A Bichito

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CERTIFICA:

Que los trabajos de investigación desarrollados en la memoria de tesis doctoral "Los líquenes en un escenario de cambio global", han sido realizados bajo su supervisión y son aptos para ser presentados por la Lda. Marta Rubio de Salcedo ante el tribunal que en su día se consigne, para aspirar al Grado de Doctor en Conservación de Recursos Naturales por la Universidad Rey Juan Carlos de Madrid

Vº Bº Director de Tesis

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Los líquenes en un escenario de cambio global

TESIS DOCTORAL

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Science is like sex: it may give some practical results, but that´s not why we do it

Richard P.Feynman

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Resumen

Introducción

La presión antrópica sobre el planeta ha alcanzado en las últimas décadas un nivel de impacto considerable, situándonos ante una situación de cambio global (Steffen et al 2004). Una de las principales consecuencias de la actividad humana es la emisión de gases invernadero, modificando la composición atmosférica que desemboca en lo que actualmente conocemos como cambio climático (IPCC 2007). Paralelamente, hay otros motores de cambio global que interaccionan entre sí, en muchos casos de forma sinérgica. Es el caso de los cambios en los usos del suelo, la desertificación, la modificación del régimen de incendios o la fragmentación y pérdida de los hábitats, siendo éste último otro de los principales motores de cambio global (Fahrig 2003).

El término biodiversidad representa una visión holística de la naturaleza e incide en el hecho de que no se perciba como un conjunto de componentes individuales (Primark y Ros 2002). La pérdida de biodiversidad a todos los niveles constituye una de las principales preocupaciones medioambientales de la sociedad en nuestros días (Thuiller et al. 2004). Muchos trabajos ya han alertado sobre el efecto negativo que el cambio global ejerce sobre la biodiversidad, implicando desde pérdidas de diversidad genética hasta reducciones del área de distribución de ecosistemas (Chen et al. 2011; Thuiller et al. 2011; Summers et al. 2012). El efecto de los motores del cambio global es variable, pero a nivel regional se ha detectado (Bellard et al. 2012) que el cambio climático ha sustituido a la fragmentación de los hábitats como la principal amenaza a la biodiversidad. Por otro lado, la mayor parte de paisajes forestales del planeta se han transformado en un mosaico de fragmentos de diferentes tamaños y grado de aislamiento. Esta pérdida y fragmentación de bosques ha afectado a la dinámica poblacional de las especies y a la riqueza y diversidad de las comunidades (Fahrig 2003; Hanski 2005),

Para conseguir una protección efectiva de la biodiversidad es importante conocer, entre otros aspectos, los patrones de distribución de las especies a gran escala, pero también a escalas más pequeñas (Albert et al 2001, Ranius et al 2002, Belinchón et al 2007). La mayor parte de trabajos que abordan el análisis de los efectos del cambio climático y de la fragmentación y pérdida de los bosques se centran en grupos de organismos “carismáticos” (Young et al. 1996; Santos & Tellería 1998; Lavorel & Garnier 2002; Virgós 2002; Root et al. 2003; Diamond et al. 2011). Sin embargo, aun tenemos un conocimiento muy escaso sobre los efectos que el cambio global ejercen sobre otros grupos de organismos, como pueden ser los líquenes. Esta falta de estudios, puede estar comprometiendo el desarrollo de estrategias de conservación dirigidas al mantenimiento o recuperación de la calidad de los hábitats donde estos organismos viven o el desarrollo de medidas dirigidas a especies concretas (Ellix 2013).

Una fórmula de protección de hábitats y especies *in situ* es la creación de Redes de Reservas. En muchas ocasiones estas redes se diseñan y se planifican en función de la distribución de las especies más conocidas, como las plantas vasculares o las aves (Araújo et al 2007). Pero hay estudios que señalan que esta fórmula no asegura la conservación de todos los taxones (p.e. Rey-Benayas y de la Montaña 2003). Es necesario, por tanto, saber hasta qué punto esta fórmula es adecuada y asegura una protección efectiva de otros grupos de organismos, con el objetivo final de proponer modificaciones y/o ampliaciones de las redes de reservas, permitiendo maximizar la protección de toda la biodiversidad.

Por otra parte, teniendo en cuenta que los ecosistemas mediterráneos se sitúan entre los más vulnerables a nivel global (Lavorel et al 2008) y que los líquenes son particularmente sensibles a cambios en su entorno (Nash y Olafsen 1995; Sillet et al 2000; Belinchón et al 2009, 2011), se hace necesario evaluar la respuesta potencial de las especies de líquenes en la Península Ibérica. Las respuestas esperadas frente al cambio climático son variables y dependen del taxón estudiado, siendo en muchos casos respuestas muy específicas (Kharouba et al 2012). Aún así, de cara a la toma de decisiones, es útil agrupar a las especies y hacer predicciones generalizables sobre el futuro de las mismas en función de su vulnerabilidad (Kharouba et al 2012, Summers et al 2012, Arribas et al 2012). En este marco conceptual, los rasgos funcionales y atributos ecológicos (Ellis et al 2013) pueden suponer una gran ventaja predictiva, ya que determinados rasgos o combinaciones pueden asociarse a mayores grados de sensibilidad o vulnerabilidad de las especies (Diamond et al 2011, Summers et al 2012).

Como hemos comentado al inicio de esta introducción, la pérdida de biodiversidad constituye una de las principales preocupaciones medioambientales de la sociedad

El estudio de los efectos derivados de la fragmentación de hábitats debe ser contemplado con una perspectiva espacial y requiere la integración de los diversos factores demográficos, genéticos y ecológicos que condicionan la supervivencia de una población.

La UICN (2001) estableció una serie de categorías de amenaza basadas en diferentes criterios. En España contamos con una Lista Roja de la Flora Vascular Española (2008), elaborada a partir del uso de una metodología de trabajo común, utilizando criterios semicuantitativos y explícitos para justificar la catalogación de las plantas amenazadas en las categorías UICN. La supervivencia o viabilidad de una población, entendida como la probabilidad de que esa población persista en un futuro, puede interpretarse como una variable que depende de dos factores fundamentalmente: el número de individuos que compone la población y el comportamiento de los individuos de la población (supervivencia, crecimiento y reproducción) (Iriondo et al. 2009). En el caso de los líquenes, estamos muy lejos de poder hacer esto. En España, existen una serie de trabajos que han tenido como objetivo hacer una llamada de atención sobre el grado de amenaza de especies liquénicas (Atienza y Segarra 2000; Martínez et al. 2003). Pero, en ningún caso se han podido basar en los criterios indicados por la UICN. Debido, principalmente, al desconocimiento que tenemos sobre la dinámica poblacional de las especies liquénicas. Nos faltan datos como: reducción del número de individuos maduros, distribución geográfica reducida (todavía existen muchos huecos en el conocimiento de la distribución de los líquenes en la Península Ibérica), número de individuos de la población, número de individuos maduros, probabilidad de extinción, etc. (IUCN 2001).

Aunque en los últimos años nuestro grupo ha acumulado algunas evidencias de cómo responden los organismos a la acción de algunos de los principales factores de cambio que están afectando actualmente a nuestra biodiversidad, tanto a nivel de comunidad (Belinchón et al. 2007, 2011; Aragón et al. 2009), como a nivel poblacional (Belinchón et al. 2009, 2011; Martínez et al. 2012.; Otálora et al. 2010a), así como en temas de especificidad entre los organismos simbiontes (Otálora et al. 2010b), quedan aún muchas incógnitas en relación a la respuesta que puedan tener las comunidades liquénicas y determinadas especies en particular a la acción combinada de la fragmentación y los cambios ambientales relacionados con el clima. Gran parte de esas incógnitas pasan por reconocer que la dispersión y establecimiento de los individuos constituyen parámetros fundamentales en el ciclo de vida de cualquier organismo (Clobert et al. 2001; Ozinga et al. 2005; Figura 1). En el caso de los líquenes epífitos, algunos trabajos relacionan el patrón de distribución de las especies con limitaciones en la dispersión relacionados con la distancia (Dettki et al. 2000; Zoller et al. 2000; Walser 2004). Otros estudios atribuyen las limitaciones dispersivas al tipo de reproducción (Hedenås y Ericson 2000; Hedenås et al. 2003; Löbel et al. 2009), o se habla de limitaciones en el establecimiento, siendo determinante la calidad del hábitat (Werth et al. 2006) o el tipo de hábitat (Lättman et al. 2009). Pero, todavía estamos lejos de conocer el funcionamiento de las especies liquénicas en relación a estos aspectos.

Por todo ello, es necesario empezar a obtener datos de calidad sobre el estado de las poblaciones de especies liquénicas “amenazadas” que nos permitan evaluar de una forma cuantitativa el grado de amenaza de cada especie. Se requiere información que nos permita definir variables corológicas, demográficas y de hábitat apropiadas para el diagnóstico de la situación de riesgo de los taxones amenazados. Las obtención de estos datos proporcionará información básica sobre el estado de conservación de las poblaciones para implementar medidas efectivas para su recuperación. Se considera que la información recogida en ellos constituye la mínima necesaria para elaborar un diagnóstico acertado sobre los factores externos y procesos vitales que son claves o condicionan la viabilidad de las poblaciones.

Los líquenes como organismo modelo

Un liquen es una asociación simbiótica entre un micobionte hongo (hongo) y un fotobionte (alga verde y/o cyanobacteria). Es una interacción estable y con estructura y fisiología propias. El hongo proporciona al fotobionte un entorno favorable, protegiéndolo de las radiaciones directas del sol y la desecación, y favoreciendo la captación de sales minerales. Por su parte, el alga y/o cyanobaceria realiza la fotosíntesis, permitiendo que el liquen no dependa de fuentes externas de carbono orgánico (Nash 1998, Brown 2001). Esta simbiosis permite a los líquenes extender ampliamente su nicho ecológico (Brown 2001).

Los líquenes son una parte importante de la biodiversidad en términos generales. Pueden llegar a suponer una alta proporción de los seres vivos, principalmente en ambientes extremos (Lesica et al 1991, Dettki y Essen 1998). Además, son componentes fundamentales en los ecosistemas, por ejemplo en los forestales (Sillet et al 2000), donde contribuyen al ciclo de nutrientes y proporcionan una fuente importante de refugio y alimento a la microfauna.

Los líquenes son sensibles a modificaciones de todo tipo en su hábitat, por lo que se han utilizado como indicadores de sensibilidad ambiental en multitud de estudios (McCune 2000, Jüriado et al 2012). Esta sensibilidad se debe, en parte a que necesitan un determinado equilibrio entre el aporte de luz y de agua. Este equilibrio es necesario para que el correcto mantenimiento de la asociación liquénica (Farrar 1976), así como la activación metabólica (principalmente fotosíntesis y la respiración (Palmqvist y Sundber 2000), pero también otras actividades como la generación de metabolitos secundarios protectores, (Gauslaa y Solhaug 2001). Como los líquenes son organismos poiquilohídricos carecen de mecanismos para la captación y pérdida de agua (Esseen and Renhorn 1998), y toman la mayoría de sus nutrientes de fuentes atmosféricas. Por ello, los líquenes son ampliamente dependientes de las modificaciones climáticas (Nash and Olafsen 1995; Belinchón et al 2009, Escolar et al 2012). Se ha demostrado que los líquenes son especialmente sensibles a cambios y modificaciones en las condiciones climáticas a escala pequeña (Belinchón et al. 2009; Martínez et al. 2012). Pero también los factores climáticos y paisajísticos, van a marcar la distribución de los líquenes a gran escala.Estas son algunas de las razones por la cual los líquenes constituyen uno de los grupos de organismos más adecuados para evaluar el impacto del cambio global sobre los ecosistemas (Aragón et al 2009, Werth et al 2005).

Otra razón que apoya su uso como organismos modelo es que se trata de especies que, en términos generales, presentan ciclos de vida largos con tasas de crecimiento relativamente lentas (Öckinger y Nilsson 2010), de forma que la composición de especies de líquenes puede estar reflejando, no sólo efectos inmediatos, si no también efectos relacionados con acciones en el pasado (Otálora et al.   paper mónica de genética lobaria pulmonaria).

Además, los líquenes son un grupo heterogéneo y amplio desde un punto de vista taxonómico, ecológico, fisiológico o morfológico. La variabilidad en sus características morfológicas como el tamaño o la forma de crecimiento, los diferentes tipos de ambientes y sustratos en que se desarrollan, y sus respuestas fisiológicas variadas, les permiten estar presentes en prácticamente todos los hábitats del planeta, incluso en los más extremos (Nash 1998). Esto también facilita su utilización como organismos modelo, permitiendo utilizarlos para evaluar los efectos a nivel global, como es el caso del cambio climático (Sancho et al 2007).

De entre los líquenes frecuentemente utilizados como organismo modelo, destaca *Lobaria pulmonaria* L. (Hoffm). Es un liquen epífito, bastante conocido desde un punto de vista ecológico (Gu et al 2001, Snäll et al 2005; Belinchón et al. 2009, 2011; Otálora et al., Martínez et al. 2012). Aunque gran parte de los estudios ecológicos de la especie se enmarcan en bosques boreales (MacKenzie et al 2001, 2001, Gauslaa et al 2007), hay bastantes estudios sobre su ecología en ambientes mediterráneos (Belinchón et al 2009, 2011; Martínez et al 2012). Estos estudios coinciden en que se trata de una especie sensible a modificaciones antrópicas en su hábitat, y en la importancia del microclima y el microhábitat para el desempeño de esta especie. Las características del árbol (ya que la especie es principalmente epífita), especialmente la especie, modifican en gran medida las respuestas de la *L. pulmonaria* (Belinchón et al 2009, 20011). En la Península Ibérica, está clasificada como “vulnerable” (Martínez et al 2003), a partir de la información disponible. La obtención de información más detallada y completa permitiría hacer un diagnóstico más realista del estado de conservación de la especie.

La Península Ibérica como área de estudio

La cuenca mediterránea se encuentra en una situación especialmente delicada ante la amenaza del cambio global (Sala et al 2000), debido a sus condiciones ecológicas particularmente marcadas por una posición transicional climática y y la actividad humana mantenida durante milenios (Lavorel et al 2008).

La Península Ibérica, principalmente encuadrada en la región mediterránea, cuenta también con territorio en las Regiones Atlántica y Alpina, aunque en proporciones menores. El clima es, por tanto, muy variable. Además, la Península Ibérica presenta una gran variabilidad de ombroclimas y de condiciones microclimáticas especiales, dependiendo de la situación espacial y la orografía (Rodó y Comín 2001). Esta heterogenidad ambiental supone un ventaja a la hora de utilizar la Península como área de estudio, ya que permite contar con gran cantidad de hábitats y condiciones ambientales en un área no muy extensa.

La Península cuenta un paisaje claramente modificado por el hombre. Se trata de un paisaje, en su mayor parte, altamente fragmentado, debido al uso humano de carácter histórico que presenta (Thirgood, J. V. 1981). La influencia humana, junto con cambios climáticos anteriores, son los principales responsables de las modificaciones sufridas en la Península Ibérica (Mesa 2002, Valladares et al. 2004). Además de dichas modificaciones históricas, este territorio sufre actualmente y seguirá sufriendo previsiblemente en un futuro próximo una fuerte presión humana (Morillo y Gómez-Campo 2000). Los modelos climáticos disponibles predicen aumento de las temperaturas y descenso de las precipitaciones, sumado a un aumento de la variabilidad y de los eventos extremos (IPCC 2007, Moreno et al 2005).

Es por todo lo anteriormente citado que, en términos generales, la Península Ibérica se considera un territorio que va a sufrir los riesgos derivados del cambio global, especialmente del cambio climático. Los ecosistemas y especies de la Península Ibérica están claramente expuestos al daño acumulado y futuro que supone la presión antrópica. A esta alta exposición al riesgo cabe añadir que muchas especies encuentran en esta región su límite de distribución meridional, lo cual les confiere un grado superior de vulnerabilidad. Esta peculiaridad propicia que algunas poblaciones peninsulares de estas especies representen situaciones marginales, que ven agravada su situación dado que habitan sistemas boscosos muy fragmentados. En el caso de la Península Ibérica, gran parte del bosque mediterráneo ha sido destruido para obtener cultivos y pastos, mientras que el resto fue transformado en monte bajo para la producción intensiva de carbón y leña (Blondel y Aronson 1999; Mesa 2002). En este sentido, los ecosistemas mediterráneos, entre los que se encuentran los bosques mediterráneos, se sitúan entre los más vulnerables a nivel global (Lavorel et al. 1998; Mooney et al. 2001). Los modelos climáticos de los que disponemos en este momento predicen calentamientos muy notables acompañados de fuertes descensos en las precipitaciones, especialmente en primavera y verano (Christensen et al. 2007). Esta vulnerabilidad climática se incrementa por el hecho de que muchos de sus elementos biológicos tienen distribuciones muy reducidas o encuentran aquí su límite más meridional, además de por su elevado nivel de fragmentación que acentúa su fragilidad (Scarascia-Mugnozza et al. 2000).

Objetivos

Con esta tesis pretendemos valorar y evaluar algunos de los factores que pueden estar comprometiendo la conservación de especies liquénicas. El objetivo final es recabar la información necesaria que nos permita proponer medidas fundamentadas para la prevención o minimización de los factores de amenaza y poder desarrollar estrategias de conservación eficaces..

Los objetivos específicos se enmarcan en dos bloques.

El **Bloque I**, con un enfoque multiespecífico, incluye los capítulos 1 y 2.

> **Capítulo 1**: "*Poor efectiveness of the Natura 2000 network protecting Mediterranean lichen species*" El objetivo principal de este capítulo es evaluar si la red europea de reservas Natura 2000 ofrece una protección efectiva de una gran diversidad de especies liquénicas. Como objetivos secundarios proponemos: (a) determinar la distribución potencial de 18 especies de líquenes con ecologías diferentes y distribución reducida en la Península Ibérica; (b) evaluar si la Red Natura 2000 presenta una capacidad diferencial de protección para los líquenes en función de la Región Biogeográfica.
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> **Capítulo 2**: "*Climatic change effects on lichens: traits and vulnerability*". El objetivo principal de este trabajo es detectar qué rasgos y atributos específicos pueden propiciar una mayor vulnerabilidad frente al cambio climático. Como objetivos parciales planteamos: (a) el cálculo de variaciones de área bioclimática de un grupo representativo de especies de la Península Ibérica; y (b) la detección de relaciones entre dichas variaciones y los atributos o rasgos específicos, para detectar aquellos que favorecen la vulnerabilidad frente al cambio climático.

Paralelamente, el **Bloque II** (**capítulos 3**, **4** y **5**) tiene como principal objetivo obtener información de calidad sobre la ecología, demografía y fisiología de una única especie de liquen epífito: *Lobaria pulmonaria* L. (Hofm.). para obtener un diagnóstico acertado sobre los factores externos y procesos vitales que son claves o condicionan la viabilidad de las poblaciones de esta especie. Para ello, se afronta un estudio detallado de 4 poblaciones de la especie, con el fin de evaluar el estado de las mismas a nivel poblacional, ecofisiológico y demográfico.

> **Capítulo 3**: "*Microhabitat selection by the epiphytic lichen* Lobaria pulmonaria*: the host tree species does matter*". Este estudio pretende establecer los efectos a nivel poblacional de las variables de microhábitat sobre *Lobaria pulmonaria*. Los objetivos

específicos son: (a) comparar la presencia y abundancia de *L. pulmonaria* en función de la especie de árbol sobre la que crece (*Quercus pyrenaica* (Willd.) o *Fagus sylvatica* (L.)); (b) evaluar y comparar la estructura poblacional de tamaños entre ambos árboles; (c) identificar las características del microhábitat que modifican la respuesta reproductiva y de estado de salud de *L. pulmonaria*.

Capítulo 4: "Microconditions tune *Lobaria pulmonaria* vitality in a Mediterranean forest". El objetivo de este trabajo es detectar variaciones en la vitalidad (eficacia fotosintética) de *L. pulmonaria*. Como objetivos concretos se pretenden testar los efectos de del microhábitat sobre la vitalidad de *L. pulmonaria*: (a) la cobertura de dosel; (b) la temperatura y la humedad relativa del aire; (c) especie de forófito; (d) microhabitat; y (e) la variabilidad intrínseca del individuo, así como su tamaño.

Capítulo 5: "Patterns of demographic variation in a threatened, long-lived, epiphytic lichen". El objetivo de este trabajo es averiguar los patrones y tasas demográficas de *Lobaria pulmonaria*, y ver cómo varían en función de las condiciones microecológicas. Los objetivos específicos son: (a) ajustar las tasas vitales de *L. pulmonaria*; (b) evaluar qué proporción de la variabilidad en las tasas corresponde a causas espaciales o temporales; (c) comprobar si las respuestas demográficas a escalas intermedias coinciden con las respuestas a menor escala; (d) testar si hay "compensación demográfica" en el tiempo y/o el espacio.

Metodología general

La metodología se detalla en cada uno de los capítulos. En este apartado, se presenta una versión resumida de los métodos, en función de los dos bloques mencionados en los objetivos.

Bloque I: Los capítulos 1 y 2 abordan sus objetivos desde un enfoque multiespecífico y a gran escala. La herramienta principal de análisis son "Modelos de distribución de especies" (SDMs) (Guisan y Zimmermann 2000), utilizando variables explicativas macroambientales.

> En el **capítulo 1**, el trabajo se restringe a España peninsular, mientras que en el **capítulo 2** incluye toda la Península Ibérica.
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> En el **capítulo 1** seleccionamos 18 especies liquénicas con áreas de distribución reducidas en la Península Ibérica. Este grupo de especies supone un buena representación de características ecológicas y hábitats. El **capítulo 2** estudia 41 especies liquénicas presentes en la Península Ibérica, aportando un conjunto amplio de rasgos funcionales y atributos ecológicos.
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> Las variables explicativas del **capítulo 1** son geológicas, topográficas, de cobertura del terreno, y climáticas. En el **capítulo 2** se analizaron variables climáticas actuales y futuras (2080, según varias proyecciones).
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> Ambos capítulos analizan los datos mediante modelos de distribución de especies con datos de sólo presencia. En el **capítulo 1**, en base al algoritmo ENFA (implementado con Biomapper (Hirzel et al 2004)). En el **capítulo 2**, utilizando un consenso entre los resultados que arrojaron GLMs (Modelos Lineales Generalizados, McCullagh y Nelder 1989), GAM (Modelos Aditivos Generalizados, Hastie y Tibshirani 1986) y CART (Árboles de Regresión y Clasificación, Brieman et al 1986). La relación entre la vulnerabilidad y los rasgos específicos se testó con GLMs.

Bloque II: Incluye los capítulos 3, 4 y 5, en los que se estudian las respuestas de la especie *Lobaria pulmonaria* a nivel poblacional, demográfico y ecofisiológico en distintas poblaciones del Sistema Central. Las variables analizadas definen el microhábitat y están a escala de parcela, árbol y/o individuo: Los análisis estadísticos se llevan a cabo mediante "Modelos Mixtos Lineales Generalizados" (GLMMs) (Zuur et al 2009).

> *Lobaria pulmonaria* es un liquen principalmente epífito considerado como Vulnerable en la Península Ibérica (Martínez et al 2003). Se trata de una especie sensible a las

modificaciones de su hábitat a varias escalas (Belinchón et al 2009, 2011). Estudiamos la respuesta poblacional y fisiológica de la especie en el Sistema Central. Para ello, establecimos 4 parcelas de estudio distribuidas en las áreas protegidas del "Hayedo de Montejo" (Sierra del Rincón, Madrid) y "Parque Natural de la Sierra Norte de Guadalajara" (Sierra de Ayllón, Guadalajara) (Tabla 1). Se trata de dos zonas próximas entre sí, que cuentan con un clima mediterráneo de montaña. Las poblaciones se encuentran en bosques de *Quercus pyrenaica* (Willd.) y en bosques mixtos en los que el árbol predominante es *Fagus sylvatica* (L.). Dos parcelas son de bosque mixto, donde estudiamos los individuos de *L. pulmonaria* creciendo sobre haya y melojo; en las otras dos parcelas, exclusivas de melojar, estudiamos individuos sobre melojo. Marcamos 725 individuos de *L. pulmonaria* (200 individuos en las parcelas 1-3, 125 en la 4), y se realizó un seguimiento exhaustivo durante los años 2011 y 2012. Se obtuvieron datos de todas las parcelas para los **capítulos 3** y **5**, mientras que en el **4**, se incluyeron únicamente datos de la parcela 1 (tabla 1).

Tabla 1: Parcelas de estudio de Lobaria pulmonaria, características y capítulos en los que se ha obtenido información de cada una de ellas.

Área protegida	Provincia	Parcela	Tipo de bosque	Tamaño (ha)	Posición X;Y (m)	Capítulos
Hayedo de Montejo	Madrid	1	Mixto	1	4555119;455864	3,4,5
		2	Robledal	0.25	4555109;458677	3,5
P.N. Sierra Norte de Guadalajara	Guadalajara	3	Mixto	0.25	4564030;467755	3,5
		4	Robledal	0.65	4549449;462976	3,5

En la tabla 2 presentamos todas las variables analizadas en el **Bloque II**, detallando cuáles se incluyeron en cada capítulo como variables explicativas y variables respuesta. Los valores de las variables microclimáticas derivan de valores de temperatura y humedad del aire recogidos cada hora por 12 sensores (HOBO V2 Pro) repartidos en las 4 parcelas. Las variables que describen el árbol y la posición del individuo se tomaron al principio del seguimiento. Para la presencia y abundancia de estructuras de reproducción, se utilizó el dato inicial. El tamaño inicial y crecimiento de los individuos se calculó mediante análisis de imagen de fotografías de los individuos marcados (Nikon Coolpix 4500, Nikon, Japan y *Adobe Photoshop*). La eficiencia cuántica del fotosistema II (Fv/Fm) se midió utilizando un fluorímetro de campo (Handy Pea). El reclutamiento se valoró realizando un muestreo mensual verificando el número de individuos nuevos en 360 cuadrados de 20x20cm.

Los análisis estadísticos se llevaron a cabo mediante GLMMs (Modelos Mixtos Lineales Generalizados), en los **capítulos 3** y **4**. En el **capítulo 5,** para el ajuste de las tasas vitales de *L. pulmonaria,* se utilizaron Modelos Lineales Generalizados y Polinómicos. Los modelos predictivos de los **capítulos 4** y **5** se seleccionaron mediante criterios de información de Akaike (AICc y cAIC respectivamente).

Tabla. 2: Variables utilizadas en cada capítulo del Bloque II como variables explicativas o respuesta. Nivel de estudio, nombre y descripción de la variable (unidades de la variable), capítulo en que se analiza.

Descripción de la variable	Capítulo					
	3	4	5	3	4	5
Nivel de parcela	Explicativa			Respuesta		
Humedad media relativa del aire(%) durante la toma del dato y 4 horas previas		x				
Humedad relativa del aire (%) durante la toma del dato		x				
Humedad relativa media del aire del semestre (%)			x			
Temperatura del aire (ºC) durante la toma del dato		x				
Temperatura media del aire (ºC) durante la toma del dato y 4 horas previas		x				
Temperatura media del aire del semestre (ºC)			x			
Temporada cobertura dosel [Mayo-Octubre]/ sin dosel [Noviembre-Abril]		x				
Horas totales de luz del semestre			x			
Horas totales de actividad (luz + humedad>90%)			x			
Nivel de árbol						
Especie de árbol (*Q.pyrenaica* / *F.sylvatica*)	x	x	x			
Diámetro del árbol a 1.3 m (cm)	x					
Diámetro del árbol a 0 m (cm)	x					
Grosor de la corteza (mm)	x					
Cobertura de briófitos en el tronco: inferior (<1m)/ superior(>1m) (%)	x					
Apertura del dosel arbóreo (%)		x	x			
Presencia de individuos de *L. pulmonaria* reproductores			x	x		
Presencia de individuos de *L. pulmonaria* no reproductores				x		
Abundancia de individuos de *L. pulmonaria* reproductores				x		
Abundancia de individuos de *L. pulmonaria* no reproductores				x		
Nivel de individuo						
Diámetro máximo del talo al inicio del periodo (mm)				x		
Tamaño del talo en área al inicio del periodo (mm^2)		x	x			
Tamaño del talo en área al final del periodo (mm^2)			x			
Crecimiento del talo (variación relativa del área en 24 meses) (%)						x
Supervencia del individuo en el semestre						x
Reclutamiento: individuos nuevos en el cuadrado de muestreo/ periodo						x
Altura en el tronco sobre la que crece el individuo (cm)	x	x	x			
Orientación en el tronco sobre la que crece el individuo (º)	x	x	x			
Crece directament sobre: corteza/briófito/otro liquen	x					
Tamaño del adulto próximo (<20cm) (mm^2)			x			
Presencia / ausencia de estructuras reproductoras				x		
Presencia / ausencia de apotecios				x		
Presencia / ausencia de estructuras de reproducción asexual				x		
Presencia / ausencia de soredios				x		
Presencia / ausencia de isidios				x		
Abundancia de soredios				x		
Abundancia de isidios				x		
Presencia / ausencia de signos de blanqueo, parasitación o depredación				x		
Eficiencia cuántica del fotositema II: Fv/Fm (micromoles/m2s)					x	

Conclusiones generales

1. La Red Natura 2000, diseñada a partir de la distribución de plantas vasculares, no asegura una protección eficaz a todas las especies de líquenes. Los hábitat forestales mediterráneos reciben mayor atención, frente a hábitats no forestales, térmicos y secos, generalmente costeros. Las especies de líquenes asociadas a estos hábitats no forestales presentan tasas de protección claramente insuficientes. Además, la efectividad de esta red presenta un efecto regional: ofrece mejores tasas de protección a especies asociadas a la región Mediterránea que a especies Atlánticas.

2. El cambio climático esperado para 2080 provocará un pérdida de espacio bioclimático para la mayoría de los líquenes estudiados. Sólo algunas especies, asociadas a hábitats térmicos y secos, tendrán áreas bioclimáticas mayores en el futuro próximo. Los atributos ecológicos y rasgos funcionales específicos permiten predecir a grandes rasgos la sensibilidad o vulnerabilidad de una especie. Rasgos como un tamaño pequeño de talo o que el fotobionte sea un alga verde; así como algunos atributos (como utilizar un árbol como sustrato) minimizan el efecto del cambio climático.

3. La heterogeneidad ambiental a escala de microhabitat afecta a *Lobaria pulmonaria* en el bosque mediterráneo, a varios niveles: poblacional, ecofisiológico y demográfico, en todas las etapas y tasas de su ciclo vital.

4. A escala espacial, la especie de árbol sobre el que crece *L. pulmonaria* ejerce una gran influencia sobre su desempeño a los tres niveles estudiados y además, modifica el efecto de otras variables a escala temporal (p.e. horas de luz) o menor escala espacial (p.e. orientación en el tronco).

    a. Si *L. pulmonaria* crece sobre roble melojo (*Q. pyrenaica*), se favorece la colonización y el reclutamiento y se alcanzan tamaños poblacionales mayores, con una estructura de tamaños sesgada hacia individuos pequeños. Además, el melojo favorece la reproducción temprana: el tamaño mínimo para desarrollar estructuras de reproducción es casi la mitad que si el árbol es un haya. La vitalidad de *L. pulmonaria* en melojo responde a un modelo simple: se ve comprometida en momentos secos y orientaciones sur, que favorecen la exposición excesiva a la luz y la desecación.

    b. Si el sustrato es un haya (*F. sylvatica*), *L. pulmonaria* se ve más limitada por las condiciones de microhábitat que si se trata de un melojo. Las poblaciones son de menor tamaño, y requieren árboles más gruesos y con corteza más desarrollada. El tamaño y la vitalidad de los individuos responde a un modelo más complejo, que incluyen más variables (p.e. la altura en el tronco). Por otro lado, las tasas de supervivencia son ligeramente mayores sobre haya, así como los tamaños individuales alcanzados.

5. A una menor escala espacial, destaca la importancia de la posición en el tronco del árbol tiene fuertes repercusiones sobre *L. pulmonaria*, regulando su exposición a la desecación y el exceso de luz y controlando, por tanto, el número y duración de periodos

activos. Sobre haya, cuanto más cerca del suelo crece un individuo, más grande puede llegar a ser y más vitalidad presenta. En cualquier especie de árbol, los individuos en las partes más bajas del tronco tienen mayores tasas de crecimiento y más probabilidad de desarrollar estructuras de reproducción sexual (apotecios). La posición en orientación es también importante. Una posición en la cara norte del tronco de un haya supone un aumento del tamaño, la supervivencia e incluso el reclutamiento. Independientemente del árbol, estar al norte mejora la vitalidad, el crecimiento y el reclutamiento.

6. La respuesta de *L. pulmonaria* también varía a escala temporal. La vitalidad depende principalmente de la humedad relativa del aire, ya que los líquenes tienen que estar hidratados para activarse. Las tasas demográficas también varían a lo largo del año: los periodos de verano (más horas de luz y menos humedad) favorecen la supervivencia, mientras que los de invierno (menos horas de luz, más humedad y frío) favorecen las tasas de crecimiento y reclutamiento.

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Referencias

Albert M. J., Escudero A., Iriondo J. M. (2001). Female reproductive success of narrow endemic *Erodium paularense* in contrasting microhabitats. Ecology, 82: 1734-1747.

Aragón, G., Martínez, I., Izquierdo, P., Belinchón R., Escudero, A. (2009). Effects of forest Management on epiphytic lichen Diversity in Mediterranean forests. Applied Vegetation Science, 13: 183-192.

Araújo, M. B., Lobo, J. M., Moreno, J. C. (2007). The effectiveness of Iberian protected areas in conserving terrestrial biodiversity. Conservation Biology, 21: 1423–1432.

Arribas, P., Abellán, P., Velasco, J., Bilton, D.T., Lobo, J.M., Millán, A., Sánchez-Fernández, D. (2012). La vulnerabilidad de las especies frente al cambio climático, un reto urgente para la conservación de la biodiversidad. Ecosistemas, 21: 79-84.

Atienza V., Segarra J.G. (2000). Preliminary red list of the lichens of the Valencian Community (eastern Spain). Forest, Snow and Landscape Research, 75: 391-400.

Belinchón, R., Martínez, I., Escudero, A., Aragón, G., Valladares, F. (2007). Edge effects on epiphytic communities in a Mediterranean *Quercus pyrenaica* forest. Journal of Vegetation Science, 18:81-90.

Belinchón, R., Martínez, I., Otálora, M.A.G., Aragón, G., Dimas, J., Escudero, A. (2009). Fragment quality and matrix affect epiphytic performance in Mediterranean forest landscape. American Journal of Botany, 96: 1974-1982.

Belinchón R., Martínez, I., Aragón, G., Escudero A., de la Cruz, M. (2011). Fine spatial pattern of an epiphytic lichen species is affected by habitat conditions in two forest types in the Iberian Mediterranean Region. Fungal Biolog,y 115: 270-1278.

Bellard, C., Bertelsmeie, C., Leadley, P., Thuiller, W., Courchamp, F. (2012) Impacts of climate change on the future of biodiversity. Ecology Letters, 15: 365-377.

Blondel J., Aronson J. (1999). Biology and wildlife of the Mediterranean region. Oxford University Press, New York.

Breiman L, Friedman JH, Olshen RA, et al. (1984) *Classification and Regression Trees*. Chapman and Hall, New York.

Brown, T. E. (2001). Lichens: the organisms. In: Brodo, I. M., Durán, SI y Sharnoff, S. (eds.), Lichens of North America. Yale University press/New Haven and London: 3-8.

Chen, I.; Hill, J. K., Ohlemüller, R., Roy, D. B., Thomas, C. D. (2011). Rapid range shifts of species associated with high levels of climate warming. Science, 333: 1024-1026.

Christensen J.H., Hewitson B., Busuioc A., Chen A., Gao X., Held I., Jones R., Kolli R.K., Kwon W-T., Laprise R., Rueda V.M., Mearns L., Menéndez C.G., Räisänen J., Rinke A., Whetton A.S.P. (2007). Regional climate projections. Contribution of working group I to the fourth assessment report of the intergovernmental panel on climate change. In: Solomon S., Qin D., Manning M., Chen Z., Marquis M., Averyt K.B., Tignor M. and Miller H.L. (eds) Climate change 2007: The physical science basis. Cambridge University Press, Cambridge, United Kingdom and New York, NY, USA, 847-943

Costa M., Morla C., Sainz H. (2001). Los bosques ibéricos. Editorial Planeta, Madrid.

Dettki, H., Esseen, P. A. (1998). Epihpytic macrolichens in managed and natural forest landscapes: a comparison at tow spatial scales. Ecography, 21: 613-624.

Diamond, S. E., Frame, A. M., Martin, R. A., Buckley, L. B. (2011) Species' traits predict phenological responses to climate change in butterflies. Ecology, 92: 1005-1012.

Doblas-Miranda, E., Retana, J. (2011). Amenazas y oportunidades ante el cambio global en los montes españoles: el proyecto MONTES Consolider. Ecosistemas, 20:114-123.

Ellis, C. J. (2013). A risk-based model of climate change threat: hazard, exposure, and vulnerability in the ecology of lichen epiphytes. Botany, 91: 1-11.

Escolar, C., Martínez, I., Bowker, M. A., Maestre, F.T. (2012) Warming reduces the growth and diversity of biological soil crust in a semi-arid environment, implications for ecosystem. Philosophical Transactions of the Royal Society of Biological Sciences, 367: 3087-3099.

Esseen, P.-A., Renhorn, K. E. (1998). Edge effects on an epiphytic lichen in fragmented forests. Conservation Biology, 12: 1307-1317.

Farrar, J. F. (1976). The lichen as an ecosystem: observation and experiment. In: Brown, D., Hawksworth, D. L. and Bailey, R. H. (eds), Lichenology: progress and problems. Proc. of an Int. Symp. held at the Univ. of Bristol. Academic Press, pp. 385/407.

Gauslaa, Y., Palmqvist, K., Solhaug, K. A., Holien, H., Hilmo, O., Nybakken, L., Myhre, L. C., Ohlson, M. (2007). Growth of epiphytic old forest lichens across climatic and succesional gradients. Canadian Journal of Forestry Research, 37: 1832-1845.

Gauslaa, Y., Solhaug, K. A. (2001). Fungal melanins as a sun screen for symbiotic green algae in the lichen *Lobaria pulmonaria*. Oecología, 126: 462-471.

Gu, W. D., Kuusinen, M., Konttinen T., Hanski, I. (2001). Spatial pattern in the occurrence of the lichen *Lobaria pulmonaria* in managed and virgin forests. Ecography, 24: 139-150.

Guisan, A., Zimmermann, N. E. (2000). Predictive habitat distribution models in ecology. Ecology Letters, 135: 147-186.

Hastie T.J., Tibshirani R. (1990). Generalised Additive Models. Chapman and Hall, London.

Hirzel, A. H., Hausser, J., Perrin, N. (2004). Biomapper 4.1. Lab of Conservation Biology, Department of Ecology and Evolution, University of Lausanne.

IPCC (2007) Climate change 2007: The scientific basis. In: Contributions of Working Group I to the Fourth Assessment Report of the Intergovernmental Panel on Climate Change: “The Physical Science Basis”, (eds Solomon S, Qin D, Manning M, Chen Z, Marquis M, Averyt KB, Tignor M, Miller HL), Cambridge University Press, Cambridge. pp. 1–18.

Iriondo, J. M., Albert, M.J., Giménez, L., Domínguez, F., Escudero A. (Eds.). (2009). Inventario Nacional de Biodiversidad. Poblaciones en peligro: variabilidad demográfica de la flora vascular amenazada de España. Ministerio de Medio Ambiente, Rural y Marino.242 pp.

Kharouba, H. M., McCune, J. L., Thuiller, W., Huntley, B. (2012) Do ecological differences between taxonomic groups influence the relationship between species’ distributions and climate? A global meta-analysis using species distribution models. Ecography: 35, 1-8.

Lavorel, S., Canadell, J., Rambal, S., Terradas, J. (1998). Mediterranean terrestrial ecosystems: research priorities on global change effects. Global Ecology and Biogeography Letters, 7:157-166.

Lesica, P.; McCune, B., Cooper, S., Hong, W.S. (1991). Differences in lichen and bryophyte communities between old-growth and managed second-growth forests in Swan Valley, Montana. Canadian Journal of Botany, 69: 1745-1755.

MacKenzie, T. D. B., Król, M., Norman, P.A., Campbell, D.A. (2002). Seasonal changes in chlorophyll fluorescence quenching and the induction and capacity of the photoprotective xanthophyll cycle in *Lobaria pulmonaria*. Canadian Journal of Botany, 80: 255-261.

MacKenzie, T. D. B., MacDonald, T. M., Dubois, L. A., Campbell, D. A. (2011). Seasonal changes in temperature and light drive acclimation of photosynthetic physiology and macromolecular content in *Lobaria pulmonaria*. Planta: 214: 57-66.

Martínez , I., Aragón, G., Sarrión, F. J., Escudero, A., Burgaz, A. R., Coppins, B. J. (2003). Threated lichens in the central Spain (saxicolous species excluded). Cryptogamie, Mycologie: 24: 73-97.

Martínez, I.; Flores, T.; Otálora, M. A. G.; Belinchón, R.; Prieto, M.; Aragón, G.; Escudero, A. (2012). Multiple scaleenvironmental modulation of lichen reproduction. Fungal Biology116: 1192-1201.

McCullagh P., Nelder J.A. (1989) Generalised Linear Models. Chapman and Hall, London.

McCune, B. (2000). Lichen communities as indicators of forest health. The Bryologist, 103: 353-356.

Mesa, S. (2002). Historia de los bosques de la Península Ibérica. En: Charco, J (Ed), La regeneración natural del bosque mediterráneo en la Península Ibérica. Arba-Ministerio de Medio Ambiente, Madrid: 153–170.

Moreno Rodríguez, J. M. (coord.) et al (2005) Principales conclusiones de la evaluación preliminar de los impactos en España por efecto del cambio climático. Oficina Española de Cambio Climático, Ministerio de Medio Ambiente, Madrid. 39 pp

Morillo, C., Gómez-Campo, C. (2000) Conservation in Spain 1980-2000. Biological Conservation, 95: 165-174

Nash III, T. H. (2008): Introduction. En: Nash III, T.H. (ed.), Lichen Biology. 2nd Cambridge University Press, Cambridge. 1-8

Nash, T.H., Olafsen , A. G. (1995). Climate change and the ecophysiological response of artic lichens. The Lichenologist 27: 559-565.

Öckinger E, Nilsson S. 2010. Local population extinction and vitality of an epiphytic lichen in fragmented old-growth forest. Ecolog: 91: 2100-2109.

Palmqvist, K., Sundberg, B. (2000). Light use efficiency of dry matter gain in five macro-lichens: relative impact of microclimate conditions and species-specific traits. Plant, Cell and Environmen:, 23: 1-14.

Primark, R.B., Ros, J. (2002). Introducción a la biología de la conservación. Ariel. Barcelona.

Ranius T. (2002). Influence of stand size and quality of tree hollows on saproxylic beetles in Sweden. Biological Conservation, 103: 85-91.

Rey-Benayas, J.M., de la Montaña, E. (2003). Identifying areas of high-value vertebrate diversity for strengthening conservation. Biological Conservation, 114: 357–370.

Rodó, X., Comín, F. (2001). Fluctuaciones del clima mediterráneo: conexiones globales y consecuencias regionales. En: Zamora, R., Pugnaire, F. (eds.), Ecosistemas mediterráneos: análisis functional. Serie de Textos Universitarios 32, CSIC-AEET, Granada: 1-36.

Sala, O.E., Chapin III, F.S., Armesto, J.J., Berlow, E., Bloomfield, J., Dirzo, R., Huber-Sanwald, E., Huenneke, L.F., Jackson,R.B., Kinzig, A., Leemans, R., Lodge, D.M., Mooney, H.A., Oesterheld, M., Poff, N.L., Sykes, M.T., Walker, B.H., Walker,M., Wall, D.H. (2000). Global biodiversity scenarios for the year 2100. Science, 287:1770-1774.

Sancho, L. G., Green, A. T.G., Pintado, A. (2007). Slowest to fastest: extreme range in lichen growth rates supports their use as an indicator of climate change in Antartica. Flora, 202: 667-673.

