklin 2009). Por tanto, los modelos a escala continental o regional son útiles para describir patrones biogeográficos (*Capítulo 1*), mientras que los estudios a nivel de paisaje van dirigidos a la comprensión ecológica detallada o la planificación de la conservación biológica (*Capítulo 3*).

Por otro lado, es importante que la variabilidad del espacio ambiental esté bien representada por la muestra, es decir, por la información referente a los registros de presencia que se utiliza para el modelado (Vaughan & Ormerod 2003; Peterson *et al.* 2011). En este sentido, los resultados obtenidos a partir del modelado de unidades de vegetación (enfoque *top-down*, *Capítulo 2*), pronosticaron un menor grado de amenaza para la vegetación alpina y subalpina de Pirineos para el año 2080 que las predicciones realizadas por Engler *et al.* (2011) a partir del modelado de especies, bajo el mismo

escenario de cambio climático. La diferencia entre estos resultados se debe, muy probablemente, a la diferente precisión planimétrica de los dos estudios, siendo por lo general la precisión de las unidades de vegetación mucho más alta que se alcanza en el caso de las especies.

1.2. Patrones espaciales de riqueza de especies de plantas para la mejora de atlas florísticos

El uso de modelos de distribución de especies nos permite generar representaciones geográficas de la distribución de la riqueza de especies de plantas en un territorio dado (*Capítulo 1*). Los patrones de riqueza obtenidos en esta Tesis doctoral se pueden considerar de gran exactitud, ya que se modelaron 2.738 especies de un total de 3.415 especies descritas en Cataluña (aproximadamente el 80% del total de su flora).

Una de las variables más importantes que determinan la composición de la vegetación en Cataluña a escala grosera es la heterogeneidad espacial de la unidad básica de estudio (Pausas *et al.* 2003). Así mismo, Rosenzweig (1995) señala que las áreas altamente heterogéneas deberían albergar un mayor número de especies que zonas de menor heterogeneidad espacial. Los patrones espaciales de riqueza de plantas obtenidos en el *Capítulo 1* señalan los Pirineos, la cordillera Litoral y la cordillera Prelitoral como las áreas con mayor riqueza de especies, las cuales se corresponden con elementos geomorfológicos de elevada heterogeneidad ambiental. Por otro lado, regiones de riqueza relativamente baja se localizan principalmente en las áreas centrales de Cataluña, posiblemente debido tanto a la baja heterogeneidad ambiental como al papel de las actividades agrícolas en estas áreas.

Además de obtenerse valiosos mapas de riqueza florística, una contribución destacable en el conocimiento sobre la riqueza de plantas de un territorio es la estimación del número mínimo de especies presentes en las zonas donde los datos son aún incompletos debido a una menor intensidad de muestreo. Los resultados del *Capítulo 1* confirman que el modelado de la distribución de las especies de manera individual y la suma de las presencias predichas para cada especie puede ser una estrategia útil en la descripción de la variación espacial de la riqueza de especies, sobre todo para las regiones poco muestreadas (Pineda & Lobo 2009).

1.3. El efecto del cambio climático

Los resultados de los *Capítulos 2 y 3* de esta Tesis doctoral muestran posibles efectos del cambio climático sobre algunos componentes de la diversidad vegetal. Los modelos de distribución de especies que evalúan los efectos del cambio climático en la distribución de las especies y unidades de vegetación predicen una reducción masiva de la diversidad de plantas.

El estudio del efecto del cambio climático sobre la diversidad vegetal se llevó a cabo mediante dos aproximaciones diferentes y a dos niveles de organización de plantas. Por un lado, se empleó un modelo de distribución de especies (MDE) estático para el análisis de unidades de vegetación en la región alpina y subalpina del Pirineo Oriental, y por el otro, se desarrolló un modelo dinámico para evaluar el efecto del cambio climático en un endemismo ibérico (*Vella pseudocytisus* subsp. *pau*).

Las unidades de vegetación alpinas y subalpinas del Pirineo Oriental pueden verse gravemente amenazadas por el cambio climático (*Capítulo 2*). Nuestros modelos proyectan un aumento en la altitud media de las áreas de ocupación potencial de las unidades de vegetación alpina y subalpina, lo que coincide ampliamente con los resultados obtenidos en estudios previos realizados tanto a escala continental europea (Engler *et al.* 2011) como a escala regional (Dirnböck *et al.* 2003; Benito Garzón *et al.* 2008; Benito *et al.* 2011) en base a registros de especies, y confirman la tendencia general de declive de la vegetación alpina frente al cambio climático. Este aumento en la altitud media puede tener consecuencias revolucionarias (al estilo de lo que diría Pierre Dansereau) para las formaciones alpinas y subalpinas de Pirineos, ya que como en cualquier sistema montañoso, a mayor altitud menor superficie disponible. Por otro lado, a mayor altitud las condiciones fisiográficas pueden hacer este desplazamiento poco probable, debido a una escasa disponibilidad de sustrato, pendientes acusadas, contrastes meteorológicos, lo que podría dar lugar a disminuciones todavía más drásticas de las áreas modeladas como idóneas para el futuro de las unidades de vegetación estudiadas.

Sin embargo, el uso de una aproximación estática para predecir el efecto del cambio climático sobre las especies o comunidades vegetales puede dar lugar a subestimaciones en los riesgos de extinción de las mismas (*Capítulo 3*), debido a que pueden ser ignoradas importantes interacciones entre las características vitales de las

plantas e idoneidad de hábitat. Un estudio relativamente reciente sobre los impactos del cambio climático en la biodiversidad española mediante el uso del algoritmo Maxent (Felicísimo *et al.* 2011), sugiere que *Vella pseudocytisus* subsp. *pau* no estaría amenazada como consecuencia del calentamiento global, al predecir una superposición espacial del 25% entre las áreas de distribución potencial actual y futura (para el año 2100, bajo el escenario de cambio climático CGCM2 A2). Por el contrario, nuestros resultados pronostican que mientras las poblaciones permanecerán más o menos inalteradas durante la primera mitad del siglo XXI, en la segunda mitad del siglo se producirá una pérdida abrupta de individuos (*Capítulo 3*), estimándose la extinción de la especie para el año 2070 bajo este mismo escenario de cambio climático.

1.3.1. La importancia del potencial dispersivo de las especies ante el cambio climático

Una de las necesidades básicas en la biología de la conservación es la evaluación de la viabilidad a largo plazo de las poblaciones de especies dentro de una gama de posibles intervenciones de gestión ante posibles cambios ambientales (Midgley *et al.* 2010). La capacidad de las plantas para migrar y mantener el ritmo de cambio en sus hábitats idóneos puede ser de vital importancia para la supervivencia de las especies (Davis & Shaw 2001; Jump & Peñuelas 2005). Por tanto, modelos que no incorporen el efecto de fenómenos como la dispersión de las especies pueden llegar a resultados que difieran en gran medida de las distribuciones futuras reales debido a limitaciones para su dispersión (Pearson & Dawson 2003).

Nuestros resultados confirman que la frecuencia de los eventos de dispersión a larga distancia juega un papel importante en la supervivencia de *Vella pseudocytisus* subsp. *pau* para el año 2050 (*Capítulo 3*). No obstante, los resultados mostraron que un mayor número de eventos de dispersión a larga distancia podría reducir la supervivencia de *V. pseudocytisus* subsp. *pau* en el territorio. Concretamente, la dispersión de una fracción de semillas superior al 1% mediante eventos a larga distancia puede comprometer la supervivencia de esta especie para el año 2050. El hecho de que una mayor capacidad para dispersarse a larga distancia pueda suponer una desventaja para la viabilidad a largo plazo de *Vella pseudocytisus* subsp. *pau*, podría indicar una elevada fragmentación de su hábitat, con grandes distancias entre fragmentos de hábitat idóneo que aumenta su mortalidad en relación con la dispersión. A escala paisajística, el éxito en la dispersión y, por lo tanto, el éxito en la colonización de nuevos hábitats

adecuados, no sólo dependerá de la capacidad dispersiva de las especies, sino también de las distancias entre parches de hábitat idóneo y la configuración del paisaje circundante (Eriksson *et al.* 2002).

A pesar de que se debe realizar un análisis más detallado para evaluar el grado de fragmentación del paisaje, la fragmentación del hábitat natural impulsada por el hombre en el área de estudio, fundamentalmente derivada de la producción agrícola, puede suponer un gran desafío para la migración de *Vella pseudocytisus* subsp. *pau*. Gracias al desarrollo de un modelo dinámico, pudimos identificar áreas refugio que puedan albergar poblaciones viables en el futuro, apoyando así la planificación de políticas relacionadas con su conservación.

1.4. Implementación de una herramienta de modelado en línea

El conocimiento relativamente maduro adquirido en MDE nos ha permitido implementar una herramienta de modelado en línea en el Sistema de Vegetación Ibérica y Macaronésica (SIVIM). Esta aplicación permite, desde el año 2012, el modelado de la distribución geográfica de los taxones y sintaxones almacenados en uno de los portales de referencia sobre diversidad vegetal en la Península Ibérica, proporcionando valiosa información preliminar para el estudio de la diversidad vegetal.

2. General discussion

In this section the most significant results obtained in this thesis are discussed.

2.1. Methodological improvements

Biological systems are governed by complex processes that act at different spatial and temporal scales. In the study of the distribution of species and plant communities, the resolution and the scope determine the geographical scale of the study and influence the applicability of the results (Elith & Leathwick 2009).

In this thesis the analysis of plant diversity using different geographic scales (local, landscape and regional) and plant organizational levels (species, communities and floras) are addressed with the aim of developing useful distribution models for conservation biology that provide reliable predictions of the distribution of the species (*Chapters 1 and 3*) and plant communities (*Chapter 2*).

The ecological relevance of the variables that determine the environmental space (conceptual space defined by the environmental variables to which the species or community respond) with respect to the objectives of the study (Elith & Leathwick 2009) should be considered during the modelling of the geographical distribution of species and communities. The ability to model the relationships between species and their environment is usually lost in large-scale studies, leading to models related to the general climate range limits of the species (Franklin 2009). Therefore, continental or regional scale models are useful for describing biogeographical patterns (*Chapter 1*), while landscape-level studies are aimed at detailed ecological understanding or biological conservation planning (*Chapter 3*).

On the other hand, it is important that the variability of the environmental space is well represented by the sample, i.e. the information relating to presence records which is used for modelling (Vaughan & Ormerod 2003; Peterson *et al.* 2011). In this sense, the results obtained from the modelling of vegetation units (top-down approach, *Chapter 2*), predicted a lower degree of threat to the alpine and subalpine vegetation of the Pyrenees for the year 2080 than predictions made by Engler *et al.* (2011) from the modelling of species, under the same scenario of climate change. It is most likely that the difference between these results is due to the different planimetric precision of the two studies, with the accuracy of vegetation units generally being much higher than that obtained in the case of species.

2.2 Spatial patterns of plant species richness for the improvement of the floristic atlas

The use of species distribution models (SDMs) allows us to generate geographical representations of the distribution of plant species richness in a given territory (*Chapter 1*). Richness patterns obtained in this thesis can be considered of great accuracy as 2,738 species were modelled from a total of 3,415 described species in Catalonia (approximately 80% of the total flora).

One of the most important variables that determine the composition of the vegetation in Catalonia to a large scale is the spatial heterogeneity of the basic unit of study (Pausas *et al.* 2003). Likewise, Rosenzweig (1995) notes that the highly heterogeneous areas should accommodate a greater number of species than areas of lower spatial heterogeneity. The plant richness spatial patterns obtained in *Chapter 1* indicate the Pyrenees, the coastal mountain range and the pre-coastal mountain range as areas with greater species richness, which corresponds to geomorphologic elements of high environmental heterogeneity. On the other hand, regions of relatively low richness are mainly located in the central areas of Catalonia, possibly due to low environmental heterogeneity from the role of agricultural activities in these areas.

In addition to obtaining valuable species richness maps, a remarkable contribution to knowledge about the plant richness of a territory is the estimate of the minimum number of species present in areas where the data are still incomplete due to a lower intensity of sampling. Results from *Chapter 1* confirm that the modelling of the distribution of species individually and the sum of the presences predicted for each species can be a useful strategy in the description of the spatial variation of species richness, above all for the under-sampled regions (Pineda & Lobo 2009).

2.3. The effect of climate change

Results of *Chapters 2* and *3* of this doctoral thesis show possible effects of climate change on some components of plant diversity. Species distribution models assessing the effects of climate change on the distribution of species and vegetation units predict a massive reduction in plant diversity.

The study of the effect of climate change on plant diversity was carried out by two different approaches and two levels of organization of plants. On the one hand, a static SDM for the analysis of vegetation units in the alpine and subalpine region of the

Oriental Pyrenees was used, and on the other hand, a dynamic model was developed to assess the effect of climate change on an Iberian endemism (*Vella pseudocytisus* subsp. *pau*).

Alpine and subalpine vegetation units of the Oriental Pyrenees may be seriously threatened by climate change (*Chapter 2*). Our models project an increase in the average altitude of the areas of potential occupation of alpine and sub-alpine vegetation units, which broadly coincides with the results obtained in previous studies carried out both at a European continental scale (Engler *et al.* 2011) and at a regional scale (Dirnböck *et al.* 2003; Benito Garzón *et al.* 2008; Benito *et al.* 2011) based on records of species, and confirm the general trend of decline of the alpine vegetation to climate change. This increase in average altitude can have revolutionary consequences (in the style of what Pierre Dansereau would say) for the alpine and subalpine Pyrenees formations, since as in any mountainous system, the higher the altitude, the less surface is available. On the other hand, at higher altitudes, the physiographic conditions could make this shift unlikely because of a limited availability of substrate, steep slopes and weather contrasts, which could lead to still more drastic decreases in the modelled areas as suitable for the future of the vegetation units studied.

However, the use of a static approach to predict the effect of climate change on plant communities or species can result in underestimates of the risks of extinction thereof (*Chapter 3*), since important interactions between the vital characteristics of plants and habitat suitability could be ignored. A relatively recent study on the impacts of climate change on Spanish biodiversity using the Maxent algorithm (Felicísimo *et al.* 2011), suggests that *Vella pseudocytisus* subsp. *pau* would not be threatened as a result of global warming, predicting a spatial overlap of 25% between the areas of current and future potential distribution (by 2100, under the CGCM2 A2 climate change scenario). On the other hand, our results predict that while populations will remain more or less unchanged during the first half of the 21st century, during the second half of the century there will be an abrupt loss of individuals (*Chapter 3*), estimating the extinction of the species by 2070 under this same climate change scenario.

2.3.1. The importance of the dispersive potential of species to climate change

One of the basic needs in conservation biology is the evaluation of the long-term viability of populations of species to a range of possible management interventions in

response to possible environmental changes (Midgley *et al.* 2010). The plants' ability to migrate and maintain the pace of change in suitable habitats may be of vital importance for the survival of the species (Davis & Shaw 2001; Jump & Peñuelas 2005). Therefore, models that do not incorporate the effect of phenomena such as the dispersal of the species can reach results that differ greatly from future real distributions due to limitations of its dispersal (Pearson & Dawson 2003).

Our results confirm that the frequency of long distance dispersal events plays an important role in the survival of *Vella pseudocytisus* subsp. *pau* by 2050 (Chapter 3). However, the results showed that a greater number of long-distance dispersal events could reduce the survival of *V. pseudocytisus* subsp. *pau* in the territory. Specifically, the dispersal of a fraction of seeds over 1% through long distance events can compromise the survival of this species by 2050. The fact that a greater capacity for long-distance dispersal may lead to a disadvantage for the long-term viability of *Vella pseudocytisus* subsp. *pau*, could indicate a high fragmentation of its habitat, with large distances between fragments of suitable habitat that increases its mortality in relation to dispersion. At a landscape scale, success in the dispersal and, therefore, success in the colonization of new suitable habitats, will depend not only on the dispersive capacity of the species, but also on the distances between fragments of suitable habitat and the configuration of the surrounding landscape (Eriksson *et al.* 2002).

While a more detailed analysis should be carried out to assess the degree of fragmentation of the landscape, the human-driven habitat fragmentation in the study area, mainly for agricultural production, can be a major challenge for the migration of *Vella pseudocytisus* subsp. *pau*. Due to the development of a dynamic model, we could identify refuge areas which can host viable populations in the future, thus supporting the planning of policy related to its conservation.

2.4. Implementation of an online modelling tool

The relatively mature knowledge obtained in SDMs has enabled us to implement an online modelling tool within the Iberian and Macaronesian Vegetation Information System (SIVIM). From 2012, this application allows the modelling of the geographical distribution of the taxa and syntaxa stored in one of the portals of reference on plant diversity in the Iberian Peninsula, providing valuable preliminary information for the study of plant diversity.

CONCLUSIONES

1. Conclusiones

1.1. Conclusiones generales

La presente Tesis doctoral estudia la aplicabilidad del modelado de la distribución de especies en el análisis de la diversidad vegetal, mediante el uso de distintas técnicas de modelado (MDE), escalas geográficas y niveles de organización de plantas, siendo ésta una investigación aplicada a la biología de la conservación vegetal. A continuación se enumeran las principales conclusiones obtenidas, las cuales se exponen ampliamente en los apartados de discusión y conclusiones de los diferentes capítulos en inglés, y de manera más abreviada, en los resúmenes en castellano.

Capítulo 1:

1.- La aplicación de MDE nos ha permitido obtener mejores patrones de la distribución espacial de la riqueza florística para Cataluña, frente a los patrones previamente proyectados basándose en los datos recogidos por el BDBC.

2.- Estos patrones son de incalculable valor para la conservación vegetal, ya que pueden ser utilizados como herramientas en la identificación de áreas de alta riqueza florística, así como en la detección de áreas que requieren un mayor esfuerzo de muestreo y/o conservación, ofreciéndonos una estimación del número mínimo de especies presentes en las zonas donde los datos son aún incompletos, con un número mínimo previsto de 300 especies por cuadrícula UTM de 10 km de lado.

