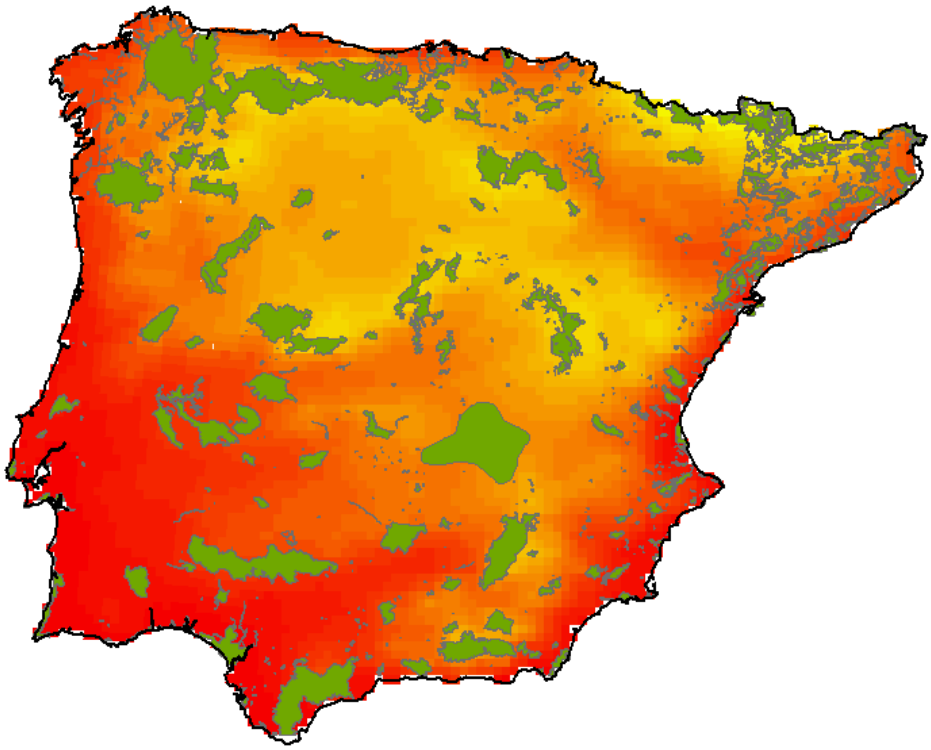
Global change impacts and conservation priorities in the Iberian Peninsula

María Triviño De la Cal



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CERTIFICAN:

Que los trabajos de investigación desarrollados en la memoria de tesis doctoral: **"Global change impacts and conservation priorities in the Iberian Peninsula"**, son aptos para ser presentados por la Lda. María Triviño De la Cal ante el Tribunal que en su día consigne, para aspirar al Grado de Doctor en Ciencias Ambientales por la Universidad Rey Juan Carlos de Madrid.

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A mis padres Carlos y Marisa

A mi hermana Cristina

Créditos

Fotografías de Mikel Sastre Morro:

Portada: petirrojo (*Erithacus rubecula*), carbonero común (*Parus major*), tarabilla norteña en vuelo (*Saxicola rubetra*), jilguero (*Carduelis carduelis*), curruca capirotada (*Sylvia atricapilla*) y verdecillo (*Serinus serinus*).

Fotografía fragmentación capítulo I: Ellen Damschen & Forest Service (http://news.wustl.edu/news/Pages/13040.aspx)

Ellen Damschen y John Orrock están estudiando la eficacia de los corredores en un experimento a largo plazo en Savannah River en Carolina del Sur.

Ilustraciones de Marga del Dedo Garcimartín

Agradecimientos: Pico mediano *(Dendrocopos medius)*

Capítulo III*:* Reyezuelo sencillo *(Regulus regulus)*

Capítulo IV: Zarcero pálido oriental *(Hippolais pallida)*

Ilustración Resumen: Ilusión óptica aves o mujer

Ilustación que puede representar tanto el rostro de una mujer como unas aves llegando al nido, por lo tanto intenta ser una metáfora de la modelización del medio ambiente y sus distintas interpretaciones.

http://www.taringa.net/posts/imagenes/9654412/Ilusiones-opticas_Juega-con-tu-mente_.html

RESUMEN

Ilusión óptica Aves o Mujer

Antecedentes

Esta tesis se encuadra en el estudio de los efectos del cambio global sobre la biodiversidad de los ecosistemas ibéricos y en el desarrollo de medidas de conservación que los tengan en cuenta.

EFECTOS DEL CAMBIO GLOBAL SOBRE LA BIODIVERSIDAD

¿Por qué se debe conservar la biodiversidad?

La biodiversidad o diversidad biológica es una medida de la amplia variedad de seres vivos que habitan la Tierra y los patrones naturales que la conforman. El término biodiversidad abarca todos los niveles de la vida, desde información genética a comunidades, incluyendo su composición, estructura y función (McNeely et al. 1990; Salwasser 1990). Además esta información puede encontrarse a muy diversas escalas espaciales o temporales (Noss 1990). Los estudios indican que durante las últimas décadas la biodiversidad está descendiendo de manera alarmante (ej., Pimm & Raven 2000) y se considera que estamos viviendo la llamada "sexta gran extinción" (Barnosky et al. 2011). Como respuesta a la pérdida de la biodiversidad surgió una nueva disciplina científica, llamada biología de la conservación, que se consolidó en la década de 1980 y que integra contribuciones de disciplinas tan diferentes como la ecología, la biogeografía, la genética, la sociología, la paleo-biología o las ciencias políticas. El principal objetivo de la biología de la conservación es estudiar las causas de la pérdida de la biodiversidad y plantear medidas para minimizarla (ej., Simberloff 1988).

¿Cuáles son las causas de la actual alta y rápida tasa de pérdida de biodiversidad?

Existen un gran número de amenazas que afectan a la biodiversidad, entre las más importantes se pueden citar: la pérdida de hábitat, las especies invasoras, la aparición de nuevas enfermedades, la sobrexplotación de especies, la contaminación, la expansión e intensificación agrícola o las catástrofes naturales como sequías o huracanes favorecidas por el cambio climático (Chapin et al. 2000; Foley et al. 2011; Wilson 1989). Se ha de poner especial atención a las interacciones entre estas amenazas ya que, el efecto sinérgico entre ellas suele ser mucho mayor que el efecto individual (Brook et al. 2008). Por tanto la conservación de la biodiversidad es dinámica y compleja y presenta grandes retos que deberán ser abordados durante este siglo.

Un nuevo reto para la conservación de la biodiversidad: el cambio global

El cambio global es una combinación de rápidos cambios ambientales a escala global que implican una gran amenaza tanto para los sistemas ecológicos como para la sociedad humana. Conseguir entender y predecir los impactos que los diferentes componentes del cambio global, como el cambio climático o los cambios de usos del suelo, tienen sobre las comunidades ecológicas supone en la actualidad uno de los mayores retos para la biología de la conservación.

El cambio climático es, probablemente, el componente del cambio global que ha recibido mayor atención científica, mediática y política. El incremento en las temperaturas medias de la atmósfera y de los océanos, la subida del nivel mar y el cambio de los patrones y de la frecuencia de los fenómenos meteorológicos extremos demuestran que el cambio climático es una realidad (IPCC 2007; Oreskes 2004) que se ha convertido una de las mayores amenazas para la biodiversidad . (Millennium Ecosystem Assessment 2005; Lovejoy 2006; Pressey et al. 2007). También resulta de especial importancia el estudio de los llamados 'puntos de inflexión' o 'tipping points'. Cuando se supera un cierto umbral de cambio en los ecosistemas los cambios producidos pueden resultar irreversibles. Por lo tanto, un pequeño cambio adicional puede provocar una respuesta desproporcionada en el sistema (Leadley et al, 2010).

¿Por qué debemos preocuparnos si ya hubo cambios climáticos en el pasado?

Hasta hace poco se pensaba que los cambios climáticos durante y después del Pleistoceno habían sido graduales, mientras que el calentamiento durante el siglo XX y principios del siglo XXI se estaba produciendo a unas tasas de velocidad sin precedentes (IPCC 2007). Sin embargo, nuevos estudios geofísicos sugieren que los cambios climáticos durante el Pleistoceno Tardío fueron abruptos, a unas altas tasas de velocidad y durante un corto período de tiempo (Steffensen et al. 2008). Así que, aunque se hayan producido cambios climáticos en el pasado de igual magnitud y velocidad que los actuales, lo que debe preocuparnos en la actualidad es la combinación de estos cambios climáticos con un gran número de nuevas amenazas, en especial con la destrucción y fragmentación del hábitat (ej., Hof et al. 2011; Travis 2003). En un paisaje fragmentado las especies van a ver limitada su capacidad de dispersión a zonas ambientalmente más adecuadas. Además, una estructura espacial consistente en parches de hábitats pequeños y fragmentados reduce la diversidad ambiental disponible, una cualidad necesaria para que las especies puedan persistir ante cambios ambientales globales (Figura 1), y sustenta poblaciones de menor tamaño que tendrán menor variabilidad genética y fenotípica (Jump & Peñuelas 2005), un prerrequisito para que puedan tener lugar rápidas respuestas adaptativas. Finalmente, la destrucción y fragmentación del hábitat reduce el número de potenciales refugios micro-climáticos comprometiendo, aún más, las posibilidades de supervivencia de las especies (ej., Araújo, 2009).

¿Cómo responde la biodiversidad ante el cambio global?

Existe un gran número de evidencias que demuestran que los ecosistemas ya están respondiendo al cambio global. Por ejemplo, se están produciendo cambios en la biología y distribución de un gran número de plantas y animales, tanto terrestres como acuáticos (ej., Chen

et al. 2011). Se han observado i) *cambios espaciales* (cambios en la distribución del rango) que son aquellos que más comúnmente se miden, ii) *cambios temporales* (fenológicos) y iii) *a nivel individual* (cambios fisiológicos, de comportamiento, micro-evolutivos) (IPCC 2007; Parmesan 2006). Muchos de estos cambios son rápidos, y a menudo, aumentan el riesgo de extinción local de las especies nativas, ya favorecen la introducción de especies invasoras y de nuevos agentes patógenos.

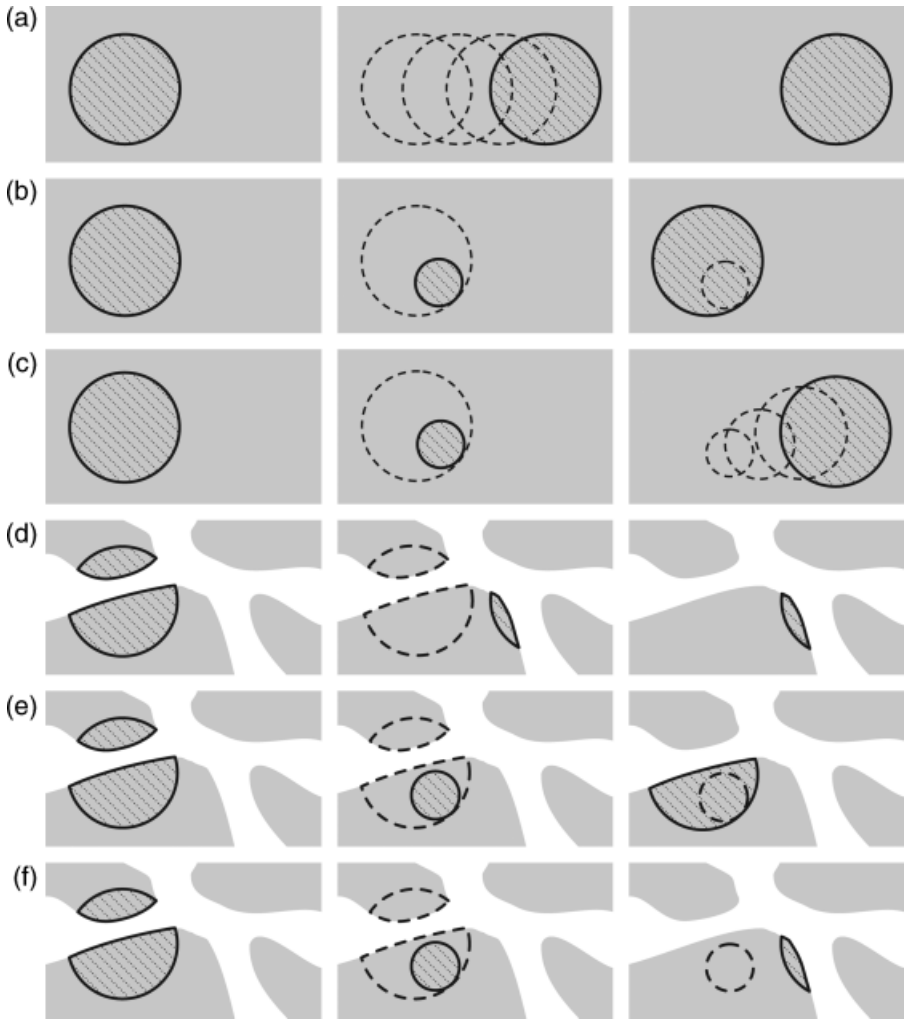

Figura 1 (Hof et al, 2011) ||La influencia de la fragmentación del hábitat sobre la capacidad de las especies de seguir el cambio climático mediante dispersión. Las áreas grises son hábitat adecuado para la presencia de especies, los círculos representan la distribución de especies y los círculos de línea discontinua su distribución pasada. (a)–(c) representan un mundo antes del impacto del ser humano con un hábitat continuo y (d)–(f) un mundo donde los hábitats han sido modificados por el ser humano. En (a) los cambios climáticos son graduales, en (b), los cambios son extremadamente rápidos y las especies deben sobrevivir en pequeñas áreas y expandirse cuando las condiciones vuelven a ser adecuadas y c) las especies también persisten en pequeñas áreas pero esta vez siguen las condiciones ambientales gradualmente. En un mundo fragmentado (d)–(f), el área disponible como refugio ante condiciones ambientales adversas es menor, lo cuál reduce las posibilidades de persistencia.

Se han documentado cuatro posibles respuestas de las especies ante cambios ambientales drásticos en el pasado: a) tolerancia, b) desplazamiento, c) migración o d) extinción. *Tolerancia*: las poblaciones de un gran número de especies han persistido en el mismo sitio desde el último máximo glacial (hace unos 21.000 años). *Desplazamiento*: muchas otras especies han desplazado sus hábitats, moviéndose distancias cortas (entre 1 y 10 km), hacia sitios con elevaciones, pendientes u otras características que permitían condiciones ambientales adecuadas para la supervivencia. *Migración*: se han documentado migraciones de entre 100 y 1000 km para muchas otras especies. Algunas especies se han extinguido como consecuencia de cambios ambientales drásticos (e.j., *Megaloceros giganteus*), mientras que otras han sufrido una pérdida de su diversidad genética, asociada a episodios de cuasi-extinción, o cuellos de botella (ej., *Picea martinezii*). Las respuestas de las especies a menudo son una combinación de estas cuatro posibilidades. Por ejemplo, algunas poblaciones de *Alces alces* han persistido en algunos lugares (tolerancia), otras se han desplazado a otras regiones (desplazamientos y migraciones), y la especie también ha sufrido severas pérdidas de información genética (Dawson et al. 2011 y referencias ahí incluidas).

Para concluir, es importante mencionar que las especies han respondido de forma individual ante los cambios ambientales en el pasado, por lo tanto, las comunidades biológicas no responden o se mueven como una única unidad. Cada especie se mueve a una tasa de velocidad diferente y, a veces, en direcciones diferentes, y en consecuencia los ecosistemas cambian y surgen otros nuevos (Lovejoy, 2006).

LA PENÍNSULA IBÉRICA: IMPORTANCIA Y AMENAZAS

La importancia de la Península Ibérica para la conservación

El área de estudio de esta tesis abarca el territorio peninsular de España y Portugal. En la mayoría de las ocasiones las fronteras políticas carecen de significado ecológico y por tanto las políticas de conservación necesarias para asegurar la persistencia de las especies deben ser aplicadas a una escala ecológica apropiada, como es el caso de la Península Ibérica. El territorio peninsular incluye una amplia variedad de biomas, relieves, condiciones climáticas y tipos de suelos, la altitud varía desde el nivel del mar hasta los 3.483 metros. Los paisajes son muy variados, desde zonas desérticas hasta áreas de alta productividad vegetal. La Península Ibérica presenta una enorme diversidad de tipos de vegetación, desde bosques caducifolios o de coníferas, zonas de matorral mediterráneo a zonas ocupadas mayoritariamente por plantas anuales (Benayas et al. 2002; Cowling et al. 1996).

La Península Ibérica forma parte de una de las regiones de mayor biodiversidad del planeta: la región Mediterránea (Myers et al. 2000). Además alberga la mitad de la biodiversidad europea y un gran porcentaje de sus especies endémicas (Williams et al. 2000). Esta alta biodiversidad se debe en parte a su gran heterogeneidad ambiental y en parte a la estabilidad climática de la que ha gozado durante los últimos miles de años y que permitió que sirviera como refugio de la biodiversidad durante las glaciaciones del Cuaternario (Hewitt 2000).

Amenazas para la conservación en el Mediterráneo y en la Península Ibérica

A pesar de la importancia de la región Mediterránea para la conservación, sus ecosistemas han sido modificados por el ser humando durante milenios y están expuestos a múltiples amenazas que han ido en aumento desde 1990 (Vogiatzakis et al. 2006). Los efectos sinérgicos entre estas amenazas, como por ejemplo la combinación de la expansión urbanística, la introducción de nuevas especies invasoras y el aumento de la frecuencia de fuegos, pueden tener efectos devastadores (Underwood et al. 2009). Por ello se espera que los ecosistemas mediterráneos, debido a su alta susceptibilidad ante cambios climáticos y de usos de suelo, sean los que sufran mayores cambios de biodiversidad bajo posibles escenarios futuros para el 2100 (Sala et al. 2000).

¿Son eficaces las actuales medidas de conservación?

Se espera que la red de áreas protegidas sea menos eficaz en el futuro ya que solamente en torno a la mitad de las áreas protegidas en la región Mediterránea conservará un clima similar al actual a finales del siglo XXI. Además, de las áreas protegidas que se espera que mantengan las mismas condiciones climáticas, un tercio han sido ya profundamente modificadas, eliminando o limitando su potencial de servir como refugios en el futuro (Klausmeyer & Shaw 2009). Por lo tanto, se necesitan medidas de mitigación y adaptación al cambio global que permitan hacer frente a este tipo de problemas.

AVES COMO OBJETO DE ESTUDIO

En tres capítulos de esta tesis se han utilizado las aves como objeto de estudio. Las aves son fáciles de observar y relativamente fáciles de reconocer. Además, su presencia y hábitos despiertan el interés de miles de apasionados ornitólogos y aficionados a la observación de aves. El apoyo para la conservación de las aves suele ser mayor que para otro tipo de taxones debido a su atractivo para el gran público y su potencial para que las actividades con aves puedan convertirse en una fuente de ingresos (Verissimo et al. 2009).

Muchas estrategias de conservación están enfocadas en la conservación de aves. Por ejemplo, Birdlife International y sus socios colaboradores han identificado cerca de 11.000 áreas importantes para las aves o Importante Bird Areas (IBAs) (Birdlife International 2010) y en el contexto europeo, la Directiva Aves se ha centrado en establecer una red de áreas de especial protección para las aves (European Commission 2009). A pesar de que varios estudios han demostrado que las aves son un pobre sustituto de la biodiversidad (Lund & Rahbek, 2002; Moore et al. 2003; Williams et al. 2006).

Por lo tanto, no es sorprendente que los cambios de abundancia y comportamiento de las aves, aparentemente, como consecuencia del cambio global sean de los mejor documentados en el mundo animal. Asimismo, nuestro conocimiento acerca de la biología de las aves está mejor documentada que en cualquier otro tipo de taxón. Estas han sido las principales circunstancias que han nos motivado a utilizar a las aves como objeto de estudio.

ESTRATEGIAS DE CONSERVACIÓN BAJO ESCENARIOS DE CAMBIO GLOBAL

¿Qué medidas se adoptan para la conservación de la biodiversidad?

La conservación de la biodiversidad es un problema global que normalmente se afronta con estrategias regionales a corto plazo ya que las políticas de conservación se aplican a nivel nacional o regional. Las estrategias de conservación pueden llevarse a cabo a través de dos modalidades: *in situ*, como por ejemplo el establecimiento de áreas protegidas, y *ex situ*, como los bancos de germoplasma. Estas dos modalidades son complementarias y permiten garantizar la conservación de las especies y su patrimonio genético (CBD 1992). La sub-disciplina científica denominada "planificación sistemática de la conservación" surgió para mejorar la localización, configuración, implementación y gestión de las áreas que han sido designadas para asegurar la persistencia de la biodiversidad y otros valores naturales (Margules & Pressey, 2000). Desde sus orígenes, a comienzos de la década de 1980, la "planificación sistemática de la conservación" ha propuesto novedosos métodos cuantitativos y ha influido tanto a las Organizaciones No Gubernamentales internacionales como a políticos y gestores de la conservación. Sin embargo, la planificación de la conservación para ser efectiva debe tener en cuenta dos factores. En primer lugar, la biodiversidad no es estática, ni temporal ni espacialmente, sino que está mantenida y generada por procesos naturales dinámicos. En segundo lugar, el ser humano está modificando el planeta cada vez más rápidamente (Pressey et al. 2007). Por estas dos razones, las medidas de conservación se deberían centrar, no solo en los patrones de biodiversidad, sino en los procesos ecológicos ya que, por ejemplo, ecosistemas pobres en especies pueden ser cruciales para el funcionamiento de ciclos de materiales y flujos de energía (Gillson et al. 2011).

¿Qué estrategias de conservación se han propuesto ante el reto del cambio global?

Se han propuesto diversas actuaciones para la mitigación y adaptación al cambio global. Entre las medidas propuestas se incluyen: la expansión del área de la red de áreas protegidas, el aumento de la heterogeneidad ambiental dentro de las áreas protegidas o una gestión más sostenible de las áreas no protegidas (ej., Heller & Zavaleta 2009). También es necesario la identificación y gestión tanto de refugios estacionarios (lugares en los cuáles las especies tienen más posibilidades de sobrevivir a pesar del cambio climático) como de refugios desplazados (lugares en los cuáles las especies tienen posibilidades de encontrar condiciones adecuadas después de haber sido desplazadas por el cambio climático) (Araújo 2009). En particular, se intentan implementar aquellas actuaciones con efectos positivos en todos los ámbitos, como por ejemplo, promocionar el comercio de carbono para preservar los bosques tropicales maduros y evitar su deforestación (Paterson et al. 2008). De entre todas las recomendaciones para la gestión de la biodiversidad bajo escenarios de cambio climático en esta tesis nos hemos centrado en el desarrollo de dos estrategias que son las que más atención han recibido en la literatura científica: a) favorecer la conectividad (desarrollado en el capítulo **I** de la tesis) y b) gestión de áreas protegidas/zonas prioritarias de conservación teniendo en cuenta proyecciones de cambio climático (desarrollado en el capítulo **IV** de la tesis).

Favorecer la conectividad del paisaje

En una era en la que la fragmentación y pérdida de hábitat es una de las mayores amenazas para la biodiversidad del planeta (Butchart et al. 2010; IUCN 2011) y que, además, se está viendo agravada por el cambio climático (Araújo et al. 2011a; Hannah et al. 2007), las estrategias de conservación no pueden depender únicamente de áreas protegidas aisladas que funcionen como islas para conservar y proteger la biodiversidad. Es fundamental reconocer la naturaleza dinámica de la diversidad biológica e incorporar conexiones entre las áreas protegidas que faciliten su persistencia (ej., Cabeza 2003) y garanticen la estabilidad futura de la biodiversidad biológica bajo escenarios de cambios ambientales globales (ej., Williams et al. 2005). Para minimizar estas amenazas, se debe favorecer la conectividad del paisaje mediante la identificación y protección de conexiones entre áreas con un hábitat de alto valor para la conservación (Fahrig & Merriam 1994; Hanski 1999). La conectividad facilita la dispersión y movimiento de las especies, y por tanto, evita extinciones locales (causada por la estocasticidad demográfica o ambiental) en poblaciones pequeñas debido al intercambio de individuos con otras poblaciones de mayor tamaño. Además, bajos posibles escenarios de cambio global, los corredores ecológicos facilitarán el movimiento de las especies desde sus actuales áreas de distribución hacia nuevas áreas con condiciones climáticas adecuadas en el futuro (ej., Araújo 2009).

Una red de áreas protegidas eficiente ante los cambios ambientales necesita diseñar redes de conexiones, por ejemplo, aprovechando la red de vías pecuarias, las riberas de los ríos, etc. Se debe tener en cuenta la estructura del paisaje para identificar áreas naturales o semi-naturales críticas para favorecer la conectividad antes de que están áreas se pierdan por el desarrollo urbanístico u otro tipo de modificación de usos del suelo. Existe una amplia literatura científica sobre herramientas utilizadas para favorecer la conectividad y muchos investigadores han empezado a desarrollar aproximaciones cuantitativas para la identificación de rutas de dispersión entre las áreas protegidas bajo escenarios de cambio climático (ej., Phillips et al. 2008; Vos et al. 2008; Williams et al. 2005). Sin embargo, un gran desafío todavía pendiente para la biología de la conservación y la ecología del paisaje consiste en desarrollar procedimientos automatizados para identificar conexiones eficientes para multitud de especies de interés para la conservación (Beier et al. 2011).

Áreas protegidas: ¿cómo integrar el cambio global?

El establecimiento de áreas protegidas es una parte fundamental de las estrategias de conservación a pesar de que han sido criticadas por tener una localización geográfica, diseño o gestión inadecuadas (ej., Joppa & Pfaff 2009; Mascia & Pailler 2011). A escala global, se han designado cientos de miles de áreas protegidas y cada año se sigue incrementando la cifra. Sin embargo, a pesar de su importancia, la capacidad para poder medir su eficacia a la hora de proteger la biodiversidad todavía sigue siendo un gran reto para los biólogos de la conservación (ej., Cabeza & Moilanen 2003; Joppa et al. 2008; Rodrigues et al. 2004). Entre otras razones, la falta de una información completa y coherente sobre la distribución geográfica de los organismos, sus interacciones y su papel en los procesos ecológicos, supone un obstáculo para establecer áreas protegidas fiables (ej., Lobo 2008).

En un contexto de cambio global resulta todavía más complicado evaluar la efectividad de las áreas protegidas, ya que los ecosistemas que se suponían que tienen que preservar están en continuo cambio y se espera que la red de espacios protegidos sufra grandes alteraciones tanto en su riqueza como en su composición de especies (ej., Hannah et al. 2007; Hole et al. 2009). Por tanto, las políticas de mitigación y adaptación al cambio global requieren que las actuales prácticas de manejo de las áreas protegidas sean revisadas y que se adopten mecanismos más flexibles y proactivos. Finalmente, para hacer frente a la complejidad de retos que afectan a las áreas protegidas, se recomienda estrategias de gestión adaptativa (ej., Baron et al. 2009; Lawler et al. 2009). La gestión adaptativa es un proceso de toma de decisiones con el objetivo de reducir la incertidumbre a lo largo del tiempo mediante el aprendizaje de las acciones que resulten más efectivas a través de un proceso de monitorización del área de estudio.

Objetivos y estructura de la tesis

El **objetivo general** de esta tesis doctoral es abordar algunos de los retos que plantea el incorporar los efectos del cambio global a las prioridades de conservación de la biodiversidad en la Península Ibérica. En particular, se centra en estudiar cómo favorecer la conectividad entre las áreas protegidas de la Península, en explorar las variables ambientales más importantes para proyectar las distribución de las aves en el futuro, en mejorar las evaluaciones de riesgo del cambio global sobre las aves y finalmente en estudiar prioridades de conservación para las aves, tanto para las condiciones ambientales actuales como para las condiciones proyectadas hacia el futuro.

Los **objetivos metodológicos específicos** son los siguientes:

1. Identificar las conexiones más eficientes para favorecer la conectividad entre las áreas protegidas de la Península Ibérica mediante la utilización de un algoritmo heurístico.
2. Identificar las variables ambientales más relevantes para proyectar la distribución potencial de las aves en el futuro.
3. Las evaluaciones de riesgo del cambio global sobre la biodiversidad normalmente se han centrado en el nivel de exposición a estos cambios. Nuestro objetivo es llevar a cabo una evaluación de riesgo del cambio global para las aves de la Península Ibérica combinando medidas de exposición a los cambios ambientales futuros con el grado de vulnerabilidad de cada especie a esos cambios.
4. Establecer prioridades de conservación teniendo en cuenta los efectos del cambio global (cambio climático, cambio de usos de suelo, de cobertura vegetal, etc.) sobre la biodiversidad mediante la utilización del software Zonation para la planificación espacial de la conservación.

Los **objetivos aplicados específicos** son los siguientes:

5. ¿Cuáles son los grupos de áreas protegidas en la Península Ibérica que requieren mantener un alto grado de conectividad mediante corredores ecológicos?
6. ¿Son las variables climáticas, más fácilmente accesibles, suficientemente explicativas para proyectar la distribución futura de las aves o es necesario invertir tiempo y dinero para incluir otro tipo de variables ambientales?
7. ¿Qué especies de aves son las más expuestas ante el cambio global? ¿Son las especies más expuestas las más vulnerables?

8. ¿Son las actuales redes de espacios protegidos efectivas a la hora de representar las prioridades de conservación de las aves? ¿Qué zonas de la Península Ibérica conserva un alto potencial de conservación?

Con el fin de cumplir estos objetivos, la presente memoria incluye cuatro capítulos. A continuación se expone un pequeño resumen de cada uno de los capítulos resaltando las preguntas que se plantearon y los resultados más relevantes que se obtuvieron:

- El **primer capítulo** está dedicado a promover la conectividad entre hábitats favorables para múltiples especies. Para ello se procede a la identificación de conexiones eficientes entre áreas protegidas con condiciones ambientales similares. El estudio se subdivide en distintas etapas: a) identificación de hábitats con condiciones ambientales similares (asumiendo que albergan especies con requerimientos ambientales similares), b) identificación de barreras ambientales (ej., regiones con unas condiciones ambientales muy distintas de las áreas protegidas ambientalmente similares que se pretenden conectar) y c) selección de conexiones eficientes, en términos de coste, entre las áreas protegidas ambientalmente similares y evitando las barreras. Para este estudio se desarrolla un algoritmo heurístico y se aplica un novedoso marco conceptual que demuestra ser efectivo para la identificación de conexiones entre áreas protegidas ambientalmente similares.

- El **segundo capítulo** está dedicado a investigar la importancia de variables climáticas frente a variables de vegetación y de su configuración espacial a la hora de describir y proyectar las distribuciones actuales y futuras de las aves de la Península Ibérica. Con ese fin, se utilizaron los datos de distribución de 168 especies de aves reproductoras de la Península Ibérica para ajustar modelos de distribución de especies usando cuatro conjuntos de variables ambientales: i) climáticas, ii) de vegetación, iii) de configuración espacial de la vegetación y iv) todas las variables al mismo tiempo. Concretamente, se contestaron las siguientes preguntas: a) ¿qué grupo de variables tienen un mayor poder predictivo: climáticas, de vegetación o de configuración espacial de la vegetación? este estudio demuestra que los modelos que utilizan variables climáticas generalmente tienen un mejor ajuste que los modelos que utilizan otro tipo de variables; b) ¿existe una congruencia entre las proyecciones futuras usando distintos grupos de variables ambientales? Los resultados muestran que los diferentes tipos de variables ambientes producen diferentes tipos de proyecciones futuras, sin embargo esta discrepancia se reduce cuando sólo se utilizan para las proyecciones especies para las cuáles los modelos se ajustan muy bien.

- En el **tercer capítulo** se lleva a cabo una evaluación de riesgo de los impactos del cambio global sobre las aves de la Península Ibérica teniendo en cuenta tanto el nivel de exposición al cambio como las características intrínsecas de las especies para afrontar esos cambios ambientales. Por lo tanto, se examinaron los efectos combinados de la exposición y vulnerabilidad de las aves a los cambios ambientales. La vulnerabilidad se midió teniendo en cuenta características como la fecundidad y el tamaño corporal, junto con el estado de conservación de la especies según la IUCN (International Union for Conservation of Nature). Específicamente, se intentaron contestar las siguientes preguntas: a) ¿las especies con alto grado de exposición a cambios ambientales son también vulnerables a estos cambios y están amenazadas según la IUCN? En nuestro estudio, las especies altamente expuestas al cambio global actualmente están menos amenazadas y poseen características biológicas que las hacen menos vulnerables; b) ¿las regiones con una alta concentración de especies con alto grado de exposición a cambios ambientales coinciden con las regiones dónde se concentran las especies más vulnerables y amenazadas? Las regiones con alta concentración de especies altamente expuestas al cambio global difieren de las regiones con alta concentración de especies vulnerables o amenazadas según los criterios de la IUCN.