Sillet, S. C., McCune, B., Peck, J.E., Rambo, T.R., Ruchty, A. (2000). Dispersal limitations of epiphytic lichens result in species dependent on old-growth forests. Ecological Applications, 10: 789-799.

Snäll T., Pennanen, J, Kivistö L., Hanski, I. (2005). Modelling epiphyte metapopulation dynamics in a dynamic forest landscape. Oikos, 109: 209-222.

Steffen, W., Sanderson, A., Tyson, P.D., Jäger, J., Matson, P.A., Moore III, B., Oldfield, F., Richardson, K., Schellnhuber, H.J., Turner, B.L., Wasson, R.J. 2004. Global change and the earth system: A planet under pressure. 336 pp. Springer-Verlag. Berlin, Heidelberg y New York.

Summers, D. M, Bryan, B. A, Crossman, N. D, Meyer W. S. (2012) Species vulnerability to climate change, impacts on spatial conservation priorities and species representation. Global Change Biology: 18, 1365-2486.

Thirgood, J. V. (1981). Man and the Mediterranean forest (Vol. 981). London: Academic Press.

Thuiller W, Lavergne, S., Roquet, C., Boulangeat, I., Lafourcade, B., Araújo, M. B. (2011) Consequences of climate change on the tree of life in Europe. Nature: 470, 531-534.

UICN. (2001). IUCN Red List Categories and Criteria version 3.1

Valladares, F., Camarero, J. J., Pulido, F., Gil-Pelegrín, E. (2004). El bosque mediterráneo, un sistema humanizado y dinámico. En: Valladares, F. (ed.), Ecología del bosque mediterráneo en un mundo cambiante. Ministerio de Medio Ambiente, Madrid: 13-26.

Werth, S., Tommervik, H., Elvebakk, A. (2005). Epiphytic macrolichen communities along regional gradients in northern Norway. Journal of Vegetation Science, 16: 199-208.

Zuur, A., Ieno, E. N., Walker, N., Saveliev, A. A., Smith, G. M. (2009). Mixed effets models and extensions in ecology with R. Springer, NY USA. 574pp

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BLOQUE I:

ENFOQUE MULTIESPECÍFICO A GRAN ESCALA

CAPÍTULOS 1 Y 2

CAPÍTULO 1

Capítulo 1

Poor effectiveness of the Natura 2000 network protecting Mediterranean lichen species

MARTA RUBIO-SALCEDO, ISABEL MARTÍNEZ, FRANCISCO CARREÑO AND ADRIÁN ESCUDERO. (2013) Journal for Nature Conservation, 21:1-9.

Abstract

Evaluation of the effectiveness of protected areas networks for conserving diversity is a demanding topic in Biological Conservation. In the last few years, there has been an increasing number of studies on species distribution modelling which can be easily used to test the efficiency of reserve networks. Unfortunately, this effort has been focused on the so called charismatic species. Our main goal is to test the effectiveness of the Natura 2000 network by using non-charismatic species. We determined potential distribution patterns for 18 lichen species in Spain and evaluated the effectiveness of the Natura 2000 network in protecting them. Models were implemented with ENFA (Ecological-Niche Factor Analysis) because this modelling approach only requires presence data since the reliability of absence data is really poor. Habitat suitability maps were obtained and high suitability areas were characterized using 10 environmental predictors. The high suitability areas maps were overlaid with the Natura 2000 network cover, considering the different biogeographical regions present in mainland Spain. The effectiveness of the Natura 2000 was quite low in most species. The analysis per region showed that Mediterranean lichen species growing in forests are better protected than species found in coastal, drier and warmer areas. Our results indicate that the Natura 2000 network, a protection system based on vascular plants, does not guarantee the protection of Mediterranean lichen species. Thus, this type of gap analysis and especially the inclusion of "non-charismatic" organisms such as lichens should be considered in studies to define protected areas.

Keywords: conservation, ENFA, gap analysis, non-charismatic species, SDM (Species Distribution Model), Spain

Introduction

Establishment of conservation areas has been probably the most used tool for achieving the objective of get biodiversity conservation, although it must be also important to get an effectiveness management of these areas and to apply conservation actions outside protected areas (Primack, 2008). However, creation of new protected areas has been addressing in most of the cases to the protection of “charismatic species or groups of organisms”, even more the effectiveness of these individual areas and networks has been based on this efficiency to guarantee the conservation of these species. This fact is based on what has become a paradigm in Biological Conservation: the idea that by conserving charismatic species or those species located at the upper parts of the trophic networks, it will be also possible to get protecting whole biodiversity. With the idea of the need to establish conservation areas, Europe has developed the Natura 2000 network which is an ecological European network of conservation areas. Legislation that establishes guidelines for developing this network are the Directive 92/43/CEE related to the conservation of natural habitats and the wildlife fauna and flora, and the Directive 009/147/CEE related to the conservation of birds. Its purpose is to ensure the long-term survival of species and most threatened habitats in Europe, helping to stop the biodiversity loss caused by the adverse impact of human activities and it is the main instrument for nature conservation in the European Union.

Moreover, in the last years, different studies have been developed in order to establish the effectiveness of protected areas to conserve as much biodiversity as possible (Rey Benayas and de la Montaña, 2003; Araújo et al., 2007; Sánchez-Fernández et al., 2008). In this way, different studies have tried to evaluate if areas rich in species of some specific known groups will be also rich in species of groups less known or less charismatic. One of the first studies with this objective was developed by Prendergast et al. (1993) which included a limited number of taxa and found a limited coincidence among them. Other studies have focused on whether the presence or abundance of some or all species in a given assemblage is correlated with species richness or abundance of other taxonomic groups (Maes et al., 2005; Fleishman and Murphy, 2009). In some cases, researches have reported low degrees of correlations among the distribution of different groups of organisms (Ricketts et al., 2002; Kleintjes et al., 2004; Hess et al., 2006), whereas in other cases a positive correlation have found (Kerr et al., 2000; Bani et al., 2006; Larsen et al., 2007).

And recently, a few studies have focused on evaluating the coincidence of potential distribution areas where found a higher number of species of different groups of organisms

(Mac Nallyand and Fleishman, 2004; Maes et al., 2005). In the case of Maes et al. (2005), they found a high coincidence of geographic areas in Flandes with high predicted species richness among four faunal groups, but much lower between plants and each of the four faunal groups.

On the other hand, knowledge of species distribution pattern and their relationship to different environmental drivers is crucial for biodiversity conservation and management (Hortal et al., 2004; Seoane et al., 2005; Martínez et al., 2006). Species distribution pattern is the basis for selecting areas of high biodiversity and for optimizing available resources in protected areas (Godown and Peterson, 2000). It is also becoming part of policies and actions of Territorial Planning (Godown and Peterson, 2000; Hortal et al., 2004).

In this sense, species Distribution Models (*SDM*) (Guisan and Zimmermann, 2000) are one of the best available tools for obtaining distribution and/or probability of occurrence information (Carter et al., 2006). This type of models is especially useful when we have not data of precision about occurrences or in those cases when there is scarce information such as in the case of little known groups of organisms. Despite there is a complete panoplia of models tools for dealing with this goal (Hirzel and Arlettaz, 2003; Guisan and Thuiller, 2005; Hirzel and Le Lay, 2008), when available data are only presence data, several tools are recommended (Walker and Cocks, 1991; Carpenter et al., 1993; Hirzel et al., 2002). Many different algorithms and software are available. Among presence only methods ENFA is on the best known ones. Its main advantage, comparing to other similar algorithms is that ENFA, using Biomapper, gives you back very useful information about the niche of the species (in the Hutchinsonian meaning; Hutchinson, 1957), in terms of which niche is the ecological space occupied by a species.

Most modeling distribution studies have focused on ‘charismatic’ organisms like birds (Godown and Peterson, 2000; Seoane et al., 2005), butterflies (Fleishman et al., 2003; Hortal et al., 2004), mammals (Cassinello et al., 2006) or plants (Randin et al., 2009; Meier et al., 2011), probably because data quality was rationality higher. However, ‘non-charismatic’ organisms have received little attention. Lichens could be included in this group of ‘non-charismatic’ organisms because they are unknown by general public and they are not a priority in conservation policies, and few predictive models have been developed for lichens (Edwards et al., 2006; Martínez et al., 2006; Bollinger et al., 2007; Ellis et al., 2007a, b). This is really impacting since groups such as algae, bryophytes and fungi including lichens comprise more than 85% of “botanic” biodiversity (Ellis et al., 2007a). This is a serious conservation concern since most of the networks and protected areas are designed based on the distribution of “charismatic species” (Martínez et al., 2006) and it is assumed that this diversity should be efficiently protected. Preliminary results working with 11 Peltigerales species showed that Natura 2000 network protected most of the lichens (Martínez et al., 2006). The authors indicated that lichen species were quite well-included in the Natura 2000 network because they were epiphytic species growing in temperate forests and with a distribution area centered in northern and central Europe, reaching in the Iberian Peninsula their southern distribution limit in Europe. They also explained that temperate forests are well represented in the Spanish Natura 2000 network; and so the relatively high effectiveness of the Natura 2000 network in the protection of this type of lichen species. Since these lichens had forests requirements, authors openly asked if this result would be extrapolate to terricolous or saxicolous lichens.

The main purpose of this study was to evaluate the effectiveness of the Natura 2000 network in protecting rare lichen species which do not strictly occur in forest habitats. Even more, we hypothesized that the establishment of a network based on the presence of some species or habitats do not guarantee the conservation of all types of organisms. Our hypothesis is that terricolous, saxicolous and epiphyte Mediterranean lichen species with reduced distribution areas will not be as well protected as lichen species mainly growing in temperate forest habitats. In order to test our hypothesis we aimed to (1) determine the potential distribution of 18 lichen species with different ecological characteristics and reduced distribution in mainland Spain; (2) compare the obtained potential distribution maps with the areas protected by the Natura 2000 network and evaluate the effectiveness of the network in protecting these species; and (3) evaluate if the effectiveness of the network varies between biogeographical regions.

Materials and methods

Study area

The study area was Peninsular Spain (that is, Spain excluding the Canary and Balearic Islands and territories from North Africa). This territory extends 493 486 km^2 and is well known for its heterogeneous landscape. It is located in the temperate zone, but the climate varies from Atlantic and Mediterranean to Alpine in the highest mountains (Martínez et al., 2006).

The study area was divided into a grid of 4928 cells of 10 km x 10 km, following Martínez et al. (2006). All biological and environmental data were georeferenced to this grid.

Abiotic data sets: Ecogeographical Variables (EGV)

The abiotic variables used in this study were: maximum elevation (m) (maximum elevation found in each cell), mean elevation (m) (mean value in each cell), altitudinal range (m) (difference between maximum and minimum altitude in each cell), type of soil cover meaning a gradient of perturbation (2 forests / 1 shrublands / 0 pastures and agricultural lands), bedrock type (1 calcareous / 0 non-calcareous), summer precipitation (mm) (total precipitation in June, July and August), total precipitation (mm), drought period (number of months when the precipitation curve is below the temperature curve), maximum temperature (ºC) (mean of the highest daily temperatures of the hottest month in each cell) and mean annual temperature (ºC) (average temperature of the whole year in each cell).

Table 1: List and codes of the ecogeographical variables (EGVs) considered in the study.

Type	Variable	Code
Topography	Maximum elevation	MAX-ALT
	Mean elevation	MED-ALT
	Altitudinal range	RAN-ALT
Land-Cover	Type of cover (2-forests/1-shrublands/0-pastures and agricultural lands)	COB
Geology	Bedrock type (calcareous /non-calcareous)	ROCA
Climate	Summer precipitation	PV
	Annual precipitation	PT
	Drought period	SEQ
	Maximum temperature	T-MAX
	Mean annual temperature	T-MED

Abiotic variables were classified into topographic, land use, geological and climatic groups (Table 1). Climatic variables were derived from the simulation model for Spain CLIMOEST (Palomares et al., 1999); topography parameters were derived from the Shuttle Radar Topography Mission (SRTM) data recorded in February 2000 at a 100 m resolution (Farr et al., 2007); bedrock type was obtained from geological cartography (Rodríguez-Fernández, 2004); land-cover map was obtained from the Spanish Ministry of the Environment; and the Natura 2000 network sites were obtained from the "Banco de Datos de la Naturaleza" (for further details on obtaining variables, see Martínez et al., 2006).

Species selection

When choosing the species, we use the checklist of the lichens and lichenicolous fungi of the Iberian Peninsula and Balearic Islands (Llimona and Hladun, 2001); available at *http://botanica.bio.ub.es/checklist.htm*); only *Vahliella saubinetii (Mont.)* P. M. Jørg. follows a different nomenclature (Jørgensen, 2008).

We specifically selected species terricolous, saxicolous and also epiphyte lichen species which do not strictly grow in temperate forest habitats and with reduced distribution areas. Moreover, we selected those species with a marked Mediterranean distribution.

Presence data for each species were obtained from bibliographic sources and herbaria. As those data were highly heterogeneous in resolution and format, we revised, edited, homogenized and stored them in a new data base. We deleted redundant, not accurate enough and not totally reliable points. We also discarded those species with less than 16 presence observation points, as more than 15 independent observations are needed to develop the models.

Finally, we selected 18 species: *Buellia cedricola* Werner*, Cetraria crespoae* (Barreno et Vázquez) Kärnefelt*, Cladonia mediterranea* P.A. Duving. et Abbayes*, Dirina ceratoniae* (Ach.) Fr.*, Fuscopannaria ignobilis* (Ahti) P.M Jørg., *Fuscopannaria olivacea* (P.M Jørg.) P.M Jørg.*, Koerberia biformis* A.Massal*, Nephroma tangeriense* (Maheu et A. Gillet) Zahlbr.*, Pyrrhospora lusitanica* (Räsänen) Hafellner*, Peltigera monticola* Vitik*, Pertusaria paramerae* A. Crespo et Vêzda*, Ramalina rosacea* Hochs. ex Schaer*, Solenopsora holophaea* (Mont.) Samp.*, Staurolemma omphalarioides* (Anzi) P.M Jørg. et Henssen*, Teloschistes chrysophthalmus* (L.) Th. Fr.*, Vahliella saubinetii (Mont.)* P. M. Jørg.*, Waynea adscendens* V.J. Rico and *Xanthoria resendei* Poelt et Tav.

Presence data of each lichen species were registered within each cell at a 10 km x 10 km resolution (Fig.1). The spatial data were used to create shapefiles in *ArcView 3.2.* Shapefiles were edited, projected and managed using *ArcGis 9.2* and then converted into raster format.

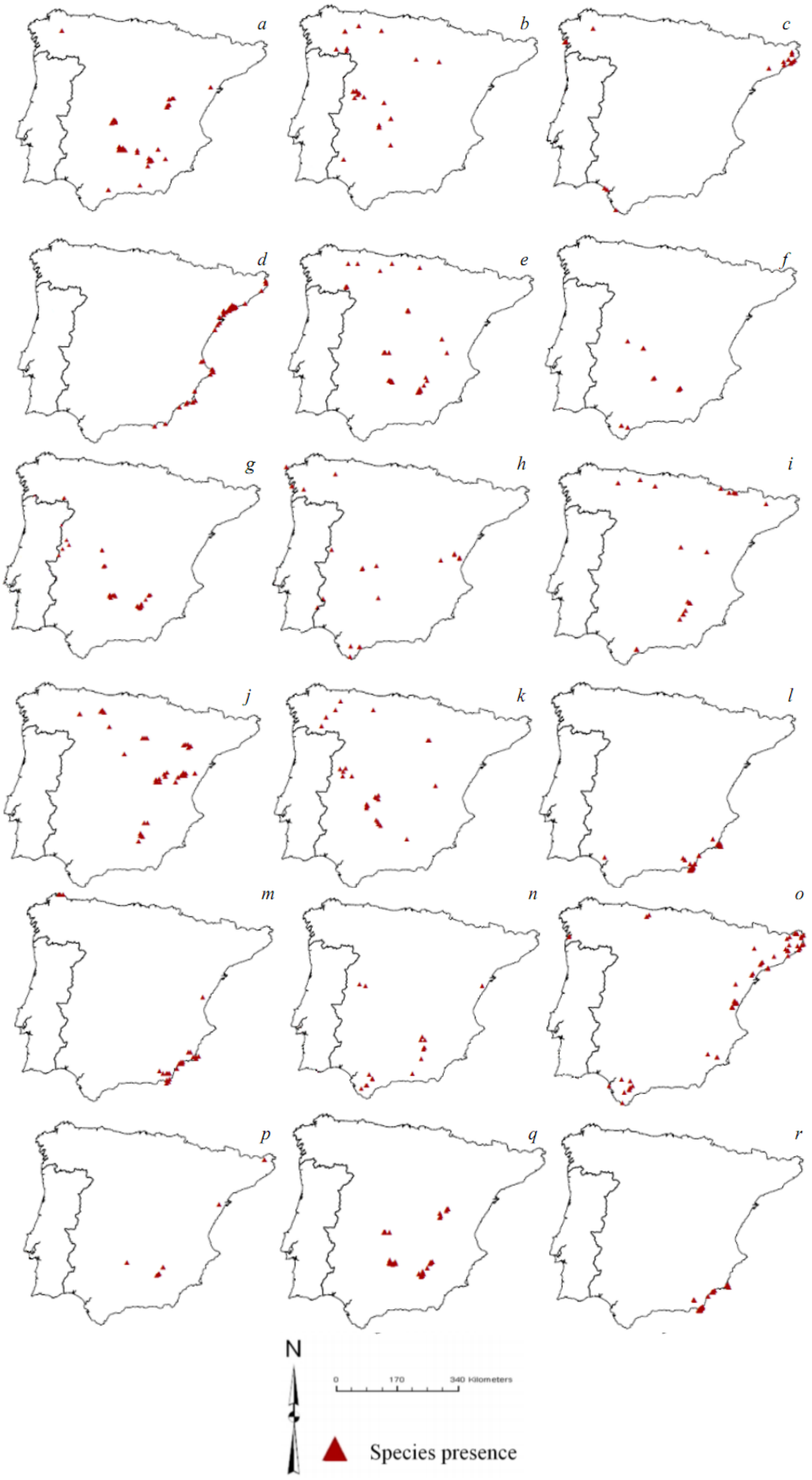

Figure1. **Distribution maps of the studied species in Spain. (a)** ***B. cedricola*****, (b)** ***C. crespoae*****, (c)** ***C. mediterranea*** **(d)** ***D. ceratoniae*****, (e)** ***F. ignobilis*****, (f)** ***F .olivacea*****, (g)** ***K. biformis*****, (h)** ***N. tangeriense*****, (i)** ***P. monticola*****, (j)** ***P. paramerae*****, (k)** ***P. lusitanica*****, (l)** ***R. rosacea,*** **(m)** ***S. holophaea*****, (n)** ***S. omphalarioides*****, (o)** ***T. chrysophthalmus*****, (p)** ***V. saubinetii,*** **(q)** ***W. adscendens*****, (r)** ***X. resendei*****.**

Data analysis

Some models are better suited to reflect the nature of the species' response (Guisan and Zimmermann, 2000). In our case, we have selected Ecological Niche Factor Analysis (ENFA) because provides us valuable information about the abiotic variables that are driving the species niche. Ecological Niche Factor Analysis (ENFA) provides a method for obtaining improved distribution models, because it can be used with presence-only datasets (Hirzel et al., 2002), and is considered one of the most successful methods when using only presence data (Brotons et al., 2004; Chefaoui et al., 2005). ENFA was performed with *Biomapper 4.1* (Hirzel et al., 2004), freely available at *www2.unil.ch/biomapper.*

ENFA generates a non-correlated number of factors that have ecological meaning, based on the assumption that species are not randomly distributed over a set of ecogeographical variables. First factor corresponds to "marginalization", while other factors represent decreasing amounts of information on the "specialization of the species".

Marginality can be understood as the degree of difference between the mean distribution of a species and average conditions in the study area. ENFA generates a global coefficient of marginality with the absolute value fluctuating between 0 and 1, although it can exceed one (Hirzel et al., 2002). Large values indicate that a species has habitat requirements different from average conditions. The global specialization coefficient ranges from 1 to infinite, expressing the ratio of global variance to species variance. The tolerance value is useful for comparing the results of different species. The tolerance value is the inverse to specialization and ranges from 0 to 1. Tolerance values close to 1 indicate that the species has a wide ecological niche, whereas values close to 0 indicate that the species has a narrow ecological niche (Hirzel et al., 2002).

The number of factors used to build the habitat suitability maps explained at least 70% of the variance. Model validation was carried out by means of a jack-knife cross-validation process (Fielding and Bell, 1997). To validate the models, a *jack-knife* cross validation is used. This process computes a confidence interval about the predictive accuracy of the habitat suitability model. The species locations are randomly partitioned into *n* mutually exclusive but identically size sets. The *n*-1 partitions will be used to compute an habitat suitability model and the left-out partition will be used to validate it on independent data. This process is repeated *x* times, each time by leaving out a different partition (Hirzel et al., 2004).

Biomapper was used to create the habitat suitability maps, and the probability of occurrence was calculated in each cell. The obtained maps were then classified as follows: very low habitat suitability (0%-33%), medium habitat suitability (34%-66%) and high habitat suitability (67%-100%).

Evaluation of the Natura 2000 network

To evaluate the effectiveness of the Natura 2000 network, areas of the highest probability of occurrence (67-100%) were selected for each species and overlapped with the Natura 2000 cover layer. This layer consists of the ultimate Natura 2000 places selected from those initial SPAs and SCIs which the Habitat Directive suggested. Each pixel of the Natura 2000 layer was overlaid with the corresponding pixel in the high suitability maps to obtain final maps using Idrisi 32. The effectiveness of the Natura 2000 network regarding different Biogeographical Regions was evaluated considering Atlantic, Alpine and Mediterranean Regions (Galicia et al., 2006), and the percentage of overlap was calculated for each species.

Results

Distribution models

Most of the models were built with the 10 previously described EGVs (Table 1) except those for *R. rosacea* and *V. saubinetti* due to problems of multicollinearity between the EGVs. In these models, the final number of variables was reduced to five and four variables in *V. saubinetti* and *R. rosacea,* respectively (data not shown).

Global marginality values ranged between 2.25 (*Peltigera monticola)* and 0.63 (*T. chrysophthalmus*) (Table 2). Most species had marginality values near 1 or higher, indicating that species requirements are very different from average conditions in the studied area. However, *N. tangeriense* and *T. chrysophthalmus* had lower marginality values, indicating that their habitat requirements are closer to the Spanish average conditions. Global tolerance values indicated that most of the studied species have narrow ecological niches (Table 2). Tolerance values ranged from 0.06 in *X. resendei* to 0.77 in *T. chrysophthalmus*.

A significant fraction of the variance was explained by reduced factors for each species, with values ranging from 72.9% in *S. omphalarioides* to 94.3% in *F. olivacea* (Table 2).

Habitat suitability maps showed markedly differences among species. The only common feature was that most of the studied species avoid central areas, as well as southern and northern plateaus (Fig. 2).

According to the *jack-knife* cross validation, predicted suitability was over 50 in more than 50% of the validation cells, except in *C. mediterranea* (44.90%; SD=0.44). Cross validation values ranged from 44.90% in *C. mediterranea* to 69.40% in *F. olivacea*, suggesting that our models are accurate enough (Table 2).

Table 2: Global marginality, specialization and tolerance values for the 18 studied species. N: total number of cells (10x10km) where each species was found, M: marginality, S: specialization, T: tolerance, F: number of factors used for map generation, V: explained variance, PD: predicted suitability, SD: standard deviation.

	N	M	S	T	F	V	PD	SD
B. cedricola	44	0.96	3.44	0.29	2	76.5	53.3	0.49
C. crespoae	32	0.94	2.46	0.41	4	85.9	44.9	0.44
C. mediterranea	18	1.00	4.90	0.20	2	85.7	53.7	0.31
D. ceratoniae	37	1.33	5.90	0.17	2	91.3	52.2	0.43
F. ignobilis	33	1.07	2.06	0.49	4	79.9	54.4	0.36
F. olivacea	16	0.94	15.25	0.07	2	94.3	69.4	0.25
K. biformis	39	0.74	3.49	0.29	2	78.4	53.5	0.29
N. tangeriense	28	0.69	2.57	0.39	3	81.9	54.2	0.32
P. lusitanica	25	0.84	2.37	0.42	3	80.8	55.0	0.38
P. monticola	35	2.25	1.79	0.56	3	73.8	50.0	0.60
P. paramerae	21	0.95	2.24	0.45	3	77.9	55.6	0.42
R. rosacea	16	1.46	1.51	0.66	3	93.0	62.5	0.44
S. holophaea	25	1.67	4.53	0.22	2	81.2	55.0	0.39
S. omphalarioides	16	1.16	3.42	0.29	2	72.9	52.1	0.38
T. chrysophthalmus	50	0.63	1.30	0.77	4	75.6	52.2	0.19
V. saubinetii	**17**	**0.83**	**4.39**	**0.23**	**2**	**93.4**	**62.5**	**0.48**
W. adscendens	27	0.91	6.33	0.16	2	80.5	50.0	0.42
X. resendei	16	2.19	15.72	0.06	2	88.3	50.0	0.46

Effectiveness of the Natura 2000 network

The area of high suitability for each species and the percentage of this area protected by the Natura 2000 network can be seen in Table 3 and Figure 3. Percentages of protected high suitability area were over 50% in only *F. saubinetti* and *K. biformis* (65% and 51.6%, respectively). A very low percentage of protected high suitability area was obtained in five species (less than 25%) since *C. mediterranea* (14.8%) to .: *R. rosacea* (20.7%). The remaining studied species had percentages between 39.2% (*P. monticola*) and 25.7% (*T. chrysophthalmus*).

Most of the studied species presented a Mediterranean distribution. However, the percentage of potential distribution area in the Atlantic Region was over 25% in species like *C. mediterranea* and *P. monticola* (Table 3; Fig. 3) and over 15% in other five species such as *C. crespoae* or *V. saubinetti* (Table 3).

The analysis of the effectiveness of the Natura 2000 network per biogeographical region showed that the effectiveness of the network is much lower in the Atlantic area (i.e., protection of these areas is less than the total average), except in the case of V. saubinetii where 69% of its potential Atlantic territory was protected (Table 3).

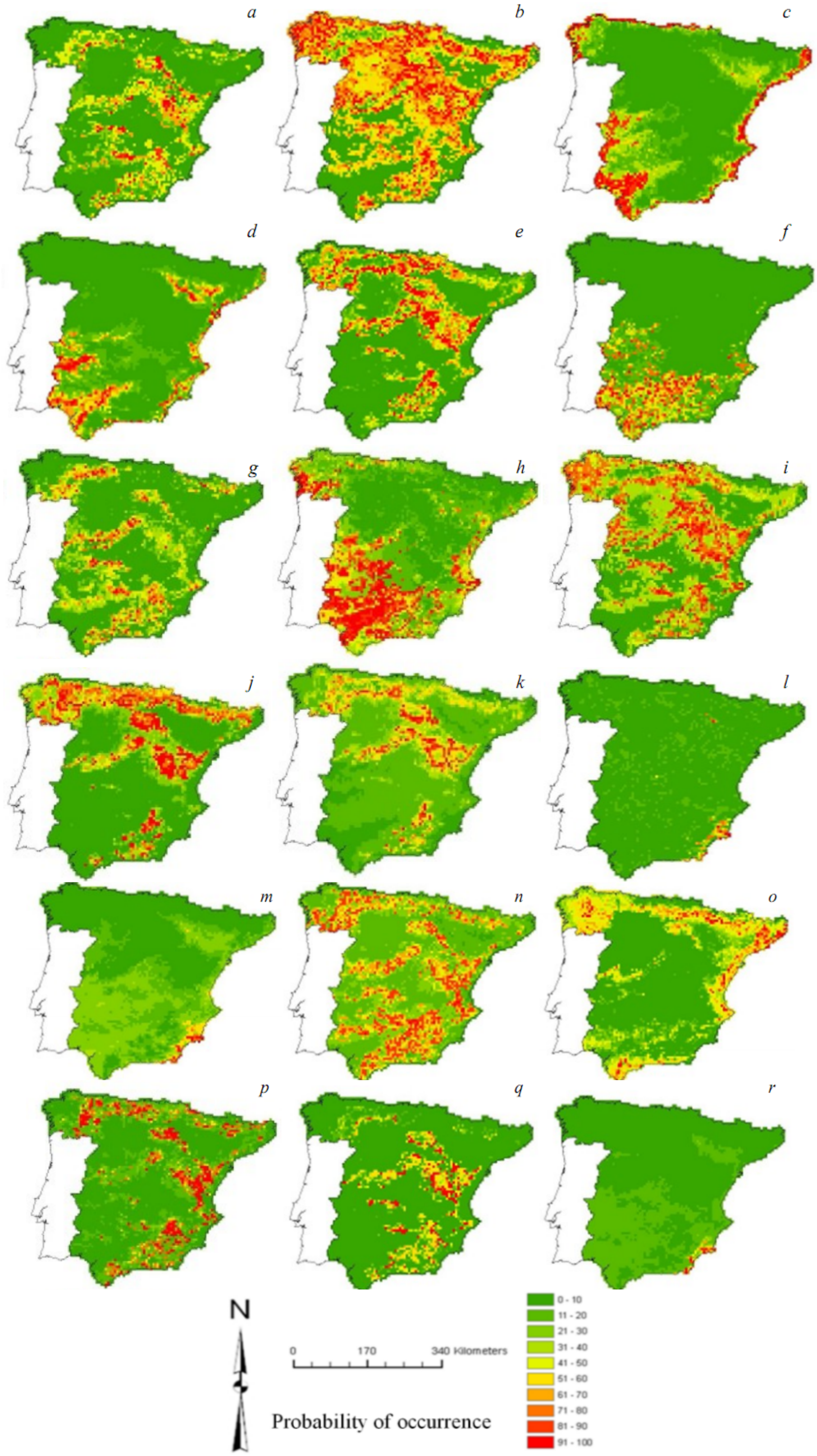

Figure 2. Habitat suitability maps for each of the studied species in Spain. Habitat suitability values are represented by different colors on the map (0= low suitability, 100= high suitability). (a) *B. cedricola*, (b) *C. crespoae*, (c) *C. mediterranea* (d) *D. ceratoniae,* (e) *F. ignobilis*, (f) *F .olivacea*, (g) *K. biformis*, (h) *N. tangeriense*, (i) *P. monticola*, (j) *P. paramerae*, (k) *P. lusitanica*, (l) *R. rosacea*, (m) *S. holophaea*, (n) *S. omphalarioides*, (o) *T. chrysophthalmus,* (p) *V. saubinetii*, (q) *W. adscendens*, (r) *X. resendei*

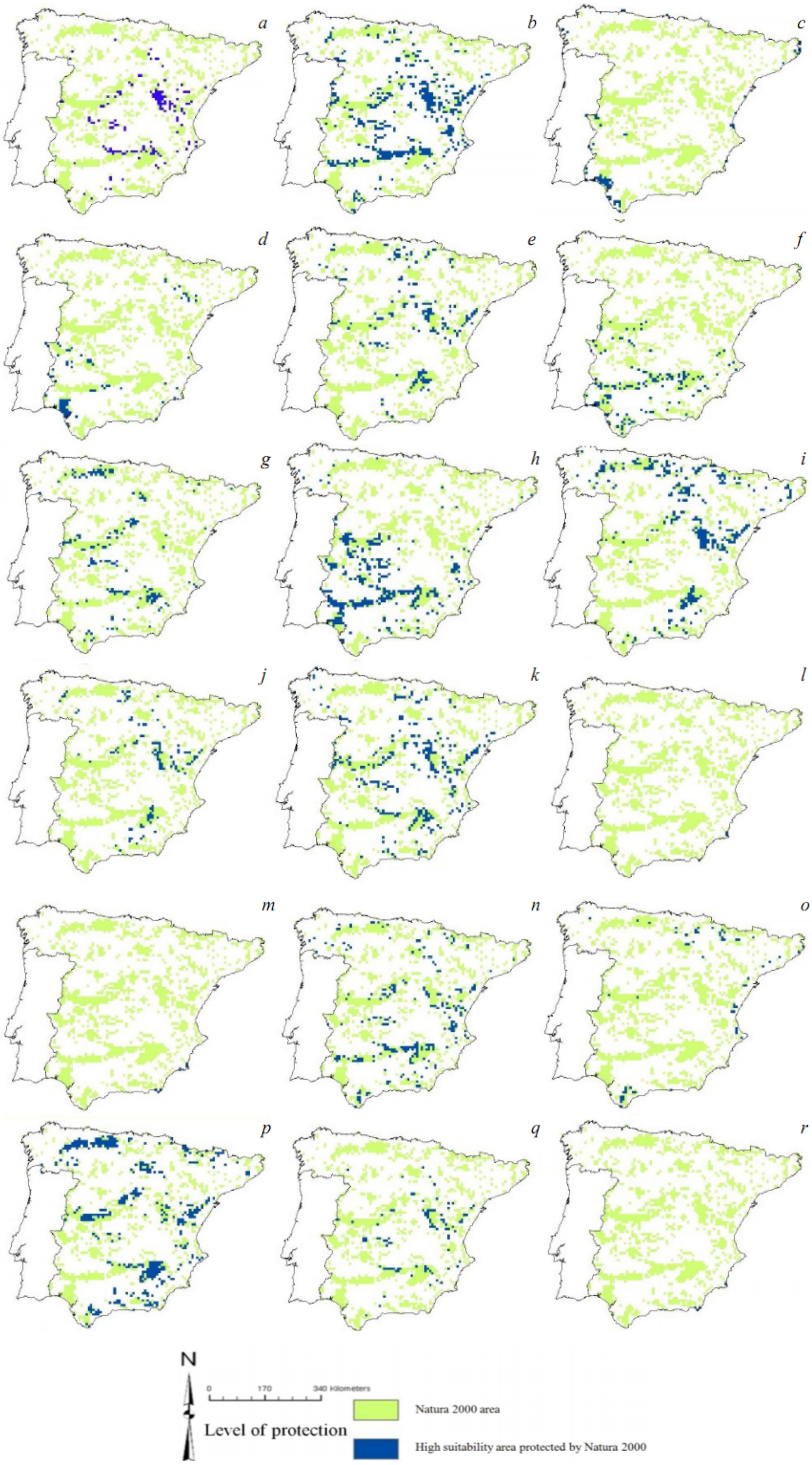

Figure 3: Area of maximum probability of occurrence included in the Natura 2000 network. (a) *B. cedricola*, (b) *C. crespoae*, (c) *C. mediterranea* (d) *D. ceratoniae,* (e) *F. ignobilis*, (f) *F .olivacea*, (g) *K. biformis*, (h) *N. tangeriense*, (i) *P. monticola*, (j) *P. paramerae*, (k) *P. lusitanica*, (l) *R. rosacea*, (m) *S. holophaea*, (n) *S. omphalarioides*, (o) *T. chrysophthalmus,* (p) *V. saubinetii*, (q) *W. adscendens*, (r) *X. resendei*

Table 3. Number of cells and the percentage of the study area they represent for each species. Maximum probability of occurrence: number of cells and percentage where the probability of occurrence is >66% according to the model, Al: Alpine, M: Mediterranean, At: Atlantic.

Species	Maximum probability of occurrence				Maximum probability of occurrence under Natura 2000 protection			
	Total	Al[b]	M[c]	At[d]	Total	Al[b]	M[c]	At[d]
B. cedricola	364(8.2%)	0	363(99.7%)	1(0.3%)	141(38.8%)	0	141(38.8%)	0
C. crespoae	1448(32.7%)	3(0.2%)	1120(77.3%)	325(22.4%)	433(29.9%)	0	416(37.1%)	17(5.2%)
C. mediterranea	440(9.9%)	0	310(70.5%)	130(29.5%)	65(14.8%)	0	58(18.7%)	7(5.4%)
D. ceratoniae	447(10.1%)	0	447(100%)	0	82(18.3%)	0	82(18.3%)	0
F. ignobilis	512(11.6%)	1(0.2%)	414(80.9%)	97(18.9%)	167(32.6%)	0	152(36.7%)	15(15.5%)
F. olivacea	392(0.9%)	0	392(100%)	0	134(34.2%)	0	198(50.5%)	0
K. biformis	310(7%)	10(3.2%)	262(84.5%)	38(12.3%)	160(51.6%)	3(30%)	143(54.6%)	32(84.2%)
N. tangeriense	983(22.2%)	0	901(91.7%)	82(8.3%)	313(33.4%)	0	305(33.8%)	8(9.7%)
P. monticola	755(17%)	20(2.6%)	537(71.1%)	198(26.2%)	296(39.2%)	5(25%)	238(44.3)	53(26.8%)
P. paramerae	309(7%)	0	274(88.7%)	35(11.3%)	116(37.5%)	0	107(39%)	9(25.7%)
P. lusitanica	1047(26.5%)	0	834(79.75)	213(20.3%)	279(26.6%)	0	254(30.4%)	25(11.7%)
R. rosacea	29(0.7%)	0	29(100%)	0	6(20.7%)	0	6(20%)	0
S. holophaea	39(0.9%)	0	39(100%)	0	6(15.38%)	0	6(15.4%)	0
S. omphalarioides	625(14.1%)	3(0.5%)	540(86.4%)	82(14.1%)	239(38.2%)	0	223(41.3%)	16(19.5%)
T.chrysophthalmus	226(5.1%)	5(2.2%)	188(83.2%)	33(14.6%)	58(25.7%)	1(20%)	51(27.1%)	6(18.2%)
V. saubinetti	629(14.2%)	23(3.6%)	486(77.3%)	120(19.1%)	409(65%)	19(30%)	307(63.2%)	83(69.1%)
W. adscendens	220(5%)	0	219(99.5%)	1(0.4%)	94(42.7%)	0	94(42.9%)	0
X. resendei	25(0.6%)	0	25(100%)	0	4(16%)	0	4(16%)	0

Discussion

The effectiveness of the Natura 2000 network in protecting Mediterranean lichen species is quite low if we compare our results with Martínez et al. (2006). In most of the species studied by these authors, over 40% of their potential areas were protected by the network. However, this was true in only 3 species in our current study (*K. biformis*, *V. saubinetii* and *W. adscendens*). It should be noted that the ecological and distributional characteristics of the lichen species are very different between both studies. Martínez et al. (2006) studied lichen species which mainly grow in temperate forests and were distributed throughout Northern and Central Europe, with the Iberian Peninsula being their southern distribution limit in Europe. Most of the species included in the present study are from the Mediterranean region and occur in Mediterranean forests and coastal areas. Our results show that *Vahliella saubinetii* is the best protected species, probably because it grows in dense and well-preserved Mediterranean forests (Aragón, 2002), being most of these forests included in the Natura 2000 network (Morillo and Gómez-Campo, 2000). This is in agreement with Martínez et al. (2006) who suggested that the effectiveness of the network is higher in the Mediterranean area where almost all of the few well-preserved forests are included in the reserves network (Morillo and Gómez-Campo, 2000).

Another group of species with less than 25% of their potential area protected by the Natura 2000 network includes species such as *C. mediterranea* (14.8%) or *X. resendei* (16%). All of these species live in warm, dry habitats, and mainly occur in coastal areas. Ours results indicate that this habitat type is poorly represented in the Natura 2000 network, although the habitats that they represent were included in the Habitat Directive. Coastal areas in Spain are highly threatened and have a high risk of human impact. Population density in these areas is four times higher than in the rest of the country and only 42% of coastline has an undetermined use (Morillo and Gómez-Campo, 2000). Cogoni et al., (2011) showed that no lichens were present in highly disturbed areas in coastal areas of Sardinia. One of the most plausible explanations in our study is that the coastal areas with certain degrees of alteration still have a high biodiversity and constitute the last habitats available for many species. This inadequacy will aggravate on the long-term when, in addition to all those threats, range shifts and reductions due to climate change will lead at decreasing species representation over the entire protected area system.

With regard to the specificity of the studied species by regions, one group of species was only present in the Mediterranean region (*D. ceratoniae, F. olivacea, R. rosacea, S.*

holophaea, X. resendei) and two other species are almost completely Mediterranean (*B. cedricola* and *W. adscendens*). These species have protection percentages ranging from 15.4% to 50.5%. In the case of species growing in both Mediterranean and Atlantic regions, the effectiveness of the network is much lower in the Atlantic region. This could be due to the fact that Atlantic habitats in Spain are not as well represented in the Natura 2000 network as Mediterranean habitats, which are rarer in Europe. Our results indicated that the protection provided by the Natura 2000 network is less effective in warm, dry coastal areas (less than 20% of the potential area) for the studied species. However, this reserve network seems to be more effective in protecting lichen species occurring in well-preserved Mediterranean forests (Martínez et al., 2006).

Due to our inability to develop strategies that reconcile economic development and conservation, biodiversity conservation is primarily based on reserve networks (Lobo, 2008). At a global scale, if the conservation goal is high species representation, the expansion of the network must take biodiversity patterns into account (Rodrigues et al., 2004). As we cannot assist all species under threat (Myers et al., 2000), we assume that a reserve network would comprise the core of global biodiversity (James et al., 2001).

An important issue is the extent to which a group of organisms can act as a surrogate for lesser-known groups (Pharo et al., 1999). Surrogates are useful in the case of taxa like lichens that are difficult to identify. Vascular plants are often used as a surrogate for total biodiversity in conservation evaluation and play a critical role in land management. They seem to be a reasonable surrogate for lichens and at a local scale reserves selected for vascular plants can capture large percentages of bryophytes and lichens (Pharo et al., 1999, 2000). However, at larger scales, the number of unique species that are not coincident with vascular plants may be of more concern (Pharo et al., 2000).

Our results show that a reserve network based mainly on vascular plant data (like Natura 2000) is not totally effective for other taxonomic groups like lichens. Gaps in the Natura 2000 network have previously been found in other studies (Araújo et al 2007; Apostolopoulou and Pantis, 2009). Recommendations for the conservation of unusual vascular plants are often made by forest managers. Similarly, recommendations could be made for lichens. However, this is difficult in practice, since their conservation status is usually unknown, and the conservation of lichens still receives scarce attention by Governmental Organizations in most countries (Martínez et al., 2006). However, there are many studies in different areas which have indicated the needed to develop tools which increase lichen conservation (Roux et al. 2001; Martínez et al. 2003; Scheidegger and Werth, 2009).

Based on our findings, gap analysis studies are important in detecting interesting conservation areas outside protected areas and can also contribute to validating existing protected areas (Chefaoui et al., 2005; D'Amen et al., 2011).Our results also suggest that the use of only presence data for these overlooked taxa is a valuable tool in improving the conservation of poorly known species. Studies like this, including “non- charismatic” species like lichens, may be useful in improving reserve design (de la Montaña and Rey-Benayas, 2003; Kathi et al., 2004). Moreover, the identification of potential distribution areas can help to locate suitable sites for reintroduction programs or favour success in regional planning (Chefaoui et al., 2005; D'Amen et al., 2011).

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References

Apostolopoulou, E., & Pantis, J. D. (2009). Conceptual gaps in the national strategy for the implementation of the European Natura 2000 conservation policy in Greece. *Biological Conservation*, 142, 221-237.

Aragón, G. (2002). *Líquenes del Parque Natural de Cazorla, Segura y Las Villas (Jaén, España.)* Ph.D. thesis, Universidad Complutense de Madrid.

Araújo, M. B., Lobo, J. M., & Moreno, J. C. (2007). The effectiveness of Iberian protected areas in conserving terrestrial biodiversity. *Conservation Biology,* 21, 1423-1432.

Bani, L., Massimino, D., Bottoni, L., & Massa, R. (2006). A multiscale method for selecting indicator species and priority conservation areas: a case study for broadleaved forests in Lombardy, Italy. *Conservation Biology,* 20, 512-526.

Bollinger, J., Bergamini, A., Stofer, S., Kienast, F., & Scheidegger, C. (2007). Predicting the potential spatial distributions of epiphytic lichen species at the landscape scale. *The Lichenologist,* 39, 279-291.

Brotons, L., Thuiller, W., Araújo, M. B., & Hirzel, A. H. (2004). Presence-absence versus presence-only modelling methods for predicting bird habitat suitability. *Ecography,* 27, 437-448.

Carpenter, G., Gillison, A. N., & Winter, J. (1993). DOMAIN: a flexible modelling procedure for mapping potential distributions of plants and animals. *Biodiversity and Conservation,* 2, 667-680.