3.- De las tres técnicas de modelado empleadas en la descripción de patrones espaciales de la riqueza de plantas, MARS y Maxent proporcionaron mapas de riqueza más precisos que los obtenidos a través de GLM.

4.- Los modelos de distribución de especies MARS, GLM y Maxent proporcionan una alternativa útil a las aproximaciones clásicas sobre la distribución espacial de la riqueza de especies en Cataluña al mejorar los atlas florísticos existentes.

Capítulo 2:

5.- El cambio climático amenaza seriamente a la vegetación alpina y subalpina de Pirineos, siendo las unidades de vegetación alpinas las más vulnerables a la pérdida de área idónea debido al calentamiento global.

A medida que el clima se vuelva más cálido y seco, las unidades de vegetación estudiadas deberán desplazarse en altitud en búsqueda de condiciones idóneas para su

supervivencia. La extensión altitudinal de los Pirineos permite a los matorrales y bosques subalpinos migrar en altitud a medida que aumenten las temperaturas y disminuyan las precipitaciones. Sin embargo, el cinturón de vegetación alpina de los Pirineos está limitado en altitud al no existir espacio disponible en las zonas culminícolas, lo que llevaría a pérdidas dramáticas en las áreas idóneas para las diferentes unidades de vegetación alpina.

6.- Los modelos que predicen cambios futuros en la distribución de las unidades de vegetación (enfoque *top-down*) pueden ser tan útiles como los utilizados en estudios previos para especies, con el objetivo de obtener mejores herramientas para la planificación de políticas relacionadas con la conservación de la biodiversidad.

Nuestros resultados proporcionan información importante sobre las áreas de ocupación de las unidades de vegetación estudiadas y a la luz de las tendencias observadas se recomienda implementar esfuerzos de conservación adicionales para asegurar el futuro de dichas comunidades vegetales, más aún cuando estas comunidades albergan tanto especies endémicas (por ejemplo *Dianthus vigoi*, *Festuca bordevei*, *Festuca yvesii*, *Armeria muelleri*) como especies amenazadas (*Oxytropis lapponica*, *Pedicularis tuberosa*, *Vaccinium vitis-idaea*).

Capítulo 3:

7.- El cambio climático tendrá un fuerte impacto sobre las poblaciones del endemismo ibérico *Vella pseudocytisus* subsp. *pau*, afectando a su persistencia en el territorio de tal manera que se prevé la extinción de la especie para el año 2070 si no se toman las medidas adecuadas para su conservación.

8.- El potencial dispersivo resultó ser clave en la viabilidad a largo plazo de *Vella pseudocytisus* subsp. *pau*, sin embargo, una mayor capacidad para dispersarse a larga distancia va en contra de la supervivencia de la especie, lo que podría estar indicando una elevada fragmentación de su hábitat, con grandes distancias entre los parches de hábitat idóneo para la especie que aumentan su mortalidad en relación con la dispersión.

9.- La identificación de áreas refugio que puedan albergar poblaciones viables en el futuro es fundamental para una correcta planificación de las políticas relacionadas con su conservación. Las poblaciones localizadas al norte de la ciudad de Teruel deberían recibir una mayor atención así como un mayor esfuerzo de conservación ya

que según nuestros resultados serían las únicas área capaces de albergar poblaciones viables en presencia del cambio climático.

Capítulo 4:

10.- La implementación de una herramienta de modelado en el portal SIVIM se realizó con éxito en el año 2012, y desde entonces está disponible para el modelado de la distribución geográfica de especies y comunidades.

1.2. Consideración final

Los modelos de distribución de especies son herramientas de gran valor en la investigación de la biología de la conservación vegetal, al proporcionar alternativas precisas para la descripción de patrones biogeográficos, predicción de los efectos del cambio climático, evaluación del potencial dispersivo de las especies, así como para el diseño de reservas y planes de conservación.

Finalmente, es importante destacar el papel de la escala en el modelado de la distribución de especies y comunidades vegetales, ya que ésta determinará tanto la aplicabilidad de los resultados como su significación biológica.

2. Conclusions

2.1. General conclusions

This doctoral thesis examines the applicability of modelling the distribution of species in the analysis of plant diversity through the use of various techniques of modelling (SDMs), geographical scales and levels of plant organization, as research applied to plant conservation biology. The main findings emerging from this study are set out below.

Chapter 1:

1.- The application of SDMs has allowed us to obtain better spatial distribution patterns of the floristic richness of Catalonia compared to the previously projected patterns based on data collected by the BDBC.

2.- These patterns are of incalculable value for plant conservation as they can be used as tools for the identification of areas of high floristic richness and in the detection of areas that require a greater sampling and/or conservation effort. This gives an estimate of the minimum number of species present in areas where data are still incomplete, with a predicted minimum number of 300 species per UTM grid.

3.- From the three modelling techniques used in the description of spatial patterns of plant richness, MARS and Maxent provided richness maps that were more accurate than those obtained through GLM.

4.- MARS, GLM and Maxent species distribution models provide a useful alternative to the classical approaches to the spatial distribution of species richness in Catalonia by improving the existing floristic atlas.

Chapter 2:

5.- Climate change is a serious threat to the alpine and subalpine vegetation of the Pyrenees, with alpine vegetation units most vulnerable to the loss of suitable area due to global warming.

As the climate becomes warmer and drier, vegetation units studied must shift in altitude in search of conditions for their survival. The altitude in the Pyrenees range allows scrublands and subalpine forests to migrate in altitude with increasing temperatures and decreasing precipitation. However, the belt of alpine vegetation of the Pyrenees is limited by altitude as there is no more space available at higher altitudes.

This would lead to a dramatic decline in areas suitable for the different units of alpine vegetation.

6.- Models that predict future changes in the distribution of vegetation units (*top-down* approach) can be as useful as those used in previous studies for species, with the goal of obtaining better tools for the planning of policies related to the conservation of biodiversity.

Our results provide important information in the areas of occupation of studied vegetation units and in the light of trends, it is recommended that additional conservation efforts to ensure the future of these plant communities are implemented, even more so when these communities are home to endemic species (e.g. *Dianthus vigoi*, *Festuca bordevei*, *Festuca yvesii*, *Armeria muelleri*) as well as threatened species (*Oxytropis lapponica*, *Pedicularis tuberosa*, *Vaccinium vitis-idaea*).

Chapter 3:

7.- Climate change will have a strong impact on the populations of the Iberian endemism *Vella pseudocytisus* subsp. *pau*, affecting its persistence in the territory in such a way that the extinction of the species is expected for the year 2070 if appropriate conservation measures are not taken.

8.- The dispersive potential proved to be critical to the long-term viability of *Vella pseudocytisus* subsp. *pau*, however, a greater capacity for long-distance dispersal runs counter to the survival of the species. This could be indicating a high fragmentation of its habitat with large distances between patches of suitable habitat for the species that increase mortality in relation to dispersal.

9.- The identification of refuge areas which can host viable populations in the future is essential for correct planning of policies related to its conservation. Populations located to the north of the city of Teruel should receive greater attention as well as a major effort of conservation since, according to our results, they would be the only area capable of accommodating viable populations in the presence of climate change.

Chapter 4:

10.- The implementation of a tool for modelling in the SIVIM portal was successful in the year 2012, and since then, is available for the modelling of the geographical distribution of species and communities.

2.2. Final consideration

Species distribution models are tools of great value in the research of plant conservation biology, by providing precise alternatives for the description of biogeographical patterns, prediction of the effects of climate change, evaluation of the dispersive potential of species, as well as for the design of reserves and conservation plans.

Finally, it is important to highlight the role of scale in the modelling of the distribution of species and vegetation communities, since this will determine both the applicability of the results and their biological significance.

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INFORMES DEL DIRECTOR

En Xavier Font i Castell, director de la Tesi doctoral de Nora Pérez García, que porta per títol “Inferencia espacial y predicción de la distribución de plantas: un estudio a diferentes escalas”, emet el següent informe relatiu al factor d'impacte i a la participació de la doctoranda en cadascun dels articles inclosos en la memòria de la esmentada Tesi.

Capítol 1. *Predicting vascular plant richness patterns in Catalonia (NE Spain) using species distribution models.* Pérez, N.; Font, X. Publicat a la revista *Applied Vegetation Science* el 2012, amb index d'impacte (2012) de 2,263.

Contribució de la doctoranda: Preparació de variables explicatives, anàlisi de les dades, interpretació dels resultats, redacció de la primera versió del manuscrit i revisions posteriors.

Contribució dels altres autors: Gestió de les dades d'observacions de plantes, participació en la interpretació dels resultats, supervisió i participació en la redacció del manuscrit.

Capítol 2. *Drastic reduction in the potential habitats for alpine and subalpine vegetation in the Pyrenees due to twenty-first-century climate change.* Pérez-García, N.; Font, X.; Ferré, A.; Carreras, J. Publicat a la revista *Regional Environmental Change* el 2013, amb index d'impacte (2012) de 1,945.

Contribució de la doctoranda: Preparació de variables explicatives, anàlisi de les dades, interpretació del resultat, redacció de la primera versió del manuscrit i revisions posteriors.

Contribució del altres autors: Generació de la cartografia dels habitats, assessorament en la interpretació dels resultats, supervisió i participació en la redacció.

Capítol 3. *Climate vulnerability assessment of an edaphic endemic plant (*Vella pseudocytisus subsp. pau*) by using a spatially explicit demographic dispersal model.* Pérez-García, N.; Domínguez, F. Sotmès a la revista *Global Change Biology*, amb index d'impacte (2012) de 6,918.

Contribució de la doctoranda: Preparació de variables explicatives i generació de capes climàtiques, realització d'inventaris florístics, participació en el seguiment demogràfic de l'especie *Vella pseudocytisus* subsp. *pau*, anàlisi de les dades, interpretació del resultat, redacció de la primera versió del manuscrit.

Contribució dels altres autors: Seguiment demogràfic de les poblacions de *Vella pseudocytisus* subsp. *pau*, assessorament en la interpretació dels resultats, supervisió i participació en la redacció del manuscrit final.

Capítol 4. *The Iberian and Macaronesian Vegetation Information System (SIVIM, www.sivim.info), five years of online vegetation's data publishing.* Font, X.; Pérez-García, N.; Biurrun, I.; Fernández-Gonzalez, F.; Lence, C. Publicat a la revista *Plant Sociology* el 2012. Revista ja referenciada en la Web of Knowledge, pero pendiente encara de evaluació de su indice d'impacte.

Contribució de la doctoranda: Implementació i test de l'algoritme MaxEnt en el portal web del SIVIM (Sistema de Informació de la Vegetación Ibérica y Macaronésica). Participació en la redacció del manuscrit final.

Contribució dels altres autors: Disseny i desenvolupament informàtic, redacció de la primera versió del manuscrit i revisions posteriors.

Tots els articles que formen part de la memòria de la Tesi doctoral de Nora Pérez García han estat publicats o sotmesos a revistes científiques d'àmbit internacional.

Finalment, certifico que cap dels coautors dels articles abans esmentats ha utilitzat aquests treballs per a l'elaboració de cap altre Tesi doctoral.

Barcelona, 5 de setembre de 2013.

Dr. Xavier Font i Castell

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APÉNDICE



Predicting vascular plant richness patterns in Catalonia (NE Spain) using species distribution models

Nora Pérez & Xavier Font

Keywords

GLM; MARS; Maxent; Mediterranean area; Model comparison; Predictive modelling; Species richness

Nomenclature

Bolòs et al. (2005)

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Abstract

Question: Given the current state of knowledge on plant species richness in Catalonia, how can we improve definition of sampled species richness patterns? We propose a concrete methodology that will highlight the most speciose areas and those areas that are insufficiently sampled.

Location: Catalonia, covering 31 980 km² in northeast Spain.

Methods: This study provides a quantitative assessment of plant richness using sampling units of 10 km × 10 km ($n = 319$). Generalized linear models (GLM), multivariate adaptive regression splines (MARS) and a maximum entropy model (Maxent) were used for all plant species contained in the Catalonia Database of Biodiversity (Banc de Dades de Biodiversitat de Catalunya, BDBC). The projected presence/absence maps were combined to create species richness maps based on distribution models for 2738 species.

Results: The modelling techniques were highly correlated, and we did not distinguish any differences in projections of geographic patterns of species richness among the modelling algorithms. However, MARS and Maxent achieved the best prediction success, whereas GLM tended to over-predict species number per quadrat. The MARS map gave the highest predictive performance based on both Kappa and the true skill statistic, and for the two components of disagreement (quantity and allocation disagreement). We were able to identify one previously known region of high diversity, the Pyrenees, and two additional areas, the coastal range and the pre-coastal mountain range.

Conclusions: We obtain improved distribution patterns for plant species in Catalonia over the previously sampled patterns, and, most importantly, we provide an estimate of the number of species present in those areas where sampling data are incomplete, with an expected 300 species. The model-predicted richness maps presented here can be used to detect zones with low and high species richness and to develop strategies for either restoring or protecting landscape biodiversity as part of national conservation plans.

Introduction

One of the major challenges for conservation biology is to stop the ongoing and accelerating decline of biodiversity (Pimm et al. 1995). One way to increase the efficiency of conservation is to focus efforts on species-rich sites or 'biodiversity hotspots' (Myers et al. 2000). Plant diversity hotspots are well identified on a global scale, but smaller, local hotspots must be identified within these regions to allow effective conservation of plants on both global and local scales (Murray-Smith et al. 2008). The estimation of geo-

graphical distribution of species richness is necessary to understand the ecological and evolutionary determinants of spatial patterns of biodiversity (Rosenzweig 1995; Ricklefs 2004). However, it is not easy to evaluate species richness distributions across heterogeneous regions where collecting efforts have not been sufficient or adequately planned (Hortal et al. 2007).

Recently, species distribution modelling (SDM) has emerged as a novel approach for generating distributions based on the relationship between species' presence or abundance records and environmental variables. Large

amounts of distributional data are collected in biodiversity databases. Thanks to both the advances in geographic information system (GIS) techniques and the availability of digital maps of environmental variables, a wide variety of modelling techniques specifically designed to model species distributions are currently available (see Guisan & Thuiller 2005). Thus, predictive models of single-species geographical distributions and species richness provide an attractive alternative to using incomplete or spatially biased survey data as a basis for conservation planning (Parviainen et al. 2009).

In addition to the fact that the Mediterranean area is considered a hotspot of biodiversity (Myers et al. 2000), mainly because of its plant richness, the existing transition between temperate and Mediterranean climates makes Catalonia (NE Spain) especially interesting from a biodiversity point of view (Pausas et al. 2003). Catalonia has an altitudinal range from sea level to 3143 m a.s.l, containing a large variety of floristic regions that shelter a broad diversity of plant species, ranging from Mediterranean flora to Medio-European (including Atlantic and Sub-Mediterranean) and Boreo-alpine elements (Ninot et al. 2007). A remarkable amount of progress has been made in describing the vegetation of this region, whose flora is perhaps better known than that of any other Mediterranean area of comparable size (Greuter 1999). However, some regions in Catalonia remain poorly surveyed. Furthermore, researchers generally prefer to visit sites that are known to have high species richness rather than survey new sites where species richness is unknown (Dennis & Thomas 2000).

The variety of existing SDM algorithms has the potential to estimate substantially different species distributions depending on the algorithm used (Carpenter et al. 1993; Loiselle et al. 2003). Because this difference could have serious consequences for the interpretation of the richness patterns in Catalonia, we used three different algorithms (GLM, MARS and Maxent) in this study. We aimed to identify richness areas based on the current distribution of all vascular plant species described in Catalonia using these three modelling techniques, which were applied to each plant species individually. We specifically focussed on (1) examining whether these modelling techniques provide an adequate methodology to improve the sampled species richness in Catalonia; (2) identifying areas of high plant species richness in Catalonian landscapes; and (3) detecting areas where sampling has probably been lacking to date.

Methods

Study area

Catalonia is a region on the northeast of the Iberian Peninsula (Fig. 1; 40° 30'–42° 40'N, 0° 15'–3° 20'E), covering an area of ca. 31 980 km². Catalonia presents a wide range

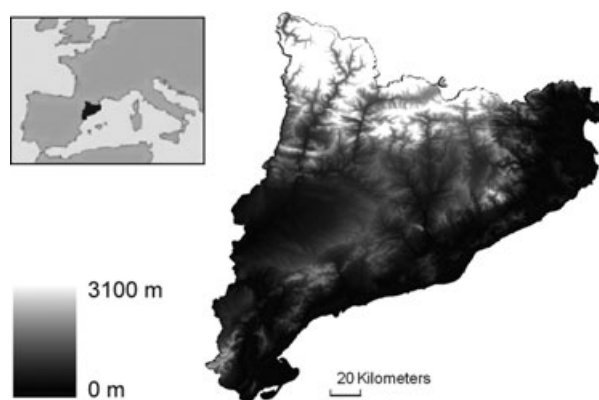


Fig. 1. Location of the study area (Catalonia).

of physiographic, biogeographic and orographic features, mainly due to the presence of the Pyrenees in the north and the Mediterranean Sea to the east. The majority of the area has a Mediterranean climate, with decreased rainfall from north to south and from the coast to the central plains. A continentality gradient is also present from the coast to the inland regions. The presence of numerous relief units results in highly variable climates (Pausas et al. 2003; Ninot et al. 2007).

The basic spatial unit for this analysis was the universal transverse Mercator (UTM) 10 km × 10 km grid system (100-km² projected area) because this is the mapping grid used in plant recording schemes in the Catalonia Database of Biodiversity (Banc de Dades de Biodiversitat de Catalunya, BDBC). The area of study is composed of 319 such units, hereafter called 'quadrats', which were included in UTM zone 31T.

