Universidad Rey Juan Carlos

TESIS DOCTORAL

Incidencia de la fragmentación del hábitat y el clima en los patrones de diversidad taxonómica, funcional y filogenética de las comunidades de líquenes epífitos

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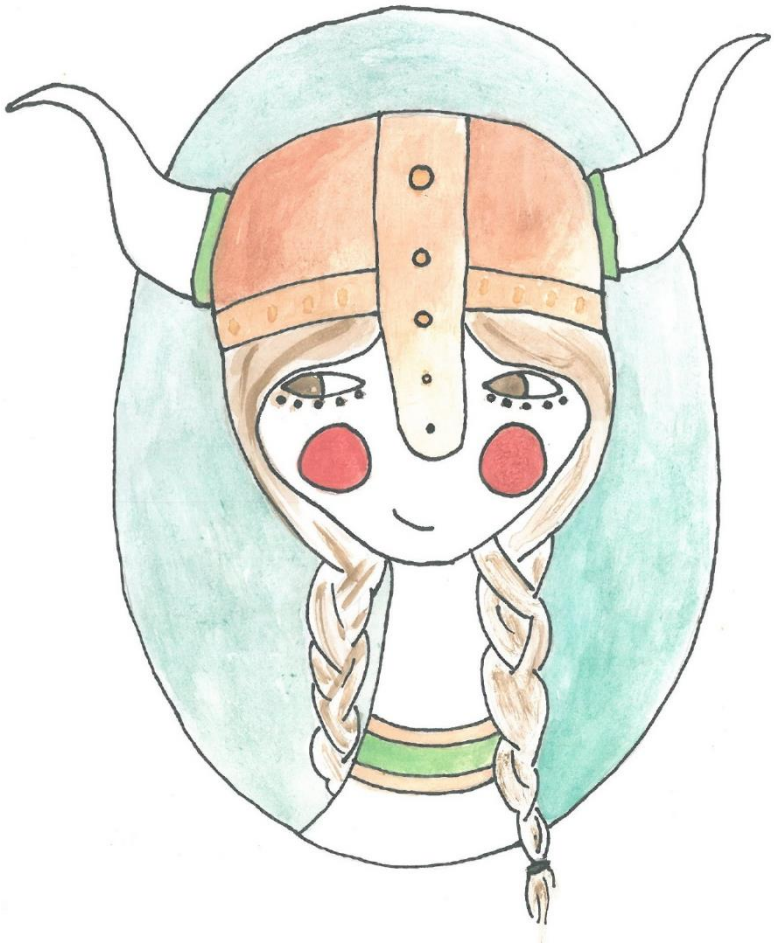

No matter the layers we hide,
A viking is still a viking
G.

ÍNDICE

Resumen

1 | RESUMEN ABREVIADO

Entender los factores que determinan los patrones de biodiversidad ha sido, y continúa siendo, uno de los retos centrales en Ecología. En el contexto actual de cambio global, evaluar la incidencia de los principales motores de cambio sobre los patrones de diversidad nos permite entender cómo es la respuesta de las comunidades en el presente y, potencialmente, cuál será su respuesta en escenarios futuros. A este respecto, la fragmentación del hábitat y el cambio climático han sido identificados como dos de los principales motores de cambio global, causantes de la actual pérdida de biodiversidad. Pero la biodiversidad es un concepto complejo y el modo de cuantificarla ha ido variando a lo largo del tiempo. Tradicionalmente, el estudio de la biodiversidad se ha basado en el estudio de los cambios en la composición y riqueza de especies (diversidad taxonómica). Sin embargo, esta aproximación tiene sus limitaciones ya que considera a todas las especies ecológicamente equivalentes y evolutivamente independientes, es decir, no tiene en cuenta el papel que juega cada especie dentro de la comunidad en función de sus rasgos y relaciones evolutivas. Para superar estas limitaciones y complementar la información proporcionada por la diversidad taxonómica, se analizan otras dos dimensiones de la diversidad, las llamadas diversidad funcional y diversidad filogenética. La diversidad funcional refleja la diversidad de rasgos morfológicos, fisiológicos y ecológicos presentes en una comunidad y cuantifica el papel y función de las especies en los ecosistemas. Por su parte, la diversidad filogenética refleja la historia evolutiva de la comunidad. A pesar de estar cada vez más reconocido el hecho de que ninguna de las tres dimensiones de la diversidad puede ser utilizada como subrogado de las demás, todavía se sabe poco sobre cómo se relacionan entre sí. Además, los escasos estudios que integran las tres dimensiones de la diversidad encuentran respuestas diferentes de estas en función de los factores ambientales y de la escala considerados. Por todo ello, el objetivo general que persigue la presente tesis es evaluar el efecto de la fragmentación del hábitat y el clima en los patrones de diversidad de las comunidades de líquenes epífitos, mediante una aproximación que integre las dimensiones taxonómica, funcional y filogenética.

Para ello muestreamos las comunidades de líquenes epífitos a lo largo de la Península Ibérica y a lo largo de Europa. En el primer caso seleccionamos dos sistemas de hayedos fragmentados localizados bajo condiciones climáticas contrastadas, en concreto, trabajamos en 22 fragmentos en la región Atlántica y 25 fragmentos en la región Mediterránea. Por otra parte, trabajamos en 23 bosques de haya localizados a lo largo de un gradiente latitudinal desde el sur de Suecia al sur de Italia (aproximadamente 3000 km), cubriendo un amplio

gradiente climático. En ambas aproximaciones, registramos la composición de las comunidades cuantificando la cobertura de cada una de las especies presentes. Además, obtuvimos la información de cuatro rasgos cualitativos para toda la comunidad de líquenes epífitos y, para los macrolíquenes, medimos diez rasgos cuantitativos relacionados con la actividad fotosintética, el balance hídrico y la adquisición de nutrientes. Por último, para cada uno de los bosques, construimos un árbol filogenético combinado utilizando cuatro marcadores moleculares (nuITS, nuLSU, mtSSU y RPB1).