Carter, G. M., Stolen, E.D., & Breininger, D. R. (2006). A rapid approach to modelling species-habitat relationships. *Biological Conservation,* 127, 237-244.

Cassinello, J., Acevedo, P., & Hortal, J. (2006). Prospects for population expansion of the exotic aoudad (*Ammostragus lervia*; Bovidae) in the Iberian Peninsula: clues from habitat suitability modelling. *Diversity and Distributions,* 12, 666-678.

Chefaoui, R. M., Hortal, J., & Lobo, J. M. (2005). Potential distribution modelling, niche characterization and conservation status assessment using GIS tools: a case study of Iberian *Copris* species. *Biological Conservation,* 122, 327-338.

Cogoni, A., Brundu, G., & Zedda, L. (2011). Diversity and ecology of terricolous bryophyte and lichen communities in coastal areas of Sardinia (Italy). *Nova Hedwigia*, 92: 159-175.

D'Amen, M., Bombi, P., Pearman, P. B., Dirk, R., Schmatz, N., Zimmermann, E., & Bologna, M. A. (2011). Will climate change reduce the efficacy of protected areas for amphibian conservation in Italy? *Biological Conservation,* 144, 989–997.

de la Montaña, E., & Rey-Benayas, J. M. (2003). ¿Coinciden los espacios naturales protegidos con las áreas relevantes de diversidad de herpetofauna en España peninsular y Baleares? *Ecosistemas,* 11, 11-15.

Edwards, J. T. C., Cutler, D. R., Zimmermann, N. E., Geiser, L., & Moisen, G. G. (2006). Effects of sample survey design on the accuracy of classification tree models in species distribution models. *Ecological Modelling,* 199, 132-141.

Ellis, C. J., Coppins, B. J., Dawson, T. P., & Seaward, M. R. D. (2007a). Response of British lichens to climate change scenarios: Trends and uncertainties in the projected impact for contrasting biogeographic groups. *Biological Conservation,* 140, 217-235.

Ellis, C. J., Coppins, B. J., Dawson, T. P., & Seaward, M. R. D. (2007b). Predicted response of the lichen epiphyte *Lecanora populicola* to climate change scenarios: trends and uncertainties in the projected impact for contrasting biogeographic groups. *Biological Conservation*, 135, 396-404.

Farr, T. G., Rosen, P. A., Caro, E., Crippen, R., Duren, R., Hensley, S., Kobrik, M., Paller, M., Rodríguez, E., Roth, L., Seal, D., Shaffer, S., Shimada, J., Umland, J., Werner, M., Oskin, M., Burbank, D., & Alsdorf, D. (2007). The Shuttle Radar Topography Mission. *Geophysics,* 45, 1-33.

Fielding, A. H., & Bell, J. F. (1997). A review of methods for the assessment of prediction errors in conservation presence/absence models. *Environmental Conservation,* 24, 38-49.

Fleishman, E., & Murphy, D. D. (2009). A realistic assessment of the indicator potential of butterflies and other charismatic taxonomic groups. *Conservation Biology,* 23, 1109-1116.

Fleishman, E., Mac Nally, R., & Fay, J. (2003). Validation tests of predictive models of butterfly occurrence based on environmental variables. *Conservation Biology,* 17, 806-817.

Galicia, D., Hervás, J., Martínez, R., & Seoane, J. (2006). *Identificación y definición de regiones naturales en España para el desarrollo de la Red Natura 2000*. TRAGSA-Ministerio de Medio Ambiente de España, Madrid.

Godown, M. E., & Peterson, A. T. (2000). Preliminary distributional analysis of US endangered bird species. *Biodiversity and Conservation,* 9, 1313-1322.

Guisan, A., & Thuiller, W. (2005). Predicting species distribution: offering more than simple habitat models. *Ecology Letters,* 8, 993-1009.

Guisan, A., & Zimmermann, N. E. (2000). Predictive habitat distribution models in ecology. *Ecological Modelling,* 135, 147-186.

Hess, G. R., Bartel, R.A., Leidner, A. K., Rosenfeld, K. M., Rubino, M. J., Snider, S. B., & Ricketts, T. H. (2006). Effectiveness of biodiversity indicators varies with extent, grain, and region. *Biological Conservation,* 132, 448-457.

Hirzel, A. H., & Arlettaz, R. (2003). Habitat suitability for complex species distributions by the environmental-distance geometric mean. *Environmental Management,* 32, 614-623.

Hirzel, A. H., & Le Lay, G. (2008). Habitat suitability modelling and niche theory. *Journal of Applied Ecology,* 45, 1372-1381.

Hirzel, A. H., Hausser, J., & Perrin, N. (2004). *Biomapper 4.1.* Lab of Conservation Biology, Department of Ecology and Evolution, University of Lausanne.

Hirzel, A. H., Hausser, J., Chessel, D., & Perrin, N. (2002). Ecological-Niche Factor Analysis: how to compute habitat-suitability maps without absence data? *Ecology,* 83, 2027-2036.

Hortal, J., García-Pereira, P., & García-Barros, E. (2004). Butterfly species richness in mainland Portugal: predictive models of geographic distribution patterns. *Ecography,* 27, 68-82.

Hutchinson, G.E. (1957). Concluding remarks. *Cold Spring Harbor Symposia on Quantitative Biology*, 22 (2): 415-427.

James, A., Gaston, K. J., & Balmford, A. (2001). Can we afford to conserve biodiversity? *BioScience,* 51, 43-49.

Jørgensen, M. (2008). *Vahliella*, a new lichen genus. *The lichenologist,* 40, 221-225.

Kathi, V., Devillers, P., Dufrêne, M., Legakis, A., Vokou, D., & Lebrun, P. (2004). Testing the value of six taxonomic groups as biodiversity indicators at a local scale. *Conservation Biology,* 18, 667-675.

Kerr, J. T., Sugar, A., & Packer, L. (2000). Indicator taxa, rapid biodiversity assessment, and nestedness in an endangered ecosystem. *Conservation Biology,* 17, 168-177.

Kleintjes, P. K., Jacobs, B. F., & Fettig, S. M. (2004). Initial response of butterflies to an overstory reduction and slash mulching treatment of a degraded pinion-juniper woodland. *Restoration Ecology,* 12, 231-238.

Larsen, F. W., Bladt, J., & Rahbek, C. (2007). Improving the performance of indicator groups for the identification of important areas for species conservation. *Conservation Biology*, 21, 731-740.

Lobo, J. M. (2008). *Hacia una estrategia global para la conservación de la diversidad biológica.* Presented at the Jornadas sobre Biodiversidad Valenciana y Arácnidos, Valencia.

Llimona, X., & Hladun, N. (2001). Checklist of the lichens and lichenicolous fungi of the Iberian Peninsula and Balearic Islands. *Bocconea,* 14, 576-582.

Maes, D., Bauwens, D., Bruyn, L. de, Anselin, A., Vermeersch, G., Van Landuyt, W., Knijf, G. de, & Gilbert, M. (2005). Species richness coincidence: conservation strategies based on predictive modelling. *Biodiversity and Conservation,* 14, 1345-1364.

Martínez, I., Carreño, F., Escudero, A., & Rubio, A. (2006). Are threatened lichen species well-protected in Spain? Effectiveness of a protected areas network. *Biological Conservation,* 133, 500-511.

Meier, E. S., Jr Thomas, C. E., Kienast, F., Dobbertin, M., Niklaus, E., & Zimmermann, N. E. (2011). Co-occurrence patterns of trees along macro-climatic gradients and their potential influence on the present and future distribution of *Fagus sylvatica* L. *Journal of Biogeography,* 38, 371–382

Morillo, C., & Gómez-Campo, C. (2000). Conservation in Spain 1980-2000. *Biological Conservation,* 95, 165-174.

Myers, N., Mittermeier, R. A., Mittermeier, C. G., da Fonseca, G. A. B., & Kent, J. (2000). Biodiversity hotspots for conservation priorities. Conservationists are far from able to assist all species under threat. *Nature,* 403, 853-858.

Mac Nally, R., & Fleishman, E. (2004). A successful predictive model of species richness using 'indicator' species. *Conservation Biology,* 18, 646-654.

Palomares, O. S., Serrano, F. S., & Carretero, M. P. (1999). *Modelos y cartografía de estimaciones climáticas termo-pluviométricas para la España Peninsular*. Madrid: INIA.

Pharo, E. J., Beattie, A. J., & Binns, D. (1999). Vascular plant diversity as a surrogate for bryophyte and lichen diversity. *Conservation Biology,* 13,282-292.

Pharo, E. J., Beattie, A. J., & Pressey, R. L. (2000). Effectiveness of using vascular plants to select reserves for bryophytes and lichens. *Biological Conservation,* 96, 371-378.

Prendergast, J. R., Quinn, R. M., Lawton, J. H., Eversham, B. C., & Gibbons, D. W. (1993). Rare species, the coincidence of diversity hotspots and conservation strategies. *Nature,* 365, 335-337.

Primack, R. B. (2008). *A primer of conservation biology*. Sinauer Associates Inc., U.S., 2nd Revised edition.

Randin, C.F., Engler, R., Normand, S., Zappa, M., Zimmermann, N. E., Pearman, P. B., Vittoz, P., Thuiller, W., & Guisan, A. (2009). Climate change and plant distribution: local models predict high-elevation persistence. *Global Change Biology,* 15, 1557-1569.

Rey-Benayas, J. M., & Montaña, E.de la. (2003). Identifying areas of high-value vertebrate diversity for strengthening conservation. *Biological Conservation,* 114, 357-370.

Ricketts, T. H., Daily, G. C., & Ehrlich, P. R. (2002). Does butterfly diversity predict moth diversity? Testing a popular indicator taxon at local scales. *Biological Conservation,* 103, 361-370.

Rodrigues, A. S. L., Andeman, S. J., Bakarr, M. I., Boitani, L., Brooks, T. M., Cowling, R. M., Fishpool, L. D. C., da Fonseca, G. A. B., Gaston, K. J., Hoffmann, M., Long, J. S., Marquet, P. A., Pilgrim, J. D., Pressey, R. L., Schipper, J., Sechrest, W., Stuart, S. N., Underhill, L. G., Waller, R. W., & Watts, M. E. J. (2004). Effectiveness of the global protected area network in representing species diversity. *Nature,* 428, 640-643.

Rodríguez-Fernández, L. R. (2004). *Mapa geológico de España*. In: J. A. Vera (Ed.), Geología de España. Madrid: SGE-IGM.

Roux, C., Bricaud, O., & Tranchida, F. (2001). The importance of lichens and lichenicolous fungi in the specific biodiversity and management of the Chambord nature reserve, (France). *Bulletin de la Societe Linneenne de Provence* 52: 161-183

Sánchez-Fernández, D., Bilton, D. T., Abellán, P., Ribera Velasco, I., & Millán, A. (2008). Are the endemic water beetles of the Iberian Peninsula and the Balearic Islands effectively protected? *Biological Conservation,* 191, 1612-1627.

Seoane, J., Bustamante, J., & Díaz-Delgado, R. (2005). Effect of expert opinion on the predictive ability of environmental models of bird distribution. *Conservation Biology,* 19, 512-522.

Scheidegger, C., & Werth, S. (2009). Conservation strategies for lichens: insights from population biology. *Fungal Biology Reviews*, 23: 55-66.

Walker, P. A., & Cocks, K. D. (1991). HABITAT: A procedure for modelling a disjoint environmental envelope for a plant or animal species. *Global Ecology and Biogeography Letters,* 1, 108-118.

Capítulo 2

Capítulo 2

Climate change effects on Iberian lichens: traits and vulnerability

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Under review in Global Change Biology

Abstract

There is ample evidence of species distributional changes in response to recent climate change, mainly leading to a biodiversity reduction. It is equally clear that the response is species-specific. Most studies are species-biased towards better known taxons, and the inclusion “cryptic species” like lichens is needed for an integrated approach. Our ability to predict the nature and extent of species reaction to climate change, however, appears limited thus far. In this sense, the use of functional traits and ecological attributes might be helpful in order to improve the interpretation of predictive models. In this study, we have tested which lichen traits/attributes could be considered as drivers of climate change impact magnitude. We have calculated present and future distributions for 41 lichen species in the Iberian Peninsula, using ensemble climatic suitability maps (derived from GLM, GAM and CART models). We calculated 7 impact metrics as surrogates of climate change consequences on species distributions, and then tested traits/attributes effects on them. Forecasted distributions were species-specific and impacts were trait-mediated. Presenting smaller thallus size, being epiphyte and presenting green-algae biont provided protection against climate change. So they did rarity and small current distributions (ecological attributes). Surprisingly, we did not detect a significant effect of other lichen traits/attributes, so further research is needed in this sense. We also highlight the critical importance of the comparison of different metrics when assessing climate change impacts.

Introduction

Many authors in the last years have pointed out the negative influence of climate change on biodiversity since loss of genetic diversity to loss of ecosystems distribution area (e.g. Chen *et al.*, 2011; Thuiller *et al.*, 2011; Summers *et al.*, 2012). Some studies even suggest that climate change could surpass habitat destruction as the greatest global threat to biodiversity (Bellard *et al.,* 2012). Evidence is accumulating rapidly that species are shifting their latitudinal distributions, elevation ranges and phenologies in response to recent climate changes (Lavorel & Garnier 2002; Root *et al.,* 2003; Parmesan & Yohe 2003; Diamond *et al.,* 2011; Chen *et al.,* 2011). However, some species could enlarge their distribution areas thanks to the broadening of their bioclimatic areas (Ellis *et al*., 2007a; Soane & Carrascal, 2007; Bello *et al.,* 2010). Despite the lack of agreement on biodiversity loss patterns, the majority of models indicate alarming consequences due to the speed and magnitude of the climate change (Parmesan & Yohe 2003; Pereira *et al.,* 2010; Chen *et al.,* 2011; Thuiller *et al.,* 2011).

In this sense, predictive modeling is a powerful tool widely used to create an initial understanding of climate impacts (Thuiller *et al.,* 2006; Ellis *et al.* 2007a; Pereira *et al.,* 2010). The bioclimatic envelope approach is a common application of predictive modeling popularly applied in examining climatic impacts. This technique reflects both direct and indirect influences of climate on those distributions (Pearson & Dawson 2003; Carter *et al.,* 2006; Zimmermann *et al.,* 2010; Araújo & Peterson 2012). Even though, many authors have provided warnings about the lack of inclusion in these models of important parameters such as dispersal, habitat change, biotic interactions and possible evolutionary or plastic phenotypic responses (Araújo *et al.,* 2005a; Bascompte, 2009; Zimmermann *et al,.* 2010; Araújo & Peterson 2012; Bellard *et al.,* 2012). Nevertheless, they have been proved to be very useful as a first approximation to forecast the potential effects of climate change on a large-scale species distributions (Guisan & Zimmermann, 2000; Guisan & Thuiller, 2005; Pearson & Dawson, 2003; Pereira *et al.,* 2010).

The prevailing idea when using predictive models is that climate is the key limiting factor shaping species distribution at macroscale (Araújo & Luoto, 2007), although there are many other factors than climate that can affect geographical distributions of species (Meier *et al.,* 2010, 2012; Kissling *et al.,* 2012). Some studies have proved that lichens are constrained by climate at different scales (Aptroot & Herk, 2002, 2007, Herk *et al.,* 2002; Insarov & Schoroeter, 2002; Søchting, 2004; Giordani & Icerti, 2008; Aragón *et al*., 2012; Escolar *et al*., 2012). Even more, climate change influence has been tested on lichens before (Ellis et al., 2007a, 2007b; Lisewski & Ellis, 2010) using predictive models.

The Iberian Peninsula is a highly adequate territory to evaluate the effect of climate change on biodiversity because, although climate change impacts will be heterogeneous, a large proportion of the Iberian Peninsula would be in risk cause of warming. According to the IPCC models, the Iberian Peninsula is one of the areas more likely to suffer a great temperature increase and an important change in precipitation regime (IPCC, 2007; Moreno *et al*., 2005). Changes in precipitation and seasonality, not only warming, play an important role in determining the potential impacts of climate change (Engler *et al.,* 2011; but see Escolar *et al.,* 2012).

In order to improve the interpretation of predictive models, some recent studies have evaluated the role of specific traits and attributes in species responses to climate change. In this sense, specific characteristics are used as a tool to understand and predict ecosystem functions and their responses to environmental change. Species climate-distribution relationships should vary according to their different life history strategies. Identifying main characteristics that determine species sensitivity and vulnerability to environmental change is crucial to ecological forecasting and conservation planning (Anglert *et al.,* 2011; Diamond *et al.,* 2011; Kharouba *et al.,* 2012; Summers *et al.*, 2012).

In plant ecology, certain ecological attributes and traits, including habitat tolerance, leaf area, rarity, range size and dispersal ability have been proved to exert an effect on the accuracy of distribution models. Those traits must be considered because might be also affecting individual species´ realized response to climate change (McPherson & Jetz, 2007; Pöyry *et al.,* 2008; Chen *et al.,* 2011), not only their exposure to this hazard. Despite theoretical support, it remains unclear whether the study of those attributes and traits affecting vulnerability will yield to predictable differences in the rate and extent of range shifts in response to climate change (Angert *et al*., 2011). There is little consensus related to the capacity of species to track their suitable climatic conditions, because this range shift depends on traits, as well as the influence of other external factors. Those external factors such as habitat fragmentation or the relative quantity of specific habitats may constrain migration and have an overriding effect on the magnitude of observed range shifts (Angert *et al*., 2011; Chen *et al*., 2011).

Very little is known about the role and applicability of attributes and functional traits of non-vascular cryptogams, particularly bryophytes and lichens. It is widely recognized that a vas proportion of biodiversity is represented by “cryptic biodiversity”, but, to date, mainstream research has frequently neglected those groups: most of the studies have been biased towards animals and vascular plants (Thuiller *et al*., 2011; Diamond *et al*., 2011; Triviño *et al*., 2011; Crossman *et al*., 2012). What is more, only a few studies have considered how lichen traits determine the different effects on ecological processes (but see Lakatos *et al*., 2006; Asplund & Wardle 2013; Giordani *et al*., 2013), despite their significant contribution to biodiversity (Ellis &2007a; Ellis, 2013) and their functional importance in many ecosystems (Cornelissen *et al*., 2007; Edman *et al*., 2008; Asplund & Wardle, 2013).

In plants, functional traits and ecological attributes include morphological, ecophysiological, biochemical and regeneration characteristics (Eviner & Chapin, 2003; Bello *et al*., 2010). Knowledge about which lichens characteristics could be considered as trait is really scarce. Despite this, we identified 8 ecological attributes and traits, based on literature, as potentially influential for lichens: tallus size, growth form, primary photobiont type, distribution range and rarity, specificity to substrate, main substrate type and reproduction (Lange *et al*., 1986; Eldridge and Rosentreter 1999; Gauslaa & Sölhaug, 1999; Ellis & Coppins, 2006; Löbel *et al*., 2006; Werth *et al*., 2007; Hedenäs & Ericson, 2008; Shiver *et al*., 2011; Aragón *et al*., 2012; Kharouba *et al*., 2012; Ellis, 2013; Merinero *et al*., 2013).

The main objective of this study is to detect potential distribution variations (shifts/contractions/enlargements) due to climate change in a subset of lichen biodiversity in the Iberian Peninsula. Besides, we want to determine which lichen traits and attributes might affect specific responses to climate change.

For this purpose, we first predicted the distributions for 41 lichen species in the Iberian Peninsula under current and future climatic conditions. Second, we quantified impacts in their distribution using different metrics as proxies of the species sensitivity (**exposure**, **susceptibility** and **vulnerability** *sensu* Settele *et al*., 2008). Finally, we tested which species´ traits/attributes could be considered as inherently drivers of lichen sensitivity to climate change.

Materials and methods

Study area

The study area corresponds to the Iberian Peninsula. This territory extends 581.436 km^2 and it is well known for its heterogeneous landscape. It is located in Southwest Europe, in the temperate zone, comprising climates from Atlantic and Mediterranean to Alpine in the highest mountains (Costa *et al*., 2005).

Species selection

Lichen species included in this study correspond in most of the cases to only recently revised taxa (Martínez *et al*., 2003; Aragón & Otálora, 2004; Aragón *et al*., 2005; Otálora *et al*., 2008, 2010, Prieto *et al*., 2010, 2012; Muñiz & Hladún, 2011). This overcomes problems such as insufficiently well recorded species and assures that presence points capture the entire suitable environmental species range. As well, avoids false presence points linked to taxonomically difficult species which presences could be doubtful.

The species set also encompasses a wide range of biological, functional and ecological characteristics. We selected species by geographical distribution ranges from Mediterranean to temperate distributions, from rare to common species with different sizes, growth forms, types of reproduction, types of substrate and specificity towards them or even different photobionts. We believe that this set of species represents an appropriate sub-sample of the Iberian lichen diversity for the purposes of the study.

Presence data points

We obtained point-based presence-only records for each species from bibliographic sources and herbaria. We selected 41 lichen species (Appendix, Table 1) with >20 independent presence points (Chefaoui & Lobo, 2008) to provide sufficiently robust predictions and accuracy calculations. We homogenized and stored them in two data bases of different resolutions: the first one containing presence points for some species at 1 km^2 and the rest at 10 km^2.

We used coarse extents for modeling and projecting, depending on the input data quality: some of the models were referred to a 584675 cells grid, when working at 1km^2 scale. The rest were referred to a 6089 cells grid if the resolution was 10 km^2 (Appendix, Table 2).

Independent climatic variables

We obtained raw climatic variables for the Iberian Peninsula from Ninyerola *et al.* (2005) climatic model, available at http://opengis.uab.es/wms/iberia/espanol/es_cartografia.htm. We transformed those monthly data into “Bioclimatic variables” (http://www.worldclim.org/bioclim) by R (R Development Core Team 2008; dismo package). We made a pre-selection of the bioclimatic variables to reduce collinearity between them and then selected the most meaningful based on their importance for lichen biology. The final set contains five variables describing baseline climate data: BIO1 (annual mean temperature, ºC), BIO8 (mean temperature of the wettest quarter, ºC), BIO9 (mean temperature of the driest quarter, ºC), BIO12 (annual precipitation, mm) and BIO17 (precipitation of driest quarter, mm) (Variables depiction and values in appendix, Table 3).

Future climate scenarios

Future climate for 2080 (2051–2080) was represented by the A1B scenario (Nakicenovic & Swart, 2000) of three regional climate model (RCM) runs. The runs originated from the ENSEMBLES EU project where global circulation model (GCM) data were physically downscaled for the 4th IPCC assessment report (IPCC, 2007). RCMs downscale the very coarse resolution climate model output of CGMs (usually 1 – 2 ° Lat/Lon per grid cell) to a much finer spatial resolution (usually 10 – 30‘ Lat/Lon) on a physical process basis. Thus, an RCM is fed by the global output of GCMs in order to provide boundary conditions and global weather input for the downscaling. For this project we have used three RCMs, HadRM3, HIRHAM3 and RACMO2 (Hewitt 2004) fed by three different GCMs (HadCM3, ECHAM5, and Arpège). The choice of RCM’s was done to represent a wide range of climate projection in the future. All RCM scenarios were interpolated to the same 30 arc seconds (~1 km) spatial resolution for 30-year monthly mean values of temperature and precipitation. These monthly values were used to calculate the 19 bioclimatic variables of Worldclim for the 2080 time period (see appendix, Table 4).

Modeling and projecting

Bioclimatic envelope models are sensitive to the mathematical functions utilized to describe the distributions of species (Araújo *et al*., 2005b; Araújo & New, 2007; Pereira *et al*., 2010). The debate so far has concerned trade-offs between the usefulness of various statistical methods. We believed that our goals were more likely to be achieved by using a combination of techniques and scenarios. This would yield lower mean error than any of the constituent individual forecasts (Thuiller, 2003; Araújo & New, 2007). We quantified species exposure to climate change using an ensemble of various model projections.

We used three alternative techniques to model the current presence of the single species: GLM, GAM and CART. **(1) GLM** (McCullagh & Nelder, 1989): We built Generalized Linear Models, followed by both backward and forward stepwise variable selection procedure based on AIC (Akaike´s information criterion, (Akaike 1974)) to select the most significant variables. Model fit was evaluated by the adjusted D^2 (adj. D^2) following Weisberg (1980). The agreement between predictions and observations was assessed using the standard area-under-the curve, AUC, measure of a receiver-operating characteristics (ROC) plot (Fielding & Bell, 1997). To avoid working with poorly calibrated models, only projections from models with AUC>0.7 (Swets, 1988) were considered in all subsequent analyses. In addition, we evaluated model accuracy using Cohen´s kappa (Cohen, 1960). **(2) GAM** (Hastie & Tibshirani, 1986): Generalized Additive Models are non parametric extensions of generalized linear models, in which linear predictor is substituted by an additive predictor. GAMs are more data-driven than GLMs, allowing both linear and complex additive responses shapes (Poyry *et al*., 2008). A step-wise variable selection procedure was also carried out. Model fit was evaluated using deviance %. As for GLMs, AUC and kappa were calculated, and models with AUC<0.7 discarded. **(3) CART** (Brieman *et al*., 1984): CART is a procedure that runs a 10-fold cross-validation to select the best trade-off between the number of leaves in the tree and the explained deviance. CART is less commonly used than the previous two methods, but they are accurate and useful (Thuiller, 2003). Trees were pruned to their optimal size using the complexity parameter (Venables & Ripley, 2002). CART models were evaluated using Cohen´s kappa (Cohen 1960). If k<0.4 (Araújo *et al*., 2005b), only GLM and GAM were considered to built ensemble map.

For each species, we used the initial number of presence records (Appendix, Table 2) and 200 pseudo absences randomly selected all across the study area (Chefaoui and Lobo 2008). This is a good approximation as lichens records are especially prone to false absences (Ellis *et al.* 2007a). Even "well recorded" species are unlikely to have been detected at all sites across landscape, so good absence data are not available. Species presence input data ranged from 20 to 159 points (Appendix, Table 2).

When fitting models for species with less than 50 presence points not all of the five climatic variables were used. We used the rule-of-thumb of including one explicative climatic variable for each 10 presence points, to avoid overparametrization. Each model (GLM, GAM, CART) was run for every species, and then calibrated models were used to project species distributions. The likelihood of occurrence was projected for individual species on present-day modeled climate data (Ninyerola *et al*., 2005) and future climate of 2080 using the A1B scenario of three RCMs.

Ensemble and binary maps

Finally, an ensemble projection map was developed for each species. This ensemble map was built combining the single output climate suitability maps: likelihood under current conditions was an average of the projected maps (obtained from the three algorithms), whilst the likelihood under future conditions was an average of nine combinations (of three algorithms and three possible scenarios). This allowed us to assess the projection uncertainty from both variability originating from the choice of statistical methods and the variability in modeled climate.

To produce binary maps of present and future climate suitability, we reclassified the ensemble maps for each species into presence/absence values. We tested two different thresholds likelihood value for discriminating presences and absence: 0.5 and 0.7. As both presented very similar results in proportional range shifts, we fixed the threshold in 0.7, in order to be more conservative (Rubio-Salcedo *et al*., 2013). Binary maps were used to calculate species-specific impact metrics described in Table 1.

We also assumed unlimited dispersal capability for the studied species. This optimistic assumption has shown to provide good estimates of species habitat loss (Engler *et al*., 2011; Meier *et al*., 2012).

Species traits

Lichen species traits and attributes with potential importance were considered and grouped into “functional” and “ecological” traits. We obtained the data from bibliographic sources (except current distribution). The functional ecological characterization of lichens is far from being quantitatively detailed, so we simplified lichen traits as the following factors:

Functional traits: (1) **Tallus size** (mm): average maximum diameter of the thallus, considering L=large (diameter≥5mm), S=small (diameter<5mm). This threshold size splits species data into two balanced groups, very close to the micro and macrolichens groups. Thallus size is related to water holding capacity and/or maintenance cost. (2) **Growth form**: This factor describes the main growth forms of lichens (classified as in Asplund & Wardle, 2013), the studied species are grouped into: C= crustose, S=squamulose, Fr=fruticose, Fo=foliose. Lichen morphology is related to water uptake and holding capacity and surface protection to external damage. (3) **Photobiont type**: primary photobiont in the symbiosis, a two-level-factor: G=green-algae, C=cyanobacteria. For tripartite lichens (more than one photobiont), only the primary photobiont is considered. **Photobiont type** is related to lichen physiology. Cyanolichens entirely depend on liquid water for positive carbon gain (Lange *et al*., 1986), whilst green-algae lichens and tripartite lichens can be activated by humid air only (Nash III, 2008). What is more, thallus hydration values for net photosynthesis are also different, and photobiont plays an important role on water holding capacity (Merinero *et al*., 2013). (4) **Reproduction type**: main reproductive strategy of the species in the study area: A=asexual, S=sexual, B=both. Dispersal limitations is one of the main sources of uncertainty when predicting species distributions under changing climate (Araújo & Guisan, 2006). Species producing long-distance travelling propagules will be more likely to track adequate climatic conditions (Kharouba *et al*., 2012). On the contrary, species limited by dispersal will have reduced opportunity to respond to rapid climate change (Araújo and Pearson 2005; Werth *et al.* 2007). When reproducing asexually, the lichen produces vegetative propagules where both symbionts are together. This way of reproducing ensures the symbiosis at the expenses of a loss of genomic variability and dispersal ability, because sexual propagules can migrate further (Löbel *et al*., 2006; ***Hedenäs*** and Ericson 2008). (Functional trait values for each species, all obtained from bibliographic sources, are shown in appendix, Table 5).

Ecological attributes: (5) **Current distribution**: km^2 of calculated climatic suitable area for present conditions (real distribution ranges are not available for most lichens). Widely distributed species, not so strict in their requirements, may have less limited ability to expand their range boundaries or habitat niches and therefore they could be resistant to a changing climate (Angert *et al*., 2011; Kharouba *et al*., 2012; Summers *et al*., 2012). (6) **Rarity**: We have considered a species as rare both from a geographical or ecological point of view (i.e. locally abundant species, but linked to rare habitats in the Iberian Peninsula) and considered frequent the rest of the species: R=rare, F= frequent. Narrowly distributed species and rare species often present smaller population sizes, linked to higher sensibility against hazards (Iriondo *et al*., 2009), and are supposed to be more vulnerable and sensitive to environmental changes due to their lower ecological tolerance and flexibility (Gregori & Gaston, 2000). (7) **Specificity for the substrate**, showing whether the species is specialist or it is able to colonize multiple substrates. A species considered a strict epiphyte, saxicolous or terricolous lichen was considered S=specialist; contrarily, if it can colonize more than one substrate, we considered it G=generalist (e.i. some species that can grow on both trees and rocks). Ecological generalization decreases vulnerability (Angert *et al*., 2011): the more different substratum a species can use, the better it can migrate and adapt, as they may have the flexibility and tolerance needed to move between hosts, rock types or soils. (8) **Substrate type** (Asplund & Wardle, 2013): type of substrate where the lichen species can grow on: E= epiphyte or corticolous, T= terricolous, S= saxicolous. Not all available substrates present the same ecological implications. Saxicolous lichens are usually more exposed to drying out, meanwhile terricolous are supposed to compete more directly with vascular plants for resources. On the other hand, epiphytes are strongly dependent on their host dynamics (Shiver *et al*., 2011) and their own response to climate change (Felicísimo *et al*., 2012). (Ecological attributes values for each species, obtained from bibliographic sources except current distribution, are shown in Appendix, Table 5).

Climate change impact evaluation

To evaluate the impacts of climate change on the lichen species we calculated seven impact metrics which are estimations of specific distributions, exposure to climate change, susceptibility and vulnerability (see Table 1 for variables description).

Table 1: Impact metrics. List of grouped variables and description of its calculation. Variables grouped in: distribution, exposure, susceptibility and vulnerability. Vulnerability according to Settele *et al*. (2008).

Metric	Variable	Description	Unit
Distribution	Current distribution	Climatic suitable area under current conditions. (Threshold likelihood=70%)	km^2
	Future distribution	Climatic suitable area under future conditions. (Threshold likelihood=70%)	km^2
Exposure	Exposure	Future distribution-current distribution	km^2
Sensitiveness	Gain	Suitable areas only under future conditions (net gain) /current distribution·100	%
	Loss	Suitable areas only under current conditions (net loss) /current distribution·100	%
	Relative exposure	Exposure/current distribution·100	%
	Shift	(Net gain + net loss) / (current distribution + future distribution)·100	%
Vulnerability	Vulnerability	Five risk classes: LR=“low climate change risk” (loss<51%) R=“climate change risk” (51<loss<71) HR=“high risk” (71<loss<85) HHR=“very high” (85<loss<95) HHHR=“extremely high risk” (loss>95%)	

Using binary consensus maps, we calculated **current distribution** and **future distribution** (km^2), in connection with range size for both current and future conditions. On the basis of these figures, we also calculated distribution variation as an approach of **exposure**: the extent to which climate change may increase or decrease the likelihood of a species' occurrence in our study area. In this sense, large **exposure** negative values are associated to higher risk of the species when facing climate change.

We also considered species **susceptibility**, using 4 different variables (Table 1) as proxies of species sensitivity to climate change. First, overlapping future and current climatic suitable areas, we calculated specific area **gain**: new areas that would fit the species climatic requirements in the future scenario as a ratio of its current distribution. This metric indicates that species is less sensitive to climate risks, gaining new climatic areas gives it the chance to migrate. **Loss** shows the proportional area loss: the larger its values, the higher the species sensitivity. Likewise, we calculated **relative exposure** for a species in relation to its current distribution. Higher positive values mean the lowest risks. We also calculated species distribution range **shift**. The nearest the value is to 100, the lesser the current and **future distributions** overlap. This approach provides a measure of the distances the species would face to migrate.

Finally, we also classified the lichen species by their **vulnerability**, according to Settele et al (2008), into five risk categories (Table 1). Depending on the species **loss** (percent loss of distributional range) species vulnerability ranges in five classes from “low climate change risk” to “extremely high risk”.

Traits-impacts relation

We used generalized linear models (GLMs) to test for associations between each species´ traits/attributes and each impact metrics. For factors with more than two levels, we used lm and TukeyHSD test (in R). Eight traits and attributes (see appendix, Table 5) were tested as explanatory variables; response variables were the seven variables named as impact metrics (described in Table 1), except **current distribution**, used as a predictor like a proxy of distribution range breadth,

To avoid multicollinearity, we ensure all predictor variables presented correlations <0.7. Residuals from GLMs were generally uniformly distributed.

Current and **future distributions** were square root-transformed to satisfy model assumption of normality. The response variables **shift** and **exposure** are normally distributed, and link function used was "identity". The **susceptibility** variables **relative exposure**, **gain** and **loss**

presented trimodal distributions, so we could not directly test the effects of species traits on them. We did analyze the effects of traits on **gain** using only the sub-sample of those species which presented a positive value for **exposure** (future distribution>current distribution). **Gain** was natural-log-transformed and link function was “identity”. **Loss** was analyzed similarly: only the sub-sample of species with negative **exposure**. We analyzed the absolute of **loss** using link=”logit”. Likewise, **vulnerability** was not analyzed as it directly relates to **loss**.

Results

Model accuracy was species-specific and variable. AUC values ranged (GAMs: $0.76<AUC<0.95$; GLMs $0.78<AUC<0.97$), being all of them acceptable, as well as kappa values (GAMs: $0.34<k<0.87$; GLMs: $0.37<k<0.83$; CART: $0<k<0.95$, excluding CART models $k<0.4$ (Appendix, Table 2)). The importance of climate was also species-dependent: models explained 23-100 % of the variance in lichen distribution when using GAMs, whereas D^2 values (GLMs) oscillated between 0.22 and 0.77.

Projected potential areas and calculated range shifts

Our results showed variability on the distributions for the current and future conditions. For the present climatic conditions, distributions varied from 5440 Km^2 for *Staurolemma omphalarioides*, to almost 10-fold larger range for *Chaenoteca chrysocephala* (49127 Km^2) (Table 2). The mean value for the current distribution was 20541Km^2, meanwhile this mean value is reduced more than a 30% (13998 Km^2) in the future conditions. What is more, exposure values for most of the studied species (31 out of 41) are negative and quite high (mean=-6543 Km^2, Table 2) In this regard, general results showed a projected loss in bioclimatic space for this lichens set.

Three trends on the impact metrics were observed. First, a group of 7 “high **susceptibility**” species: they only presented **loss** (**loss**>70%), with no **gain** at all, and negative values of **exposure** (Table 2). Those 7 species (i.e. *Peltigera elisabethae, Peltigera hymenina, Peltigera leucophlebia, Peltigera membranace, Peltigera polydactylon, Peltigera venosa, Solorina saccata*) would face the highest risk, as their ranges would be dramatically reduced. According to their **vulnerability** values, they range from “risk” (R) to “very high climate change risk” (HHR). The second trend comprised ten “low **susceptibility**” species, with the lowest impacts: positive values for **exposure** linked in most cases to a great **gain** (e.g. *Callicium glaucellum* **gain**=238.5%). Most of them (6) are under “low risk” (LR) **vulnerability** class, although the other 4 could be considered under “risk” (R/HHR) due to their **loss** values (**loss**>50%) and high **shift** values (e.g. *Calicium glaucellum* **shift**=95.05%). Finally, the rest (24) of species could be grouped in a “variable **susceptibility**” heterogeneous group. They had in common high **loss** values (**loss**>50%) and negative **exposure**, but also very variable **gains** (**gain** values ranging 0.29%-57.83%) and showed variable degrees of **susceptibility** and **vulnerability.**

Table 2: Specific impact values of climate change. Distribution: extension (Km2) of climatic suitability areas (likelihood threshold>70%) under current and future climatic conditions. Exposure: Future distribution-current distribution (Km2). Susceptibility metrics: gain= area only under future conditions= (net gain/current distribution)·100; loss=area only under future conditions= (net loss/current distribution)·100; relative exposure= (exposure/current distribution); shift: (net gain + net loss)/(current distributions + future distribution). Vulnerability: climate change risk classes according to Settele *et al*. (2008): LR="Low risk", R="Risk", HR="High risk", HHR="very high risk", HHHR="Extremely high risk". Mean ± standard deviation values for the species set.

	Distribution (Km^2)			Susceptibility (%)				
Species	**Current**	**Future**	**Exposure (Km^2)**	**Gain**	**Loss**	**Relative exposure**	**Shift**	**Vulnerability**
B.cedricola	14159	41472	27313	229.18	36.28	192.9	67.64	LR
C.glaucellum	8300	28100	19800	327.71	89.16	238.55	95.05	HHR
C.cinereum	11111	1484	-9627	0.85	87.49	-86.64	78.87	HHR
C.daedaleum	22396	4863	-17533	2.52	80.80	-78.29	68.81	HR
C.crespoae	22684	6475	-16209	14.07	85.53	-71.46	77.75	HHR
C.chrysocephala	49127	26479	-22648	12.22	58.32	-46.1	45.90	R
C.mediterranea	18336	30660	12324	111.99	44.78	67.21	60.20	LR
D.ceratoniae	8610	8215	-395	49.78	54.37	-4.59	53.42	R
F.ignobilis	22297	27403	5106	84.45	61.55	22.9	65.66	R
K.biformis	15184	15024	-160	90.5	91.56	-1.05	97.88	HHR
L.aragonii	24105	10435	-13670	27.72	84.43	-56.71	78.41	HR
L.furfuraceum	45735	74121	28386	159.26	97.19	62.07	97.85	HHHR
L.lichenoides	25196	9761	-15435	12.05	73.31	-61.26	61.74	HR
L.pulvinatum	22100	21700	-400	67.42	69.23	-1.81	68.94	R
L.amplissima	16700	2000	-14700	6.59	94.61	-88.02	90.37	HHR
L.pulmonaria	17500	6200	-11300	28	92.57	-64.57	89.76	HHR
L.scrobiculata	19800	25100	5300	58.08	31.31	26.77	39.42	LR
N.laevigatum	24800	20500	-4300	47.98	65.32	-17.34	62.03	R
N.parile	17000	3200	-13800	9.41	90.59	-81.18	84.15	HHR
N.resupinatum	30800	10800	-20000	19.16	84.09	-64.94	76.81	HR
P.canina	20600	7900	-12700	14.56	76.21	-61.65	65.84	HR
P.collina	30800	10500	-20300	9.09	75.00	-65.91	62.71	HR
P.elisabethae	24300	4900	-19400	0	79.84	-79.84	66.89	HR
P.horizontalis	22900	3100	-19800	3.93	90.39	-86.46	83.91	HHR
P.hymenina	21300	2900	-18400	0	86.38	-86.38	76.66	HHR
P.leucophlebia	19400	4000	-15400	0	79.38	-79.38	66.37	HR
P.membranacea	30300	7000	-23300	0	76.90	-76.9	62.80	HR
P.monticola	22329	5916	-16413	6.56	80.07	-73.51	68.88	HR
P.neckeri	14100	17400	3300	80.85	57.45	23.4	61.90	R
P.polydactylon	12800	2200	-10600	0	82.81	-82.81	71.62	HR
P.praetextata	21400	5400	-16000	7.48	82.24	-74.77	71.91	HR
P.venosa	17400	4800	-12600	0	72.41	-72.41	57.27	HR
P.paramerae	42820	7055	-35765	12.5	96.02	-83.52	93.17	HHHR
P.imbecillum	7716	542	-7174	0.29	93.26	-92.98	87.66	HHR
P.lusitanica	14159	22469	8310	82.73	24.04	58.69	41.34	LR
S.holophaea	9900	26900	17000	174.75	3.03	171.72	47.82	LR
S.saccata	28200	8800	-19400	0	68.79	-68.79	52.71	R
S.omphalarioides	5440	2438	-3002	44.67	99.85	-55.18	99.73	HHHR
S.fuliginosa	16600	11200	-5400	57.83	90.36	-32.53	88.48	HHR
T.chrysophthalmus	9604	5193	-4411	24.31	70.24	-45.93	62.81	HR
W.adscenderes	14159	39311	25152	225.64	48	177.64	72.54	LR
Mean±	**20541±**	**13998±**	**-6542.70±**	**51.32±**	**73.30±**	**-21.97±**	**0.70±**	
SD	**9657.04**	**14449.70**	**14976.41**	**74.45**	**21.6**	**85.41**	**0.15**	

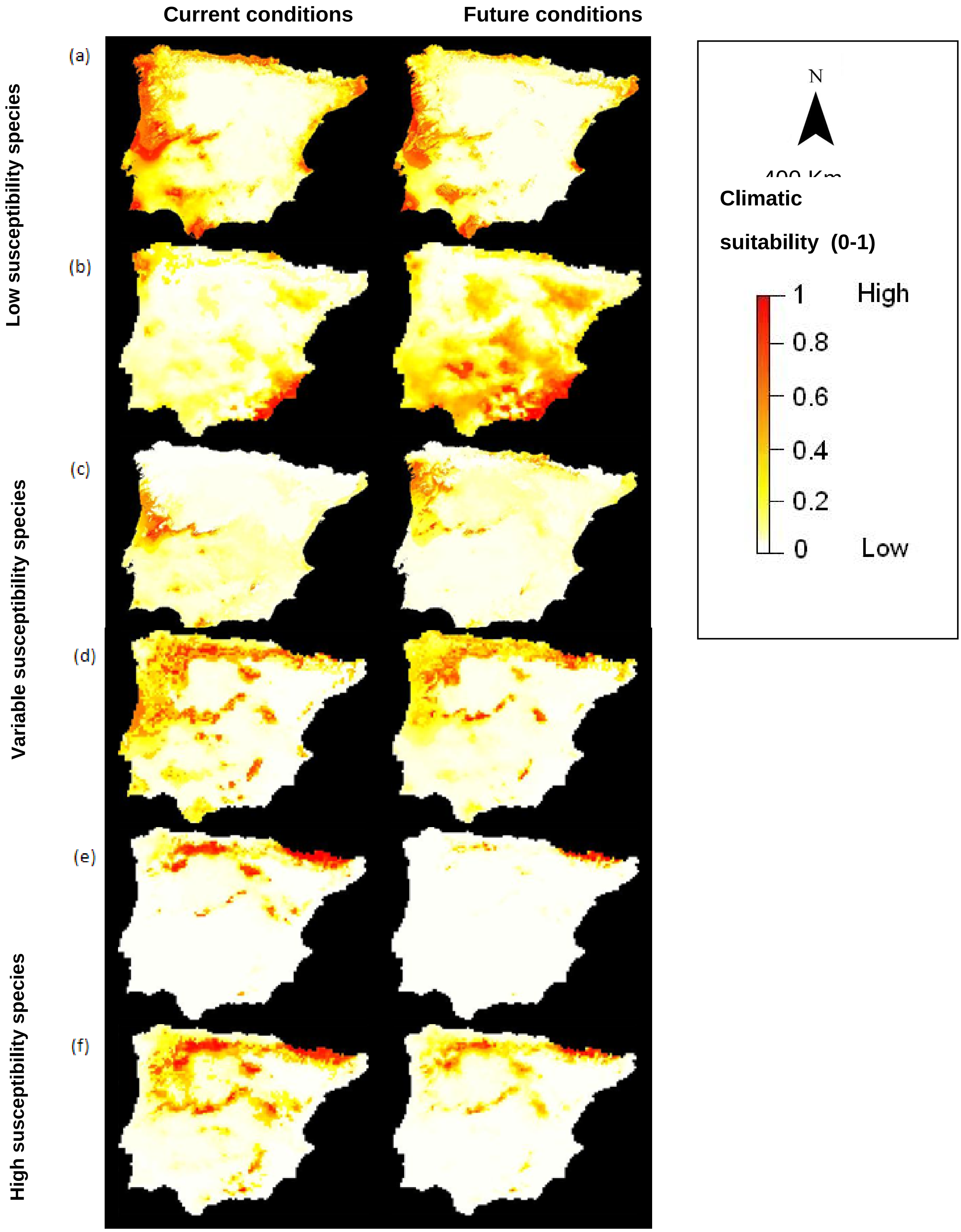

Figure 1: Climatic suitability maps. Low susceptibility species: (a) *Cladonia mediterranea* (b) *Solonopsora holophaea*; variable susceptibility species: (c) *Staurolemma omphalarioides* (d) *Lobaria pulmonaria*; high susceptibility species: (e) *Peltigera elisabethae* (f) *Solorina saccata.*

A visual inspection of the per-species ensemble probability maps (Appendix, Fig. 1) supported the idea of the three trends mentioned above and showed spatially explicit distributions, **exposure** and **shift** values. The “low **susceptibility**” group of (10) species was characterized by a clear increase of their distribution (i.e. *C. mediterranea* Fig. 1(a)). Of the “high **susceptibility**” group, all species presented reductions in their distributions when facing climate change (i.e. *S. saccata* Fig. 1(f)), and their climatic suitability areas did not move, only shrank. An extreme case of this trend was *P. elisabethae* (Fig. 1(f)), restricted in the future conditions to some areas of the Cordillera Cantábrica and the Pyrenees. The largest “variable **susceptibility**” group was comprised of species mainly loosing climatic space, but with different degrees of shifting: from *Lobaria pulmonaria* (Fig. 1(d)), which suffered mainly a reduction in its distribution (**relative exposure**=-66.57%, **loss**=92.57%, **shift**=89.76%, see Table 2), to *S. omphalarioides* (Fig. 1 (c)) which presented a clear displacement northwards (also see Table 2, **shift**=99.73%), but not such shrank in distribution thanks to distribution gains (**gain**=44.67, Table 2).