Plant species data

In this study, we used all georeferenced plant species occurrence records from the BDBC, which uses the taxonomy updated by Bolòs et al. (2005). The scientific literature and, secondarily, herbaria are the most important data sources for this database. Prior to modelling, we examined all of the records to identify and exclude any with errors in georeferencing, obvious misidentifications and duplicate species records for one quadrat. Additionally, a species had to be represented in at least five quadrats to be modelled (see Vargas et al. 2004; Pearson et al. 2007; Raes et al. 2009). In total, the species data for our study consisted of 2 543 274 records for 2738 species (of the 3415 species in the database).

Environmental data

Both the quality and the interpretability of models and the derived richness maps strongly depend on variable

selection. Ninety-three variables were collected as predictive factors that influence the potential distribution of vascular plants (see Pausas et al. 2003). Each variable belonged to one of the following three types of environmental data: (1) geographical data, which included 14 variables; (2) climatic data, 72 variables; and (3) geological data, seven variables. These sets of explanatory variables have already been successfully used in both flora and fauna studies in Catalonia (e.g. Pausas & Sáez 2000; Pausas et al. 2003; Hawkins & Pausas 2004). The spatial resolution of the plant species data (10 km × 10 km) dictated the analysis resolution. We used ArcInfo workstation tools (ESRI 2009) to generate the environmental data.

Geographical set

The spatial patterns of biodiversity in Catalonia are strongly influenced by topographic features due to the heterogeneity of the territory (Pausas et al. 2003). Therefore, data on altitude, slope and orientation were obtained from a digital elevation model of Catalonia (resolution 20 m). We united the digital elevation model to a UTM 10-km × 10-km layer and calculated the maximum, minimum and average values of the altitude and slope data for each UTM quadrat. We also determined the percentage of every quadrat area oriented to each cardinal point (N, S, E, W, NE, NW, SE and SW).

Climatic set

Data on temperature, precipitation and radiation were derived from maps of the Digital Climatic Atlas of Catalonia (resolution 180 m; Ninyerola 2000). Seasonal data were chosen because in the Mediterranean climate seasons are easily distinguishable, making seasonal climatic factors the most important. Seasonal minimum temperature, maximum temperature, mean temperature, precipitation and radiation data were summarized as average, minimum and maximum values for each UTM quadrat.

Data on water deficit and potential evapotranspiration were obtained from the Climatic Atlas of Catalonia (<http://mediambient.genocat.cat/cat/inici/jsp>, ICC 1996). From this map, we first obtained the proportion of every quadrat area that corresponded to the following seven categories of water deficit: <0, 0–100, 100–200, 200–300, 300–400, 400–500 and >500 mm. Second, we obtained the percentage corresponding to each of the following five categories of potential evapotranspiration: 286–427, 427–572, 572–712, 712–855 and 855–997 mm.

Geological set

The different soil types present in the territory were obtained from the hydrogeological map of the Cartographic Institute of Catalonia (DPTOP & SGC 1992). The original 39 bedrock types on the map were grouped into the following seven main types as per Pausas et al. (2003): gypsum, siliceous schist, siliceous granites, siliceous conglomerates, marls, limestones and Quaternary substrates. Due to the presence of different soil types in the same quadrat, we estimated the area occupied by each substrate in each quadrat.

Analyses

We modelled the potential distribution of 2738 plant species using three different methods. We applied a maximum entropy model (Maxent) that, according to Elith et al. (2006), consistently outperforms more established methods, including presence-only methods or presence–absence methods, particularly when sample sizes are low. We also applied a generalized linear model (GLM) and multivariate adaptive regression splines (MARS) using the BIOMOD tool (Thuiller 2003), as implemented for R software (R Development Core Team 2009, Vienna, Austria).

A total of 93 variables for this study is a large number of factors that may be highly correlated. To avoid problems such as multicollinearity, which can result in model overfitting (Peterson et al. 2007), we reduced the number of predictors using a principal components analysis (PCA). We performed a PCA on the 93 observed predictors for the 319 quadrats of Catalonia. We selected the first 14 PCA axes as our environmental predictors (PCA01–14) because each of them separately explains more variance than would be expected by chance (1.07%) and they jointly explain 80.22% of the data variance.

Maxent model calibrations

We used the maximum entropy model (Maxent version 3.2.19, available at <http://www.cs.princeton.edu/~schapire/maxent>; Phillips et al. 2006), a presence-only algorithm that requires known species occurrence points and environmental variables. Maxent estimates the potential geographic distribution of the species by finding the probability distribution of maximum entropy, or closest to uniform distribution, subject to constraints derived from the occurrence data (Phillips et al. 2006). We automatically ran 2738 models (using the Maxent commands) with auto-features (Araújo & New 2007). For each run, a maximum number of 10 000 background quadrats were selected at random as pseudo-absences, the maximum number of iterations was 500, the convergence threshold

was set to 10^{-5} and regularization was set to the default value (Phillips et al. 2006). To evaluate the quality of predictions, we made a random partition of the occurrence localities for each species and divided the databases into two subsets: calibration and evaluation. The former, a random sample from 80% of the total database, was used to calibrate (train) the models, whereas the latter, comprising the remaining data, was used to evaluate (test) the model predictions (Fielding & Bell 1997).

Maxent model evaluation

We used receiver operating characteristic (ROC) analysis, which characterizes the species model performance at all possible thresholds with a single number that represents the area under the curve (AUC). This method does not require discrete presence/absence predictions and is therefore a measure that integrates many thresholds (Pearce & Ferrier 2000; McPherson et al. 2004). Although the AUC has been recently criticized, this method has been extensively used in the species distribution modelling literature because it measures the ability of a model to discriminate between sites where a species is present and those where it is absent (Hanley & McNeil 1982).

Maxent richness map

To develop plant species richness maps, a threshold was set to convert the continuous SDM predictions to discrete presence/absence predictions. We selected the threshold using the criterion of 'maximum training sensitivity plus specificity', which has recently been shown to produce successful predictions (Liu et al. 2005; Jiménez-Valverde & Lobo 2007). Once the threshold was set, the plant species richness map was developed through combining the presence/absence maps for individual species by summing the predicted presences (Lehmann et al. 2002). Thus, distribution maps of the 2738 species were overlapped to obtain an estimation of the potential species richness for each quadrat (i.e. a species richness map).

BIOMOD model calibrations

The methods included in the analysis framework were generalized linear models (GLM) and multivariate adaptive regression splines (MARS). GLMs have been one of the most commonly used techniques in species distribution modelling and are able to predict current species distribution (Austin & Meyers 1996; Brito et al. 1999). The MARS model provides an alternative regression-based method for fitting non-linear responses using piece-wise linear fits. Due to the lack of independent data for model evaluation,

we used a random data splitting procedure, as in the Maxent model calibration. For each species, the following procedure was used.

1 For GLM (McCullagh & Nelder 1989) with linear terms, we used a step-wise procedure to select the most parsimonious model and the most significant variables. The statistical criterion used for selecting models of increasing fit was the Akaike information criterion (AIC) (Akaike 1974; MathSoft 1999).

2 MARS (Friedman 1991) represents a relatively new technique that utilizes classical linear regression and was recently tested in an extensive study comparing 16 predictive techniques (Elith et al. 2006). We used the default values, in which the maximum interaction degree is equal to 1.

BIOMOD model evaluation

The accuracy of the species models was evaluated using the area under the relative operating characteristic curve, which considers many different thresholds to transform probability values from models into binary presence-absence form (Pearce & Ferrier 2000).

BIOMOD richness maps

To create species richness maps derived from GLM and MARS, we followed the same procedure as in Maxent.

Performance assessment of the richness maps

To be reliable, predictive modelling should always include a testing phase (MacNally 2000). Two measures of association, Kappa and the true skill statistic (TSS), were used to assess the predicted species composition of the three richness maps. Moreover, we calculated two components of disagreement between the richness maps in terms of the quantity and spatial allocation of the categories (related to our study species presences and absences). Otherwise, Pearson correlation (COR) was applied to assess the prediction performance of the predicted species richness.

For Kappa, we compared the predicted to the sampled local species composition for a set of 21 UTM quadrats (UTM assessment set) that had already been thoroughly studied by botanical experts and had floristic compositions that are considered to be very well known (Table 1). This UTM assessment set is representative of the environmental heterogeneity of the territory, containing coastal and inland areas as well as the Pyrenees (Fig. 2). We evaluated how well the different modelling approaches identified the sampled species composition in the UTM assessment set using Cohen's Kappa (κ) statistic (Cohen 1960). For this, we created a contingency matrix for each quadrat of the

Table 1. UTM assessment set.

UTM	Locality	Cited species	Predicted species by GLM (κ ; TSS)	Predicted species by MARS (κ ; TSS)	Predicted species by Maxent (κ ; TSS)
31T EG07	Castelló d'Empúries	1098	1033 (0.712; 0.649)	1124 (0.787; 0.752)	1026 (0.755; 0.688)
31T DG84	Girona	1111	968 (0.751; 0.683)	1012 (0.788; 0.733)	1068 (0.781; 0.728)
31T DG99	Sant Climent Sescebes	1171	917 (0.543; 0.464)	1212 (0.674; 0.643)	1047 (0.719; 0.660)
31T CG36	Isona	804 *	648 (0.707; 0.431)	448 (0.776; 0.396)	435 (0.799; 0.404)
31T DG66	Santa Pau	886	997 (0.687; 0.602)	955 (0.732; 0.646)	1025 (0.743; 0.672)
31T BF89	Aitona	715	906 (0.737; 0.643)	788 (0.851; 0.770)	670 (0.895; 0.785)
31T BF99	Sarroca de Segrià	756	591 (0.814; 0.622)	622 (0.843; 0.680)	569 (0.833; 635)
31T DG08	Grèixer	1251	926 (0.651; 0.603)	1080 (0.727; 0.695)	1046 (0.697; 0.652)
31T CF79	La Llacuna	745	637 (0.785; 0.579)	567 (0.772; 0.547)	631 (0.738; 0.514)
31T CG46	Abella de la Conca	1054	919 (0.541; 0.440)	1049 (0.710; 0.650)	831 (0.650; 0.530)
31T CF34	Cambrils	535 **	685 (0.803; 0.661)	735 (0.817; 0.726)	681 (0.851; 0.752)
31T BF81	Santa Bàrbara	861	1423 (0.553; 0.579)	1006 (0.841; 0.812)	883 (0.804; 0.712)
31T DG46	Vidrà	963	1082 (0.696; 0.637)	1069 (0.736; 0.682)	1064 (0.752; 0.691)
31T CH21	Boí	1046	1332 (0.692; 0.685)	1132 (0.845; 0.826)	1121 (0.795; 0.755)
31T CH41	Espot	1050	1270 (0.705; 0.687)	1131 (0.756; 0.718)	1139 (0.721; 0.669)
31T DG38	Riber de Freser	1265	1239 (0.569; 0.655)	1279 (0.712; 0.699)	1295 (0.672; 0.650)
31T CF27	Montsant	1106	724 (0.666; 0.553)	744 (0.694; 0.587)	952 (0.749; 0.673)
31T DG57	Olot	1136	1273 (0.574; 0.545)	1028 (0.725; 0.671)	1026 (0.703; 0.636)
31T DF28	Barcelona	1207	884 (0.599; 0.532)	903 (0.673; 0.611)	1042 (0.677; 0.620)
31T DG58	Beget	1078	965 (0.597; 0.513)	1132 (0.745; 0.706)	1036 (0.755; 0.692)
31T DG72	Maçanet de la Selva	1119	1277 (0.713; 0.694)	1201 (0.756; 0.730)	1162 (0.765; 0.726)

*Number of species used for statistical analysis in the 31T CG36 quadrat is 407. The number of records in this locality has not been updated.

**CF34 grid includes only 25% of emerged land.

κ ; TSS = Kappa and true skill statistic values.

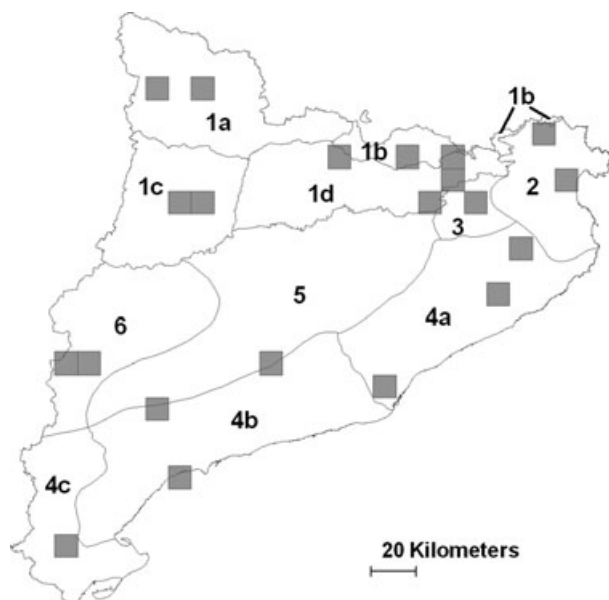


Fig. 2. Location of the UTM assessment set within the Catalan physiogeographic territories, according to Bolòs et al. (2005). The grey squares represent the UTM quadrats used for the UTM assessment set. Catalan biogeographic territories. **1** Pyrenees, subdivided into: **1a** Central Pyrenees; **1b** Eastern Pyrenees; **1c** Central Pre-Pyrenees; **1d** Eastern Pre-Pyrenees. **2** Ruscinic territory. **3** Olositanic territory. **4** Catalanidic territory, subdivided into: **4a** northern; **4b** central; **4c** southern. **5** Ausosegarric territory. **6** Sicoric territory.

Table 2. Contingency matrix used to evaluate the predicted species composition of the richness maps. *a*, number of species for which their presence in a quadrat was correctly predicted by the model; *b*, number of species for which their presence in a quadrat was not sampled but the model predicted their presence; *c*, number of species for which their presence in a quadrat was sampled but the model predicted their absence; *d*, number of species for which their absence in a quadrat was correctly predicted by the model.

		Sampled species	
		Present species	Absent species
Predicted species by the model	Present species	<i>a</i>	<i>b</i>
	Absent species	<i>c</i>	<i>d</i>

UTM assessment set, comparing the sampled and predicted species composition (Table 2). We built a total of sixty-three 2×2 contingency matrices corresponding to the three models and the 21 quadrats. Regarding the Kappa value, we used the following ranges for assessing the richness maps: $0.40 \leq K < 0.55$ was moderate, $0.55 \leq K < 0.70$ was good, $0.70 \leq K < 0.85$ was very good, $0.85 \leq K < 0.99$ was excellent and $0.99 \leq K \leq 1.00$ was perfect (Monserud & Leemans 1992). Nevertheless, we have to be aware that there is controversy about the universal standards of claims for high accuracy. As Pontius et al. (2007) and Pontius & Millones (2011) point out, it

makes no sense to have universal standards for accuracy in practical applications, because a universal standard is not related to any specific research question or study area (Pontius et al. 2007; Foody 2008; Pontius & Millones 2011). Moreover, in spite of its wide use, several studies have criticized the Kappa statistic for being inherently dependent on prevalence, and have claimed that this dependency introduces bias and statistical artefacts to estimates of accuracy (Cicchetti & Feinstein 1990; Byrt et al. 1993; Lantz & Nebenzahl 1996; McPherson et al. 2004; Pontius & Millones 2011). The TSS corrects for this dependency while still retaining all of the advantages of Kappa (Allouche et al. 2006). Regarding TSS, we proceeded in the same way as for Kappa, evaluating the prediction success of the different modelling approaches. For this, we created a contingency matrix for each quadrat of the UTM assessment set that compares the sampled and predicted species composition using TSS. Like Kappa, TSS takes into account both omission and commission errors, and success as a result of random guesses, and ranges from -1 to $+1$, where $+1$ indicates perfect agreement and values of zero or less indicate a performance no better than random (Allouche et al. 2006).

Kappa analysis and its variants has become a standard component of almost every accuracy assessment (Congalton & Green 2009). However, Pontius & Millones (2011) found that Kappa and its variants (i.e. TSS) are flawed metrics. Thus, they recommend replacing these indices with a more useful and simpler approach by summarizing the contingency matrices in terms of quantity disagreement and allocation disagreement. Quantity disagreement is the amount of difference between the reference map (sampled species composition) and a comparison map (predicted species composition) that is due to the less than perfect match in the proportions of the categories. Allocation disagreement is the amount of difference between the reference map and a comparison map that is due to the less than optimal match in the spatial allocation of the categories, given the proportions of the categories in the reference and comparison maps (Pontius & Millones 2011). The disagreement analysis was based on the built contingency matrices for each quadrat of the UTM assessment set.

In order to observe the relationship between the sampled and predicted richness, we carried out a linear regression analysis. Then we calculated Pearson correlations (between the sampled and predicted richness) to evaluate the performance of the richness maps. These calculations take into account how much the predictions vary from the observations. In addition, the adequacy of the richness maps was assessed by detecting outliers that disproportionately influenced the fit of the maps, examining the standard errors of coefficients, plotting the residuals vs the fitted values, plotting the residuals in a normal probability

plot, and examining the leverage of the observations. Alternatively, to identify the most poorly studied areas according to the results of the distribution richness maps, we analysed the standardized Pearson residuals to detect quadrats that show negative standard residuals lower than -1.95 (Lobo et al. 2004). Finally, the autocorrelation of the residuals of the linear models was checked using generalized least squares; we did not find spatial autocorrelation. These analyses were performed using the R program.