Tanto la fragmentación del hábitat como el clima tienen un efecto en los patrones de diversidad de las comunidades de líquenes. Sin embargo, los factores concretos que determinan los patrones de diversidad taxonómica, funcional y filogenética varían en función de la dimensión de la diversidad. De manera general, la fragmentación ejerce un impacto negativo disminuyendo la diversidad de las comunidades de líquenes epífitos mientras que variables relacionadas con la estacionalidad de la temperatura y la precipitación son los determinantes climáticos más importantes de los patrones de diversidad a lo largo de Europa. Por otra parte, y de manera consistente a lo largo de la tesis, los resultados muestran que la diversidad funcional está relacionada con la filogenética (relación positiva) y taxonómica (relación positiva o negativa) mientras que estas últimas no se encuentran relacionadas entre sí. Este resultado sustenta la hipótesis de que las comunidades responden a las presiones ambientales a través de los rasgos funcionales de las especies que las componen. En relación a los rasgos estudiados, encontramos que los rasgos cualitativos de líquenes (forma de crecimiento, tipo de fotobionte y estrategia reproductiva) son buenos indicadores de los efectos de la fragmentación y de las variaciones climáticas a escala de bosque. Sin embargo, rasgos cuantitativos finos relacionados con la actividad fotosintética, el balance hídrico y la adquisición de nutrientes no responden con la misma intensidad a los cambios climáticos. Al analizar en detalle los determinantes de la variación funcional de las comunidades de líquenes a escala continental encontramos que, en contra de lo esperado en plantas vasculares, la variabilidad intraespecífica tiene una contribución muy importante, incluso mayor que el recambio de especies.

En conclusión, los patrones de diversidad funcional, filogenética y taxonómica están influidos por distintos factores abióticos y proporcionan una información complementaria de la respuesta de las comunidades frente a tales factores. Este resultado pone de manifiesto la importancia de usar un enfoque integrador y considerar explícitamente las tres dimensiones de la diversidad para poder tener una visión completa de la dinámica de las comunidades. Aun así, es cierto que, tras evaluar la relación entre las tres dimensiones de la diversidad a lo

largo de gradientes ambientales a distintas escalas espaciales, comprobamos que la diversidad funcional juega un papel clave pudiendo explicar, al menos en parte, la respuesta de las diversidades filogenética y taxonómica. En concreto, los rasgos *tipo de fotobionte*, *forma de crecimiento y estrategia reproductiva* aparecen como indicadores ecológicos de alerta temprana que informan sobre los efectos de la fragmentación del hábitat y el clima. Sin embargo, las variables climáticas a escala de bosque explican un bajo porcentaje de la variabilidad de los rasgos cuantitativos relacionados con la actividad fotosintética, el balance hídrico y la adquisición de nutrientes por lo que podrían responder a factores a microescala o estar más relacionados con su efecto en el funcionamiento de los ecosistemas. Por último, la variabilidad intraespecífica aparece como un componente clave, incluso superior que el recambio de especies, a la hora de determinar los cambios funcionales en las comunidades de líquenes epífitos.

2 | SUMMARY

Understanding the factors that determine the patterns of biodiversity is one of the major goals in Ecology. Assessing the effect of the main drivers of global change over the patterns of biodiversity is crucial to understand the response of the communities under contrasting environmental conditions. In this line, habitat fragmentation and climate change have been identified as major drivers of global change, responsible of the increasing biodiversity loss. Traditionally, the study of biodiversity has been based on composition and richness (i.e. taxonomic diversity). However, this species-centric approach is limited by the assumption that all species are ecologically equivalent and evolutionary independent. To overcome this limitation and to complement the information provided by the taxonomic diversity, two new facets of biodiversity are quantified, the so-called functional and phylogenetic diversities. The functional diversity reflects the variety of morphological, physiological and ecological traits found in the community and quantifies the role and function of species in the ecosystems, while phylogenetic diversity reflects the evolutionary history of a community. Previous studies have found differences in the response of the three diversity dimensions to environment and in relation with the different scales considered. Moreover, the relationships between these different dimensions is still unclear. For these reasons, the general aim of this PhD thesis is to assess the effect of habitat fragmentation and climate over the patterns of biodiversity in lichen epiphytic communities, by integrating the taxonomic, functional and phylogenetic dimensions.

We surveyed the epiphytic lichen communities across the Iberian Peninsula and Europe. In the Iberian Peninsula, we selected beech forest remnants located under contrasting climatic conditions, in particular, we selected 22 beech forest remnants within the Atlantic region and 25 beech remnants in the Mediterranean region. In Europe, we selected 23 beech forests located along a latitudinal gradient from southern Sweden to southern Italy (ca. 3000 km), reflecting a broad climatic gradient. For all the forests surveyed, both in the Iberian Peninsula and across Europe, we quantified the cover of all epiphytic lichen species occurring in the communities. In addition, we recorded four qualitative traits, and for macrolichens, we also quantified ten quantitative traits related to photosynthetic performance, water use strategy and nutrient acquisition strategy. Finally, for each forest, we built a combined phylogenetic tree using four molecular markers (nuITS, nuLSU, mtSSU y RPB1) and including all lichen species occurring in these forests.

Both, habitat fragmentation and climate, modify the patterns of biodiversity in lichen epiphytic communities. However, the specific factors that determine the taxonomic,

functional and phylogenetical diversity patterns vary depending on the diversity dimension considered. Overall, habitat fragmentation showed a negative impact decreasing the diversity of epiphitic lichen communities, while variables related with temperature and precipitation seasonality were the most important climatic determinants of diversity patterns throughout Europe. On the other hand, our results showed that functional diversity is related with phylogenetical diverity (positive relationship) and with taxonomic diversity (positive and negative relationships), while these latter are not related to each other. This result supports the hypothesis that species present in natural communities respond to environmental changes throught their functional traits. Regarding the different traits studied, soft qualitative traits such as growth form, type of photobiont and reproductive strategy are good indicators of the effects of fragmentation and climatic changes at forest scale. However, the hard quantitative traits related to photosynthetic performance, water use strategy and nutrient acquisition strategy do not respond with the same intensity to climatic changes.