In spite of the variable impacts, note that **shift** values showed that future climatic conditions lead to a distribution displacement in all species (Table 2). Species like *S.omphalarioides,* with a very high **shift** value (99.73%) (see also Fig. 1(c)), showed that their future and current potential areas overlap almost nothing.

According to **vulnerability** values (Table 2), only 6 species are not under a risk class (LR). Of the rest, 14 species are under the highest risk categories: “very high” (HHR) and “extreme risk” (HHHR).

Vulnerability classes did not always match with **susceptibility** and **exposure** values. Some species, as *L. furfuraceum*, presented low **susceptibility** values plus a positive **exposure**, but are under a high risk class (*L.furfuraceum*, HHHR) and its current and future distributions do not overlap (Table 2, see also appendix, Fig.1). On the other hand, species as *Pertusaria paramerae* (**susceptibility** and **vulnerability** values did matched: **relative exposure**=-83.52%, **gain**=12.50%, **loss**=96.02%, **shift**=93.17%, **vulnerability**=HHHR), show more consistent impacts of climate change.

Impacts and traits/attributes

When we analyzed the relationship between species traits/attributes and climate change impact metrics, thallus size emerged as the most important one. Smaller thallus size was significant when considering **future distribution**, **exposure** and **loss** as responses. These consistent results showed that species with smaller thallus size presented an advantage when facing climate change (Table 3). Potobiont type was the other noteworthy functional trait: green-algae lichens presented significantly higher **gain** values when tracking suitable climatic conditions (Table 3).

Table 3: Trait effects on impact metrics. GLMs results: coefficient estimate±standard deviation, p-value. Impact metrics evaluated: future distribution: extension (Km^2) of climatic suitability areas under future conditions (likelihood>70%); exposure: Future distribution-current distribution (Km^2); gain= area only under future conditions= (net gain/current distribution)·100; loss=area only under future conditions= (net loss/current distribution)·100. Only significant traits are shown.

Impact metric	Trait	Level	Estimate±SD	P-value
Future distribution	Size	Large (intercept)	84.92±10.95	<0.001
		Small	41.42±15.68	0.0118
	Substrate type	Epiphyte (intercept)	120.93±10.682	<0.001
		Saxicolous	6.897±27.235	0.814
		Terricolous	-45.046±16.777	0.0107
Exposure	Size	Large (intercept)	-13478±2918	<0.001
		Small	13965±4177	0.00184
	Rarity	Frecuent (intercept)	-10602±2860	<0.001
		Rare	10087±4579	0.033576
	Current distribution	Intercept	5305.2±5211.0	0.3149
		Curret distribution	-0.5828±0.2301	0.0154
Gain	Photobiont	Cyanobacteria (intercept)	3.4197±0.2858	<0.001
		Green-algae	1.451±0.3690	0.00434
Loss	Size	Large (intercept)	4.1938±0.2249	<0.001
		Small	-0.7994±0.3615	0.0351

When considering ecological attributes, substrate type had an effect on **future distribution**: epiphytic lichens presented larger **future distributions** in response to climate change, in comparison to terricolous (no significant differences among saxicolous and epiphytes and/or terricolous were detected). **Rarity** and **current distribution** were also relevant when evaluating **exposure**: range-reduced and rare species tended to exhibit the greater advancements (Table 3).

We did not to detect any effect of the studied traits/attributes on the response variable **shift**. Furthermore, no effects of the other studied traits were found, apart from the ones already commented. Neither reproduction type, nor substrate specificity nor growth form had any significant outcome on any of the used metrics to detect range variations (data not shown).

Discusion

Different authors such as Aptroot & Herk (2007) have already pointed out that lichens area among the most sensitive organisms responding to climate changes. This study provides one of the first examinations of projected climate change impacts on lichens (but see Ellis *et al*., 2007a, 2007b). Our results are strongly indicating a loss of bioclimatic space for most species (31) and an increase for some others (10). The present study also highlights how **distributions**, **susceptibility** and **vulnerability** might be species-specific and trait-mediated.

General tendencies show geographical shifts for all the study species. Moreover, most forecasted shifts meant a contraction in distributions, leading species to reduced ranges. When considering the study species as a set, the mean value for the future distribution suffered a 30% reduction (comparing with current conditions). This is consistent with experimental evidence, demonstrating a decline in lichen occurrence following the simulated effects of climate change (Aptroot & Herk, 2007; Ellis *et al*., 2007a; Escolar *et al*., 2012). Many of them are linked to old forests and high mountain areas. Mountain habitats —as proved for butterflies (Wilson *et al*., 2005) or plants (Holzingger *et al*., 2008)— imply higher risks due to added difficulties to altitudinal shifts. Lichen results are according to many previous studies all across life diversity (Root *et al*., 203; Chen *et al*., 2011; Bellard *et al*., 2012). The convergence of those predictions to a species loss, accounting for many different organisms, can be regarded as an indicator of robustness of this general trend and might be interpreted as a major threat for biodiversity.

Nevertheless, climatic change can also have positive effects on bioclimatic ranges. In our study, 10 species enlarged their distributions. Six of them (<15%) are not under risk, according to vulnerability classification (Settele *et al*., 2008). These clearly Mediterranean species presented positive impacts when facing climate change. Long-term monitoring studies already pointed out that warm-temperate lichens have increased their European distributional ranges, whereas cold and wet environment species have decreased or disappeared (e.g. Van Herk *et al*., 2002). This is consistent with some other taxa: Seoane & Carrascal (2007) found a positive population trend in the Iberian Peninsula for Iberian birds facing climate change.

It is worth emphasizing the usefulness of a combined use of different metrics to calibrate climate change impacts on a species distribution. Of the 10 lichens enlarging distributions mentioned above, 4 are under threat when considering vulnerability. In this sense, these lichens showed exposure values leading us to think that they are not under a serious risk when facing climate change, whilst they belong to a vulnerability class of risk. E.g. *L. furfuraceum* is under “extremely high risk” (HHHR) according to its vulnerability, but its exposure, relative exposure and gain values are reassuring.

If the climatic niche of a species reduces in area (e.g. *S. saccata* or *P. hymenina*), such depletion is clearly a threat for the species conservation (IUCN, 2009), at least locally. The bioclimatic potential area might become too small to allow healthy populations to survive (Iriondo et al 2009). Even though, local extinctions do not necessarily lead to global extinction. That would be the case of some of the lichens in this study (i.e. *P. horizontalis* or *L. amplissima*) that present distributional ranges broader than the Iberian Peninsula.

When facing area depletion, species could also experience some adaptations: as phenotipic plasticity or rapid evolution. Rates of evolutionary change are usually much slower than required for species to evolve necessary adaptations in the face of climate change (Engler *et al*., 2011), and it is more likely in short-lived species (Pearson & Dawson, 2003) which is not the case of most lichens. Empirical evidence suggests that plastic contribution is often more important (Ellis, 2013 and references) in lichens. They seem to be able to acclimate through plasticity (Gauslaa *et al*., 2006). In this sense, further research is needed to evaluate lichen capacity for each of these responses.

Some lichens will face geographic relocation of their climatic suitable conditions (e.g. *C. glaucellum*, shift=0.95). If failing to adapt, they can track appropriate climatic requirements in space and follow them through migration. This process is dependent on species dispersal characteristics (Werth *et al*., 2007; Meier *et al*., 2012), but also on the landscape structure (Pearson & Dawson, 2003)**,** including natural barriers and fragmentation (Belinchón *et al*., 2007; Meier *et al*., 2012). Dispersal-limited species and those restricted to fragmented or isolated habitat patches will have reduced opportunity to respond to climate change by migrating. This is of special concern in the Mediterranean area and Iberian Peninsula, where fragmentation is significant threat (Scarascia-Mugnozza *et al*., 2000; Belinchón *et al*., 2007, 2009). Migration also depends on biotic interactions. Community assemblages under a changed climate may be dissimilar to those occurring in the present-day conditions (Lavorel & Garnier, 2002; Bascompte, 2009). New climatic conditions could create favorable habitats for superior competitors (Engler *et al*., 2011), grazers or even affect lichenization process (Nash III, 2008). As a result, readjustments of species ranges to climate change are complex and very individualistic.

Traits/attributes effect

Our analysis showed a significant effect of some lichen species´ functional traits and ecological attributes on climate change impacts.

Smaller thallus sizes meant a protection against climate change, and revealed as the most important lichen trait. Smaller species turn out to be less exposed, susceptible and vulnerable. Although our size classification is quite coarse the significant effect of size on 3 impact metrics gives our result robustness. This can be due to the fact that larger thallus require more water availablility (Merinero *et al*., 2013), and a higher biomass implies higher costs of maintenance, as is the case of plants (Milla & Reich, 2007).

Some other traits influenced future distribution of species and their susceptibility to change. So it was substrate type: terricolous lichens -compared to epiphytes- presented smaller future distributions. Lichens growing directly on the soil are usually more exposed to competition with plants, more exposed and supposed to respond more directly to climatic parameters. Conversely, epiphytes clearly depend on future forest spatial dynamics and distributions. If they present more than one potential host plant may be buffered form range shifts: land abandonment is currently creating forest patches and thus would promote epiphyte species migration (Meier *et al*., 2012). But specialist epiphytes should be also of concern due to their high dependence to their host tree dynamics (Shiver *et al*., 2011; Felicísimo *et al.,* 2012).

As expected, green-algae lichens presented less susceptibility, comparing to cyanolichens. For lichens presenting distributional enlargement, expansion was greater when accounting for green-algae lichens. This is probably due to green photobiont better performance when facing dryer conditions (Lange *et al*., 1986). Cyanolichens are linked to wetter and cooler places, where liquid water is more likely to be available for longer periods. In the Iberian Peninsula forecasted drier conditions (IPCC, 2007), the lower photosynthetic efficiency of cyanobacterial may limit cyanolichens establishment and growth.

Both rarity and current distribution (as a surrogate of real distributional range) are, contrary to our expectations, positive attributes when facing climate change. Rare species are linked to habitat types relatively unusual nowadays in the Iberian Peninsula. Those habitats with extreme Mediterranean conditions could become more common when climatic conditions change in the next few decades (IPCC, 2007). *C. mediterranea* (gain=111.99%) or *S. holophaea* (gain=174.75%) are rare species which bioclimatic niches are linked to warm and dry areas (Rubio-Salcedo *et al.* 2013). Ellis & Coppins (2007) also found similar results: an increase of suitable areas in Scotland for “southern species” (which require warmer temperatures better tolerate drought).

But this should be read prudently; e.g. *Cladonia mediterranea* is locally abundant in sandy coastal areas, rocks and dunes. These habitats are worrying threatened and disturbed (Morillo & Gómez-Campo, 2000; Cogoni *et al*., 2011) and sea level rising is forecasted to be intense (Moreno *et al*., 2005; IPCC, 2007). This example highlights how complex interactions between global change factors are not accounted for in these models, and these interactions could decrease or increase in future extinction risk (Pereira *et al*., 2010).

In the same way, narrow current distributions lead to the larger distributions under future conditions. This striking result supports the concept that frequent species with broader ranges are less prone to gain new areas, contrary to our expectations. However, some evidence also supports this idea: Lenoir *et al*. (2008) found that mountain plants with narrower distributions moved further upward when facing climate change.

We did not detect any effect of specificity, growth form and reproduction type on impact metrics. In this regard, further effort in this area is needed to understand how these traits and attributes influence species´ responses to climate. Particularly astonishing is the lack of significant effect of reproduction type, in spite of its proved implication on dispersal ability. Theoretically, lichens with asexual reproduction appear to have lower capacity for migration compared with spore-dispersed species (***Hedenäs*** & Ericson, 2008), but we could not find support to this. Furthermore, it should be noted that asexual reproduction in lichens also presents higher establishment success (facilitated by larger sores of resources and no need to relichenization). This advantage may be traded off against limited dispersion or in situ adaptation thanks to higher genetic variability associated to sexual reproduction.

Our results provide a valuable means of exploring how Iberian lichens will respond to climate change and how specific traits and attributes are involved. Nevertheless, an appropriate interpretation of our results requires an assessment of the assumptions and limitations of our analyses (Thuiller, 2003; Pearson & Dawson, 2003; Zimmermann *et al*., 2010; Araújo & Peterson, 2012). Sources of uncertainty as "working assumptions" (Araújo & Peterson, 2012), input data quality (Ellis *et al*., 2007a, 2007b), historical factors (Zimmermann *et al*., 2010) or small scale effects (Ellis, 2013) should be considered in discussion. Lichens are especially sensitive to smaller-scale environmental conditions (Jüriado *et al*., 2011; Rubio-Salcedo *et al.* 2014), so the response of many species to large-scale climate will be modified by small-scale factors. Besides, lichen species have to cope with additional co-occurring threats, as pollution (Giordani *et al*., 2002) and habitat destruction (Morillo & Gómez-Campo, 2000; Cogoni *et al*., 2011), some of which may act in synergy with climate change (Bellard *et al*., 2012; Ellis *et al.* 2007a).

Conclusions

This study provides a good estimation of projected climate change impact on Iberian lichens. Our results are species-specific and show a great loss of bioclimatic space, with some exceptions for Mediterranean species linked to dry and warm areas.

When evaluating biodiversity responses to climate change, more comprehensive conservation strategies are needed, as an integrated approach including taxons like lichens. In the absence of detailed ecological information, a focus on traits may play a valuable role in coupling distributional patterns for lichen species. Thallus size, substrate type and photobiont type revealed as important lichen traits driving climate change distributional responses. Rarity and current distribution range are ecological attributes also involved in specific responses to climate change. Surprisingly, we did not detect a significant effect of other traits/attributes theoretically important. Further research is needed In this sense.

We also highlight the critical importance of the methodological approaches. Combining complementary modeling techniques helps results to be more accurate and robust. Plus, when assessing the climate change impacts on species distributions we suggest the comparison of different metrics, as they do not necessarily lead to the same conclusions.

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References

Akaike H (1974) A new look at the statistical model identification. *IEEE Transactions on Automatic Control*, **19**, 716-723.

Angert LA, Crozier LG, Rissler LE, Gilman SE, Tewksbury JJ, Chunco AJ (2011) Do species' traits predict recent shifts at expanding range edges? *Ecological Letters*, **14**, 677–689.

Aptroot A, van Herk CM (2002) Lichens and global warming. *International Lichenological Newsletter,* **35**, 57-58.

Aptroot A, van Herk CM (2007) Further evidence of the effects of global warming on lichens, particularly those with Trentepohlia phycobionts. *Environmental Pollution,* **146**, 293-298.

Aragón G, Otálora MAG (2004) Ecological and chorological novelties of the genus Leptogium in the Iberian Peninsula. *Nova Hedwigia*, **78**, 353-366.

Aragón G, Otálora MAG, Martínez I (2005) New data of the genus *Leptogium* (ascomycetes lichenized) in the Iberian Peninsula. *Nova Hedwigia,* **80**, 199-226.

Aragón G, Martínez I, García A (2012) Loss of epiphytic diversitiy along a latitudinal gradient in southern Europe. *Science of the Total Environment*, **426**, 188-195.

Araújo MB, Guisan A (2006) Five (or so) challenges for species distribution modelling. *Journal of Biogeography*, **33**,1365-2699.

Araújo MB, Luoto M (2007) The importance of biotic interactons for modelling species distributions under climate change. *Global Ecology and Biogeography*, **16**, 743-753.

Araújo MB, New M (2007) Ensemble forecasting of species distributions. *TRENDS in Ecology and Evolution,* **22**, 42-47.

Araújo MB, Pearson RG (2005) Equilibrium of species' distributions with climate. *Ecography*, **28**, 693–695.

Araújo MB, Peterson T (2012) Uses and misuses of bioclimatic envelope modeling. *Ecology* **93**,1527-1539.

Araújo MB, Whittaker RJ, Ladle RJ, Erhard M (2005a) Reducing uncertainty in projections of extinction risk from climate change. Global Ecology and Biogeography 14, 529-538.

Araújo MB, Pearson R, Thuiller W, Erhard M (2005b) Validation of species–climate impact models under climate change. *Global Change Biology,* **11**, 1–10.

Asplund J, Wardle DA (2013) The impact of secondary compounds and functional characteristics on lichen palatability and decomposition. *Journal of Ecology,* **101**, 689-700.

Bascompte J (2009) Disentangling the web of life. *Science*, **325**, 416–419.

Belinchón R, Martínez I, Escudero A, Aragón G, Valladares F. (2007) Edge effects on epiphytic communities in a Mediterranean Quercus pyrenaica forest. *Journal of Vegetation Science*, **18**, 81-90.

Belinchón R, Martínez I, Otálora MAG, Aragón G, Dimas J, Escudero A (2009) Fragment quality and matrix affect epiphytic performance in Mediterranean forest landscape. *American Journal of Botany*, **96**, 1974-1982.

Bellard C, Bertelsmeier C, Leadley P, Thuiller W, Courchamp F (2012) Impacts of climate change on the future of biodiversity. *Ecology Letters*, **15**, 365-377.

Bello F, Lavorel S, Díaz S *et al*. (2010) Towards an assessment of multiple ecosystem processes and services via functional traits. *Biodiversity and Conservation*, **19**, 2873-2893.

Breiman L, Friedman JH, Olshen RA, et al. (1984) *Classification and Regression Trees*. Chapman & Hall, New York.

Carter G M, Stolen ED, Breininger DR (2006) A rapid approach to modelling species–habitat relationships. *Biological Conservation*, **127**, 237–244.

Chefaoui RM, Lobo JM (2008) Assessing the effects of pseudo-absences on predictive distribution model performance. *Ecological Modelling,* **210**, 478-486.

Chen I, Hill JK, Ohlemüller R, Roy DB, Thomas CD et al. (2011) Rapid range shifts of species associated with high levels of climate warming. *Science*, **333**,1024-1026.

Cogoni A, Brundu G, Zedda L (2011) Diversity and ecology of terricolous bryophyte and lichen communities in coastal areas of Sardinia (Italy). *Nova Hedwigia*, **92**, 159–175.

Cohen J (1960) A coefficient of agreement for nominal scales. *Educational and Psychological Measurements*, **20**, 37-46.

Corenelissen JHC, Lang SI, Soudzilovskia, NA *et al.* (2007) Comparative cryptogam ecology, a review of bryophyte and lichen traits that drive biogeochemistry. *Annals of Botany,* **99**, 987–1001.

Costa M, Morla C, Sáinz H (eds.) 2005. *Los montes ibéricos, una interpertación geobotánica*. Editorial Planeta. Barcelona.

Crossmann ND, Bryan BA, Summers DM (2012) Identifying priority areas for reduciong species vulnerability to climate change. *Diversity and Distributions*, **18**, 60-72.

Diamond SE, Frame AM, Martin R, Buckley LB (2011) Species' traits predict phenological responses to climate change in butterflies. *Ecology,* **92**, 1005-1012.

Edman M, Eriksson AM, Villard D (2008) Effects of selection cutting on the abundance and fertility of indicator lichens *Lobaria pulmonaria* and *Lobaria quercizans*. *Journal of Applied Ecology*, **45**, 26-33.

Eldridge DJ, Rosentreter R (1999) Morphological groups, a framework for monitoring microphytic crusts in arid landscapes. *Journal of Arid Environments*, **41**, 11-25.

Ellis C (2013) A risk-based model of climate change threat, hazard, exposure, and vulnerability in the ecology of lichen epiphytes. *Botany*, **91**,1-11.

Ellis C, Coppins BJ (2006) Contrasting functional traits maintain lichen epiphyte diversity in response to climate and autogenic succession. *Journal of Biogeography*,**33** 1643–1656

Ellis C, Coppins BJ, Dawson TP, Seaward MRD (2007a) Response of British lichens to climate change scenarios, trends and uncertainties in the projected impact for contrasting biogeographic groups. *Biological Conservation,* **140**, 217-235.

Ellis C, Coppins BJ, Dawson TP (2007b). Predicted response of lichen epiphyte K to climate change scenarios in clean-air region of Northern Britain. *Biological Conservation*, **135**, 396-404.

Engler R, Radin C, Thuiller W *et al.* (2011) 21st century climate change threatens mountain flora unequally across Europe. *Global Change Biology*, **17**, 2330-2341.

Escolar C, Martínez I, Bowker MA, Maestre FT. (2012) Warming reduces the growth and diversity of biological soil crust in a semi-arid environment, implications for ecosystem. *Philosophical Transactions of the Royal Society of Biological Sciences*, **367**, 3087-3099.

Eviner VT, Chapin FS (2003) Functional Matrix, a conceptual framework for predicting multiple plant effects on ecosystem processes. *Annual Review of Ecology, Evolution, and Systematics*, **34**, 455 -485.

Felicísimo AM, Muñoz J, Mateo RG, Villalba CJ (2012) Vulnerabilidad de la flora y vegetación españolas ante el cambio climático. *Ecosistemas,* **21**, 1-6.

Fielding AH, Bell JF (1997) A review of methods for the assessment of prediction errors in conservation presence/absence models. *Environmental Conservation*, **24**, 38-49.

Gauslaa Y, Solhaug KA (1999) High-light damage in air-dry thalli of the old forest lichen Lobaria pulmonaria -- interaction of irradiance, exposure duration and high temperature. *Journal of Experimental Botany*, **50**, 697-705.

Gauslaa Y, Lie M, Solhaug KA, Ohlson M (2006) Growth and ecophysiological acclimation of the foliose lichen Lobaria pulmonaria in forests with contrasting light climates. *Oecología,* **147**, 406-416.

Giordani P, Incerti G (2008) The influence of climate on the distribution of lichens, a case study in a borderline area (Liguria, Nw Italy). *Plant Ecology*, **2**, 257-272.

Giordani P, Brunialti G, Alleteo D (2002) Effects of atmospheric pollution on lichen biodiversity (LB) in a Mediterranean region (Liguria, northwest Italy). *Environmental Pollution*, **118**, 53-64.

Giordani P, Incerti G, Rizzi G, Nimis PL, Modenesi P (2013) Functional traits of cryptogams in Mediterranean ecosystems are driven by water, light and substrate interactions. *Journal of Vegetation Science*. Doi: 10.1111/jvs.12119

Gregory RD, Gaston KJ (2000) Explanations of commonness and rarity in British breeding birds, separating resource use and resource availability. *Oikos*, **88**, 515-526.

Guisan A, Thuiller W (2005) Predicting species distribution, offering more than simple habitat models. *Ecology Letters*, **8**, 993–1009.

Guisan A, Zimmermann NE (2000) Predictive habitat distribution models in ecology. *Ecological Modeling* ,**135**, 147-186.

Hastie TJ, Tibshirani R (1990) Generalised Additive Models. Chapman & Hall, London.

Hedenås H, Ericson L (2008) Species occurrences at stand level cannot be understood without considering the landscape context, Cyanolichens on aspen in boreal Sweden. *Biological Conservation*, **141**, 710-718.

Herk CM, Aptroot A, van Dobben HF (2002) Long-term monitoring in the Netherlands suggests that lichens respond to global warming. *Lichenologist,* **34**, 141-154.

Hewitt CD (2004) Ensembles-based predictions of climate changes and their impacts, Eos*, Transactions American Geophysical Union*, **85**, 566–566.

Holzinger B, Hülber K, Camenisch M, Grabherr G (2008) Changes in plant species richness over the last century in the eastern Swiss Alps, elevational gradient, bedrock effects and migration rates. *Plant Ecology*, **195** ,179-193.

Insarov G, Schroeter B (2002) Lichen monitoring and climate change. In: *Monitoring with Lichens-Monitoring Lichens*.(eds Nimis PL, Scheidegger C, Wolseley PA),. Kluwer, Amsterdam.

IPCC (2007) Climate change 2007: The scientific basis. In: *Contributions of Working Group I to the Fourth Assessment Report of the Intergovernmental Panel on Climate Change: “The Physical Science Basis”*, (eds Solomon S, Qin D, Manning M, Chen Z, Marquis M, Averyt KB, Tignor M, Miller HL), pp. 1–18. Cambridge University Press, Cambridge.

Irondo JM, Albert MJ, Giménez-Benavides L, Domínguez Lozano F, Escudero A (Eds.) (2009) *Poblaciones en peligro, viabilidad demográfica de la flora vascular amenazada de España.* Dirección General de Medio Natural y Política Forestal (Ministerio de Medio Ambiente, y Medio Rural y Marino). Pp 1-242, Madrid.

IUCN (International Union for the Conservation of Nature) (2009) IUCN Red List of threatened species. Version 2009.2. http,//www.iucnredlist.org

Jüriado I, Liira J, Csencsics D, Widmer C, Adolf C, Kohv K, Scheidegger C (2011) Dispersal ecology of the endangered woodland lichen Lobaria pulmonaria in managed hemiboreal forest landscape. *Biodiversity and Conservation,* **20**, 1803–1819.

Kharouba HM, McCune JL, Thuiller W, Huntley B (2012) Do ecological differences between taxonomic groups influence the relationship between species' distributions and climate? A global meta-analysis using species distribution models. *Ecography,* **35**, 1-8.

Kissling WD, Dormann CF, Groeneveld J, *et al.* (2012)Towards novel approaches to modelling biotic interactions in multispecies assemblages at large spatial extents. *Journal of Biogeography*, **39**, 2163-2178.

Lakatos M, Rascher U, Büdel B. (2006) Functional characteristics of corticolous lichens in the understory of a tropical lowland. *New Phytologist,* **172**,679-95.

Lange OL, Kilian E, Ziegler H. (1986). Water vapor uptake and photosynthesis of lichens, performance differences in species with green and blue-green algae as phycobionts. *Oecología,* **71**, 104-110.

Lavorel S, Garnier F (2002) Predicting changes in community composition and ecosystem functioning from plant traits, revisiting the Holy Grail. *Functional Ecology,* **16**, 545-556.

Lenoir J, Gegout JC, Marquet, PA, de Ruffray P, Brisse H (2008) A significant upward shift in plant species optimum elevation during the 20th century. *Science*, **320**, 1768–1771.

Lisewski V, Ellis JC (2010) Epiphyte sensitivity to a cross-scale interaction between habitat quality and macroclimate, an opportunity for range-edge conservation. *Biodiversity and Conservation*, **19**, 3935-3949.

Löbel S, Snäll T, Rydin H (2006) Species richness patterns and metapopulation process, evidence from epiphyte communities in boreo-nemoral forests. *Ecography*, **29**, 169-182.

Martínez I, Burgaz AR, Vitikainen O, Escudero A (2003) Distribution pattern of the genus Peltigera Willd. *The Lichenologist,* **35**, 301-323.

McCullagh P, Nelder JA (1989) Generalised Linear Models. Chapman & Hall, London.

McPherson JM, Jetz W (2007) Effects of species´ ecology on the accuracy of distribution models. *Ecography,* **30**, 135-151.

Meier ES, Kieanast F, Pearman PB *et al.* (2010) Biotic and abiotic variables show little redundancy in explaining tree species distributions. *Ecography,* **33**, 1038-1048.

Meier ES, Lisschke H, Schmatz DR, Zimmermann.NE (2012) Climate, competition and connectivity affect future migration and ranges of European trees. *Global Ecology and Biogeography*, **21**,164-178.

Milla R, Reich PB (2007) The scaling of leaf area and mass, the cost of light interception increases with leaf size. *Proceedings of the Royal Society of Biological Sciences*, **274**, 2109-2114.

Moreno Rodríguez J.M. (coord.) et al (2005) Principales conclusiones de la evaluación preliminar de los impactos en España por efecto del cambio climático. 39 pp. Oficina Española de Cambio Climático, Ministerio de Medio Ambiente, Madrid.

Morillo C, Gómez-Campo C (2000) Conservation in Spain 1980–2000. *Biological Conservation*, **95**, 165–174.

Muñiz D, Hladún N (2011) Sociedad Española de Liquenología, SEL. Barcelona.95 pp + 98 fotografías.

Nakicenovic N, Swart R (Cambridge University Press, Cambridge, 2000)

Thomas H. Nash III (ed) Lichen Biology (2008) 2nd edn. London, Cambridge University Press. Pp. 486

NINYEROLA M., X. PONS AND J.M. ROURE (2005) Atlas Climático Digital de la Península Ibérica. Universidad Autónoma de Barcelona, Bellaterra.

Otálora MAG, Martínez I, Molina MC, Aragón G, Lutzoni F (2008) Phylogenetic relationships and taxonomy of the Leptogiumlichenoides group (Collemataceae, Ascomycota) in Europe. *Taxon,* **57**, 907-921.

Otálora MAG, Martínez I, Aragón G, Molina MC, Lutzoni F (2010) Disentangling the Collema-Leptogium complex through a molecular phylogenetic study of the Collemataceae (Peltigerales, lichen-forming Ascomycota). *Mycologia,* **102**, 279-290.

Parmesan C, Yohe G (2003) A globally coherent fingerprint of climate change impacts across natural systems. *Nature*, **421**, 37-42.

Pearson RG, Dawson TP (2003) Predicting the impacts of climate change on the distribution of species, are bioclimate envelope models useful? *Global Ecology and Biogeography*, **12**, 361-371.

Pereira HM, Leadley PW, Proença V et al. (2010) Scenarios for Global Biodiversity in the 21st Century. *Science*, **330**, 1496.

Pöyry J, Luoto M, Heikkinen RK, Saarinen K (2008) Species traits are associated with the quality of bioclimatic models. *Global Ecology and Biogeography*, **17**,403–414.

Prieto M, Aragón G, Martínez I (2010) The genus Catapyrenium s. lat. (Verrucariaceae) in the Iberian Peninsula and the Balearic Islands. *The Lichenologist,* **42**, 637-684.

Prieto M, Martínez I, Aragón G, Gueidan C, Lutzoni F (2012) Molecular phylogeny of *Heteroplacidium, Placidium* and related catapyrenoid genera (Verrucariaceae, lichen-forming Ascomycota). *American Journal of Botany,* **99**, 23-35.

R Core Team (2013) R, A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. URL http,//www.R-project.org/.

Root TL, Price JT, Hall KR, Schneider SH, Rosenzweig C, Pounds JA (2003) Fingerprints of global warming on wild animals and plants. *Nature,* **421**, 57-60.

Rubio-Salcedo M, Martínez I, Carreño F, Escudero A (2013) Poor effectiveness of the Natura 2000 network protecting Mediterranean lichen species. *Journal for Nature Conservation*, **21**, 1-9.

Scarascia-Mugnozza G, Oswald H, Piussi P, Radoglou K (2000) Forests of the Mediterranean region, gaps in knowledge and research needs. *Forest Ecology and Management*, **132**, 97-109.

Seoane J, Carrascal LM (2007) Interspecific differences in population trends of Spanish birds are related to habitat and climatic preferences. *Global Ecology and Biogeography,* **17,** 111-121.

Settele J, Kudrna O, Harpke A *et al.* (2008) Climatic Risk Atlas of European Butterflies. BioRisk 1 (special issue), 1-710. Pensoft, Sofia-Moscow.

Shiver R, Cutler K, Doak DF (2011) Comparative demography of an epiphytic lichen, support for general life history patterns and solutions to common problems in demographic parameter estimation. *Oecologia*, **170**,137–146.

Søchting U (2004) *Flavoparmelia caperata* – a probable indicator of increased temperatures in Denmark. *Graphis Scripta*, **15**, 53-56.

Summers DM, Bryan BA, Crossman, ND, Meyer WS (2012) Species vulnerability to climate change, impacts on spatial conservation priorities and species representation. *Global Change Biology*, **18**, 1365-2486.

Swets J. (1988) Measuring the accuracy of diagnostic systems. *Science*, **240**, 1285-1293.

Thuiller W, Lavorel S, Sykes MT, Araú jo MB (2006) Using niche-based modelling to assess the impact of climate change on tree functional diversity in Europe. *Diversity and Distributions,* **12**, 49–60.

Thuiller W, Lavergne S, Roquet C, Boulangeat I, Lafourcade B, Araújo MB (2011) Consequences of climate change on the tree of life in Europe. *Nature*, **470**, 531-534.

Triviño M, Thuiller W, Cabeza M, Hickler T, Araújo MB. The Contribution of Vegetation and Landscape Configuration for Predicting Environmental Change Impacts on Iberian Birds. *PLoS ONE* 6(12), e29373. Doi: 10.1371/journal.pone.0029373

Thuiller W (2003) BIOMOD – optimizing predictions of species distributions and projecting potential future shifts under global change. *Global Change Biology*, **9**, 1353-1362.

Van Herk CM, Aptroot A, Van Dobben HF (2002) Long-term monitoring in the Netherlands suggest that lichens respond to global warming. *The Lichenologist*, **34**, 141-154.

Venables W N, Ripley BD (2002) Modern Applied Statistics with S. Fourth Edition. Springer.

Weisberg S (1980) Applied Linear Regression. John Wiley and Sons. New York. 352pp.

Werth S, Holderegger R, Wagner HH, Csencsics D, Scheidegger C (2007) Landscape-level gene flow in Lobaria pulmonaria, an epiphytic lichen. *Molecular Ecology,* **16**, 2807-2815.

Wilson RJ, Gutiérrez D, Gutiérrez J, Martínez D, Agudo R, Monserrat VJ (2005) Changes to the elevational limits and extent of species ranges associated with climate change. *Ecology Letters,* **8**, 1138-1146.

Zimmermann NE, Edwards TC, Graham CG, Pearman PB, Svenning JC (2010) New trends in species distribution modelling. *Ecography,* **33**, 1-5.

Appendix

Table 1: List of species modelled in the study. Complete names.

Buellia cedricola Werner
Calicium glaucellum Ach.
Catapyrenium cinereum (Pers.) Körb.
Catapyrenium daedaleum (Kremp.) Stein
Cetraria crespoae (Barreno & Vázquez) Kärnefelt
Chaenoteca chrysocephala (Turner ex Ach.) Th. Fr.
Cladonia mediterranea P.A.Duvign. & Abbayes
Dirina ceratoniae (Ach.) Fr.
Fuscopannaria ignobilis (Anzi) P.M. Jørg.
Korberia biformis A. Massal.
Leptogium aragonii Otálora
Leptogium furfuraceum (Harm.) Sierk
Leptogium lichenoides (L.) Zahlbr.
Leptogium pulvinatum (Hoff.) Otálora
Lobaria amplissima (Scop.) Forss.
Lobaria pulmonaria (L.) Hoffm.
Lobaria scrobiculata (Scop.)
Nephroma laevigatum Ach.
Nephroma parile (Ach.) Ach.
Nephroma resupinatum (L.) Ach.
Peltigera canina (L.) Willd.
Peltigera collina (Ach.) Schrad.
Peltigera elisabethae Gyeln.
Peltigera horizontalis (Huds.) Baumg.
Peltigera hymenina (Ach.) Delise
Peltigera leucophlebia (Nyl.) Gyeln.
Peltigera membranacea (Ach.) Nyl.
Peltigera monticola Vitik.
Peltigera neckeri Hepp ex Müll. Arg.
Peltigera polydactylon (Neck.) Hoffm.
Peltigera praetextata (Flörke ex Sommerf.) Zopf
Peltigera venosa (L.) Hoffm.
Pertusaria paramerae Crespo & Vezda
Placidium imbecillum (Breuss) Breuss
Pyrrhospora lusitanica (Räsänen) Hafellner
Solenopsora holophaea (Mont.) Samp.
Solorina saccata (L.) Ach.
Staurolemma omphalarioides (Anzi) P.M. Jørg. & Henssen
Sticta fuliginosa (Hoffm.) Ach.
Teloschistes chrysophthalmus (L.) Th. Fr.
Waynea adscenderes V.J. Rico

Table 2: Modeling details: N= number of presence points used; scale: scale of the input data and projections (Km^2); variables= climatic variables included as predictors (1=Annual mean temperature ºC, 8=Mean temperature of the wettest quarter of the year ºC, 9= Mean temperature of the driest quarter of the year ºC, 12= Annual mean precipitation mm, 17= mean precipitation of the driest quarter of the year mm); cross validation results for the GLM model: D^2, AUC and kappa values, for the GAM: % of variance explained, AUC and kappa, for the CART kappa value. Kappa values for CART in bold mean that the consensus map was built only using GLM and CART.

				GLM-Step			GAM			CART
Species	**N**	**Scale**	**Variables**	**D^2**	**AUC**	**k**	**%**	**AUC**	**k**	**k**
B.cedricola	49	1	1,8,9,12,17	0.75	0.96	0.80	79.5	0.95	0.87	0.88
C.glaucellum	22	10	1,8	0.35	0.87	0.56	45.7	0.83	0.47	0.62
C.cinereum	23	1	1,8	0.38	0.86	0.60	40.8	0.82	0.59	**0.00**
C.daedaleum	23	1	1,8	0.37	0.87	0.57	38.9	0.87	0.57	**0.00**
C.crespoae	26	1	8,12	0.22	0.78	0.37	30.8	0.79	0.34	0.68
C.chrysocephala	20	1	8,12	0.44	0.81	0.63	74.2	0.82	0.48	0.86
C.mediterranea	30	1	1,8,12	0.35	0.86	0.47	44.7	0.84	0.46	0.81
D.ceratoniae	79	1	1,8,9,12,17	0.77	0.97	0.83	99.4	0.91	0.80	0.94
F.ignobilis	45	1	1,8,9,12	0.68	0.84	0.82	77.1	0.90	0.72	0.94
K.biformis	89	1	1,8,9,12,17	0.34	0.85	0.44	45.9	0.86	0.48	0.63
L.aragonii	25	1	8,12	0.32	0.84	0.50	46.2	0.83	0.51	0.86
L.furfuraceum	20	1	8,9	0.73	0.97	0.77	73.7	0.94	0.76	0.93
L.lichenoides	24	1	8,12	0.36	0.86	0.51	38.1	0.84	0.47	0.89
L.pulvinatum	65	10	1,8,9,12,17	0.35	0.89	0.60	73.0	0.84	0.51	0.77
L.amplissima	77	10	1,8,9,12,17	0.32	0.85	0.49	39.9	0.84	0.44	0.52
L.pulmonaria	115	10	1,8,9,12,17	0.28	0.85	0.46	45.5	0.85	0.45	0.57
L.scrobiculata	108	10	1,8,9,12,17	0.32	0.87	0.50	39.3	0.86	0.49	0.66
N. resupinatum	41	10	1,8,9,12	0.63	0.94	0.76	100	0.81	0.58	0.85
N.laevigatum	100	10	1,8,9,12,17	0.34	0.88	0.49	41.4	0.87	0.47	0.32
N.parile	37	10	1,8,9	0.40	0.85	0.59	51.2	0.79	0.53	0.95
P.canina	123	10	1,8,9,12,17	0.22	0.79	0.38	35.4	0.84	0.47	0.62
P.collina	114	10	1,8,9,12,17	0.40	0.90	0.58	48.6	0.90	0.59	0.58
P.elisabethae	31	10	1,9,17	0.65	0.97	0.77	74.8	0.94	0.72	0.89
P.horizontalis	68	10	1,8,9,12,17	0.36	0.88	0.55	55.9	0.89	0.6	0.71
P.hymenina	26	10	8,12	0.46	0.90	0.64	49.7	0.86	0.61	0.78
P.leucophlebia	23	10	1,17	0.47	0.91	0.64	56.8	0.92	0.59	0.89
P.membranacea	62	10	1,8,9,12,17	0.51	0.93	0.68	54.1	0.89	0.69	0.78
P.monticola	26	1	1,8	0.37	0.90	0.61	49.8	0.88	0.63	0.65
P.neckeri	99	10	1,8,9,12,17	0.22	0.80	0.42	28.8	0.81	0.44	0.93
P.polydactylon	38	10	1,8,12	0.24	0.81	0.44	25.1	0.78	0.40	0.56
P.praetextata	159	10	1,8,9,12,17	0.26	0.84	0.45	34.8	0.83	0.44	0.45
P.venosa	22	10	1,9	0.58	0.94	0.75	82.4	0.90	0.70	0.87
P.paramerae	21	1	1,17	0.36	0.90	0.54	39.4	0.89	0.57	0.88
P.imbecillum	32	1	1,17	0.19	0.80	0.38	23.0	0.76	0.40	**0.00**
P.lusitanica	20	1	1,9	0.32	0.84	0.45	33.1	0.84	0.46	**0.00**
S.holophaea	21	10	1,12	0.36	0.80	0.79	39	0.88	0.76	0.81
S.saccata	40	10	1,8,9,12	0.40	0.89	0.55	47.7	0.87	0.59	0.72
S.omphalarioides	20	1	9,12	0.31	0.81	0.44	33.1	0.77	0.48	0.89
S.fuliginosa	41	10	1,8,9,12	0.32	0.85	0.44	53.5	0.81	0.44	0.64
T.chrysophthalmus	58	1	1,8,9,12,17	0.29	0.82	0.41	39.0	0.81	0.40	0.50
W.adscenderes	24	1	8,17	0.65	0.94	0.72	74.6	0.94	0.72	0.95

Table 3: Climatic variables values for present conditions. List of codes, resolution (Km2), variable description (unit), mean value ± standard deviation and range (minimum-maximum value).