- En el **cuarto capítulo** se identifican sitios prioritarios para la conservación de las aves de la Península Ibérica teniendo en cuenta sus distribuciones potenciales tanto en el presente como en el futuro. Además se evalúan la efectividad de las actuales redes de áreas protegidas, tanto la red nacional de espacios protegidos como la europea Red Natura 2000, para proteger los sitios identificados como prioritarios. Finalmente, se identifican aquellas regiones que tienen un alto potencial de conservación debido a todavía no están protegidas pero conservan un elevado valor ecológico porque no han sido altamente modificadas por el ser humano. Los resultados muestran una falta de efectividad de las actuales redes de espacios protegidos en representar las prioridades de conservación identificadas para las aves. Aunque los sitios prioritarios están mejor representados en la red europea Natura 2000 que en la red nacional de espacios protegidos. Además se encontró que más de la mitad de los sitios identificados como prioritarios para la conservación conservan un elevado valor ecológico y no están incluido en la red nacional de espacios protegidos por lo que tienen un gran potencial de conservación

Metodología general

Para el desarrollo de la presente tesis doctoral se han utilizado distintos tipos de metodologías. Todos los materiales y métodos están descritos de forma detallada y con sus respectivas referencias en cada uno de los capítulos. Sin embargo, a continuación se presenta un resumen de los métodos utilizados.

Datos ambientales

*Datos de áreas protegidas (Capítulos **I** y **IV**)*

Se utilizaron dos redes de espacios protegidos: la red de espacios protegidos a nivel nacional y la designada a nivel europeo, más conocida como Red Natura 2000. Los datos de ambas redes de áreas protegidas fueron obtenidos a través de los ministerios de Medio Ambiente de Portugal y España (ICNB 2011; MARM 2011). Para el capítulo **IV** se utilizaron los datos actualizados en Diciembre del 2011 ya que la creación y designación de nuevas áreas protegidas es un proceso dinámico y en continua expansión (Europarc-España 2010). Los datos geográficos de España y Portugal se unieron usando ArcGIS 10 (ESRI 2006). Las áreas protegidas designadas solamente por convenios internacionales como los sitios UNESCO (reservas UNESCO del Hombre y la Biosfera y los Humedales de Importancia Internacional (Ramsar)) fueron utilizadas en el capítulo I y el material suplementario del capítulo **IV**.

*Datos del índice del impacto humano (Capítulo **I**)*

El índice del impacto humano o "Human Footprint Index" refleja la influencia del hombre sobre el paisaje. La Sociedad para la Conservación de la Naturaleza (Wildlife Conservation Society, WCS) y el Centro para la Red de Información Internacional de Ciencias de la Tierra (Center for International Earth Science Information Network CIESIN) de la Universidad de Columbia se unieron para medir la influencia del ser humano sobre la superficie terrestre. Este índice está basado en los siguientes datos: densidad de la población, transformación del terreno (uso del suelo, ciudades y carreteras), grado de accesibilidad (líneas de costa y ríos) e infraestructura eléctrica (Sanderson et al. 2002). Los datos fueron descargados desde la página web: http://www.ciesin.columbia.edu/wild_areas/register1.html a una resolución de 1 x 1km. El índice del impacto humano tiene un rango de variación entre 0 (no existe impacto humano) y 100 (área complemente dominada por el ser humano).

*Datos de especies (Capítulos **II**, **III** y **IV**)*

Se utilizaron los datos de distribución de 168 aves reproductoras de la Península Ibérica. Los datos fueron obtenidos del Atlas de las Aves Reproductoras de España (Martí & del Moral 2003) y del Atlas de las Aves Reproductoras de Portugal (Equipa Atlas 2008) y representan los

datos de ausencia y presencia de las especies en 5923 cuadrículas UTM a una resolución de 10x10 km. Esta es la mayor resolución a la que se encuentra disponibles los datos en la Península Ibérica. Excluimos las aves acuáticas y marinas debido a que la modelización de sus hábitats hubiese requerido variables que no estaban disponibles. Además se excluyeron las especies con menos de 20 presencias para evitar los problemas derivados de modelización de especies con pequeños tamaños de muestra (Stockwell & Peterson 2002).

*Datos climáticos (Capítulo **I, II, III** y **IV**)*

Para el capítulo **I** se utilizaron datos mensuales de cuatro variables climáticas (temperatura máxima, temperatura mínima, precipitación anual y desviación estándar de la temperatura mínima) para el período 1961-1990. Estas variables fueron seleccionadas porque se consideran importantes a la hora de caracterizar la distribución de la especies a grandes escalas (Hawkins et al. 2003; Whittaker et al. 2007). Los datos climáticos a una resolución de 1x1 km fueron obtenidos a través del Instituto de Meteorología (Portugal) y de la Agencia Estatal de Meteorología (España) (para una descripción más detallada de los datos consultar Araújo et al. 2011b).

Para los capítulos **II**, **III** y **IV** se utilizaron datos climáticos, derivados de la Unidad de Investigación Climática (Climate Research Unit CRU), para el período 1971-1990 a una resolución de 10' (equivalente aproximadamente a 16km a la latitud de nuestra área de estudio). Se utilizaron datos mensuales de tres variables climáticas: temperatura media invernal, precipitación anual y los días acumulados de crecimiento. Se considerada que estas variables son ecológicamente importantes para describir los patrones de distribución de las aves (ej., Gregory et al. 2009; Huntley et al. 2008). Estas variables fueron interpoladas, utilizando el método "krigging" implantado en el software de Sistemas de Información Geográfica (SIG) ArcGIS 9.2., a una resolución de 10km para coincidir con la resolución de los datos de las especies de aves.

*Datos de vegetación y su configuración espacial (Capítulos **II** y **III**)*

Los datos de la cobertura potencial vegetal fueron simulados con el modelo dinámico de vegetación (DVM) LPJ-GUESS (Hickler et al. 2004; Smith et al. 2001). El modelo ha sido ajustado para representar las principales especies de árboles europeas y un número de grupos funcionales de plantas (Hickler et al. 2009; Hickler et al. 2012). Los datos de vegetación de las especies individuales también fueron agrupados en tres tipos de hábitats que reflejan la estructura de la vegetación: forestal, matorral y pastizal, ya que para muchas especies de aves es más importante la estructura de la vegetación que su composición (Karr & Roland 1971; Root

1988; Rotenberry & Wiens 1980). La variable cuantitativa continua que se utilizó para los análisis fue el índice de superficie de hoja (Leaf Area Index LAI), que es la relación entre el total de la superficie foliar y la superficie de terreno en la cuál crece la vegetación. Los datos de vegetación estaban a una resolución de 10' y fueron interpolados a una resolución de 10x10 km para coincidir con la resolución de los datos de las especies de aves.

La configuración espacial de la vegetación se calculó, para cada uno de los tres tipos de hábitats: forestal, matorral y pastizal, sumando el LAI de los diferentes de grupos funcionales incluidos en cada uno de los diferentes hábitats. Usando ArcGIS 9.2., se calcularon tres bandas concéntricas, cada una de 10 km de anchura, entorno a cada celda de cada tipo de hábitat. Estos datos nos dan información acerca de la configuración espacial y composición entorno a cada celda.

*Datos de tipos de usos del suelo (Capítulos **II**, **III** y **IV**)*

Los datos de tipos de usos del suelo fueron derivados de CORINE Land Cover (CLC) (European Commission 1993). Sus 44 categorías fueron agregadas en 6 tipos de usos del suelo: Urbano, Agrícola, Cultivos permanentes, Pastizales, Bosques y Otros (para una completa descripción de la metodología que se siguió ver (Dendoncker et al. 2007). El porcentaje de tipo de uso de suelo en cada cuadrícula UTM fue calculado usando la herramienta Zonal Statistics implementada en ArcGIS 9.2.

*Datos ambientales para el futuro (Capítulos **II**, **III** y **IV**)*

Utilizamos datos de escenarios climáticos dentro del programa europeo ALARM para el período 2051-2080 (Fronzek et al. 2012). Los escenarios climáticos fueron simulados con el modelo de global de circulación HadCM3, usando el escenario BAMBU (Business As Might be Usual) del proyecto ALARM (que corresponde al escenario de emisión A2). Los escenarios futuros de vegetación potencial fueron obtenidos de un estudio anterior (Hickler et al. 2012) al igual que los escenarios futuros de cambios de tipo de uso de suelo (Rounsevell et al. 2006).

*Datos de las características de las aves (Capítulo **III**)*

No todas las especies son igual de vulnerables a la extinción, y su grado de vulnerabilidad está directamente relacionado con determinadas características tanto biológicas como no biológicas. Por ello, en el capitulo **III**, se recopilaron datos de rasgos o características de aves, basados en una revisión bibliográfica, que reflejan su vulnerabilidad ante el cambio global. Las características utilizadas fueron las siguientes: *(i) Número promedio de polladas por año*. Hay cada vez mayor número de evidencias de que las aves están adelantando la fecha de puesta de

huevos y este fenómeno está asociado a la subida de la temperatura media. En muchas ocasiones, este adelanto provoca un desfase entre la puesta y los picos de abundancia de comida, lo cuál repercute negativamente en el éxito reproductor de las aves (Both et al. 2009; Dunn & Winkler 2010; Jiguet et al. 2007; Thackeray et al. 2010). Las especies con mayor número de polladas, por lo tanto, tendrán más oportunidades de sincronizar sus puestas con los picos de abundancia de comida; *(ii) Tamaño de puesta*, promedio de huevos por pollada. Esta es otra medida de la tasa de fecundidad de las aves, ya que baja fecundidad está asociada con una mayor vulnerabilidad a la extinción; (*iii) Tamaño corporal*, representado por la longitud media de las aves desde el pico hasta la cola. Grandes tamaños corporales han sido asociados con mayores tasas de extinción debido a que las especies más grandes suelen tener menores tasas reproductivas (ej., Pimm et al. 2006) y más tiempo entre generaciones (ej., Cardillo & Bromham 2001) lo que incrementa la tasa de reposición. No obstante, estudios recientes han cuestionado esta correlación entre tamaño corporal y propensión a la extinción (Amano & Yamaura 2007; Fritz et al. 2009; Pocock 2010); *(iv) Amplitud de hábitat*, como una medida del grado de especialización del hábitat utilizado. Las especies generalistas serán capaces de tolerar un mayor nivel de cambios ambientales que las especies especialistas (Foden et al. 2008). Un estudio, llevado a cabo por Julliard et al. (2004), mostró que en Francia las poblaciones de aves especialistas se estaban reduciendo a un mayor ritmo que las poblaciones de aves generalistas; *(v) Amplitud de nicho climático*, como una medida de la tolerancia ambiental. Una menor tolerancia ambiental hace que las especies sean más susceptibles a los cambios ambientales (ej., Ehrenfeld 1970; Foden et al. 2008); *(vi) Posición de nicho o marginalidad*, como medida del grado de especialización del nicho (Dolédec et al. 2000); *(vii) Tamaño relativo de rango*, calculado como la proporción entre el número total de ocurrencias y el número total de celdas del área de estudio. Se ha incluido como una medida de rareza que es uno de los mejores predictores de la propensión a la extinción (McKinney 1997 y referencias ahí incluidas).

Los datos de *(i) número promedio de polladas por año, (ii) tamaño de puesta y (iii) tamaño corporal* fueron obtenidos de la página web: http://www.enciclopediadelasaves.org. Los valores de *(iv) amplitud de hábitat* fueron recopilados del Apéndice I del Atlas de las aves reproductoras de España (Martí & del Moral 2003) y la metodología de como se calculó está descrita en Carrascal y Lobo (2003). Los valores de *(v) amplitud de nicho climático y (vi) posición de nicho o marginalidad* fueron calculados a escala europea utilizando un método de ordenación denominado 'outlying mean index' (OMI) desarrollado por Dolédec et al. (2000). OMI se utiliza para estimar el rango de las condiciones ambientales utilizadas por cada especie (amplitud de nicho) y su posición media dentro del espacio ambiental (posición de nicho). Para más detalles ver Dolédec et al. 2000 y para casos de estudio ver Hof et al. 2010 y Thuiller et al. 2004.

Modelos de distribución de especies (Capítulos *II*, *III* y *IV*)

Para anticiparse a la amenaza del cambio global y priorizar acciones de conservación, se han desarrollado varias herramientas de modelización para predecir la distribución y diversidad de especies. Una de las metodologías más utilizadas en las últimas décadas son los modelos de distribución de especies. El objetivo de estos modelos es predecir la distribución espacial más probable de una especie o comunidad biológica. Para lograrlo relacionan el suceso de ocurrencia u ocurrencia/ausencia de la especie con los valores de variables ambientales que tienen influencia en la distribución utilizando métodos estadísticos correlativos (Figura 2). Son técnicas estadísticas relativamente nuevas muy útiles en estudios de ecología, evolución, biogeografía, conservación y cambio climático (Franklin 2009; Peterson et al. 2011). Una de las aplicaciones más populares de los modelos de distribución de especies es proyectar la distribución potencial de las especies bajo condiciones de cambio climático y evaluar los impactos potenciales sobre la biodiversidad.

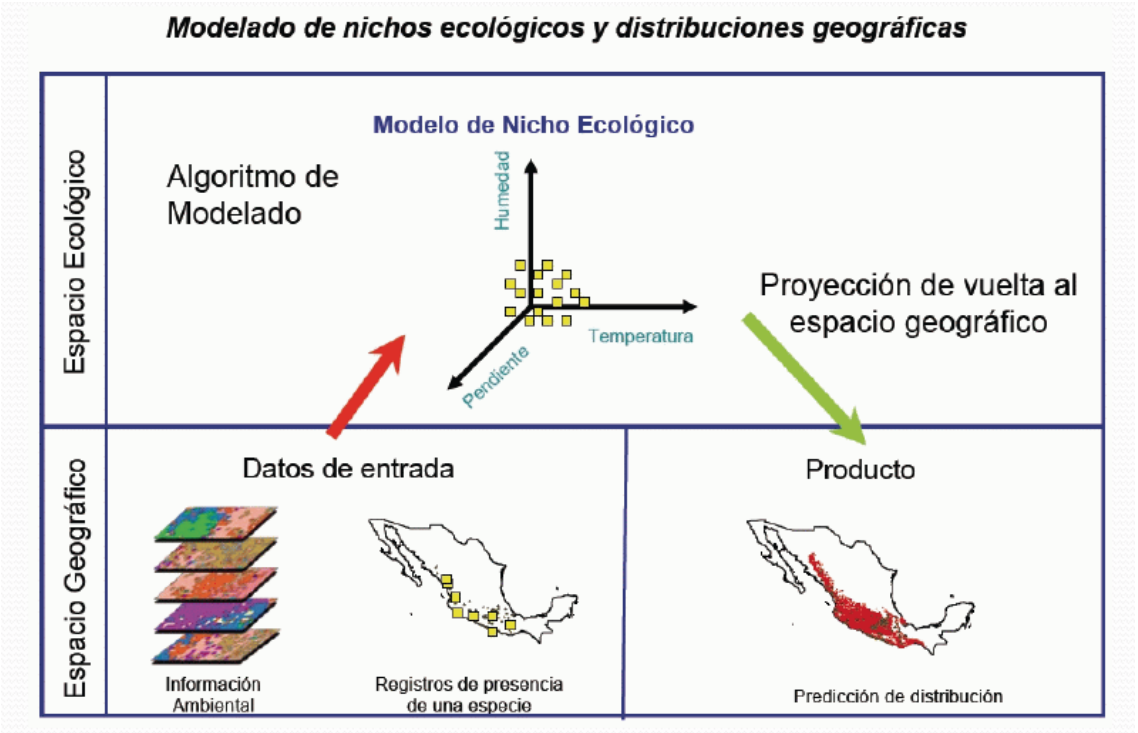

Figura 2: Adaptada por Noberto Martínez de E. Martínez-Meyer & A.T. Peterson, 2006

Los modelos usados en esta tesis fueron construidos utilizando la librería BIOMOD (Thuiller et al. 2009) en R (R Development Core Team 2009) (versión 1.15) usando los parámetros por defecto. Los dos algoritmos utilizados para modelar la distribución de las especies fueron Random Forest (RF) (Breiman 2001; Cutler et al. 2007) y Boosted Regression

Trees (BRT) (Elith et al. 2008; Friedman 2001). La base de datos completa para las 168 especies de aves reproductoras fue dividida al azar en dos subcategorías: calibración y evaluación, con 70% y 30% de los datos respectivamente, y este procedimiento se repitió cinco veces para asegurarnos de que el proceso de evaluación era independiente del procedimiento de división aleatorio. Las proyecciones futuras se hicieron asumiendo que la dispersión era ilimitada, que es un escenario más probable para especies de aves y la extensión geográfica del área de estudio que la otra alternativa posible de dispersión nula. Los modelos fueron evaluados utilizando cuatro técnicas distintas: i) *sensitivity*, que mide el porcentaje de presencias correctamente predichas, ii) *specificity*, que mide el porcentaje de ausencias correctamente predichas, iii) the area under curve (AUC) of the receiver operating characteristic (ROC) (Swets 1988) y iv) the true skill statistics (TSS) (Allouche et al. 2006).

Hay multitud de técnicas estadísticas disponibles para calibrar los modelos y se sabe que producen resultados marcadamente distintos al projectar las distribuciones futuras de las especies (Pearson et al. 2006; Thuiller et al. 2004a). Las técnicas comúnmente utilizadas para validar los modelos miden la concordancia entre la distribución potencial, resultante de los modelos, y la distribución observadas de las especies (Araújo & Guisan 2006). Sin embargo, un buen poder discriminatorio de los modelos para las condiciones actuales no garantiza que sea igual de efectivo para proyecciones futuras (e.j., Thuiller 2004), especialmente cuando se requieren predicciones fuera del rango ambiental en el cuál el modelo está basado (e.j., Araújo et al. 2005). Una metodología para reducir la incertidumbre y la variabilidad de resultados posibles es mediante el uso de un “ensemble forecasting”, que combina los resultados de los modelos mediante técnicas de consenso (Araújo & New 2007). En esta tesis, se utilizó un método de consenso basado en la media de todas las probabilidades generadas por RF y BRT y el método TSS fue elegido para convertir los valores de probabilidades en datos de ausencia-presencia (Marmion et al. 2009).

Incertidumbre y limitaciones

Los resultados obtenidos son sensibles a las limitaciones de los datos de entrada tanto de las especies como de las variables ambientales. Es frecuente que los datos de entrada de las especies tengan sesgos debido, por ejemplo, a un inadecuado esfuerzo de muestreo, identificaciones erróneas, etc. (Elith 2009; Hortal et al. 2008). Además, los catálogos de biodiversidad están sesgados porque la mayoría de las especies todavía no han sido formalmente descritas (lo que se ha denominado como ‘the Linnean Shortfall’) y la distribución geográfica de la mayoría de las especies todavía no está bien muestreada (lo que se ha denominado como ‘the Wallacean Shortfall’) (Brown & Lomolino 1998).

Existen diversas fuentes de incertidumbre que hay que tener en cuenta cuando se utilizan modelos de distribución de especies. Una de las principales fuentes de incertidumbre proviene de la selección del algoritmo utilizado para la modelización (e.j., Heikkinen et al. 2006; Pearson et al. 2006). Otras fuentes de incertidumbre proceden de la selección de los escenarios futuros de cambio climático (e.j., Beaumont et al. 2008), de las variables ambientales elegidas (e.j., Synes & Osborne, 2011) o de la selección de umbrales para convertir los datos de salida de los modelos (probabilidades de presencia) en datos binarios de presencia/ausencia (Nenzén & Araújo, 2011). Para tratar de entender y reducir la incertidumbre se puede cuantificar y representar espacialmente (Diniz-Filho et al. 2009; Beaumont et al. 2011) o combinar los resultados de los modelos mediante técnicas de consenso (e.j., García et al. 2011).

Dado las diferentes fuentes y niveles de incertidumbre, hacer recomendaciones de gestión de sitios o especies específicas basadas en modelos de poca resolución y a una escala continental resultaría inapropiado. Sin embargo, ignorar la información proporcionada por esos modelos sería igualmente imprudente, resultando una gestión de la biodiversidad reactiva en lugar de proactiva.

Métodos para determinar prioridades de conservación (Capítulo *IV*)

La conservación de áreas naturales parece la forma más eficaz de conservar la diversidad biológica a largo plazo (Primack 1993). Desde la década de 1980 se han desarrollado muchas herramientas para determinar prioridades de conservación, basándose en diversos criterios como riqueza de especies, grado de endemicidad y rareza o grado de amenaza (Brooks et al. 2006). Este apartado se centra en los algoritmos de selección eficiente de reservas ya que ha sido la metodología utilizada en el capítulo IV de la tesis. Esta aproximación se ha desarrollado en los últimos 20 años y ha supuesto en buena medida la superación de propuestas más clásicas como el diseño de reservas basado en la biogeografía de islas (Wilson & Willis 1975). Los algoritmos para la selección eficiente de reservas pueden aplicarse a escala global, regional, o local. Su uso principal se ha hecho a escala regional, en la identificación de lugares candidatos a ser incluidos en redes de reservas, y a escala global, como ayuda en la identificación de zonas prioritarias en la conservación de la diversidad. Esta metodología está basada en el principio de complementariedad, que asegura que las nuevas áreas seleccionadas para formar parte de la red de reservas complementan a las ya existentes incluyendo, por ejemplo, nuevas especies que todavía no estaban representadas ni protegidas.

En esta tesis, la selección de zonas prioritarias para la conservación de aves en la Península Ibérica se llevó a cabo utilizando el software para la planificación de la conservación Zonation (Moilanen et al. 2011y ver referencias incluidas en el manual) teniendo en cuenta: a) la probabilidad estimada de ocurrencia de las especies de aves tanto en el período actual como en las proyecciones del futuro, b) requerimientos de conectividad básicos de las especies, tanto desde la distribución actual hacia la distribución futura como desde la futura hacia la presente. Zonation asigna un valor a cada celda del área de estudio basándose en los requerimientos ecológicos de las especies y permitiendo una clasificación jerárquica de las prioridades de conservación. A continuación se selecciona un determinado porcentaje de superficie para conservar identificando las áreas prioritarias para el mayor número de especies.

Los objetivos de conservación utilizados en los análisis del capítulo **IV** fueron basados en las distribuciones de las aves tanto en el presente como en el futuro. Cuando se establecen prioridades de conservación teniendo en cuenta los efectos del cambio climático se deben considerar las distribuciones potenciales actuales y futuras, así como la conectividad entre ambas (e.j., Kujala et al. in review; Carroll et al. 2010). La conectividad se implementó a través de la técnica 'interacción de especies' de Zonation, que permite medir la conectividad entre dos áreas de distribución (Moilanen & Kujala 2008; Rayfield et al. 2009). El cálculo de la distancia media de dispersión se basó en los cambios observados en el rango de distribución de las aves en las últimas décadas (ver Brommer & Møller 2010 y las referencias ahí incluidas). La distancia de dispersión media estimada por década fue de 11.04 km y para el período de tiempo total de nuestro estudio fue de 77.31 km. Se utilizaron dos medidas de conectividad para cada especie. La primera es una conectividad del presente hacia el futuro y se denomina 'source areas', ya que las áreas de valor más elevado representan las áreas de dónde se espera que haya dispersión hacia las áreas adecuadas en el futuro. El segundo tipo de conectividad es desde el futuro hacia el presente, y se denomina 'stepping stones' porque son áreas que no son necesariamente de importancia en el presente pero ayudan a las especies a alcanzar las zonas adecuadas en el futuro. Por lo tanto, para llevar a cabo la priorización de zonas Zonation tienen en cuenta las distribuciones actuales, futuras, 'sources areas' y 'stepping stones'.

Conclusiones Generales

Integrando los resultados de los cuatro capítulos de esta tesis doctoral, se pueden extraer las siguientes conclusiones:

1) En el primer capítulo de la tesis se muestra como el algoritmo heurístico (desarrollado para poder utilizar nodos terminales de distintas características) resulta adecuado y útil para identificar conexiones entre áreas protegidas (u otro tipo de hábitat natural) utilizando datos ambientales como sustitutos de la biodiversidad. Además, para la identificación de conexiones entre áreas protegidas se favorecen aquellas zonas del paisaje que ambientales sean similares a las áreas protegidas que unen.

2) El principal interés de la biología de la conservación es la persistencia de las especies, a menudo en paisajes fragmentados. Los datos de dispersión de especies se deberían combinar con otros factores que determinen la persistencia de las especies a diferentes escalas temporales y espaciales

3) La capacidad de discriminación de los modelos de nicho no siempre se ve mejorada por la inclusión de datos de la cobertura vegetal y su configuración espacial, como en un principio se podría esperar. En el caso particular de las especies de aves en la Península Ibérica a una resolución de celda de 10x10 km, era suficiente la inclusión de datos climáticos para caracterizar la distribución actual de cerca de la mitad de las especies. Para algunas especies los datos de vegetación ayudaban a mejorar el rendimiento de los modelos pero los datos de configuración espacial de la vegetación, por sí solos, no ayudaba a mejorar la capacidad de discriminación de los modelos para ninguna de las especies estudiadas. Algunos de los factores que han podido determinar estos resultados son los siguientes: i) la importancia de variables climáticas frente a variables no climáticas depende de la escala del estudio, ii) en los países Mediterráneos el ser humano ha modificado el paisaje durante milenios por lo tanto la vegetación que observamos está altamente antropizada y iii) entre las variables de vegetación incluidas no sé tiene en cuenta factores importantes como la cantidad de materia muerta o la edad de los árboles. Se puede concluir que la decisión de incluir factores no climáticos en los modelos requiere un estudio específico de cada caso basado en la auto-ecología de las especies.

4) Se podría esperar que para las aves de hábitats forestales la inclusión de especies arbóreas en los modelos como variables predictoras tuviese más relevancia que para aves de hábitats esteparios o urbanos. Sin embargo, con nuestros datos y nuestros

análisis no emerge ningún patrón general en relación a la importancia de variables de vegetación para los distintos grupos de aves clasificadas por sus preferencias de hábitat.

5) Las evaluaciones de los impactos del cambio global sobre la biodiversidad que combinan medidas de exposición de las especies a los cambios ambientales con medidas que reflejan su capacidad intrínseca para hacer frente a estos cambios muestran un escenario relativamente menos pesimista que las evaluaciones de riesgo basadas solamente en el grado de exposición a los cambios, que hasta la fecha son la gran mayoría. Más concretamente, nuestro estudio muestra que las especies que se predice estarán altamente expuestas a los futuros cambios ambientales tienen actualmente un menos grado de amenaza y cuentan con unas características biológicas que las hacen menos vulnerables a la extinción local que las especies que están menos expuestas a los cambios ambientales. A pesar de que los resultados dependen del grupo taxonómico y de la región geográfica de estudio, se puede concluir que la capacidad de respuesta de las especies ante el cambio global depende de sus características biológicas y que la coincidencia entre el grado de exposición a una amenaza y la vulnerabilidad ante ella no se puede dar por sentado.

6) Los análisis del tercer capítulo de esta tesis también revelan que una gran proporción de especies de aves que actualmente no se encuentran amenazadas, según los criterios de la IUCN (categorías de Vulnerable, En Peligro o Críticamente Amenazado), podrían verse amenazadas en el futuro como resultado de los cambios climáticos, de vegetación y de tipos de uso de suelo.

7) Los resultados del cuarto capítulo muestran que las actuales redes de espacios protegidos no son muy efectivas representando las prioridades de conservación identificadas para las aves de la Península Ibérica. Aunque los sitios prioritarios están mejor representados en la red europea Natura 2000 que en la red nacional de espacios protegidos.

8) Un gran porcentaje del área de las prioridades de conservación identificadas en nuestro estudio conserva un elevado valor ecológico y no está protegido bajo la red nacional de espacios protegidos por lo que esta área tiene un importante potencial de conservación.

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Lista de manuscritos

Los siguientes capítulos de esta tesis doctoral han sido redactados en inglés con el objetivo de ser publicados en revistas científicas de ámbito internacional. A continuación se detalla el título, la lista de coautores y el estado de publicación de cada capítulo.

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Capítulo 2 Triviño, M., Thuiller, W., Cabeza, M., Hickler, T., Araújo, M.B. (2011). The Contribution of Vegetation and Landscape Configuration for Predicting Environmental Change Impacts on Iberian Birds. *PLoS ONE* **6**, e29373.

Capítulo 3 Triviño, M., Cabeza, M., Thuiller, W., Hickler, T., Araújo, M.B. Risk assessment for Iberian birds under global change. Enviado a *Conservation Letters*.

Capítulo 4 Triviño, M., Kujala, H., Araújo, M.B., Thuiller, W., Cabeza, M. Conservation priorities under climate change: Identifying threats and opportunities for the Iberian protected area networks. Manuscrito inédito.

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Chapter I

Linking like with like: optimising connectivity between environmentally-similar habitats

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Linking like with like: optimising connectivity between environmentally-similar habitats

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Abstract

Habitat fragmentation is one of the greatest threats to biodiversity. To minimise the effect of fragmentation on biodiversity, connectivity between otherwise isolated habitats should be promoted. However, the identification of linkages favouring connectivity is not trivial. Firstly, they compete with other land uses, so they need to be cost-efficient. Secondly, linkages for one species might be barriers for others, so they should effectively account for distinct mobility requirements. Thirdly, detailed information on the auto-ecology of most of the species is lacking, so linkages need being defined based on surrogates. In order to address these challenges we develop a framework that a) identifies environmentally-similar habitats; b) identifies environmental barriers (i.e., regions with a very distinct environment from the areas to be linked), and; c) determines cost-efficient linkages between environmentally-similar habitats, free from environmental barriers. The assumption is that species with similar ecological requirements occupy the same environments, so environmental similarity provides a rationale for the identification of the areas that need to be linked. A variant of the classical minimum Steiner tree problem in graphs is used to address c). We present a heuristic for this problem that is capable of handling large datasets. To illustrate the framework we identify linkages between environmentally-similar protected areas in the Iberian Peninsula. The Natura 2000 network is used as a positive 'attractor' of links while the human footprint is used as 'repellent' of links. We compare the outcomes of our approach with cost-efficient networks linking protected areas that disregard the effect of environmental barriers. As expected, the latter achieved a smaller area covered with linkages, but with barriers that can significantly reduce the permeability of the landscape for the dispersal of some species.

Keywords: Connectivity, Environmental surrogates, Graph theory, Iberian Peninsula, Minimum Steiner tree problem, Protected areas, Spatial conservation planning.

Introduction

Habitat fragmentation ranks among the highest threats to global biodiversity (Butchart et al. 2010; IUCN 2010) and this threat is likely to be exacerbated with climate change (Hannah et al. 2007; Araújo et al. 2011a). To minimise this threat, landscape connectivity should be enhanced with the identification and protection of linkages between areas of high conservation value (Fahrig and Merriam 1994; Hanski 1999). The underlying idea is that connectivity facilitates species dispersal, thus the rescue of small populations from local extinction (due to demographic or environmental stochasticity), while favouring the recolonization of suitable habitats (Bull et al. 2007). A major challenge in conservation and landscape ecology is to develop automated procedures that effectively identify linkages for multitude of species of conservation concern (Beier et al. 2011)

Several approaches have been developed to identify linkages between natural areas. These approaches are usually derived from two different bodies of literature: *reserve design* and *corridor design*. Reserve design typically involves strategies to achieve maximum representation of species in reserves given sets of constraints. Such constraints are often derived from the Island Biogeography and Metapopulation theories and seek to achieve a spatial reserve configuration that maximises species persistence (for a review see Araújo 2009). Mathematical programming techniques have been proposed to address species persistence in reserve design. The techniques included rules to achieve contiguous reserve systems (e.g. Williams 2002; Cerdeira et al. 2005; Önal and Briers 2005; Önal and Wang 2008; Wu et al. 2011), contiguous areas of distribution for the focal species (e.g. Cerdeira et al. 2010) or approaches where spatial criteria are incorporated in the objective function to be optimised (for a review see Williams et al. 2005). Criteria include compactness (e.g. Williams and ReVelle 1998; Rothley 1999; McDonnell et al. 2002; Fischer and Church 2003; Önal and Briers 2003), diameter (e.g. Önal and Briers 2002) and proximity between pairs of reserves (e.g. Önal and Briers 2002; Alagador and Cerdeira 2007).

Corridor design seeks to optimally link habitats where species of conservation interest occur. The primary input for corridor design is a permeability surface representing the cost of moving across landscape units (Taylor et al. 1993). Ideally, movement costs should be tuned for individual species, but since information is usually lacking for large numbers of species, multi-species corridor design focuses on general measures of landscape permeability (Chetkiewicz and Boyce 2009).