In summary, patterns of functional, phylogenetic and taxonomic diversity are determined by distinct abiotic factors and provide complementary information about the response of the communities to cope with these contrasting environments. This result highlights the need to use a pluralistic approach considering the three dimensions of diversity to obtain a complete picture of the dynamic of the communities. However, after analyzing the relationships between taxonomic, functional and phylogenetic dimensions along wide environmental gradients and at different spatial scales, we observed that functional diversity has a key role mediating, at least in part, changes in phylogenetic and taxonomic diversity. In particular, the soft traits *type of photobiont, growth form* and *reproductive strategy*, were identified as valuable early-warning ecological indicators of habitat fragmentation and climate. In turn, the effect of climate over the hard traits related with photosynthetic performance, water use strategy and nutrient acquisition was lower. Finally, intraspecific trait variability showed high relative contribution, even more important than species turnover, explaining the functional changes in lichen epiphytic communities.

3 | ANTECEDENTES

Uno de los retos en ecología de comunidades es entender los procesos y reglas que determinan la coexistencia de las especies y la composición de las comunidades (Gleason 1926, Pavoine & Bonsall 2011). En este sentido, alcanzar un conocimiento detallado sobre los patrones de diversidad y los factores subyacentes, es uno de los objetivos centrales en esta disciplina. Ante el contexto actual de cambio global, evaluar los efectos de un amplio abanico de condiciones ambientales sobre las comunidades biológicas permite predecir su respuesta ante escenarios futuros y, en consecuencia, adoptar estrategias de gestión y conservación eficaces para mitigar los impactos del citado cambio. Con tal fin, es cada vez más evidente la necesidad de utilizar una perspectiva multidimensional que no sólo considere la riqueza y composición de las especies que conforman las comunidades, sino que también tenga en cuenta las funciones que dichas especies desempeñan en los ecosistemas y la diversidad de linajes que representan. Por todo ello, evaluar la diversidad taxonómica, funcional y filogenética de las comunidades biológicas y los efectos que los principales motores de cambio global ejercen sobre ellas puede ayudarnos a entender cómo está distribuida la biodiversidad en el espacio hoy en día y, potencialmente, como serán las comunidades en el futuro.

3.1. Fragmentación del hábitat y cambio climático como motores de cambio global

La fragmentación del hábitat y el cambio climático han sido identificados como dos de los principales motores de cambio global, causantes de la actual pérdida de biodiversidad (Gibb & Hochuli 2001, Schimiegelow & Mönkkönen 2002, Leadley et al. 2010, Bálint et al. 2011). La creciente conversión de hábitats naturales en terrenos agrícolas o urbanísticos ha transformado grandes áreas continuas de bosque en pequeños fragmentos aislados. Desde mediados del siglo XVIII la cobertura forestal a nivel mundial se ha reducido en más de un tercio (Hansen et al. 2013) y las previsiones para 2030 indican una reducción continuada a una tasa de pérdida más lenta (d'Annunzio et al. 2015). Por su parte, desde la época preindustrial, la temperatura global ha aumentado 0.2 ºC por década hasta que, en 2017, se registró un incremento de 1 ºC respecto a los valores preindustriales (Allen et al. 2018). Para finales del siglo XXI, las estimaciones sobre cambio climático frente a diversos escenarios futuros apuntan a un incremento de la temperatura comprendido entre los 0.3 ºC y los 4.8 ºC, acompañado por una alteración en el régimen de precipitaciones, con eventos extremos de mayor intensidad y duración (Pachauri & Meyer 2014).

La **fragmentación del hábitat** puede ir acompañada por una reducción en la cantidad de territorio, que pasa a estar distribuido en fragmentos de menor tamaño en los que el efecto borde y el contacto con el hábitat circundante son mayores (Fahrig 2003, Haddad et al. 2015), y en los que la conectividad y el potencial de dispersión de las poblaciones son menores (Guerin et al. 2014). La existencia de fragmentos de hábitat más pequeños lleva asociada una disminución no sólo en la riqueza de especies que albergan sino, presumiblemente, en la diversidad de rasgos funcionales y de diversidad genética (Guerin et al. 2014). El impacto de la fragmentación sobre la biodiversidad puede responder a distintas causas como, por ejemplo, el espacio disponible, la heterogeneidad ambiental y el efecto borde. En primer lugar, por una cuestión de azar, se reduce el espacio disponible y, con él, la cantidad de recursos y áreas de refugio con lo que los fragmentos resultantes pueden albergar un menor número de individuos y de especies. En segundo lugar, la heterogeneidad ambiental en el interior de fragmentos más pequeños es menor (Gignac & Dale 2005), de manera que también se reduce el número de especies diferentes capaces de persistir bajo un rango de condiciones ambientales más estrecho. En tercer lugar, la cantidad de borde aumenta respecto a la cantidad de zona central o *core area* (Sih et al. 2000), ambas con condiciones microclimáticas muy contrastadas. En el caso de los bosques, las zonas centrales se caracterizan por tener mayor humedad, menor insolación y menores oscilaciones térmicas de tal manera que una reducción en el tamaño de los fragmentos perjudica la presencia de especies que requieran tales condiciones ambientales. Por el contrario, en los bordes del fragmento, se verán favorecidas especies más tolerantes a condiciones más secas, a la insolación y a la fluctuación de la temperatura y, además, será mayor la llegada de propágulos desde otros lugares (incluyendo aquellos de especies generalistas) (Schimiegelow & Mönkkönen 2002). Por tanto, los impactos del llamado "efecto borde" pueden ser tanto positivos como negativos dependiendo de las especies evaluadas, aunque aquellas especies con requerimientos de hábitat más especializados o aquellas que originalmente ocupaban grandes superficies continuas de hábitat natural se verán potencialmente perjudicadas (Swihart & Gehring 2003). En todo caso, un estudio que analizó la cobertura global de los bosques a lo largo de los cinco continentes y utilizó una serie temporal de 35 años (Haddad et al. 2015), reveló que la disminución del área de los fragmentos, la creación de bordes y el aumento del aislamiento entre fragmentos asociados al proceso de fragmentación, conducía no sólo a pérdidas de biodiversidad sino también a la degradación del funcionamiento de los ecosistemas (Haddad et al. 2015).