Code	Resolution (Km^2)	Variable description (unit)	Mean±sd	Range
BIO1_1	1	Annual mean temperature (ºC)	13.89±2.75	1.23;19.21
BIO8_1	1	Mean temperature of the wettest quarter of the year (ºC)	10.18±3.59	-2.01;22.3
BIO9_1	1	Mean temperature of the driest quarter of the year (ºC)	20.29±5.66	-5.46;26.59
BIO12_1	1	Annual precipitation (mm)	742.20±315.95	157.60;210.9
BIO17_1	1	Precipitation of the driest quarter of the year (mm)	79.67±48.64	1.60;334.2
BIO1_10	10	Annual mean temperature (ºC)	13.33±2.77	1.95;19.17
BIO8_10	10	Mean temperature of the wettest quarter of the year (ºC)	9.57±3.59	-1.18;20.88
BIO9_10	10	Mean temperature of the driest quarter of the year (ºC)	19.68±5.68	-4.62;26.38
BIO12_10	10	Annual precipitation (mm)	789.3±320.67	200.30;2372.60
BIO17_10	10	Precipitation of the driest quarter of the year (mm)	88.65±50.59	6.95;350.89

Table 4: Climatic variables values for future conditions (2080) according to A1B scenario and different Regional climate models (RCMs): HadRM3 / HIRHAM3 / RACMO2. List of codes, resolution (Km2), variable description (unit), mean value ± standard deviation and range (minimum-maximum value).

Code	Resolution (Km^2)	RCM	Variable description (unit)	Mean±sd	Range
BIO1_1	1	HIRHAM3	Annual mean temperature (ºC)	16.05±2.74	2.56;22.1
BIO8_1	1	HIRHAM3	Mean temperature of the wettest quarter of the year (ºC)	11.77±4.33	-4.13;28.22
BIO9_1	1	HIRHAM3	Mean temperature of the driest quarter of the year (ºC)	23.46±4.94	-4.02;30.83
BIO12_1	1	HIRHAM3	Annual precipitation (mm)	625.30±29.27	136.20;2545.00
BIO17_1	1	HIRHAM3	Precipitation of the driest quarter of the year (mm)	46.40±3.90	0.00;305.40
BIO1_10	10	HIRHAM3	Annual mean temperature (ºC)	16.09±2.75	4.17;21.54
BIO8_10	10	HIRHAM3	Mean temperature of the wettest quarter of the year (ºC)	11.91±4.27	-1.27;27.18
BIO9_10	10	HIRHAM3	Mean temperature of the driest quarter of the year (ºC)	23.43±4.83	-2.92;29.96
BIO12_10	10	HIRHAM3	Annual precipitation (mm)	634.50±29.52	186.00;2008.00
BIO17_10	10	HIRHAM3	Precipitation of the driest quarter of the year (mm)	47.779±3.98	0-256.50
BIO1_1	1	RACMO2	Annual mean temperature (ºC)	16.25±2.74	1.71;22.33
BIO8_1	1	RACMO2	Mean temperature of the wettest quarter of the year (ºC)	9.60±3.32	-4.23;26.64
BIO9_1	1	RACMO2	Mean temperature of the driest quarter of the year (ºC)	24.66±5.01	-3.14;31.98
BIO12_1	1	RACMO2	Annual precipitation (mm)	602.60±29.50	98.22;2606.00
BIO17_1	1	RACMO2	Precipitation of the driest quarter of the year (mm)	52.08±4.64	0.80;399.70
BIO1_10	10	RACMO2	Annual mean temperature (ºC)	16.28±2.77	4.29;21.44
BIO8_10	10	RACMO2	Mean temperature of the wettest quarter of the year (ºC)	9.72±3.26	-1.45;23.48
BIO9_10	10	RACMO2	Mean temperature of the driest quarter of the year (ºC)	24.59±4.93	-0.60;31.00
BIO12_10	10	RACMO2	Annual precipitation (mm)	609.00±29.99	149.30;2109.00
BIO17_10	10	RACMO2	Precipitation of the driest quarter of the year (mm)	52.77±4.80	1.76-339.70
BIO1_1	1	HadRM3	Annual mean temperature (ºC)	16.79±2.68	2.28;22.74
BIO8_1	1	HadRM3	Mean temperature of the wettest quarter of the year (ºC)	11.07±3.45	-2.96;24.13
BIO9_1	1	HadRM3	Mean temperature of the driest quarter of the year (ºC)	24.87±6.11	-3.87;31.58
BIO12_1	1	HadRM3	Annual precipitation (mm)	615.00±27.23	87.17;2324.00
BIO17_1	1	HadRM3	Precipitation of the driest quarter of the year (mm)	50.69±4.09	0.76;276.00
BIO1_10	10	HadRM3	Annual mean temperature (ºC)	16.82±2.68	5.09;21.99
BIO8_10	10	HadRM3	Mean temperature of the wettest quarter of the year (ºC)	11.19±3.33	-0.54;20.88
BIO9_10	10	HadRM3	Mean temperature of the driest quarter of the year (ºC)	24.81±6.03	-1.49;30.83
BIO12_10	10	HadRM3	Annual precipitation (mm)	622.30±27.60	187.70;2073.00
BIO17_10	10	HadRM3	Precipitation of the driest quarter of the year (mm)	51.52±4.22	4.89-238.10

Appendix, Table 5: Species traits for the studied species. Functional traits: Thallus size: mean diameter of the adult tallus: S=small, L=large; growth form: biotype or growing form of the thallus: C=crustose, S=squamulose, Fr=fruticose, Fo=foliose; photobiont type: primary photobiont present in the species: G=green-algae, C=cyanobacteria; reproduction: main reproductive strategy: S= sexual, A=asexual, B=both. Ecological attributes: current distribution: Km^2 of suitable climatic area under current conditions (likelihood>70%); rarity: F=frequent species in the study area, F= rare species in the study area; specificity: specificity to the substrate: s= specific g=generalist; substratum type: main substrate where the species grows on: E=epiphyte, T=terricolous, S=saxicolous.

	Functional traits				Ecological attributes			
Species	Thallus size	Growth form	Photobiont type	Reproduction type	Current distribution	Rarity	Specificity	Substratum type
B.cedricola	S	C	G	S	14159	R	S	E
C.glaucellum	S	C	G	S	8300	F	S	E
C.cinereum	S	S	G	S	11111	F	G	T
C.daedaleum	S	S	G	S	22396	R	S	T
C.crespoae	S	Fr	G	S	22684	R	S	E
C.chrysocephala	S	C	G	S	49127	F	S	E
C.mediterranea	S	Fr	G	A	18336	R	S	T
D.ceratoniae	S	C	G	S	8610	R	S	E
F.ignobilis	S	S	C	S	22297	R	S	E
K.biformis	S	Fo	C	B	15184	R	S	E
L.aragonii	S	Fo	C	S	24105	F	G	S
L.lichenoides	L	Fo	C	B	25196	F	G	S
L.furfuraceum	S	Fo	C	A	45735	R	S	E
L.pulvinatum	S	Fo	C	S	22100	F	G	T
L.amplissima	L	Fo	C	S	16700	F	S	E
L.pulmonaria	L	Fo	G	B	17500	F	S	E
L.scrobiculata	L	Fo	C	B	19800	F	G	E
N.laevigatum	L	Fo	C	S	24800	F	G	E
N.parile	L	Fo	C	A	17000	R	G	E
N.resupinatum	L	Fo	C	S	30800	F	G	E
P.canina	L	Fo	C	S	20600	F	G	T
P.collina	L	Fo	C	B	30800	F	G	E
P.elisabethae	L	Fo	C	A	24300	F	S	T
P.horizontalis	L	Fo	C	S	22900	R	G	E
P.hymenina	L	Fo	C	S	21300	F	S	T
P.leucophlebia	L	Fo	G	S	19400	R	S	T
P.membranacea	L	Fo	C	S	30300	F	S	T
P.monticola	L	Fo	C	S	22329	F	S	T
P.neckeri	L	Fo	C	S	14100	F	G	T
P.polydactylon	L	Fo	C	S	12800	F	G	T
P.praetextata	L	Fo	C	B	21400	F	G	T
P.venosa	L	Fo	G	S	17400	R	S	T
P.paramerae	S	C	G	S	42820	F	S	E
P.imbecillum	S	S	G	S	7716	F	S	T
P.lusitaica	S	C	G	S	14159	R	S	E
S.holophaea	S	S	G	S	9900	R	S	S
S.saccata	L	Fo	C	S	28200	F	S	T
S.omphalarioides	S	Fo	C	S	5440	R	S	E
S.fuliginosa	L	Fo	C	A	16600	R	G	E
T.chrysophthalmus	S	Fr	G	S	9604	F	S	E
W.adscendens	S	S	G	B	14159	F	S	E

BLOQUE II:

ENFOQUE MONOESPECÍFICO A MICROESCALA

CAPÍTULOS 3, 4 Y5

Capítulo 3

Capítulo 3

Microhabitat selection by the epiphytic lichen *Lobaria pulmonaria*: the host tree species does matter

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Abstract

Detailed knowledge of the habitat requirements of species is required because it greatly affects the demographic rates and the persistence of species. In this study, we investigated the effects of microhabitat heterogeneity on the population dynamics of the locally threatened lichen *Lobaria pulmonaria*. We studied four *L. pulmonaria* populations in Central Spain and collected microhabitat data for individuals growing on beech and oak. The microhabitat affected the life stages of *L. pulmonaria.* The host tree species was a main driver, causing different patterns of population dynamics. Reproduction started earlier on oak where the recruitment was higher and viability poorer. By contrast, beech provided a more stable habitat where *L. pulmonaria* populations exhibited a delay in reproduction and healthier and larger individuals. These responses to microhabitat heterogeneity must be considered when developing conservation strategies for this species, ensuring a suitable habitat for colonization, recruitment and for the long-term maintenance.

Key words: Epiphyte; Central Spain; host tree; *Lobaria pulmonaria*; Mediterranean Region; population dynamics; population structure

Introduction

In conservation biology, the first step toward conserving species is to identify the underlying mechanisms that determine the distribution patterns and abundance of a species. Therefore, an efficient conservation initiative demands detailed knowledge about species-specific habitat requirements (Ranius, 2002). To determine the performance of a species, it is necessary to identify the important habitat characteristics and the spatial scale at which they operate. These characteristics affect the abundance of the species while habitat factors will determine population growth rate and persistence.

Several studies of plants have shown that microhabitat heterogeneity at a fine scale, i.e., microhabitat heterogeneity, may affect the plant demography by influencing the plant size, competition, population size, and/or genetic structure (e.g. Albert et al., 2001). Predictions of population persistence require an understanding of environmental patterns, including how plant population dynamics respond to microhabitat heterogeneity and how it can affect reproductive success.

Lichens function as sensitive indicators of environmental changes (e.g. Belinchón et al., 2009; Jüriado et al., 2012). In particular, epiphytic lichens are functional components of forest ecosystems (Sillet et al., 2000, Edman et al., 2008), contributing to nutrient cycles and providing food and habitats for animals, while they also represent a major part of the species diversity (Sillet et al., 2000). Many lichens are facing major threats to their conservation. The general lack of ecological knowledge about lichen population dynamics prevents a better understanding of the occurrence of lichens.

Most studies of lichens define the habitat quality based on the environmental factors that determine the presence or abundance of a species (Scheidegger and Werth, 2009; Belinchón et al., 2011). However, little is known about the habitat requirements for individual establishment, growth, and reproduction (see Hilmo et al., 2011). Many epiphytic lichens can grow on various tree species with different properties. Lichens, especially species confined to old-growth forests, are sensitive to habitat change (Belinchón et al., 2009, 2011; Otálora et al., 2011) and respond to minor differences in the habitat structure or specialized microhabitats (Jüriado et al., 2011, 2012). Thus, finer resolution habitat studies are required to understand the habitat components that affect the selection of sites, as well habitat-specific establishment, growth, and reproductive capacity.

Lobaria pulmonaria (L.) Hoffm. is a widespread epiphytic lichen frequently used as a model organism in ecological studies (Gu et al., 2001; Snäll et al., 2005; Werth et al., 2007; Belinchón et al., 2009, 2011; Jüriado et al., 2012; Martínez et al., 2012). *Lobaria pulmonaria* can colonize many tree species and it is also possible to find *L. pulmonaria* individuals on rocks (Istomina, 1996; Burgaz and Martínez, 2003). It is susceptible to changes in forest habitats (e.g., Gauslaa et al., 2006a; Edman et al., 2008) and has been described as an indicator species in high ecological continuity forests (Rose, 1976). *Lobaria pulmonaria* is declining and is considered endangered in many parts of Europe (Gärdenfors, 2010).

Previous studies have shown that the presence, cover, establishment, and growth of *L. pulmonaria* are affected greatly by the forest (Snäll et al., 2004; Belinchón et al., 2009; Martínez et al., 2012) and tree characteristics (Belinchón et al., 2009, 2011; Hilmo et al., 2011). This lichen species is presumably more limited by the habitat quality than by its dispersal ability (Gu et al., 2001; Öckinger et al., 2005; Werth et al., 2007; Belinchón et al., 2009).

However, little is known about the variables that affect the different life stages of *L. pulmonaria* populations and the stages that limit population development as a possible bottleneck (Sillet et al., 2000). Thus, we evaluated the microhabitat characteristics of *L. pulmonaria* throughout its life cycle in Mediterranean forests. Our general hypothesis was that the host tree species, its characteristics and lichen position on it would be the main factors controlling the performance of *Lobaria pulmonaria*. We hypothesized that *L. pulmonaria* individuals would have tree-specific patterns of establishment, growth, reproductive capacity, and viability. Our specific objectives were as follows.

1. To compare the abundance and probability of occurrence of *L. pulmonaria* on two host tree species.

2. To evaluate the effects of host tree species on population structure.

3. To identify the microhabitat factors that affect the reproductive capacity and viability of *L. pulmonaria* individuals.

Materials and methods

Study area and data collection

The study was carried out in the Sistema Central Range in the Iberian Peninsula, including the Sierra de Ayllón and Sierra del Rincón. The climate is typically Mediterranean and is characterized by a drought period in the summer (an average of 1.8 months).

The field work was carried out in two different habitats: *Fagus sylvatica* L. mixed forests and *Quercus pyrenaica* Willd. forests. *Fagus sylvatica* (beech) is a deciduous tree that is widespread throughout Western Europe and one of its southernmost distribution limits was in the study area, usually mixed with other tree species. *Quercus pyrenaica* is a semideciduous oak, which is virtually endemic in the Iberian Peninsula. In this study, we designated “beech forests” as forests with >60% *F. sylvatica* trees, which were accompanied mainly by *Q. pyrenaica* and minor proportions (<10%) of other woody plants such as *Ilex aquifolium* L., *Crataegus monogyna* Jacq., or *Sorbus aucuparia* L. We designated “oak forests” as forests that were composed mainly of *Q. pyrenaica* trees with low percentages of other trees and bushes (<10% of species such as *Crataegus monogyna* or *Prunus spp*.).

We used four square plots, with two in each type of forest. (See supplementary material S1 and S2).

A total of 1460 trees were recorded in all of the plots. Only oak and beech were considered for further analysis, as the other recorded tree species represented only a small proportion of the data (<10% of the trees and <2.3% of the *L. pulmonaria* individuals). Finally, 1315 trees were included in the models: 840 oak (57%) and 475 beech (32%). We recorded variables at the tree and *L. pulmonaria* individual level. At the tree level we considered: the host tree species (*F. sylvatica* or *Q. pyrenaica*); the diameter of the trunk measured at the base and at 1.3 m; the roughness of the bark (the depths of the cracks were measured using a digital caliper); the percentage cover of bryophytes on the trunk based on two strips, i.e., from the ground to 1 m (lower strip) and from 1 m to 2 m (upper strip) (Table 1).

Table 1 List of variables recorded at the tree and individual level, and the codes used. An asterisk (*) indicates a variable excluded from the models because of a high correlation level.

Tree level	Code	Individual level	Code
Tree species	Sp	Maximum thallus diameter (mm)	Size
*Diameter at the tree base (cm)	DBB	Height in the tree (cm)	Height
Tree diameter at breast height (cm)	DBH	Exposure aspect on the tree (°)	Or
Roughness of the bark (mm)	Roughness	Attachment site: bark/bryophyte/lichen	EPI(C/B/L)
Bryophyte cover on:			
Lower strip of the trunk (%)	BL		
Upper strip of the trunk (%)	BH		

Every *L. pulmonaria* individual ≥2 mm in diameter was considered. It is not trivial to define a *L. pulmonaria* “individual” because a single thallus may be formed by several lobes that have grown together. In this case, we defined an individual as a single lobe or a group of lobes, which were spatially differentiated from each other.

At the individual level we recorded the following variables: the longest diameter of the thallus (to estimate the individual size); the presence (1) or absence (0) of sexual reproduction (apothecia); and the presence of asexual structures (isidia and soredia) estimated as % of cover of the thallus surface by the same person. Juvenile individuals as those with no reproductive structures. We also ranked each individual's health status as unhealthy or healthy, as a proxy of their individual viability. Unhealthy individuals had a high proportion of bleached areas, grazed areas, and/or the presence of parasites (i.e., *Plectocarpon lichenum* (Sommerf.) D. Hawksw.). Three variables were recorded to specify the individual microhabitat: the height from the ground (from 0 to 200 cm, to the nearest cm); exposure aspect on the trunk (0–359°, to the nearest degree); and the type of growth substrate, i.e., bark, bryophytes, or other lichens (Table 1).

Data analysis

We excluded variables with correlation values >0.7 to avoid problems of multicollinearity (See Supplementary Material, S2).

Global models

The individual size was used as a response variable to test the effects of environmental variables and it was also used as an explanatory predictor to assess the effect of individual size on the existence of reproductive structures. We identified the variables driving *L. pulmonaria* behavior by fitting generalized linear mixed models (GLMM) using the SAS Macro program, which iteratively calls the SAS Procedure MIXED until convergence (GLIMMIX ver. 8 for SAS/STAT; available at http://ftp.sas.com/techsup/download/stat/). This modeling approach was used because our data had an unbalanced and hierarchical structure where individuals were nested within trees and trees were nested within plots. A hierarchical data structure implies a correlation between data points at different scales. This correlation inflates the degrees of freedom, thereby increasing the chance of making a type I error. To overcome these problems, we analyzed the data using a multilevel approach where we considered trees and plots as random factors, and applied mixed modeling as necessary (Verbeke and Molenberghs, 1997).

Beech and oak are suitable host trees for *L. pulmonaria* so we previously tested two different model extensions. First, we modeled the occurrence and abundance of *L. pulmonaria*, as well as the abundance of juveniles and reproductive individuals per tree. The explanatory variables were: species (Sp), diameter at breast height (DBH), DBH*Sp (the interaction between both variables), roughness, bryophyte cover on the lower trunk (BL), and bryophyte cover on the upper trunk (BH) (Table 1). Second, we modeled the size, the presence of apothecia, the presence of asexual structures, the presence and abundance of soredia and isidia, and the health status of the individuals studied. In these models, the explanatory variables were: Sp, size (only for reproductive structures and health status), DBH, height above ground (Height), the exposure aspect (Or), roughness, the attachment site (EPI), BL, and BH (Table 1).

Specific models

The results of the global models indicated that the tree species was highly significant so we analyzed the data by differentiating between beech models and oak models to detect the different performances of *L. pulmonaria.*

For the presence of *L. pulmonaria*, we fitted GLMM models using a binomial estimation and the “logit” link function with “plot” as a random factor. Similarly, we fitted a mixed model to describe *L. pulmonaria* abundance, the abundance of juveniles, and the abundance of reproductive individuals. We also selected “plot” as a random factor and used the “log” link function with a Poisson distribution.

For the “individual size” models, we performed a log-transformation for “size” because its distribution was biased strongly toward very small sizes. In the GLIMMIX model, “tree” was nested in “plot” (random factors). “Normal” distribution and the link function “identity” were used.

The relationship between size, the probability of reproduction, and being unhealthy

In the “apothecia presence” models, “plot” was not a random factor because we purposely selected two plots containing individuals with apothecia and two without them. Thus, “tree” was the only random factor. The distribution of the variable was “binomial” and the link function was “logit.”

The other models explained the factors with effects on asexual reproductive structures, i.e., the presence and abundance of soredia, isidia, and both structures together, and the presence of unhealthy individuals. In all of the models, “tree” was nested in “plot” and both were random factors. In these models, the distribution of the response variables was “binomial” and the link function was “logit.”

To estimate the probability curves for each reproductive structure relative to the individual size, we constructed generalized linear models (GENMOD SAS v. 9). In the same way, we calculated a probability curve for unhealthy status. We analyzed the three reproductive structures, i.e., apothecia, soredia, and isidia. The significance of each predictor was estimated using a deviance test (Guisan et al. 2002). “Binomial” distribution and “logit” link function were assumed for the response variable.

The relationship between the probability of being reproductive *(p)* and individual size can be quantified using a logistic regression (Wesselingh et al., 1997), according to the formula:

$$p = \frac{1}{1+\exp(\mu+ax)}$$

where the parameters μ and α determine the intercept with the *x*-axis and the slope of the curve, respectively. They may be related to the threshold size for reproduction (Méndez and Karlsson, 2004) or the development of unhealthy symptoms.

Results

Descriptive data

We recorded 10918 *L. pulmonaria* individuals growing on oak and 2760 on beech, whereas the percentage of occupied trees was higher in the beech. However, the occupied oaks hosted a higher number of individuals. On both tree species, *L. pulmonaria* presence was favored by larger tree diameter, greater bark roughness, and a higher abundance of bryophytes (See Supplementary material, S3).

The mean size of *L. pulmonaria* individuals was 107.16 ± 135.65 mm, with a range of 2–2220 mm in diameter. A comparison between the tree species showed that the mean individual size was higher on beech (Supplementary material, S3). *Lobaria pulmonaria* grew mainly on northerly exposed surfaces in both host species, on the lower trunk, and preferentially on the bark (Supplementary material, S4). The individual size differed depended on the growth substrate. The mean size of individuals that grew on bark was larger than those that grew on bryophytes. The analysis of the reproductive capacity showed that over half of the total individuals were juvenile, with a slightly higher proportion on beech. Most of the reproductive individuals exhibited asexual reproduction. Only a small number exhibited sexual reproduction, which was slightly higher on oak. Unhealthy individuals were more abundant on oak than beech (Supplementary material, S3).

As population structure is a difficult measure to assess we will therefore be limited to size distribution. Figure 1 clearly shows that both trees host populations skewed to small individuals. But the skewness is much more marked on oaks. Very big individuals can be found in both populations, but represent a greater proportion of the population on beech.

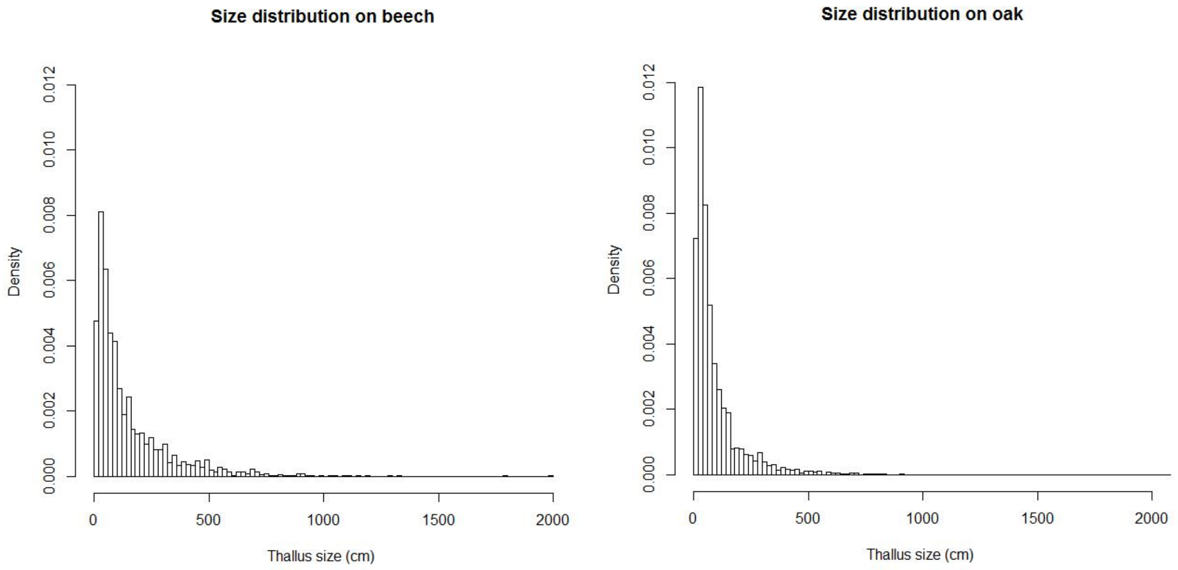


Fig. 1 Size distribution of *Lobaria pulmonaria* populations per host tree. X-axis: individual size as maximum diameter (mm), y-axis: density (0-1).

Global models

GLIMMIX models constructed to explain the abundance and presence of *L. pulmonaria* individuals, as well as the abundance of juvenile and reproductive individuals (Table 2), showed that the tree species and the interaction between the tree species and tree diameter were significant in most cases.

Table 2. Summary of the generalized linear mixed models used to examine the effects of environmental factors on the occurrence and abundance of *Lobaria pulmonaria*, and on the abundance of juvenile and reproductive individuals.

Occurrence of *Lobaria pulmonaria*					**Abundance of *Lobaria pulmonaria***				
Fixed factors	*DF*	*Estimator*	*F-Value*	*P-value*	*Fixed Factors*	*DF*	*Estimator*	*F-Value*	*P-value*
Sp	91.1	–4.6539	8.28	0.005	Sp	1305	–2.0816	206.67	< 0.0001
DBH	1308	0.04639	18.94	< 0.0001	DBH	1305	0.008419	92.93	< 0.0001
					DBH*Sp	1305	0.009746	18.93	< 0.0001
					Roughness	1305	0.02986	11.86	0.0006
					BL	1305	0.004462	5.04	0.0249
Abundance of juveniles					**Abundance of reproductive individuals**				
Fixed factors	*DF*	*Estimator*	*F-Value*	*P-value*	*Fixed Factors*	*DF*	*Estimator*	*F-Value*	*P-value*
Sp	1306	–2.0467	135.57	< 0.0001	Sp	1305	–2.1757	217.71	< 0.0001
DBH	1306	0.009583	71.89	< 0.0001	DBH	1306	0.006378	75.55	< 0.0001
DBH*Sp	1305	0.008182	9.95	0.0016	DBH*Sp	1305	0.01334	28.41	< 0.0001
Roughness	1305	0.03356	10.65	0.0011	BL	1305	0.00654	11.61	0.0007

Notes: Only significant factors are shown. The data are the Wald-type F-statistic (F-value), degrees of freedom (DF), coefficient of the variable in the model (Estimator), and the significance value (*P-value*). See Table 1 for the abbreviations of the variables.

The probability of the occurrence of *L. pulmonaria* was higher on larger trees (Table 2). The abundance was determined by the host species, the tree diameter, and the interaction of these two variables, as well as the bark roughness and the bryophyte cover on the lower strip on the tree (Table 2). The tree species and diameter (and their interaction) were also positively correlated with the abundance of juveniles and reproductive individuals. We also found that increased bark roughness correlated with the abundance of juvenile individuals, whereas the abundance of reproductive individuals was greater in trees with a higher bryophyte cover at the base. The random variable plot was not significant for any model (not shown).

The tree species was also a key factor that affected the individual size and the presence and abundance of reproductive structures (Supplementary material, S4 and S5). In this case, the random variable plot also had no significant effect, whereas the random variable tree had a significant effect in the model.

Specific models

The juvenile abundance was greater on larger trees with coarser bark, regardless of the tree species. However, the abundance of reproductive individuals on beech depended only on the tree diameter, while it was also favored by the bark roughness and low bryophyte cover at the tree base in oak (Table 3).

In the global model (Supplementary material, S4), a greater tree diameter favored the presence of larger individuals, but the variables that affected the size of *L. pulmonaria* size differed in the specific models (Table 4). In beech, larger tree diameter and a coarser bark were associated with increased individual size, whereas the exposure aspect of individuals on the tree and the microhabitat were significant factors in oak (Table 4). In both trees, the microhabitat was important: a northern exposure allowed *L. pulmonaria* to grow and reach a larger size. The height on the trunk was only significant in beech because larger individuals were located on the lowest parts of the trunk (Table 4). In addition, the type of growth substrate also had effects in both tree species.

A comparison of the per-tree-species models showed that fairly similar variables incluenced the presence and abundance of reproductive structures in both tree species (Tables 5 and 6). Individual thallus size always had a positive effect on reproduction (sexual and asexual) (Tables 5 and 6). Furthermore, microhabitat variables affected the development of reproductive structures. The height of individuals on the trunk had opposite effects on the reproductive types, i.e., individuals with apothecia were more abundant at the tree base, whereas the upper parts of the trunk favored the presence and abundance of soredia and isidia. In oak, however, the presence and abundance of isidia were modulated by height, whereas this effect was not observed in soredia. A northerly exposure appeared to have an important effect on the presence and abundance of reproductive structures, especially in beech where exposure was a significant factor in every model (Tables 5 and 6). However, the type of substrate also affected the reproductive type (Tables 5 and 6).

The individual viability linked to unhealthy symptoms differed in the two tree species (Table 7). In both cases, larger individuals were more likely to be unhealthy. Other factors linked to the microhabitat affected the *L. pulmonaria* population health because we found more unhealthy individuals on the lower parts of the trunk. In beech, bryophytes also promoted the unhealthy status of *L. pulmonaria* individuals, but only in those growing at <1 m (Table 7).

The random variable tree detected significant effect in all models, which suggests that many other factors at the tree level (not included in the models) were also responsible for the differences in the modeled variables.

Table 3. Summary of the generalized linear mixed models used to examine the effects of environmental factors on the abundance of juveniles and reproductive individuals of *L. pulmonaria* in separate models, depending on the host tree species, i.e., *Quercus pyrenaica* and *Fagus sylvatica*.

Abundance of juveniles on *Quercus pyrenaica*					**Abundance of juveniles on *Fagus sylvatica***				
Fixed factors	*DF*	*Estimator*	*F-Value*	*P-value*	*Fixed Factors*	*DF*	*Estimator*	*F-Value*	*P-value*
DBH	790	0.008537	12.79	0.0004	DBH	22.9	0.02076	65.40	< 0.0001
Roughness	789	0.03388	9.60	0.002	Roughness	457	0.1069	8.99	0.029
Abundance of reproductive individuals on *Quercus pyrenaica*					**Abundance of reproductive individuals on *Fagus sylvatica***				
Fixed factors	*DF*	*Estimator*	*F-Value*	*P-value*	*Fixed Factors*	*DF*	*Estimator*	*F-Value*	*P-value*
DBH	789	0.006106	9.90	0.0017	DBH	181	0.02085	42.73	< 0.0001
Roughness	789	0.02175	6.25	0.0126					
BL	789	–0.00602	14.21	0.0002					
BH	789	0.007227	5.98	0.0147					

Notes: Only the significant factors are shown. The data are the Wald-type F-statistic (F-value), degrees of freedom (DF), coefficient of the variable in the model (Estimator), and the significance value (*P-value*). See Table 1 for the abbreviations of the variables

Table 4 Summary of the generalized linear mixed models used to examine the effects of environmental factors on *Lobaria pulmonaria* individual size in separate models, depending on the host tree species, i.e., *Quercus pyrenaica* and *Fagus sylvatica*.

Individual size on *Quercus pyrenaica*				
Fixed factors	*DF*	*Estimator*	*F-Value*	*P-value*
Or	11000	0.07634	31.44	< 0.0001
EPI	11000	B > C > L	151.36	< 0.0001
Individual size on *Fagus sylvatica*				
Fixed factors	*DF*	*Estimator*	*F-Value*	*P-value*
DBH	164	0.003643	6.96	0.0091
Roughness	140	0.06389	11.38	0.001
Height	2730	–0.00175	17.77	< 0.0001
Or	2719	0.2036	41.95	< 0.0001
EPI	2724	C > B > L	72.66	< 0.0001

Notes: Only significant factors are shown. The data are the Wald-type F-statistic (F-value), degrees of freedom (DF), coefficient of the variable in the model (Estimator), and the significance value (P-value). See Table 1 for the abbreviations of the variables.

Table 5. Summary of the generalized linear mixed models used to examine the effects of different factors on the presence and abundance of reproductive structures on *Fagus sylvatica*.

Apothecia presence					**Asexual presence**				
Fixed factors	*DF*	*Estimator*	*F-Value*	*P-value*	*Fixed factors*	*DF*	*Estimator*	*F-Value*	*P-value*
Size	2715	2.0895	329.77	< 0.0001	Size	2715	2.2163	599.23	< 0.0001
Height	2715	–0.01151	35.51	< 0.0001	EPI	2699	C > L > B	6.47	0.0016
Or	2742	0.7340	27.05	< 0.0001	Or	2644	0.2939	8.97	0.0028
Soredia presence					**Soredia abundance**				
Fixed factors	*DF*	*Estimator*	*F-Value*	*P-value*	*Fixed factors*	*DF*	*Estimator*	*F-Value*	*P-value*
Size	2733	2.2161	504.67	< 0.0001	Size	2727	1.1317	1013.98	< 0.0001
Or	2526	0.3112	8.61	0.0034	Or	2647	0.2080	16.61	< 0.0001
Epi	2610	C > L > B	6.07	0.0024	EPI	2720	C > L > B	14.58	< 0.0001
					Height	2626	0.001442	5.46	0.0195
Isidia presence					**Isidia abundance**				
Fixed factors	*DF*	*Estimator*	*F-Value*	*P-value*	*Fixed factors*	*DF*	*Estimator*	*F-Value*	*P-value*
Size	2713	1.4725	392.17	< 0.0001	Size	2722	1.1912	495.82	< 0.0001
Height	1856	0.004198	12.94	0.0003	Height	2736	0.002097	5.27	0.0218
Or	2640	0.3375	11.75	0.0006	Or	2751	0.3291	17.09	< 0.0001
EPI	2741	C > L > B	6.16	0.0022	EPI	2745	L > C > B	5.59	0.0026

Notes: Only significant factors are shown. The data are the Wald-type F-statistic (F-value), degrees of freedom (DF), coefficient of the variable in the model (Estimator), and the significance value (P-value). See Table 1 for the abbreviations of the variables

Table 6. Summary of the generalized linear mixed models used to examine the effects of different factors on the presence and abundance of reproductive structures on *Quercus pyrenaica*.

Apothecia presence					**Asexual presence**				
Fixed factors	*DF*	*Estimator*	*F-Value*	*P-value*	*Fixed factors*	*DF*	*Estimator*	*F-Value*	*P-value*
Size	10400	2.1158	1181.90	< 0.0001	Size	11300	2.0848	2277.75	< 0.0001
Height	9570	–0.00287	10.78	0.0010	Or	11300	0.1789	18.18	< 0.0001
EPI	1400	L > C > B	6.45	0.0016	EPI	11300	C > B > L	83.73	< 0.0001
Soredia presence					**Soredia abundance**				
Fixed factors	*DF*	*Estimator*	*F-Value*	*P-value*	*Fixed factors*	*DF*	*Estimator*	*F-Value*	*P-value*
Size	11300	2.1074	2266.06	< 0.0001	Size	11300	0.9963	3148.35	< 0.0001
Or	11300	0.2076	23.69	< 0.0001	Or	11300	0.1847	59.79	< 0.0001
Epi	11300	C > L > B	58.02	< 0.0001	Epi	11300	C > L > B	62.84	< 0.0001
					BL	282	0.007310	5.28	0.0223
					BH	290	–0.00840	4.11	0.0435
Isidia presence					**Isidia abundance**				
Fixed factors	*DF*	*Estimator*	*F-Value*	*P-value*	*Fixed factors*	*DF*	*Estimator*	*F-Value*	*P-value*
Size	11300	1.4530	1736.69	< 0.0001	Size	11300	1.0882	1769.40	< 0.0001
Height	11300	0.003535	37.92	< 0.0001	Height	11300	0.005060	126.7	< 0.0001
EPI	11300	C > B > L	49.43	< 0.0001	EPI	11300	C > B > L	40.14	< 0.0001

Only significant factors are shown. The data are the Wald-type F-statistic (F-value), degrees of freedom (DF), coefficient of the variable in the model (Estimator), and the significance value (P-value). See Table 1 for the abbreviations of the variables.

Table 7. Summary of the generalized linear mixed models used to examine the effects of different variables on the health status of *Lobaria pulmonaria* on *Quercus pyrenaica* and *Fagus sylvatica.*

Unhealthy individuals on *Fagus sylvatica*

Fixed factors	*DF*	*Estimator*	*F-Value*	*P-value*
Size	2685	0.8786	263.95	< 0.0001
Height	2708	–0.00316	9.48	0.0021
Or	2699	0.1573	3.91	0.0482
EPI	2657	C>B>L	18.63	< 0.0001
BL	224	0.03465	12.24	0.0006
BH	276	–0.03843	9.07	0.0028

Unhealthy individuals on *Quercus pyrenaica*

Fixed factors	*DF*	*Estimator*	*F-Value*	*P-value*
Size	11300	0.8502	388.17	< 0.0001
Height	11300	–0.00264	10.76	0.0010
EPI	11300	C > L > B	15.26	< 0.0001

Notes: Only significant factors are shown. The data are the Wald-type F-statistic (F-value), degrees of freedom (DF), coefficient of the variable in the model (Estimator), and the significance value (P-value). See Table 1 for the abbreviations of the variables.

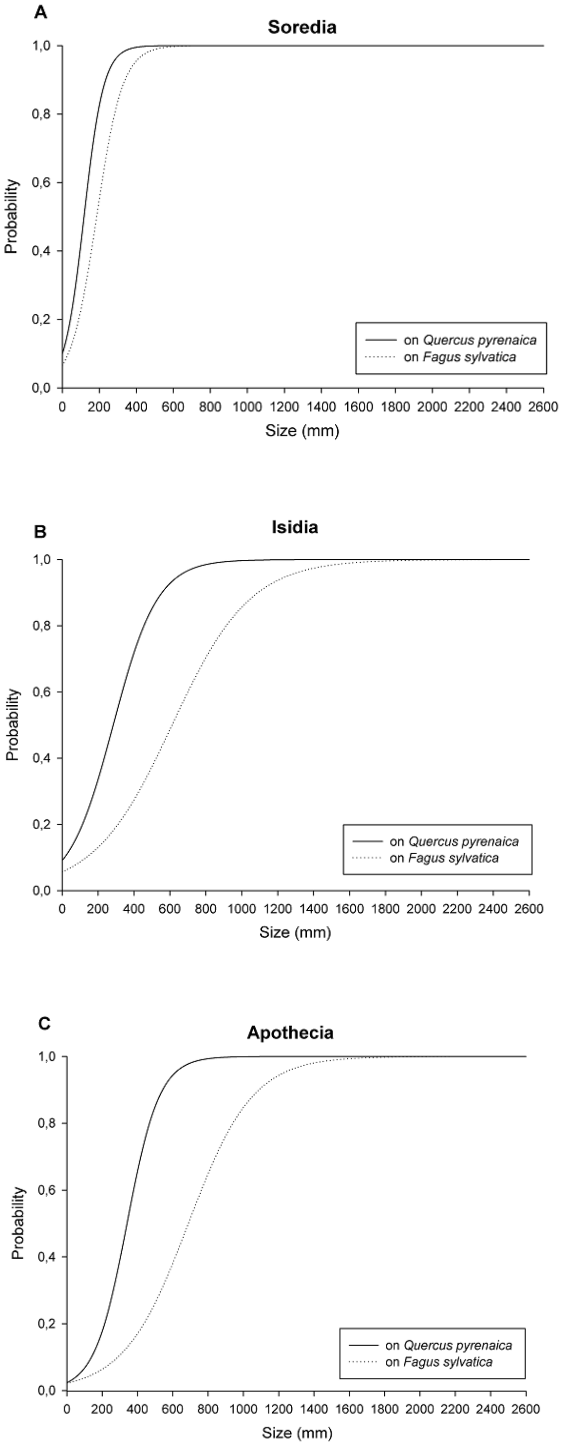
Relationships between size, the probability of reproduction, and being unhealthy

All of the logistic models used to analyze the relationships between individual size, reproductive capacity, and health status were highly significant (size: $p < 0.0001$ in all models). The tree species was a key factor for reproduction and health in *L. pulmonaria*, although only the species-specific curves are shown (Fig. 2).

The probability of a reproductive structure being present at a given individual size is shown in Fig. 2. The curves were different for oak and beech. Size-dependence pattern was common, but the threshold size for the development of reproductive structures was much smaller in individuals on oak for all types of reproduction. For example, with a tree diameter of 350 mm , an individual had a 50% probability of developing apothecia if it was growing on oak, whereas it needed to be almost twice that size (690 mm) to have the same probability on beech Supplementary material, S6).

The probability of an individual being unhealthy increased with thallus size, ($p <$ 0.0001). Once again, *L. pulmonaria* performed differently on oak and beech (Fig. 3). On oak, an individual had a 50% probability of being unhealthy when it measured 41 mm, whereas on beech, viability was not reduced to 50% before size of 271mm (Supplementary material, S6).

Fig. 2 Reproductive probability of *Lobaria pulmonaria* relative to individual size. A: Presence of soredia. *x*-axis: thallus size (mm); *y*-axis: sexual reproduction (by apothecia) probability. B: Presence of isidia. *x*-axis: thallus size (mm); *y*-axis: asexual reproduction (by isidia) probability. C: Presence of apothecia. *x*-axis: thallus size (mm); *y*-axis: sexual reproduction (by apothecia) probability.



Discussion

The host tree species and microhabitat heterogeneity affected the performance of *L. pulmonaria* individuals in the study Mediterranean forests. We observed different patterns of establishment, size, reproductive capacity, and health status on the two tree species. These different patterns may be decisive for the mid- and long-term survival of this lichen species, leading to different population viability and vulnerability.

Species occurrence and abundance

The occurrence and abundance of *L. pulmonaria* individuals were driven mainly by the host tree species and tree diameter, and both were important variables related to the habitat quality for this species. Occupied oaks had a greater abundance of *L. pulmonaria* than beech, as well as smaller individuals, which suggested a higher success in their colonization and establishment on oak, probably due to coarser bark. Short-distance dispersing propagules are more likely to be retained in the cracks and crevices of trees with rougher bark, such as oak, even when they are young (Belinchón et al., 2009; Scheidegger and Werth, 2009). Although *L. pulmonaria* was linked to a large diameter in both host tree species, it required a greater diameter in beech than oak, probably because beech need to reach a larger size to provide *L.pulmonaria* a good habitat, i.e. a coarse bark.

Occurrence and abundance results are consistent with previous studies at landscape scales and they reflect the importance of habitat quality for this species (Gu et al., 2001; Öckinger et al., 2005; Werth et al., 2007; Edman et al., 2008; Belinchón et al., 2009, 2011; Jüriado et al., 2011, 2012). Öckinger et al. (2005) found that *L. pulmonaria* occupied larger trees with a greater cover of bryophytes than unoccupied trees with a similar size. Many studies have shown that the tree diameter is an important predictor of occupancy by *L. pulmonaria* (Gu et al., 2001; Öckinger et al., 2005; Snäll et al., 2005; Edman et al., 2008; Belinchón et al., 2009, 2011). Larger trees have been available for colonization for longer periods while they also provide a larger and more suitable surface, including bark roughness, moisture, and nutrient conditions (Snäll et al., 2003). Furthermore, Gustafsson and Eriksson (1995) indicated that the bark chemistry of large, old trees often differed from that of younger and smaller trees, which may facilitate lichen establishment.

In our study, bryophyte cover appeared to be a favorable habitat for colonization by new individuals; probably because they facilitate the attachment of dispersal propagules and provide a more humid microenvironment (Colesie et al. (2012) found similar results on a terricolous lichen). Sillet et al. (2000) indicated that tree species with as smooth bark as beech, such as *Betula papyrifera* or *Populus tremuloides*, were disadvantageous for colonization by macrolichens. They also noted that epiphytic mosses changed the bark surface, potentially affecting the establishment and growth of lichens. Mosses can store water, accumulate nutrients, and form a spongy surface, which could either promote or inhibit lichen establishment (Colesie et al., 2012).

Individual size

On beech, we found larger individuals on broader trees with coarser bark, a northerly exposure, and nearer to the ground. These microhabitat conditions are strongly related to water availability because they are positions where lichens will dry more slowly. However, in oak, the size depended only on the tree diameter. These results suggest that individuals growing on beech may have been more limited by the microhabitat conditions than those growing on oak.