Graph theory provides an appropriate framework for corridor design (Urban and Keitt 2001; Calabrese and Fagan 2004). If one assumes that each landscape unit is a node in a graph (with an associated permeability measure) and edges between pairs of nodes represent the ability of a species to directly move between the corresponding landscape units, then the most efficient way to link a set of particular nodes (called terminals) is readily-expressed by a classical optimisation problem, called minimum Steiner tree (MST) problem in graphs (Du and Hu 2008). MST was introduced in the context of spatial conservation planning by Sessions (1992), who discussed the limitations of algorithms to find optimal MST solutions for real conservation problems that are characterized by vast amount of data. Subsequently, Williams (1998) and Conrad et al. (2010) worked on extensions of the MST problem to obtain solutions where linkage costs are balanced with suitability of the selected linkages. Recently, an open access software package (LQGraph) was released to implement MST for corridor design (Fuller et al. 2006; Fuller and Sarkar 2006).

The identification of efficient linkages when several types of terminal nodes (i.e., habitat units) exist, and nodes for linking these different types may not coincide, is a new variant of the MST problem. In this work, we address this problem as a major step of a framework to effectively promote connectivity for multiple species. The framework consists of: a) identification of environmentally-similar habitats (expected to accommodate groups of species with similar environmental requirements); b) identification of environmental barriers (i.e., regions with a very distinct environment from the environmentally-similar areas to be linked), and; c) selection of cost-efficient linkages between environmentally-similar habitats, free from environmental barriers (i.e., not including regions environmentally distinct from the habitats to be linked). We handle a) and b) using cluster analysis and we tackle c) using a heuristic that treats the problem as a sequence of MST problems.

We illustrate the framework using the Iberian Peninsula protected areas as the habitat units to be linked. We use climatic variables to assign protected areas into classes (under the assumption that climatically-similar areas hold similar pools of species) and to characterise landscape permeability for each species pool. Linkages between environmentally similar protected areas were favourably established across Natura 2000 areas (European Community Directive 92/43/EEC) because these are already under some form of protection. In contrast, areas highly modified by human activities, i.e., with high Human Footprint (Sanderson et al. 2002), were excluded from candidate linkages as they are unlikely suitable for species dispersal. The outcomes of our approach for selecting linkages between protected areas are compared with networks selected using an identical approach but ignoring climatic information.

Methods

The framework is exemplified using Iberian Peninsula protected areas as the habitat units (i.e., terminals) to be connected. The Iberian Peninsula map was divided into 580,696 cells following the UTM 1 km x 1 km grid. The map resolution was chosen to ensure consistency with the resolution of the climatic dataset (see below) and to generate a sufficiently high number of cells to challenge the practicability of the linkage algorithm proposed herein (see below).

Protected areas data were obtained from the Portuguese and Spanish Environmental Ministries and included 681 areas encompassing a wide range of national and international conservation conventions and cells with some amount of protected areas were treated as terminal nodes for analysis (80,871 cells, aprox. 14% of the cells in the Iberian Peninsula) (Figure S1.1 in the Supplementary Material). Natura 2000 areas not overlapping with protected areas were not considered as terminal nodes.

The Natura 2000 network (European Community Directive 92/43/EEC) is a European scale conservation scheme designed to complement nationally-defined protected areas. It is widely present across the European landscape and therefore has potential to be used for connectivity purposes (Saura and Pascual-Hortal 2007). We used Natura 2000 point/polygon data (downloaded from http://www.eea.europa.eu/data-and-maps/data/natura-1) (Figure S1.1 in the Supplementary Material) to calculate the proportion of each cell not covered by Natura 2000 areas. These values were used as linkage-costs c(s), for each cell s. We settled c(s) = 0 for each terminal cell.

We used the Human Footprint Index (Sanderson et al. 2002; downloaded from: http://www.ciesin.columbia.edu/wild_areas/register1.html), at 1 km x 1 km cell size (Figure S1.1 in the Supplementary Material), as a measure of human modification, *hf(s)* (Baldwin et al. 2010; Theobald 2010). The human footprint index ranges from 1 (low human impact) to 100 (high human impact). Since a negative relationship between human footprint and permeability of the cells for species‟ dispersal was assumed, cells with *hf(s)* over a specified threshold (see below) were not considered as candidates for linkages. We settled *hf(s)*=0 for terminal cells.

Monthly data of four climatic variables (maximum temperature, minimum temperature, total precipitation and standard deviation of the minimum temperature), from 1961 to 1990, were averaged to characterize current climatic conditions in the Iberian Peninsula (Figure S1.1 in the Supplementary Material). These variables were selected because they are considered important drivers of species‟ distributions at large spatial scales (Hawkins et al. 2003;

Whittaker et al. 2007). Climatic data, at 1km x 1km, were provided by the Instituto de Meteorologia (Portugal) and the Agencia Estatal de Meteorologia (España) (for a full description of data see Araújo et al. 2011b).

Environmental classification of protected areas

We carried out a Principal Components Analysis (PCA) to reduce the dimensionality and the correlative effects of the climatic data. We retained the two PCA components that explained the greatest proportion of the data variability (Figure S2.1, Table S2.1 and Table S2.2 in the Supplementary Material). These components were then used to group Iberian 5 protected areas into climatically similar clusters. Specifically, we computed the arithmetic mean of the two PCA components in the centroids of all individual protected areas. These centroids were chosen as units for the cluster analysis. We developed a k-means algorithm (Fielding 2007) for grouping protected areas into homogeneous climatic units (i.e., minimizing the summed Euclidean distances of each class-member to its respective class-centroid). The algorithm is a simulated annealing approach (Aarts et al. 1997), which, at each iteration, randomly selects a protected-area centroid and considers the possibility of its allocation in a different class. We used 10,000 iterations for each 50 uniformly selected initial classification-seeds, and saved the best solution. The number of climatic types (k=4) was selected a priori to limit the number of climatic clusters in Iberian Peninsula (i.e., alpine, continental, Mediterranean, and oceanic), in line with the Koppen-Geiger climatic classification for the region (Peel et al. 2007) (Table S2.3 in the Supplementary Material).

Identification of barriers

We considered two types of barriers: one defined by the Human Footprint Index and the other defined by climate data. Areas with high human footprint *hf(s)* values were assumed to be poorly permeable to species‟ movement. We defined a threshold, *H*, and excluded as candidate areas for linkages between protected areas the cells s, for which $hf(s)>H$. We used $H \in \{50, 60\}$, as low values of *H* would retrieve an excessively fragmented landscape (i.e., many landscape barriers) and high values of *H* resulted in highly disturbed cells being included (Figure S3.1 and Table S3.1 in the Supplementary Material).

In addition to the human footprint barriers we also considered climatic barriers. Here, the centroid of each climatic class in the final cluster was used as an archetype of the climate of that class, and the Euclidean distances, in the climatic space, of each (unprotected and protected) cell

to the centroid of each class were computed. This retrieves *k* values, *di(s)*, for each cell, expressing the dissimilarity of cell *s* to every climatic class-*i*.

Since the goal is to link climatically similar protected areas across cells that do not differ significantly from the mean climatic conditions of protected areas, we defined a threshold value *Bi* assuming that cells with *di(s)*>*Bi* are climatic barriers, thus not adequate for linking protected areas of class-*i*. We defined *Bi* according to two scenarios. In the first scenario, *Bi* was defined as the largest dissimilarity *di(s)*, among the protected cells s in every protected area of class-*i* (*max di(s)*). In the second and more restrictive scenario, the barriers for class-*i* were established as the top 25% *di(s)* values for cells s not belonging to *i*, i.e., (*Q3 di(s)*) (Table S4.1 in the Supplementary Material).

The linkage algorithm

Linking protected areas within each class-i, with minimum cost and with no environmental barriers for class-*i*, is a generalization of the (node weighted) MST problem in graphs, where protected areas act as terminal nodes. The MST is the special case when only one class exists. The MST is a difficult problem, and heuristics are the only option to handle even moderate size instances (say a few hundred of nodes and a few dozens of terminals). A simple heuristic for the MST problem is what is called the minimum spanning tree approach (see Du and Hu 2008). First, minimum cost paths (min cost paths: Dijkstra 1959) are computed between every pair of terminals. Next, these min cost paths are used to weight the edges of a complete graph whose nodes are terminals, and the minimum spanning tree for this graph (Kruskal 1956; Prim 1957) is obtained. Finally, the union of paths, corresponding to the edges of the minimum spanning tree, is pruned from redundant nodes (i.e., nodes that are not necessary to link all terminals of each class). The pruning process ends when the solution is minimal, i.e., every node is needed for linkage.

We extended this approach when there are $k>1$ classes. For each of the $k!$ permutations of the k climatic classes, we applied the above MST procedure to link protected areas of the class appearing first on the permutation. We then assigned "cost zero" to every cell of that linkage, and proceed as above to link the protected areas belonging to the second class of the permutation. This was repeated for the third, fourth, and k classes. At the end, the solution consisting of the union the k linkages was turned minimal. The final climate network was the minimum cost network among the $k!$ networks considered (see a schematic diagram of the algorithm in Figure 1).

In our implementation, special concern was given to data structures to allow the heuristic to run large instances, such as the Iberian Peninsula example.

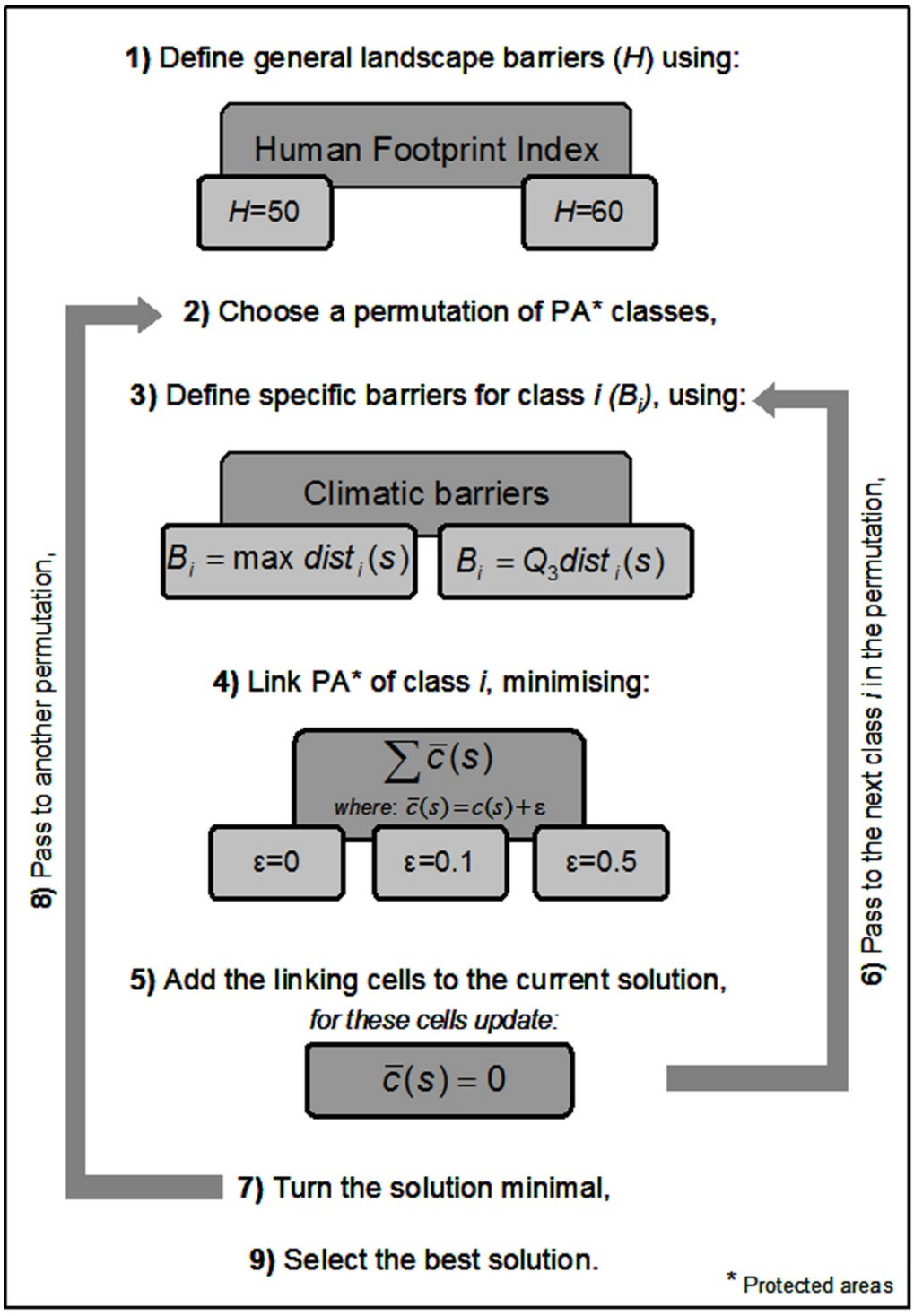

Figure 1 Simplified overview of the procedures implemented in the connectivity algorithm.

It should be noted that, depending on the specific parameterization of climatic barriers (*Bi*) and the human footprint threshold (*H*), pairs of protected areas of the same class might not be linked in the final solution. This can happen when all paths connecting two protected areas belonging to some class-*i* include some cell, *s*, with *di(s)>Bi* or *hf(s)>H*. In other words, for some climatic classes, the resulting climate network can have more than one connected component (Figure 2a). A connected component of class-*i* is a maximal (with respect to inclusion) subset of (protected and unprotected) cells connecting protected areas of class-*i* that are not barriers for that class. This generalizes the notion of a connected component in a graph (e.g. Rayfield et al. 2011).

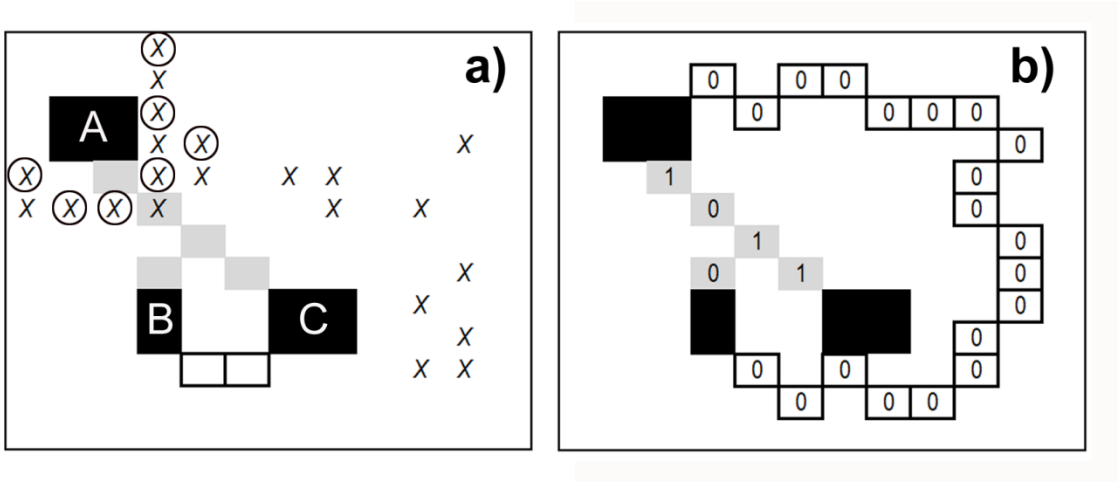

Figure 2. Comparison of climate-concerned networks (CCN) (filled squares) and climate-unconcerned networks (CUN) (open circles) in terms of efficiency: **a)** total area selected, **b)** total area selected not listed in Natura 2000; and effectiveness (number components in protected area networks), for the most conservative scenario under consideration (H=50, B_i>Q_3 $d_i(s)$), using distinct area-penalty parameterizations (ε values in parenthesis). Arrows represent comparisons of CCN and CUN sharing similar costs.

Our algorithm generates a climate network with the minimum number of connected components for each class. We used the number of components (which strictly depends on the values used for *Bi* and *H*) as an indicator of linkage effectiveness. A large number of components for a given class reflect a highly fragmented network. This may indicate an ineffective linkage for that class.

We also considered balancing the cost of the final solution with the number of selected cells using an area-penalty. For every cell, *s*, we added a positive fixed term ε to the cost, *c(s)*, obtaining the modified cost $\bar{c}(s) = c(s) + \varepsilon$. Larger ε values determine fewer cells in the solution (Figure 2b). We tested three different values (ε=0; ε=0.1 and ε=0.5).

Comparing network effectiveness

We compared the climate networks with linkages obtained without use of climatic information, i.e., using the procedure described above, but assuming that all protected areas belong to the same climatic class and that no climatic barriers exists. We denote these networks as simple networks.

We obtained climate networks and simple networks for each of the 12 parameterizations above described (2 human footprint thresholds x 2 climatic barriers assumptions x 3 area-penalty values). We compared solutions in terms of efficiency (i.e., total 20 surface areas and total cost) and effectiveness. To assess effectiveness of simple networks we recovered the protected areas climatic classification and for each climatic class-*i* we removed the barriers for that class. Then, we counted the number of connected components of class-*i*, which we compared with the number of connected components in the corresponding climate network.

Results

Outputs from the two types of networks (climate and simple networks) obtained under different parameterizations (ε x H x Bi) showed marked variability on the extent (Table 1), effectiveness (Figure 3) and spatial location (Figure 4, and Table S5.1 in the Supplementary Material) of linkages connecting the Iberian protected areas. While climate networks ranged from 5,328km^2 to 6,666 km^2, simple networks varied from 4,873km^2 to 6,373 km^2. This means that climate networks required 3.2% to 14.4% more area than simple networks, and also identified more linkages outside the Natura 2000 network (3.8% to 19.2% more area). Models penalizing the number of cells and the total area in the solution (ε=0.5) retrieved more distinct solutions between the approaches; a trend that is true for both H=50 and H=60 scenarios (Table 1).

Table 1. Summary of networks of Iberian protected areas, obtained with climate data (climate networks; CN) and without climate data (simple networks; SN) using different parameterizations of the human footprint threshold H, the area-penalty parameter ε, and climatic barriers Bi. Percentage-differences (Δ (%)) between CN and SN are presented for the total selected area, the selected area outside Natura 2000 network, the total number of protected area components and for the number of components within each of the climatic classes (alpine, continental, Mediterranean and oceanic).

									Number of components in protected area networks												
			Total selected area (km^2)			Selected area outside Natura (km^2)			Alpine			Continental			Mediterranean			Oceanic			Total		
B_i	H	ε	CN	SN	Δ (%)	CN	SN	Δ (%)	CN	SN	Δ (%)	CN	SN	Δ (%)	CN	SN	Δ (%)	CN	SN	Δ (%)	CN	SN	Δ (%)
$max\ d_i$	50	0.0	6,361	6,140	3.6	2,083	1,988	4.8	1	1	0.0	19	25	-24.0	59	63	-6.3	31	31	0.0	110	120	-8.3
		0.1	5,934	5,639	5.2	2,163	2,026	6.8	1	1	0.0	19	23	-17.3	59	62	-4.8	31	31	0.0	110	117	-6.0
		0.5	5,331	4,901	8.8	2,473	2,244	10.2	1	1	0.0	19	25	-24.0	59	63	-6.3	31	31	0.0	110	120	-8.3
	60	0.0	6,577	6,373	3.2	2,034	1,959	3.8	1	1	0.0	8	15	-46.7	43	45	-4.4	17	17	0.0	69	78	-11.5
		0.1	5,890	5,622	4.7	2,138	2,010	6.4	1	1	0.0	8	14	-42.9	43	46	-6.5	17	17	0.0	69	78	-11.5
		0.5	5,328	4,873	9.3	2,562	2,229	14.9	1	1	0.0	8	13	-38.5	43	45	-4.4	17	17	0.0	69	76	-9.2
$Q3\ d_i$	50	0.0	6,383	6,140	4.0	2,126	1,988	6.9	3	15	-80.0	20	31	-35.5	59	70	-15.7	32	34	-5.9	114	150	-24.0
		0.1	5,985	5,640	6.1	2,193	2,026	8.2	3	14	-78.6	20	30	-33.3	59	69	-14.5	32	34	-5.9	114	147	-22.4
		0.5	5,506	4,901	12.3	2,531	2,244	12.8	3	11	-72.7	20	27	-25.9	59	69	-14.5	32	33	-3.0	114	140	-18.6
	60	0.0	6,666	6,362	4.8	2,143	1,956	9.6	2	15	-86.7	8	22	-63.6	43	51	-15.7	17	20	-15.0	70	108	-35.2
		0.1	6,029	5,622	7.2	2,223	2,010	10.6	2	14	-85.7	8	20	-60.0	43	53	-18.9	17	20	-15.0	70	107	-34.6
		0.5	5,576	4,875	14.4	2,657	2,229	19.2	2	11	-81.1	8	17	-52.9	43	54	-20.4	17	19	-10.5	70	101	-30.7

As expected, climate networks performed better in terms of avoiding climatic barriers than equivalent simple networks. In fact, by identifying and bypassing climatic barriers, climate networks included 6.0% to 35.2% less protected area components than simple networks, a fact that is contingent on the spatial pattern of unsuitable areas provided by *H* and *Bi*. Differences in the number of components vary with the climatic classes, because linkages between protected areas in particular classes are more challenged by barriers.

When barriers included the 25% more dissimilar cells outside protected areas of each type (*Bi > Q3 di(s)*), greater differences between the climate and simple networks were obtained for the alpine protected area network (Table 1). With climate networks, linkages for these protected areas retrieved few components (2 to 3) being 72.7% to 86.7% more effective at guaranteeing connectivity than linkages in the simple networks. Turning *H*=50 to *H*=60 greatly affected comparisons of both approaches for the continental protected areas, as effectiveness gains with climate networks varied approximately from 30% to 60%. This means that the general (landscape) barriers are the major determinant of fragmentation for these protected areas. Differences between approaches were less marked when connecting Mediterranean and oceanic protected areas, with gains in effectiveness being approximately 15% for climate networks. Using *H*=50, effectiveness gains in oceanic 5 protected areas were narrower (3.0 to 5.9%).

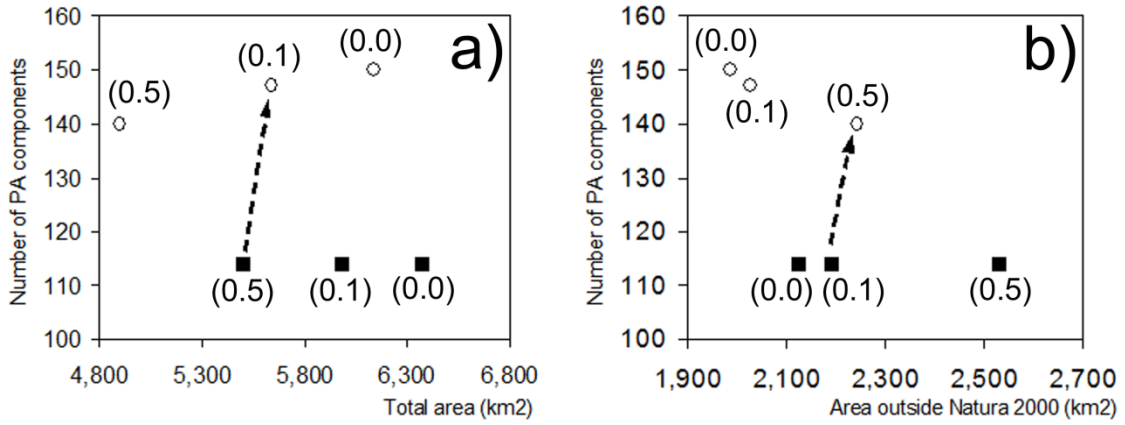

Figure 3. Comparison of networks delineated with climate data (climate networks; CN) (filled squares) with simple networks without climatic data (simple networks; SN) (open circles) in terms of efficiency: a) total area selected, b) total area selected not listed in Natura 2000; and effectiveness (number components in protected area networks), for the most conservative scenario under consideration (*H*=50, *Bi>Q3 di(s)*), using distinct area-penalty parameterizations (εvalues in parenthesis). Arrows represent comparisons of pairs of networks sharing similar costs.

Comparing efficiency and effectiveness of climate and simple networks enables the assessment of the extent to which a fixed budget produces solutions performing differently in terms of realized linkage achievements. Climate networks are inevitably more costly than simple networks when the same parameterization is used. Therefore, we manipulated area-penalty to obtain climate and simple networks with similar costs. For example, analysing the more conservative scenario (i.e., with more barriers) (H=50, $B_i > Q_3\ d_i(s)$), the climate networks requiring less surface area targeted 5,506 km^2, encompassing 114 protected area components, while a similar-size simple networks (5,640 km^2) contained 147 protected area components (Figure 3a). An equivalent loss of linkage effectiveness for the simple networks occurred when the selected area outside Natura 2000 was used as a measure of efficiency (Figure 3b). In this case the most-costly simple network (2,244 km^2) presented more 22.8% protected areas components than the climate network using a similar amount of area outside Natura 2000 (2,193 km^2). These differences are directly translated to the spatial patterns obtained for both network types (Figure 4).

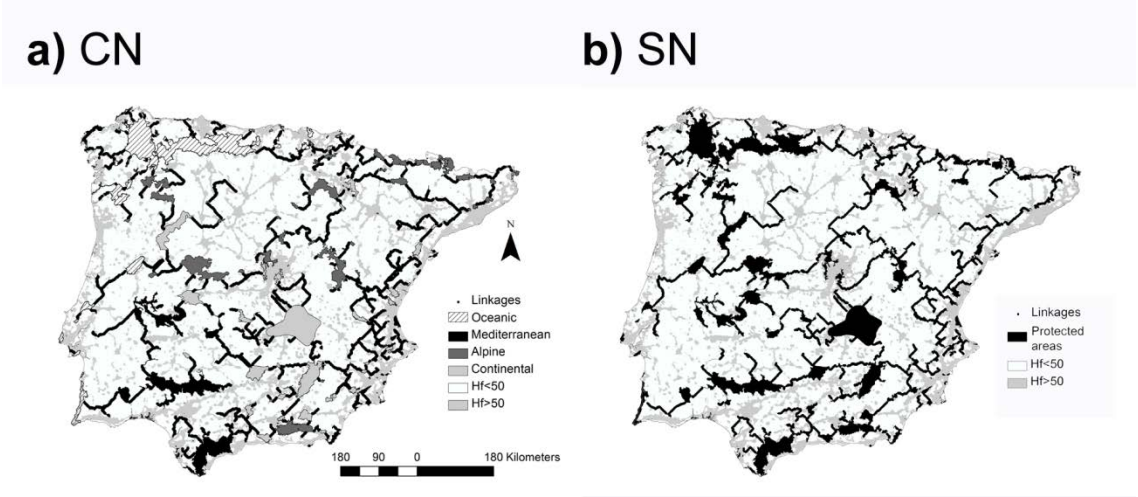

Figure 4. Maps of linkages for the Iberian Peninsula protected areas obtained with climate data (climate networks; CN), using an area-penalty ε=0.1 and climatic barriers $B_i > Q_3\ d_i(s)$, and without climate data (simple networks; SN) using an area-penalty ε=0.5. Both networks are delineated over a similar amount of land not listed within Natura 2000 (see Table 1). Landscape barriers (light grey areas) are defined after applying a threshold value (H=50) to filter out the areas with the highest human footprint values.

Discussion

We have shown that extending the MST to account for different types of terminal habitats provides a useful framework for identifying linkages between natural areas using environmental data. The framework is based on the assumption that the environment drives, at least partially, species' distributions, so that habitats with similar environments are likely to share similar assemblages of species or act as potential 'sources' and 'sinks' for species' dispersal. It follows from this assumption that linkages between protected areas should preferentially be established between environmentally-similar areas. Although this assumption is problematic for the selection of complementary sets of areas in reserve selection (see, Araújo et al. 2001; Araújo et al. 2004; Hortal et al. 2009), it is reasonable to expect that when species occupying a given environment are, for whatever reason, forced to move elsewhere, they preferentially move to similar environments (Chetkiewicz et al. 2006; Sawyer et al. 2011). The choice of the relevant environmental attributes to be used should be concerted with the autoecology of focal species and the scale of analysis (i.e., extent and resolution of the study area). For example, we used climate to obtain a broad characterization of species' permeability in Iberian Peninsula as it is seen highly correlated with plant and animal species' distributions at such spatial extent and grain size (Hawkins et al. 2003; Whittaker et al. 2007). Several other environmental variables could be used instead (e.g., vegetation types, topographic, geologic, biogeographic, phylogenetic and disturbance data, or different combinations of them).

Two problems may arise when using climatic variables in our framework in a context of climate change. First, sets of climatically-similar habitats are likely to be shuffled with climate change and therefore an habitat unit A initially targeted to be linked with a similar unit B, may no longer need such linking, but requires a linkage with a new similar unit C. Second, areas identified as linkages for a given habitat class may lose climatic suitability for that class. In an extreme scenario, they may even turn into barriers to species' movements. To develop conservation maps robust to climate change (without relying on projected emissions of greenhouse gases, air-ocean circulation models, and climate-envelope models), several studies support the use of more steady factors driving biodiversity patterns and processes, like topographic and geomorphologic variation (Anderson and Ferree 2010; Beier and Brost 2010; Game et al. 2011).

Our framework is flexible enough to accommodate simple conservation purposes. For example, natural habitats may be so heavily fragmented that no continuous swaths of land are left to be conserved. Furthermore, there are species able to cross some amount of inhospitable land. In cases such as these, linking habitats with stepping-stones may open opportunities for

effective and less-conflicting conservation measures, because stepping stones require lesser area than continuous linkages. Our framework may be easily adapted to delineate stepping-stones optimally. This can be accomplished by using adjacency rules between cells that integrate a "functional distance" defined by the distance that the least mobile focal species are able to move across unsuitable habitat. Once a given cell is chosen for linkage at least one other cell, distancing no more than the "functional distance", needs also to be selected.

The cost-optimised networks obtained with our framework only require a unique path between each pair of habitat units of the same class. This may not be the most precautionary option to take (Pinto and Keitt 2009). One can increase network robustness by identifying multiple paths to link habitats of the same class. Our framework is able to reach this by replacing the execution of the last step of the linkage algorithm (i.e., turning the solution minimal), with the removal of only the non-terminal cells that are connected to no more than one other cell. Then, if non-overlapping linkages are desired, the heuristic can be repeatedly run removing all the selected non-terminal cells from the previous solutions. Clearly, this can be executed only for those habitat classes with greater numbers of threatened species or for the classes requiring longer linkages, as these are less likely to be implemented or are more exposed to threats (Beier and Noss 1998). Furthermore, in circumstances where lengthy linkages are not critical to maintain long distance dispersal events, it may be wiser to avoid linking distant habitat units. For example, the analysed region may be sub-divided in order to obtain sub-areas with higher densities of habitat units for each habitat class. Independent solutions for each of these sub-areas may be obtained thereafter.

Finally, it is critical to realize that if the main interest of conservation is the persistence of species in fragmented landscapes, the sole integration of species' movement patterns is insufficient. Species' dispersal data should be combined with other factors that determine species' persistence at various spatial and temporal scales. Therefore the framework here presented should be considered as part of a broader analysis towards the promotion of such complex and integrative objective as it is allowing species to persist.

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Authors' contribution

MBA developed and proposed the idea. DA, MT, JOC, MC, and MBA designed the analysis. JOC designed and implemented (in Fortran) the algorithm for environmental clustering of protected areas, for the connectivity algorithm, and for the method for comparing climate and simple networks. RB implemented (in C++) the linkage algorithm. MT handled the environmental and geographical data. DA run the models and analysed the results. DA and MT wrote the paper with substantial contributions from JOC and MBA as well as comments from the remaining authors.