Por su parte, el aumento de las temperaturas y la alteración en el régimen de precipitaciones ligados al **cambio climático** tienen efectos significativos en los patrones de distribución de las especies llegando incluso a actuar como causa de extinción de las mismas (Thomas et al. 2004, Bálint et al. 2011). El cambio climático afecta a todos los niveles de la biodiversidad, desde los organismos a los biomas (Bellard et al. 2012), y además puede afectar a las especies de manera directa ocasionando un estrés fisiológico o, de manera indirecta, modificando, por ejemplo, las interacciones entre las mismas (Harley 2011). De este modo, considerando los rangos de tolerancia fisiológica de diferentes especies frente a las condiciones ambientales, pueden detectarse cambios en la abundancia y distribución de las especies a lo largo de extensos gradientes ambientales, por ejemplo, en latitud o altitud (Bálint et al. 2011). Como hemos mencionado previamente, el cambio en las condiciones climáticas también afecta a las relaciones interespecíficas que se refleja en cambios en la composición y dinámica de las comunidades y, en último término, en el funcionamiento de los ecosistemas (Bellard et al. 2012). Para poder comprender los efectos del cambio climático sobre la biodiversidad es importante tener en cuenta cómo las especies pueden hacerle frente, ya sea modificando su distribución espacial, su fenología o su fisiología (Bellard et al. 2012). De esta manera, los estudios basados en extensos gradientes latitudinales nos ofrecen la oportunidad de evaluar el efecto de un amplio abanico de condiciones climáticas sobre la distribución de la biodiversidad. Esto nos permite tener una imagen más realista y precisa de la respuesta de las comunidades naturales frente a condiciones climáticas contrastadas dado que dichas comunidades se localizan a lo largo de gradientes de temperatura o humedad (McGill et al. 2006).

3.2. La biodiversidad: un concepto complejo y multidimensional

Qué se entiende por biodiversidad y cómo se cuantifica son cuestiones que se han tratado desde distintos puntos de vista a lo largo del tiempo. De manera tradicional, la biodiversidad se ha abordado desde una perspectiva taxonómica, en la que se evaluaba el número, abundancia y composición de especies (Rosenzweig 1995). Esta aproximación ha sido de gran utilidad en ecología y ha servido para esclarecer patrones generales a distintas escalas, desde la vecindad hasta la escala global, explicando, por ejemplo, la variación de la riqueza de especies en función de la altitud o la latitud (Mittelbach 2002, Sanders & Rahbek 2012). En la actualidad, se reconocen las limitaciones de esta aproximación ya que la biodiversidad se identifica como un concepto complejo y multidimensional. Como tal, para complementar la información que proporciona la dimensión **taxonómica**, los ecólogos han cuantificado

otras dos dimensiones de la diversidad, la **funcional** y la **filogenética** (Devictor et al. 2010). Las especies dejan de verse como entidades ecológicamente idénticas y filogenéticamente independientes para pasar a verse como entidades que desempeñan distintas funciones en los ecosistemas y que se relacionan evolutivamente (Swenson 2011). En particular, la diversidad funcional refleja la diversidad de rasgos morfológicos, fisiológicos y ecológicos dentro de las comunidades biológicas (Petchey & Gaston 2006), mientras que la diversidad filogenética refleja la historia evolutiva de las especies que forman dichas comunidades (Webb et al. 2002). A pesar de que el número de trabajos integrando la respuesta de las tres dimensiones de la diversidad se ha incrementado en la última década, todavía son escasos los estudios de este tipo. Hay que destacar que la mayoría de ellos encuentra diferencias en la respuesta de las tres dimensiones de la diversidad cuando se analizan a distintas escalas y que, además, se encuentran relacionadas con distintos factores ambientales (Devictor et al. 2010, Purschke et al. 2013, Arnan et al. 2015, Dainese et al. 2015). Asimismo, existe un sesgo de estudios hacia los grupos taxonómicos más conspicuos tales como plantas vasculares, mamíferos y aves (Thuiller et al. 2011). Por el momento, ninguna de estas tres dimensiones puede ser utilizada como subrogado de las demás ya que proporcionan información complementaria. En consecuencia, para establecer conclusiones extrapolables, parece necesario profundizar en la respuesta e interrelación entre las tres dimensiones de la diversidad ampliando los grupos de organismos, rasgos funcionales y gradientes ambientales estudiados.

Las implicaciones de la aproximación multidimensional a la biodiversidad son tanto teóricas como aplicadas, y comprenden desde los procesos de ensamblaje de comunidades hasta la conservación y el desarrollo de planes de gestión focalizados en paliar los efectos de los distintos motores de cambio global. En lo que respecta al ensamblaje de comunidades, una visión plural de la diversidad ayuda a desentrañar la respuesta de las comunidades frente a diferentes eventos ecológicos e históricos. Teniendo en cuenta que la aproximación funcional se basa en la asunción de que las especies serán capaces de persistir en las comunidades según los rasgos funcionales que posean (Götzenberger et al. 2012, Shipley et al. 2016), cuantificar la diversidad funcional sería crucial para entender cómo distintos factores tanto bióticos como abióticos filtran aquellas especies con un determinado conjunto de rasgos (Le Bagousse-Pinguet et al. 2017). Además, considerar la diversidad filogenética de la comunidad no sólo podría integrar la información de rasgos funcionales no medidos, sino que ayudaría a profundizar en el conocimiento de los procesos evolutivos que han dado forma a los patrones de diversidad actuales (Webb et al. 2002, Gerhold et al. 2015). Desde

un punto de vista aplicado, los recursos destinados a conservación son limitados y, como tal, dónde invertir dichos recursos es una cuestión clave. Tradicionalmente, la distinción de áreas prioritarias para conservación se ha basado en un criterio taxonómico según el cual lo importante era conservar un alto número de especies o unas determinadas especies (Myers et al. 2010). Sin embargo, esta tendencia está cambiando en torno a dos ideas: una mayor diversidad filogenética favorece la respuesta de las especies frente a los cambios ambientales (Forest et al. 2007) y una mayor diversidad funcional asegura el funcionamiento y estabilidad de los ecosistemas (Cadotte et al. 2011). En definitiva, analizar los patrones de distribución de las tres facetas de la biodiversidad permitirá identificar puntos calientes que requieran una especial atención ayudando no sólo a conservar un gran número de especies sino también de funciones y linajes. En relación con el cambio global, abordar el estudio de las comunidades *per se* considerando, además, sus rangos funcionales y su diversidad genética y cómo responden a los factores abióticos, puede mejorar nuestro conocimiento sobre los cambios en la estructura, dinámica y función de los ecosistemas (McGill et al. 2006) no sólo en el presente sino también en el futuro (Guerin et al. 2014).