Results

Prediction of plant species richness in Catalonia

The spatial pattern of plant diversity in Catalonia was well summarized with GLM, MARS and Maxent models. The predicted species richness maps produced a much smoother pattern than that found in the sampled species richness map (Fig. 3). Based on visual examination and statistical evaluation, there was little variation between modelling methods (i.e. the patterns of relative richness did not vary among models; Table 3). For the three models analysed, the stacked and summed predicted distributions of 2738 plant species indicate that areas with concentrations of the greatest species richness occur along the

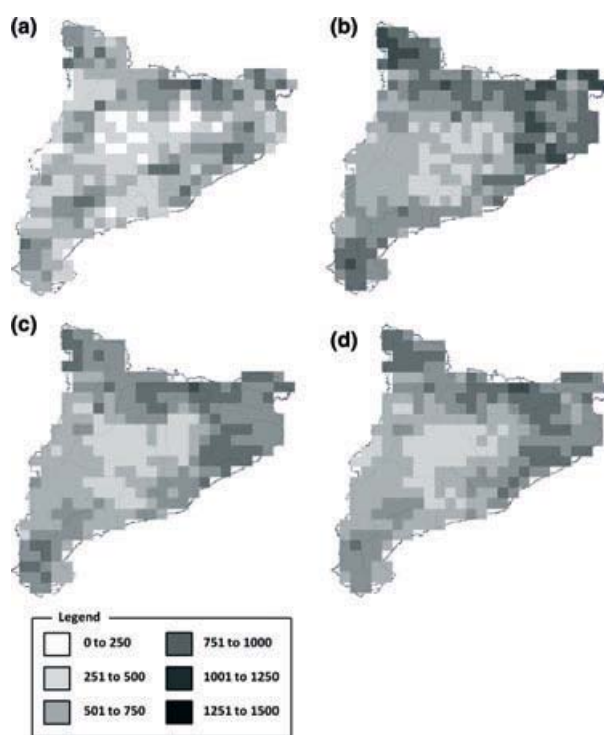


Fig. 3. (a) Sampled species richness in Catalonia according to the BDBC, (b) predicted species richness according to GLM, (c) predicted species richness according to MARS and (d) predicted species richness according to Maxent in Catalonia.

Table 3. Pair-wise correlation coefficient for the predicted richness among three modelling techniques and sampled richness based on the BDBC database (observed).

	Observed	MARS	GLM
MARS	0.67		
GLM	0.49	0.89	
Maxent	0.72	0.92	0.82

Pyrenees, the pre-coastal mountain range and the coastal range (Fig. 3). Ribes de Freser (quadrat 31T DG38) was the locality in which the highest number of both sampled and predicted species were concentrated, containing 1268 sampled species and 1279, 1239 and 1295 predicted species, as determined by MARS, GLM and Maxent, respectively. In contrast, low predicted richness values were common in inland areas. Central Catalonia, which includes the regions of Bages, southern Solsonès, southern Berguedà, Anoia and Segarra, was the least species-rich area, followed by the plain of Lleida, which includes the regions of Pla d’Urgell, Urgell, Segrià and Noguera.

Accuracy of species distribution models

We considered four classes of model accuracy. The low accuracy ($AUC < 0.7$) class included 173 species for GLM, 229 species for MARS and 1069 species for Maxent, representing 6.32%, 8.36% and 39.04% of the total data, respectively. The fair accuracy class ($0.7 < AUC < 0.8$) included 554 species for GLM (20.23%), 263 species for MARS (9.6%) and 435 species for Maxent (15.88%); this class included species with several occurrences (e.g. *Equisetum ramosissimum* and *Aristolochia rotunda*) as well as more scarce species (such as *Diplotaxis viminea* and *Berberis vulgaris*). Good accuracy status ($0.8 < AUC < 0.9$) was assigned to findings of 833 species (30.62%) for GLM, 850 species (31.05%) for MARS and 518 species (19%) for Maxent; this class also included both highly abundant species and more scarce species. The high accuracy class ($AUC > 0.9$) included 1195 species for GLM (43.66%), 1585 species for MARS (57.91%) and 715 species for Maxent (26.11%).

Finally, the results of the species distribution model evaluation indicate that MARS is the model that best predicts species actual distributions (Fig. 3c) (GLM: $AUC_m = 0.865$, $SD = 0.098$; MARS: $AUC_m = 0.902$, $SD = 0.085$; Maxent: $AUC_m = 0.736$, $SD = 0.187$).

Performance assessment of the richness maps

For the three statistical values (Kappa, TSS and COR) and the two components of disagreement, there is no obvious difference between the MARS and Maxent richness maps (Table 4), indicating that the overall prediction perfor-

Table 4. Statistical assessment criteria for prediction richness maps.

Criteria	GLM	MARS	Maxent
Kappa	0.671	0.760	0.755
TSS	0.589	0.680	0.659
Quantity Disagreement	6.952	4.095	3.428
Allocation Disagreement	11.857	9.904	11.333
COR	0.492	0.671	0.717

mance of these two richness maps is very close. In fact, the highest correlation coefficient for predicted richness was obtained between MARS and Maxent ($r = 0.918$). However, there is a difference between these maps and the GLM richness map, which showed the lowest values for the three statistics and the highest values for the two components of disagreement (Table 4).

Based on both Kappa statistics and TSS, the MARS map achieved the highest success ($\kappa_{mean} = 0.760 \pm 0.055$, $TSS_{mean} = 0.680 \pm 0.094$) in predicting the sampled species composition in the assessment data (21 UTMs with floristic composition thoroughly studied) (Table 4, Fig. 4). Kappa and TSS values obtained for the maximum entropy algorithm ($\kappa_{mean} = 0.755 \pm 0.061$, $TSS_{mean} = 0.659 \pm 0.088$) allow us to conclude that the predictive power of Maxent in identifying plant species richness is ‘very good’. Moreover, the richness maps derived from Mars and Maxent produced a baseline with an average of 4.1% ($\pm 3.0\%$) and 3.4% ($\pm 2.2\%$) quantity disagreement and an average of 9.9% ($\pm 3.6\%$) and 11.3% ($\pm 2.9\%$) allocation disagreement, respectively (Fig. 5). The maps obtained by Mars and Maxent produced a baseline with 85.76% and 85.14% agreement, respectively, which highlights that the species richness distribution in the landscape derived from the models is ‘very good’. Furthermore, the component of quantity disagreement for these two algorithms reflects a prediction of more than the reference quantity of presence for ten and seven quadrats, respectively, of the UTM assessment set (Table 1). This highlights a potential improvement in richness patterns over prior knowledge of

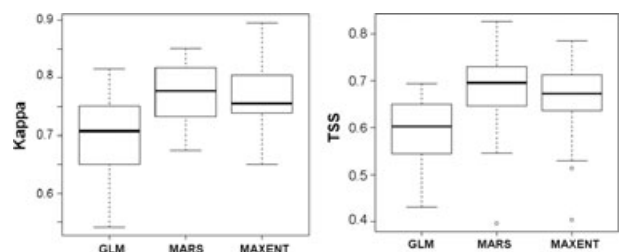


Fig. 4. Results of the richness map assessment of the 21 Kappa and TSS values computed for each model. The boxes represent the interquartile range, and the median is marked as a bold line within these bars; the line extensions from each box are the largest and the smallest values and the circles represent outliers.

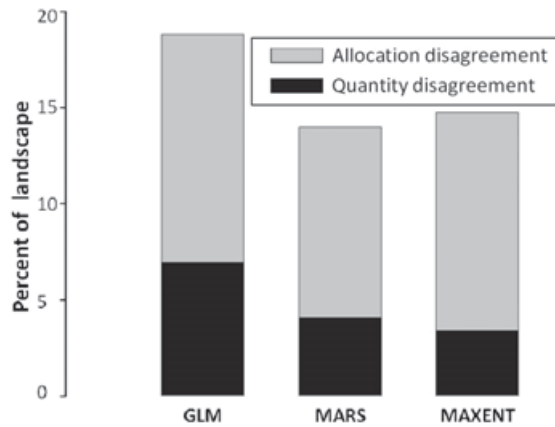


Fig. 5. Quantity disagreement and allocation disagreement for each matrix of the UTM assessment set.

the plant species richness in these quadrats. The Kappa, TSS and COR values obtained for the GLM analysis ($\kappa_{\text{mean}} = 0.671 \pm 0.086$, $\text{TSS}_{\text{mean}} = 0.589 \pm 0.081$) could indicate that its ability to predict plant species richness for Catalonia is ‘moderate’. However, the separation of the overall disagreement into components of quantity ($6.9 \pm 4.5\%$) and allocation ($11.8 \pm 5.0\%$) shows that most of the error is allocation error, revealing that this map is actually more useful for our particular purpose (produces good quality plant species richness maps) than implied by the reported measures of association (Kappa and TSS), which tend to focus more on the allocation error than on the quantity error. This evaluation of the predictive richness maps based on both Kappa and TSS statistics and on analysis of the two components of disagreement agrees with the results obtained from the Pearson correlation analysis (Table 4), confirming that the MARS and Maxent algorithms have higher accuracy in measurements than GLM as predictors of plant species richness for Catalonia.

Neither the examination of residuals nor that of spatial autocorrelation showed especially aberrant features. These results suggest that the models predict reasonably well the plant species richness in the more poorly sampled quadrats. However, 12 quadrats showed negative standard residuals below -1.95 (fitted values higher than observed; Fig. 6). These 12 quadrats contain fewer species than predicted by the explanatory variables, probably because the number of database records for each quadrat may not always reflect a comparable sampling effort. The results of the three modelling techniques indicate that these quadrats are the most poorly studied areas and are, therefore, the areas that should be focused on in future flora studies (31TCG85, 31TCG58, 31TDG54, 31TCG48, 31TCG17, 31TEG02, 31TCF56, 31TCF98, 31TCH51, 31TCG55, 31TCH52 and 31TDG65).

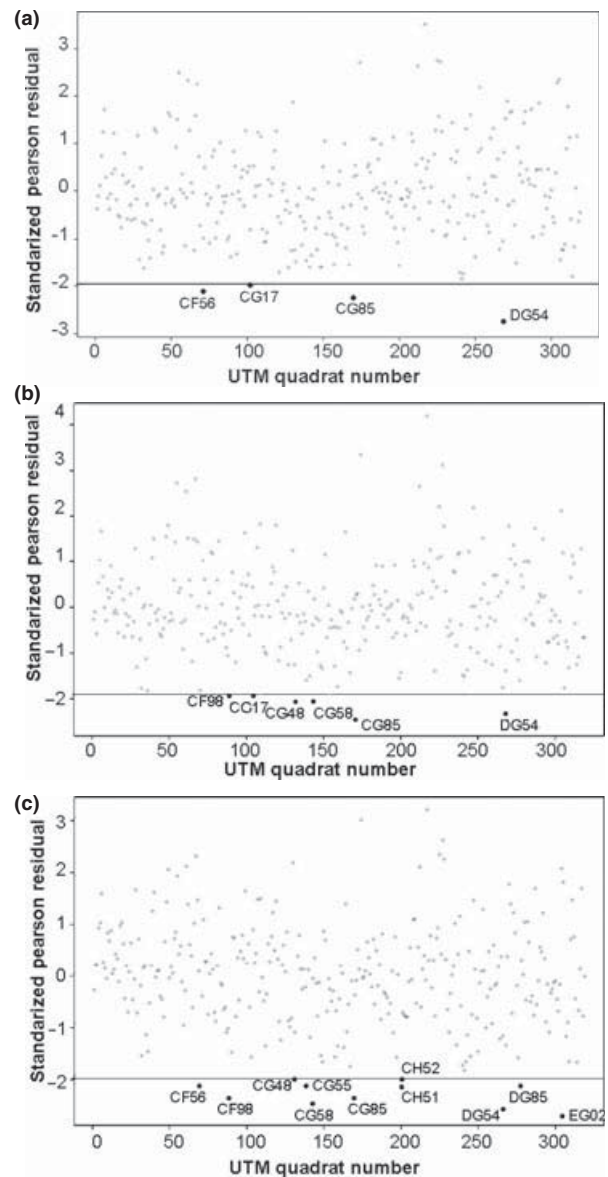


Fig. 6. Standardized Pearson residual scores for (a) the GLM, (b) MARS and (c) Maxent. Lines delimit the UTM quadrats with negative residuals less than -1.95 .

Discussion

Most studies describe species richness patterns based on a small group of indicator species, genera or families (MacNally & Fleishman 2004; Murray-Smith et al. 2008; Schouten et al. 2009). Hence, this study can be considered of great importance in plant species diversity assessment because 2738 species were modelled of a total of 3415 species in Catalonia (ca. 80% of the total flora of Catalonia).

When considering the accuracy of maps produced through a modelling system, it is important to note that

high scores of global performance measures do not necessarily imply that maps will be better suited to management applications. Although the predictive performance of Maxent for species distribution, based on the AUC values, was fair, both the richness map produced by this model and the map produced by MARS were best supported by the performance analysis based on Kappa and TSS statistics, the two components of disagreement, Pearson correlations and by known plant species richness. Moreover, the highest correlation coefficient for predicted richness was obtained between MARS and Maxent, indicating that these models provided reasonably similar predictions of species richness. The GLM tends to over-predict the species richness in Catalonia, reaching values of ca. 1400 species in the richest quadrats. According to Pausas et al. (2003), this value is too large and does not represent the true species richness of these areas.

The use of distribution modelling methods allows us to produce a geographical representation of the plant species richness distribution over the territory. As shown in the results, the spatial patterns of species richness in Catalonia are neither uniformly nor randomly distributed across the landscape. Generally, high species richness areas are predicted to occur along the Pyrenees, the pre-coastal mountain range and the coastal range, which are ancient geomorphological features that have high environmental heterogeneity. One of the most important variables determining vegetation composition at a coarse scale in Catalonia was quadrat heterogeneity, which showed a positive relationship to plant species richness in the quadrats (Pausas et al. 2003). Spatial heterogeneity is a surrogate for niche diversity, and it follows that highly heterogeneous areas should support more species than areas of lower heterogeneity (Rosenzweig 1995). The high plant species richness node observed in Barcelona (possibly due to the nearby presence of numerous universities and research centres) was predicted to be moderately rich, whereas the northern Catalan coast and the Ebro delta were predicted to have a higher richness than has been sampled. Regions of relatively low richness occur mainly in the central areas, possibly due to both the low environmental heterogeneity and the role of the agricultural activities in these areas, which we did not explore in this paper.

According to Pausas et al. (2003), the weighted mean, the minimum and the maximum number of species per quadrat in Catalonia were 620, 120 and 1222, respectively. The weighted mean, the minimum and the maximum number of species per quadrat predicted by MARS were 767, 313 and 1279, respectively, and with Maxent, these values were 764, 305 and 1295, respectively. It is important to point out that the two algorithms raised the minimum number to at least 300 species (i.e. the predicted richness in the poorest areas predicted by the

SDMs was higher than estimated in Pausas et al. 2003). Therefore, the two models increased the expected number of species present in the least sampled regions. Our results highlight that we have improved upon the patterns of species richness developed by Pausas et al. (2003), increasing the weighted mean and the minimum number of species per quadrat and obtaining potentially valuable distribution richness maps, especially in the most poorly sampled quadrats. Furthermore, the maximum number of expected species predicted by MARS and Maxent coincides closely with the prediction made by Pausas et al. (2003). Hence, from a botanical point of view, we believe that our results fit the reality of vascular plant richness in Catalonia.

In addition, analysis of the standardized Pearson residuals has allowed us to identify the most poorly studied areas, i.e. the quadrats that had the highest differences between sampled and predicted species number; these quadrats should be the focus of future sampling efforts. Once the modelling was completed, the Generalitat of Catalonia organized the '1–4 June 2010 Catalonia Bio-prospecting campaign', during which we conducted a survey in the two taxonomically poorest studied quadrats of the region. Thanks to this survey we increased the number of species encountered in these two quadrats from 76 and 83, to 417 and 361, respectively. So, these sampled values reached the minimum number of expected species predicted by the modelling algorithms. Moreover, MARS and Maxent predicted, for each quadrat, an actual number of species close to the surveyed number for the two quadrats (respectively, 337 and 347 with MARS; 419 and 425 with Maxent). Consequently, the results indicate that these two modelling algorithms are useful techniques to estimate plant species richness in Catalonia.

As stated above, we found some variation in modelling success between the different modelling techniques. This confirms that it is worthwhile to consider prediction outputs from multiple models when making assessments of species richness trends (Thuiller 2003; Elith et al. 2006). Our results confirm that modelling species distributions separately for each species and summing the predicted presences can be a useful strategy for assessing spatial variation in species richness, particularly for poorly sampled regions (Pineda & Lobo 2009). The model-predicted richness maps presented here can be used to detect zones with low and high species richness and to derive strategies for either restoring or protecting landscape biodiversity as part of national conservation plans. Although we are confident that the modelled maps reflect the actual richness pattern, we must stress that areas with lower values for the three models are not necessarily less important for conservation.

Conclusions

The species distribution models used in this study provided improved distribution patterns of plant species richness in Catalonia over the previously sampled patterns, and, most importantly, provided an estimate of the number of species present in those insufficiently sampled areas. Therefore, with this approach, we have developed patterns of species richness that are more reliable than those expounded in Pausas et al. (2003), thus providing a useful alternative to classical richness approximations for Catalonia.

Of the three modelling techniques used in this work, MARS and Maxent were the two methodologies that provided more accurate species richness maps than GLM.

Finally, this study has shown that it is possible to generate indices of plant richness in Catalonia using species distribution models. These indices are of potential value for management institutions, as they can be used as tools to identify target areas that require more survey and conservation efforts.

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Drastic reduction in the potential habitats for alpine and subalpine vegetation in the Pyrenees due to twenty-first-century climate change

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Abstract Recent climate change is already affecting both ecosystems and the organisms that inhabit them, with mountains and their associated biota being particularly vulnerable. Due to the high conservation value of mountain ecosystems, reliable science-based information is needed to implement additional conservation efforts in order to ensure their future. This paper examines how climate change might impact on the distribution of the main alpine and subalpine vegetation in terms of losses of suitable area in the Oriental Pyrenees. The algorithm of maximum entropy (Maxent) was used to relate current environmental conditions (climate, topography, geological properties) to present data for the studied vegetation units, and time and space projections were subsequently carried out considering climate change predictions for the years 2020, 2050 and 2080. All models predicted rising altitude trends for all studied vegetation units. Moreover, the analysis of future trends under different climate scenarios for 2080 suggests an average loss in potential ranges of 92.3–99.9 % for alpine grasslands, 76.8–98.4 % for subalpine (and alpine) scrublands and 68.8–96.1 % for subalpine forest. The

drastic reduction in the potential distribution areas for alpine grasslands, subalpine scrublands and *Pinus uncinata* forests highlights the potential severity of the effects of climate change on vegetation in the highest regions of the Pyrenees. Thus, alpine grasslands can be expected to become relegated to refuge areas (summit areas), with their current range being taken over by subalpine scrublands. Furthermore, subalpine forest units will probably become displaced and will occupy areas that currently present subalpine scrub vegetation.