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Supplementary Material

1) Data

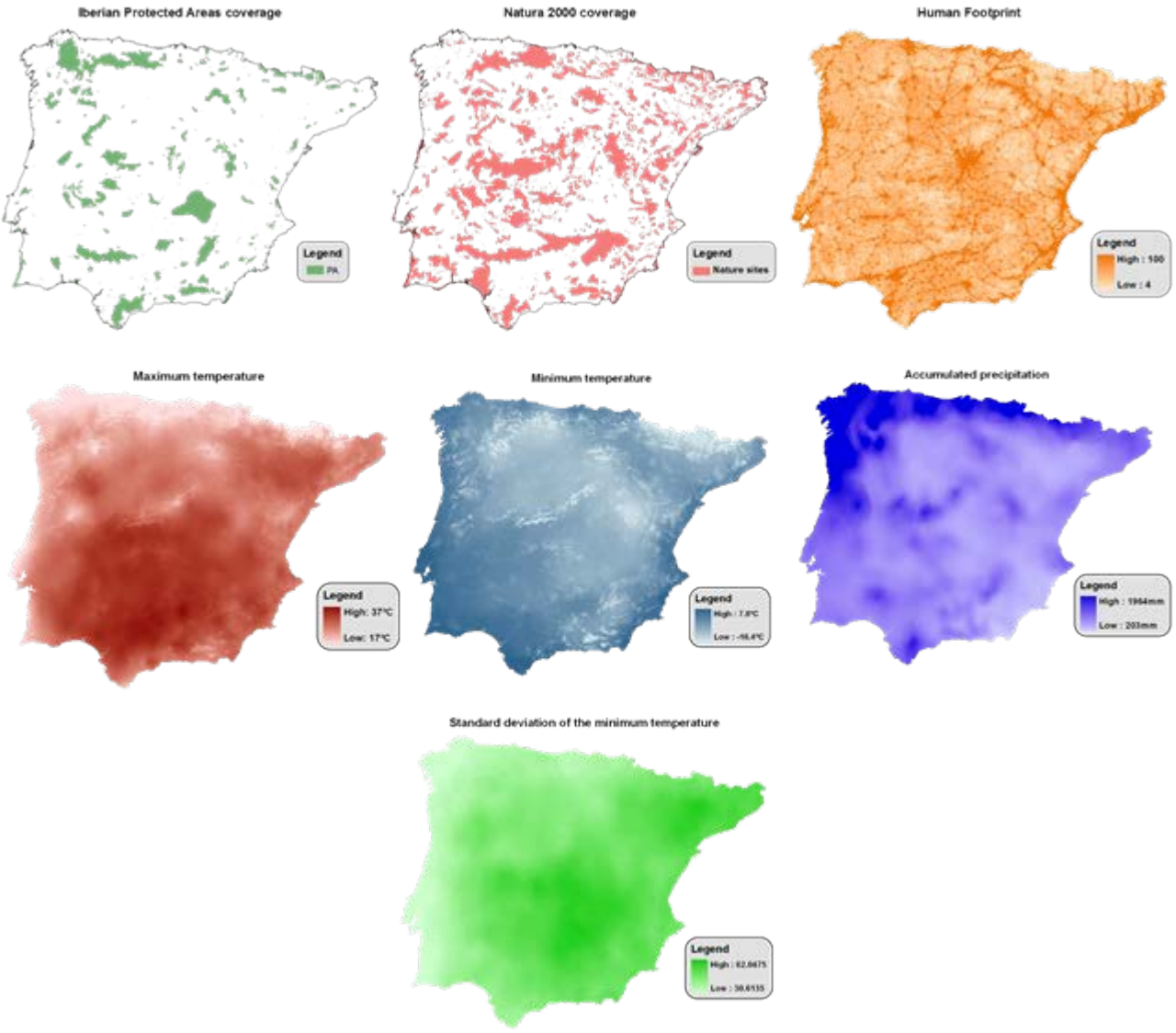


Figure S1.1. Spatial distribution of the different data used in this study.

2) Climatic characterization

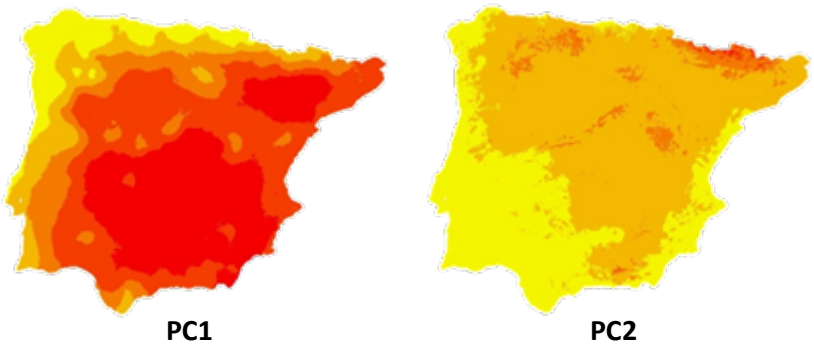


Figure S2.1 Spatial pattern in Iberian Peninsula of the first (PC1) and second (PC2) principal components.

Table S2.1 Characterization of the first four principal components (eigenvalues and explained variance).

Factors	Eigenvalue		Variance (%)	
	Value	Cumulative	Value	Cumulative
1	2.307438	2.307438	57.68596	57.6860
2	1.190173	3.497611	29.75432	87.4403
3	0.349566	3.847177	8.73914	96.1794
4	0.152823	4.000000	3.82058	100.0000

Table S2.2 Characterization of the first four principal components (eigenvectors per variable).

Eigenvectors	Factor 1	Factor 2	Factor 3	Factor 4
Max tmp	**0.578674**	-0.305971	0.381001	-0.652960
Min tmp	-0.018986	**-0.903150**	0.036006	0.427391
Accum prec	-0.576365	0.023014	**0.815590**	-0.045682
Std min tmp	**0.576696**	0.300287	0.433999	0.623613

Table S2.3 Characterization of Iberian Peninsula PA sizes.

PA class	Mean area (km^2)	Standard deviation of area (km^2)
All PAs	97.043	610.787
Continental	87.883	501.469
Oceanic	132.326	1062.756
Alpine	123.936	387.563
Mediterranean	75.687	434.564

3) Landscape barriers

Table S3.1 Correspondence of human footprint values to different land uses.

Human footprint value	Type of area
91-100	Areas in city centres of big cities like Madrid or Barcelona
61-90	Suburban areas
50-60	Natural areas close to cities. Rural areas
19-49	Natural areas modified by humans activities
4-18	Isolated areas further away from cities such as mountains

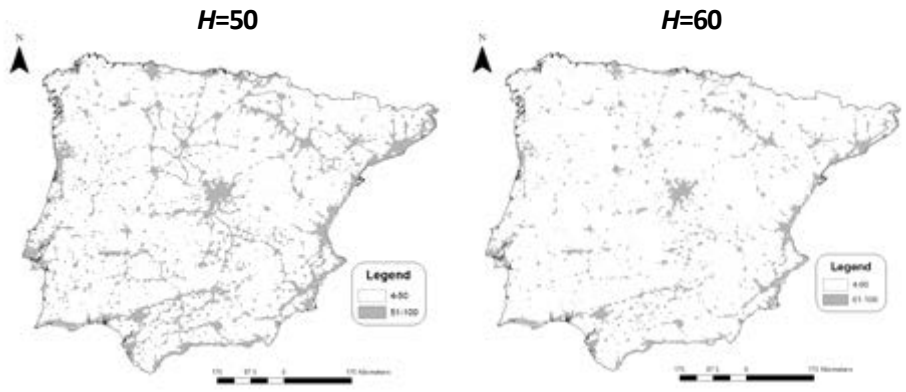
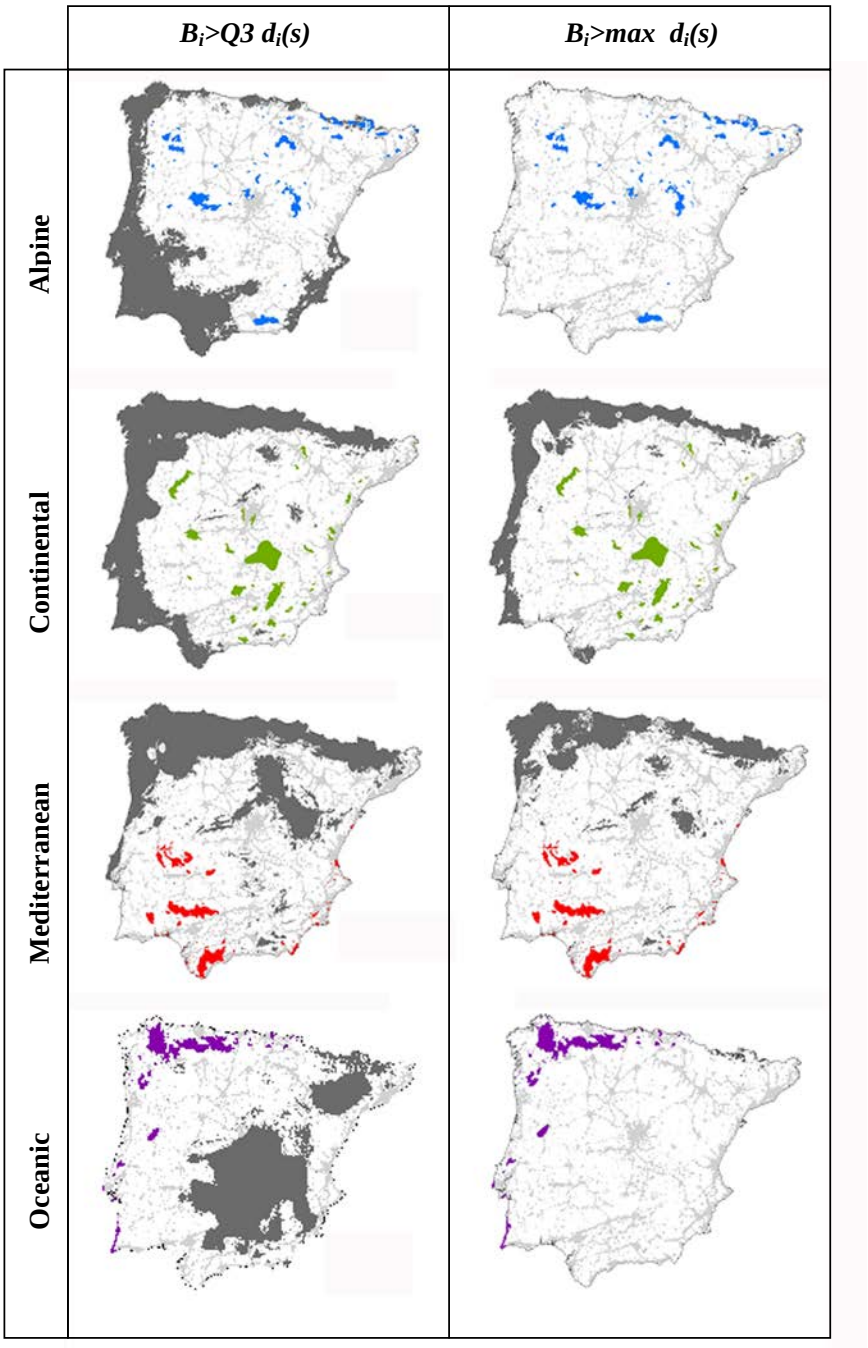


Figure S3.1 Location maps of landscape barriers (light grey areas), derived from the use of two threshold values over human footprint index (*H*=50 and *H*=60).

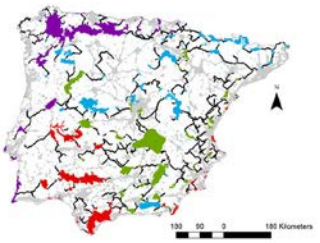
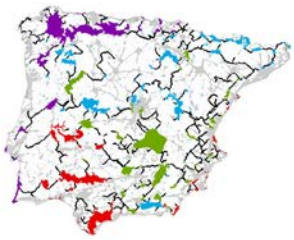
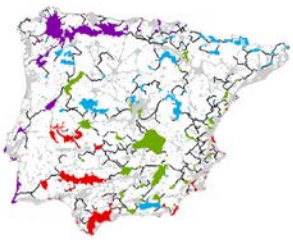
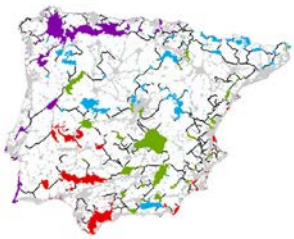
4) Climatic barriers

Table S4.1 - Location maps of climatic barriers (dark grey areas) for different climatic classes of protected areas (blue: alpine; green: continental; red: Mediterranean; purple: oceanic), under two barrier assumptions $B_i > Q3\ d_i(s)$ and $B_i > max\ d_i(s)$. Landscape barriers are also presented (light grey areas).



5) Linkages results

Table S5.1 - Maps of climate networks (CN) and simple networks (SN) (black lines) linking Iberian Peninsula protected areas. CN were defined for four climatic classes (blue: alpine; green: continental; red: Mediterranean; purple: oceanic) and SN obtained without climate data (olive-green: protected areas). Networks were produced for different area-penalties (epsilon, ε), landscape barriers (light grey) and climatic barriers assumptions (see Figure S3.1 to locate climatic barriers).

	ε = 0.0	ε = 0.1	ε = 0.5
A)	**Landscape barriers (H=50) & climatic barriers B_i>$Q3\ d_i(s)$**		
CN			
SN			
B)	**Landscape barriers (H=50) & climatic barriers B_i>$max\ d_i(s)$**		
CN			
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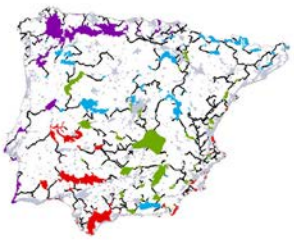
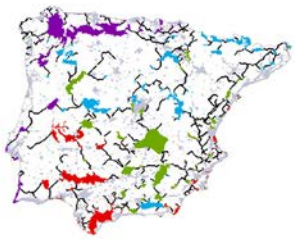
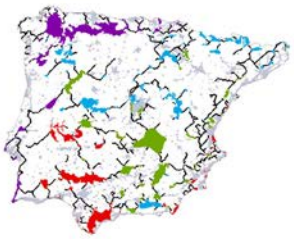
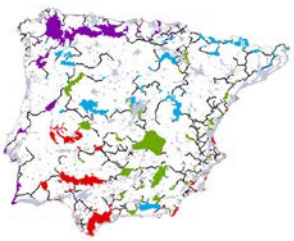
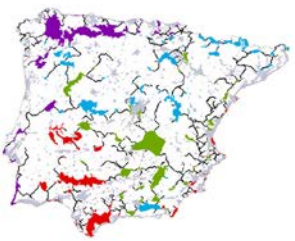
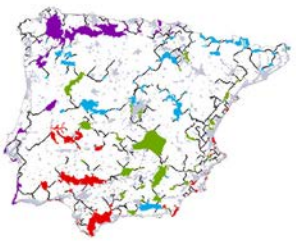
	ε = 0.0	ε = 0.1	ε = 0.5
C)	**Landscape barriers (*H*=60) & climatic barriers B_i>*Q3* $d_i(s)$**		
CN			
SN			
D)	**Landscape barriers (*H*=60) & climatic barriers B_i>*max* $d_i(s)$**		
CN			
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Table S5.2 Running times (sec.) of the linkage algorithm to obtain climate networks, using several parameterizations threshold values for the Human Footprint Index (*H*); area-penalty parameter (ε) and climatic barriers (B_i)

		Running times (sec.)	
		B_i	
H	ε	$max\ d_i$	$Q3\ d_i$
50	**0.0**	4,560	2,945
	0.1	3,840	2,689
	0.5	3,399	2,278
60	**0.0**	5,279	3,830
	0.1	4,534	3,321
	0.5	4,079	2,907

Chapter II

The Contribution of Vegetation and Landscape Configuration for Predicting Environmental Change Impacts on Iberian Birds

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The Contribution of Vegetation and Landscape Configuration for Predicting Environmental Change Impacts on Iberian Birds

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Abstract

Although climate is known to be one of the key factors determining animal species distributions amongst others, projections of global change impacts on their distributions often rely on bioclimatic envelope models. Vegetation structure and landscape configuration are also key determinants of distributions, but they are rarely considered in such assessments. We explore the consequences of using simulated vegetation structure and composition as well as its associated landscape configuration in models projecting global change effects on Iberian bird species distributions. Both present-day and future distributions were modelled for 168 bird species using two ensemble forecasting methods: Random Forests (RF) and Boosted Regression Trees (BRT). For each species, several models were created, differing in the predictor variables used (climate, vegetation, and landscape configuration). Discrimination ability of each model in the present-day was then tested with four commonly used evaluation methods (AUC, TSS, specificity and sensitivity). The different sets of predictor variables yielded similar spatial patterns for well-modelled species, but the future projections diverged for poorly-modelled species. Models using all predictor variables were not significantly better than models fitted with climate variables alone for ca. 50% of the cases. Moreover, models fitted with climate data were always better than models fitted with landscape configuration variables, and vegetation variables were found to correlate with bird species distributions in 26-40% of the cases with BRT, and in 1-18% of the cases with RF. We conclude that improvements from including vegetation and its landscape configuration variables in comparison with climate only variables might not always be as great as expected for future projections of Iberian bird species.

Keywords: Climate change; birds; bioclimatic envelope models; dynamic vegetation models, Iberian Peninsula.

Introduction

Global environmental changes pose great challenges to biodiversity, with ongoing impacts on species distributions and abundances already being recorded (e.g. Lenoir et al. 2008; Parmesan 2006; Walther et al. 2009). Attempts to estimate the future effects of global change on biodiversity have often relied on environmental envelope models (Heikkinen et al. 2006). These models relate known species distributions to environmental variables to project future altered potential distributions under global change scenarios (e.g. Araújo et al. 2006; Pompe et al. 2008; Thuiller et al. 2011). Most of the studies have used climatic factors alone to project species distributions into the future. Nevertheless, there are many factors other than climate that can affect the geographical distributions of species (e.g. Hampe 2004; Melles et al. 2011). This is particularly true for animal species for which climate is often used as a surrogate for resource availability or nesting suitability.

A large number of studies have included non-climatic factors for modelling contemporary species distributions. Such factors included, among others, land cover and land use (Luoto et al. 2007; Pearson et al. 2004; Thuiller et al. 2004a), vegetation cover (Seoane et al. 2004), topography (Luoto and Heikkinen 2008), or a combination of all of them (Brotons et al. 2007). However, only a small number of assessments exploring the potential impacts of future global environmental changes have included predicted land use or vegetation changes to complement climatic information (but see Araújo et al. 2008; Jetz et al. 2007; Kissling et al. 2010; Preston et al. 2008) because of the scarcity of relevant non-climatic data projected into the future. To our knowledge, none of these previous studies has incorporated vegetation dynamics modelled in a mechanistic way as we have done in this study. The question remains: how would changes in non-climatic environmental factors affect projections of future altered species distributions? We address this question using Iberian birds as a case study.

European bird species have already shown phenological (e.g. Lehikoinen et al. 2004; Møller et al. 2004) and distributional changes (e.g. Brommer 2004; Thomas and Lennon 1999) and they are projected to shift their ranges substantially as a result of global change (Huntley et al. 2007). However, improvements of projections of future range shifts could be expected if information on vegetation dynamics was included because bird species distributions are known to be, at least partially, determined by vegetation and its spatial configuration (e.g. Julliard et al. 2006; Root 1988; Rotenberry and Wiens 1980). Variables characterizing aspects of vegetation have been used to model potential current distributions of birds (e.g. Peterson et al. 2002; Seoane et al. 2004), but they have rarely been incorporated in models projecting future range shifts under scenarios of global environmental change (Lawler et al. 2006). Furthermore, most

attempts to incorporate vegetation dynamics into forecasts of species distributional changes have not considered vegetation dynamics, such as those simulated by Dynamic Vegetation Models (DVMs), but rather used statistical interpolation of vegetation patterns (Hughes et al. 2008; Preston et al. 2008). For example, Lawler et al (2006) simulated changes in the vegetation distribution with the Mapped Atmospheric-Plant-Soil System (MAPSS), an equilibrium model that provides future static snapshots, but no year-to-year variability. The spatial configuration of vegetation cover is also thought to be important for explaining bird distributions (e.g. Pearson 1993; Saab 1999), because it accounts for the amount of available habitat in the surrounding area, but again little attempts have been made to incorporate landscape dynamics in forecasts of biodiversity change.

In this study, we used distribution data for 168 breeding bird species in the Iberian Peninsula to fit models using combinations of climatic variables, vegetation characteristics, and their derived landscape configuration. Models were used to assess the importance of alternative aspects of the environment for projecting future potential bird ranges. Specifically, we address the following questions: (i) what sets of variables have greater predictive power: climate, vegetation or landscape configuration? (ii) Are projections using different environmental predictor variables coincident?

Materials and Methods

Species data

We used distributional records in the Iberian Peninsula for 168 native breeding bird species. Distribution data were extracted from the Spanish Atlas of Breeding Birds (Martí and del Moral 2003) and from the Portuguese Atlas of Nesting Birds (Equipa Atlas 2008) reporting the presence and absence of bird species in 5923 10x10 km resolution UTM cells. This is the highest-resolution animal distribution data available for the Iberian Peninsula. Our analyses of bird distributions excluded marine and aquatic species because modelling of their habitats would require information about variables that is not available to us. Species with less than 20 records were also excluded to avoid problems of modelling species with small sample sizes (Stockwell and Peterson 2002).

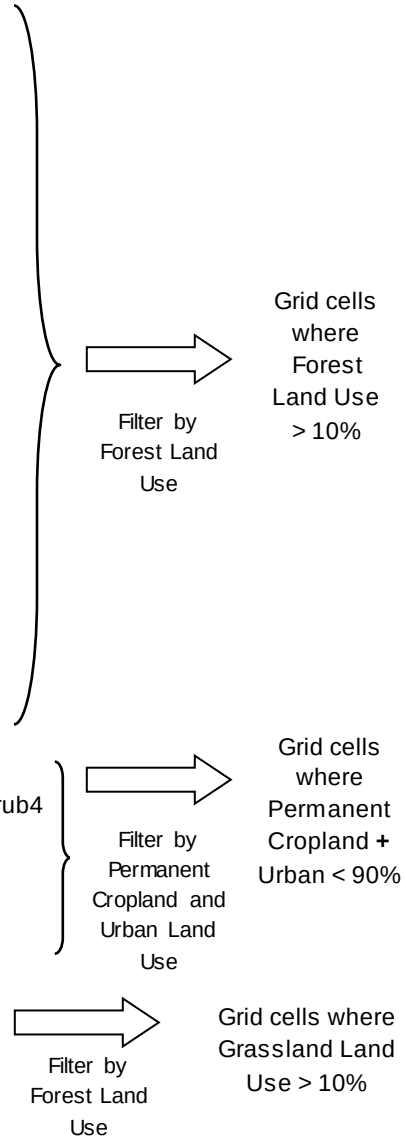
Environmental data for the baseline period

Variables were selected from a larger pool based on expert knowledge and data mining; the latter was done with the specific goal of reducing the number of variables and remove collinearity among them. Overall, four groups of continuous predictor variables were used to fit the models (Table 1): (i) *climatic* (3 variables), (ii) *vegetation* (17 variables), (iii) *landscape configuration* (3 variables) and (iv) *global* (including all previous variables).

For the (i) ***climatic group***, a set of aggregated climate parameters were derived from the Climate Research Unit at 10' resolution. The CRU CL 2 and CRU CL 2.1 dataset at resolution of 10' (~16km at the latitude of the study) was chosen to represent current climate (average from 1971 to 1990). Average monthly temperature and precipitation in grid cells covering the mapped area of the Iberian Peninsula were used to calculate mean values of three different climate parameters: mean winter temperature, annual precipitation and accumulated degree days. These variables are considered ecologically important for explaining bird distribution patterns (e.g. Araújo et al. 2009; Gregory et al. 2009; Huntley et al. 2008) and limit species distribution as a result of widely shared physiological constraints (e.g. Crick 2004; Whittaker et al. 2007). Finally, variables were interpolated using kriging implemented within Geographical Information System (GIS) software ArcGIS 9.2 (ESRI 2006) to a resolution of 10 km to match the bird distribution datasets.

Table 1 Environmental variables used to build alternative models.

Variable name	Variable description
Climate data set	
1 mwintertmp	Mean winter temperature (ºC)
2 annpre	Annual precipitation (mm)
3 acmgddaug	Accumulated degree days (January to August)
Vegetation data set	
Forest type	
1 Bet.pen	*Betula pendula*
2 Bet.pub	*Betula pubescens*
3 Car.bet	*Carpinus betulus*
4 Cor.ave	*Corylus avellana*
5 Fag.syl	*Fagus sylvatica*
6 Fra.exc	*Fraxinus excelsior*
7 Pic.abi	*Picea abies*
8 Pin.hal	*Pinus halepensis*
9 Que.ile	*Quercus ilex*
10 Que.pub	*Quercus pubescens*
11 Que.rob	*Quercus robur*
12 Til.cor	*Tilia cordata*
13 Total.Forest	Sum of all the forest types
Shrubland type	
14 MRS	Mediterranean Raingreen Shrub4
15 Jun.oxy	*Juniperus oxycedrus*
16 Que.coc	*Quercus coccifera*
Grassland type	
17 c3	Herbaceous
Landscape data set	
1 Forest.R30	Accumulated forest in a radius of 30 km
2 Shrub.R30	Accumulated shrubland in a radius of 30 km
3 Grass.R30	Accumulated grassland in a radius of 30 km



The (ii) ***vegetation group*** comprised potential natural vegetation composition and structure, simulated with the DVM LPJ-GUESS (Hickler et al. 2004; Smith et al. 2001). The model simulates the competition between main tree species and PFTs. Forest dynamics resemble successional patterns, adopting a forest "gap model" approach. The model has been parameterized to represent the main European tree species and a number of plant functional types (PFTs) (Hickler et al. 2009; Hickler et al. 2012). LPJ-GUESS reproduced the main general patterns in European potential vegetation at a coarse scale, but the model did not reproduce the fine-scale mosaic of different vegetation types existing in many areas. Discrepancies were, for example, caused by the fact that some real-world drivers, such as different soil nutrient levels, are not accounted for by the model. However, the model results we used present the first assessment of dynamic future vegetation changes at the level of important tree species and PFTs over continental Spain and Portugal. General vegetation features in the Iberian Peninsula, such as the distinction between forests, shrublands and grasslands, corresponded better with the potential natural vegetation in the Iberian Peninsula than in earlier studies with dynamic global vegetation models (Hickler et al. 2012). The model also reproduced the main features of the coarse-scale distribution of major tree species covered by the Third Spanish Forest Inventory (Villanueva 2004) (Figures S1). The PFTs were also grouped into three broad habitat types, reflecting the vegetation structure rather than individual tree species or PFTs: forest, shrubland, and grassland. The sum of the LAI of all species and PFTs belonging to each of the three broad habitat type group was then used in the analyses. Many bird species are rather dependent on such structural vegetation features than on individual tree species (Karr and Roland 1971; Root 1988; Rotenberry and Wiens 1980). Furthermore, the model output for these structural ecosystem features is more robust than the simulated patterns for individual species or PFTs, and they are less likely to be fundamentally changed by forest management. A PCA was performed in order to investigate for collinearity among variables and potentially select a reduced set of variables. However, variables were not highly correlated so all were kept. The vegetation was represented by the continuous variable Leaf Area Index (LAI), which is the ratio of total upper projected leaf surface of vegetation divided by the surface area of the land on which the vegetation grows. LAI is a dimensionless value, typically ranging from 0 to 8 for a dense forest. The variables were originally at 10' (~16km at the latitude of the study) resolution and were interpolated at 10km resolution to match the bird distribution datasets.

Because potential vegetation cover variables modelled with LPJ-GUESS do not account for current and future land use, we combined them with land use information derived from CORINE Land Cover (CLC) as follows (European Commission 1993). Categories from CLC were aggregated and represented by 6 land cover classes: Urban, Cropland, Permanent Crops,

Grasslands, Forest and Others (for a complete description of the methodology see Dendoncker et al. 2007, despite in this reference they use the PELCOM dataset, the analyses were re-done using CORINE dataset and are the ones used for this study). The percentage of each land use type within the UTM grid cells was calculated using the Zonal Statistics tool implemented in ArcGIS 9.2. Grid cells were classified as forested when 10% or more of their surface were covered by Forest. If, for example, the vegetation model predicted forest but less than 10% of the grid cell was forested according to the land cover data, non-forest vegetation cover was assumed in the analysis. From the grid cells classified as shrublands we excluded the ones in which the sum of non-compatible land use types (Permanent Croplands, Croplands and Urban) represented 90% or more of the grid area. Finally, cells were classified as grasslands when their area was covered by at least 10% of Grasslands. Thus, we assume that a certain fraction of available habitat within a grid cell is sufficient for populations to persist. Different classes were not exclusive between each other and grid cells could hold more than one vegetation type at the same time. If, for example, a grid cell was covered by 17% of forest and 16% of grassland according to land cover data and was occupied by Quercus ilex (PFT of forest type) and c3 (PFT of grassland type) according to the vegetation model, that grid cell was considered both as "forest" and as "grassland".

The (iii) ***landscape configuration group*** was calculated based on the accumulated sum of the different PFTs values included in each habitat type: forest, shrubland, and grassland. Using ArcGIS 9.2., three concentric bands, each 10 km wide, were delimited around each grid cell for the three habitat types. Within each band and for each habitat type, the accumulated vegetation abundance was calculated. These data provided information of the spatial arrangement and composition of the landscape around each grid cell. From the nine variables created only the three variables of radius equal to 30 km were retained due to the high correlation between the three different radiuses (Spearman's correlations, r= 0.8- 0.9) and also because they capture a broader range of landscape and were the variables least correlated with the original habitat types.

Finally, the (iv) ***global group*** included the three previous data sets.

Environmental data for the future

We used a European climate scenario from the EU framework program Assessing Large-scale environmental Risks for biodiversity with tested Methods (ALARM) at a resolution of 10' for the period 2051-2080 (Fronzek et al. 2012). The climate scenario was derived from a simulation with the global climate model HadCM3, using the BAMBU (Business As Might Be

Usual) scenario (which corresponds to A2 SRES) of the ALARM project. Scenarios for future potential natural vegetation were developed by a previous study (Hickler et al. 2012) as well as the scenarios for future land use change (Rounsevell et al. 2006). Land use projections used to constrain potential vegetation cover from LPJ-GUESS were based on the BAMBU scenario (Spangenberg 2007) (for details see (Dendoncker et al. 2006 ; Rounsevell et al. 2006)).

Data analysis

The models were built using the BIOMOD library (Thuiller et al. 2009) in R (R Development Core Team 2009) (version 1.15), using the default settings and parameters. Two ensemble modelling techniques were selected: Random Forests (RF) (Breiman 2001; Cutler et al. 2007) and Boosted Regression Trees (BRT) (Elith et al. 2008; Friedman 2001). Both techniques are effective in dealing with non-linearities and interactions among variables. Random forest uses a bootstrap aggregation algorithm by fitting multiple un-pruned classification trees on sub-samples of the original data. The prediction is then the average of the predictions of all trees weighted by their internal predictive accuracy (out-of-bag estimator). We fitted random forest using a maximum of 700 trees and using a random half of the predictor variables for each tree. BRT is a boosting algorithm in which very short classification trees (seven nodes) are repeatedly built on the residuals from the previous tree to improve the fit using cross-validation to stop the process. In BRT models the maximum number of trees was set to 3000, the learning-rate was 0.001 and the interaction-depth was 4 as suggested by Elith et al. (2008). The full dataset for the 168 breeding bird species was randomly partitioned into two subsets (calibration and evaluation), with 70% and 30% respectively, and this overall procedure was repeated five times to make sure that the evaluation procedure was independent of the random splitting procedure. Future projections were made assuming unlimited dispersal, which is a more likely scenario among birds at the geographical extent of the study area than the alternative no dispersal scenario.

Models were assessed using four evaluation methods: the area under curve (AUC) of the receiver operating characteristic (ROC) (Swets 1988), the true skill statistics (TSS) (Allouche et al. 2006), sensitivity that measures the percentage of presences correctly predicted and specificity that measure the percentage of absences correctly predicted. The specificity and sensitivity were determined separately after using an AUC and TSS protocol to convert probabilities of occurrence into presences and absences (Figure 1).

There is a large number of statistical techniques available to fit environmental envelope models and they are known to produce markedly different future projections of species range shifts when projections are made into the future (Araújo and Guisan 2006; Pearson et al. 2006; Thuiller et al. 2004b). Commonly used evaluation metrics measuring agreement between predicted potential and observed distributions are useful to verify the models' discrimination ability (Araújo and Guisan 2006). However, discrimination between predicted potential and observed distributions is known to be a relatively poor surrogate of the models' ability to predict future distributions well (Araújo et al. 2005a). Therefore, there are little guidelines for selection of the models to use under future scenarios (Araújo and New 2007). A possible approach to handle inter-model variability and reduce uncertainty is to use ensemble forecasting by generating multiple copies of the models and combining them using consensus techniques (see for review (Araújo and New 2007)). In this study, a consensus approach based on the mean of the probabilities from the sets of projections made by RF and BRT was selected (see also (Araújo et al. 2011; Araújo et al. 2005b; Marmion et al. 2009)) and TSS method was chosen to convert probabilities values into presence-absence data.