3.3. Los líquenes como organismos modelo en estudios ecológicos: una aproximación funcional

Los líquenes ofrecen un excepcional modelo de estudio para evaluar el impacto de diferentes factores ambientales sobre la diversidad ya que son organismos poiquilohídricos cuya actividad fisiológica está estrechamente determinada por las condiciones ambientales que les rodean (Nash 2008). En concreto, carecen de mecanismos para regular activamente su contenido hídrico y, dado que están fisiológicamente activos gracias a ciclos de hidratación-deshidratación, su actividad fisiológica va a estar íntimamente ligada a las condiciones de su entorno (Green et al. 2001). Por otra parte, al carecer de raíces, adquieren todos los nutrientes de la atmósfera por lo que su contenido en nutrientes va a depender de la cantidad de dichos elementos en el ambiente. Estas características los sitúan entre los organismos más sensibles a las condiciones ambientales y les confieren un gran valor como indicadores de alerta temprana de la respuesta de otros organismos menos sensibles con los que coexisten (Giordani et al. 2012, Matos et al. 2015). Además, tienen una contribución clave en el funcionamiento de los ecosistemas, siendo refugio para una gran variedad de invertebrados y estando implicados, entre otros, en los ciclos del agua y de los nutrientes, y en las redes tróficas de los ecosistemas (Ellis 2012).

A pesar de su valioso papel como indicadores ecológicos y como organismos clave en el funcionamiento de muchos ecosistemas, como por ejemplo los forestales (Giordani et al. 2012, Ellis 2012), la mayoría de los trabajos que se han desarrollado hasta el momento en relación a la diversidad filogenética y funcional de las comunidades, se han centrado en grupos de organismos bien conocidos. En particular, la denominada ecología funcional se ha desarrollado basándose principalmente en estudios con plantas vasculares, desarrollando protocolos detallados y estandarizados (Cornelissen et al. 2003, Pérez-Harguindeguy et al. 2013) y describiendo patrones de respuesta a escala global (Reich et al. 2003, Wright et al. 2004). Sin embargo, hay una necesidad de extender los paradigmas existentes en plantas a otros grupos de organismos especialmente si consideramos que una gran proporción de la biodiversidad está representada por lo que denominamos "diversidad críptica", en la que incluiríamos a los líquenes. El primer paso para entender la respuesta de estos organismos utilizando una aproximación funcional es seleccionar el conjunto de rasgos a medir, incluyendo aquellos que informen sobre cómo afrontan distintos desafíos, por ejemplo, respecto a la dispersión, establecimiento y persistencia bajo determinadas condiciones ambientales (Weiher et al. 1999). Por otro lado, es muy importante tener en cuenta la cantidad de recursos que hay que invertir para obtener estos rasgos y la información que proporcionan. En este sentido, podemos distinguir dos tipos de rasgos, los llamados 'gruesos' o *soft* (*sensu* Belluau & Shipley 2018) son menos costosos de medir y dan una visión más integradora de diferentes funciones, pero informan poco sobre funciones fisiológicas concretas. Por el contrario, los rasgos 'finos' o *hard* (*sensu* Belluau & Shipley 2018) son mucho más costosos de medir, pero dan una información más precisa sobre funciones fisiológicas concretas. Por tanto, comprender no sólo la respuesta de estos rasgos frente a distintas condiciones ambientales sino evaluar hasta qué punto los rasgos gruesos son subrogados de los finos, puede ayudarnos a establecer un marco de trabajo que nos guíe en la selección de los rasgos ecológicamente más importantes para estos organismos y en el establecimiento de protocolos de trabajo.

4 | OBJETIVOS Y ESTRUCTURA DE LA TESIS

El objetivo general de la presente tesis doctoral se centra en evaluar el efecto de la fragmentación del hábitat y el clima en los patrones de diversidad taxonómica, funcional y filogenética de las comunidades de líquenes epífitos. Para la consecución de este objetivo general, la tesis se estructura en seis objetivos específicos que se materializan en seis capítulos:

Capítulo 1: Evaluar el efecto de la fragmentación de hábitat, el clima y la calidad de hábitat en la diversidad taxonómica, funcional y filogenética de las comunidades de líquenes epífitos en hayedos de la Península Ibérica. Además, analizamos si el efecto de estos factores abióticos sobre las tres dimensiones de la diversidad ocurre de forma directa o de forma indirecta a través de la diversidad funcional. Por último, testamos cómo están interrelacionadas las tres dimensiones de la diversidad en las dos regiones biogeográficas estudiadas (Atlántica y Mediterránea).

Capítulo 2: Determinar cuáles son los principales factores abióticos que dan forma a los patrones de diversidad taxonómica, funcional y filogenética de las comunidades de líquenes epífitos presentes en hayedos a lo largo de un gradiente latitudinal europeo (desde el sur de Suecia hasta el sur de Italia). También evaluamos la correlación entre las tres dimensiones de la diversidad a lo largo del gradiente y la existencia de una configuración geográfica tanto en la composición de especies como en la estructura funcional de las comunidades en respuesta a las condiciones ambientales.

Capítulo 3: Cuantificar la contribución relativa del recambio de especies y la variabilidad intraespecífica a la hora de determinar los cambios funcionales de las comunidades de líquenes epífitos en hayedos a lo largo de Europa. Además, evaluamos el papel del clima explicando los cambios funcionales a escala de comunidad debidos tanto al recambio de especies como a la variabilidad intraespecífica.