Keywords Alpine grasslands · Climate change · Maxent · *Pinus uncinata* forest · Pyrenees · Subalpine shrubs

Introduction

Recent climate change is already affecting both ecosystems and the organisms that inhabit them (Walther et al. 2002; Parmesan 2006; Rosenzweig et al. 2008), with mountains and their associated biota being particularly vulnerable to climate change (Beniston et al. 1996; Theurillat and Guisan 2001). In fact, it has been noted that plants of alpine and subalpine areas appear to be especially sensitive to global warming (Shaw et al. 2000; Erschbamer 2001; Pauli et al. 2001). Moreover, it is likely that such effects are more intense in mountain systems under extreme and climatically marginal conditions (Beniston 2000), such as in many alpine areas with a Mediterranean climate influence, in which most of the orophilous species are relicts from glacial periods and are considered at the limit of their climatic tolerance range (Sanz-Elorza et al. 2003). Furthermore, impacts on flora from regions projected to undergo increased warming accompanied by decreased precipitation, such as the Pyrenees, will likely be greater than those on flora in regions

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where the increase in temperature is less pronounced and rainfall increases concomitantly (Engler et al. 2011).

In the last two decades, species- and community-based models have been increasingly used in conservation planning, and more recently, they have become important tools to evaluate the potential impacts of climate change on biodiversity (Guisan and Zimmermann 2000; Thomas et al. 2004; Guisan and Thuiller 2005; Ferrier and Guisan 2006). Concerning the former, species distribution models (SDMs) generate species' potential distributions in landscapes based on the relationship between species observations (presence/absence or abundance) and environmental variables. Regarding community-based models, two major approaches currently prevail (Guisan and Rahbek 2011). The first approach focuses directly on realized properties of species assemblages and uses macroecological modelling. The second approach focuses on aggregate properties of individual constituent species, used to reveal the properties of assemblage, and applies SDMs to a spatial stack of species (S-SDMs). Many studies have modelled the potential areas of species in the future under climate change scenarios of the intergovernmental panel on climate change (IPCC), but the work carried out by Thomas et al. (2004) was one of the first studies to apply SDMs to the problematic of climate change impact on organism geographic distribution for a large number of species. In Europe, the greatest modelling effort was carried out by Engler et al. (2011), who assessed the possible effects of climate change on the potential distributions of 2,632 plant species by the end of the twenty-first century in all major European mountain ranges at a fine spatial resolution (100 m; 1 km for the Spanish Pyrenees). However, most studies in Europe have focused on modelling species presence at the continental scale at a resolution of 50×50 km (Bakkenes et al. 2002; Thuiller et al. 2005) using input data taken from the Atlas Florae Europaeae (Jalas and Suominen 1972–1996). Other regional approaches have been applied for the Swiss Alps (Bolliger et al. 2000; Dirnböck et al. 2003; Walther et al. 2005; Pauli et al. 2007) and for 20 tree species on the Iberian Peninsula (Benito Garzón et al. 2008). Effects of ongoing climate warming on alpine plant species distribution have already been detected in several Iberian mountain ranges (Peñuelas and Boada 2003; Sanz-Elorza et al. 2003; Benito et al. 2011). Specially, Benito et al. (2011) pointed out that the suitable areas for species inhabiting the summits of Sierra Nevada (SE Iberian Peninsula) may disappear before the middle of the century. Thus, according to these studies, the alpine and subalpine vegetation in the Pyrenees can be expected to suffer similar trends as a consequence of the projected climate change. Hence, we expected that the vegetation belts in the Pyrenees will suffer an upwards shift, being, thus, the alpine belts the most affected by the climate change (see Benito et al. 2011; Engler et al. 2011).

In this study, we chose to model the potential distribution of entire vegetation units (as defined in CORINE; Vigo et al. 2006) rather than individual species for the following reasons: first, although vegetation units are not as sharply and objectively defined biological entities as species, for all of the vegetation units studied in this work, the mapping at our disposal, which is based on detailed orthophoto maps and intense field work, provides continuous layers of current distributions with a planimetric accuracy much greater than what is achieved in the case of species. Furthermore, the studied vegetation units are mainly defined by the presence of the dominant or key species. The behavior of the key species will determine the survival of many accompanying species, given that the former act as a nurse plant for the latter, creating appropriate micro-niches (Castro et al. 2004). Thus, investigation of the distribution of these vegetation units is consistent with investigation of the distribution of their dominant or key species. What is more, the reduction in the area that is climatically suitable for a particular vegetation unit determines the magnitude of the extinction risk for species belonging to it (Thomas et al. 2004). Moreover, to our knowledge, no detailed study has been conducted that assesses the future of the alpine and subalpine vegetation in the Pyrenees with such planimetric accuracy (resolution of approximately 0.6 km^2) under future climatic conditions. Finally, it is important to note that the studied units have a high conservation value because seven of them are habitats of community interest and two are habitats of priority interest under the 'Habitats' Directive 97/62/UE (Council Directive 97/62/UE of October 27, 1997, adapting Directive 92/43/EEC to technical and scientific progress on the conservation of natural habitats and wild fauna and flora).

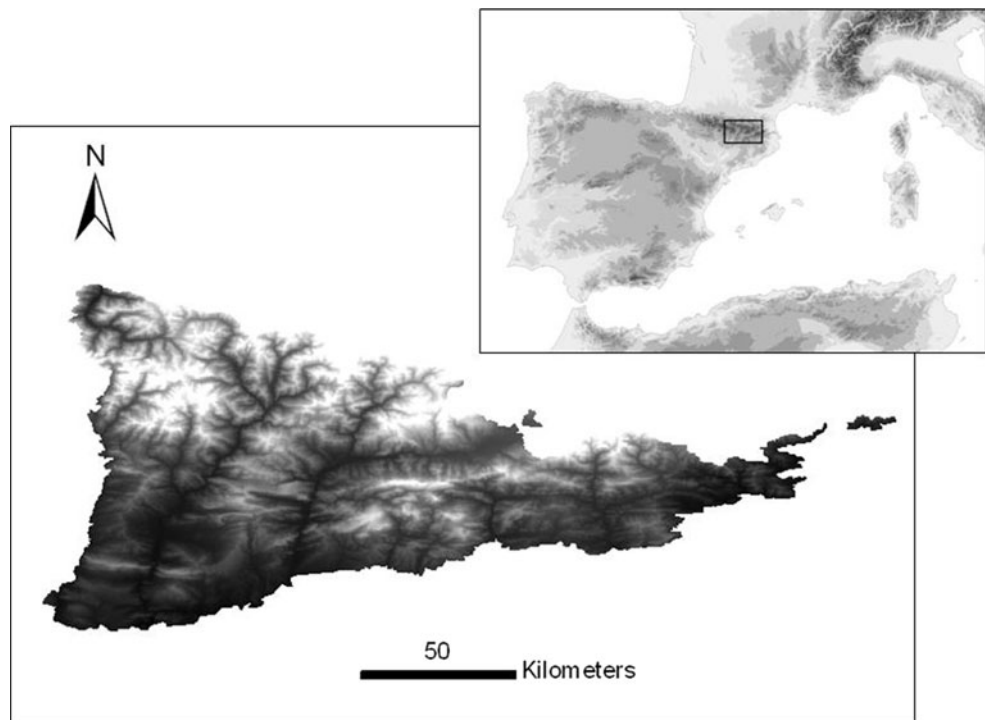
In this study, we assess the impacts of climate change on the potential distribution of six alpine grasslands, two subalpine (and alpine) scrublands and four subalpine forests of *Pinus uncinata* in the Oriental Pyrenees by the end of the twenty-first century using 700×900 m habitat samples and data expressing two IPCC-based climate change scenarios for the years 2020, 2050 and 2080.

Methodology

Study area

The study area covers a total area of $9,894 \text{ km}^2$, including the subalpine and alpine belts in the eastern half of the Spanish Pyrenees and Andorra (Fig. 1). Detailed vegetation mapping (Carreras et al. 2003; Vigo et al. 2006) and field surveys carried out mainly by Spanish botanists have provided excellent knowledge regarding the vegetation and flora in this area. In the Pyrenees, there is essentially one

Fig. 1 Map showing the location of the study area in the Oriental Pyrenees (NE Spain and Andorra)



tree species that inhabits the upper subalpine area: mountain pine (*P. uncinata*). At the tree line ecotone, open woods give way to a patchy area with small areas of dwarf scrub, grassland, tree islands and isolated trees. The vegetation above the forest limit, in the alpine zone, forms a small-scale mosaic of structurally and floristically distinct plant communities, including short grasslands clearly dominated by *Festuca eskia*, *Festuca airoides* or *Carex curvula* (on acidic substrata) and grasslands of *Kobresia myosuroides* or *Festuca gautieri* (in carbonated soils), dwarf scrub (formed by, e.g., *Rhododendron ferrugineum*, *Genista balansae*, *Vaccinium uliginosum* ssp. *microphyllum*), and sparse vegetation on rocky substrata and scree (Braun-Blanquet 1948; Carrillo and Ninot 1992). *Rhododendron* and *Genista balansae* dwarf scrub are placed on north- and south-facing slopes, respectively, and both can be either primary or secondary vegetation communities in alpine and subalpine areas severally. Traditional logging and bush burning for pasture are the main causes that explain their presence in subalpine areas as secondary vegetation communities.

Distribution data

In the Oriental Pyrenees, 57 CORINE vegetation units (legend units of the interpretation manual; Vigo et al. 2006) appear covering the surface of the alpine and subalpine belts (see Vigo et al. 2006 for further details). According to criteria such as occupation area, representativeness and

ecological importance, we selected 12 of these units (Table 1) which comprise the Pyrenees' main alpine and subalpine landscapes: subalpine forest of *P. uncinata* and subalpine (and alpine) scrublands, and grasslands distributed mainly in the alpine belt. The geo-referenced distribution data for the 12 studied vegetation units were obtained from both Catalonia habitats mapping (scale 1:50,000 with a minimum area of representation of 150 × 150 m, approximately 2.25 ha), a scientific project conducted during the period 1998–2003 (Vigo et al. 2006), and Andorra habitats mapping (scale 1:25,000 and 1.6 ha resolution; Carreras et al. 2003).

However, due to the spatial accuracy of the climate maps, the study was conducted at a resolution of approximately 0.6 km², that is, the spatial accuracy of the climate maps dictated the resolution at which spatial projection and analyses were carried out for the study area. Hence, the habitats mapping were rasterized to a 700 × 900 m grid using ArcGis 9.3 analysis tools (ESRI 2009). Lastly, these rasterized maps were converted into points which were positioned at the centers of all cells that they represent for modelling using ArcGis 9.3 conversion tools (ESRI 2009).

Environmental data

Environmental data included 36 climate layers, five layers describing geological materials and 11 topographic layers. We represented the current climate using monthly minimum

Table 1 Studied CORINE vegetation units; test omission rates (OR) at the maximum sensitivity plus specificity threshold; AUC values; and changes in the suitable area for the 12 studied vegetation units by the year 2080 under scenarios A2 and B2, and assuming universal dispersal

Vegetation unit	OR	AUC	Current potential distribution (km ²)	A2 scenario			B2 scenario		
				Maintained (%)	Increased (%)	Reduced (%)	Maintained (%)	Increased (%)	Reduced (%)
31 g <i>Rhododendron ferrugineum</i> heaths ^a	0.048	0.935	1,377.23	0.31	0.48	98.90	8.34	6.94	74.84
31 u Subalpine and alpine <i>Genista balansae</i> formations ^a	0.051	0.950	1,102.29	0.59	3.43	95.38	9.23	19.28	55.62
36a Alpine acid snow-patch communities	0.031	0.977	529.10	0.00	0.00	100.00	0.65	0.00	92.82
36 b Alpine calcareous snow-patch communities dominated by espalier <i>Salix</i> species	0.000	0.986	682.59	0.03	0.00	99.94	2.27	0.00	92.38
36 g <i>Festuca eskia</i> garland grasslands	0.034	0.906	1,615.64	0.15	0.03	99.66	11.32	0.24	74.76
36 h Acidophile <i>Carex curvula</i> grasslands	0.026	0.981	404.85	0.00	0.00	100.00	3.25	0.61	86.98
36 i Alpine <i>Festuca airoides</i> grasslands	0.049	0.973	1,247.68	0.05	0.00	99.90	1.03	0.01	95.14
36 m Alpine calcicolous <i>Kobresia myosuroides</i> swards ^a	0.049	0.986	363.64	0.00	0.00	100.00	0.09	1.35	97.05
42 f Mesophile and acidophilus <i>P. uncinata</i> forests ^a	0.076	0.888	2,072.51	2.64	6.99	87.72	24.01	17.27	26.41
42 g Xerophile <i>P. uncinata</i> forest of siliceous adrets ^a	0.062	0.907	1,862.03	0.56	6.24	92.65	18.76	18.16	52.28
42 h Xerophile <i>P. uncinata</i> forest of calcareous adrets ^b	0.059	0.964	887.85	0.14	2.08	97.63	9.54	18.68	67.38
42 i Mesophile calcareous <i>P. uncinata</i> forests ^b	0.050	0.956	1,105.09	0.36	4.80	94.47	8.80	17.97	74.64

Areas maintained, lost and gained by 2080. All performance metrics are based on the data partition (80 % training, 20 % test) generated for each vegetation unit

^a Habitats of community interest under the habitats directive

^b Habitats of priority interest under the habitats directive

temperature (Tmin), monthly maximum temperature (Tmax) and monthly precipitation (Ptotal) data layers provided by the WorldClim database. These data layers are generated through the interpolation of mean monthly climate data (averaging the period corresponding to 1950–2000) from climate stations onto a 0.6 km² resolution grid (Hijmans et al. 2005).

The spatial biodiversity patterns in the Pyrenees are strongly influenced by topography and geological properties (Pausas et al. 2003). Based on geological maps of Catalonia (scale 1:250,000) from the Cartographic Institute of Catalonia (ICC 1996), we carried out a simplification to obtain five geological variables (carbonate materials, silicon materials, substrates with sulfate, quaternary deposits and water bodies). Then, these geological data were adapted to the reference grid, and we calculated the percentage of each cell containing each type of geological material. Additionally, topographic data were obtained from a digital elevation model of Catalonia (DEM; with a

resolution of 20 × 20 m) developed from the topographic database of Catalonia at a 1:50,000 scale (ICC 2010). From this map, we calculated the maximum, minimum and average for both the altitude and the slope for each cell of the study area. Moreover, we obtained the percentages of each cell facing north, south, east, west and plane surfaces from the DEM. Finally, these data were adapted to a resolution of 700 × 900 m, allowing them to be overlaid with climate data.

To avoid multi-collinearity problems, which can result in model over-fitting (Peterson et al. 2007), we reduced the number of environmental predictors using a principal component analysis (PCA) in the software Ginkgo (version 1.7, <http://biodiver.bio.ub.es/vegana/>). We selected the first ten PCA axes as our environmental predictors (PCA01-10; Table S1 in Online Resources) because each of these axes separately explains more variance than would be expected by chance (1.78 %), and they jointly explain 97 % of the variance in the data.

Climate change scenarios

To simulate the distribution of the investigated vegetation units under possible future climate conditions, we used global climate model data from the IPCC third assessment report provided by the WorldClim database (<http://www.worldclim.org/futdow.htm>).

We used two different climate projections for the 1990–2080 time period developed by the UK Hadley Center for Climate Prediction and Research (Mitchell et al. 2004; Mitchell and Jones 2005). These were derived from a global circulation model (HadCM3; Carson 1999) and are based on two different socioeconomic scenarios proposed by the IPCC (Nakicenovic and Swart 2000): A2FI and B2FI (hereafter referred to as A2 and B2, respectively). The A2 scenario storyline describes a very heterogeneous world with a continuously increasing global population and regionally oriented economic growth that is more fragmented and slower than in other scenarios. The B2 scenario describes a world in which the emphasis is on local solutions to economic, social and environmental sustainability, with a continuously increasing population (lower than A2) and intermediate economic development.

With projected average warming of +4.99 °C over our study area by 2080, the A2 projection represents the most severe climate change scenario that we considered, while B2 was the mildest (+3.58 °C). Greenhouse gas emissions from the two scenarios will affect global climate change in different ways, with A2 having a more drastic effect on vegetation compared to B2. The future climatic condition trends in the study area are shown in Fig. 2 as changes in air temperature and precipitation.

Vegetation units distribution modelling

We used Maxent (Phillips et al. 2006) version 3.3.1 to relate current environmental conditions to vegetation occurrence data (i.e., points of vegetation units' presences derived from CORINE habitats mapping) and subsequently carried out spatial and temporal projections for the two possible future climate scenarios. Maxent estimates the potential geographic distribution of studied vegetation units by finding the probability distribution of maximum entropy, or closest to uniform, subject to constraints derived from occurrence data (Phillips et al. 2006). Maxent has been found to represent a promising and robust approach for modelling species distributions in both current (Elith et al. 2006; Hernandez et al. 2006) and future environments (Hijmans and Graham 2006).

Occurrence data often exhibit a spatial bias in survey efforts, which will impact the quality of predictions (Phillips et al. 2009). However, the coverage of the vegetation units across the Oriental Pyrenees is continuous,

consistent and has a good planimetric resolution, so one of the advantages of modelling these types of data over their associated species occurrences is that the sampling distribution for these vegetation units in the study region is exactly known (with much greater precision than the climate data). Before projecting the model, we applied a mask representing rocky areas to avoid projections at locations that are unsuitable, regardless of climate, topography and geological properties.