The relative importance of environmental variables was also calculated for RF and BRT. In Random Forests, variable importance is determined by comparing the misclassification error rate of a tree with the error rate that occurs if the values of a predictor variable are randomly permuted (Cutler et al. 2007). In Boosted Regression Trees variable importance is based on the number of times a variable is selected for binary splitting, weighted by the squared improvement to the model as a result of each split, and averaged over all the individual trees (Friedman and Meulman 2003). Because measures of variable importance are calculated differently in RF (Mean Decrease Accuracy and Mean Decrease Gini) and BRT, a ranking system was created to compare environmental selection among the different model types. Environmental variables were ranked from 1 (most important) to 23, although only the three first ones were analysed to compare across all groups of variables (only three variables for the climatic group).

Bird species were classified into eight categories based on their main habitat use: Forest, Shrubland, Grassland, Grassland/Forest, Shrubland/Forest, Grassland/Shrubland, Grassland/Shrubland/Forest and Others (including bird's species which do not depend on any vegetation type such as those specialized on urban areas or cliffs). In order to define the degree of habitat specialization of species we counted the number of habitat types used for breeding or feeding and considered that the more habitats used the less specialized are the species. The information was gathered from the Spanish Atlas of Breeding Birds (Martí and del Moral 2003) and complemented by consultation with experts (Table S1).

Results

Average discrimination ability of models based on cross validated AUC and TSS values differed statistically among the different groups of predictor variables (Friedman test, $p < 0.001$), being lower for landscape models and higher for models including all predictor variables together (Figure 1). Models including climatic variables alone were generally better than models fitted solely with vegetation or landscape variables, although not always significantly better than models including vegetation (Wilcoxon test, $p<0.05$) (Table 2). The comparison between the models including all variables and the models including climate, vegetation or landscape showed that the all-variables models were significantly better than any other model, except for the models fitted with climatic variables alone for which the all-variables-model was significantly better only in 50% of the cases (Table 3). Regarding the differences in discrimination ability between modelling techniques, we found that Random Forests adjusted projections to the data more closely than Boosted Regression Trees in almost all of the cases and regardless of the four evaluation techniques used (Figure 1).

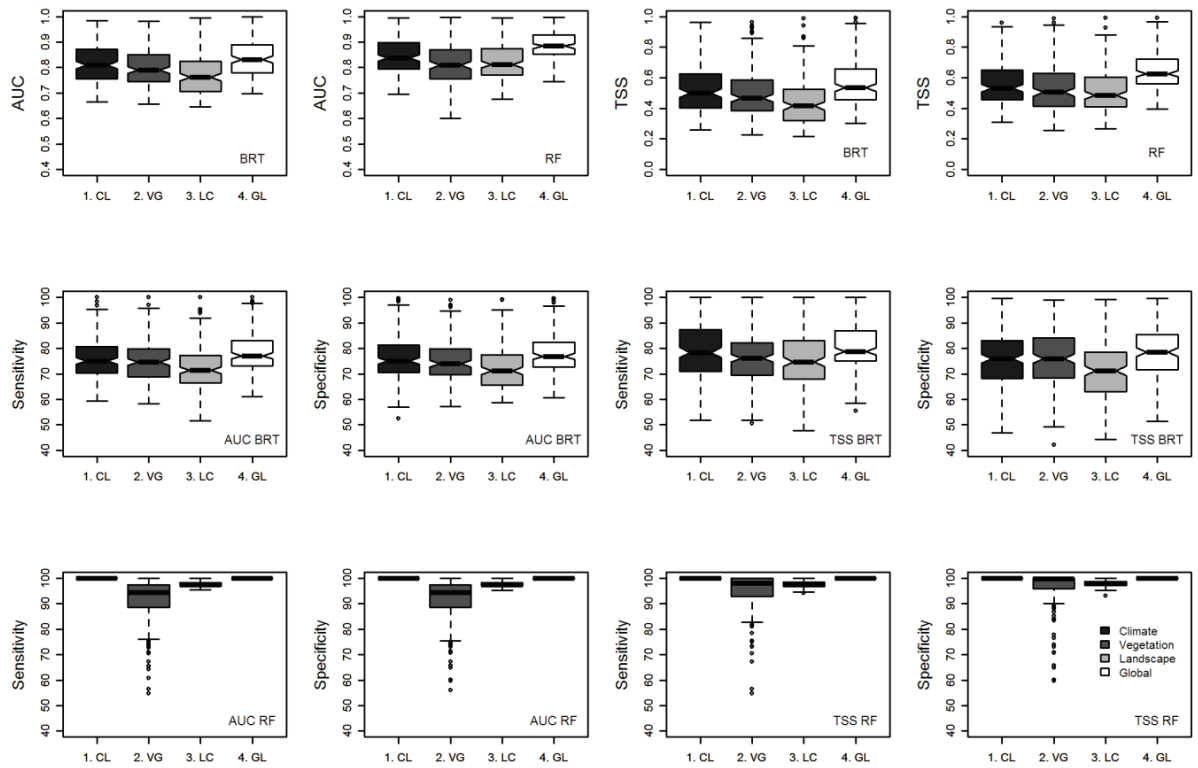


Figure 1. Four evaluation methods to compare model performance using different predictor variables. Boxplot summarizing results of measures of performance (AUC and TSS) of each dataset used (Climate, Vegetation, Landscape and Global) for the cross validation results for BRT and RF models. Percentage of presence and absence correctly predicted (sensitivity and specificity) were also provided. Median values (line across box), range excluding outliers (error bars), interquartile range containing 50% of values (box) and outliers (circles) from results. Untransformed values have been used.

Spatial correspondence among projections of species richness for the four sets of models was very high for the baseline period, but substantially variable for future scenarios. Inter-model variability was constrained by model performance (Figure 2). That is, species for which models performed notably well (high-performance species) had lower inter-model variability than species for which models performed well (good-performance species) and poorly (poor-performance species) (Table 4). Overall, the pairwise correlation among future projections for the 168 species varies considerably (Spearman's correlations, r= 0.26 – 0.8). However, pairwise comparisons for groups of species with models of similar accuracy (grouped according to AUC values) showed that higher correlation between model predictions was obtained for the models with higher accuracy: high-performance species (Spearman's correlations, r= 0.5-0.94; maximum number of species=32); good-performance species (r= 0.37- 0.6; maximum number of species=63); and poor-performance species (r= 0.17- 0.44; maximum number of species=37).

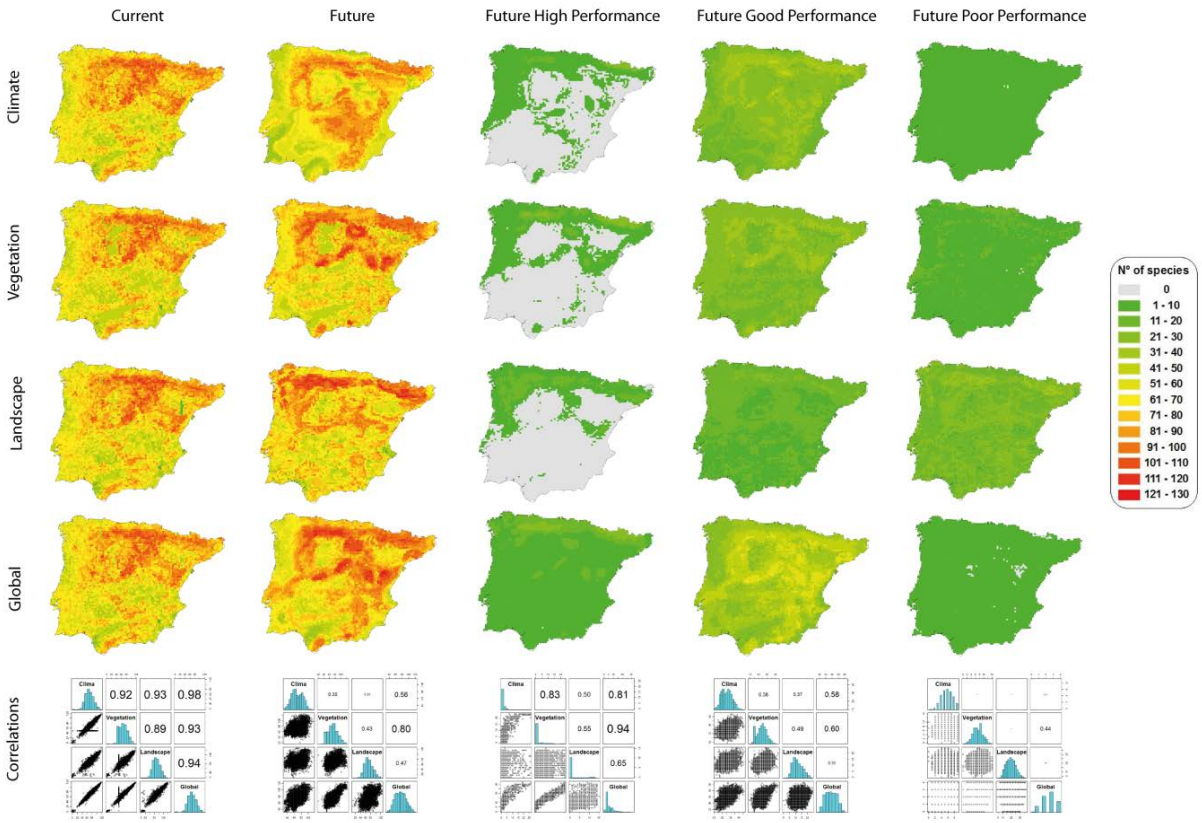


Figure 2. Spatial pattern comparison of bird distributions. The maps represent the total number of species per each 10 km cell for the four model types (Climate, Vegetation, Landscape and Global) and for two time periods (current and future projections). The correlation graphs indicate the level of agreement between the four model types for each column. The calculations for the first two columns (current and future) were done using the total number of bird species (N = 168) whereas the last three columns illustrate subsets of the future projection based on model performance categories (AUC method): high (N = 32), good (N= 63) and poor (N = 37).

Table 2: Results of pairwise Wilcoxon test of the effect of predictor variables (climate, vegetation and landscape configuration) on model performance estimated by AUC and TSS.

Predictor variables	**Climate-Vegetation**				**Climate-Landscape**				**Vegetation-Landscape**			
Evaluation method	AUC		TSS		AUC		TSS		AUC		TSS	
Model technique	BRT	RF **	BRT	RF	BRT ***	RF **	BRT ***	RF **	BRT **	RF	BRT **	RF
Wilcoxon test	*W*=13512; *p*=0.0575	*W*=14459; ***p*=0.0019**	*W*=13326; *p*=0.096	*W*=13410; *p*=0.077	*W*=15853; ***p*=1.1e-06**	*W*=14168; ***p*=0.0063**	*W*=15727; ***p*=2.5e-06**	*W*=14155; ***p*=0.0066**	*W*=14528; ***p*=0.0014**	*W*=11319; *p*=0.3801	*W*=14595; ***p*=0.001**	*W*=12470; *p*=0.562

Table 3: Results of pairwise Wilcoxon test comparison between each individual model (climate, vegetation and landscape configuration) and the global model based on performance estimated by AUC and TSS.

Predictor variables	**Climate-Global**				**Vegetation-Global**				**Landscape-Global**			
Evaluation method	AUC		TSS		AUC		TSS		AUC		TSS	
Model technique	BRT	RF ***	BRT	RF***	BRT ***	RF ***	BRT ***	RF ***	BRT ***	RF ***	BRT **	RF ***
Wilcoxon test	*W*=9839; *p*=0.0059	*W*=7566; ***p*=1.8e-08**	*W*=10030; *p*=0.01203	*W*=7666; ***p*=3.6e-08**	*W*=8258; ***p*=2.0e-06**	*W*=5940; ***p*=1.4e-14**	*W*=860; ***p*=1.6e-05**	*W*=6878; ***p*=7.7e-11**	*W*=6396; ***p*=1.1e-12**	*W*=5737; ***p*=1.8e-15**	*W*=6568; ***p*=5.2e-12**	*W*=5889; ***p*=8.5e-15**

Table 4: Number of species from the 168 species classified in different accuracy classes of AUC and TSS based on two modelling techniques

Predictor variables	**Climate**				**Vegetation**				**Landscape**			
Evaluation method	AUC		TSS		AUC		TSS		AUC		TSS	
Model technique	BRT	RF	BRT	RF	BRT	RF	BRT	RF	BRT	RF	BRT	RF
High-performance	28	35	17	19	23	27	15	21	17	28	5	10
Good-performance	61	78	28	32	53	60	21	25	35	71	19	30
Fair-performance	70	53	79	90	78	46	80	74	75	59	66	85
Poor-performance	9	2	44	27	14	28	51	48	41	5	78	43
Fail	0	0	0	0	0	7	1	0	0	5	0	0

AUC: High = AUC>0.9, Good=0.9<AUC<0.8; Fair = 0.7<AUC<0.8; Poor = 0.6<AUC<0.7. Fail AUC<0.6

TSS: High = TSS>0.8, Good=0.8<TSS<0.6; Fair = 0.6<TSS<0.4 and Poor = 0.2<TSS<0.4. Fail TSS<0.4

After ranking the relative importance of all the environmental variables, we calculated the fraction of species for which the models selected climatic, vegetation or landscape variables among the three most important ones. Results were different depending on the method used (Figure 3). Using the procedure for assessment of variable importance in BRT, we found that vegetation was selected as important for a larger fraction of bird species (26.2- 40.5%) than that estimated with RF models (Accuracy 1.2- 7.7%, and Gini index 12.5- 18.4%). For the three measures of variable importance used (BRT, Accuracy and Gini index), the fraction of species for which the models selected non-climatic variables increased from the first most important variable (1.2 - 26.2%) to the second (4.8 - 37.5%) and third variable selected (7.7 – 40.5%).

The main type of habitat used by the bird species was not associated with the choice of variables entering into the models (Figure 4) neither did the degree of habitat specialization (Table 5). As it can be seen in figure 4, vegetation variables were selected as the first, second, or third most important variable for a constant fraction of bird species. For example, vegetation was associated with ~ 35% of forest bird specialists in all cases. Unlike the expectation, no clear variable discrimination emerged in models using vegetation variables among forest, shrubland or grassland birds.

Table 5 Fraction of bird species for which the model included vegetation variables as the first (V1), second (V2) or third (V3) most important variables. Species are grouped by their degree of habitat specialization based on the number of habitat types they use for breeding and feeding. **High specialization** means the species use one habitat type (N = 90), **mid specialization** means the species use two habitat types (N = 51) and **low specialization** means the species use three habitat types (N = 9).

Model technique	BRT			RF (Gini index)		
Specialization level	**V1**	**V2**	**V3**	**V1**	**V2**	**V3**
High specialization	52.3 %	54 %	58 %	52.4 %	54.5 %	61.3 %
Mid specialization	25 %	34.9 %	20.3 %	33.3 %	39.4 %	29 %
Low specialization	6.8 %	3.2 %	4.3 %	0 %	0 %	0 %

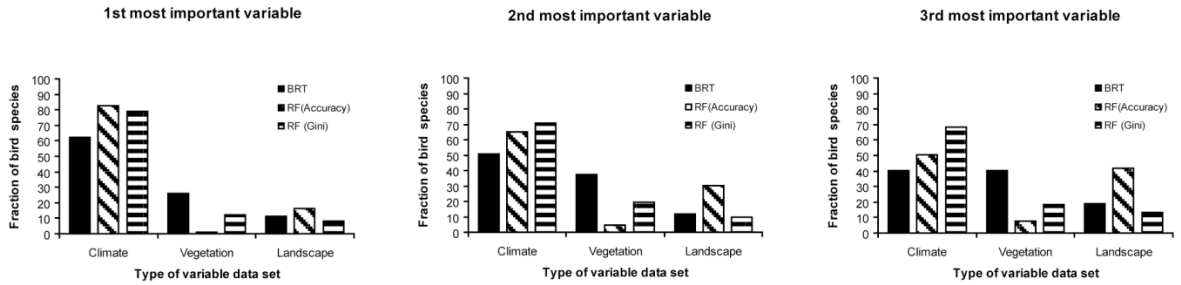


Figure 3. **Ranking of variable importance for BRT and RF models.** Fraction of the 168 bird species for which the model selected climatic, vegetation or landscape variables as the first, the second or the third most important variable.

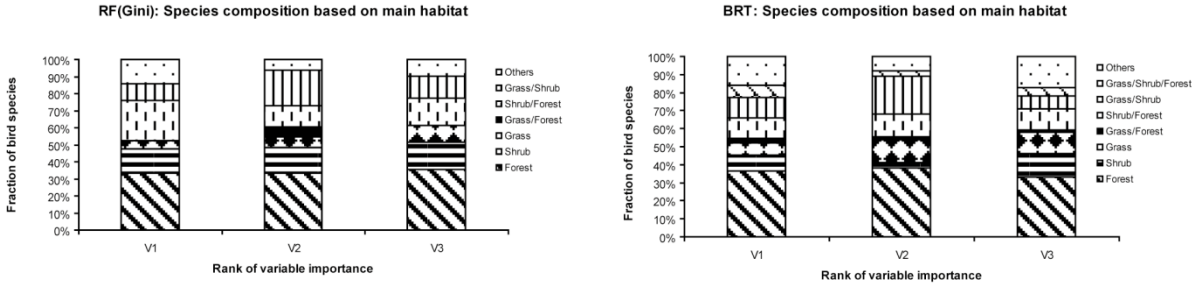


Figure 4. Importance of vegetation variables among bird species with different habitat preferences. Species composition based on the main habitat used by the bird species selecting vegetation variables as the first, second or third most important for explaining their distribution. For BRT model species number for V1 = 44, V2 = 63 and V3 = 69 whereas for RF model (Mean Decrease Gini measure) the species number for V1 = 21, V2 = 33 and V3 = 31.

Discussion

In this study we asked whether adding vegetation and landscape configuration variables in environmental envelope models would significantly increase discrimination ability of models and whether different sets of variables would affect the spatial representation of climate change impacts on bird species. We showed that models using climatic variables generally fit the data better than models using vegetation or landscape configuration variables. However, improvements of discrimination with the climate models, as compared with the two alternative models, were significant in all cases only for the climatic-landscape model comparison. Disagreement existed between future projections using different predictors, but the discrepancy decreased when species with high levels of discrimination ability in ensembles of forecasts were retained. Finally, the importance of variables appeared to be species specific and, despite the importance of climatic variables, vegetation and landscape configuration were also important for explaining the distribution patterns of a number of bird species.

Climatic variables perform better than non-climatic variables when predicting potential distributions of birds

Authors have repeatedly suggested that greater care should be given to the choice of environmental predictors when modelling the potential distributions of species (e.g. Austin and Van Niel 2011). Previous studies have suggested that non-climatic variables should be incorporated in bioclimatic models for projecting future range shifts (e.g. Araújo and Luoto 2007; Seoane et al. 2004), but the impossibility of validating future projections (Araújo et al. 2005a; Araújo and Rahbek 2006) makes it complicated to measure the relative importance of non-climatic variables. It is well-established that the configuration and composition of vegetation are good predictors of bird species distributions because they are associated with many of their breeding, feeding or nesting requirements (e.g. Lee and Rotenberry 2005 and references therein). For example, Seoane et al. (2004) found that vegetation models were significantly more accurate than topo-climatic models. However, our results showed that vegetation or landscape models did not outperform climatic models. Indeed, for half of the modelled species consideration of all variables did not result in better discrimination than that obtained with models only accounting for climate variation. Possible explanations for this result are that: (i) the relative importance of climatic versus non-climatic predictors is scale dependent (e.g. Whittaker et al. 2001). For example, in a previous study, land cover data did not improve model accuracy at coarse resolution (50 km) in Europe (Thuiller et al. 2004a). In another study, using a finer resolution (10 and 1 km), the inclusion of land use improved model discrimination ability (Pearson et al. 2004). In effect, the resolution and extent of our study might be too coarse to capture the dependence of birds on vegetation; (ii) vegetation in Mediterranean countries has

been modified by humans for millennia. The human impact is not represented by the simulated potential vegetation. We sought to address this issue by tailing vegetation to land use, but the land cover data used herein is still a rather coarse approximation of real land cover and its associated habitat characteristics. However, the correspondence between species potential distributions and simulated potential vegetation might be higher in regions where the actual vegetation has been little influenced by human activities; (iii) the vegetation model used here was parameterized to represent the main dominant tree species and vegetation types across Europe, but it did not include all important trees in the Iberian Peninsula. Furthermore, as with any process-based vegetation model, simulated vegetation patterns do not always correspond well with real patterns; (iv) the coarse vegetation and land use variables used in this study do not account for all important habitat characteristics, such as forest age and size structure in plantations and the amount of deadwood.

Discrepancies between future projections could be partly explained by the expected decrease in the correlation between climate and simulated vegetation across time. This is because, firstly, the vegetation model accounts for potential effects of increasing atmospheric CO2 on productivity and water cycling (Hickler et al. 2009; Hickler et al. 2008). "CO2 fertilization" and reductions in stomatal conductance and water losses might alleviate some of the negative effects of increasing drought on vegetation (Gerten et al. 2005; Hickler et al. 2009). Secondly, the vegetation model simulates transient vegetation shifts, not the equilibrium response to the climatic forcing. Over a few decades, only a small fraction of the long-term equilibrium response of the vegetation can be expected (Hickler et al. 2012). This non-equilibrium is much more important for the discrepancies in the projections than the CO2 effects (Hickler et al. 2009; Hickler et al. 2012).

Species characteristics influence model accuracy

Species characteristics have been shown to influence model accuracy and many biological traits such as body size or dispersion rate and also population trends have been measured for evaluating their influence on modelling results (McPherson and Jetz 2007). Species with narrower or spatially more aggregated ranges (e.g. Segurado and Araújo 2004; Seoane et al. 2005) and higher habitat specialization (e.g. Poyry et al. 2008; Seoane and Carrascal 2008) can generally be predicted with higher accuracy. Our results support the conclusions from these studies, as the species with the highest accuracy values across all model types (climate, vegetation, landscape configuration and global) included high-mountain species with very narrow ranges and low prevalence, such as Tengmalm's owl *Aegolius funereus*,

bearded vulture *Gypaetus barbatus*, rock ptarmigan *Lagopus mutus*, capercaillie *Tetrao urogallus* and ring ouzel *Turdus torquatus*. In our study, the ranking of species by accuracy values was similar across models as it was shown when future projections for the subgroup of species with good model performance were compared (Figure 2). Therefore, other relevant environmental or biological predictors might be required for those species that were difficult to model.

The importance of predictors is species specific

It is difficult to determine what are the most important environmental variables constraining species distributions, especially when a large number of species is considered. Nevertheless, we note that most of the divergence in future projections was caused by species that were difficult to model with our predictors, i.e., that performed poorly with the measures of discrimination ability used to verify model performance. Models discriminating data well yielded less variable projections into the future. More work is needed to identify whether animal species can be grouped based on their response to global environmental changes as well as identify which functional traits made them more resistant to these changes.

We conclude that the discrimination ability of envelope models is not always improved by inclusion of vegetation and landscape configuration variables. In the particular case of bird species in the Iberian Peninsula, climate was sufficient to describe current distributions for ca. 50% of the species and in some of the remaining cases vegetation could help improving the fit of the models but not landscape configuration. With our data and analysis, no general patterns emerged with regards to the selection of vegetation variables by models of different guilds of species. So, the decision as to whether to include specific non-climatic factors in the models requires case specific considerations based on the auto-ecology of the species.

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Authors' contribution

MT, WT and MBA conceived and designed the experiments. MT and WT analysed the data. TH contributed with data. MT wrote the paper with significant contributions from MBA, MC, TH and WT.

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Supplementary Material

Table S1. Main habitats (G = grassland, S = shrubland, F = forest, O = others) for the 168 bird species included in the study. The information was gathered from the Spanish Atlas of Breeding Birds (Martí and del Moral 2003) and complemented by consultation with the following experts: Carlos Ponce, Sergio Pérez Gil and Alejandro Aparicio Valenciano.

Common name	Scientific name	Main habitat
Goshawk	*Accipiter gentilis*	F
Eurasian Sparrowhawk	*Accipiter nisus*	F
Long-tailed Tit	*Aegithalos caudatus*	F
Tengmalm's Owl	*Aegolius funereus*	F
Eurasian Black Vulture	*Aegypius monachus*	F
Skylark	*Alauda arvensis*	G/S
Common Kingfisher	*Alcedo atthis*	F
Red-legged Partridge	*Alectoris rufa*	G/S
Tawny Pipit	*Anthus campestris*	G/S
Water Pipit	*Anthus spinoletta*	G/S
Tree Pipit	*Anthus trivialis*	S/F
Common Swift	*Apus apus*	O
White-rumped Swift	*Apus caffer*	O
Pallid Swift	*Apus pallidus*	O
Iberian Imperial Eagle	*Aquila adalberti*	S/F
Golden Eagle	*Aquila chrysaetos*	G/S/F
Short-eared Owl	*Asio flammeus*	G
Long-eared Owl	*Asio otus*	S/F
Little Owl	*Athene noctua*	S/F
Eurasian Eagle Owl	*Bubo bubo*	S/F
Cattle Egret	*Bubulcus ibis*	G/S
Eurasian Thick-knee	*Burhinus oedicnemus*	G
Common Buzzard	*Buteo buteo*	G/S/F
Greater Short-toed Lark	*Calandrella brachydactyla*	G
Lesser Short-toed Lark	*Calandrella rufescens*	G/S
European Nightjar	*Caprimulgus europaeus*	F
Red-necked Nightjar	*Caprimulgus ruficollis*	S/F

Linnet	*Carduelis cannabina*	G/S
European Goldfinch	*Carduelis carduelis*	G/S
European Greenfinch	*Carduelis chloris*	S/F
Eurasian Siskin	*Carduelis spinus*	F
Rufous-tailed Scrub-robin	*Cercotrichas galactotes*	S
Short-toed Treecreeper	*Certhia brachydactyla*	F
Common Treecreeper	*Certhia familiaris*	F
Cetti's Warbler	*Cettia cetti*	O
Dupont's Lark	*Chersophilus duponti*	S
White Stork	*Ciconia ciconia*	G/F
Black Stork	*Ciconia nigra*	F
Short-toed Snake-eagle	*Circaetus gallicus*	F
Northern Harrier	*Circus cyaneus*	G/S
Montagu's Harrier	*Circus pygargus*	G/S
Zitting Cisticola	*Cisticola juncidis*	G
Great Spotted Cuckoo	*Clamator glandarius*	S
Haw finch	*Coccothraustes coccothraustes*	S/F
Stock Dove	*Columba oenas*	G/S/F
Common Wood-pigeon	*Columba palumbus*	F
European Roller	*Coracias garrulus*	S/F
Common Raven	*Corvus corax*	F
Carrion Crow	*Corvus corone*	F
Jackdaw	*Corvus monedula*	G/S/F
Common Quail	*Coturnix coturnix*	G/S
Common Cuckoo	*Cuculus canorus*	F
Azure-winged Magpie	*Cyanopica cyana*	F
House Martin	*Delichon urbica*	O
Great Spotted Woodpecker	*Dendrocopos major*	F
Middle Spotted Woodpecker	*Dendrocopos medius*	F
Lesser Spotted Woodpecker	*Dendrocopos minor*	F
Black Woodpecker	*Dryocopus martius*	F
Black-winged Kite	*Elanus caeruleus*	G/S
Corn Bunting	*Emberiza calandra*	G/S

Rock Bunting	*Emberiza cia*	F
Cirl Bunting	*Emberiza cirlus*	F
Yellow hammer	*Emberiza citrinella*	S
Ortolan Bunting	*Emberiza hortulana*	S
European Robin	*Erithacus rubecula*	S/F
Lesser Kestrel	*Falco naumanni*	G
Peregrine Falcon	*Falco peregrinus*	O
Eurasian Hobby	*Falco subbuteo*	S/F
Common Kestrel	*Falco tinnunculus*	G/S/F
European Pied Flycatcher	*Ficedula hypoleuca*	F
Chaffinch	*Fringilla coelebs*	F
Crested Lark	*Galerida cristata*	G/S
Thekla Lark	*Galerida theklae*	S
Eurasian Jay	*Garrulus glandarius*	F
Bearded Vulture	*Gypaetus barbatus*	O
Griffon vulture	*Gyps fulvus*	G/S/F
Bonelli's Eagle	*Hieraaetus fasciatus*	G/S/F
Booted Eagle	*Hieraaetus pennatus*	F
Eastern Olivaceous Warbler	*Hippolais pallida*	S
Melodious Warbler	*Hippolais polyglotta*	S
Red-rumped Swallow	*Hirundo daurica*	G/S/F
Eurasian Wryneck	*Jynx torquilla*	F
Rock Ptarmigan	*Lagopus mutus*	G
Red-backed Shrike	*Lanius collurio*	S/F
Southern Grey Shrike	*Lanius meridionalis*	S/F
Woodchat Shrike	*Lanius senator*	S/F
Red Crossbill	*Loxia curvirostra*	F
Woodlark	*Lullula arborea*	G/S
Common Nightingale	*Luscinia megarhynchos*	S
Bluethroat	*Luscinia svecica*	G/S
Calandra Lark	*Melanocorypha calandra*	G
European Bee-eater	*Merops apiaster*	S
Black Kite	*Milvus migrans*	F

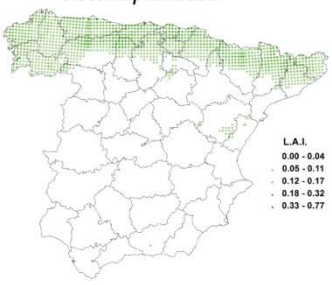
Red Kite	*Milvus milvus*	F
Rufous-tailed Rock-Thrush	*Monticola saxatilis*	O
Blue Rock-Thrush	*Monticola solitarius*	O
White-winged Snowfinch	*Montifringilla nivalis*	G
White Wagtail	*Motacilla alba*	G
Grey Wagtail	*Motacilla cinerea*	O
Yellow Wagtail	*Motacilla flava*	G
Spotted Flycatcher	*Muscicapa striata*	S/F
Egyptian Vulture	*Neophron percnopterus*	G/S
Black-eared Wheatear	*Oenanthe hispanica*	G/S
Black Wheatear	*Oenanthe leucura*	O
Wheatear	*Oenanthe oenanthe*	G/S
Golden Oriole	*Oriolus oriolus*	F
Great Bustard	*Otis tarda*	G
Scops Owl	*Otus scops*	S/F
Coal Tit	*Parus ater*	F
Blue Tit	*Parus caeruleus*	F
European Crested Tit	*Parus cristatus*	F
Great Tit	*Parus major*	F
Marsh Tit	*Parus palustris*	F
House Sparrow	*Passer domesticus*	G
Spanish Sparrow	*Passer hispaniolensis*	G
Tree Sparrow	*Passer montanus*	G/S
Grey Partridge	*Perdix perdix*	S
European Honey-buzzard	*Pernis apivorus*	F
Rock Sparrow	*Petronia petronia*	G/F
Black Redstart	*Phoenicurus ochruros*	S
Redstart	*Phoenicurus phoenicurus*	G/S
Western Bonelli's Warbler	*Phylloscopus bonelli*	F
Chiffchaff	*Phylloscopus collybita*	F
Magpie	*Pica pica*	S/F
Eurasian Green Woodpecker	*Picus viridis*	F
Alpine Accentor	*Prunella collaris*	S

Dunnock	*Prunella modularis*	G/S
Pin-tailed Sandgrouse	*Pterocles alchata*	G
Black-bellied Sandgrouse	*Pterocles orientalis*	G
Eurasian Crag Martin	*Ptyonoprogne rupestris*	O
Alpine Chough	*Pyrrhocorax graculus*	G
Red-billed Chough	*Pyrrhocorax pyrrhocorax*	G
Bullfinch	*Pyrrhula pyrrhula*	F
Firecrest	*Regulus ignicapilla*	F
Goldcrest	*Regulus regulus*	F
Penduline Tit	*Remiz pendulinus*	O
Sand Martin	*Riparia riparia*	O
Whinchat	*Saxicola rubetra*	G/S
African Stonechat	*Saxicola torquata*	G/S
Woodcock	*Scolopax rusticola*	F
Citril Finch	*Serinus citrinella*	F
European Serin	*Serinus serinus*	F
Nuthatch	*Sitta europaea*	F
Eurasian Collared Dove	*Streptopelia decaocto*	O
Turtle Dove	*Streptopelia turtur*	F
Tawny Owl	*Strix aluco*	G/F
Spotless Starling	*Sturnus unicolor*	O
Starling	*Sturnus vulgaris*	G
Black-capped Warbler	*Sylvia atricapilla*	S/F
Garden Warbler	*Sylvia borin*	S/F
Subalpine Warbler	*Sylvia cantillans*	S
Whitethroat	*Sylvia communis*	S
Spectacled Warbler	*Sylvia conspicillata*	S
Orphean Warbler	*Sylvia hortensis*	G/S
Sardinian Warbler	*Sylvia melanocephala*	S
Dartford Warbler	*Sylvia undata*	S
Alpine Swift	*Tachymarptis melba*	O
Capercaillie	*Tetrao urogallus*	G/S
Little Bustard	*Tetrax tetrax*	G

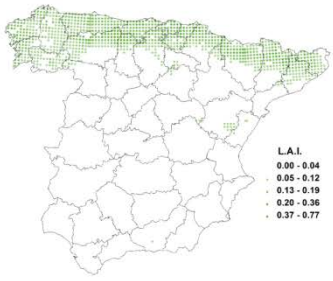
Wallcreeper	*Tichodroma muraria*	O
Winter Wren	*Troglodytes troglodytes*	S/F
Blackbird	*Turdus merula*	S/F
Song Thrush	*Turdus philomelos*	S/F
Ring Ouzel	*Turdus torquatus*	S
Mistle Thrush	*Turdus viscivorus*	F
Barn Owl	*Tyto alba*	G
Hoopoe	*Upupa epops*	G/S/F
Northern Lapwing	*Vanellus vanellus*	G

Figure S1. Comparison between the simulated LAI of the main tree species and presence data from the Third Spanish Forestry Inventory (IFN = Inventario Forestal Nacional). Inventory data was not available for all simulated tree species. The first column of maps represents the model outputs, the second column the result from the combination of LPJ-GUESS results with a land use dataset (see Materials and Methods for further details), and the third column represents the presence data of the IFN. The model reproduced the broad distinction between northern and southern trees, but the simulated distribution of more northerly distributed species generally expanded further to the south than according to the inventory data. This was too some extent expected as the model represented potential natural vegetation. The Mediterranean region has a long history of large-scale anthropogenic impacts. Most areas once occupied by forest were transformed into croplands and pastures hundreds and in many cases even thousands of years ago (e.g. Kaplan et al, 2009), while the rest of the remaining forest has been intensively managed (Bohn et al, 2003). Also the imposition of real land use patterns could only partly remove this mismatch because the land use data only distinguished forest and non-forest areas, without tree species-specific information. As a result, the simulated distribution was maintained in the simulated data as long as the land use data indicated that the forest cover was, at least, 10% (see Materials and Methods). Another explanation for the wider simulated ranges might be that the inventory might not cover all small outlier populations.