The proportion of small individuals in the population shows recruitment on both trees, but shows higher rates of recruitment and / or early survival on oak. This is probably due to the rougher bark. Similarly, Öckinger and Nilsson (2010) showed that the establishment of new *L. pulmonaria* individuals was easier in certain tree species. But it might be also explained, at least partially, by the larger abundance of reproducing individuals on oak, and therefore, abundance of propagules.

Reproductive capacity

Less than half of the individuals present in our study area were reproductive. The abundance of reproductive individuals (asexual and sexual) on beech was affected only by the tree diameter, whereas larger oak with coarser bark and less bryophyte cover hosted more reproductive individuals. This appears to contradict the positive effect of bryophytes on colonization. However, the facilitative effects of bryophyte during colonization and establishment might turn into competition for resources when individuals become larger and start reproducing. Another possible explanation is that reproducing individuals are bigger and heavier so they detach more readily from mossy oak bark.

Sexual structures were present in <10%. Different authors suggest that the scarcity of fertile individuals is a common trend in different geographic regions. Denison (2003) indicated that the proportion of sexual thalli in *L. pulmonaria* populations was usually <25%. Zoller et al. (1999) and Walser et al. (2004) also suggest that asexual reproduction is the major strategy in *L. pulmonaria* populations. Different authors have noted that the presence of sexual reproduction in *L. pulmonaria* increases with the population size (Scheidegger et al., 1995; Edman et al., 2008; Öckinger and Nilsson, 2010). On beech, we found both smaller populations and lower percentage of fertile individuals. Because *L. pulmonaria* is a heterothallic species (Zoller et al., 1999; Walser et al., 2004; Singh et al., 2012), it is possible that in beech, the lower number of *L. pulmonaria* fertile individuals could be a consequence of the scarcity of suitable mating types for sexual reproduction, as suggested by Jüriado et al. (2011). Therefore, larger populations on oak are more likely to contain more genets and a higher probability of producing apothecia.

The analysis of sexual reproduction showed that the largest individuals had a higher probability of forming apothecia, which was tuned by the microhabitat conditions. Individuals growing near the ground more likely presented apothecia, whereas individuals growing in comparatively higher areas of the trees produced asexual structures with higher probability, mainly isidia. These results are highly consistent with those reported by Martínez et al. (2012) based on a study throughout the Iberian Peninsula. A northerly exposure was also favorable, mainly on beech trees. The water retention capacity is lower on beech trunks compared with oak trunks (Belinchón et al., 2009). Thus, *L. pulmonaria* individuals growing on beech require a greater amount of moisture so a northerly orientation facilitates the development of apothecia.

Another important point is that a minimum threshold size is required before the development of all reproductive structures (Larsson and Gauslaa, 2011; Martínez et al., 2012, but see Jackson et al., 2006). *Lobaria pulmonaria* develops its reproductive structures according to a sequence that is linked to its size, i.e., soredia, followed by isidia and apothecia (Deninson, 2003; Martínez et al., 2012). Although a threshold size is required, this minimum size is habitat-dependent, which was demonstrated by our results. The threshold size is driven significantly by the host tree species and also by the microhabitat conditions.

Various underlying causes or mechanisms might explain this phenomenon. The microhabitat conditions, which are slightly more stressful *a priori* on oak (Belinchón et al., 2009), might tune *L. pulmonaria* to an earlier reproductive status, thereby reducing its ongoing growth rate. However, the conditions that favor a high growth rate are not necessarily the optimal conditions (Gauslaa et al., 2006b), which might have been the case for beech in our study area. Reproductive *L. pulmonaria* individuals grow much more slowly (Larsson and Gauslaa, 2011; Gauslaa et al., 2012) compared with juvenile individuals. Individuals might grow for a longer period on beech because the microhabitat conditions do not allow them to become reproductive as early as they would on oak. This may mean that they invest greater resources in reaching a larger size. However, this response could also be a result of greater herbivory stress and the presence of lichenicolous fungi on oak.

Individual viability and health status

We considered that *L. pulmonaria* individuals were unhealthy if they were bleached, if they presented parasites, or if they exhibited signs of herbivory. Lichens are an important food source for many organisms and the effects of herbivory damage are well documented on lichens (Benesperi and Tretiach, 2004; Asplund and Wardle, 2013; Cornejo and Scheidegger, 2013).

We detected differences in health status of *L. pulmonaria* in the two host tree species, although larger individuals growing near the ground exhibited more damage, regardless of the tree species. We considered that the largest individuals were older so they had been exposed to grazers or pathogens for longer periods. Several studies have reported similar results, such as Benesperi and Tretiach (2004) who found that the intensity of snail damage on *Peltigera* species was correlated to the lichen size. However, Asplund and Gauslaa (2008) found that recently established juvenile *L. pulmonaria* individuals were particularly vulnerable to mollusk grazing because they had lower defensive compound concentrations. The proximity to the ground is also a risk factor in other *Lobaria* species (Asplund et al., 2010) because the grazing pressure and severity increases with the proximity to the ground and on bryophyte covered trunks (Gauslaa et al., 2006b).

On beech, also northern exposures promoted unhealthy signs. A location with a northerly exposure at the tree base, and with more bryophytes, implies higher humidity, so they are more favorable conditions for pathogens. Mollusks often have patchy distributions in forests, which depend on the microhabitat (Kleewein, 1999), and their grazing impact is usually higher in shady places with slower desiccation, i.e., ideal conditions for mollusk activity (Asplund and Gauslaa, 2008).

Lobaria pulmonaria performance main differences among host trees species

Oak were a more favorable habitat for colonization and recruitment, and established populations became larger, although they were biased toward a smaller size. Surprisingly, the mean sizes in the population were smaller, but individuals did reproduce because they did not needed to reach the same size as those found on beech to become reproductive. The bark roughness and higher frequency of unhealthy individuals on oak suggested that a greater incidence of grazers and parasites made them a “more unstable” habitat, which accelerated the life cycle.

Lobaria pulmonaria individuals might be more limited by the microhabitat conditions on beech. Older trees with greater diameters and coarser bark were required for *L. pulmonaria* establishment and the populations were not as large as those found on oak, which was due mainly to a longer generation time (Larsson and Gauslaa, 2011). However, *L. pulmonaria* individuals reached larger sizes and delayed their reproduction. The slow accumulation of *L. pulmonaria* on beech may be attributed to establishment limitation and to the time required to reach an appropriate size for reproduction. Beech provide a less favorable microhabitat for recruitment but an adequate microhabitat may be created if certain conditions are met (dense bryophyte cover and large trees), which facilitate the establishment of new individuals.

Conclusions

Lobaria pulmonaria responds strongly to variations in the habitat conditions at a fine scale because microhabitat heterogeneity affects all of its life stages. Of the variables addressed in the present study, the host tree species had the main effects while other microhabitat conditions, such as the height and exposure orientation on the trunk, the bark roughness, and bryophyte cover also affected the performance of *L. pulmonaria*. Thus, the different distribution patterns depended on the microhabitat characteristics, which must be taken into account when developing conservation strategies for this species. The relationships between the factors that affect *L. pulmonaria* can be understood better using integrated approaches. It is important to appreciate that the presence of a low number of reproductive individuals will limit the regeneration of a population while a high turnover of individuals due to an unstable habitat can also compromise the future of the population. Conservation strategies needs to consider all of these issues. We must ensure that suitable habitats are available (oak) that allow colonization by new individuals, but we must not forget the requirements for a suitable habitat that ensures the long-term maintenance of the population (beech).

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References

ALBERT M. J., A. ESCUDERO AND J.M. IRIONDO. 2001. Female reproductive success of narrow endemic *Erodium paularense* in contrasting microhabitats. *Ecology* 82: 1734-1747.

ASPLUND J., P. LARSSON, S. VATNE AND Y. GAUSLAA. 2010 Gastropod grazing shapes the vertical distribution of epiphytic lichens in forest canopies. *Journal of Ecology* 98: 218-225.

ASPLUND J. AND Y. GAUSLAA. 2008. Mollusc grazing limits growth and early development of the old forest lichen *Lobaria pulmonaria* in broadleaved deciduous forests. *Oecologia* 155: 93-99.

ASPLUND J. AND D. A. WARDLE. 2013. The impact of secondary compounds and functional characteristics on lichen palatability and decomposition. *Journal of Ecology* 101: 689-700.

BELINCHÓN R., I. MARTÍNEZ, M. A. G. OTÁLORA, G. ARAGÓN, J. DIMAS AND A. ESCUDERO. 2009. Fragment quality and matrix affect epiphytic performance in a Mediterranean forest landscape. *American Journal of Botany* 96: 974-1982.

BELINCHÓN R., I. MARTÍNEZ, G. ARAGÓN, A. ESCUDERO AND M. DE LA CRUZ. 2011. Fine spatial pattern of an epiphytic lichen species is affected by habitat conditions in two forest types in the Iberian Mediterranean Region. *Fungal Biology* 115: 270-1278.

BENESPERI R. AND M. TRETIACH. 2004. Differential land snail damage to selected species of the lichen genus *Peltigera*. *Biochemical Systematics and Ecology* 32: 127-138.

BURGAZ A. R. AND I. MARTÍNEZ. 2003. Peltigerales: Lobariaceae, Nephromataceae, Peltigeraceae. Flora Liquenológica Ibérica. Universidad de Murcia. España.

COLESIE C., S. SCHEU, T. G. A. GREEN, B. WEBER, R. WIRTH AND B. BÜDEL. 2012. The advantage of growing on moss: facilitative effects on photosynthetic performance and growth in the cyanobacterial lichen *Peltigera rufescens*. *Oecologia* 169: 599–607.

CORNEJO C. AND C. SCHEIDEGGER. 2013. Morphological aspects associated with repair and regeneration in *Lobaria pulmonaria* and *L. amplissima* (Peltigerales, Ascomycota). *Lichenologist* 45: 285-289.

DENISON W. C. 2003. Apothecia and ascospores of *Lobaria oregana* and *Lobaria pulmonaria* investigated. *Mycologia* 95:513-518

EDMAN M., A. M. ERIKSSON AND M.A. VILLARD. 2008. Effects of selection cutting on the abundance and fertility of indicator lichens *Lobaria pulmonaria* and *Lobaria quercizans*. *Journal of Applied Ecology:* 45: 26-33.

GÄRDENFORS U. 2010. Red List of Swedish Species. ArtDatabanken, SLU, Uppsala.

GAUSLAA Y., M. LIE, K. A. SOLHAUG AND M. OHLSON. 2006. Growth and ecophysiological acclimation of the foliose lichen *Lobaria pulmonaria* in forests with contrasting light climates. *Oecologia* 147: 406–416.

GAUSLAA Y., H. HOLIEN, M. OHLSON AND T.-SOLH ØY. 2006b. Does snail grazing affect growth of the old forest lichen *Lobaria pulmonaria*? *Lichenologist* 38: 587-593.

GAUSLAA Y., D.S. COXSON AND K. A. SOLHAUG. 2012. The paradox of higher light tolerance during desiccation in rare old forest cyanolichens than in more widespread co-occurring chloro- and cephalolichens. *New Phytologist* 195: 812-822.

GU W. D., M. KUUSINEN, T. KONTTINEN AND I. HANSKI. 2001. Spatial pattern in the occurrence of the lichen *Lobaria pulmonaria* in managed and virgin forests. *Ecography* 24: 139-150.

GUISAN A., T. C. EDWARDS AND T. HASTIE. 2002. Generalized linear and generalized additive models in studies of species distributions: setting the scene. *Ecological Modelling* 157: 89–100.

GUSTAFSSON L. AND I. ERIKSSON. 1995, Factors of importance for the epiphytic vegetation of aspen *Populus tremula* with special emphasis on bark chemistry and soil chemistry. *Journal of Applied Ecology* 32: 412–424.

HERFINDAL I., J.P. TREMBLAY, B.B. HANSEN, E.J. SOLBERG, M. HEIM AND B.E. SÆTHER. 2009. Scale dependency and functional response in moose habitat selection. *Ecography* 32: 849-859.

HILMO O., L. ROCHA, H. HOLIEN AND Y. GAUSLAA. 2011. Establishment success of lichen diaspores in young and old boreal rainforests: a comparison between *Lobaria pulmonaria* and *L. scrobiculata*. *Lichenologist* 43:241-255

ISTOMINA N.B. 1996. The biology of *Lobaria pulmonaria* (L.) Hoffm. and *Menegazzia terebrata* (Hoffm.) Massal. in southern taiga forests of the European Russia. PhD dissertation, Cand. Sci. (Biol), Moscow, Russia.

JACKSON, B.H., ST. CLAIR, L.L., EGGIT, D.L. 2006. Size is not a realiable measure of zexual fecundity in two species of lichenized fungi. *Bryologist* 109: 157-165.

JÜRIADO I., J. LIIRA, D. CSENCSICS, I. WIDMER, C. ADOLF, K. KOHV AND C. SCHEIDEGGER . 2011. Dispersal ecology of the endangered woodland lichen *Lobaria pulmonaria* in managed hemiboreal forest landscape. *Biodiversity and Conservation* 20: 1803–1819.

JÜRIADO I., L. KARU AND J. LIIRA. 2012. Habitat conditions and host tree properties affect the occurrence, abundance and fertility of the endangered lichen *Lobaria pulmonaria* in wooded meadows of Estonia. *Lichenologist* 44: 263-276.

KLEEWEIN D. 1999. Population size, density, spatial distribution and dispersal in an Austrian population of the land snail *Arianta arbustorum styriaca* (Gastropoda: Helicidae). *Journal of Molluscan Studies* 65: 303-315.

LARSSON P. AND Y. GAUSLAA. 2011. Rapid juvenile development in old forest lichens. *Botany* 85: 65-72.

MARTÍNEZ I., T. FLORES, M. A. G. OTÁLORA, R. BELINCHÓN, M. PRIETO, G. ARAGÓN AND A. ESCUDERO. 2012. Multiple-scale environmental modulation of lichen reproduction. *Fungal Biology* 116: 1192-1201.

MCCARTHY P.M. AND J.A. HEALY .1978. Dispersal of lichen propagules by slugs. *Lichenologist* 10:131-132.

MÉNDEZ M. AND P.S. KARLSON. 2004. Costs and benefits of carnivory in plants: insights from the photosynthetic performance of four carnivorous plants in a subarctic environment. *Oikos* 86: 105-112.

NINYEROLA M., X. PONS AND J.M. ROURE. 2005. Atlas Climático Digital de la Península Ibérica. Universidad Autónoma de Barcelona, Bellaterra.

ÖCKINGER E. AND S. G. NILSSON. 2010. Local population extinction and vitality of an epiphytic lichen in fragmented old-growth forest. *Ecology* 91: 2100-2109.

ÖCKINGER E., M. NIKLASSON AND S.G. NILSON. 2005. Is local distribution of the epiphytic lichen *Lobaria pulmonaria* limited by dispersal capacity of habitat quality? *Biodiversity and Conservation* 14: 759-773.

OTÁLORA M. A. G., I. MARTÍNEZ, R. BELINCHÓN, I. WIDMER, G. ARAGÓN, A. ESCUDERO AND C. SCHEIDEGGER. 2011. Remnants fragments preserve genetic diversity of the old forest lichen Lobaria pulmonaria in a fragmented Mediterranean mountain forest. *Biodiversity and Conservation* 20: 1239–1254.

RANIUS T. 2002. Influence of stand size and quality of tree hollows on saproxylic beetles in Sweden. *Biological Conservation* 103: 85-91.

ROSE F. 1976. Lichenological indicators of age and environmental continuity in woodlands. in: D. H. Brown, D. L. Hawksworth, and R. H. Bailey (eds) Lichenology: Progress and Problems. Academic Press, London, pp 279-307.

SCHEIDEGGER C., FREY, B., ZOLLER, S.(1995) Transplantation of symbiotic propagules and thallus fragments: methods for the conservation of threatened epiphytic lichen populations. Mitteilungen der Eidgenössishen Forschungsanstalt WSL 70: 41-62.

SCHEIDEGGER C. AND S. WERTH. 2009. Conservation strategies for lichens: insights from population biology. *Fungal Biological Reviews* 23: 55-66.

SILLETT S. C., B. MCCUNE, J.E. PECK, T.R. RAMBO AND A. RUCHTY. 2000. Dispersal limitations of epiphytic lichens result in species dependent on old-growth forests. *Ecological Applications* 10: 789-799.

SNÄLL T., P.J. RIBEIRO AND H. RYDIN. 2003. Spatial occurrence and colonisations in patch-tracking metapopulations of epiphytic bryophytes: local conditions versus dispersal. *Oikos* 103: 566-578.

SNÄLL T., A. HAGSTRÖM, J. RUDOLPHI AND H. RYDIN. 2004. Distribution pattern of the epiphyte *Neckera pannata* on the spatial scales importance of past landscape structure connectivity and local conditions. *Ecography* 27: 757-766.

SNÄLL T., J. PENNANEN, L. KIVISTÖ AND I. HANSKI. 2005. Modelling epiphyte metapopulation dynamics in a dynamic forest landscape. *Oikos* 109: 209-222.

SINGH G., F. DAL GRANDE, C. CORNEJO, I. SCHMITT AND C. SCHEIDEGGER. 2012. Genetic basis of self-incompatibility in the lichen-forming fungus *Lobaria pulmonaria* and skewed frequency distribution of mating-type idiomorphs: implications for conservation . *PLoS ONE* 7: e51402.doi:10.1371/journal.pone.0051402.

VERBEKE G. AND G. MOLENBERGHS. 1997. Linear mixed models inpractice. A SAS-oriented approach. Springer, New York.

WALSER J. C., F. GUGERLI, R. HOLDEREGGER, D. KUONEN AND C. SCHEIDEGGER. 2004. Recombination and clonal reproduction in natural populations of *Lobaria pulmonaria*. *Heredity* 93: 322-329.

WERTH S., R. HOLDEREGGER, H.H. WAGNER, D. CSENCSICS AND C. SCHEIDEGGER. 2007. Landscape-level gene flow in *Lobaria pulmonaria*, an epiphytic lichen. *Molecular Ecology* 16: 2807-15.

WESSELINGH R. A., P. G. L. LINKHAMER, T. J. DE JONG AND A. B. BOORMAN. 1997. Threshold size for flowering in different habitats: effects of size-dependent growth and survival. *Ecology* 78: 2118-2132.

ZOLLER S., F. LUTZONI AND C. SCHEIDEGGER. 1999. Genetic variation within and among populations of the threatened lichen *Lobaria pulmonaria* in Switzerland and implications for its conservation. *Molecular Ecology* 8: 2049-2059.

Supplementary material

Table S1 Plot characteristics. T: annual mean temperature; P: total precipitation; DBH: mean tree diameter . Precipitation and temperature data source: Ninyerola et al. (2005).

Plot	Locality name	Coordinates X; Y (m)	Size (Ha)	Forest type	Number of trees	Number of beech	Number of oak	Altitude (m a.s.l.)	T (°C)	P (mm)	DBH (cm)
1	Montejo 1	4555119; 455864	1	Mixed beech	606	350	202	1320	9.5	954	27.84
2	Montejo 2	4555109; 458677	0.25	Oak	159	0	123	1294	9.5	954	26.02
3	Cantalojas	4564030; 467755	0.25	Mixed beech	156	114	9	1580	8.6	1153	38.93
4	Santuy	4549449; 462976	0.65	Oak	539	0	519	1410	8.9	744	14.59

Table S2 Values of the tree variables for each host tree species, i.e., *Quercus pyrenaica* or *Fagus sylvatica*.

Tree variable	***Quercus pyrenaica***		***Fagus sylvatica***	
Number of trees	840		475	
Occupation (%)	43		58	
Total no. individuals	10918		2760	
Individuals/tree	29.42±27.68		10.03±12.82	
	With *L. p*	Without *L. p*	With *L. p*	Without *L. p*
DBH	31.48±14.64	14.44±8.49	39.04±26.60	17.18±10.53
Roughness	10.37±3.47	8.72±3.71	1.27±1.46	0.60±1.16
BL	31.15±19.77	14.02±11.08	16.60±14.82	7.77±10.94
BH	15.68±14.68	3.60±5.76	9.35±12.43	3.29±6.76

Total number of trees recorded; occupation as the percentage of trees that hosted *Lobaria pulmonaria*; total no. individuals: the total number of *L. pulmonaria* individuals studied in each forest type; Individuals/tree: mean ± standard deviation (SD) for the number of individuals in each occupied tree; DBH: mean ± SD for the tree diameter at the breast height in occupied (with *L. pulmonaria, L. p.*) and unoccupied (without *L. pulmonaria, L. p.*) trees; roughness; bryophyte cover (%) on the tree trunks in the lower (BL) and upper (BH) strips.

Table S3 *Lobaria pulmonaria* individual variable values in both host tree species, i.e., *Quercus pyrenaica* and *Fagus sylvatica.*

Individual variable	***Quercus pyrenaica***	***Fagus sylvatica***
Mean size **±** SD (mm)	95.35±118.90	153.87±180.39
Attached to		
Bark	5956(54.5)/99.48±120.07	1395(50.5)/194±211.09
Bryophyte	3813(34.9)/53.88±64.57	1032(37.4)/81.52±77.55
Lichen	1149(10.5)/101.39±126.99	333(12.1)/121.65±140.98
Exposure		
North	3649(33.5)	985(35.7)
West	3029(27.7)	692(25.1)
East	2341(21.4)	717(26.0)
South	1899(17.4)	366(13.2)
Height		
H1	4504(42.1)	1609(58.3)
H2	3399(31.3)	526(19.0)
H3	1969(17.0)	359(13.0)
H4	1046(9.6)	266(9.7)
Reproductive structures		
Juvenile	5778(52.9)	1716(62.1)
Apothecia	1118(10.2)	211(7.6)
Asexual	4405(40.3)	1036(37.5)
Soredia	3925(35.9)	982(35.6)
Isidia	2186(20.0)	365(13.2)
Soredia Cover	(8.2)	(8.8)
Soredia + Isidia Cover	(6.0)	(6.0)
Unhealthy	5792(53.0)	1036(37.5)

Mean size of individuals ± standard deviation (SD); number of individuals and percentage (in brackets) at different attachment sites (bark/bryophyte/other lichens)/mean size of the individuals ± standard deviation growing at each attachment site. The number of individuals and the percentage (in brackets) for the following variables: exposure (North (316–45°), East (46–135°), South (136–225°), West (225–315°)); the height on the trunk (H1 = 0–49 cm, H2 = 50–99 cm, H3 = 100–149 cm, H4 = 150–200 cm); the number and percentage (in brackets) of individuals with or without reproductive structures, i.e., juveniles, apothecia, asexual (soredia and/or isidia), only soredia, and only isidia; the mean cover of soredia and/or isidia in individuals with these structures; the number and percentage (in brackets) of unhealthy individuals.

Fig. S1 Location of the study area in the Sistema Central Range, Spain. Red squares represent the surveyed plots: 1 = Montejo 1, 2 = Montejo 2, 3 = Cantalojas, 4 = Santuy.

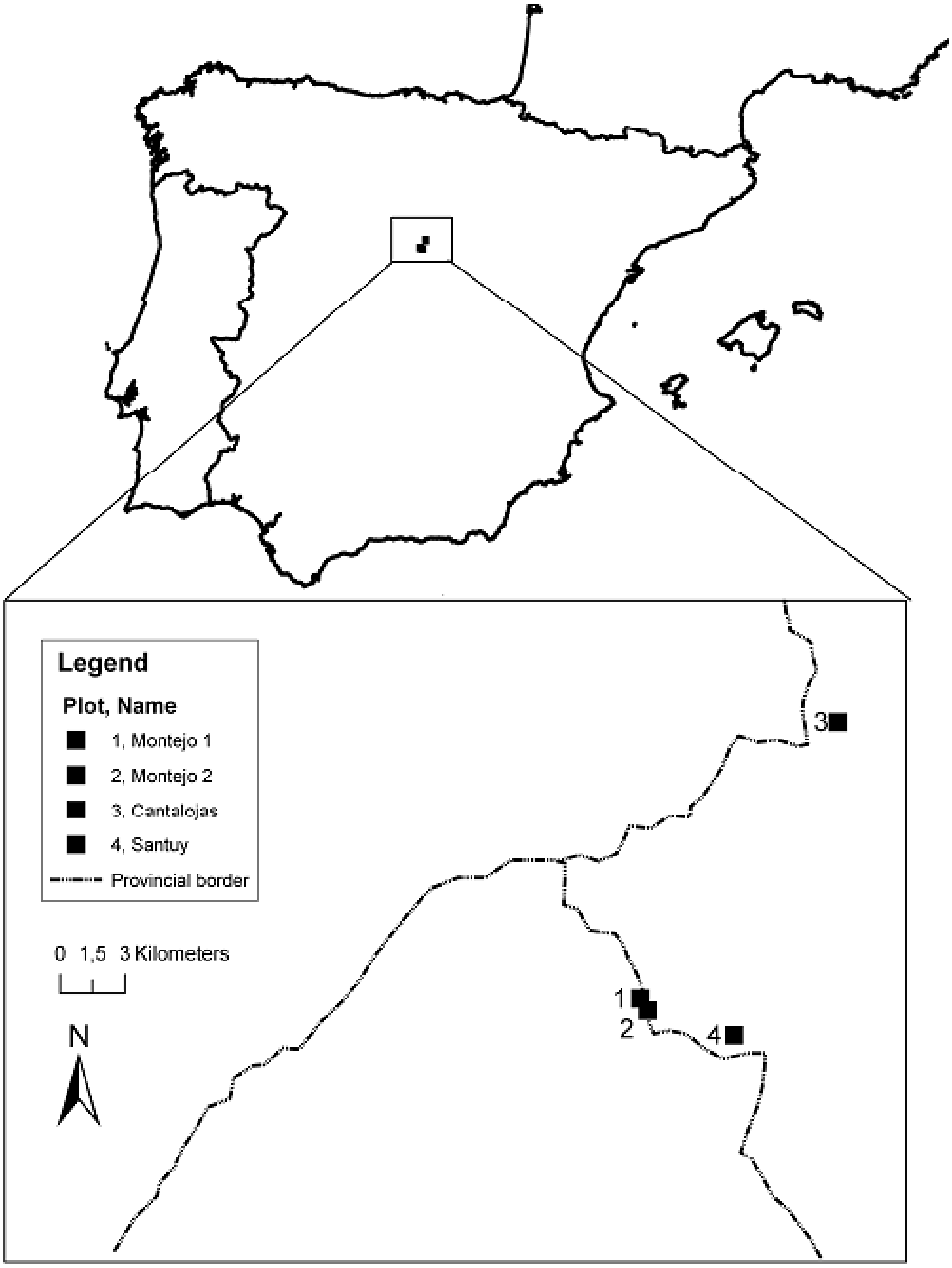

Table S4 Results of the generalized linear mixed models used to examine the effects of environmental variables on the individual size of *Lobaria pulmonaria*. Only significant factors are shown. The data are the Wald-type F-statistic (F-value), degrees of freedom (DF), coefficient of the variable in the model (Estimator), and the significance value (*p*-value).

Individual size				
Fixed factors	*DF*	*Estimator*	*F-Value*	*p-value*
Sp	505	0.4610	36.97	< 0.0001
DBH	515	0.002544	5.53	0.0190
Height	14000	–0.00064	12.61	0.0004
Or	14000	0.09743	59.90	< 0.0001
EPI	14000	C > B > L	174.38	< 0.0001

Table S5. Summary of the generalized linear mixed models used to examine the effects of different factors on the presence and abundance of reproductive structures. Only significant factors are shown. The data are the Wald-type F-statistic (F-value), degrees of freedom (DF), coefficient of the variable in the model (Estimator), and the significance value (*p*-value). See Table 1 for the abbreviations of the variables.

Apothecia presence					**Asexual presence**				
Fixed factors	*DF*	*Estimator*	*F-Value*	*p-value*	*Fixed factors*	*DF*	*Estimator*	*F-Value*	*p-value*
Sp	2049	–1.6463	161.37	< 0.0001	Sp	378	–1.1847	71.56	< 0.0001
Size	13000	2.0886	1575.78	< 0.0001	Size	14000	2.1041	2910.74	< 0.0001
EPI	13000	L > C > B	7.77	0.0004	EPI	14000	C > B > L	88.93	< 0.0001
Height	13000	–0.00390	26.82	< 0.0001	Or	14000	0.1985	26.74	< 0.0001
					BL		0.007585	4.33	0.0381
Soredia presence					**Soredia abundance**				
Fixed factors	*DF*	*Estimator*	*F-Value*	*p-value*	*Fixed factors*	*DF*	*Estimator*	*F-Value*	*p-value*
Sp	409	–1.0359	54.33	< 0.0001	Sp	280	–0.2418	7.07	0.0083
Size	14000	2.1293	2806.77	< 0.0001	Size	14000	1.0227	4205.99	< 0.0001
Or	14000	0.2242	32.03	< 0.0001	Or	14000	0.1933	80.35	< 0.0001
EPI	14000	C > B > L	63.03	< 0.0001	EPI	14000	C > B > L	79.39	< 0.0001
					BL	489	0.005531	5.02	0.0255
					Height	13000	0.000670	5.39	0.0203
Isidia presence					**Isidia abundance**				
Fixed factors	*DF*	*Estimator*	*F-Value*	*p-value*	*Fixed factors*	*DF*	*Estimator*	*F-Value*	*p-value*
Sp	628	–1.4142	110.71	< 0.0001	Sp	456	–0.8455	34.90	< 0.0001
Size	14000	1.4511	2144.40	< 0.0001	Size	14000	1.1046	2249.67	< 0.0001
Height	13000	0.003697	51.99	0.0273	Height	13000	0.004641	131.65	< 0.0001
EPI	14000	C > B > L	55.27		EPI	14000	C > B > L	45.93	< 0.0001
Or	14000	0.08284	4.87	< 0.0001					

Table S6. Threshold sizes (mm) and the probabilities of developing reproductive structures or an unhealthy status for *Lobaria pulmonaria* on two different host tree species, i.e., *Quercus pyrenaica* or *Fagus sylvatica*. The reproductive structures considered were soredia, soredia + isidia, and apothecia.

Probability	Reproductive structure	Threshold Size	
		Quercus pyrenaica	*Fagus sylvatica*
50%	Soredia	118	190
99%	Soredia	500	680
50%	Soredia+Isidia	640	690
99%	Soredia+Isidia	1225	1750
50%	Apothecia	350	690
99%	Apothecia	1100	2000
50%	Unhealthy status	41	279
99%	Unhealthy status	1164	1715

Capítulo 4

Capítulo 4

Which factors affect *Lobaria pulmonaria* vitality in the Spanish Mediterranean Region?

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Abstract

For conservational purposes, there is a need for ecophysiological studies in order to understand species susceptibility to environmental stress in contrasting microhabitats. Lichens are sensitive to habitat change at different scales, responding to minor differences in habitat structure and seasonal variations. The threatened lichen *Lobaria pulmonaria* is particularly susceptible to these changes. In this study in a Mediterranean forest, we wanted to clarify *L. pulmonaria* vitality variations throughout two years and under contrasting microhabitat conditions. For this purposes, we monthly monitored 217 *L. pulmonaria* individuals ranging different thallus sizes and growing on different microsites on two host trees (beech *Fagus sylvatica* and oak *Quercus pyrenaica*). We analyzed individual vitality data computing Generalized Linear Mixed Models (GLMMs). Vitality values revealed no clear seasonal pattern, but did show the importance of air relative humidity for *L. pulmonaria* vitality. Microhabitat played a subordinate but important role, mainly when temporal conditions where stressing. However, *L. pulmonaria* vitality response was different between the two host tree species: on oak, vitality was diminished by dry air conditions and southern aspects on the trunk, factors tuning water availability. By contrast, *L. pulmonaria* individuals growing on beech presented as well vitality depression if they grew attached to the upper parts of in the trunk, especially in southern orientation, where desiccation is higher.

Introduction

When attempting to protect a threatened species there is one important step in conservation biology: to identify target species´ vitality and performance. As conditions can change considerably among habitats and seasons within the species´ distribution range, its response will probably greatly vary at both spatial and temporal scales. Such information is needed to evaluate the fate of the species under different ecological scenarios. Long-term studies are essential, as they might reflect long-term risks for the lichen species (Gauslaa et al 2001, Gaio-Oliveira et al 2004). Besides, field measurements permit an interpretation of lichen performance under their stressful environmental conditions in nature (Sojo et al 1997, Gauslaa and Solhaug 2000, Larsson et al 2012).

There is a need for ecophysiological studies in order to understand specific susceptibility to environmental stress of thalli in contrasting microhabitats. In case the threatened species is a lichen, information about its performance is usually more scarce. Lichens are stable symbiotic association between a fungus (mycobiont) and algae and/or cyanobacteria (photobiont). Both bionts strongly interact: the photobiont produces simple sugars by photosynthesis; in contrast, the fungi build the structure of the lichen thallus, within which they provide conditions for a long term, stable association with their photobionts. Predicting the long-term performance and vitality of poikilohydric photosynthetic organisms such as lichens is not straightforward, because the applicability of higher plant models is limited (but see Jonsson et al 2008, Jonsson čabrajič et al, 2010, 2010b). In lichens, photosynthesis, and therefore vitality, is thus driven by external environmental conditions, but also influenced by their internal physiological status (Sundberg et al 1997; Dahlman and Palmqvist 2003; Nash 2008).

As poikilohydric organisms, lichens need to be wet to be photosynthetically active, but they also need light. Therefore, their activity is controlled by a delicate balance between light availability and desiccation risk, as a physiological trade-off between activity and fatal desiccation (Gauslaa et al 2006).

On the one hand, lichens metabolism is dependent on thallus water content, so water could be judged the primary limiting resource (Armstrong 1974, Lange et al 1986, Maguas et al 1995). Hydration is important for lichen vitality increasing the duration of photosynthetically active periods (Dahlman and Palmqvist 2003), But, lichens require a fluctuating water content for a proper maintenance of the symbiosis (Farrar 1976) and for growth (Merinero et al 2014 and subsequent references). In the dehydrated state lichens become inactive but resistant to long-term high and low temperatures and other stressing environmental conditions (Soni and Strasser 2008, Gauslaa et al 2012). Desiccation protects against light damage: light transmittance diminishes in dry conditions disconnecting of the photosystem II (PS II) (Palmqvist and Sundberg 2000, Gauslaa and Solhaug 2000, 2001). Moreover, foliose lichens curling during desiccation protects them against photoinhibition (Bartak et al 2006). Hydration is needed for damage repairing (Gauslaa and Solhaug 1999, 2004) as well as for the production of photoprotective secondary compounds (Gauslaa et al 2001, Solhaug et al 2010).

Irradiance level received during hydration periods is a key factor for lichen photosynthesis (Palmqvist and Sundberg 2000, Dahlman and Palmqvist 2003). Light can be a limiting factor but also an excess is detrimental for lichen vitality causing photoinhibitory damage (Sojo et al 1997, Pintado et al 1997, Gauslaa and Solhaug 1996, 1999, 2000). Solar radiation is one of the factors showing higher seasonal and spatial variation in temperate forests (Gauslaa and Solhaug 2000). Thus, light might be a limiting resource when scarce, yet a stress factor when excessive, even at fine temporal and spatial scales.

Lichens, especially species confined to old-growth forests, are sensitive to habitat change and respond to minor differences in the habitat structure (Belinchón et al 2009, 2011; Otálora et al 2011, Jüriado et al 2011, 2012, Rubio-Salcedo et al 2014). Pintado and Sancho (2002) found that *Ramalina capitata* acclimated when growing in places of the rock where liquid water did not leak. At the same water content, individuals on driest microsites reached higher levels of activation. In Maritime Antartica, *Catillaria corymbosa* showed structural and physiological differences among sympatric populations depending on microhabitat light exposure level (Sojo et al 1997). Individuals in protected microhabitats presented more reproductive structures (soredia), chlorophyll content, water retention and photosynthetical rates.

Besides this, lichens are sensitive to variation in conditions throughout time. Like most photosynthetic organisms in seasonal climates, lichens are known to acclimate temporally by tuning various functions to seasonal climatic changes. (McEvoy et al 2007; Gauslaa et al 2013). In temperate climates, there are strong temperature and rainfall variations. In deciduous woods there is a strong seasonal change in the light environment associated with canopy closure (MacKenzie et al 2001, 2002).

Lobaria pulmonaria (L.) Hoffm. is an epiphytic lichen frequently used as a model organism in ecological studies (Gu et al 2001, Snäll et al 2005, Werth et al 2007; Jüriado et al 2012, Martínez et al 2012). It is highly susceptible to habitat changes, at the forest scale (Snäll et al 2004, Belinchón et al 2009, Hilmo 2012), tree level (Belichón et al 2011, Hilmo et al 2011) and microsite with in a tree (Rubio-Salcedo et al 2014). In the center of the Iberian Peninsula, this species lives on deciduous mountain forests, occupying deciduous trees like oak or beech.

Lobaria pulmonaria is particularly susceptible to excessive light (Gauslaa and Solhaug 1999, Larsson et al 2009). One reason for the sensitivity of *L. pulmonaria* to habitat and microhabitat conditions is related to its reduced resistance to high light. Light stress may cause photoinhibitory damage, both when the lichen thallus is wet and desiccated (Gauslaa and Solhaug 1996, 2000, Gauslaa et al 2001). Despite of its sensitivity, *L. pulmonaria* is found in largely contrasting climatic regions (Rose 1988). This lichen produces secondary metabolites, as melanic compounds that act as sun screen (UVA, UVB and visible wavelength, Gauslaa and Solhaug 2001). *Lobaria pulmonaria* growth rate can vary as a result of varying water, light and temperature conditions in the particular habitat (McCune et al 1996; Shirazi et al 1996; Muir et al 1997; Palmqvist and Sundberg 2000). Moreover, it responds differently to changing conditions throughout time. It grows faster during Spring and Fall in boreal forest, with warm, bright and wet conditions (MacKenzie et al 2001, 2002).

In Mediterranean habitats water availability is often a limiting factor (Valladares et al 2004). The ecophysiological mechanisms underlying lichen performance and the role of microhabitat are poorly understood under Mediterranean conditions (but see Gaio-Oliveira et al 2004). Even though the species is in its southern distributin limit, we found large reproducing *L.pulmonaria* populations (>10000 individuals/ha, Rubio-Salcedo et al 2014) in Mediterranean forests in Central Spain.

Our main hypothesis is that *Lobaria pulmonaria* vitality in a Mediterranean forest will reflect a slightly fluctuating but good ecophysiological status of the population. We also expect reductions in vitality under stressing conditions at fine scale. The sources of variation we will test are: (a) seasonal pattern associated to defoliation of the host trees: vitality will increase during Spring and Summer thanks to denser canopy cover; (b) microclimatic adverse conditions (extreme temperatures and very low air humidity rate) will decrease *Lobaria pulmonaria* vitality; (c) different host tree species will lead to different *L.pulmonaria* vitality patterns in response to microhabitat; (d) individuals growing on shelter positions (northern aspect and lower parts of the trunk), where conditions are more humid and less light-exposed will therefore show higher vitality values; (e) each individual respond depending on its own physiological state and features as size. Larger thallus will be active for longer and present higher vitality.

To test our hypotheses, we monthly monitored vitality (Fv/Fm) of 217 *Lobaria pulmonaria* individuals for 2 years, under different microclimatic conditions. Individuals covered a comprehensive range of sizes and are placed in diverse microhabitat conditions.

Materials and methods

Study species

Lobaria pulmonaria (L.) Hoffm. is a widespread epiphytic lichen, ranging from Northern Europe, Asia and America to Africa (REFS). *Lobaria pulmonaria* has an important ecological role being an umbrella species in natural old forest (Scheidegger and Werth 2009) as it inhabits forest with high lichen diversity. Therefore it has been used as an indicator species of ecological integrity in forests (Rose 1976, Nascimbene et al 2010). Although still widespread, *Lobaria pulmonaria* is declining and considered endangered in many parts of Europe (Gärdenfors 2010), including our study region in Central Spain. Despite this, it still forms abundant populations at the local scale. *Lobaria pulmonaria*, with the green alga *Dictyochloropsis* as the main photobiont and the cyanobacterium *Nostoc* in cephalodia becomes rehydrated and photosynthetically active solely through water vapor uptake from humid air.

Study area and data collection

This study was carried out in the protected area "Hayedo de Montejo", in the Sistema Central Range in the Iberian Peninsula. Field measurements were conducted monthly from 2011 March to 2013 February. The climate in this area is Mediterranean, characterized by a drought summer period (1.8 months), with an annual rainfall of 954 mm and a mean annual temperature of 9.5°C (1320 m a.s.l.).

We settled one 100x100m plot (Lat=45551191m, Long=458642m) in a mixed forest mainly consistent of *Fagus sylvatica* L. (beech) and *Quercus pyrenaica* Willd. (oak), the two tree species where *Lobaria pulmonaria* is more likely to be found in this area. *Fagus sylvatica* L. (beech) is a deciduous tree that is widespread throughout Western Europe and one of its southernmost distribution limits was in the study area. *Quercus pyrenaica* Willd.(oak) is a virtually endemic oak in the Iberian Peninsula.

We measured temporal variations in temperature and air relative humidity. To record hourly data, we placed five Hobo ® Pro V2 data loggers (Onset, USA) within the plot. Microclimatic variables are: air relative humidity (RH, %) during data collection and also mean RH value for the previous 4hours (HR4); air temperature (T, ºC) and mean value for air temperature the previous 4hours during data collection (T4). We also considered two "seasons" in relation to defoliation: defoliated season from November to April, and well developed canopy cover the rest of the year.

A total of 54 trees (diameter at 130cm >20cm) were randomly selected: 37 beeches and 17 oaks hosting a variable number of *L.pulmonaria* individuals. Tree features were recorded at the beginning of the study: diameter at 130cm (DBH, cm), bark roughness (mm) and canopy openness (%) (Table 1). Image analysis of hemispherical digital pictures (Englund et al 2000) was used to quantify each tree developed canopy cover. Digital photographs were taken from a horizontal position close to each tree, at breast height and at ground level, using a horizontally levelled digital camera (Nikon Coolpix 4500, Nikon, Japan) aimed at the zenith, using a fish-eye lens of 180º field of view (FCE8, Nikon). Photographs were analysed using Gap Light Analyser (GLA) software ver. 2.0. (Frazer et al 1999). This software estimates several irradiance variables but we used canopy openness (%), because the rest of estimates highly correlate in our study area (Merinero et al in prep).

Table 2: List of explicative variables recorded at temporal (month level) and spatial scales (tree and individual levels). An asterisk (*) indicates a variable included in the models, the others in the same level were excluded due to high correlation.

Month (temporal)	Tree level (spatial)	Individual level (spatial)
Air relative humidity air (HR,%) during the data collection	*Tree species (*Fagus*/*Quercus*)	Thallus maximum diameter (mm)
*Air Mean relative humidity (HR4,%) 4 hours prior and during data collection	Diameter at 0cm above ground (cm)	*Initial thallus size (mm^2 on 2011 March)
Air temperature (T, ºC) during the data collection	Tree diameter at 130cm above ground (cm)	24-months growth rate Δsize=(ln(size1)-ln(size0)*100)/ ln(size0)
Mean air temperature (T4, ºC) 4 hours prior and during data collection	Roughness of the bark (mm)	Exposure aspect on the tree (°)
Defoliation season (binary variable): [November-April]=defoliated trees	Canopy openness (%)	Height above the ground (cm)
		Reproductive / non reproductive (any sexual or asexual reproductive structures)

From a previous study in the same plot, 400 *L.pulmonaria* individuals (200 on oak, 200 on beech) were marked, labelled and monitored in order to detect individual growth and survival rates (Rubio-Salcedo et al in prep.) taking photographs every 6months during the period 2011 January- 2013 January. Of those monitored individuals, we discarded those presenting too small size (thallus diameter>15mm) to use Handy Pea leaf-clips (Hansathech chlorophyll fluorescence system). That resulted on 217 L. pulmonaria individual: 80 on oak, 137 on beech. For each individual, we recorded its position on the tree trunk: exposure aspect (0-359 º) and height above ground (0-200 cm) (Table 1). We recorded thallus size as thallus maximum diameter (mm) and thallus initial size as thallus area at the beginning of the study (Size0, mm^2). Size was calculated by image analysis using Photoshop 6.0. Thallus growth was calculated as % variation in area (following Gauslaa et al 2006), analyzing and comparing first and last photographs. Likewise, we noted presence/absence of any reproductive structure (i.e. sexual structures, apothecia and/or asexual structures: isidia and/or soredia).