We employed recommended default parameters for this version of the model, including regularization multiplier = 1, maximum iterations = 500, convergence threshold = 0.00001 and a maximum of 10,000 background points. To evaluate the quality of the predictions under current climatic conditions, we carried out a random partitioning of the occurrence localities for each vegetation unit and divided the databases into two subsets: calibration and evaluation. The former subset, a random sample from 80 % of the total database, was used to calibrate (train) the models, whereas the latter subsample, comprising the remaining data, was used to evaluate (test) the model's predictions (Fielding and Bell 1997).

The results provided by Maxent were evaluated from the evaluation dataset (20 % of total data), employing the area under the receiver operating curve (AUC, ROC) method (Manel et al. 2001). The ROC curve characterizes the model's performance at all possible thresholds using a single number that represents the area under the curve (AUC). This procedure has been extensively used to evaluate models (Hanley and McNeil 1982; Fielding and Bell 1997). For models found to have a good predictive performance (test AUC >80 %), we projected the model from the present (1990) to each interval of 30 years until the year 2080.

Before performing migration simulations (described below), the model results were imported into ArcGIS 9.3 (ESRI 2009) to produce maps of potentially suitable areas. We reclassified the probabilistic projections of each Maxent model into binary values (presence–absence grids) representing either suitable or unsuitable areas. This conversion required the selection of a threshold above which a pixel was reclassified as potentially suitable, whereas it was unsuitable below the threshold. We tested the threshold that maximizes sensitivity plus specificity under the current climate (see Liu et al. 2005; Jiménez-Valverde and Lobo 2007; Fitzpatrick et al. 2008).

Dispersal scenarios

We used three simple dispersal scenarios, universal, zero or limited dispersal, to estimate the percentage gain or loss of the geographic range for each vegetation unit. The universal dispersal scenario assumes that vegetation can

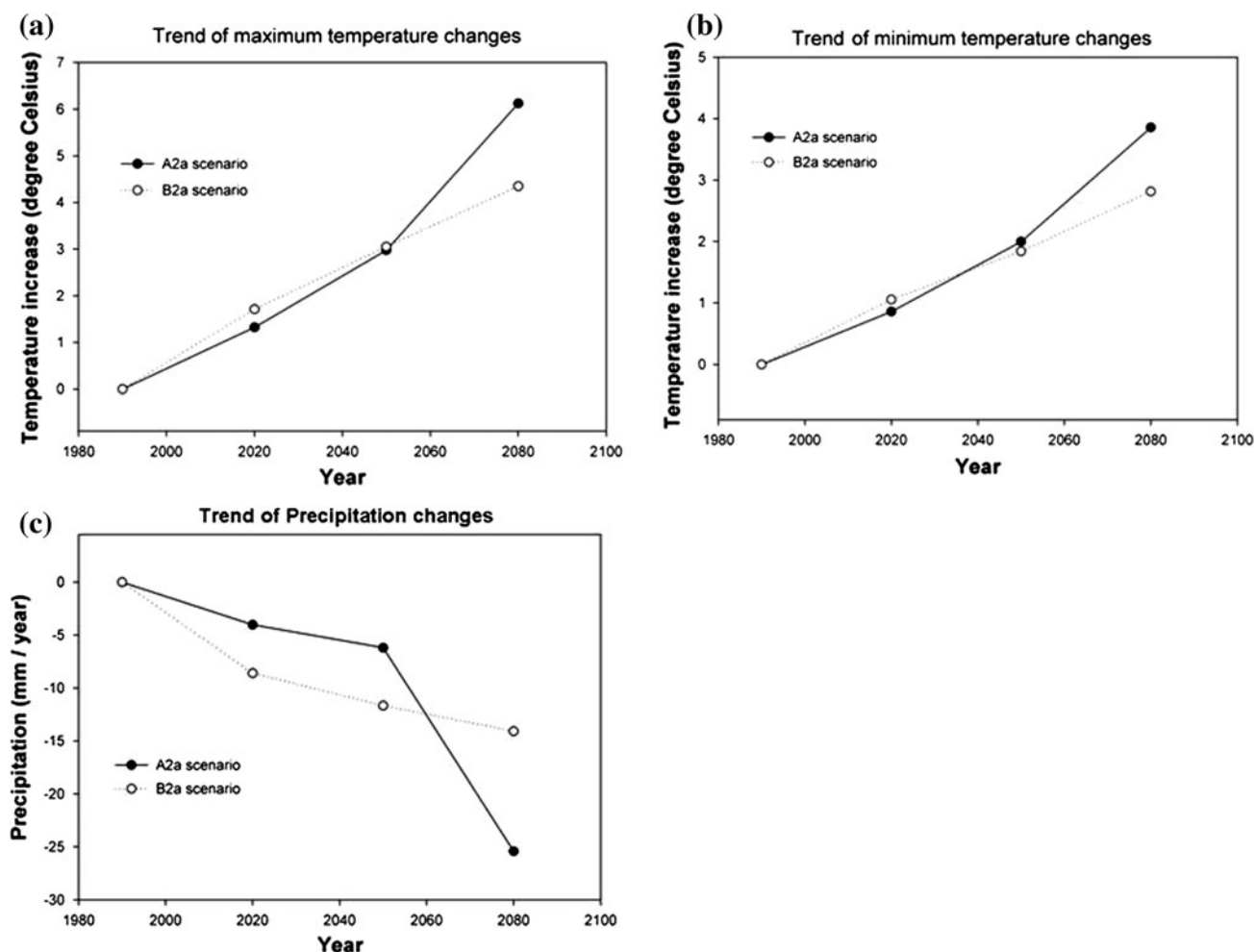


Fig. 2 Changes in the mean annual air temperature and accumulated annual mean precipitation according to the HadCM3 Global Circulation Model projected under the IPCC SRES A2 and B2 scenarios in

the Spanish Pyrenees and Andorra. **a** Trend of maximum temperature changes, **b** Trend of minimum temperature changes, **c** Trend of Precipitation changes

track their shifting climate envelopes, and the future distribution of vegetation will mirror the future spatial extent and location of those environments that are suitable for them. Therefore, we are assuming that all pixels projected to become potentially suitable as a result of climate change will be occupied by the vegetation units. This assumption might be conservative (i.e., optimistic), but it has been shown to provide good estimates of species loss levels for mountain areas (Engler et al. 2009). The zero dispersal scenario assumes that vegetation will persist only in areas where the modelled current and future geographic ranges overlap. In cases where there is no overlap, vegetation units are assumed to become extinct. However, historical constraints will cause realized species ranges to fill only limited proportions of the fundamental range, which is defined as the range that would be achieved should all dispersal constraints be overcome (Gaston 2003). Thus, using the limited dispersal scenario, we quantify the extent to which vegetation units

fill their current modelled climatic potential range in the study area (i.e., the capacity to occupy their full suitable area). For this objective, we computed the current realized/potential range size ratio (R/P) (Gaston 2003) across the study area, where P is the number of climatically suitable pixels defined by the Maxent model maps, and R is the number of climatically suitable pixels within the occupied distribution maps of the vegetation units. Thus, we obtained an indicator of the amount of the suitable area that was actually occupied (dispersal ability simulator). We assumed that maintained areas remain constant, and we applied this indicator to expansion areas after assuming universal dispersal. This scenario represents an intermediate dispersal scenario. We thus obtained the percentage of area lost, but we do not know where that loss occurs.

The spatial overlap between the modelled current and future vegetation presence/absence grids was calculated using ArcGis 9.3 tools (ESRI 2009) for each climate

scenario and time period, producing cell counts of current and future distributions.

Changes in vegetation units' distribution

Using the predictions for each vegetation unit, the maintenance, expansion or reduction in their ranges with respect to their current potential distribution was quantified for each scenario. The maintained distribution area was predicted from the area occupied at the present time that was also expected to be occupied in the future (year 2080). Expansion was defined as the area not occupied at present that was likely to be occupied by the vegetation unit in the future. Reduction was calculated from the area occupied at present that will most likely not be occupied in the future.

Finally, we calculated both the altitudinal shifts and the potential area loss of the modelled vegetation units for the year 2080 as follows:

$$[(\text{Area}_{2080} \times 100) / \text{Area}_{\text{current}}] - 100.$$

A unit is expected to become extinct when it is predicted to lose 100 % of its suitable area. However, because the link between area losses and extinction formally requires a population viability analysis in addition to predictions of spatial distribution analysis (Botkin et al. 2007), we only discuss our projections in terms of suitable area losses, that is, the percentage change in the size of the area.

Results

Algorithm performance

The models developed using Maxent had good to excellent predictive ability, as measured by the AUC values (Table 1). The AUC ranged from 0.888 to 0.986. The relatively high AUC values indicate that the distributions of the vegetation units are well described by the climate, topography and geological properties of the study area. Additionally, for the chosen threshold, all models showed low omission rates, indicating that only a small percentage of test points fell outside the area predicted as suitable (Table 1).

Projected distribution by 2080

Our models predict that climate change will have a substantial impact on the geographic ranges of the 12 studied vegetation units (Table 1), with the climate change severity scenario and dispersal scenario influencing the magnitude of the modelled range change responses. An increase in climate change severity (A2 scenario) increases the risk of loss of potential areas for all modelled vegetation units.

Considering our results, the following trends are apparent (Table S2, and Figures S1 and S2 in Online Resource).

Alpine grasslands (vegetation units 36 in Table 1)

By 2080, the size of the area occupied by alpine grasslands was significantly reduced under the two climate scenarios, losing 99.9 % (± 0.1 standard deviation) of the area of occupation on average under the conditions of the A2 scenario and 92.3 % (± 7.5 standard deviation) under the conditions of the B2 scenario. For the six studied alpine grassland, assuming universal dispersal, the modelled geographic ranges decline with increasing climate change severity. When incorporating the current R/P range size ratio, or if zero dispersal is assumed, the same trends in direction occur, but declines in the modelled range size are more severe. Therefore, these vegetation units were predicted to suffer an intense and rapid reduction in their ranges (Table 1; Fig. 3a), with particularly strong effects being seen for the snow-patch communities of acid soils (36a; Figure S1c and Figure S2c in Online Resource), the grasslands of *Carex curvula* (36 h; Fig. 4; Figure S1f and Figure S2f in Online Resource) and the swards of *Kobresia myosuroides* (36 m; Figure S1h and Figure S2h in Online Resource); these are formations that appear at higher elevations and seem to show a low capacity to maintain or expand their ranges, which could lead to their extinction by the year 2080.

Regarding changes in altitudinal trends, it is expected that the studied group of alpine grasslands (group 36 in the legend for CORINE habitat mapping of Catalonia and Andorra) will rise between 310 and 415 m by the year 2080, reaching a mean altitude of 2,733 m under the A2 scenario and 2,627 m under the conditions of the B2 scenario.

Subalpine (and alpine) scrublands (vegetation units 31 in Table 1)

Our models predict a great reduction in the modelled geographic ranges of the two high mountain scrub formations by 2080, with this potential area loss being greater with increasing climate change severity and decreasing dispersal rates. For the *Rhododendron ferrugineum* heaths (31 g), the modelled geographic range declines by 98.9 % under the more severe scenario (A2) assuming universal dispersal and by 74.8 % under the B2 scenario with universal dispersal. When zero dispersal is assumed, the modelled range size for this formation decreases more dramatically, losing 99.7 % of its potential area under the A2 scenario and 91.6 % under B2. Finally, when incorporating the R/P ratio, we observe an intermediate situation, in which the loss of suitable area is 99.2 % under the conditions of the A2 scenario and 78.6 % under the less

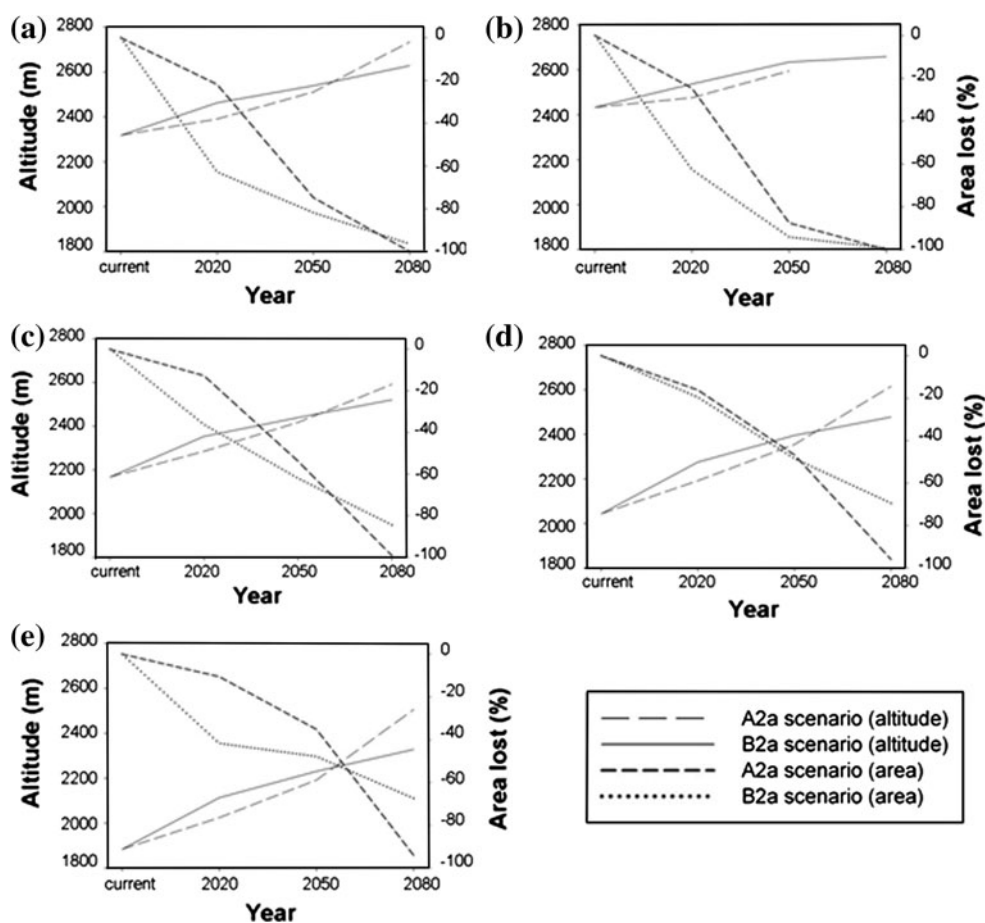


Fig. 3 Quantifying the change trends expressed as losses in the potential range and as an increase in the mean altitude for the two change scenarios assuming universal dispersal: **a** alpine grasslands (units of group 36); **b** alpine acid snow-patch communities (unit 36a);

c *Rhododendron ferrugineum* heaths (unit 31g); **d** *Genista balansae* scrublands (unit 31u); and **e** subalpine *P. uncinata* forests (units of group 42)

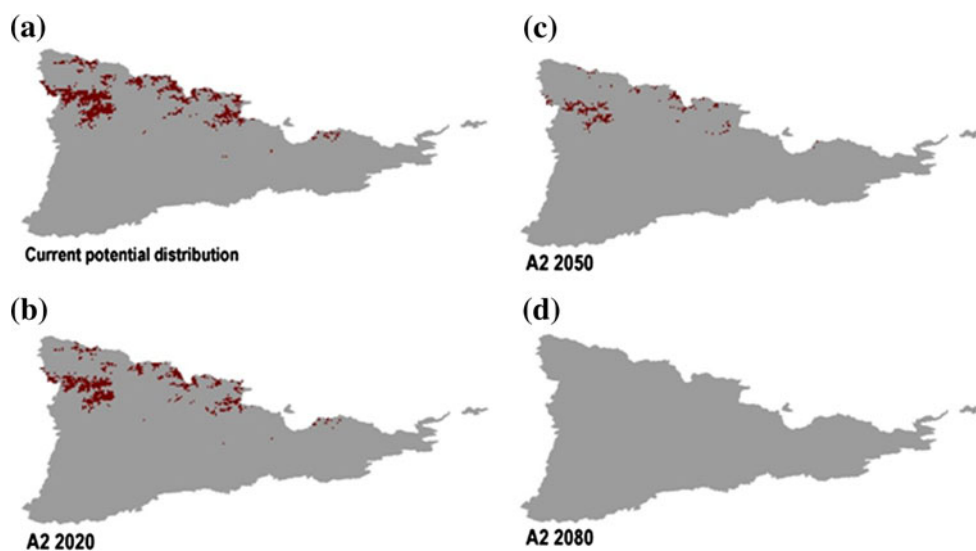


Fig. 4 Potential distribution of acidophile *Carex curvula* grassland (unit 36 h) in the present and under the climate projections of scenario A2 (2020, 2050 and 2080) assuming universal dispersal

severe scenario (B2). The *Genista balansae* formations (31u) are predicted to suffer a slightly less drastic decline, losing 95.4 % of their area by 2080 under the A2 scenario and 55.6 % under the B2 scenario assuming universal dispersal. When zero dispersal is assumed, this subalpine scrubland shows a reduction in its potential area of 99.4–90.8 % (scenarios A2 and B2, respectively). Figure 3c, d show the general trends of reduction in the ranges of these subalpine scrubs.

Regarding the changes in altitudinal trends, our results show an altitudinal increase for these subalpine scrublands of between 394 and 498 m by the year 2080, reaching an average altitude of 2,603 m under the A2 scenario and 2,500 m under the B2 scenario.