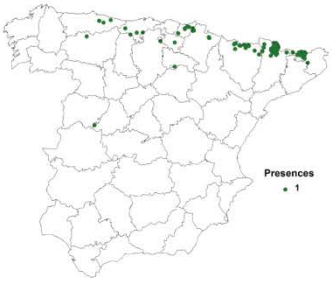
Betula pendula



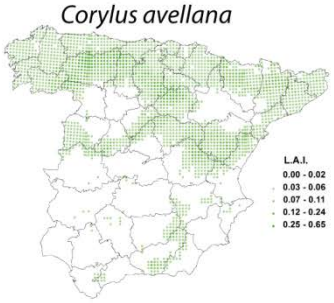
Betula pendula filtered by LU



Betula pendula from IFN



Corylus avellana



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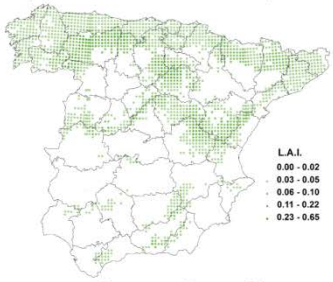

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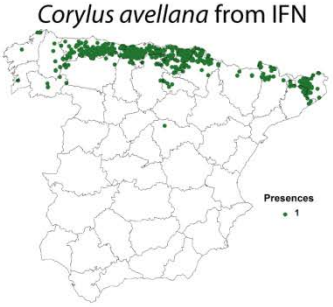
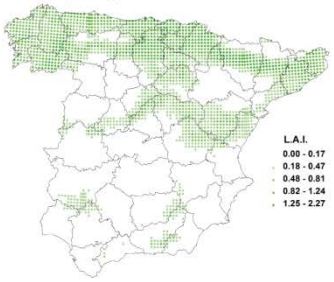


Fagus sylvatica



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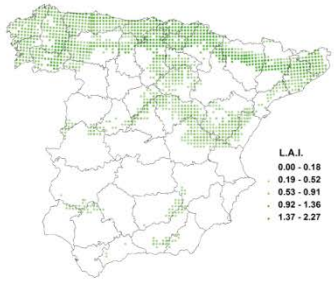

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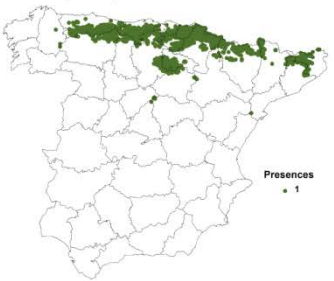
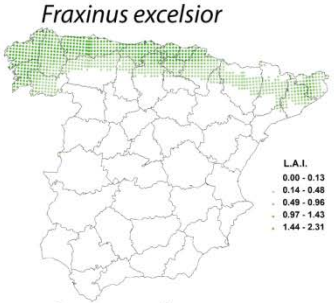


Fraxinus excelsior



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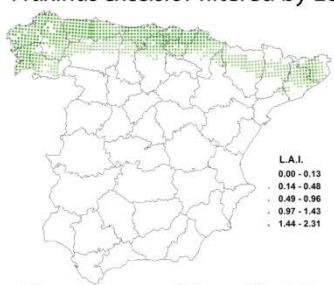
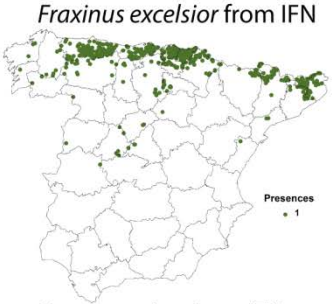
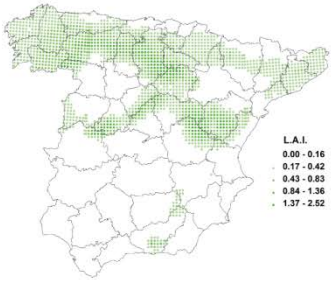


Fraxinus excelsior from IFN



Quercus robur



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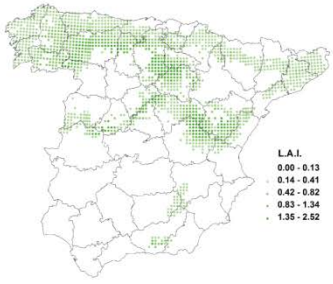
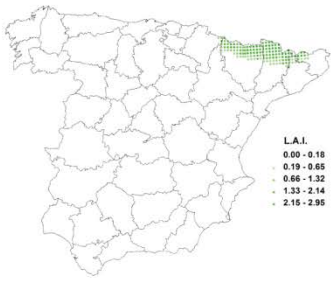


Quercus robur from IFN

Picea abies



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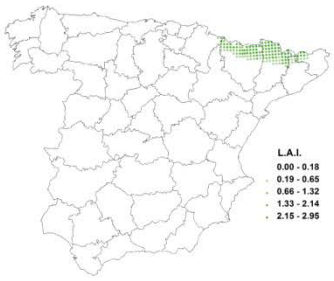
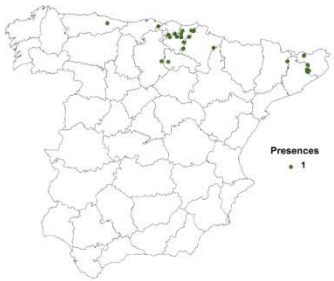
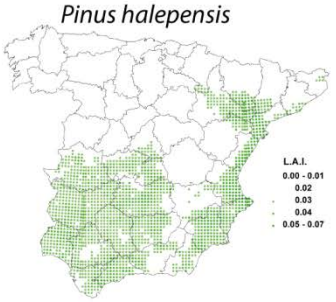


Picea abies from IFN



Pinus halepensis



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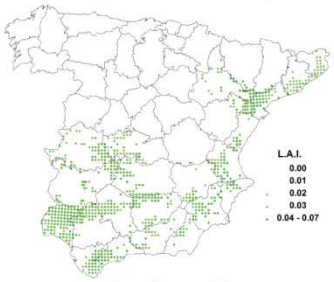

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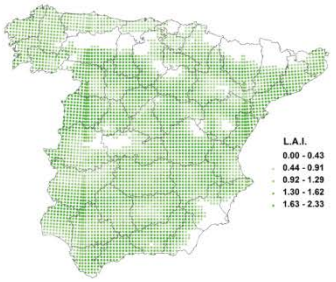
Quercus ilex



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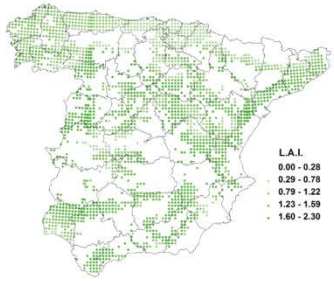

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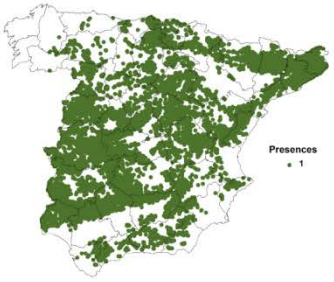
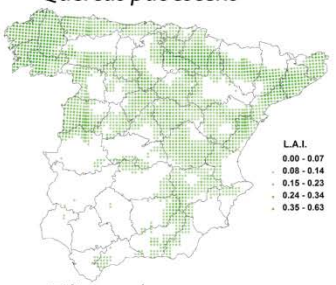


Quercus pubescens



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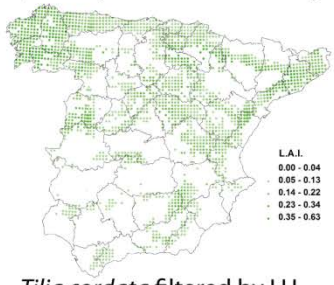

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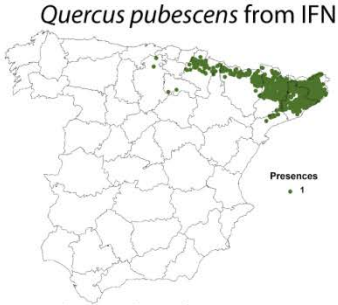
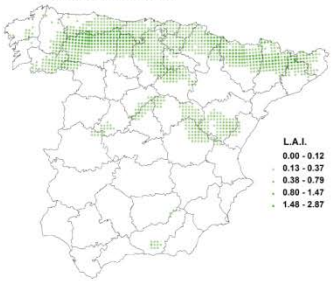


Tilia cordata



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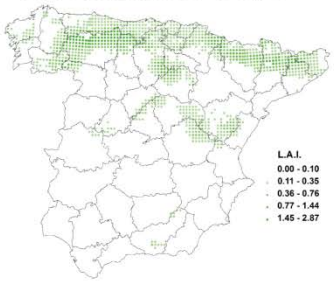

Tilia cordata from IFN

Chapter III

Risk assessment for Iberian birds under global change

Manuscript submitted to *Conservation Letters*

Risk assessment for Iberian birds under global change

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Abstract

Conservation policies are often implemented without consideration of the effects of environmental changes on biodiversity. However, changes in both climate and land cover are expected to threaten species persistence. In this study, we develop and implement an approach to rank bird species according to their exposure to future global environmental changes as well as to their intrinsic susceptibility to them. We first built environmental envelope models and projected future potential habitats under climatic, vegetation, and land cover changes. Then, we identified groups of bird species that a) are predicted to lose suitable environmental conditions in the future, b) possess characteristics that render them vulnerable to environmental changes, and c) are already categorized as 'threatened'. This evaluation framework enables proactive conservation prioritization of species in the face of global change.

***Keywords**:* Biological traits; Birds; Environmental envelope models; Global change; Iberian Peninsula; Local extinction risk; Vulnerability.

Introduction

There is growing evidence that global environmental changes are already affecting biodiversity and its effects are expected to become greater during the 21st century (e.g. Parmesan 2006). Recently, an increasing number of studies have used environmental envelope models to explore the impacts of global change on biodiversity (e.g. Pereira et al. 2010). These models relate known species distributions to environmental variables to project future potential distributions under global change. Environmental envelope models provide an estimate of the potential level of exposure of species distributions to global change, but they do not characterize species susceptibility to these changes (Araújo and Peterson 2012). Therefore, for a given level of exposure species will have varying abilities to respond to it. In order to carry out species risk assessments in the context of global change, it would be desirable, whenever possible, to combine measurements of exposure to threats with measurements of species vulnerability to them (e.g. Dawson et al. 2011; Foden et al. 2008; Williams et al. 2008).In this study, species' vulnerability is defined as the species intrinsic capacity to cope with changes without considering the level of exposure to them as part of it (Araújo and Williams 2000).

A species' capacity to cope with global change depends on a variety of biological characteristics including intrinsic species characteristics, such as fecundity rate, and other non-organismal characteristics such as range size. For the sake of simplicity, we refer to both organismal and non-organismal characteristics as 'traits', although only the former are traits in the strict sense (Violle et al. 2007). The idea that certain organismal traits like body size or fecundity make species more susceptible to extinction is well-established (e.g. Cardillo et al. 2006) and evidence has also been presented that non-organismal traits, such niche breadth, correlate with species vulnerability to external pressures (Williams et al. 2007). In recent years, some authors tried to go further and identify traits that would increase species vulnerability to global environmental changes (Angert et al. 2011; Devictor et al. 2012; Foden et al. 2008; Jiguet et al. 2007). For example, Foden et al. (2008) proposed groups of traits that are associated with species vulnerability to climate change, such as specialized habitat requirements or narrow environmental tolerances that are likely to be exceeded because of climate change. In a more specific study, Jiguet et al. (2007) found that traits associated with population declines of birds in France were: low ecological tolerance, low heat tolerance and small brood number.

Clearly, species extinction risks are determined not by the exposure to external threats or by organisms and non-organismal characteristics but by the interactions of all these factors. For example, once species population sizes (a non-organisms characteristic of a species) have been drastically reduced by anthropogenic land-use changes, they are more likely to be vulnerable to

stressors, such as climate change or diseases (Hof et al. 2011) (measures of exposure to threatening processes). In this study, we examine the combined effects of exposure and vulnerability of Iberian bird species distributions to environmental changes. Vulnerability is measured as the union of organismal and non-organismal trait measurements together with species IUCN conservation status. Specifically, we address the following questions: (i) Are species highly exposed to environmental changes also highly vulnerable to them?; (ii) Are species highly exposed to environmental changes highly threatened according to IUCN?; (iii) Are regions harbouring the greatest concentration of species highly exposed to environmental changes also the regions where vulnerable and threatened species occur?

Materials and Methods

Species and potential exposure to global change data

Environmental envelope models were used to quantify predicted range shifts for 168 breeding bird species in the Iberian Peninsula under global environmental change scenarios. Distributions data were extracted from the Spanish Atlas of Breeding Birds (Martí and del Moral 2003) and from the Portuguese Atlas of Breeding Birds (Equipa Atlas 2008) reporting the presence and absence of bird species in 5923 10x10 km resolution grid cells. We assessed the potential exposure of bird species to changes in climate, vegetation and landscape configuration using present (period 1971-1990) and future (period 2051-2080) model projections from a previous study (Triviño et al. 2011) (details in Appendix S1).

Traits data

We selected a number of traits, based on the literature (Table 1), that are prone to reflect species vulnerability to global change, especially for birds. The data compilation was restricted to a subset of 94 passerine bird species from the total 168 species because one of the traits, the 'habitat breadth' was only available for those species. Further details and justification on the selection of traits are included in Appendix S2.

Contemporary conservation status data

The conservation status of a species should be considered both at international and national levels because mismatches between national and international Red Lists have been reported (e.g. Marini and Garcia 2005) and conservation efforts should target species that are threatened at both regional and global scales. We used three different Red Lists to define the number of threatened (included in the Vulnerable (VU), Endangered (EN) or Critically Endangered (CR) categories) bird species in the Iberian Peninsula. We employed the IUCN Red

List of globally threatened species (4 species) from the IUCN webpage (www.iucnredlist.org), the Spanish Red List of nationally threatened species (23 species) (Madroño et al. 2004), and the Portuguese Red List (34 Species) (S.N.P.R.C.N. 1990) (Table 2).

Table 1 Bird traits used in this study as a proxy for vulnerability to environmental changes for the 94 bird species. For further details see Appendix S2.

Traits	Source of data	Sign (*)	Why it is included?
1. Mean nº of broods	www.enciclopediadelasaves.org	↓	Higher number of broods less mismatch with food peaks
2. Clutch size	www.enciclopediadelasaves.org	↓	Low reproductive rate more vulnerable
3. Length	www.enciclopediadelasaves.org	↑	Measure of body size: bigger species are more vulnerable
4. Habitat breadth	Extracted from Appendix I of the Spanish Breeding Atlas (Martí and del Moral 2003)	↓	Habitat specialization
5. Climatic niche breadth	Methodology used described in Appendix S2	↓	Environmental tolerance
6. Marginality	See Appendix S2	↑	Environmental tolerance
7. Relative range size	See Appendix S2	↓	Environmental tolerance

(*) The association to species vulnerability: 'arrows facing up' mean that the higher the trait values the higher the vulnerability and 'arrows facing down' are the other way around.

Table 2 Bird species included in different IUCN conservation status categories (excluding Data Deficient (DD) species) at a national level (Portugal (N = 162) and Spain (N = 165) and at a global scale (N = 168).

IUCN conservation status category						
Location	**EX**	**CR**	**EN**	**VU**	**NT**	**LC**
Portugal	4 (2.5%)	8 (4.9%)	10 (6.2%)	16 (9.9%)	18 (11.1%)	106 (65.4%)
Spain	0 (0%)	0 (0%)	8 (4.8%)	15 (9.1%)	12 (7.3%)	130 (78.8%)
Global	0 (0%)	0 (0%)	1 (0.6%)	3 (1.8%)	5 (3%)	159 (94.6%)
Combined	0 (0%)	8 (4.8%)	14 (8.3%)	22 (13.1%)	22 (13.1%)	102 (60.7%)

Data analysis

Bird species were classified into groups based on their potential level of exposure to global change. We followed the methodology used in the Iberian Atlas of Climate Change Impacts on Biodiversity (Araújo et al. 2011b), which classifies species into four groups:

- (i) 'Expanding species': Percentage of potential area lost < 0
- (ii) 'Stables species': 0 < Percentage of potential area lost < 30
- (iii) 'Contracting species': 30 < Percentage of potential area lost < 70
- (iv) 'Major contracting species': Percentage of potential area lost > 70

The percentage of potential area lost, equated to a measure of potential exposure, was calculated using the following equation:

$$Potential\ area\ lost = (t2p - t1p)\ x\ 100\ /t1p \quad (1)$$

Where $t2p$ is the future potential area occupied by the species and $t1p$ is the present potential area occupied by the species.

We calculated the fraction of the 168 bird species (subsets of contracting, stable and expanding species) included in each one of the national and international IUCN categories (Spain, Portugal and global) and in a combined conservation status index. This is an accumulative index based on species' national and global IUCN conservation status and if the species is endemic to the study area (further described in Rocha et al. 2009). For example, a species that it is endangered at the national scale (2 points), vulnerable at the global scale (1 point) and endemic to the Iberian Peninsula (1 point) would have an index value of 4 points.

A Principal Component Analysis (PCA) was carried out to reduce dimensionality in the species traits database. From the PCA we retained the three first principal components that explained the greatest proportion of variation in the data (65%; details in Appendix S3).

In order to link the different levels of (i) potential exposure, (ii) vulnerability to changes, and (iii) current conservation status, the following statistical analyses were carried out. The association between the potential level of exposure to global change and the traits (represented by the three principal components) was tested using a Kruskal-Wallis test. Furthermore, the level of potential exposure was regressed against each of the three first principal components of the PCA, using generalised linear models (GLMs). Because species are linked by their evolutionary history, we checked whether exposure showed any phylogenetic signal that would prevent us from using traditional linear regression (Blomberg et al. 2003). We calculated the lambda estimate (Pagel 1999) using the molecular phylogeny at the species level from Thuiller

et al. (2011). There was no phylogenetic signal in the exposure variable (lambda = 0.0001). The association between potential level of exposure to global change and the current conservation status was represented using bar plots and the statistical differences tested with a χ^2 test.

We plotted the potential exposure to future global change against the species potential vulnerability for the subset of 94 passerine species to identify species facing higher risk of local extinction. The potential vulnerability was the result of multiplying each individual principal component by the combined conservation status.

Results

The PCA that was carried out to reduce dimensionality in the vulnerability traits showed that the first component was negatively related to climatic niche breadth, habitat breadth, and relative range size. These measures are all associated with environmental tolerance. The second component was positively related to clutch size and negatively related to body size. These measures are associated with fecundity (Bohning-Gaese et al. 2000). Finally, the third component was positively associated to number of broods and niche position (marginality). Although the first factor is associated with fecundity, the second provides a measure of the biogeographic context, i.e., species with high niche position use environments that are very abundant in the study area, suggesting that the third component measures the independent effects of fecundity that are associated with environmental favourability. Consequently, the interpretation was that, for PC1, the higher the values the higher the vulnerability, and for PC2 and PC3 the opposite was assumed.

Out of the 168 breeding bird species, 90 were modelled as being potentially expanding in the Iberian Peninsula, 52 were potentially stable, and 26 were potentially contracting. There was no bird species included in the category of 'major contracting species'. This first classification was used to determine if the species that are potentially susceptible to global change are the same as those already identified as threatened by the IUCN Red List. A second classification was done for the subset of 94 passerine bird species for which traits were available and the results obtained were: Expanding species = 36, Stable species = 38 and Contracting species = 20.

Are species more exposed to environmental changes also more vulnerable to them?

The three groups of bird species (expanding, stables and contracting) differed significantly in their traits, as summarized using the three principal components (Kruskal-Wallis test for PC1: $p < 0.001$; for PC2: $p < 0.05$ but for PC3 there were no significant differences: $p >$

0.05). The expanding species were the most vulnerable (see Figure 1: higher values of PC1 and lower values of PC2 and PC3). The differences between contracting and stable species were not significant (Wilcoxon test, $p < 0.05$) (Table 3), whereas significant differences were found between the stables and the expanding groups for PC1 and PC2.

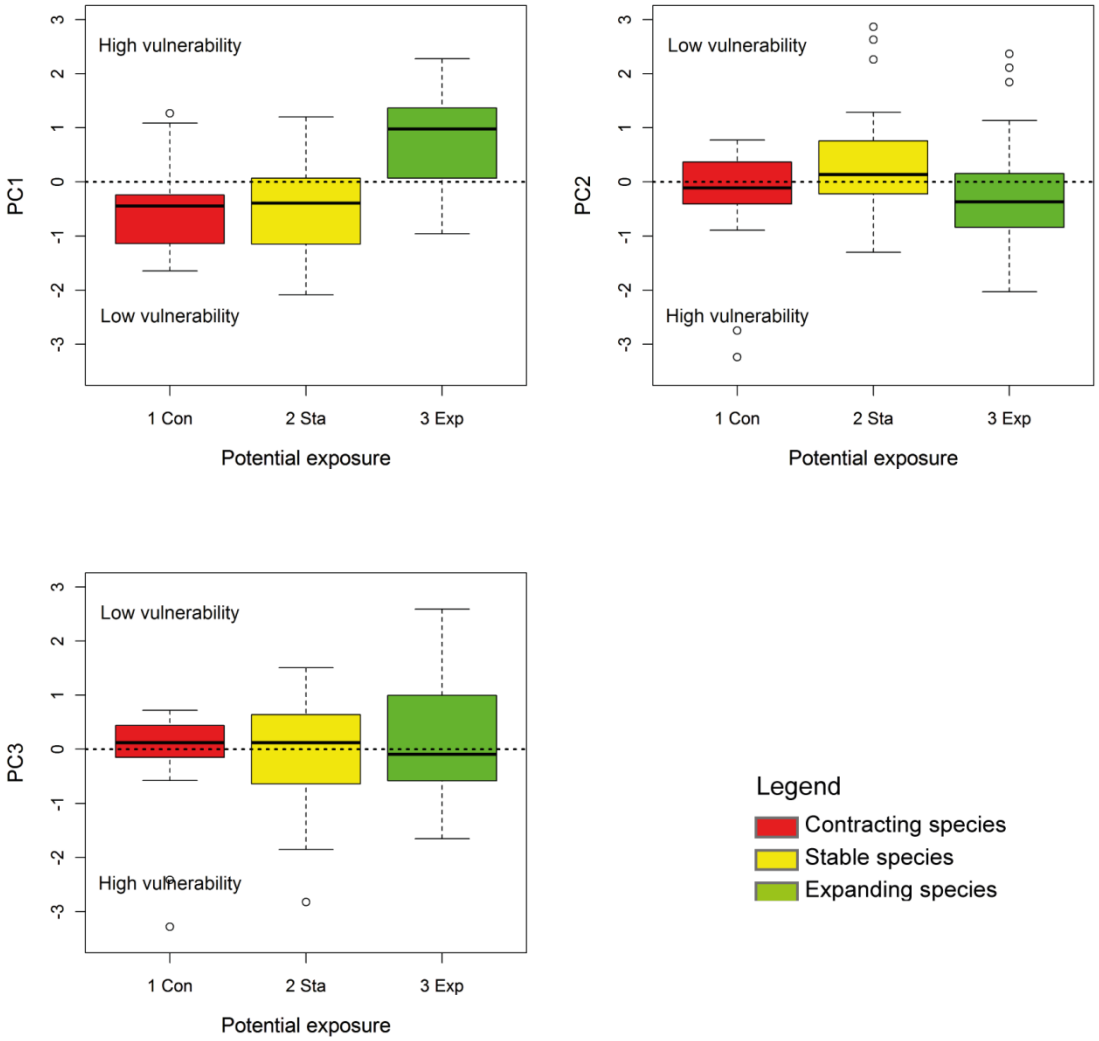

Figure 1 Boxplots comparing the traits of the three groups of bird species based on their potential exposure to future global change ("1 Con": contracting species, "2 Sta": stables species and "3 Exp": expanding species). The traits were summarized using each of the three principal components axes (PC1, PC2 and PC3) respectively.

The outputs from the Generalised Linear Models (GLMs) showed that the best statistical model, according to the Akaike information criterion (AIC), was the model including the three components of the PCA as predictor variables. The second best model included PC1 and PC3 as

predictors and it was followed by the individual model including PC1 (Table 4). The inclusion of second order polynomial of explanatory variables to account for potential nonlinear relationships did not improve AIC values, so we report results only from the linear fits.

Table 3 Results of pair wise Wilcoxon test of distribution of the traits in the three different groups ("Con": Contracting species (N= 20), "Sta": Stables species (N=38) and "Exp": Expanding species (N=36)).

Principal Component 1			Principal Component 2			Principal Component 3		
Con-Sta	**Sta-Exp*** **	**Con-Exp*** **	**Con-Sta**	**Sta-Exp** **	**Con-Exp**	**Con-Sta**	**Sta-Exp**	**Con-Exp**
W = 373	*W* = 1154	*W* = 646	*W* = 447	*W* = 447	*W* = 322	*W* = 373	*W* = 731	*W* = 387
p = 0.83	***p* = 7.5e-08**	***p* = 4e-06**	*p* = 0.14	***p* = 0.0099**	*p* = 0.35	*p* = 0.83	*p* = 0.617	*p* = 0.916

* = $p < 0.05$; ** = $p < 0.01$; *** = $p < 0.001$

Table 4 Generalized linear models of the level of environmental exposure with the three first principal components of the PCA for 94 passerine bird species in the Iberian Peninsula. Gaussian family; Res. Deviance: Residual deviance; DF: degrees of freedom; AIC: Akaike information criterion.

Variable	AIC	Null Deviance	Res. Deviance	DF	Pr(>|t|)
PC1	1129.9	1098968	857409	92	**1.88e-06*** **
PC2	1151.8	1098968	1082382	92	0.2382
PC3	1147.4	1098968	1033134	92	**0.0174***
PC1 + PC2	1128.4	1098968	808618	90	0.0615
PC1 + PC3	1112.5	1098968	682704	90	**0.00027*** **
PC2 + PC3	1140.7	1098968	921682	90	**0.003** **
PC1+PC2+PC3	1105.5	1098968	582315	86	**0.00076*** **

* = $p < 0.05$; ** = $p < 0.01$; *** = $p < 0.001$

Are species highly exposed to environmental changes highly threatened according to IUCN?

The species less exposed to global change (expanding) were the ones currently most threatened (Figure 2). There was a significant difference between expanding and stable species (χ^2 test, p <0.001), as well as between expanding and contracting species (χ^2 test, p <0.001). However, there were no differences in threat category between contracting and stable species (χ^2 test, p = 0.104).

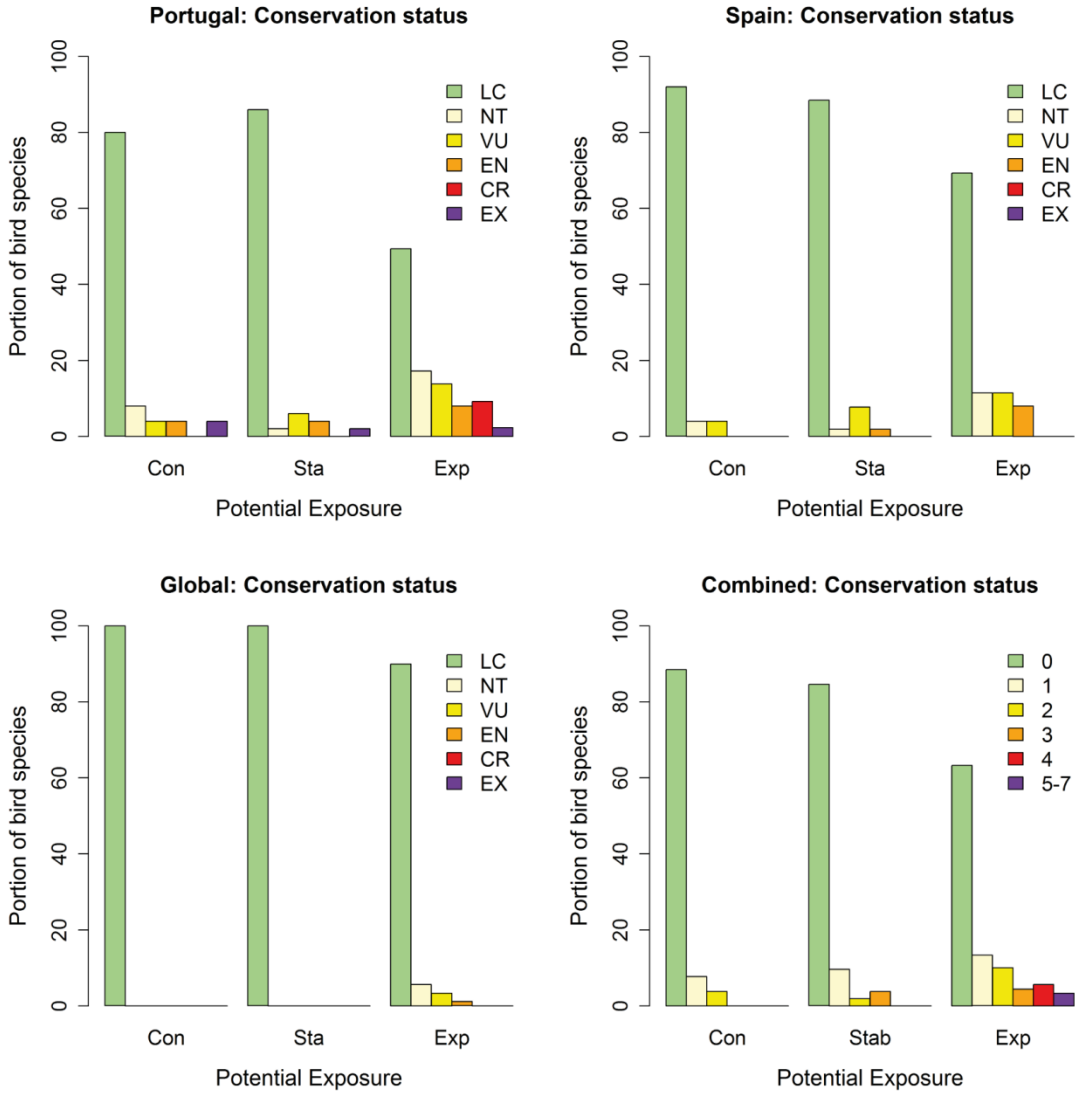

Figure 2 Bar plots comparing the distribution of the IUCN conservation status (LC = Least Concern; NT = Near Threatened; VU = Vulnerable; EN = Endangered; CR = Critical Endangered and EX = Extinct) and the combined conservation status (for Portugal, Spain and Global according to the method from Rocha et al, (2009)) among the three groups of species: "Con": Contracting (N = 26), "Sta": Stables (N = 52) and "Exp": Expanding (N = 90) for the 168 bird species considered.