We considered *Lobaria pulmonaria* vitality in relation to its photobiont photosynthetic activity. As a metric of vitality, we considered the maximal photochemical quantum yield of photosystem II, Fv/Fm. This metric is a simple non-destructive measurement, a depression in maximal PS II efficiency. It has become a sensitive and frequently used stress indicator of photosynthetic organisms (Maxwell and Johnson 2000). Fv/Fm lower values indicate a reduction in potential photosynthetic performance (injuries to the PS II), thereby, as a good estimator of lichen vitality. Every month (2011 March – 2013 February) we carried out vitality measurements on each *Lobaria pulmonaria* individual with a portable fluorometer Handy Pea (Plant Efficiency Analyser, Handsatech, UK). Lichen vitality was assessed by Fv/Fm after complete rehydration (spraying water intensively) and 20 minutes of dark adaptation. Vitality measures were always recorded at noon (±2h), and in the same thallus lobe (Barták et al 2000) avoiding reproductive and/or bleached areas. Values of Fv/Fm were calculated with the instrument from fluorescence induction curves of 5 seconds duration recorded at an irradiance of 1500 $\mu mol\ m^{-2}\ s^{-1}$ from light-emitting diodes.

Data analysis

We collected vitality data for two years. Data set comprised 22 monthly subsets, 2012 January and 2012 September are missing due to logistic problems. Each subsets comprises 217 individual data, so the data set includes a total of 4774 individual vitality data (1760 *L.pulmonaria* individuals growing on oak, 3014 on beech).

Previous studies (Rubio-Salcedo et al 2014) showed that the individual response was highly host tree-dependent. Exploratory analysis confirmed this pattern (data not shown), so we run separated vitality models for individuals growing on oak and beech (from now on, oak and beech models).

The effect on lichen vitality of the random and fixed factors was assessed using Generalized Linear Mixed Models (GLMMs, Bolker et al 2008, Zuur et al 2009) in R environment (R

Development Core Team, 2012) using the additional package “lme4” (lme4 package, Bates et al 2013). Response variable was Fv/Fm individual values for each measuring date. The models were fitted by Restricted Maximum Likelihood criteria (REML). We constructed “the beyond the optimal model” including all possible random and fixed factors. We first selected the random structure, and once it was fixed, we selected the best fixed factors combination (Zurr et al 2009). The random saturated structure included tree and individual nested in tree as random factors. Also “month” was considered as a random factor: “month” could influence the effect of the fixed factors height and aspect on vitality response. Once random effects were optimized, we performed model selection for fixed effects. Of the temporal variables, only mean air humidity (RH4) and season (defoliated/non defoliated) were considered as fixed factors. The other temporal variables were excluded due to collinearity (Spearman correlation coefficient >0.7, p >0.05). Canopy openness was the only fixed factor at the tree scale. Both lichen position factors, aspect and height and their interaction, were included in the models. Aspect (º) was linearized as cos(aspect), to discern northern vs. southern orientation aspects. Size0 was the only individual fixed factor included in the model due to collinearity.

Among all the possible combinations of independent variables given the “beyond the optimal model”, we selected the best-fitting model that minimized the second-order Akaike information criterion (AICc). If only one model had an AICc>2 with respect to the rest of the models, it was considered the best model. When differences between several models had an AICc < 2.0, they were considered approximately equivalent in explanatory power (Burhanm and Anderson 2002). We show the results for the most complete model, including the widest range of predictor variables included in the subset of best-fitting models with AICc< 2.0.

To provide a value of the goodness-of-fit of each selected model, we also calculated pseudo-R-squared according to Nakagawa and Schielzeth (2013). For mixed-effects models, R^2 can be categorized into two types: marginal and conditional. Marginal R^2 represents the variance explained by fixed factors, whilst conditional R^2 is interpreted as variance explained by both fixed and random factors.

Results

Individual vitality values ranged Fv/Fm=0.2-0.85 µmols/m^{2}s. Mean Fv/Fm±SD values for each month also varied depending on the host tree: from the minimum values on 2012 February (Fv/Fm$_{oak}$=0.43±0.13 µmols/m^{2}s, Fv/Fm$_{beech}$=0.47±0.11 µmols/m^{2}s) to maximum values on 2011 May (Fv/ Fm$_{oak}$ =0.74±0.03, Fv/ Fm$_{beech}$ =0.77±0.02). *Lobaria pulmonaria* vitality suffered great variability temporal variation (Figure 1). In addition, there is some variability (SD) associated to microhabitat and individual characteristics. This variation was greater in the periods of poorest vitality mean values (e.g. 2012 Februray). No clear seasonal pattern was described. Despite reduction in vitality in certain dates, *L. pulmonaria* recovered. Recovery can be one moth fast (2011 October-November, figure 1) or more gradual and progressive (2012 February-March-April, figure 1).

GLMMs showed that both microclimate and microhabitat conditions exert influence on *L. pulmonaria* vitality. First, there is high importance of the random factors (Table 2): the best selected model presents the saturated structure for random factors. Second, fixed effects showed that humid dates and northern positions in the trunk promoted vitality on *L.pulmonaria* individuals regardless host tree species (Table 2). However, results suggest that the individual vitality responds differently in each host tree. Beech model is more complex comparing to oak one, and shows other important microhabitat factors tuning vitality. When growing on oak, only northern microsites enhance vitality (Table2, figure 2). When growing on beech, apart from aspect, also height in the trunk and the interaction height*aspect involves importance, and so it does individual size (Table 2, figure 2). On beech, *L.pulmonaria* larger individuals located in the lowest and northern exposures of the trunk present higher vitality. What is more, height negative effect in vitality is much more marked if it matches with southern positions (figure 3); if the individual grows on northern aspects, height exerts a minor effect on vitality.

Both models have a good global fit (following Nakagawa and Schielzeth 2013), as pseudo-R^2 values show (conditional R^2 >0.8; table 2). More than 80% of the variance is explained by both random and fixed effects together, regardless host tree. However, fixed factors explain three times more the variance in oak model comparing to oak one (marginal R^2 =0.17 and 0.57 respectively; table 2).

Table 2: Summary of coefficients for the GLMMs models used to examine the effects of random and fixed factors on Lobaria pulmonaria vitality (Fv/Fm). Best model selected for each host tree species, i.e., Quercus pyrenaica and Fagus sylvatica. Fixed factor effects: Only signicant factors are shown. Estimate ± standard error for each factor: Height= height of the thallus above the ground (cm); Aspect= linealized aspect of the thallus position on the trunk (cos(º)); RH4= mean air relative humidity of the 4 hours prior and during data collection (%), Height:Aspect= interaction of both factors, Size0= square root of initial thallus size (mm2). Random factors: standard deviation for each factor: Nind:Ntree= individual nested in tree, Date and its effect on Height and aspect effects on response variable, Residual. Marginal and conditional pseudo- R2 values for each model.

	***Fagus* model**		***Quercus* model**	
Fixed Factors				
	Estimate ±	SE	Estimate ±	SE
(Intercept)	0.4970 ±	0.06600	0.1890 ±	0.0597
Height	-0.0002 ±	0.00006		
Aspect	0.0050 ±	0.00373	0.0185 ±	0.0087
RH4	0.0028 ±	0.00112	0.0065 ±	0.0008
Height: Aspect	0.0001 ±	5.55e-5		
Size0	3.99e-8 ±	7.03e-8		
Random Factors				
	SD		SD	
Nind:Ntree (Intercept)	0.0130		0.0214	
Ntree (Intercept)	0.0124		0.0710	
Date (Intercept)	0.1210		0.0439	
Height	0.0002		0.0003	
Date (Intercept)	4.19e-8		0.0752	
Aspect	0.0075		0.0378	
Residual	0.0635		0.0567	
Pseudo-R^2 values				
R^2 marginal	0.1693		0.5694	
R^2 conditional	0.8324		0.8776	

Figure 1: *Lobaria pulmonaria* vitality during the study on different host tree. Fv/Fm mean ± SD values (error bars) for each date of collection (2011 March-2013 February). Blue points and lines= individuals growing on *Fagus sylvatica*. Red points and lines= individuals growing on *Quercus pyrenaica*.

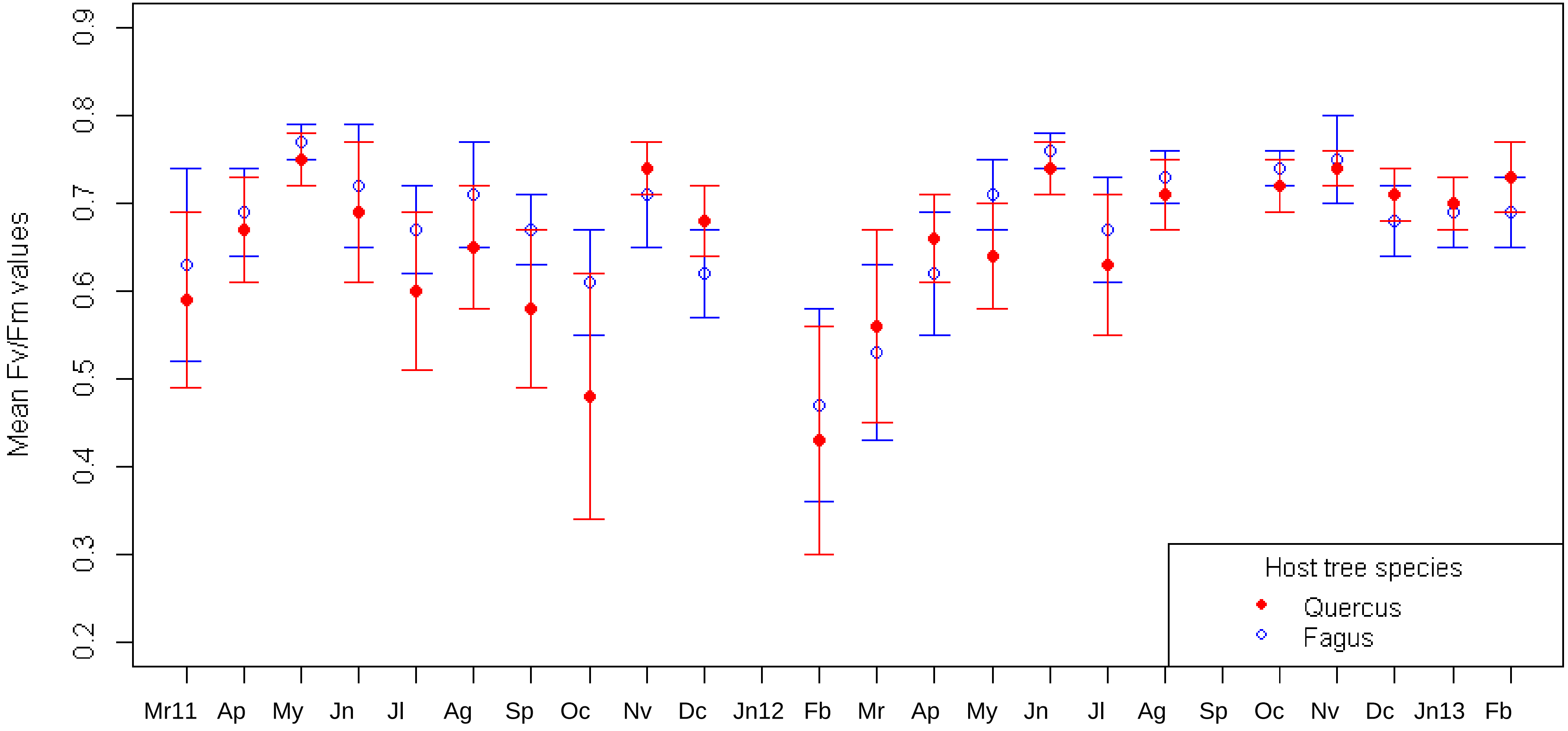


Figure 2: ***Lobaria pulmonaria*** **vitality (Fv/Fm) data (points) and projected values (lines) vs. air relative humidity (%), in different conditions spatial conditions (variables selected in the models). (a) Individuals growing on *Quercus pyrenaica* on opposite aspects of the trunk (black= northern, red=southern). (b) Individuals growing on *Fagus sylvatica*: on opposite aspects of the trunk (black= northern, red=southern) and heights above the ground (dashed line=200cm, solid line=0cm).**

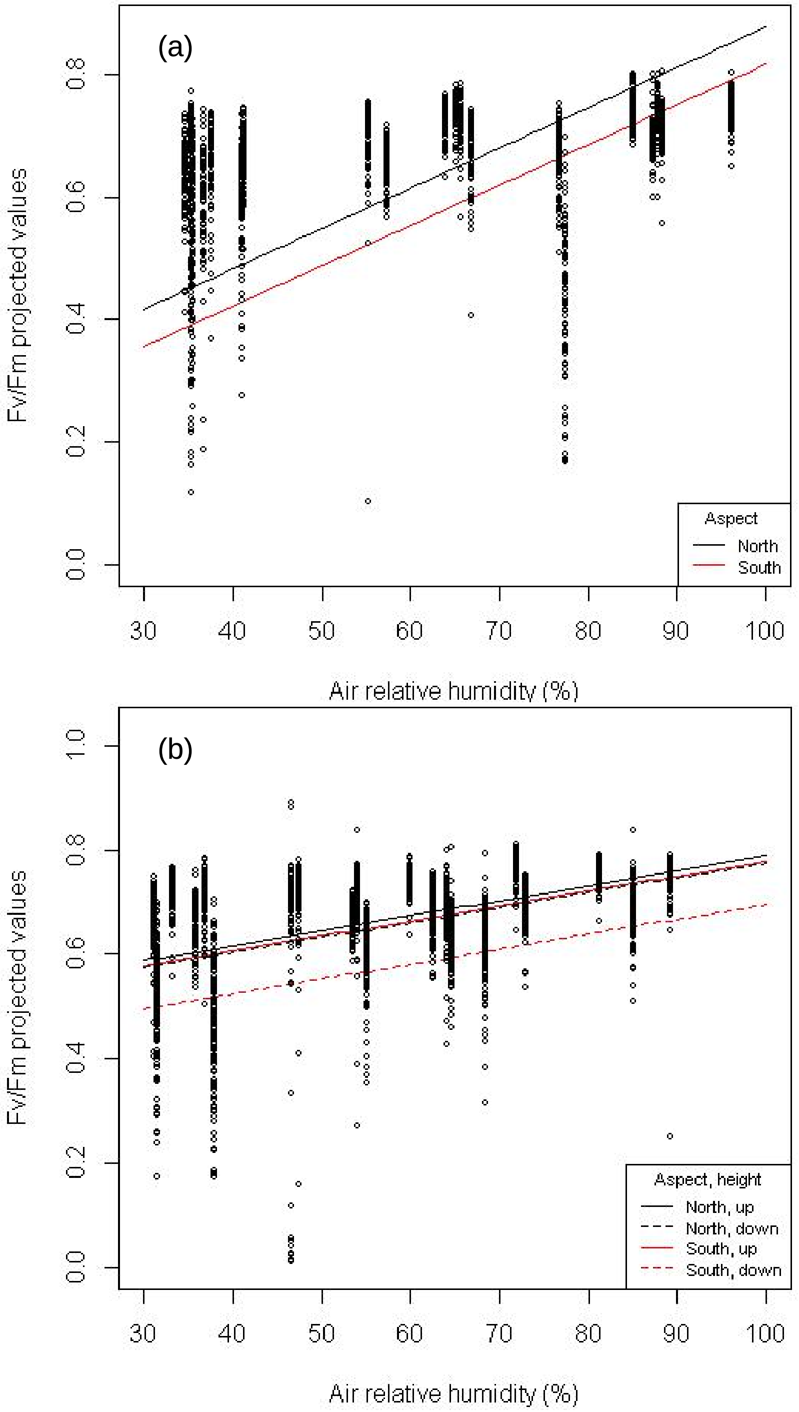
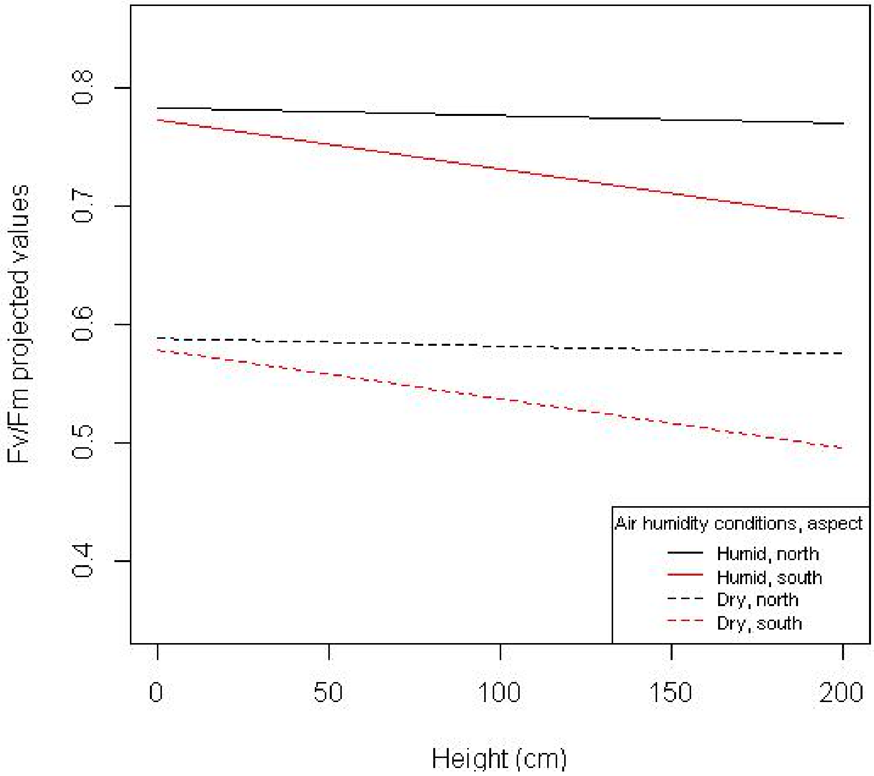


Figure 3: ***Lobaria pulmonaria*** **vitality (Fv/Fm) projected values (lines) vs. height above the ground under different air relative humidity and aspect conditions (variables selected in model). Individuals growing on** ***Fagus sylvatica*****: on opposite aspects of the trunk (black= northern, red=southern) and under extreme recorded air moisture conditions (dashed line=dry conditions (HR=30%, minimum recorded), solid line=humid conditions (HR=98%, maximum recorded).**



Discusion

Vitality values for *Lobaria pulmonaria* changed throughout the study 24-month duration. Most of the individual vitality data were in a range that could be considered as healthy for this species (FvFm 0.7-0.8 µmols/m^{2}s, e.g. Gauslaa and Solhaug 2000). This reflects that the monitored population is healthy in terms of ecophysiological state, as we expected. However, there are important vitality variations linked to microclimate and microhabitat conditions and individual response.

Under good microclimatic conditions (e.g. 2011 May) vitality is very similar among individuals, regardless microhabitat and self-individual conditions (lower SD values, figure 1). On the contrary, response is much more individual-dependent when temporal circumstances are stressing (e.g. 2012 February). Under stressful microclimatic satiations spatial factors at small scale seem to play a major role. We would say that conditions at the temporal scale drive *L. pulmonaria* response and spatial and individual factors play a subordinate role.

Temporal reductions in *Lobaria pulmonaria* vitality indicated that individual photosynthetic performance is less than optimal. Lower levels of vitality occurred in 2011 October, 2012 February and March (mean Fv/Fm <0.6 µmols/m^{2}s, minimum mean Fv/Fm=0.43 µmols/m^{2}s). After all those episodes of low vitality, we detected recovery. *Lobaria pulmonaria* can quickly recover from photoinhibitory damage in short humid periods (Jarius et al 2009). However, recovery is also damage-intensity dependent. In this case, recovery was faster and more complete in 2011 November comparing to 2012 April. In 2011 November, we detected low vitality rates in one single period. Meanwhile, in the second case vitality values were low for two consecutive periods. We believe that the longer the stressing conditions, the largest the impact and the longest the time to recover. Another explanation is that temperatures in 2012 February were lower than in 2011 October (1.7 vs 6.2 ºC), thus damage was higher because high irradiances in combination with low temperature are more harmful that at higher temperatures (Gauslaa and Solhaug 1996).

At the temporal scale, contrary to our expectations, we did not detect a clear seasonal pattern. For *L.pulmonaria*, seasonal patterns have already been described in boreal forest (Larsson et al 2012). Muir and Shirazi (1997) described growth patterns enhanced by wet season, and MacKenzie et al (2001, 2002) also relate growth variations to canopy changes. We expected that developed canopy cover would permit *L.pulmonaria* exhibit its highest vitality values. Canopy conditions in deciduous woods are *a priori* more favorable, providing *L.pulmonaria* a good protection against excess of light (Gaio-Olivera et al 2004, Gauslaa and

Solhaug 2000, Gauslaa et al 2006, 2007). Air relative humidity was a very important driver for *L. pulmonaria* vitality; however, we could not detect any effect of seasonality. A possible explanation for this striking result is that, under Mediterranean climate, where stochasticity plays a major role, weather and other changing conditions throughout the year exert lower influence in comparison to other regions. Air relative humidity conditions are much more important for *L. pulmonaria* vitality than a general trend or pattern in seasonality.

Air humidity is the main explicative variable in both oak and beech (Table2, figures 2). We strongly believe that air moisture is the limiting factor under Mediterranean conditions for *L. pulmonaria.* At 90% air relative humidity, the green alga *Dictocholorpsis reticulate* in *Lobaria pulmonaria* efficiently assimilates carbon in the absence of liquid water (Maguas et al 1995), which is ecologically very important under dry conditions (Lange et al 2011). Number and duration of periods RH > 90% will directly affect the length of active periods for photosynthesis, respiration and reparation processes (Palmqvist and Sundberg 2000, Gauslaa and Solhaug 2001, Palmqvist et al 2002, Hilmo 2002, Bidussi et al 2013).

About spatial explicative factors at fine scale, aspect is important regardless the host tree species. Northern positions on both *Fagus* and *Quercus* promote *L. pulmonaria* vitality. Aspect is such an important variable because it regulates water availability and light exposure at the microscale (Gauslaa et al 2011). This regulation is important during day, when light permits photosynthetic activity, and therefore net carbon fixation (Palmqvist and Sundberg 2000; Dahlman and Palmqvist 2003). Wet periods also permit the physiologically active processes of producing melanic compounds and other photoprotectors (Gauslaa and Solhaug 2001) and permiting nocturnal recovery from damage (Bidussi et al 2013).

Beech model shows that, apart from air humidity and aspect, other fixed factors play a role in vitality. Height means both higher light exposure and lower humidity, as moisture decreases with decreasing proximity to the ground (Geiger 1950). It also means increasing evaporative demands due to wind and sun exposure. Lower parts of beech trunks are also favorable places for *Lobaria pulmonaria* to reach larger thallus sizes and to develop reproductive structures (both sexual and asexual) (Rubio-Salcedo et al 2014). But height effect on vitality interacts with aspect: in northern orientations, where microconditions are smoother, the negative effect of height is almost no noticeable. Meanwhile, individuals growing on southern aspects do suffer more damages when growing in the upper parts of a beech trunk. Conversely, height does not affect *L. pulmonaria* vitality when this lichen is growing on oak. This is in line with population level previous results (Rubio-Salcedo et al 2014): larger individuals can be found at any height in the trunk when growing on oak, but are linked to lower parts when on beech. We strongly believe this is due to host tree species bark properties. Oak has a much coarser bark that permits easier attachment and also moisture due to higher water retention (Barkman 1985; Fritz et al 2009).

There is also a marginal effect of size0 in the beech model. Size is one of the most important lichen traits. Large lichen specimens present higher water holding capacity (Hestmark et al 1997, Gauslaa and Solhaug 1998, Merinero et al 2014). Likewise, size influences lichen growth, survival and reproduction (Armstrong and Wardle 2011, Larsson and Gauslaa 2011; Hilmo et al 2013, Rubio-Salcedo et al 2014). Larger L. pulmonaria individuals present higher vitality values because they are active for longer, thanks to their higher water holding capacity. Moreover, they probably present higher proportions of protective secondary compounds that enhance their vitality.

Selected structure of random factors, is consistent whit our hypothesis: a great proportion of inherit variability is associated to the individual itself, the host tree conditions and also microclimate. The random factor “month” incorporates many environmental factors that can vary thoughout the year as: sun light incidence (Jarius et al 2009, Palmqvist 2000, Gauslaa and Solhaug 2000, 2001, Gauslaa et al 2006, 2007, 2001), cloud cover, snow or wind conditions (Lidén and Hilmo 2005). These variables modify *Lobaria pulmonaria* vitality. They modify the number of wet periods (Palmqvist 2000), enlarg or shorten these periods (Hestmark et al 1997, Jonsson Čabrajic et al 2010, Lange et al 2001, Larsson et al 2012) and/or tune the irradiance received when wet, one of the main drivers when considering *L.pulmonaria* photosynthetical performance (Palmqvist and Sundberg 2000; Dahlman and Palmqvist 2003).

Lobaria pulmonaria has already been proved to be greatly affected by tree features (Belinchón et al 2009, 2001; Hilmo et al 2011; Martínez et al 2012), mainly tree species (Jüriado et al 2012, Rubio-Salcedo et al 2014). But vitality is thus driven by its internal physiological state (Sundberg et al 1997; Dahlman and Palmqvist 2003; Nash 2008). We considered “individual” as a random factor and size0 as an explicative factor. Other internal factors as water holding, lichen porosity, protective secondary compounds (Gauslaa and Solhaug 2001) and gelatinous substances (as occurs in Umbilicariaceae family, see Valladares et al 1993, 1997) or not detected grazing pressure (Cornejo and Scheidegger 2013) might be defining *L. pulmonaria* individual vitality. Also lichen genetic properties and prehistory (Nash 2008) are for sure modifying this lichen vitality.

Vitality models are both very explicative (conditional R^2>0.8). This results supports the idea that *L. pulmonaria* performance depends on microhabitat conditions (Belinchón et al 2011, Juriado et al 2012), and specially host tree species (Sillet et al 2000, Öckinger and Nilsson 2010, Rubio-Salcedo 2014). Oak model is quite simple: two fixed factors explain more than half of the variance (marginal R^2=0.57). On the other hand, beech model included these variables plus others: height and the interaction height*aspect, besides individual thallus size. In this model, fixed factors can only explain 17% of the variance in vitality. Higher complexity of beech vitality model is in the line of previous studies whith results at population level (Rubio-Salcedo et al 2014). It shows up that conditions tuning *L. pulmonaria* performance when it grows on oak are simpler and follow stronger patterns. Oak bark is coarser, what promotes important processes like recruitment (Zoller et al 2000, Scheidegger and Werth 2009, Öckinger and Nilson 2010). Coarser bark also enhances water availability favoring *L. pulmonaria* growth or reproductive structures development(Rubio-Salcedo et al 2014). Beech presents smoother bark, linked to less water and nutrient retention. This might be a handicap for *L. pulmonaria* vitality as for recruitment or thallus size.

More importantly from a conservation strategy point of view is that *Lobaria pulmonaria* vitality response is much more predictable when it grows on oak (only air humidity plus aspect explain more than 50% of the observed variability) in comparison to when it is growing on beech.

Conclusions

Lobaria pulmonaria vitality record revealed that the monitored population is ecophysiologycally healthy. However, vitality data presented differences linked mainly to temporal variation, and secondarily to spatial conditions at fine scale (tree and position in the tree). When low vitality levels were detected, recover is faster stressing conditions last for shorter.

During data collection, we did not detect a seasonal pattern in *Lobaria pulmonaria* vitality. However, air relative humidity, regardless the season of the year and tree defoliation, always promoted vitality.

At the spatial scale, *L. pulmonaria* presented different responses depending on host tree species: (a) vitality for individuals growing on oak was very predictable (57% of the variance explained by fixed factors), and only fixed factors were air humidity and aspect on the trunk. (b) By contrast, for individuals growing on beech only 17% of variability could be explained by fixed factors. Vitality responded positively to high air humidity and northern aspect, as on oak. However, vitality was enhanced on lower positions in the trunk, places where *Lobaria pulmonaria* reaches larger sizes, factor which in turn also enhances lichen vitality.

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References

Armstrong RA. 1974. A comparison of the growth-curves of the foliose lichen *Parmelia conspersa* determined by a cross sectional study and by direct measurement. *Journal of Experimental Botany* 32: 221-227.

Armstrong RA, Bradwell T. 2011. Growth of foliose lichens: a review. *Symbiosis* 53: 1-16.

Barkman JJ. 1958. *Phytosociology and Ecology of Cryptogamic epiphytes*. Assen van Gorcum. Sweden.

Barták M, Hájek J, Gloser J. 2000. Heterogeneity of chlorophyll fluorescence over thalli of several foiose macrolichens exposed to adverse environmental factors: interspecific differences as related to thallus hydration and high radiance. *Photosynthetica* 38: 531-537.

Barták M, Sholhaug KA, Vraáblíková H, Gauslaa Y. 2006. Curling during dissecation protects the foliose lichen *Lobaria pulmonaria* against photoinhibition. *Oecologia* 149: 553-560.

Bates D, Maechler M, Bolker B and Walker S. 2013. lme4: Linear mixed-effects models using Eigen and S4. R package version 1.0-5. http://CRAN.R-project.org/package=lme4

Belinchón R, Martínez I, Aragón G, Escudero A and de la Cruz M. 2011. Fine spatial pattern of an epiphytic lichen species is affected by habitat conditions in two forest types in the Iberian Mediterranean Region. *Fungal Biology* 115: 270-1278.

Belinchón R, Martínez I, Otálora MAG, Aragón G, Dimas J and Escudero A. 2009. Fragment quality and matrix affect epiphytic performance in a Mediterranean forest landscape. *American Journal of Botany* 96: 974-1982.

Bidussi M, Gauslaa Y, Solhaug KA. 2013. Prolonging the hydration and active metabolism from light periods into nights substantially enhances lichen growth. *Planta* 5: 1359-1366.

Bolker BM, Brooks ME, Clark CJ, Geange SW, Poulsen JR, Stevens MHH, White J-SS. 2009. Generalized linear mixed models: a practical guide for ecology and evolution. *Trends in Ecology & Evolution* 3: 127-135.

Cornejo C and Scheidegger C. 2013. Morphological aspects associated with repair and regeneration in *Lobaria pulmonaria* and *L. amplissima* (*Peltigerales*, *Ascomycota*). *Lichenologist* 45: 285-289.

Dahlman L, Palmqvist K. 2003. Growth in two foliose tripartite lichens, *Nephroma arcticum* and *Peltigera aphthosa*: empirical modelling of external vs internal factors. *Functional Ecology* 17: 821-831.

Englund SR, O'Brien JJ, Clark DB. 2000. Evaluation of digital and hemispherical photography and spherical densiometry for measuring forest light environments. *Canadian Journal of Forest Research* 30: 1999–2005.

Farrar JF. 1976. The lichen as an ecosystem: observation and experiment. In: Brown, D., Hawksworth, D. L. and Bailey, R. H. (eds), Lichenology: progress and problems. Proc. of an Int. Symp. held at the Univ. of Bristol. Academic Press: 385/407.

Frazer GW, Canham CD and Lertzman KP. 1999. Gap Light Analyzer (GLA), Version 2.0: Imaging software to extract canopy structure and gap light transmission indices from true-colour fisheye photographs, users manual and program documentation. Institute of Ecosystem Studies, Millbrook, New York, USA.

Fritz Ö, Gustafsson L and Larsson K. 2008. Does forest continuity matter in conservation? A study of epiphytic lichens and bryophytes in beech forests of southern Sweden. *Biological Conservation* 141: 655–668.

Gaio-Oliveira G, Dahlman L, Máguas C, Palmqvist K. 2004. Growth in relation to microclimatic conditions and physiological characteristics of four *Lobaria pulmaria* populations in two contrasting habitats. *Ecography* 27: 13-28.

Gärdenfors U. 2010. Red List of Swedish Species. ArtDatabanken, SLU, Uppsala, Sweden.

Gauslaa Y. 2014. Rain, dew, and humid air as drivers of morphology,function and spatial distribution in epiphytic lichens. *The Lichenologist* 41: 1-16.

Gauslaa Y, Coxson DS and Solhaug KA. 2012. The paradox of higher light tolerance during desiccation in rare old forest cyanolichens than in more widespread co-occurring chloro- and cephalolichens. *New Phytologist* 195: 812-822.

Gauslaa Y, Lie M, Solhaug KA, Ohlson M. 2006. Growth and ecophysiological acclimation of the foliose lichen *Lobaria pulmonaria* in forests with contrasting light climates. *Oecologia* 147: 406-416.

Gauslaa Y, Palmqvist K, Solhaug KA, Holien H, Hilmo O, Nybakken L, Myhre LC, Ohlson M. 2007. Growth of epiphytic old forest lichens across climatic and succesional gradients. *Canadian Journal of Forestry Research* 37: 1832-1845.

Gauslaa Y, Solhaug KA. 1996. Differences in the susceptibility to light stress between epiphytic lichens of ancient and young boreal forest stands. *Functional Ecology* 10: 344-354.

Gauslaa Y, Solhaug KA. 1999. High-light damage in air-dry thalli of the old forest lichen *Lobaria pulmonaria*—interactions of irradiance, exposure duration and high temperature. *Journal of Experimental Botany* 50: 697-705.

Gauslaa Y, Solhaug KA. 2000. High-light intensity damage to the foliose lichen *Lobaria pulmonaria* with in natural forest: the applicability of chlorophyll fluorescence methods. *The Lichenologist* 32: 271-289.

Gauslaa Y, Solhaug KA. 2001. Fungal melanins as a sun screen for symbiotic green algae in the lichen *Lobaria pulmonaria*. *Oecologia* 126: 462-471.

Geiger R. 1950. *The Climate Near the Ground*. Cambridge. Harvard University Press, UK.

Gu WD, Kuusinen M, Konttinen T and Hanski I. 2001. Spatial pattern in the occurrence of the lichen *Lobaria pulmonaria* in managed and virgin forests. *Ecography* 24: 139-150.

Hestmark G, Schroeter B, Kappen L. 1997. Intrathalline and size-dependent patterns of activity in *Lasallia pustulata* and their posible consequences for competitive interactions. *Functional Ecology* 11: 318-322.

Hilmo O. 2002. Growth and morphological response of old-forest lichens transplanted into a young and an old *Picea abies* forest. *Ecography* 25: 329-335.

Hilmo O, Gauslaa Y, Rocha L, Lindmo S, Holien H, 2013. Vertical gradients in population characteristics of canopy lichens in boreal rainforests of Norway. *Botany* 91: 814-821.

Hilmo O, Rocha L, Holien H and Gauslaa Y. 2011. Establishment success of lichen diaspores in young and old boreal rainforests: a comparison between *Lobaria pulmonaria* and *L. scrobiculata*. *Lichenologist* 43: 241-255

Jarius K, Lõhmus A, Lõhmus P . 2009. Lichen acclimatization on retention trees: a conservation physiology lesson. *Journal of Applied Ecology* 46. 930-936.

Jonsson Čabrajič AV, Lidén M, Lundmark T, Ottosson-Löfvenius M, Palmqvist K. 2010. Modelling hydration and photosystem II activation in relation to in situ rain and humidity patterns: a tool to compare performance of rare and generalist epiphytic lichens. *Plant, Cell & Environment* 33, 840-850.

Jonsson AV, Moen J, Palmqvist K. 2008. Predicting lichen hydration using biophysical models. *Oecologia* 156: 259-273.

Jonsson Čabrajič AV, Moen J, Palmqvist K. 2010b. Predicting growth of mat-forming lichens on a landscape scale comparing models with different complexities. *Ecography* 33: 949-960.

Jüriado I, Karu L and Liira J. 2012. Habitat conditions and host tree properties affect the occurrence, abundance and fertility of the endangered lichen *Lobaria pulmonaria* in wooded meadows of Estonia. *Lichenologist* 44: 263-276.

Jüriado I, Liira J, Csencsics D, Widmer I, Adolf C, Kohv K and Scheidegger C. 2011. Dispersal ecology of the endangered woodland lichen *Lobaria pulmonaria* in managed hemiboreal forest landscape. *Biodiversity and Conservation* 20: 1803–1819.

Barton K. 2013. MuMIn: Multi-model inference. R package version 1.9.13. http://CRAN.R-project.org/package=MuMIn.

Lange OL, Green TGA, Heber U. 2001. Hydration-dependent photosynthetic production of lichens: What do laboratory studies tell us about field performance? *Journal of Experimental Botany* 52: 2033-2042

Lange OL, Kilian E and Ziegler H. 1986. Water vapor uptake and photosynthesis in lichens: performance differences in species with green and blue green algae as phycobionts. *Oecologia* 71: 104–110.

Larsson P, Gauslaa Y. 2011. Rapid juvenile development in old forest lichens. *Botany* 89: 65-72.

Larsson P, Kristýna Večeřová, Cempírkováb H, Solhauga KA, Gauslaaa Y. Does UV-B infuence biomass growth in lichens defcient in sun-screening pigments? *Environmental and Experimental Botany* 67: 215-221.

Larsson P, Solhaug KA, Gauslaa Y. 2012. Seasonal partitioning of growth into biomass and area expansion in a cephalolichen and a cyanolichen of the old forest genus *Lobaria*. *New Phytologist* 194: 991–1000.

Lidén M and Hilmo O. 2005. Population characteristics of the suboceanic lichen *Platismatia norvegica* in core and fringe habitats: relation to macroclimate, substrate and proximity to streams. *The Bryologist* 108: 506-517.

MacKenzie TDB, Król M, Norman PA, Campbell DA. 2002. Seasonal changes in chlorophyll fluorescence quenching and the indicution and capacity of the photoprotective xanthophyll cycle in *Lobaria pulmonaria*. *Canadian Journal of Botany* 80: 255-261.

MacKenzie TDB, MacDonald TM, Dubois LA, Campbell DA. 2011. Seasonal changes in temperature and light drive acclimation of photosynthetic physiology and macromolecular content in *Lobaria pulmonaria*. *Planta* 214: 57-66.

McEvoy M, Gauslaa Y, Solhaug KA. 2007. Changes in pools of depsidones and melanins, and their function, during growth and acclimation under contrasting natural light in the lichen *Lobaria pulmonaria*. *New Phytologist* 175: 271–282.

Máguas C, Griffths H, Broadmeadow MSJ. 1995. Gas-exchange and carbon-isotope discrimination in lichens – evidence for interactions between CO2 concentrating mechanisms and difussion limitation. *Planta* 196: 95-102.

Martínez I, Flores T, Otálora MAG, Belinchón R, Prieto M, Aragón G and Escudero A. 2012. Multiple-scale environmental modulation of lichen reproduction. *Fungal Biology* 116: 1192-1201.

Maxwell K, Johnson GN. 2000. Chlorophyll fluorescence- a practical guide. *Journal of experimental Botany* 51: 659-668.

Merinero S, Hilmo O and Gauslaa Y. 2014. Size is a main driver for hydration traits in cyano- and cephalolichens of boreal rainforest canopies. *Fungal Ecology* 7: 59-66.

Muir PS, Shirazi AM. 1997. Seasonal growth dynamics in the lichen *Lobaria pulmonaria*. *Bryologist* 100: 458–464.

Nakagawa S, Schielzeth H. 2012. A general and simple method for obtaining R^2 from Generalized Linear Mixed-effects Models. *Methods in Ecology and Evolution* 4: 133-142.

Nascimbene J, Brunialti G, Ravera S, Frati L, Caniglia G. 2010. Testing *Lobaria pulmonaria (L.)* Hoffm. as an indicator of lichen conservation. *Ecological indicators* 10: 353-360.

Nash TH III. 1998. *Lichen Biology*. Cambridge. Cambridge University Press.

Öckinger E, Nilsson S. 2010. Local population extinction and vitality of an apiphytic lichen in fragmented old-growth forest. *Ecology* 91: 2100-2109.

Otálora MAG, Martínez I, Belinchón R, Widmer I, Aragón G, Escudero A and Scheidegger C. 2011. Remnants fragments preserve genetic diversity of the old forest lichen *Lobaria pulmonaria* in a fragmented Mediterranean mountain forest. *Biodiversity and Conservation* 20: 1239–1254.

Palmqvist K, Dahlman L, Valladares F, Tehler A, Sancho LG, Mattsson JE. 2002. CO2 exchange and thallus nitrogen across 75 contrasting lichen associations from different climate zones. *Oecologia*, 133: 295-306.

Palmqvist K, Sundberg B. 2000. Light use efficiency of dry matter gain in five macro-lichens: relative impact of microclimate conditions and species-specific traits. *Plant, Cell and Environment* 23. 1-14.

Pintado A, Sancho LG. 2002. Ecological significance of net photosynthesis activation by water vapour uptake in *Ramalina capitata* from rain-protected habitats in central Spain. *Lichenologist* 34: 403-413.

Pintado A, Valladares F, Sancho LG. 1997. Exploring phenotypic plasticity in the lichen *Ramalina capitata*: morpohlogy, water relations and chlorophyll content in northern versus southern populations. *Annals of Botany* 80: 345-353.

Rose F. 1976. Lichenological indicators of age and environmental continuity in woodlands. in: D. H. Brown, D. L. Hawksworth, and R. H. Bailey (eds) Lichenology: Progress and Problems. Academic Press, London, UK: 279-307.

Rubio-Salcedo M, Martínez I, Merinero S. 2014. Microhabitat selection by the epiphytic lichen *Lobaria pulmonaria*: the host tree species does matter. Fungal Ecology, in press.

Scheidegger C and Werth S. 2009. Conservation strategies for lichens: insights from population biology. *Fungal Biological Reviews* 23: 55-66.

Sillett SC, McCune B, Peck JE, Rambo TR and Ruchty A. 2000. Dispersal limitations of epiphytic lichens result in species dependent on old-growth forests. *Ecological Applications* 10: 789-799.

Sojo F, Valladares F, Sancho LG. 1997. Structural and physiological plasticity of the lichen *Catillaria corymbosa* in different microhabitats of Maritime Antartica. *The Bryologist* 100: 171-179.

Snäll T, Pennanen J, Kivistö L and Hanski I. 2005. Modelling epiphyte metapopulation dynamics in a dynamic forest landscape. *Oikos* 109: 209-222.

Solhaug KA, Larsson P, Gauslaa Y. 2010. Light screening in lichen cortices can be quantified by chlorophyll fluorescence techniques for both reflecting and absorbing pigments. *Planta* 231: 1003-1011.

Soni V, Strasser RJ. 2008. Survival strategies cannot be devised, the do exist already: a case study on lichens. En: Allen JF, Gantt E, Goldbeck JH and Osmong B (eds.) Photosynthesis. Energy from the sun: 14th international congress of photosynthesis: 1567-1571.

Sundberg B, Campbell D, Palmqvist K (1997) Predicting CO2 gain and photosynthetic light acclimation from fluorescence yield and quenching in cyano-lichens. *Planta* 201: 138–145.

Valladares F, Camarero J J, Pulido F, Gil-Pelegrín E. 2004. El bosque mediterráneo, un sistema humanizado y dinámico. En: Valladares, F. (ed.), Ecología del bosque mediterráneo en un mundo cambiante. Ministerio de Medio Ambiente, Madrid: 13-26.

Valladares F, Sancho LG, Ascaso C. 1997. Water storage in the lichen family *Umbilicariaceae*. *Botanica Acta* 111: 99-107.

Valladares F, Wierzchos J, Ascaso C. 1993. Porosimetric study of the lichen family *Umbilicariacea*e: anatomical interpretation and implications for water storage capacity of the thallus. *American Journal of Botany* 80: 263-272.

Werth S, Holderegger R, Wagner HH, Csencsics D and Scheidegger C. 2007. Landscape-level gene flow in *Lobaria pulmonaria*, an epiphytic lichen. *Molecular Ecology* 16: 2807-2815.

Zoller S, Frey B, Scheidegger C. 2000. Juvenile development and diaspore survival in the threatened epiphytic lichen species *Sticta fuliginosa*, *Leptogium saturninum* and *Menegazzia terebrata*: conclusions for in situ conservation. *Plant Biology* 2: 496-504.