Pinus uncinata subalpine forest (vegetation units 42 in Table 1)

In general terms, our results suggest that by the year 2080, these vegetation units will present suitable occupation areas at higher altitudes than today (Fig. 3e), reaching an average altitude of 2,505 m under the A2 scenario and 2,327 m under the B2 scenario, shifting scrublands and alpine grasslands in part. These subalpine forests were generally predicted to undergo a less drastic reduction in the area occupied than any other vegetation unit analyzed in this study (Table 1), losing 96.1 % (± 3.8 standard deviation) of their potential range on average by the year 2080 under the A2 scenario and 68.8 % (± 21.2 standard deviation) under the B2 scenario. Specifically, when assuming universal dispersal, their average area lost is 93.1 % under the conditions of the A2 scenario and approximately 55 % under the B2 scenario. When assuming zero dispersal, the modelled range size decreases, losing 99 % of the suitable area under the A2 scenario and 84.7 % under B2. When incorporating the current R/P range size ratio, the projected potential area lost by the models varied between 96 and 66 % (scenarios A2 and B2, respectively).

This is the group of vegetation units for which we found the greatest differences in potential area loss based on the climate change scenario employed.

Vegetation unit extinction by 2080

Among the group of 12 vegetation units investigated, the percentage of units going extinct in the study area (100 % threshold) varied from 0 % (universal dispersal under B2) to 25 % (under A2). The percentage of vegetation units going quasi-extinct (i.e., units with over a 90 % decrease in distribution) varied from 91.6 % (universal dispersal under A2) to 100 % (zero dispersal under A2) and was never below 33 % (universal dispersal under B2). Extinctions are expected to occur between 2050 and 2080.

Discussion and conclusions

Credible scientific predictions of future impacts on biodiversity will be required to guide conservation planning and adaptation. Engler et al. (2011) suggest that changes in precipitation, in addition to warming, play an important role in determining the potential impacts of climate change on vegetation. Furthermore, in high mountains, the effects of global warming with regard to the biota are amplified (Benito et al. 2011). This is especially true in the Pyrenees, which are strongly influenced by the Mediterranean climate, because Mediterranean climate regions are projected to be among the most significantly affected by anthropogenic climate changes and show the highest levels of confidence in projected changes in rainfall (IPCC 2007). Models that forecast species distributions based on climatic scenarios for the twenty-first century predict a dramatic increase in these climatic trends, resulting in a massive reduction in mountain plant diversity. This is a matter of concern, as mountain ecosystems represent invaluable resources, both in terms of biodiversity and the ecosystem services they provide (Körner 2003; Viviroli and Weingartner 2004). Here, we used fine mapping scale data to assess climate change impacts on the potential distribution of alpine and subalpine vegetation units in the Oriental Pyrenees, and our results point to severe changes in the occupation area. Our models projected that many of the vegetation units analyzed in this study may be threatened by climate change. For all of the analyzed vegetation units, the projected impacts of climate change on the modelled geographic ranges differed mainly in the magnitude rather than the direction of the response across climate change severity and dispersal scenarios, with all vegetation unit ranges being projected to decline. Specifically, the trend shown in our analysis was that higher elevation vegetation is more vulnerable to area losses due to climate change than vegetation at lower elevations. The altitudinal extension of the Pyrenees allows scrublands and forest with a subalpine habitat suitability to move upward as the climate becomes warmer and drier. However, the alpine vegetation belt of the Pyrenees is restricted by altitude (there is no more space available at higher altitudes), which would lead to dramatic losses in appropriate areas for different vegetation units. With the rise in altitude, the area of available habitat diminishes, the topography becomes more hostile (higher slopes) and the soil loses the power to sustain shrub and tree species (Benito et al. 2011). Therefore, as we expected and as our results show, the impact of climate change will mainly affect alpine vegetation units. Moreover, carbonated soils in the study area are limited to altitudes approximately below 2,700 m (ICC 1996); hence, calcareous vegetation units would also lack of suitable surfaces with the projected rise in altitude. As a

consequence, we should be mindful of the risks calcareous alpine vegetation would face in the future.

This study confirmed a general trend found in studies based on species data conducted for Europe (Engler et al. 2011) and on regional scales (Dirnböck et al. 2003; Benito Garzón et al. 2008; Benito et al. 2011). As the climate becomes warmer and drier for the Oriental Pyrenees, alpine vegetation units can be expected to become relegated to summits, with their current range being taken over mainly by subalpine vegetation. Several works across the world have reported a force response in the altitudinal migration of plant species in New Zealand (Wardle and Coleman 1992) and in northern Europe (Kullman 2002), or in Alps, where resampling of vegetation in some areas has shown a significant increase in the number of shrub and herbaceous species in alpine ecosystems (Grabherr et al. 1994). More specifically, in the Mediterranean mountains, some studies have suggested that changes in temperature and precipitation would lead to a shift toward vegetation types currently found under drier conditions in Mediterranean mountains (Gritti et al. 2005). In a study performed in the Spanish Central Range, Sanz-Elorza et al. (2003) reported a replacement in high mountains grassland communities dominated by *Festuca aragonensis* by shrub patches of *Juniperus communis* and *Genista balansae* from lower altitudes. Furthermore, this altitudinal shift means that there will be increasingly restricted availability of potentially suitable areas for the analyzed alpine grassland units because, as mentioned above, the higher the altitude, the less the available surface area, being calcareous alpine grasslands more vulnerable due to the lack of carbonated soils above 2,700 m in the study area. This trend for alpine grasslands has also been observed in the Alps (Dirnböck et al. 2003), where similarly to the Oriental Pyrenees, alpine plant species show more limited availability of potentially suitable areas above the timberline over the years, so they will likely experience severe fragmentation and loss of suitable areas as a result of climate change. However, in alpine and subalpine environments, where the timberline is often maintained artificially at low altitudes by human activities, preservation of traditional land uses, such as pasturing, can decrease area losses for open vegetation that would become excluded through upward shifts of trees and reforestation of areas that are already suitable for forests under current climatic conditions (Theurillat and Guisan 2001; Dirnböck et al. 2003, 2011; Engler et al. 2011). Thus, a real challenge lies in the preservation of biodiversity of the mountain summits, since the species living there lack areas of expansion and will be subjected to great pressure, both by the degradation of the conditions appropriate to each species and by the arrival of new competitive species from lower altitudes (Benito et al. 2011).

A relatively recent study on the distribution of Iberian tree species is also noteworthy (Benito Garzón et al. 2008), in which the investigators used the *random forest* algorithm (RF) and projected losses in the size of the potential distribution area of *P. uncinata* on the Iberian Peninsula of approximately 92 % by the year 2080 under the conditions of the A2 scenario. This coincides with our results, which forecast a very similar percentage of 95 % of area lost (lost area based on the weighted average of each unit in group 42, *P. uncinata* forests) by 2080 under the same climate scenario. However, despite the loss of current area, these vegetation units are expected to be capable of altitudinal displacement and will therefore survive if they can colonize similar areas created by climate change. The extinction of some of the alpine and subalpine species would lead to a reduction in genetic diversity on the Iberian Peninsula, although it may be expected to survive in other European areas (Benito Garzón et al. 2008). A study performed regarding the future of the Alps also suggests that this species will survive at high altitudes (Theurillat and Guisan 2001).

A fine spatial resolution study in Europe (Engler et al. 2011) projects that an average of ~20 % of the plant species of European mountains areas could lose their entire suitable area by 2070–2100 under the A2 climate change scenario. This coincides with our results, which forecast a similar degree of threat to high mountain Pyrenees vegetation, with an average of 25 % of vegetation units projected to lose their entire suitable area by 2080 under this climate change scenario. Specifically, Engler et al. (2011) forecast that a maximum of 100 % of alpine species and 56 % of subalpine species will lose their entire suitable area in the Spanish Pyrenees by 2070–2100 under the A2 scenario. In contrast, our results forecast a much lower degree of threat to alpine and subalpine vegetation, with maximum levels of 50 and 0 % of alpine and subalpine units, respectively, projected to lose their entire suitable area by 2080 under this climate change scenario. The difference between these results is likely due to the different planimetric precision of the two studies, with the accuracy of CORINE vegetation units usually being much higher than that achieved in the case of species. Furthermore, we should note that this value of 100 % of alpine species that are projected to lose their entire suitable area by 2070–2100 in Engler et al. (2011) is based on only four species, so the actual average for all alpine species in the Pyrenees would be certainly lower, as found in this study. Nevertheless, our results coincide with the direction of the risks of predictions made by Engler et al. (2011) for the Spanish Pyrenees.

Hence, we note that models that predict future changes in the distribution of vegetation units can be as useful as those used in previous studies for species with the aim of

obtaining better tools for policy planning related to biodiversity conservation. This study emphasizes that the investigated units could be potentially affected by climate change, and if we consider their high conservation value (as more than a half of the studied vegetation are of community interest under the ‘Habitats’ Directive 97/62/UE), we should consider implementing additional conservation efforts to ensure the future of these vegetation units. Moreover, these units shelter both endemic (e.g., *Dianthus vigoi*, *Festuca bordevei*, *Festuca yvesii*, *Armeria muelleri*) and threatened species (*Oxytropis lapponica*, *Pedicularis tuberosa*, *Vaccinium vitis-idaea*), for which conservation either in situ or ex situ is essential.

Finally, we should note some intrinsic limitations of the methodology used in this study that should be considered when interpreting our results. The first of these limitations derives from the assumption that the climate forecast performed by the third IPCC working group for the next 70 years is correct. If the expected climatic patterns we used in this study do not match the future patterns exactly, such as a less pronounced increase in temperature occurring, the trends of altitudinal and range size changes predicted in this study may differ substantially. Another limitation to consider is related to the implementation of the limited dispersal scenario. For this, we used a statistical approach by applying a dispersal ability simulator of the vegetation units in the study area to their modelled future projections. However, the conditions that have led to the current range filling of the vegetation units might not exist in the future. Typically, the climate change scenario forecast changes in climate that are much faster than what happened in the past, and plants might not be able to migrate fast enough to keep up with the change. This means that the limited dispersal scenario used in this study probably overestimate the dispersal capacity of the vegetation units. The latter limitation to consider is that our models consider only the potential distribution of vegetation units as defined by bioclimatic envelopes (i.e., estimate the potential future distribution of vegetation based solely on environmental conditions) and therefore do not consider either competition phenomena or the ability of species to resist severe climatic conditions that are not lethal for their survival. Therefore, in light of these methodological limitations, the actual loss of area of occupancy of the studied vegetation units by 2080 could be considerably lower than predicted based on the results of this work. Nevertheless, our predictions provide important information about trends in the range sizes (occupation areas) of the studied vegetation formations.

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The Iberian and Macaronesian Vegetation Information System (SIVIM, www.sivim.info), five years of online vegetation's data publishing

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Abstract

The SIVIM website was born six years ago. After a first stage of fast growing, the number of queries to its database has currently surpassed 100,000 per year. SIVIM offers its users the opportunity to access to large datasets facilitating phytosociological reviews, plant conservation management and taxonomic chorological studies, amongst others. Therefore, the number of scientific papers and books as well as other websites that cite our website is enlarged everyday. New data have been constantly brought into the project, which means that more than 130,000 phytosociological relevés are currently accessible, storing more than two million specific floristic observations. According to the Global Index of Vegetation-Plot Databases (GIVD), and taking into account the number of computerized relevés, SIVIM is the fourth largest database in the world.

New analysis tools have been developed during this year, among them the on line calculation of species and syntaxa's fidelity values, and a new remarkable tool to model the potential distribution of taxa and syntaxa (based on the maximum entropy algorithm), and their future trends in response to climate change (projections for the years 2020, 2050, and 2080). We should also emphasize ZamiaDroid, the latest integration within the project, which allows querying SIVIM by mobile devices (smartphones and tablets). With respect to programming, we implemented a new system so that users can report errors directly to SIVIM administrators.

Concerning future actions, we aim to develop an online expert system in order to survey and classify vegetation communities and to open SIVIM to participative projects, especially those related to photography of plants and vegetation types. The SIVIM project has been funded by two research projects, CGL2006-13421-C04 (2007-2009) and CGL2009-13317-C03 (2010-2012), consecutively.

Keywords: analysis tools, database, relevés, vegetation.

Introduction

The importance of having large biodiversity databases has been highlighted in several international forums, as well as in the recent national report on the climate change impacts (Moreno, 2005). Databases of plant species occurrence in conjunction with environmental data can be a powerful tool to understand ecological relations or predict the effect of external drivers on ecological processes and species reactions (Chytrý & Rafajová, 2003; Smart *et al.*, 2003; Lenoir *et al.*, 2008; Schaminée *et al.*, 2009). Descriptive studies on vegetation using phytosociological methods include, in most cases, data as relevé tables and constitute an important source of phytosociological, ecological and floristic information.

The great number of publications currently available within the Iberian Peninsula and the Macaronesian archipelagos (nearly 1,700 references are already compiled in SIVIM) give rise to a large number of accessible relevés. We estimate there are approximately 175,000 relevés available for the concerned area (Font *et al.*, 2009). These data are scattered in numerous publications (either national or international), and in a great

number of unpublished works (PhDs, Master theses, reports, and so on). The difficulty in finding some of these works, along with the large diversity detected on the information sources, frequently causes some data to go easily unnoticed even to expert users, being for non-specialists almost impossible to work with all the data from an extensive territory.

Moreover, the knowledge of the composition and distribution of plant communities is becoming increasingly necessary, partially as a consequence of surveying the habitats enclosed in the Habitats Directive 92/43/CE (the legend of which is mostly based on phytosociological vegetation units). However, not only is the knowledge of the distribution and occurrence of vegetation types important for phytosociological studies, but also for the assessment of decision making on land planning and management and for ecological research in general.

We can find a substantial number of independent projects aiming to computerize vegetation data all over the world. The Global Index of Vegetation-Plot Databases (GIVD, <http://www.givd.info>) has recorded 184 databases hosting 2,838,550 vegetation plots worldwide. The first initiative to relate these databases is being

carried out by the European Vegetation Archive (EVA; Chytrý *et al.*, 2012). However, the political, institutional, scientific and technological obstacles that should be overcome are still important. Among the scientific challenges of computerizing information on plants, we could point out the taxonomic and nomenclatural ones (Jansen & Dengler, 2010), which can be partially solved by using nomenclatural web services like that suggested by the EuroSL project (Dengler *et al.*, 2012).

A standard exchange for plot-based vegetation data (Veg-X) that allows for observations of vegetation at both individual and aggregated observation levels, and makes them available to the entire ecological community has been created (Wiser *et al.*, 2011). The access to large biodiversity data banks is leading to the emergence of new research lines on this topic, and to methodological possibilities unthinkable until now (Ozinga *et al.*, 2005; Bekker *et al.*, 2007).

SIVIM project

SIVIM was born in the frame of a nationally funded research project of the Global Change, Earth Sciences and Biodiversity Program (CGL2006-13421-C04) with the involvement of several Spanish universities (University of Barcelona, University of the Basque Country, University of Castilla-La Mancha and University of León). The project was refunded in 2010 for the next 3 years (CGL2009-13317-C03). The direct precursor of SIVIM was the BDBC project (Biodiversity Database of Catalonia, <http://biodiver.bio.ub.es/biocat/>), funded by the Generalitat (regional government) of Catalonia, which begun 17 years ago and currently hosts 21,765 relevés from Catalonia and neighboring areas (Font & Ninot, 1995). Secondly, SIVIM also includes data from the BIOVEG project (Vegetation-Plot Database of the University of Basque Country, <http://www.givd.info/>) which hosts 20,172 relevés (Biurrun *et al.*, 2012). Most of the characteristics applied in SIVIM are based on those already implemented and tested in the BDBC. SIVIM is con-

ceived as a vegetation information system designed for capturing, hosting, editing, analyzing and outputting georeferenced vegetation data. It was created with the aim of being a helpful tool, both in scientific research and in assessment of decision making on land planning and management. Since SIVIM has been developed to record phytosociological relevés, these data (the coverage of all species present in a relevé, regardless of their frequency and taxonomic status) are an important complement to the distributional data from herbarium collections and the floristic literature, both of which are preferentially focused on relatively uncommon species and taxonomically difficult groups and lack the information about species co-occurrence. In this context, it is remarkable that SIVIM holds the largest number of floristic data records in the national information system on phytodiversity. SIVIM currently stores almost 130,066 phytosociological relevés derived from 1,570 bibliographic references, mainly from the Iberian Peninsula and the Canary Islands. According to the *Global Index of Vegetation-Plot Databases* (GIVD), and taking into account the number of computerized relevés, SIVIM is the fourth largest database in the world. These relevés contain 2,141,254 floristic records (16.5 species per relevé in average), summing altogether 6,637 species. The individual floristic records contained in SIVIM are now available for consultation also in the national (<http://www.gbif.es>) and international (<http://www.gbif.org>) GBIF nodes.

SIVIM uses a taxonomic thesaurus following the proposals of the Anthos project (<http://www.anthos.es>) of the Royal Botanical Garden of Madrid for the Iberian flora, complemented by other floristic repertoires from northwest Africa and the Macaronesian archipelagos and the periodic updating derived from the project *Flora iberica*. With regards to syntaxonomical nomenclature, SIVIM follows the checklist of Rivas-Martínez *et al.* (2001, 2002, 2011), but the database structure includes separated fields for the original name (verbatim, unchangeable) and for the corrected or updated name of each relevé. The syntaxonomical thesaurus solves synonymies and allows users to address queries at different levels of the hierarchical classification of vegetation.

Website

The SIVIM website (<http://www.sivim.info>, Fig. 1) was presented at the XXI Conference of the Spanish Phytosociological Association in Madrid more than five years ago. In contrast to other vegetation databases, SIVIM offers free online access to relevés, tables, and floristic observations by versatile queries. Currently, the SIVIM portal allows the following query options: relevés of a specific syntaxon, distribution area (map) of a selected syntaxon, syntaxa or relevés in one



Fig. 1 - The SIVIM Homepage.