Capítulo 4: Analizar la variación y covariación de los rasgos de líquenes epífitos de hayedos a lo largo de un gradiente latitudinal. Aplicando el método comparado para integrar la aproximación funcional y la relación filogenética entre las especies, evaluamos hasta qué punto la variabilidad inter- e intraespecífica controlan la variación de los rasgos funcionales. Además, examinamos si los patrones de covariación entre los rasgos son consistentes entre las especies y dentro de las mismas y estudiamos la respuesta de cada rasgo frente a diferentes variables climáticas.

Capítulo 5: Identificar las condiciones climáticas en las cuales las comunidades de líquenes epífitos maximizan su diversidad taxonómica, funcional y filogenética y así comparar si los nichos óptimos de las diferentes dimensiones de la biodiversidad son congruentes o no. Además de identificar puntos calientes de biodiversidad de líquenes en Europa para las tres dimensiones de la diversidad, nos centramos en encontrar los óptimos climáticos para el conjunto de los rasgos funcionales seleccionados y de las familias de líquenes encontrados a lo largo del gradiente latitudinal.

Capítulo 6: Elaborar un listado de especies que recoja la diversidad de líquenes epífitos encontrados sobre *Fagus sylvatica* L. en hayedos a lo largo de Europa. Construir una herramienta online de acceso libre para que este listado de especies pueda ser actualizado con nuevos registros por parte de cualquier usuario.

5 | LISTADO DE MANUSCRITOS

Hurtado P, Prieto M, Aragón G, Escudero A & Martínez I. 2019. Critical predictors of functional, phylogenetic and taxonomic diversity are geographically structured in lichen epiphytic communities. *Journal of Ecology,* 00: 1─14. DOI: 10.1111/1365-2745.13189

Hurtado P, Prieto M, de Bello F, Aragón G, Giordani P, Díaz-Peña EM, Vicente R, Košuthová A, Merinero S, Benesperi R, Bianchi E, Mayrhofer H, Nascimbene J, Grube M, Wedin M, Westberg M & Martínez I. Contrasting climatic predictors determine patterns of taxonomic, functional and phylogenetic diversity in lichen communities along a European latitudinal gradient. *En preparación.*

Hurtado P, Prieto M, Aragón G, de Bello F & Martínez I. Intraspecific variability drives functional changes in lichen epiphytic communities along Europe. *En preparación.*

Hurtado P, Prieto M, Martínez-Vilalta J, Giordani P, Aragón G, López-Angulo J, Košuthová A, Merinero S, Díaz-Peña EM, Rosas T, Benesperi R, Bianchi E, Grube M, Mayrhofer H, Nascimbene J, Wedin M, Westberg M & Martínez I. Disentangling functional trait variation and covariation in epiphytic lichens along a continent-wide latitudinal gradient. *En revisión en Proceedings of The Royal Society B.*

Hurtado P, Matos P, Aragón G, Branquinho C, Prieto M & Martínez I. Are functional, phylogenetic and taxonomic optimal climatic niches congruent along a continent-wide latitudinal gradient? *En preparación.*

Hurtado P, Aragón G, Martínez I, Mayrhofer H & Prieto M. The epiphytic lichens on *Fagus sylvatica* in beech forests of Europe: towards an open and dynamic checklist. *En revisión en Herzogia.*

6 | METODOLOGÍA GENERAL

En esta sección se hace una descripción general de la metodología utilizada a lo largo de la tesis. Es importante aclarar, que la metodología aquí descrita es bastante somera ya que una información detallada de la metodología empleada en cada capítulo puede encontrarse en el apartado *Materials and Methods* de cada uno de ellos.

6.1. Áreas de estudio

6.1.1. Gradiente latitudinal en la Península Ibérica (Capítulo 1 y 6)

A lo largo de la Península Ibérica se seleccionaron 47 fragmentos de hayedo localizados en dos regiones biogeográficas diferentes, la región Atlántica y la región Mediterránea. En concreto, se muestrearon las comunidades de líquenes epífitos en 22 fragmentos en la Cordillera Cantábrica (Parque Natural Saja-Besaya; región Atlántica) y 25 fragmentos en el Sistema Central (Hayedo de Montejo, Hayedo de La Pedrosa y Hayedo de Tejera Negra; región Mediterránea).

6.1.2. Gradiente latitudinal en Europa (Capítulos 2, 3, 4, 5 y 6)

Cubriendo el rango de distribución de *Fagus sylvatica,* seleccionamos 23 bosques a lo largo de un gradiente latitudinal incluyendo seis países: Suecia, Eslovaquia, Austria, Francia, España e Italia. En Suecia se seleccionaron cuatro bosques mientras que en Eslovaquia, Austria y Francia se trabajó en tres bosques por país. En el caso de España y de Italia, dada su heterogeneidad ambiental, se seleccionaron bosques tanto en el norte (3 en el norte de España y uno en el norte de Italia) como en una localización más meridional (3 bosques en el centro de España y 3 en el sur de Italia).

En todos los casos, se seleccionaron bosques monoespecíficos de *Fagus sylvatica,* con una cobertura arbórea de más del 65%, sin manejo en los últimos cincuenta años y con presencia de *Lobaria pulmonaria* (L.) Hoffm. que es un indicador de comunidades de líquenes maduras (Rose 1988).

6.2. Diversidad taxonómica, funcional y filogenética

En relación a la **diversidad taxonómica**, se siguió el protocolo de Aragón et al. (2012) para determinar la composición de las comunidades liquénicas y la abundancia relativa de las distintas especies. Para ello se llevó a cabo un diseño anidado seleccionando parcelas dentro de cada bosque, árboles dentro de cada parcela e inventarios dentro de cada árbol.