Are regions harbouring the greatest concentration of species highly exposed to environmental changes also the regions where vulnerable and threatened species occur?

High risk regions differ in spatial patterns based on the information used. Based on the environmental envelope models, the species more exposed to expected global change, i.e., the species potentially contracting their ranges, were mainly located in the north-western part of the Iberian Peninsula, whereas the expanding species were located in dry and warm areas in the southern part of the Iberian Peninsula (Figure 3: E, F). However, the information provided by the species traits indicates a different spatial distribution of the species most at risk. On the one hand, the most vulnerable species, measured through their environmental tolerances, are concentrated in the mountainous areas. On the other, the most vulnerable species, measured through fecundity traits, were located in the Mediterranean region. Values from the third principal component showed that the most vulnerable species were concentrated in the northern region of the Iberian Peninsula (Figure 3: A-C). The highest concentration of currently threatened species was located in flat and lowland areas which are dominated by croplands (Figure 3: D).

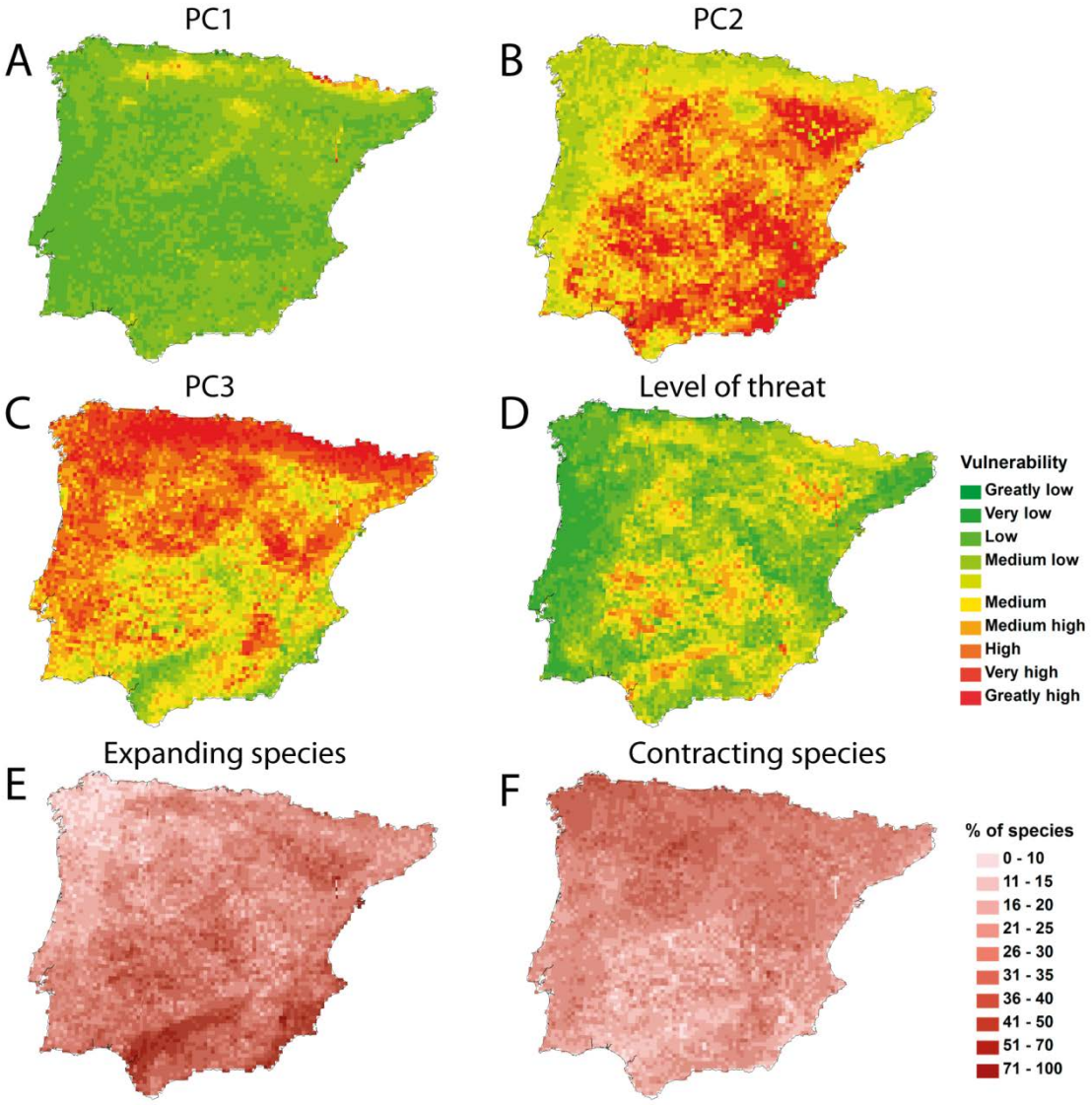

Figure 3 Risk spatial patterns. The maps A, B and C represent the mean values of PC1, PC2 and PC3 respectively for the total number of bird species (N = 94) occurring in each 10 km cell. The colour scale of PC2 and PC3 were inverted to match with the PC1 scale. The original numerical scale (ranging from -2.44 to 0.42) was converted to a categorical one to express the level of vulnerability in each 10 km cell. The map D represents the mean 'combined' conservation status of the species present in the cell. The original numerical scale (ranging from 0 to 9) was converted to the same categorical bar scale as the PCA maps. Finally, the maps E and F represent the proportion of expanding (N = 36) and contracting (N = 20) bird species respectively in each 10 km cell.

Discussion

Our study shows that risk assessments that combine estimates of species exposure to environmental changes together with metrics reflecting their intrinsic ability to cope with them provide a relatively less pessimistic view of risks than evaluations based solely on estimates of exposure. Specifically, in our study, species expected to be highly exposed to future global environmental changes were shown to be currently less threatened and possess traits that make them less vulnerable to local extinction than less exposed species. However, our analyses also reveal that a large proportion of the species that are not currently threatened could become threatened in the future as a result of climate, vegetation, and land use changes (Figure 2). Results are contingent on the particular group of species and region studied, but they highlight that species with different traits have different abilities to cope with threats and that coincidence between exposure to a threat and vulnerability to it cannot be taken for granted.

Conservation prioritization often focuses on areas with high species richness and great concentrations of endemic or threatened species (Myers et al. 2000). Our results demonstrate that such a strategy would be insufficient to tackle the challenges brought by global environmental changes (see also, Araújo et al. 2004). More specifically, in our study area, focusing conservation on high-rich areas would lead to overlooking areas with high exposure to future threats and/or high concentrations of vulnerable species (e.g. Cardillo et al. 2006). Estimates of global environmental change risk for biodiversity might be under- or over-estimated depending on the methodology and assumptions employed in the assessments (e.g. Chin et al. 2010). Our study indicates that projections that do not consider species capacity to cope with environmental changes overestimate local extinction risk. It is unclear how different uncertainties will act together to increase or decrease risk. For instance, the consideration of physiological and behavioural responses, as well as the genetic and plastic capacity of species, might provide lower estimates of local extinction risk. On the other hand, the inclusion of factors such as co-extinction, synergies and tipping points are expected to increase the estimates (Bellard et al. 2012). For example, a previous study with vertebrates in Europe (Araújo et al. 2011c) showed that highly exposed species to climate change were often poorly connected in a modelled network of species interactions and therefore they were less likely to be important for the stability of interaction networks.

Once species are ranked based on their potential risk to global change, how should such information be accounted for in processes leading to location and allocation of conservation resources? Advocates of triage, the process of prioritising the allocation of limited resources to maximise conservation returns, suggest that the management of species must be based on

concepts of cost-efficiency (e.g. Bottrill et al. 2008; Myers 1979; Wilson et al. 2011). Opponents of triage argue that the philosophical and functional consequences of letting threatened species go extinct cannot be afforded (e.g. Jachowski and Kesler 2009; Pimm 2000). We propose that species rankings based on assessments of exposure and vulnerability can help to inform a triage process. Rankings, when based on multivariate assessments of vulnerability, can be used to identify conservation actions that are appropriate for the specific threats faced by the species. In some cases, proactive conservation (prioritizing areas with low vulnerability) might be suitable, whereas in other cases reactive conservation (prioritizing areas with high vulnerability) might be the socially accepted solution (Brooks et al. 2006). For example, following the conceptual scheme in Figure 4, in line with the irreplaceability/vulnerability framework proposed by Margules and Pressey (2000), one could argue that no conservation actions are needed for species in the 'green area'. Furthermore, species located in the 'yellow area' are already identified as threatened, implying that some conservation actions are already taking place. Special attention should be paid to species located in the 'orange area' because they are not the object of conservation actions yet, but may need them in the future. Therefore, monitoring schemes and proactive conservation tools to face the threat of global change are needed for these species. Finally, the species located in the 'red area' are the species with the highest risk of local extinction and on which conservation efforts should concentrate if the costs and resources do not exceed the benefits of preserving them. Moreover, there were few species threatened at the same time both by high potential exposure to environmental changes and high vulnerability to them (see risk matrices included in Appendix S4). Different conservation actions might likewise be needed in different geographical areas depending on what the regional cause of concern is. For example, if potentially expanding species are not able to colonize new areas because of landscape fragmentation, then a reasonable conservation measure might be to increase connectivity between suitable habitats (Heller and Zavaleta 2009).

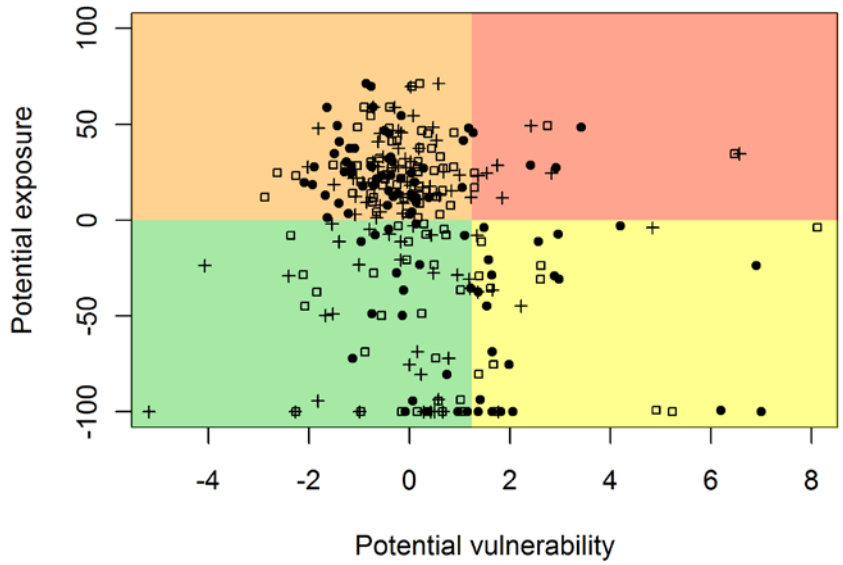

Figure 4 Plot integrating the different components to carry out the bird risk assessment. The values of potential exposure to global change were plotted against the potential vulnerability for the subset of 94 species. The potential vulnerability was calculated multiplying the values from the PCA (species traits) and the combined conservation status (LC = 0; NT = 1, VU = 2; EN = 3; CR = 4 and EX = 5). PCA values: 'black circles' = PC1, 'empty squares' = PC2 and 'crosses' = PC3. The potential exposure axis was divided, following the methodology used in Araújo et al. (2011a) into values below zero (including the expanding species) and values above zero (including the contracting and stable species). In the potential vulnerability axis, the third quartile of the first principal component was used as a splitting point. The 'green area' is occupied by species expected to expand their future ranges and that have low vulnerability. The 'yellow area' depicts regions with species already threatened that are not expected to be exposed to future threats. The 'orange area' is represented by species not yet threatened but that might become threatened in the future due to climate, vegetation and/or land use changes. Finally, the 'red area' is where species are highly exposed and highly vulnerable.

Conclusions

Conservation biology seeks to develop the science required to improve the persistence prognoses of species. Here, we identify Iberian bird species expected to be highly exposed and susceptible to environmental changes, and identify areas where many species at high risk are located. Identifying species likely to become highly threatened in the future is important for priority setting, especially when declines are hard to stop once underway. Moreover, determining species susceptible to future threats could complement monitoring schemes in the Red list status and offer an alternative to conservation plans focusing only on species experiencing high current risk of extinction.

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Appendix S1: Description of data and methods to calculate the potential exposure to global change.

We assessed the potential exposure of 168 bird species to environmental global change using present and future model projections from a previous study (Triviño et al. 2011). Our analyses excluded marine and aquatic species because modelling of their habitats would require predictor variables that were not available to us. Species with less than 20 records were also excluded to avoid problems of modelling species with small sample sizes (Stockwell and Peterson 2002). Two ensemble forecasting methods (Araújo and New 2007): Random Forests (RF) and Boosted Regression Trees (BRT) were used. A consensus approach based on the mean of the probabilities from the sets of projections made by RF and BRT was selected (Marmion et al. 2009) and TSS method was chosen to convert probabilities values into presence-absence data. We used 23 predictor variables that include: (i) climate (3 variables), (ii) vegetation characteristics: simulated potential natural vegetation using the mechanistic model LPJ-GUESS (Hickler et al. 2012) combined with land uses (17 variables) and (iii) the vegetation landscape configuration (3 variables). For projecting the future bird ranges we used a European climate scenario from the EU framework program Assessing Large-scale environmental Risks for biodiversity with tested Methods (ALARM) at a resolution of 10' for the period 2051-2080 (Fronzek et al. 2012). The climate scenario was derived from a simulation with the global climate model HadCM3, using the BAMBU (Business As Might Be Usual) scenario (which corresponds to A2 SRES) of the ALARM project. Scenarios for future potential natural vegetation were created with a dynamic model of the potential natural vegetation of Europe (Hickler et al. 2012), which resembled main actual features of the vegetation of Iberian Peninsula (Triviño et al. 2011), as well as the scenarios for future land use change (Rounsevell et al. 2006). Both land use projections and potential vegetation cover from LPJ-GUESS were also based on the BAMBU scenario (Spangenberg 2007) (for details see Dendoncker et al. 2006 ; Rounsevell et al. 2006). Models were assessed using four evaluation methods: the area under curve (AUC) of the receiver operating characteristic (ROC), the true skill statistics (TSS), sensitivity that measures the percentage of presences correctly predicted and specificity that measure the percentage of absences correctly predicted (for further details see Triviño et al. 2011).

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Appendix S2: Description of selection of biological characteristics used for the study

The need to incorporate biological characteristics or 'traits' into global change studies is increasingly acknowledged. Trait-based research has undergone a rapid expansion in recent years (Naeem and Bunker 2009) and a paradigm shift from studies of individual species to functional traits is expected (Kattge et al. 2011). Traits could be a good surrogate of species performance (Violle et al. 2007), trait-based analyses could be compared with results of envelope models (Thuiller et al. 2010) or they could be used for supporting the establishment of conservation priorities (Loyola et al. 2008).

The biological characteristics estimated in this study were: (i) Average number of broods per year, as the product of average clutch size and average number of broods per year. There is increasing evidence that birds are advancing their date of laying eggs associated with increasing mean temperature. Many times, this advance does not coincide with seasonal peaks of food abundance, which affect the reproductive success in birds (Both et al. 2009; Dunn and Winkler 2010; Jiguet et al. 2007; Thackeray et al. 2010). Species with the capacity to have multiple broods will have more opportunities to synchronize with peaks of food abundance, so if the first brood does not coincide with a peak of food, the second or the third might; (ii) Clutch size, as the average number of eggs per clutch. This trait was included as a measure of fecundity as low fecundity is associated to higher vulnerability to extinction; (iii) Body size, characterized by the mean length of the species. Large body size has been associated to extinction proneness because larger-bodied species often have lower reproductive rates (e.g. Pimm et al. 2006) and longer generation times (e.g. Cardillo and Bromham 2001) that increase the replacement time. However, recent studies have questioned the correlation between body size and extinction (Amano and Yamaura 2007; Fritz et al. 2009; Pocock 2010). Another measure of body size, wingspan, was also collected but it was not included in the study because it was highly correlated with the longitude (Spearman's correlation, $r = 0.95$); (iv) Habitat breadth, as a measure of habitat specialization. Habitat generalist species are likely to be able to tolerate a greater level of environmental changes than specialized species (Foden et al. 2008). The study carried out by Julliard et al. (2004) showed that specialized bird species were declining at much higher rates than generalists in France; (v) Niche breadth, as a measure of environmental tolerance. Narrow environmental tolerance makes species more vulnerable to environmental changes (e.g. Ehrenfeld 1970; Foden et al. 2008); (vi) Relative range size, as the ratio between the total number of presences and the total number of grid cells in the study area. The extent of the study area is the same for all the bird species. Relative range size was included as a measure of rarity that it is considered as one of the best predictors of extinction likelihood (McKinney

1997 and references therein); (vii) Marginality, as a measure of niche specialization because low values correspond to the ubiquitous or generalists species (Dolédec et al. 2000).

Values of habitat breadth were extracted from the Appendix I of the Spanish Atlas of Breeding Birds (Martí and del Moral 2003) and the methodology used was described by Carrascal and Lobo (2003). The habitat breadth index was calculated following the Levins index divided by the number of habitat categories (n) considered (Levins 1968):

$$\mathrm{HB} = \frac{(\Sigma p_i^2)^{-1}}{n}$$

where p_i is the proportion of the density for each species measured in the habitat i (dividing density in habitat i by the sum of all densities recorded in the n habitat categories. In this particular case, n = 6). This index ranges between 0.17 (only present in one habitat) and 1 (evenly distributed across the 6 habitats).

Niche breath and marginality (niche position) were calculated at European level based on an ordination approach termed 'outlying mean index' (OMI) developed by Dolédec et al. (2000). OMI estimates the range of environmental conditions used by each species (niche breath) as well as the species average position (niche position) within environmental space (for further details see Dolédec et al. 2000; Hof et al. 2010; and for case studies see Thuiller et al. 2004).

We collected information of other species-specific characteristics that were finally not included in the study because of various types of reasons. For example, the quality of the data of the 'diet specialization' trait was not good enough to be included. We also collected information of the 'migratory status' but for most of species there was not a unique classification, e.g. Alauda arvensis have 'resident' and 'wintering' populations; thus 'migratory status' was excluded from the study.

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Appendix S3: Description of the Principal Component Analysis (PCA)

Variables used to perform the PCA and their association to vulnerability to environmental changes:

1) Mean nº of broods

2) Clutch size (nº eggs/ brood)

3) Length (as a measure of body size).

4) Habitat breadth.

5) Climatic niche breadth (at European scale).

6) Marginality (at European scale).

7) Relative range size.

The selection of the three first components was based on the rule of thumbs of selecting eigenvalues higher than one (Table S1).

Table S1: Eigenvalues of the correlation matrix and related statistics.

	Eigenvalue	% Total variance	Cumulative Eigenvalue	Cumulative variance
PC1	1.886277	26.94682	1.886277	26.9468
PC2	1.376986	19.6712	3.263264	46.6181
PC3	1.285915	18.37022	4.549179	64.9883
PC4	0.944911	13.49873	5.494090	78.4870
PC5	0.600112	8.57303	6.094202	87.0600
PC6	0.561618	8.02311	6.655820	95.0831
PC7	0.344180	4.91686	7.000000	100.0000

Table S2: Eigenvectors of the correlation matrix

Trait	PC1	PC2	PC3
Nº broods	-0.33350016	0.210211087	0.562372309
Clutch size	0.00866691	0.582910472	0.478520376
Length	0.077404483	0.579803511	0.473393559
Habitat breadth	0.520626545	0.014599089	0.052273634
Climatic niche breadth	0.374316258	0.405159036	0.105953138
Marginality	0.27987633	0.336518044	0.465082447
Relative range size	0.627069098	0.047362401	0.019846707

Figure S1 Scree plot of the PCA

Appendix S4: Risk matrices

Risk matrices were created for the identification of the species most at risk. In the matrices, 'Potential exposure' was subdivided in the following categories: High = Contracting species; Medium = Stable species and Low = Expanding species. In the matrix from Table S3, 'Potential vulnerability' was calculated combining the traits information with the IUCN conservation status. First, each one of the three principal components was subdivided into three levels of vulnerability: High = for PC1 values above third quartile (75-100%), for PC2 and PC3 values below first quartile (0-25%); Medium = for PC1, PC2 and PC3 values between first and third quartile (25-75%); High = for PC1 below first quartile (0-25%) and for PC2 and PC3 above the third quartile (75-100%). Then, IUCN categories were classified into: High = Critical Endangered (CR) and Endangered (EN) species, Medium = Vulnerable (VU) species and Low = Near Threatened (NT) and Least Concern (LC) species.

Table S3. Risk matrix (subset of 94 species). *Potential Exposure* was subdivided into: H: High (Contracting, N = 20); M: Medium (Stables, N = 36); L: Low (Expanding, N = 38). *Potential Vulnerability* is the union of PC1 values and IUCN conservation status. Vulnerability (based on biological characteristics of PC1) was subdivided into: H: High (N = 24); M: Medium (N = 46); L: Low (N= 24)). Vulnerability (based on IUCN conservation status) was subdivided into: H: High (Endangered + Critically Endangered (N = 6)); M: Medium (Near Threatened + Vulnerable (N = 19)); L: Low (Least Concern (N = 69)).

	Potential Vulnerability								
Potential Exposure	**L x L**	**L x M**	**L x H**	**M x L**	**M x M**	**M x H**	**H x L**	**H x M**	**H x H**
High	2	0	0	6	2	1	8	1	0
Medium	1	2	0	18	2	0	13	0	0
Low	10	5	4	9	7	1	2	0	0

Table S4 Risk matrix (168 species). *Potential Exposure* was subdivided into: H: High (Contracting, N = 26); M: Medium (Stables, N = 52); L: Low (Expanding, N = 90). Conservation status combines the IUCN conservation status from Portugal, Spain and Globally (CR: Critically Endangered (N = 8); EN: Endangered (N = 14); VU: Vulnerable (N = 22); NT: Near Threatened (N = 22); LC: Least Concern (N = 102)). White cells represent low risk, grey cells represent medium risk and dark grey cells represent high risk.

	Conservation status				
Potential Exposure	**LC**	**NT**	**VU**	**EN**	**CR**
High	20(%)	3	2	1	0
Medium	43	1	5	3	0
Low	39	18	15	10	8

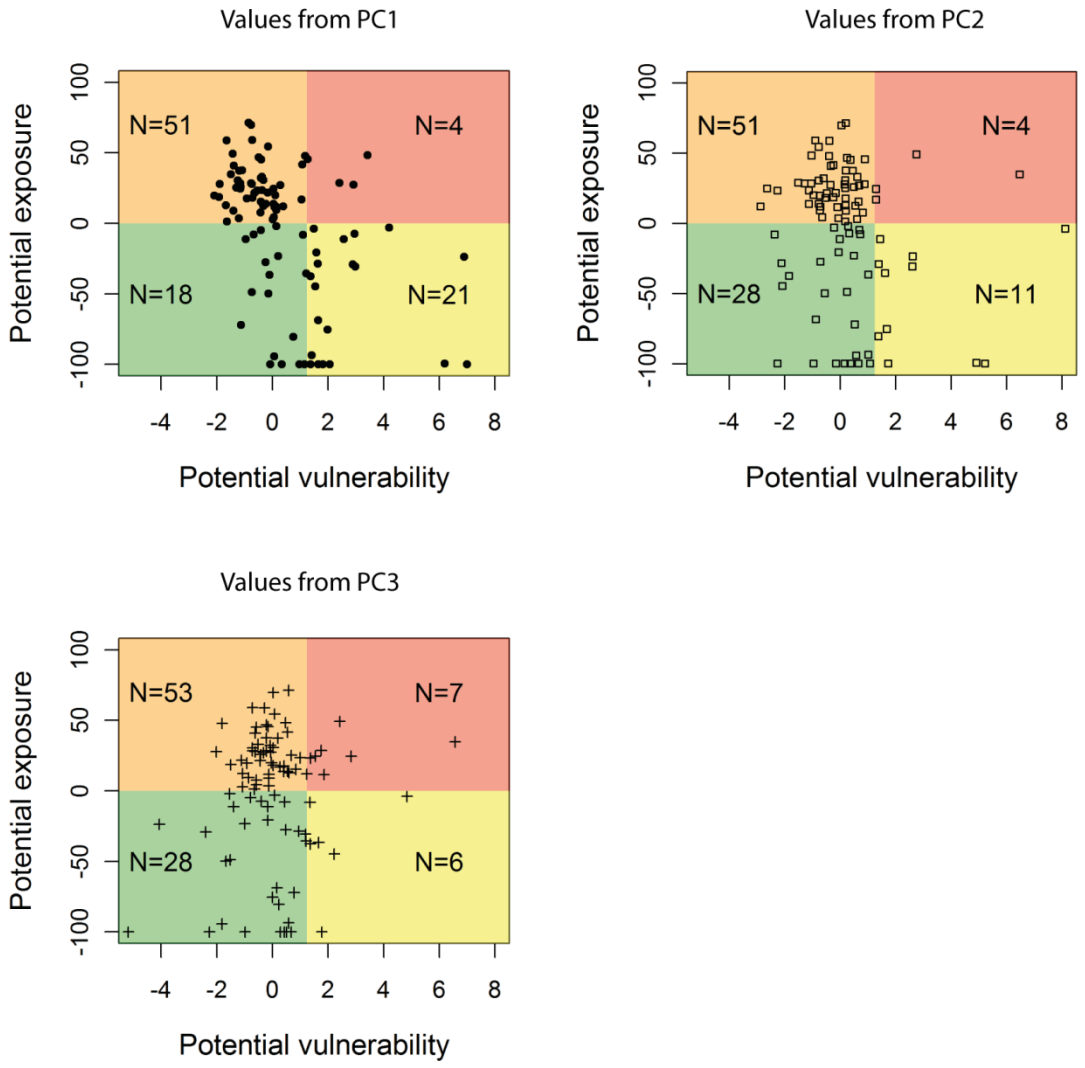

Figure S2 Plot integrating the different components to carry out the bird risk assessment. The values of potential exposure to global change were plotted against the potential vulnerability for the subset of 94 species. The potential vulnerability was calculated multiplying the values from the PCA (species traits) and the combined conservation status (LC = 0; NT = 1, VU = 2; EN = 3; CR = 4 and EX = 5). The potential exposure axis was divided, following the methodology used in Araújo et al. (2011a) into values below zero (including the expanding species) and values above zero (including the contracting and stable species). In the potential vulnerability axis, the third quartile of the first principal component was used as a splitting point. Pearson correlation values between potential exposure and potential vulnerability axis are the following ones: for PC1 values r = -0.46, for PC2 values r = -0.19 and for PC3 values r = 0.26

Chapter IV

Conservation priorities under climate change: Identifying threats and opportunities for the Iberian reserves networks

Manuscript in preparation

Conservation priorities under climate change: Identifying threats and opportunities for the Iberian protected area networks

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Abstract

Conservation policies are often implemented without consideration of the impacts of climate change on biodiversity. We identified conservation priorities based on both present and projected future distributions of 168 Iberian bird species. We then assessed threats and opportunities for conservation within the identified priorities by evaluating a) their current coverage by Protected Areas and Natura 2000 networks and b) their main present and projected future land use threats. Results show that 19% of the areas that were identified as priorities under climate change are covered by Protected Areas and 40% by Natura 2000. However, if we separate the areas important for present or future distributions, both protected area networks have a higher overlap with present priorities. Croplands are the most extensive pressure on currently unprotected priorities but their extent is expected to decrease in the future. Land use pressures are also predicted to decrease in both protected area networks but this will be foiled by climate change driven distribution shifts which will increase the mismatch between the locations of protected areas and the identified priorities. Although Iberian protected area networks are clearly beneficial for conserving present-day biodiversity, we identify several conflict locations where further efforts are needed to preserve biodiversity also in the future.

Keywords:

Protected Areas; effectiveness; environmental envelope models; Zonation software; land-use threats; birds; Iberian Peninsula

Introduction

The establishment of protected area networks is a fundamental part of local, regional and global strategies for biodiversity conservation although protected areas have often been criticized for being located in inadequate places or not being well designed or managed (e.g., Joppa and Pfaff 2009, Mascia and Pailler 2011). Worldwide, many tens of thousands of reserves have been designated and substantial additions are still made. For instance, the Convention on Biological Diversity targets call for seventeen per cent protection of terrestrial ecosystems by 2020 (Perrings et al, 2010). In spite of the heavy reliance placed on reserves, testing their effectiveness is still a challenge for conservation biologists (e.g., Cabeza and Moilanen 2003, Rodrigues et al. 2004b, Gaston et al. 2008, Joppa et al. 2008).

Climatic and land use changes are among the greatest threats to biodiversity (Jetz et al. 2007). In a context of rapid global change, testing protected area effectiveness has become even more complicated because the ecosystems that they were supposed to preserve are changing. Protected area networks are fixed in space and are expected to suffer major changes in species richness and composition (e.g. Hannah et al. 2007, Hole et al. 2009). Different types of responses to climate change have been measured for different taxa such as latitudinal and elevation range shifts (e.g., Forero-Medina et al. 2011), phenological and behavioural changes (e.g., Badeck et al. 2004) or evolutionary changes (Lavergne et al. 2011). In particular, European bird species have already shown phenological (e.g. Lehikoinen et al. 2004, Møller et al. 2004) and distributional changes (e.g. Thomas and Lennon 1999, Devictor et al. 2008, Devictor et al. 2012) and they are projected to shift their ranges substantially as a result of climate change (Huntley et al. 2007). For example, European populations of bird farmland species have been drastically reduced by agricultural intensification (e.g. Donald et al. 2001).

The Iberian Peninsula forms a part of the Mediterranean biodiversity hotspot (Myers et al. 2000) and harbours as much as half of the European terrestrial vertebrate and plant species as well as a high rate of endemism (Williams et al. 2000). It is covered by extensive networks of natural reserves that include two types of reserves with different degree of protection. While the nationally designated protected areas network has a high degree protection status, the Natura 2000 network established by the European Union (EU) is more flexible and human activities are allowed. For example, most of the land is privately owned with land use emphasis on sustainable management, both ecologically and economically. The Natura 2000 network objective is to ensure the long-term survival of its most valuable and threatened species and habitats. It is comprised of Special Areas of Conservation (SACs) designated under the Habitats Directive to conserve rare and vulnerable non-bird animals, plants and habitats, and Special Protection Areas (SPAs) designated under the Birds Directive to help conserve important sites

for rare and vulnerable birds. The Iberian Peninsula has a fundamental contribution to the European network, as Natura 2000 areas cover 28% of the Spanish territory which is the highest percentage of area contribution across EU member countries (Europarc-España 2010). Despite Iberian Peninsula's importance as a biodiversity hotspot and its extensive investment in reserve networks, the effectiveness of these areas has rarely been tested (but see, Martinez et al. 2006, Araújo et al. 2007, Hernández-Manrique et al. 2012). Moreover, the attempts to assess Iberian reserve effectiveness under climate change scenarios has been limited to small regions (e.g. Aragón et al. 2010) and hence complete assessments of the situation in the Iberia Peninsula are still lacking.

The main purpose of protected area networks is to ensure representation and persistence of species (Margules and Pressey 2000). In this study, we identify conservation priorities based on both present and projected future distributions of 168 Iberian bird species. We then assess threats and opportunities for conservation within the identified priorities by evaluating a) their current coverage by Protected Areas and Natura 2000 networks and b) their main present and projected future land use threats. We hope our results can inform about species conservation needs under climate change and offering general insights on the effectiveness of fixed protected area networks.

Material and Methods

Species data

Bioclimatic envelope models results from a previous study (Triviño et al. 2011) were used to quantify the probability of occurrence for 168 breeding bird species in the Iberian Peninsula under present and future scenarios. Distribution data were extracted from the Spanish Atlas of Breeding Birds (Martí and del Moral 2003) and from the Portuguese Atlas of Breeding Birds (Equipa Atlas 2008) reporting the presence and absence of bird species in 5923 10x10 km resolution grid cells. Our analyses excluded marine and aquatic species because modelling of their habitats would require information that is not available to us. Species with less than 20 records were also excluded to avoid problems of modelling species with small sample sizes (Stockwell and Peterson 2002).

Present (1971-1990) and projected future (2051-2080) distributions of bird species were modelled using climatic data as predictor variables and the mean consensus model from two ensemble forecasting models: Random Forests and Boosted Regression Trees. All models were run using default options of the BIOMOD package (Thuiller et al. 2009). For the future projections, a European climate scenario from the EU framework program Assessing Large-

scale environmental Risks for biodiversity with tested Methods (ALARM) was used (for further details see Triviño et al. 2011).