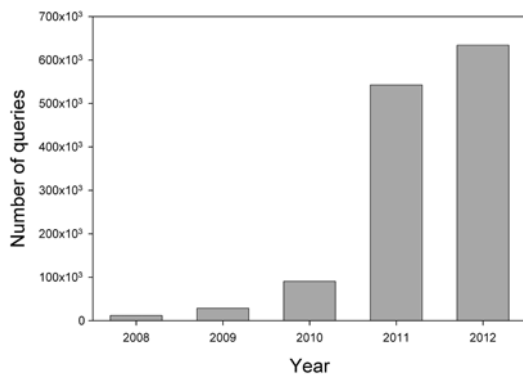


Fig. 2 - Number of queries to the SIVIM website through time (2008-2012).

or more (up to 6) selected UTM 10x10 km grid cells, syntaxa or relevés present in one or more selected localities, syntaxa or relevés including one or more selected species, taxa (and their frequencies) present in a selected syntaxon, and literature references containing relevés of a selected syntaxon. Data of both relevés and tables are downloaded in B-VegAna XML format. In general, scientists and conservation managers agree that all information on biodiversity should be public and easily available as a way to improve knowledge and prevent and halt impacts on and losses of biodiversity. The only limitation concerns the public accessibility to data containing accurate locations of threatened or protected species. These data in particular should not be finer than 10x10 or 1x1 km grid cell to avoid undesirable risks. Accurate locations of these species should only be facilitated upon request and previous justification of their use for research or conservation purposes.

Web statistics of SIVIM usage

The number of queries to the SIVIM web portal has been rising since the very beginning of the project (Fig. 2), when the website was opened. During the year 2011 the increase in the number of queries was extremely high, achieving more than 500,000 queries, a rate maintained during 2012. This increase is mostly due to GoogleBot, the Google's tracker robot, which has queried all the options of the website several times, and has indexed all the SIVIM database contents. Almost a 70% of the current queries follow this path. Thanks to all this, the contents of SIVIM are also directly accessible using the Google searcher.

If we look to the origin of the queries, most of them come from Spain and are focused in academic institutions and research centers.

Relevés survey through time

Although the SIGMA trip in Catalonia promoted by

J. Braun-Blanquet and P. Font-Quer during the year 1934 is usually considered the beginning of the phytosociology in the Iberian Peninsula, the relevés obtained from this famous expedition, which were published one year later (Braun-Blanquet *et al.*, 1935) were not the first relevés sampled at the Iberian Peninsula. This merit goes to the Scandinavian botanist J. Frodin (1926) who published 55 relevés of the central Pyrenees, using a similar recording method to the current phytosociological approach. Nearly ninety years have passed since these first surveys, and we estimate that about 175,000 relevés have been surveyed in the territory in this period (Font *et al.*, 2009, 2010). However, the surveying intensity has not been the same across time (Fig. 3), and the following four periods can be distinguished:

1926-1947 - Besides the mentioned precedents and the works carried out by Susplugas in Vallespir (Catalonia), there are few works to be highlighted for this initial period, which comprises more than 20 years. Furthermore, these works are scarce (a total of 19), and contribute few data (500 relevés).

1948-1980 - In 1948 Braun-Blanquet published his monograph dealing with Alpine vegetation of the Pyrenees (Braun-Blanquet, 1948) and from then on new phytosociological data were annually published at increasingly higher rates. In this period numerous local researchers, some of them already deceased like O. de Bolòs and S. Rivas Goday, constantly contributed with new relevés. Besides the aforementioned researchers, we should stand out S. Rivas-Martínez, J. Vigo and G. Lapraz, who published a substantial number of relevés. During this 33-year period, 343 works storing 25,000 relevés were published. Thus, during this period there was a constant gain of researchers and, consequently, of published relevés.

1981-2004 - During this 24-year period, the phytosociology experienced an authentic boom, thanks to hundreds of committed researchers who published 1,038

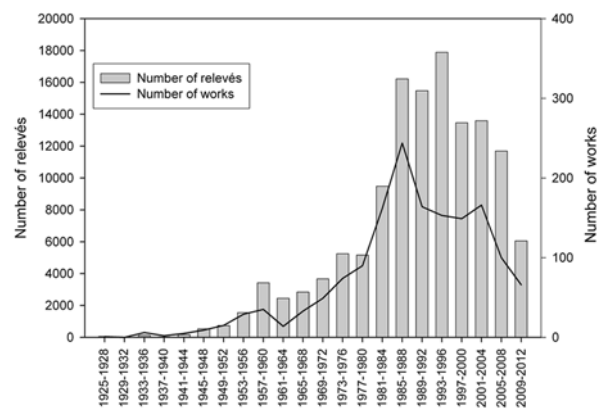


Fig. 3. Number of relevés surveyed through 4-year periods, and number of works from which these relevés come from.

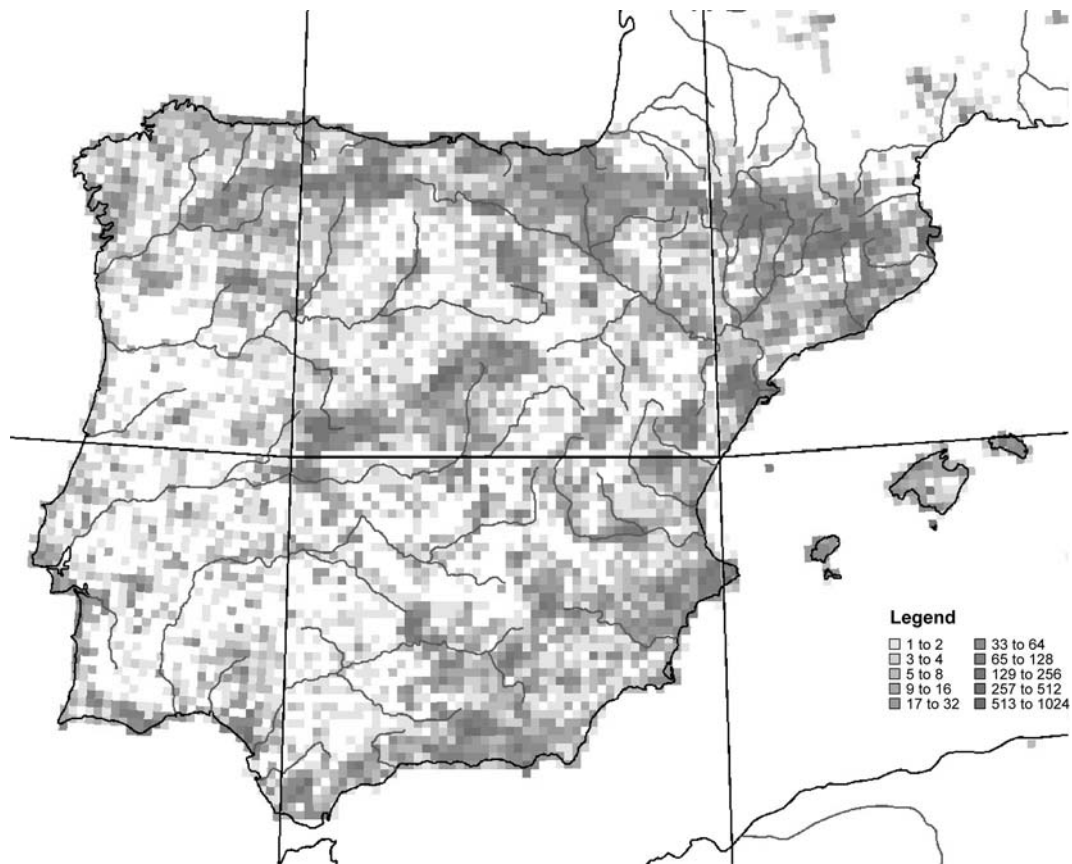


Fig. 4. Geographic distribution of the relevés computerized in SIVIM.

works (more than 43 publications per year in average) hosting more than 86,000 relevés. Throughout this period this botanical discipline was taught in almost every University in Spain, and numerous PhDs were disserted. Among them, the study performed by Sardiñero (2004), storing 1,554 relevés, holds the record of published relevés within one work.

2005-2012 - Lately, the number of publications has gradually been decelerating (20 works per year in average) due to the ageing of the researchers interested on vegetation survey (in some cases due to their retirement), to the extinction of their chairs due to the current economical crisis and also to some kind of competitiveness penalty to researchers devoted to descriptive studies on vegetation. Moreover, we should not forget the effect that changes in educational plans have had on this discipline, causing in many cases the disappearance of lectures related to phytosociology and vegetation science (Jansen & Dengler, 2010). Thus, the number of PhDs dealing with this discipline has decreased abruptly in the last years. This is the reason why we expect that the current deceleration in the volume of works will continue until reaching the levels registered during the 60s.

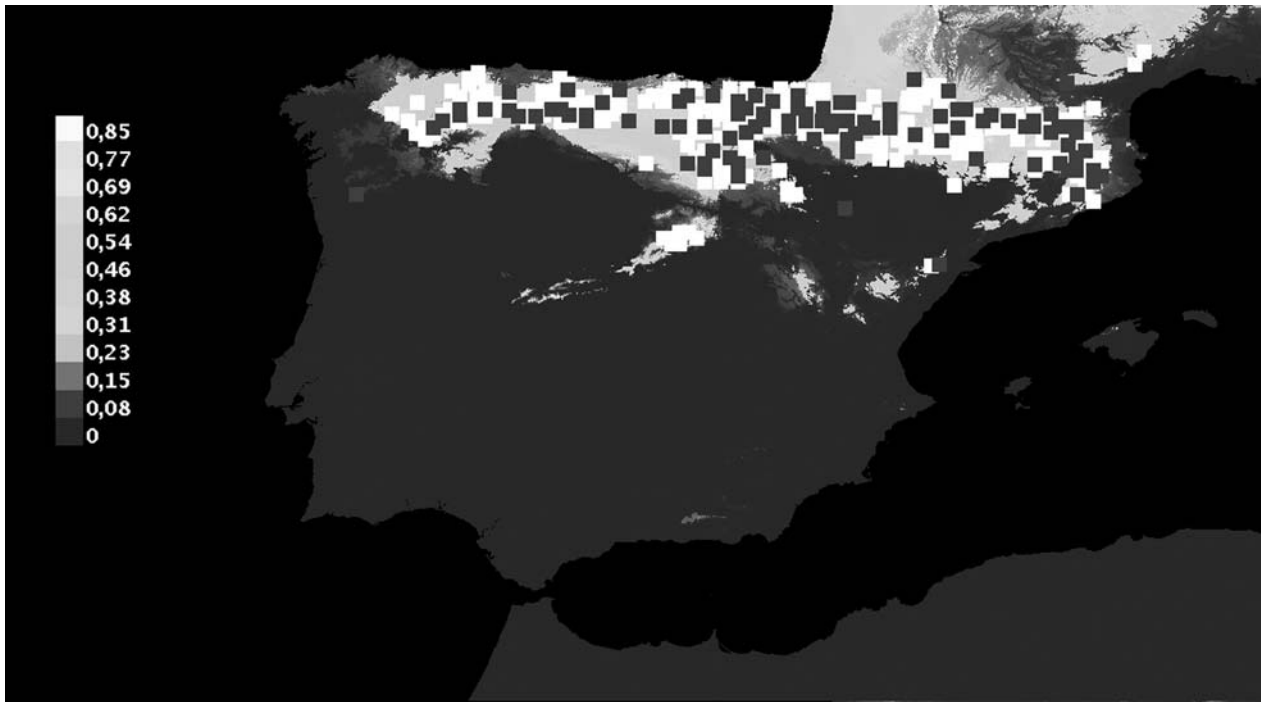
Relevés survey through the space

The 130,066 relevés contained in SIVIM are not evenly distributed through the territory, being mountain areas clearly better surveyed (Fig. 4). Among the computerized relevés accessible at the SIVIM website, 108,694 were carried out in the Spanish peninsular territory (21,765 in Catalonia; 20,172 in Basque Country and bordering territories), 2,774 correspond to relevés performed in the Macaronesian archipelagos, 1,917 to the Balearic Islands, 7,550 come from continental Portugal, 4,776 from Southern France, and 35 from Northern Africa. The remaining 4,325 relevés are not properly georeferenced. However, there are still nearly 1,500 UTM quadrats (10 x 10 km grid size) where no phytosociological relevés have been surveyed up to date, while on the other hand the UTM quadrat 31TBH52, in the Pyrenean Ordesa valley, where 893 relevés have been performed, holds the record of phytosociological surveys.

News of 2012

Plenty of innovations have been programmed during

a)



b)

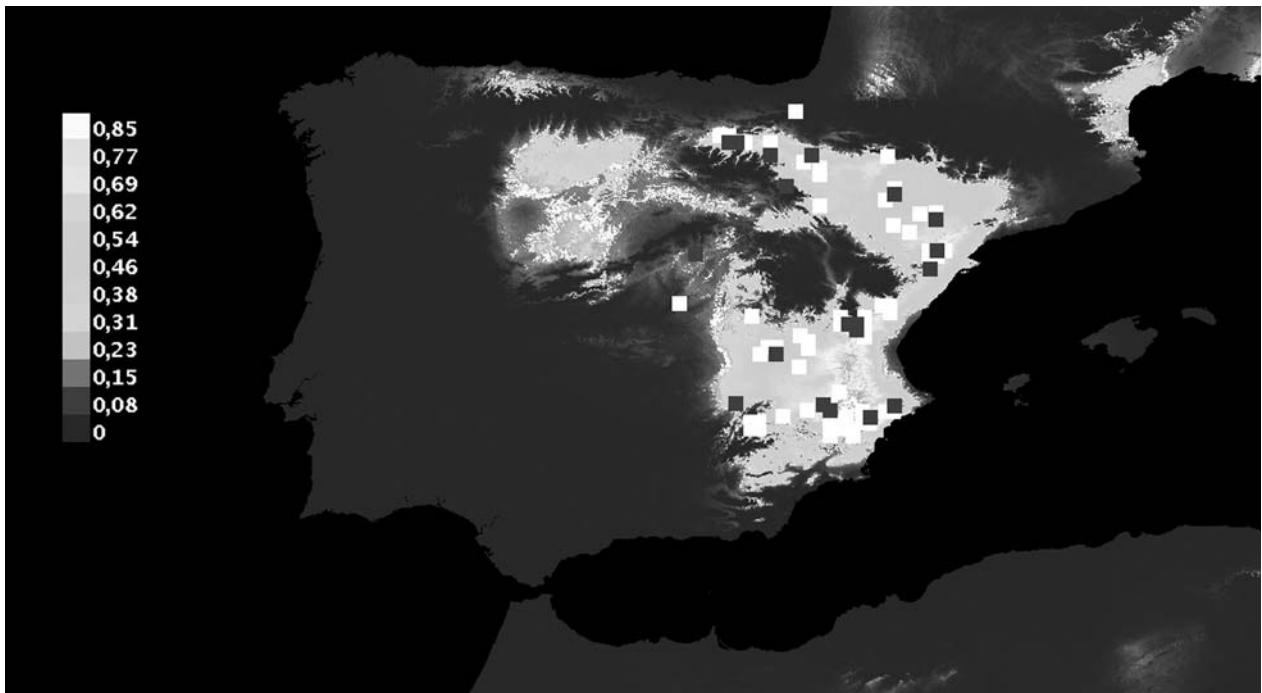


Fig. 5 - Generated maps based on the maximum entropy algorithm: a) potential distribution of *Fagus sylvatica*; b) potential distribution of *Rhamno lycioidis-Quercetum cocciferae* Br.-Bl. et O. Bolòs 1958.

the year 2012 in order to improve the SIVIM website. Among the analysis capabilities developed this year, we should highlight the implementation of a potential distribution modeling tool for taxa and syntaxa stored on the database, which is based on the maximum entropy (MaxEnt) algorithm (Phillips *et al.*, 2006). Figure 5 shows two examples of the generated maps. This

tool also provides the resulting ROC curves, which evaluate the model performance. Additionally, nowadays it is possible to calculate the fidelity values for both species and syntaxa online. This allows users to find out the fidelity of a particular taxon to the associations in the database, as well as the opposite option (i.e. to select a particular association and see which are

its faithful species). Moreover, it is worth to mention the recent integration of SIVIM in mobile devices, smartphones, and tablets, with an Android operating system. The new app ZamiaDroid (<http://biodiver.bio.ub.es/zamiaDroid>) lets the user enter georeferenced data at the field (floristic observations, and relevés), and address data query to the SIVIM is also possible. Finally, a new system has been implemented by which users can easily report errors detected in the data: nomenclatural adjustments, syntaxonomical ascriptions, georeferencing, discrepancies with respect to original sources, and so on.

Conclusions and future issues

SIVIM is conceived to offer free online access to vegetation relevés from the Iberian Peninsula, the Balearic and Macaronesian archipelagos, and the bordering territories. It includes some basic tools for data analysis among which are worth to mention the taxa and syntaxa's potential distribution mapping and the quantitative estimation of fidelity (Phi and Ochiai) of taxa to plant communities. These characteristics, together with the large amount of compiled relevés, make this Project unique among the currently available vegetation databases. The SIVIM Project represents a small contribution to the task of opening up and spreading basic biodiversity data for their extensive use in research and applied issues.

Moreover, several improvements are ongoing. Regarding the data, we are working on data quality control and we are collecting more data from Portugal and the South of France, areas from where the number of available sources at our web portal is still small. The quality control will require an additional reviewing effort and an update of the taxonomic and syntaxonomic files (thesaurus) for which new regional experts' contributions will be needed. The application of automatic filters to detect probabilistic models-based errors would be helpful. Regarding the improvement of the analysis tools, all of them based on software enhancement, we should point out the possibility of using climate change models (ECHAM5, Roeckner *et al.*, 2003) in order to project the taxa and syntaxa's potential distribution for the future (years 2020, 2050, and 2080); and a web service for automatic determination of vegetation relevés as well. Araucaria (De Cáceres *et al.*, 2009), an early experimental version of this web service, is already implemented in the BDBC. We are currently working on a second version based on probabilities, which will be gradually implemented in SIVIM over the next three years. We also consider very important to encourage the participation of users, so we have developed an application to report errors and we are working on a new application to share images of plants and their communities at SIVIM.

Finally, the linkage to other national or local databases, in a similar way to EVA (European Vegetation Archive) or others initiatives, is a key task for the immediate future.

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