Los inventarios se realizaron en dos orientaciones (norte y sur) y alturas diferentes (base y altura del pecho) debido a la heterogeneidad en la composición de las comunidades de líquenes en respuesta a los cambios en orientación y altura en el árbol. En concreto, en cada inventario, se estimó la cobertura (en porcentaje) de todas las especies de líquenes presentes. En total, se muestrearon 3808 inventarios a lo largo de la Península Ibérica (capítulo 1 y 6) y 4600 inventarios a lo largo de Europa (capítulos 2-6). En aquellos casos en los que una especie no podía ser identificada en el campo, era recogida e identificada siguiendo claves de determinación (Clauzade & Roux 1985, Smith et al. 2009) o análisis filogenéticos y blast cuando la identificación tampoco era posible con las claves.

Respecto a la **diversidad funcional**, se seleccionaron cuatro rasgos gruesos y diez rasgos finos relacionados con diferentes aspectos de la biología de los líquenes (Fig. 1).

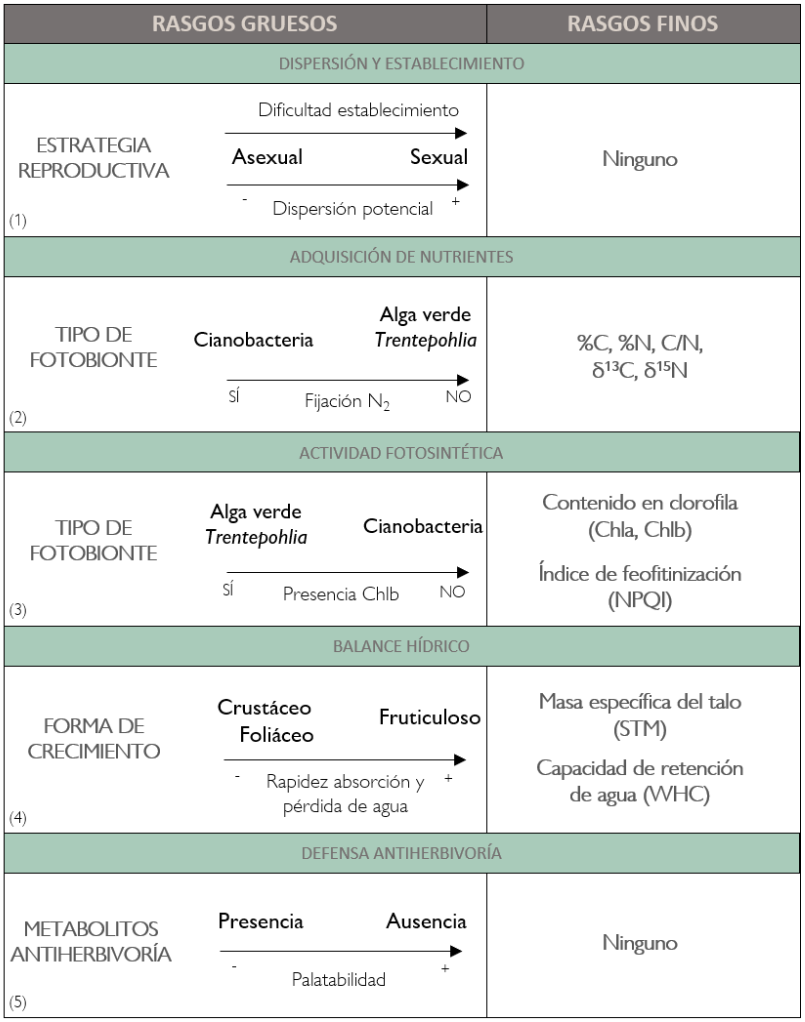

Figura 1. Esquema resumen de los rasgos seleccionados indicando las funciones con las que están relacionados. En todos los casos, los rasgos gruesos (a la izquierda en la figura) son rasgos cualitativos y las categorías dentro de cada rasgo vienen indicadas mientras que los rasgos finos (a la derecha en la figura) son cuantitativos. Abreviaturas: C, carbono; N, nitrógeno. Referencias: (1) Bowler & Rundel

1975, Scheidegger & Werth 2009; (2) Palmqvist et al. 1998; (3) Palmqvist & Sundberg 2000; (4) Gauslaa 2014; (5) Molnár & Farkas 2010.

La información sobre los cuatro rasgos gruesos (cualitativos) se obtuvo de fuentes bibliográficas mientras que se cuantificaron en el laboratorio los diez rasgos finos (cuantitativos):

- Rasgos cualitativos: la clasificación de los rasgos forma de crecimiento, tipo de fotobionte, estrategia reproductiva y presencia de metabolitos secundarios se realizó siguiendo las bases de datos ITALIC (Nimis & Martellos 2017) y Lias Light (Rambold et al. 2014).
- Rasgos cuantitativos: se cuantificaron los rasgos relacionados con la actividad fotosintética (Chla, Chlb y NPQI) siguiendo el protocolo de Barnes et al. (1992) y utilizando las ecuaciones de Wellburn (1994). En referencia a los rasgos relacionados con el balance hídrico (STM y WHC) se siguió a Merinero et al. (2014). Por último, la medición de los rasgos relacionados con la adquisición de nutrientes (%C, %N, C/N, $\delta^{13}C$ y $\delta^{15}N$) se realizó en las instalaciones de la Universidad de California (UC Davis Stable Isotope Facility) utilizando un espectrofotómetro de masas.

En cuanto a la **diversidad filogenética,** se construyeron árboles filogenéticos combinados utilizando cuatro marcadores moleculares (nuITS, nuLSU, mtSSU y RPB1). Para ello se utilizaron las secuencias de GenBank o se generaron secuencias propias siguiendo el protocolo de Prieto & Wedin (2013) cuando la información no estaba disponible en la citada base datos. Para la extracción de ADN se utilizaron especímenes recolectados en las zonas de muestreo y serán depositados en herbarios públicos próximamente.

6.3. Métricas de diversidad

Se utilizó la información de composición y cobertura de las especies, de los rasgos funcionales y de los árboles filogenéticos para calcular diferentes índices de diversidad taxonómica, funcional y filogenética a escala de comunidad para cada uno de los bosques seleccionados.

- Diversidad taxonómica: número de especies (riqueza), índice de Shannon e inverso de Simpson.
- Diversidad funcional: índice de disimilitud de Rao (Rao 1982) y *community weighted mean* (CWM) (Lavorel et al. 2008).
- Diversidad filogenética: índice de disimilitud de Rao (Rao 1982).