Protected areas data

Two protected areas datasets were used: the national-designated Protected Area network and the European-designated Natura 2000 network. We used the most recent public version of the two datasets available for the Iberian Peninsula at the time of the study (ICNB 2011, MARM 2011). Spanish and Portuguese geographic data were merged using ArcGIS 10 (ESRI 2006). We excluded from our analyses all areas designated only by international conventions like UNESCO World Heritage sites (UNESCO Man and Biosphere reserves and Wetlands of International Importance (Ramsar)) because areas designated solely by international conventions have no regulatory power to enforce protection (e.g. Jenkins and Joppa 2010). Auxiliary analyses were carried out using international-designated protected areas and are included as supplementary material (see Appendix S1).

Land-use data

Habitat loss and habitat degradation are recognized as the most important threats to biodiversity (Millennium Ecosystem Assessment 2005). In particular, agricultural intensification has been identified as the main threat to European birds (Donald et al. 2001). However, most conservation priorities schemes still do not account for threats to biodiversity and mainly focus on land purchase (Wilson et al. 2007). For that reason, in this study we use land use types as a surrogate for threat and assume that all bird species are equally affected by threats. Current and future land use information was derived from the CORINE Land Cover (CLC) data (European Commission 1993). CLC categories were aggregated into 6 land cover classes: Urban, Cropland, Permanent Crops, Grasslands, Forest and Others (for a complete description of the methodology see Dendoncker et al. 2007). We define ‘natural’ lands as those classified on land cover maps as natural vegetation type (e.g. grasslands and forests) and others categories (e.g. bare rocks and burnt areas). We define ‘agricultural’ lands as those classified as croplands and permanent croplands. Finally, we define ‘urban’ lands as those as built-up land cover categories (Table 2).

Conservation prioritization

The spatial conservation prioritization was done using Zonation software (Moilanen et al. 2012 and references therein) taking into account: (i) estimated probability of occurrence levels of bird species both presently and projected into the future, (ii) basic connectivity requirements of species from potential present distribution to projected one and from future to present.

Zonation produces a hierarchical priority ranking through the entire study area, accounting for ecological requirements of the species. The areas of highest priority across species can then be identified by selecting any given amount of area with highest priority ranks.

The conservation targets used in our analyses were present and future projected bird species distributions. When accounting for climate change in conservation prioritization both present and future predicted distribution of species and connectivity between those areas should be included (e.g. Carroll et al. 2010, Kujala et al. In press). Connectivity was implemented via the 'species interactions' technique of Zonation, which allows calculation of connectivity between two distributions (Moilanen and Kujala 2008, Rayfield et al. 2009). This technique is based on the metapopulation connectivity measure, where connectivity of any given focal site is dependent on its distance to other sites, the local value of both focal and other sites, and the dispersal ability of the respective (Hanski 1998, Moilanen and Nieminen 2002). Based on information on observed bird range shifts in the last decades (Brommer and Møller 2010) we set the dispersal distance of all species to 11 km/decade, corresponding to a dispersal distance of 77.3km for the time period of our study. We used two connectivity measures per species that makes it possible to identify priority areas that are currently important but also that facilitate dispersal to projected future distribution areas. The first connectivity was calculated from present to future, where highest values were given to present areas that are of good quality and geographically close to expected future distribution given species dispersal limitations. Under climate change these areas are expected to act as sources from where dispersal to future distributions takes place (hereafter called 'source areas'). For the second measure the connectivity was similarly calculated from future to present, and highest values were given to those future areas that are well connected to present areas and which hence are expected to help species to reach the core areas of their future distribution (hereafter called 'stepping stones'). Therefore, for each species, there were four types of distributions relevant for the conservation prioritization: present cores (PC), future cores (FC), source areas (S) and stepping stones (SS). Using the Zonation software we produced conservation prioritizations for the Iberian Peninsula across all species by i) separately accounting for each of the relevant distributions per species (hence, four different solutions), and ii) simultaneously accounting for all four relevant distributions per species (one solution, hereafter called 'altogether', Alt). From each of these five prioritization results we selected the highest 17% ranking areas, corresponding to the Nagoya goal for 2020 (Diversity 2010), for further investigation.

Data analyses

Gap Analysis is a widely used method to evaluate the effectiveness of reserve networks (Dudley and Parish 2006) which assesses the extent to which native species are being protected within protected areas (e.g. Rodrigues et al. 2004a, Kujala et al. 2011). We used gap analysis to determine how well the Iberian protected area networks represented the important areas for birds by overlapping the two protected area networks with the areas identified as conservation priorities by Zonation. We calculated three types of measure: i) the number of priority cells that overlap with protected areas or Natura 2000 sites, ii) the number of cells that overlap more than 50% and iii) the mean area of overlap.

In order to test that the effectiveness of the two protected area networks was not biased by the species pool we split the data into two subsets of species: 'agricultural' and 'non-agricultural' species. Agricultural zones are more predominant in Natura 2000 than in national protected areas (croplands and permanent croplands represent 15% of the national protected areas whereas they represent almost 24% in Natura 2000, see table 2). There are 46 species associated with agricultural areas (SEO/BirdLife 2010) and they represent 28% of the modelled species. The Zonation prioritization and the gap analysis were re-done using the two subsets of species.

To determine the spatial distribution of threats for bird persistence derived from land uses we calculated the proportions of the 'protected', the 'non-protected' and 'identified priority areas' that fall into the three land-cover categories: 'natural', 'agricultural' and 'urban'.

Finally, to estimate the opportunities and threats for conservation we calculated for the five types of identified priorities areas (PC, FC, SS, S, Alt) the areal percentage of 'protected', 'threatened' and 'potential for conservation'. We define 'protected' lands those included in the nationally designated protected area network. We define 'threatened' lands as those from agricultural and urban land cover categories. Finally, we consider lands of 'potential for conservation' those identified as priority areas, located outside protected areas and not threatened by human land uses.

Results

The effectiveness of the existing protected area networks to represent the identified Iberian bird priority areas under climate change depended on the species pool used to carry out the gap analysis. For the total pool of 168 species, almost 19% and 40% of the identified priority grid cells in the 'Altogether' solution were protected to high degree (>50% overlap) by the nationally designated protected area and by the Natura 2000 network, respectively. However, the same analyses done for the subset of 'non-agricultural' revealed that Natura 2000 did not outperform national protected areas for this group of species (Table 1).

Table 1 Three measures of overlap (proportion of cells with any overlap; proportion of cells with > 50% overlap, and the mean percentage of overlap) between identified conservation priority areas (Zonation results) and the two protected area networks: nationally designated protected areas (PAs) and Natura 2000 (Natura).

		All species			Agricultural species			Non-agricultural species		
		% cells	% cells > 50%	Mean overlap	% cells	% cells > 50%	Mean overlap	% cells	% cells > 50%	Mean overlap
PAs	Alt	48.0%	18.0%	18.8%	33.9%	11.0%	11.9%	47.2%	18.0%	18.8%
	PC	49.0%	18.6%	19.4%	34.6%	10.9%	11.7%	50.7%	19.3%	20.3%
	FC	41.0%	14.6%	15.3%	34.0%	14.0%	14.2%	41.1%	14.6%	15.3%
Natura	Alt	83.8%	39.2%	40.0%	77.3%	24.8%	27.9%	27.4%	14.0%	14.1%
	PC	83.7%	37.3%	39.2%	77.4%	24.8%	27.9%	84.5%	38.6%	40.1%
	FC	75.3%	27.8%	29.8%	77.7%	29.4%	31.3%	75.4%	28.1%	30.0%

If we separate the overlap of the two networks with present and future distributions, protected area networks have a higher overlap with present cores than with future cores (Figure 1). Under climate change the expected decrease in the protection of core areas is higher for the Natura 2000 (from 39.2 to 29.8%) than for the national designated protected area network (from 19.4 to 15.3%) (Table 1).

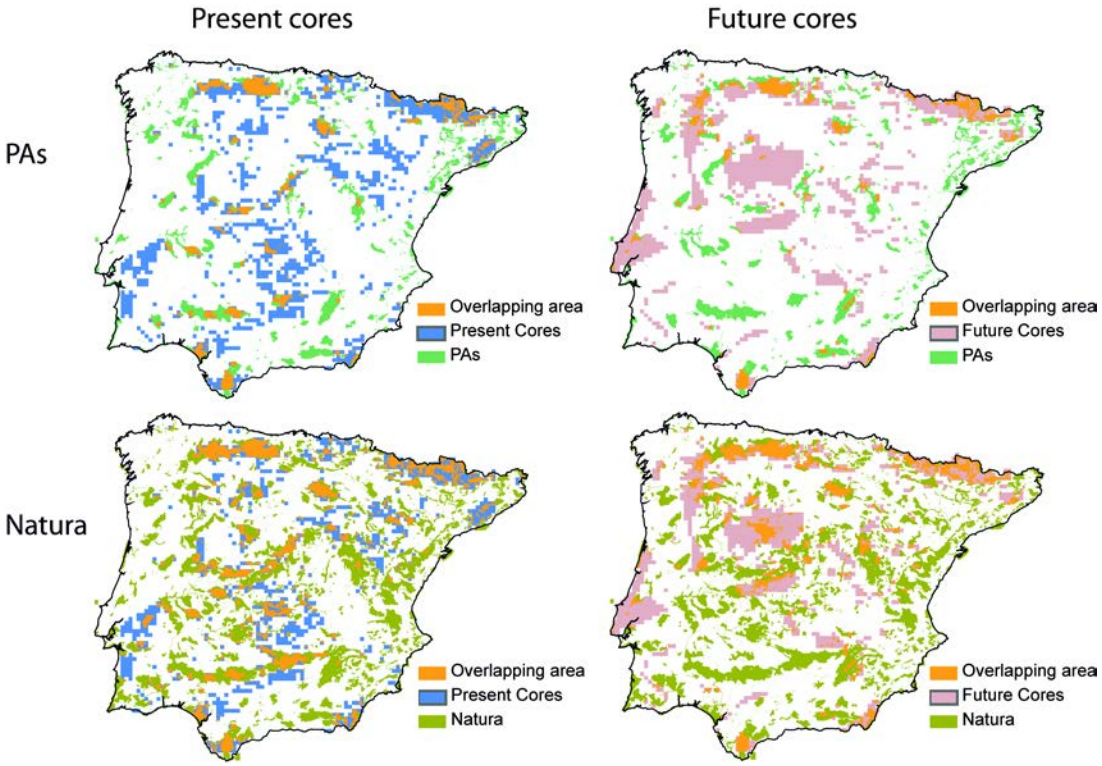

Figure 1 Overlap between identified priorities in the present (Present cores) and future (Future cores) time period and the two natural protected area networks: Protected Areas (PAs) and Natura 2000 (Natura).

Using the three land categories to calculate the spatial distribution of threats, we found that half of the non-protected area, and approximately 40% of the identified priority areas are presently threatened by land-use practices, considering everything not natural as a threat (Table 2). Within the two protected area networks majority of the land are in natural state (78.7 and 86.4% respectively), but notably almost one-quarter of the Natura 2000 network is represented by agricultural and urban zones.

While agricultural lands currently pose the most extensive pressure to biodiversity on the Iberian Peninsula, their extent is expected to decrease in the future. Urban areas constitute only a small fraction of current and future threats, but their role is nevertheless expected to increase by year 2080 (Table 2). Natural forests and grasslands currently cover over 50% of all analysed areas and their proportion is expected to further increase in the future.

Overall, all land types (‘protected’, ‘non-protected’, ‘priority areas’) are expected to undergo favourable development by year 2080, in terms of increasing naturalness and decreasing threats that rise from human land-use practices. Future cores are expected to experience the largest changes, with the steepest increase in natural lands (5.14%) and highest decrease in ‘agricultural’ areas (5.16%). Despite the favourable development one third of all identified priority areas will be threatened by land-use also in the future (Table 2).

Table 2 Spatial distribution of land-use changes through time. Natural area is represented by *Grasslands*, *Forests* and *Others* land use categories; Agricultural area is represented by *Croplands* and *Permanent Croplands* land use categories and Urban areas is represented by *Urban* land use category.

		% Natural area		% Agricultural area		% Urban area	
Zone	Area (km^2)	2080	Change 2000-2080	2080	Change 2000-2080	2080	Change 2000-2080
PAs	65,771	86.45%	2.02	12.89%	-2.20	0.66%	0.22
Natura 2000	155,805	78.73%	2.66	20.89%	-2.73	0.39%	0.08
No protected	497,302	55.26%	4.74	42.69%	-5.00	2.05%	0.26
Altogether	102,800	64.18%	3.01	34.66%	-2.99	1.17%	-0.01
Present Cores	102,800	64.49%	3.30	33.96%	-3.20	1.55%	0.10
Future Cores	102,800	66.28%	5.14	32.40%	-5.16	1.31%	0.01

There was a high spatial congruence between conservation priorities identified for 'all species' (N=168) and 'non-agricultural species' (N=122), although 'stepping stones' were notably lacking from the prioritization done for 'non-agricultural species'. The spatial distribution of the conservation priorities for 'agricultural species' (N=46) was more aggregated and compact and located in croplands areas of the Iberian Peninsula (Figure 2).

When estimating the opportunities and threats for conservation we found only small differences between the five types of identified conservation priorities. The future cores had the greatest potential for conservation (55.47%). Among all priority areas, the percentage of national protection was lower than 20% and the level of threat posed by land-use practices was close to 40%. Over 50% of all identified priority areas were not protected and currently not threatened by land-uses, future cores having the greatest potential for conservation (55.47%) (Table 3). These areas were mainly located in mountainous regions like the southern part of the Pyrenees or the Cantabric mountains as well as in the southwest of the Iberian Peninsula (Figure 3).

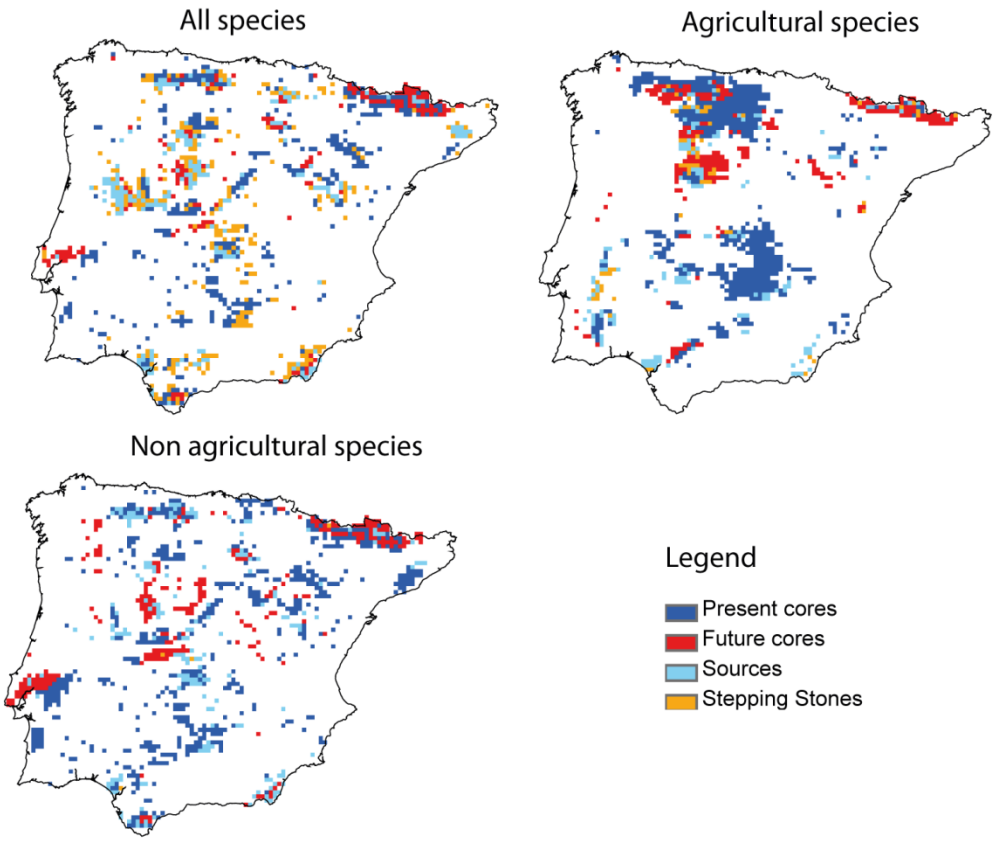

Figure 2 Top conservation priorities for Iberian bird species, including present and future projected distribution and the respective connectivity measures, when equal weight is given to present and future and the mean dispersal distance is 77, 31 km. Colours represent the classification of the top 17% priorities into their relative importance as present cores, future cores, sources and stepping stones.

Table 3 'Protected': mean percentage of overlap between the priority areas and the nationally designated protected area network; **'Threatened'**: percentage of cells that overlap with contemporary agricultural and urban areas; **'Potential for conservation'**: percentage of cells that are neither protected nor threatened at the present time.

	% Protected	% Threatened	% Potential for conservation
PC	19.4	38.6	54.3
FC	15.3	38.9	55.5
S	18.1	40.0	53.2
SS	17.9	40.0	53.1
Alt	18.8	38.8	54.1

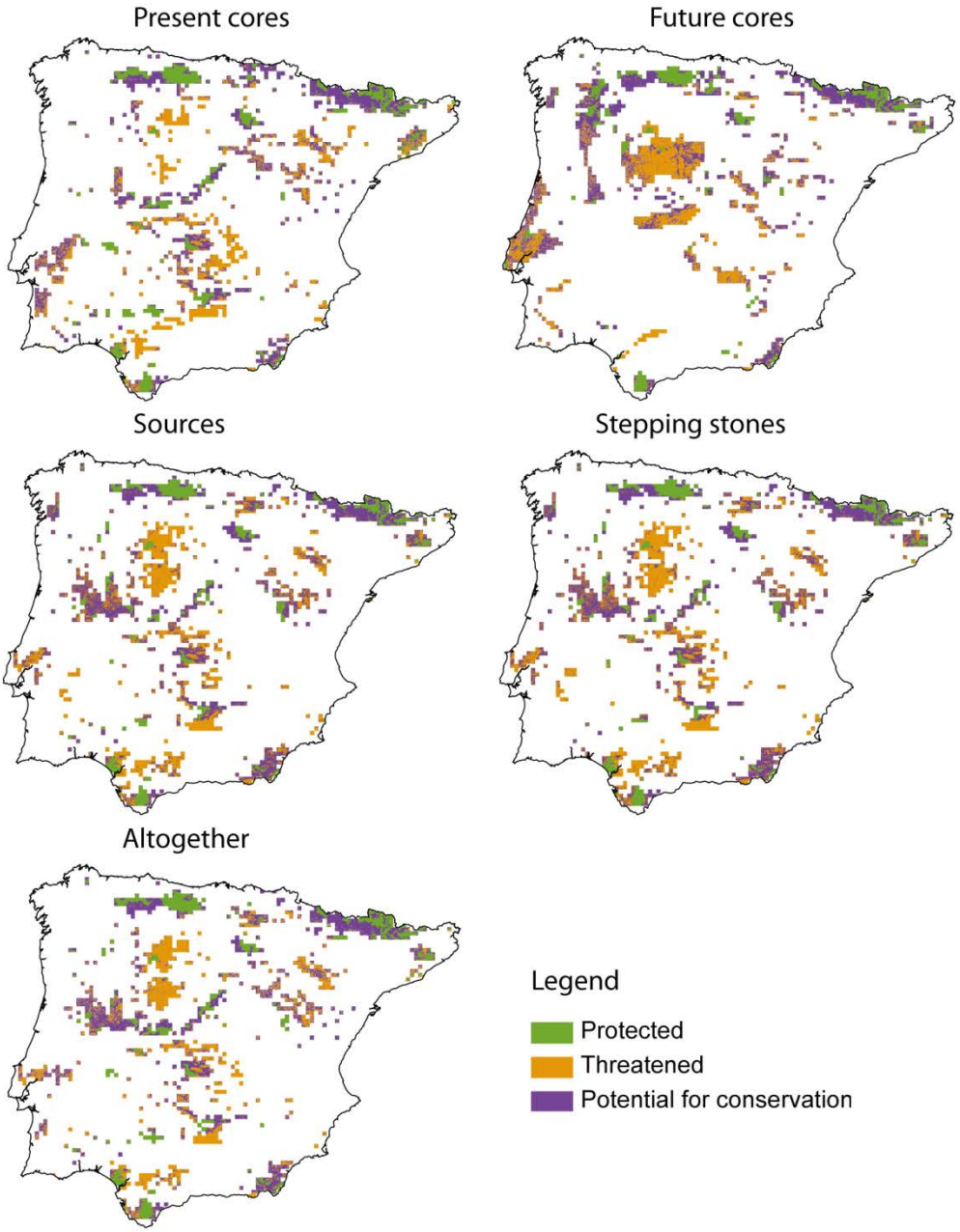

Figure 3 Maps of top conservation priority areas for Iberian bird species reclassified into three categories to show threats and opportunities for conservation. **'Protected'**: mean percentage of overlap between the priority areas and the nationally designated protected area network; **'Threatened'**: percentage of cells that overlap with contemporary agricultural and urban areas; **'Potential for conservation'**: percentage of cells that are neither protected nor threatened at the present time.

Discussion

In this study we explored threats and opportunities for conservation of Iberian birds. Our results provide the first assessment of the effectiveness of the two Iberian protected area networks to conserve bird priority areas under climate change. We found out that there are still many areas with potential for future conservation actions because most of the identified conservation priority areas are still not protected nor threatened by land uses. We showed that the two Iberian protected area networks were not efficient in representing conservation priority areas for birds but Natura 2000 sites outperformed nationally designated protected areas. Finally, land use pressures are predicted to decrease in both protected area networks but this will be foiled by climate change driven distribution shifts which will increase the mismatch between the locations of already established protected areas and the identified priorities.

Effectiveness of the Iberian protected area networks to represent identified conservation priority areas for birds.

Iberian protected area networks seemed not to be very effective in representing the identified conservation priority areas for birds and this finding is in agreement with previous studies that showed that protected areas provided poor representation for bird species (Carrascal and Lobo 2003, Araújo et al. 2007). However, it is interesting to note that Natura 2000 sites outperformed the nationally designated protected areas in representing both present and future conservation priority areas. This finding can be partly attributed to the large extension of the Natura 2000 network which it is more than double the size of the nationally designated protected area network. Another reason that explain this result is that the selection of most protected areas has been ad hoc, especially at the beginning of the century, whereas the designation of Natura 2000 are sites is rather new and specifically designated based on their biological values. Moreover, Natura 2000 include the Special Protection Areas (SPAs) designated under the Birds Directive to help conserve important sites for rare and vulnerable birds. Therefore, it is reasonable that Natura 2000 outperforms the nationally designated protected areas network as it has been specifically designed to protect bird species. However, in this study we did not take topography into account and as Natura 2000 are located in flatlands are expected to be more affected by climate change than protected areas (Araújo et al. 2011).

Does the effectiveness of protected area networks decrease under climate change scenarios?

As it would be expected since protected areas networks were designed for present-day distributions, they better represent priority areas for the present than the expected important areas for the future. This finding is in line with earlier studies that showed that current protected

areas will no longer retain suitable climatic conditions for many of the species for which they were designated (Araújo et al. 2004, Hannah et al. 2007, Huntley et al. 2008, Hole et al. 2009). However, there is ambiguous evidence of bird species' abilities to shift their ranges fast enough to keep pace with climate change (e.g. Araújo et al. 2005, Chen et al. 2011, Devictor et al. 2012) and considerable uncertainty about the rate of vegetation response and hence of appropriate habitat in areas that become climatically suitable for a species in the future (e.g. Sykes et al. 1996). A way forward to produce more realistic scenarios is by reducing models uncertainty (for example using ensemble forecasting Araújo & New, 2007), by calculating more realistic dispersal rates (see Barbet-Massin et al. 2011) or by introducing population trends information (e.g. Kujala et al. 2011).

Threats posed by land use pressures

Although there are many other types of threats affecting Iberian birds besides climate and land use changes, such as the increasing construction of infrastructures (e.g. Torres et al. 2011), poison or human disturbance of nest sites among others (Madroño et al. 2004), agricultural intensification constitutes the highest threat for European farmland birds (e.g. Donald et al. 2001). Our results showed that in the future there will be further urban expansion but decreased pressure from agriculture activities (Underwood et al. 2009). Forest cover is expected to increase as many agricultural areas have been already abandoned and the Iberian Peninsula is experiencing a forest regeneration process (e.g. Rey Benayas et al. 2007, Gil-Tena et al. 2009, Álvarez-Martínez et al. 2011). These changes will favour forest bird species, especially forest specialist, but not species associated to traditional agricultural systems (Gil-Tena et al. 2007). We acknowledge the limitation of the land use data used because with six broad land use categories the differences between traditional agricultural practices (beneficial for conservation) and intense agricultural practices are difficult to capture.

Potential for Iberian bird species conservation

The large proportion of currently unprotected but natural and semi-natural land distributed across the identified priority areas offers new conservation opportunities. Nevertheless, we showed that a substantial percentage of conservation priority areas are threatened by land use pressures both currently (~40%) and in the future (~30%) and climate change will increase the mismatch between already established protected areas and identified priority areas. Therefore, adaptive conservation measures to global change are urgently needed. There is wide agreement that more land must be protected rapidly and that protection should be expanded outside reserves (Heller and Zavaleta 2009, Mawdsley et al. 2009).

A common strategy for reducing climate change impacts on biodiversity will certainly include the establishment of new protected areas to increase the available habitat for species and ensure the existence of suitable pathways for species dispersal. The selection of new protected areas can be informed by the methodology used in this study which combines forecasts of species range shifts under climate change (e.g. Araújo et al. 2004, Williams et al. 2005, Phillips et al. 2008, Vos et al. 2008) with reserve selection software (Carroll et al. 2010).

The finding that protected areas networks are not very effective should not be interpreted as traditional protected areas are not essential for conservation strategies. Rather, the message is that if the remaining natural lands where people live and work are managed in a sustainable manner that allows persistence of native species, we can achieve significant additional biodiversity gains. These new approaches require unprecedented collaboration among stakeholders to promote conservation both inside and outside of traditional protected areas, including human managed areas (Cox & Underwood 2011).

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Appendix S1: Analyses including international protected areas and detailed composition of land use data.

Table S1 Three measures of overlap (proportion of cells with any overlap; proportion of cells with > 50% overlap, and the mean percentage of overlap) between identified conservation priority areas for the 168 bird species (Zonation results) and the protected area network including national and international designated sites.

	% cells	% cells > 50%	Mean overlap
Altogether	51.5%	22.0%	22.9%
Present Cores	53.5%	23.4%	24.3%
Futur Cores	44.5%	17.9%	18.6%

Table S2 Spatial distribution of land-use changes through time. Natural area is represented by *Grasslands*, *Forests* and *Others* land use categories; Agricultural area is represented by *Croplands* and *Permanent Croplands* land use categories and Urban areas is represented by *Urban* land use category. This table includes the broad protected area network which includes the national and international designated sites (Broad PAs)

		% Natural area		% Agricultural area		% Urban area	
Zone	Area (km^2)	2080	Change 2000-2080	2080	Change 2000-2080	2080	Change 2000-2080
Broad PAs	80,656	82.13%	4.18	17.27%	-4.32	0.60%	0.14
Natura 2000	155,805	78.73%	2.66	20.89%	-2.73	0.39%	0.08
No protected	497,302	55.26%	4.74	42.69%	-5.00	2.05%	0.26
Altogether	102,800	64.18%	3.01	34.66%	-2.99	1.17%	-0.01
Present Cores	102,800	64.49%	3.30	33.96%	-3.20	1.55%	0.10
Future Cores	102,800	66.28%	5.14	32.40%	-5.16	1.31%	0.01

Table S3 Spatial distribution of land-use changes in conservation priority areas inside and outside protected areas through time This table includes the identified conservation prioritiy areas ('Alt': Altogether; 'PC': Present Cores and 'FC': Future Cores) divided into two subsets: inside and outside the broad protected area network (including national and international areas).

	% Natural area		% Agricultural area		% Urban area	
Zone	2080	Change 2000-2080	2080	Change 2000-2080	2080	Change 2000-2080
Alt (Inside)	92.40%	0.81	7.38%	-0.82	0.22%	0.01
Alt (Outside)	57.58%	3.47	41.03%	-3.45	1.39%	-0.02
PC (Inside)	91.72%	1.15	8.06%	-1.14	0.22%	-0.01
PC (Outside)	57.86%	3.53	40.27%	-3.65	1.88%	0.13
FC (Inside)	93.42%	1.27	6.21%	-1.22	0.37%	-0.05
FC (Outside)	61.30%	5.83	37.22%	-5.85	1.49%	0.03

Table S4: Detailed composition of the two agriculture land use categories

Permanent croplands	**Percentage of surface**
Vineyards	13.97%
Fruit trees and berry plantations	12.12%
Olive groves	27.57%
Annual crops associated with permanent crops	6.05%
Agro-forestry areas	40.29%
Croplands	
Non-irrigated arable lands	60.88%
Permanently irrigated land	13.38%
Rice fields	1.03%
Complex cultivation patterns	24.71%

GENERAL CONCLUSIONS

Integrating the results from the four chapters of this thesis we can extract the following conclusions:

1) In the first chapter we showed that the heuristic algorithm, developed to use different types of terminal habitats, was suitable and useful to identify linkages between environmentally-similar protected areas (or other type of natural habitats) using environmental data as a biodiversity surrogate. It follows from this assumption that linkages between protected areas should preferentially be established between environmentally-similar areas.

2) The main purpose of conservation biology is the persistence of species, many times in fragmented landscapes. In order to establish robust linkages between natural habitats different type of data are needed and the incorporation of species movement patterns is not enough. Species' dispersal data should be combined with other factors that determine species' persistence at various spatial and temporal scales.

3) In the second chapter of the thesis we asked whether adding vegetation and landscape configuration variables in environmental envelope models would significantly increase discrimination ability of models and whether different sets of variables would affect the spatial representation of climate change impacts on Iberian bird species at a spatial resolution of 10 x 10 km. We showed that models using climatic variables generally fit the data better than models using vegetation or landscape configuration variables. However, improvements of discrimination with the climate models, as compared with the two alternative models, were significant in all cases only for the climatic-landscape model comparison. Disagreement existed between future projections using different predictors, but the discrepancy decreased when species with high levels of discrimination ability in ensembles of forecasts were retained.

4) The importance of variables appeared to be species specific and, despite the importance of climatic variables, vegetation and landscape configuration were also important for explaining the distribution patterns of some Iberian bird species. Possible explanations for these results are that: (i) the relative importance of climatic versus nonclimatic predictors is scale dependent; (ii) vegetation in Mediterranean countries has been modified by humans for millennia. The human impact is not represented by the simulated potential vegetation; (iii) the coarse vegetation and land use variables used do not account for all important habitat characteristics, such as forest age and size structure in plantations and the amount of deadwood. We can conclude that the decision as to whether to include specific non-climatic factors in the models requires case specific considerations based on the auto-ecology of the species.

5) We found out that it is difficult to determine what are the most important environmental variables constraining species distributions, especially when a large number of species is considered. Nevertheless, we note that most of the divergence in future projections was caused by species that were difficult to model with our predictors, i.e., that performed poorly with the measures of discrimination ability used to verify model performance. Models discriminating data well yielded less variable projections into the future.

6) Results from the third chapter showed that risk assessments that combine estimates of species exposure to environmental changes together with metrics reflecting their intrinsic ability to cope with them provide a relatively less pessimistic view of risks than evaluations based solely on estimates of exposure. Specifically, in our study, species expected to be highly exposed to future global environmental changes were shown to be currently less threatened and possess traits that make them less vulnerable to local extinction than less exposed species. Results are contingent on the particular group of species and region studied, but our results highlight that species with different traits have different abilities to cope with threats and that coincidence between exposure to a threat and vulnerability to it cannot be taken for granted

7) The analyses from the third chapter also reveal that a large proportion of the species that are not currently threatened according to IUCN criteria (Vulnerable, Endangered or Critical Endangered categories) could become threatened in the future as a result of climate, vegetation, and land use changes.

8) Results from the fourth chapter show that the protected área networks in the Iberian Peninsula are not very effective representing the identified conservation priority áreas for birds. A comparison, between the national designated protected áreas and the European network Natura 2000, reveal that Natura 2000 outperforms national protected áreas in representing identified bird conservation priorities.

9) The analyses carried out in the four chapter show that more than half of the surface of the identified conservation priorities maintain high ecological values and are still not protected under national legislation. Therefore, we can consider that these regions have a potential for future conservation actions.