Zuur A, Ieno EN, Walker N, Saveliev AA, Smith GM. 2009. Mixed effets models and extensions in ecology with R. Springer, NY USA.

Capítulo 5

Capítulo 5

Patterns of demographic variation in a threatened, long-lived epiphytic lichen

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Abstract

The life history of a species is the combination of traits regulating population dynamics and also individual fitness. But, quantitative characterizations of full life histories have focused on vertebrates, vascular plants or arthropods. Unfortunately, our knowledge on these critical issues for other biological groups is scarce and especially urgent in the case of certain groups such as lichenized fungi. *Lobaria pulmonaria* is one of the best known lichens, from a ecological point of veiw: we know it is sensible to habitat changes at various scales. However, fundamental aspects of its demography and how environmental variables might tune its vital rates are still not well known. This study describse *L. pulmonaria* demographical rates, and how those rates vary among temporal and spatial scales. We monitored semianualy during two years 4 *L. pulmonaria* populations in the center of Spain, growing on two different host trees: oak *Quercus pyrenaica* and beech *Fagus sylvatica*. We adjusted vital rates runing GLMs, all size-dependent, using separate models for each host trees. Environmental factors effect on vital rates was tested by model selection procedure (cAIC; N>1000). Survival resulted high (98-99%), slightly higher on beech. Mortality mainly correspond to very small individuals(<20mm^2), suggesting a possible demographic bottelneck for *L. pulmonaria* in this mediterranean habitat. Recruitment depended on the closeness of a big reproducing adult, as a propagule source and maybe due to its facilitating effect. Adult closeness was an important driver on both host trees, but almost indispensable on beech, where recruitment rates are clearly slower and lowest. Surprisingly, conditions favoring survival are summer dry lightfull conditions, meanwhile growth and recruitment are enhanced by wet, cold and less light full (winter) conditions, suggesting demographic compensation.*Lobaria pulmonaria* vital rates are tuned by both temporal and spatial changes in the habitat at small scale, therefore species viability is probably conditioned by small habiat changes. This information should be taken into account when developing conservation strategies for the species.

Introduction

The life history of a species is the combination of traits regulating population dynamics and also individual fitness (Young and Clarke, 2000; Picó, 2002; Milla et al., 2009). This set of traits governs both a species' ability to persist in a given environment and many aspects of its ecological dynamics. Development of general theories explaining the life history patterns within and across taxonomic groups has been the topic of many ecological studies (see e.g. Cole 1954; Jackson et al, 2006; Linares et al. 2007; García et al. 2008; Milla et al. 2009). But, quantitative characterizations of full life histories have focused on vertebrates, vascular plants or arthropods (van Straalen 1985; Boggs and Ross 1993) with little attention to other taxonomic groups.

Unfortunately, our knowledge on these critical issues for other biological groups is scarce and especially urgent in the case of certain groups such as lichenized fungi. Among the reasons that have been posed to explain this scarcity are the difficulties in obtaining good fitness estimates due to the “supposed” great longevity of lichens and to the fact that the stages of their life cycle may not be completely known (Jackson et al. 2006). In this sense, we still need detailed demographic research for lichens, urgently for threatened lichen species (Scheidegger and Werth 2009).

Lichens are major components in many terrestrial ecosystems (Nash 2008), yet their population ecology is at best only poorly understood. Few studies have fully quantified the life history or demographic patterns of any lichen, with particularly little attention to epiphytic species. Interest in lichen ecology has not extended to any extensive degree to their population ecology, including life history analysis. Survival, growth, and reproductive rates of lichens are the drivers that shape their community and ecosystem roles, but of these, only growth patterns have received any attention (Armstrong and Bradwell 2011; Rhoades 1983; Loso and Doak 2006). Many studies have quantified lichen growth rates, focusing on biomass accumulation or on the use of lichen sizes to date surfaces for ecological studies, rather to understand their ecological dynamics and to evaluate which factors could be influencing on demographic patterns (Benedict 2009; Bradwell and Arsmstrong 2007).

Study of the variation in vital processes from lichens is interesting not only from an ecological perspective but also from an evolutionary perspective. Such variation is critical to understand the entire distribution of a species and how its demography adjusts to environmental conditions and, even more importantly, to predict changes in range limits in response to future climate change (Gaston 2003, 2009). Although many studies have been conducted on other groups of organisms to assess this possible relationship (Lennartsson and Oostermeijer 2001; Wilson et al. 2005; Giménez-Benavides et al. 2007; Marrero-Gomez et al, 2007), very little has been done for lichens (Shriver et al. 2012).

Both temporal and spatial variation in demographic rates are known to be important in understanding population viability and more general dynamics. However, most studies have concentrated on moderate to large scale differences in demographic rates, or on temporal variation. But, small scale spatial variation should, a priori, have strong effects on population processes. How well larger scale variation encompass the patterns at smaller scales is not clear.

Here, we investigate the demographic patterns seen for *Lobaria pulmonaria* L. (Hoffm.), a threatened, epiphytic lichen, in the Spanish Mediterranean area. Previous studies indicate that microhabitat and tree host species determine the occurrence, abundance, thallus size and reproductive capacity of this species in Mediterranean Spain (Belinchón et al. 2011; Martínez et al. 2012; Rubio-Salcedo et al. 2014). While little demographic work has been done on lichens, they are appealing subjects for understanding the drivers of demo variability, because the factors driving demography are relatively easy to quantify at even very small scales.

We addressed three specific questions with this work:

A) How is variation in demography partitioned across time and space, and at different spatial scales?

B) do medium scale patterns in demographic rates reflect the same patterns seen at small scales?

C) Do we find evidence for demographic compensation across either time or space, and if so, are these patterns similar temporally as spatially?

A final goal of this work was to add to the limited data on lichen population ecology.

Materials and methods

Study species

Lobaria pulmonaria (L.) Hoffm. is a widespread epiphytic lichen, ranging from Northern Europe, Asia and America to Africa and has been used as a model organism in multiple ecological studies (Gu et al 2001, Snäll et al 2005, Martínez et al 2012). This species is susceptible to changes in forest habitats, including fragmentation, pollution and habitat degradation processes (Belinchón et al 2009, Otálora et al 2011, Jüriado et al 2012) and it has been used as an indicator species of ecological integrity in forests (Rose 1976, Campbell and Freeden 2004, Nascimbene et al 2010). However, very little is currently understood about the basic population ecology or demography of this species. Although still widespread, *Lobaria pulmonaria* is declining and considered endangered in many parts of Europe (Gärdenfors 2010), including our study region in central Spain (Martínez et al. 2003). *L. pulmonaria* is able to colonize multiple tree species, including the two oak *Quercus pyrenaica* Willd. and beech *Fagus sylvatica* L. on which it most commonly lives in our study region (Burgaz and Martínez 2003).

Data collection

The study area is located in the center of the Iberian Peninsula, in Sierra del Rincón, belonging to the Sistema Central Range. All study plots were in protected areas: two of them in the Hayedo de Montejo (Madrid province) and the other two in Sierra Norte de Guadalajara (Guadalajara province). The climate is Mediterranean, characterized by a drought period in summer time (average duration 1.8 months), but with an annual rainfall of 960 mm and a mean annual temperature of 9.5ºC mainly due to orientation and high elevation (900-2050m).

Like other lichens, *L. pulmonaria* has varying performance on different host trees species (Burgaz and Martinez 2003), so we collected data on lichens growing on two hosts: beech *sylvatica,* which is widespread throughout Western Europe and near its southernmost distribution limit in the study area, and *Quercus pyrenaica,* is a semi-deciduous oak, nearly endemic in the Iberian Peninsula. We established four 0.25 ha plots, two in predominantly oak and two in predominantly beech forest. All plots were at similar elevations and aspects and within 600 m to 16 km of one another (Table 1).

Table 1: Plots depiction and number of individuals monitored

Plot number	Number of individuals monitored	Locality name	Size (Ha)	Forest type	Altitude (m a.s.l.)
1	200	Montejo 1	0.25	Beech	1320
2	200	Montejo 2	0.25	Oak	1294
3	200	Cantalojas	0.25	Beech	1580
4	125	Santuy	0.65	Oak	1410

To measure size-specific survival and growth, 200 individuals per plot were marked with aluminum tags in 2011 (in plot 4, the sparse distributions of *L. pulmonaria* limited us to only 125 individuals). Selection of individuals was haphazard, with selection of individuals representing the range of sizes in the population (previously studied and ranging from 10 to 105040 mm^2), many different positions in the tree, as well as different trees, in order to present a wide range of microhabitats. Lichens on a total of 19 to 47 trees per plot were monitored. It is not trivial to distinguish one individual *L.pulmonaria* from other abutting individuals. We only marked and followed individual that we could clearly distinguish (although even then we do not know their genetic origins).

The field work was carried out from January 2011 to January 2013. All plots were monitored every 6 months, but the annual timing of these resurveys differed between plots. In two of our plots (one beech and one oak) we conducted surveys in January 2011, July 2011, January 2012, July 2012 and January 2013. The other two plots were established later. Plot 3 was surveyed in May 2011, October 2011, May 2012 and October 2012, the same for plot 4 except starting on October 2011. In every census individual survival was recorded, and a digital photo with a scale bar was taken (when fully hydrated) and later analyzed, using Photoshop 6.0, to determine individual area (Larsson and Gauslaa 2011).

In addition to survival and growth data, we also recorded several thallus, tree, or plot-specific information. To quantify the position of each thallus, we measured the height above ground (from 0 cm to 200 cm) and orientation on the trunk (0-359º). At the tree level, we measured: tree species (oak *Q. pyrenaica* or beech *F. sylvatica*), and canopy openness % (pictures taken with Canon EOS ED 50 and fish-eye lens of 180º field of view (see Belinchón et al 2007); canopy openness average value for south and north face of the trunk calculated with Gap Analysis 3.0). These measurements were taken at the initiation of the study and not repeated (Table 2).

At the plot level we recorded climate by placing three Hobo ® Pro V2 data loggers (Onset, USA) in each plot to record humidity and temperature at 1 hour intervals. For every inter-census six-month period we calculated the mean value for temperature (T ºC) and air moisture (HR %), averaging across all measurements of all three loggers during each period. To test whether the time available for possible photosynthesis would better correlate with performance, we also calculated the active hours of each period: we considered that *L.pulmonaria* individuals could be active during day light hours if the temperature is higher than 0ºC and air humidity is at least 90% (Table 2).

Table 2: Ecological variables and codes: at the spatial and temporal scales. Variables at the spatial scale were measured for every individual: host tree species (oak *Quercuspyrenaica* or beech *Fagussylvatica*), tree canopy openness (%), orientation aspect (0-359º; sin(orientation)=discriminate between West/East orientations; cos(orientation)=discriminates between North/South orientation) and height (0-200cm) where the individual is growing on. Variables at the temporal scale were measured and calculated for each plot and 6months period: temperature (mean temperature ºC), relative humidity of the air (%), light hours (number of day light hours linked to the latitude of the plot) and active hours (number of the light hours when *L.pulmonaria* individuals might be photosynthetically active: temperature >0ºC and relative humidity >90%).

Ecological variables and codes	
Spatial scale	Temporal scale
Host tree species (sp)	Temperature (T)
Tree canopy openness (Canopy)	Relative humidity (HR)
Orientation (OrW/E; OrN/S)	Light hours (LH)
Height (Ht)	Active hours (AH)

In addition to our demographic monitoring, we also monitored recruitment of new thalli and survival and growth of very small individuals, using a total of 360 20x20cm sampling squares (180 per plot in two of our plots: one beech and one oak). Four of these squares were placed on 45 different trees per plot, at three fixed heights in the tree (low (10-30cm), medium (60-80cm), high (130-150cm)) and also at the four main orientation aspects (N=0º, E=90º, S=180º, W=270º). When the squares were established, we mapped the size and locations of all adult *L.pulmonaria* in each. We also recorded the presence of reproductive structures on these adults, and mapped the locations of any small thalli. These plots were then remapped monthly to detect establishment of new thalli, and survival and growth of any previous recruits. As very small *L. pulmonaria* individuals are nearly round, diameter was measured and area was inferred for these measurements of very small recruits. Once each individual reached one year old, its diameter was measured. If the individual did not exist at the beginning of the period we recorded its initial diameter as 1mm (the ~ minimum size we can detect in the field).

Data analyses

Survival. For large individuals, survival was summarized for each six month period, To summarize survival for small individuals into compare time periods, we considered a small individual as surviving if it was present the first and last month of the six-months period, and dead if it existed at the beginning but not at the end of the period. We did not use information on individuals that appeared but then died within a time period.

Growth. For large individuals, growth was calculated as difference between ending and beginning size over each six month interval. For growth calculations and for all other analyses, with size expressed as the square-root of area. Since recruits are first measured after one year, we used annual change in size to estimate six month growth for these small thalli, assuming that increase in diameter each month of the first year is constant. As described below, in addition to conducting analyses to predict size and environment-specific mean growth rates, we also analyzed the residual variance in growth, as per Easterling et al (2000).

Recruitment. Raw recruitment is the total number of new individuals appearing in each sampling square over a given six-month period. To quantify the recruitment process, we broke recruitment into two variables: a binary variable for the presence of any recruits over a sampling period and, conditional on there being one or more recruits, the number of new recruits found. In both cases, adult area within a square has strong effects on the recruitment values. Thus, we included adult area per sampling quadrat in models of recruit presence, and we quantified recruit number as density: number/open area in a quadrat. Finally, we obtained a corrected number of recruits per adult area as the product of the probability of any recruits being present and the recruit density.

Predictive Models. To determine what factors influence each vital rate, we ran a set of alternative explanatory models (linear for growth and recruitment, and with a logistic link for survival). We then used AICc values to determine the support for different models. We ran these groups of models separately for the oak and beech data, due to multiple, strong differences in basic demographic rates and effects on these rates in the two types of forests. While it would be possible to include host species as an effect, the many interactions between hosts and other effects would greatly complicate the model sets, and also obscure real differences between thallus demography on the two hosts.

As another step to create relatively simple model sets, we also followed other authors in doing model construction in two steps. First, for each host type and demographic rate, we ran a set of models with differing spatial effects (Table 3) but all including a categorical "period" to include maximal temporal variation. We selected the best supported of these spatial models using AICc criteria, and then used the spatial effects from this best model in a series of models of with differing temporal effects.

Several data transformations were used to obtain the best representation of relationships between the vital rates and the explanatory variables. First, in all models, we used the square root of thallus area as the basic measure of size; for models with a simple and squared term for size, the variables used were thus sqrt(area) and area. Due to the extreme non-linearity of the relationship between size and survival, for these models, we used double log transformations of size in the models: log(log(squared root area+0.01)) and log(log(area+0.01)).

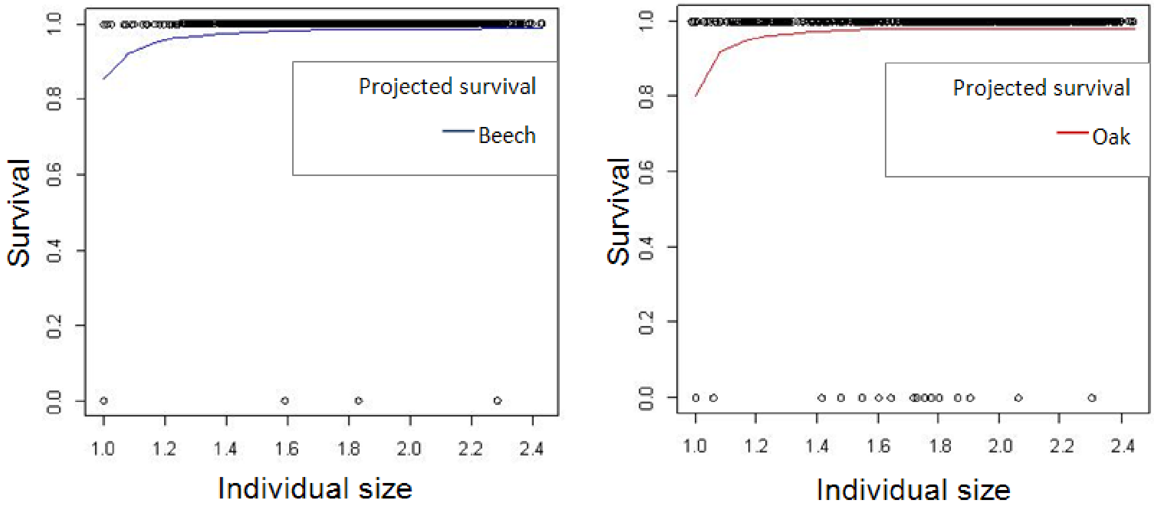
Results

L. pulmonaria demography rates

Our results indicate that *L. pulmonaria* demographic rates were strongly influenced by forest type. Anyway, there are some common patterns and some differences among host trees, as we detailed below:

Survival rates were very high in both tree species, and mainly for larger individuals, with 6 month survival of 98% across all individuals on oak and 99% on beech. Survival for recruits was lower in both host trees, but was nonetheless extremely high for such tiny individuals (88% on beech and 86% on oak). There was a modest size dependence in predicted survival rates fit to these data (Fig. 1).

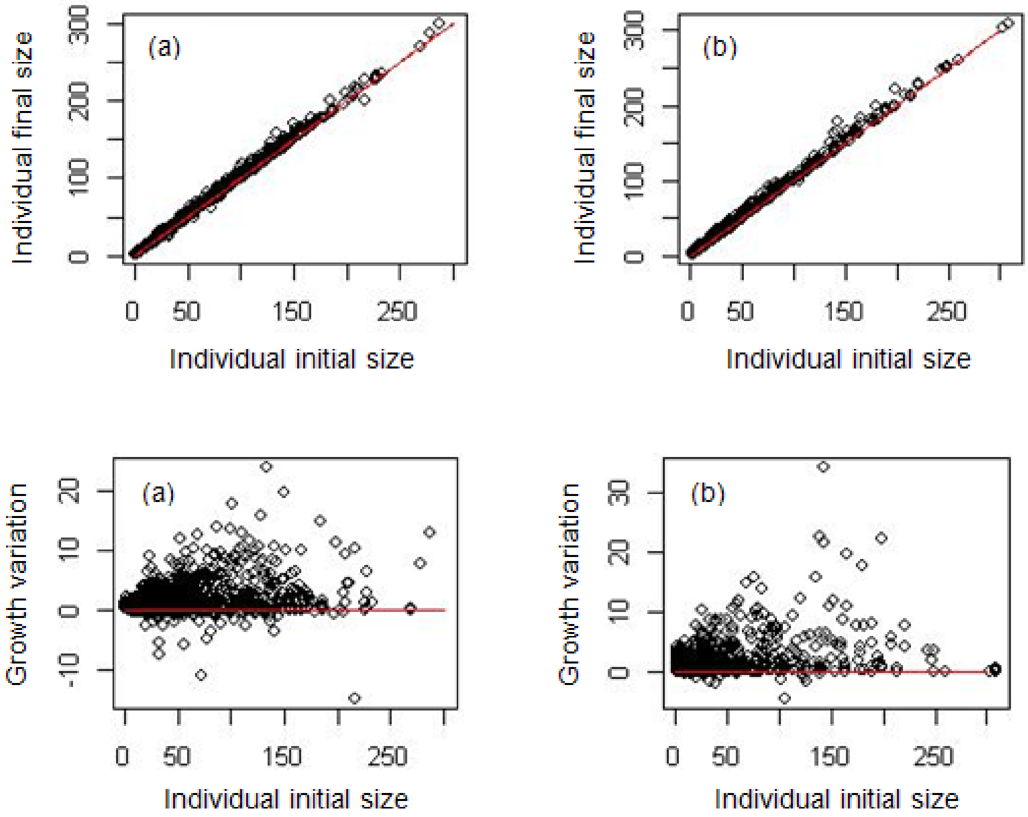
Figure 1: *Lobaria pulmonaria* survival rates. Data and projected survival values for individuals growing on beech or oak. Individual size as log(log(size0+1)).



Growth rates were size-dependent. Small individuals (20-40 mm^2) present the highest growth rate, being of 25%, and oscillating between 2.9% and 52%; medium individuals (900-1100 mm^2) have a growth rate of 8.3% (1.32%-27%), while in bigger individuals (>45000 mm^2) is 1.9% (1.11%-9.8%).

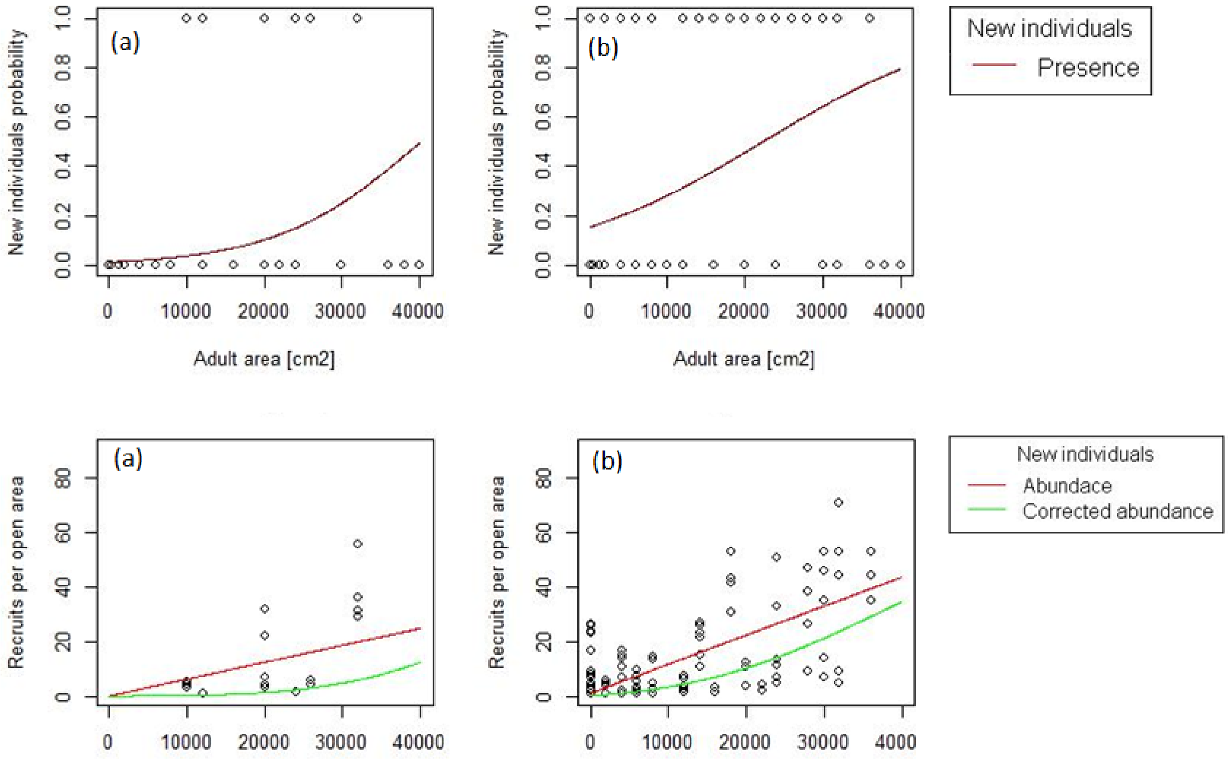
Growth rates were slow and similar on both hosts (Figure 2). We saw some evidence of size-dependency in growth rates, as well as some shrinkage. Variance in growth was lowest for large and small individuals, with the largest variance in medium-sized individuals (Fig. 2). As individuals reach big size and present slow growth rate, we can indicate that *L. pulmonaria* is a long-lived, slow-growing lichen.

Figure 2: *Lobaria pulmonaria* growth. Upper panel: growth = square root of initial size (mm^2) vs. square root of final size (mm^2) when growing on (a) beech or (b) oak. Lower panel: growth variation = (square root of final size (mm^2) – square root of initial size (mm^2)) vs. square root of initial size (mm^2) when growing on (a) beech or (b) oak. Red line= stasis line.



Recruitment. The most dramatic differences in demography between the two forest types occurred in the recruitment rates. *Lobaria pulmonaria* recruitment rate is about double on oak host trees comparing to beech, and also less dependent to adult presence (although both are, see Fig. 3). The presence of adult area is good in both cases, but almost “necessary” on beech. However, in the case of oak, although the presence of adult area improve the recruitment rate, it is possible to find recruitment although adult area lack (Fig. 3).

Figure 3: *Lobaria pulmonaria* recruitment. Upper panel: probability of appearance of new individuals vs. nearest adult area (cm^2) on (a) beech or (b) oak. Red line= presence model. Lower panel: new individuals abundance per open area vs. nearest adult area (cm^2) on (a) beech or (b) oak. Red line= abundance model; green line= corrected models as a result of presence model * abundance model.



Spatial and temporal variation in life history rates

The best supported models for each demographic rate were quite different between both tree species (Table 3).

In the best supported model, survival on oak is only influenced by light hours, with more light, as in summer, enhancing survival. In beech forests, we found more support for complex demographic effects of microhabitat. During dry periods (RH low) survival improved, and survival was higher in areas with more light: East and Southern orientations in the tree, as well as trees with more open canopy. Also the interaction canopy*OrE was significant and negative, showing the interaction between the medium and small scale.

Environmental variables affected growth rates were similar on both tree species (Table 3), being the periods with higher light (i.e. autumn-winter) when there is less growth. In beech, higher temperatures were also detrimental to growth rates. However, the positive effect of the T*LH interaction on growth shows that these temporal effects are complex. There is also substantial microsite variation in growth rates. In particular, height on the tree had a significant, negative effect on growth in both forest types. In oak forests, canopy openness positively affected growth (Table 3).

Fig. 4 represents the growth rate on oak and beech, but including the variables height in the tree where *L. pulmonaria* individuals grow and also considering two periods: winter and summer. This representations show that in the case of beech, individuals of *L. pulmonaria* always grow more in the lower areas of the trees. Besides, these individuals grow more in winter than in summer, but the influence of the height effect is lower in summer (Fig. 4). The growth pattern is less informative on oak, where *L. pulmonaria* individuals grow more in upper areas of the trees in winter, whereas in summer time they grow more in lower areas (Fig. 4).

Recruitment was positively influenced by humid periods, in both host trees, and also cold temperatures on beech (Table 3). Better places for recruitment on beech are a combination of open canopy trees and Northern/East aspects, providing a combination of light and humidity. On oak*,* recruitment rates are also influenced by position at small scale: low parts of the trunk are better places to recruit (Table 3).

Table 3: Coefficients for the best supported models for each demographic rate in the two tree species: beech and oak. Coefficients values shown for the variables included in each best supported models. Values correspond to the estimate value, except for the intercept. See table 2 for variable codes.

			Main variable		**Temporal variables**			**Spatial variables**				**Interactions**	
Vital rate		**Intercept**	**Size**	**Size^2**	**T**	**RH**	**LH**	**Or W/E**	**Or N/S**	**Ht**	**Canopy**	**OrN/S* Canopy**	**T* LH**
Survival	Beech	4.42	0.81			-0.25		0.36	-24.56		0.98	-1.59	
	Oak	-4.27	0.09				$3.8 \cdot 10^{-3}$						
Growth	Beech	21.58	0.03	$-7.2 \cdot 10^{-5}$	-2.08		$-9 \cdot 10^{-3}$			$-4 \cdot 10^{-3}$		$-4 \cdot 10^{-3}$	$9 \cdot 10^{-4}$
	Oak	7.44	0.05	-4.10^{4}			$-4.1 \cdot 10^{-3}$			$-3 \cdot 10^{-3}$	0.12		
		Intercept	**Adult size**		**T**	**RH**	**AH**	**Or W/E**	**Or N/S**	**Ht**	**Canopy**	**OrW/E* OrN/S**	
Recruitment													
Presence	Beech	-6.97	$1.26 \cdot 10^{-4}$					5.26	3.94	-0.028		$-5.3 \cdot 10^{-16}$	
	Oak	2.39	$6.41 \cdot 10^{-5}$			0.02				-0.013			
Abundance	Beech	-0.49	$5.79 \cdot 10^{-5}$				0.0158	0.28			2.48		
	Oak	-1.18	$1.06 \cdot 10^{-3}$				$7.8 \cdot 10^{-3}$						

Table 4: Mean values for variables at the temporal scale: Temperature ºC (T), relative air humidity % (HR) and number of light hours (LH) per plot and period.

Plot	Tree	Period	From-to period	LH	T	HR
1	Beech	1	Jan11-June11	2234.5	14.8	55.7
2	Oak	1			15.6	53.1
1	Beech	2	July11-Dec11	2163	11.1	67.4
2	Oak	2			11.3	67.1
1	Beech	3	Jan12-June12	2234.5	6.7	69.8
2	Oak	3			7.1	69.2
1	Beech	4	July12-Dec12	2163	10.9	71.7
2	Oak	4			11.2	72.8
3	Beech	5	May11-Oct11	2468.5	15.5	58.5
3	Beech	6	Oct11-Apr12	1929.5	4.3	63.6
4	Oak	6			5.1	68.1
3	Beech	7	May12-Oct12	2468	13.6	60.5
4	Oak	7			15.9	52.5

Discusion

Our parameterization of demographic rates for *L. pulmonaria* adds interesting knowledge to the short list of full life history characterizations for lichens. In part, our results confirm generalities about lichen life histories, with remarkably high life spans, if we take into account that this species is both large when adult (maximum thallus area in our study 40 000 cm^2) and grows comparably slow (Fig 2: stasis line). Previous studies have calculated life span for this lichen around 40 years (Öckinger and Nilsson 2010). Indeed, longevities for *L. pulmonaria* are comparable to that of many long-lived plants (Linares et al.2007; Garcia et al. 2008). However, we also find high variance in demographic performance from season to season, and due to microhabitat conditions, with especially large swings in growth rates of medium thalli and survival of small thalli (Figs. 1 and 2). Due to mircohabitat (mainly host tree species), we also found great variations in recruitment rates: more than four times-fold larger on oaks (Fig 3), due to its rougher barks (Barkman et al 1985), but also linked to other positive conditions, as could be more water retention. This observed variance in vital rates implies that individual lichens are very inflluenced by microenvironmental factors at both temporal and spatial scales. This is in the line of previous studys in the same area using a population or ecophysiological approach (Rubio-Salcedo et al 2014).

Survival is often considered the most important demographic rate (Franco and Silvertown 2004; Heppell et al. 2000). For *L. pulmonaria*, we found high and relatively invariant (Fig. 1) survival data of large individuals, almost near to 100%. Only some large individuals died: they detached linked to estochastic events (Rubio-Salcedo, personal obs.) Öckinger and Nilsson (2010) proposed this kind of esthastic events as a main cause of adult death: wind, storms, snow... In the forest we carried out our study, also livestock, mainly cows, might be causing accidental detach by scratching with tree barks. Survival is slightly lower due to very small individuals death events. We propose small individuals ($>20mm^2$) survival as a possible bottleneck for this species, as most of the registered deaths were of recently recruited individuals. Probably, they are more prone to death because they are less properly attached to the bark, as the lichen develops rizhines -support and attachment structures- while it grows (Nash 2008). It is also probable that they are more likely grazed (Gauslaa et al 2006), as they present lower proportions of protective secondary compounds. Even more, they face higher dissecation risk, as their smaller size leads them to present lower water storage capacity (Merinero et al 2014).

Lichens have no underground storage organ to buffer vital rates (growth or survival) against ephemerally poor conditions. So, their responses to microhabitat and microclimate changes are quite inmediate. Given cited lack of storage organs, high variance in growth rates is perhaps unsurprising. However, the coupling of high variance in growth with a relatively long life span is still surprising, given patterns seen in other taxa (Garcia et al.2008). Previously published lichen growth rates and those of *L. pulmonaria* (e.g. Gauslaa et al 2007)show a similar pattern of declining relative growth with size for all species (Fig.2), what would be expected from peripheral thallus growth (Armstrong and Smith1998; Aplin and Hill 1979). *Lobaria pulmonaria* grows at very similar rates regardless the host three species. That seems surprinsingly, as this species presents a clear size-distribution pattern depending on the tree it grows on. Rubio-Salcedo et al (2014), found that *L. pulmonaria* maximum sizes reached when it grows on beech is much larger than when it grows on oaks. This might be a real effect, but also due to what we have consider as "growth": in this study and in Rubio-Salcedo et al (2014), only area growth was considered. Foliose lichens grow in three dimensions, weight and area growth are usually coupled (Gauslaa et al 2009), but the relation among area growth / weight growth can strongly vary among microhabitats and variying conditions. That might be also explaining that *L. pulmonaria*, when grows on oaks, develops reproductive structures at half area than on beech. Individuals on beech might be larger in area, but not necessarily as well on weight. Individuals on oaks might have higher weights, being thicker and therefore presenting enough biomass and resources to develop reproductive structures.

Perhaps more interesting is the relationship between substrate type and recruitment (Fig.3). We found consistently higher recruitment rates of lichens on oak, compared to those in similar climate conditions on beech, almost four times higher. This suggests that *L. pulmonaria* may be better suited to oak substrate, at least for colonization. Belinchón et al (2011) found that *L. pulmonaria* is more likely found on oaks than on beech in this type of forest. Those authors proposed that this oaks, even when younger, promote *L. pulmonaria* presence and abundance at a population level. On the other hand, *Lobaria pulmonaria* individuals on beech live in a comparatively stable (Rubio-Salcedo et al 2014) and long-lived substrate, potentially allocating resources to thallus area growth (nor thickness) and other structural investments that would be beneficial over a longer period. This would explain slightly higher survival rates on beech. Previous work on lichens has demonstrated a trade-off between thallus thickness and dispersal (and thus reproduction) (Johansson et al. 2007), but the degree to which substrate influences this or other life history patterns (e.g., fecundity) remains unexplored.

In turning field data into model parameters, we faced two problems that are common to many demographic studies. First, we could not directly observe recruitment origin: both sexual and asexual propagules could lead to observed new individuals. The approach of estimating this recruitment rate using genetic studies (e.g. Otálora et al 2011) to detect parent origin is promising for other studies.

One of the most strinking results in this study is that conditions favoring survival are completely different from those favoring growth and recruitment. Wet periods with short light hours (winter periods) seem to promote growth and recruitment rates in *L. pulmonaria* in boths host trees. In this sense, we believe that macro conditions are more important that microconditons. In this type of Mediterranean forests, humidity and water availability is a major limiting factor (Valladares et al 2004). If air is humid (>90%, Máguas et al 1995), *L. pulmonaria* photobiont can activate, and photosinthetize which leads to lichen growth. Humidity, mainly rain, can activate lichen propagule movement, specially short-distance dispersion (propagules are carried by water drops). In contrast, dry, warm summer periods seem to promote survival. We think this type of performance responds to the fact that lichens can stay inactive for long periods. In the dehydrated state, lichens become inactive, but extremely resistant to long term high and low temperatures, high salt and high light conditions (Soni and Strasser 2008).

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References

Aplin PS, Hill DJ (1979) Growth analysis of circular lichen thalli. J Theor Biol 78:347–363

Armstrong RA (1973) Seasonal growth and growth rate-colony size relationships in six species of saxicolous lichens. New Phytol 72:1023–1030

Armstrong RA (1979) Growth and regeneration of lichen thalli with the central portions artificially removed. Environ Exp Bot 19:175–178

Armstrong RA (1983) Growth curve of the lichen *Rhizocarpon geographicum*. New Phytol 94:619–622

Armstrong RA (1987) Dispersal in a Population of the Lichen *Hypogymnia physodes*. Environ Exp Bot 27(3):357–363

Armstrong RA (1990) Establishment and survival of soredia and fragments of the lichen *Hypogymnia physodes*. New Phytol 114(2):239–245

Armstrong RA, Bradwell T (2011) Growth of lichens: a review. Symbiosis 53:1–16

Armstrong RA, Smith SN (1998) Does radial growth of the lichen *Parmelia conspersa* depend exclusively on growth processes at the lobe tip? Environ Exp Bot 39(3):263–269

Belinchón R, Martínez I, Aragón G, Escudero A, de la Cruz M (2011) Fine spatial pattern of an epiphytic lichen species is affected by habitat conditions in two forest types in the Iberian Mediterranean Region. Fungal Biolog,y 115: 270-1278

Belinchón R, Martínez I, Otálora MAG, Aragón G, Dimas J, Escudero A (2009) Fragment quality and matrix affect epiphytic performance in Mediterranean forest landscape. American Journal of Botany 96: 1974-1982

Benedict JB (2009) A review of lichenometric dating and its applications to archaeology. Am Antiq 74:143–172

Boggs CL, Ross CL (1993) The effect of adult food limitation on life history traits of *Speyeria mormonia*(Lepidoptera: Nymphalidae). Ecology 74:433–441

Bowler PA, Rundel PW (1975) Reproductive strategies in lichens. Bot J Linn Soc 70:325–340

Bradwell T, Armstrong RA (2007) Growth rates of *Rhizocarpon geographicum* lichens: a review with new data from Iceland. J Quat Sci 22:311–320

Chen B, Liao C (2004) Population models of farmed abalone *Haliotis diversicolor* supertexta exposed to waterborne zinc. Aquaculture 242:251–269

Cochran ME, Ellner S (1992) Simple methods for calculating age-based life history parameters for stage-structured populations. Ecol Monogr 62:345–364

Cole LC (1954) Population consequences of life history phenomena. Q Rev Biol 29:103–137

Conti ME, Cecchetti G (2001) Biological monitoring: lichens as bioindicators of air pollution assessment—a review. Environ Pollut 114:471–492

Cortés E (2002) Incorporating uncertainty into demographic modeling: application to shark populations and their conservation. Conserv Biol 16:1048–1062

Dahlgren JP, García MB, Ehrlén J (2011) Nonlinear relationships between vital rates and state variables in demographic models. Ecology (in press)

Dietrich M, Scheidegger C (1997) Frequency, diversity and ecological strategies of epiphytic lichens in the Swiss Central Plateau and the pre-Alps. Lichenologist 29:237

Doak DF, Morris WF (2010) Demographic compensation and tipping points in climate-induced range shifts. Nature 467:959–962

Easterling MR, Ellner SP, Dixon PM (2000) Size-specific sensitivity: applying a new structured population model. Ecology 81:694–708

Ellix Ch (2012) Lichen epiphyte diversity: a species, community and trtait-based review. Perspectives in Plant Ecology, Evolution and Systematics 14: 131-152

Franco M, Silvertown J (2004) A comparative demography of plants based upon elasticities of vital rates. Ecology 85:531–538

Garcia MB, Pico FX, Ehrlen J (2008) Life span correlates with population dynamics in perennial herbaceous plants. Am J Bot 95(2):258–262

Golm GT, Hill PS, Wells H (1993) Life expectancy in a Tulsa Cemetery: growth and population structure of the lichen *Xanthoparmelia cumberlandia*. Am Midl Nat 129:373–383

Goudie RI, Scheidegge, C, Hanel C, Munier A, Conway E (2011) New population models help explain declines in the globally rare boreal felt lichen *Erioderma pedicellatum* in Newfoundland. Endangered Species Research 13: 181-189

Gustafsson L, Fedrowitz K, Hazell P (2013) Survival and vitality of a macrolichen 14 years after transplantation on aspen trees retained at clearcutting. Forest Ecology and Management 291: 436-441

Haworth LA, Calkin PE, Ellis JM (1986) Direct measurement of lichen growth in the Central Brooks Range, Alaska, USA, and its application to lichenometric dating. Arct Alp Res 18:289–296

Heppell SS, Caswell H, Crowder LB (2000) Life histories and elasticity patterns: perturbation analysis for species with minimal demographic data. Ecology 81:654–665

Hijmans RJ, Cameron SE, Parra JL, Jones PG, Jarvis A (2005) Very high resolution interpolated climate surfaces for global land areas. Int J Climatol 25:1965–1978

Honegger R (1991) Functional aspects of the lichen symbiosis. Annu Rev Plant Physiol Plant Mol Biol 42:553–578

Hughes TP, Jackson JBC (1985) Population dynamics and life histories of foliaceous corals. Ecol Monogr 55:141–166

Jackson HB, St Clair LL, Eggett DL (2006) Size is not a reliable measure of sexual fecundity in two species of lichenized fungi. Bryologist 109:157–165

Johansson P, Rydin H, Thor G (2007) Tree age relationships with epiphytic lichen diversity and lichen life history traits on ash in southern Sweden. Ecoscience 14:81–91

Knops JMH, Nash TH III, Boucher VL, Schlesinger WH (1996) The influence of epiphytic lichens on the nutrient cycling of an oak woodland. Ecol Monogr 66:159–179

Larsson P, Gauslaa Y (2011) Rapid juvenile development in old forest lichens. Botany 89:65–72

Lättman H, Lindblom L, Mattsson JE et al (2009) Estimating the dispersal capacity of the rare lichen *Cliostomum corrugatum*. Biol Conserv 142:1870–1878

Linares C, Doak DF, Coma R, Díaz D, Zabala M (2007) Life history and viability of a long-lived marine invertebrate: the octocoral *Paramuricea clavata*. Ecology 88:918–928

Löbel S, Rydin H (2009) Dispersal and life history strategies in epiphyte metacommunities: alternative solutions to survival in patchy, dynamic landscapes. Oecologia 161: 569-579

Loso MG, Doak DF (2006) The biology behind lichenometric dating curves. Oecologia 147:223–229

MacDonald A, Coxson D (2013) A comparison of *Lobaria pulmonaria* population structure between subalpine fir (*Abies lasiocarpa*) and mountain alder (*Alnus incana*) host-tree species in British Columbia's inland temperate rainforest. Botany 91: 535-544

Martínez I, Flores T, Otálora MAG, Belinchón R, Prieto, M.; Aragón G, Escudero A (2012) Multiple scaleenvironmental modulation of lichen reproduction. Fungal Biology 116: 1192-1201

Matsuoka SM, Handel CM (2007) Nesting ecology of boreal forest birds following a massive outbreak of spruce beetles. J Wildl Manag 71:51–63

McFadden CS (1991) A comparative demographic analysis of clonal reproduction in temperate soft coral. Ecology 72:1849–1866

Morris WF, Doak DF (2002) Quantitative conservation biology: theory and practice of population viability analysis. Sinauer, Sunderland

Palmer TM, Doak DF, Stanton ML, Bronstein JL, Kiers T, Young TP, Goheen JR, Pringle RM (2010) Synergy of multiple partners, including freeloaders, increases host fitness in a multispecies mutualism. Proc Nat Acad Sci USA 107:17234–17239

Pfister CA (1998) Patterns of variance in stage-structured populations: evolutionary predictions and ecological implications. Proc Nat Acad Sci USA 95:213–218

Pike LH (1978) The importance of epiphytic lichens in mineral cycling. Bryologist 81:247–257

R Development Core Team (2011) R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. ISBN: 3-900051-07-0.http://www.R-project.org

Rubio-Salcedo M, Martínez I, Carreño F, Escudero A (2013) Poor effectiveness of the Natura 2000 network protecting Mediterranean lichen species. Journal of Nature Conservation 21: 1-9

Ramstad S, Hestmark G (2001) Population structure and size-dependent reproductive effort in *Umbilicaria spodochroa*. Mycologia 93:453–458

Rhoades FM (1983) Distribution of thalli in a population of the epiphytic lichen *Lobaria oregana* and a model of population dynamics and production. Bryologist 86:309–331

Rogers RW (1989) Colonization, growth and survival strategies of lichens on leaves in a subtropical rainforest. Aust J Ecol 14:327–333

Rosentreter R (1995) Lichen diversity in managed forests of the Pacific Northwest, USA. Mitt Eidgenöss Forsch 70:103–124

Salguero-Gomez R, Casper BB (2010) Keeping plant shrinkage in the demographic loop. J Ecol 98:312–323

Shriver R.K., Cutler, K. and Doak DF (2012) Comparative demography of an epiphytic lichen: support for general life history patterns and solutions to common problems in demographic parameter estimation. Oecologia 170: 137-146

Tummers B (2006) DataThief III.http://datathief.org/

van Straalen NM (1985) Comparative demography of forest floor *Collembola* populations. Oikos 45:253–265

Wikelski M, Thom C (2000) Marine iguanas shrink to survive El Nino. Nature 403:37–38

Woolhouse HW (1968) The measurement of growth rates in lichens. Lichenologist 4:32–33