6.4. Análisis estadísticos

El conjunto de herramientas estadísticas utilizado a lo largo de los seis capítulos de la tesis incluye: modelos de ecuaciones estructurales (capítulo 1); modelos lineales generalizados (GLMs), modelos de regresión lineal (OLS) y análisis de redundancia (RDA)(capítulo 2); análisis de partición de la varianza (capítulos 3 y 4); regresión filogenética, modelos mixtos controlados por la filogenia (PGLMM) y correlaciones controladas por la filogenia (capítulo 4); escalamiento multidimensional no métrico (NMDS) y el método *hillplot* propuesto por Nelson et al. (2015) (capítulo 5).

7 | CONCLUSIONES

1. Diferentes factores ambientales son los principales predictores de la diversidad taxonómica, funcional y filogenética de las comunidades de líquenes epífitos. Por tanto, adoptar una aproximación integradora que considere la respuesta de las tres facetas de la biodiversidad es necesario para conocer la respuesta de las comunidades de líquenes a la hora de hacer frente a la fragmentación del hábitat y el cambio climático.

2. Las tres facetas de la biodiversidad proporcionan información complementaria sobre la dinámica de las comunidades, aunque la diversidad funcional aparece como un componente clave. La respuesta de las comunidades para hacer frente a los cambios ambientales está mediada a través de los rasgos funcionales de las especies que componen la comunidad. Los rasgos funcionales gruesos desempeñan un papel muy valioso como indicadores ecológicos, mientras que los rasgos finos responden con menor intensidad a los factores macroclimáticos.

3. Factores relacionados con las fluctuaciones climáticas, tanto en temperatura como en precipitación, son los determinantes más importantes de la respuesta de las comunidades de líquenes a lo largo de un amplio gradiente latitudinal que se extiende desde Suecia hasta Italia. Incrementos en la estacionalidad reducen la diversidad funcional y filogenética de las comunidades. Además, las especies de líquenes modifican sus estrategias ecológicas de acuerdo con gradientes de estacionalidad, con cambios desde estrategias de conservación de recursos a estrategias de adquisición de recursos en entornos con mayor estacionalidad. Teniendo en cuenta los modelos de predicción del clima global, se prevé un empobrecimiento de la diversidad funcional y filogenétia de las comunidades de líquenes epífitos y un incremento de líquenes con estrategias de adquisición de nutrientes.

4. A escala de comunidad, y en contraposición al patrón general esperado en plantas vasculares, la variabilidad intraespecífica explicó la mayoría de la variabilidad de los rasgos funcionales. Por tanto, remarcamos la importancia de tener en cuenta la variabilidad intraespecífica para comprender el efecto de los cambios ambientales sobre los rasgos funcionales de los líquenes. Al evaluar la variación de los rasgos finos a escala de especie, la variación funcional resultó mayor entre especies que dentro de especies, pero la variabilidad intraespecífica (particularmente dentro de poblaciones)

contribuyó sustancialmente a la variación global de los rasgos. Por tanto, incluir la variación dentro de las especies es esencial para profundizar en la respuesta de los líquenes epífitos bajo diferentes escenarios climáticos, incluso en gradientes ambientales extensos.

5. Los rasgos gruesos, tales como tipo de fotobionte y forma de crecimiento, son indicadores ecológicos útiles para desarrollar métodos de evaluación rápida del efecto de los cambios macroclimáticos. Además, señalamos la necesidad de incluir tres categorías diferentes dentro de los cianolíquenes a la hora de evaluar la influencia del clima ya que estos grupos funcionales responden de manera diferente a las condiciones climáticas. En contraposición a los rasgos gruesos, más estudios son necesarios para desvelar hasta qué punto los rasgos finos pueden responder a variables ambientales a pequeña escala o si, por el contrario, son relevantes para evaluar el efecto de las comundiades sobre el funcionamiento de los ecosistemas.

6. La variación funcional de los rasgos finos está distribuida entre diferentes escalas, siendo orden y especie las escalas que mayor contribución tienen la hora de explicar la variación global de dichos rasgos. Los factores evolutivos tuvieron una alta contribución a la variación funcional global mientras que el efecto de los factores ambientales fue menor, lo que pone de manifiesto la importancia de integrar la historia filogenética de las especies en los estudios funcionales utilizando el método comparado.

7. Los rasgos funcionales de los líquenes covarían a lo largo de Europa, y los patrones de covariación son diferentes entre especies y dentro de especies con la excepción de una correlación consistente en relación a las estrategias de uso del agua. Con base en esta covariación, identificamos una estrategia ecológica relacionada con el balance hídrico de los líquenes, pero no fue posible establecer estrategias generales en relación a la actividad fotosintética y la adquisición de nutrientes. Sin embargo, confirmamos que líquenes con talos más gruesos tienden a almacenar más agua lo cual implica un compromiso entre una estrategia de hidratación rápida y una estrategia conservativa de almacenamiento de agua.

8. Las comunidades de líquenes epífitos maximizan su diversidad taxonómica, funcional y filogenética bajo distintas condiciones climáticas. Los puntos calientes de diversidad funcional son congruentes con los máximos de diversidad filogenétca y

taxonómica, lo cual implica que conservar una alta diversidad funcional permitirá conservar, indirectamente, una alta diversidad filogenética y taxonómica en las comunidades de líquenes. Sin embargo, dado que los puntos calientes de diversidad taxonómica y filogenética no fueron congrentes, sería necesaria una aproximación multidimensional para identificar áreas de alta prioridad a las que destinar los recursos y para establecer políticas de conservación efectivas.

9. Las comunidades de líquenes epífitos maximizan su diversidad en los extremos del espacio climático estudiado, siendo la región Mediterránea un punto caliente de diversidad filogenética y funcional en estos organismos que requieren una especial atención de conservación.

10. Con la información obtenida durante los muestreos, y complemetada con una revisión bibliográfica de 127 artículos científicos, hemos creado una herramienta *online* de acceso libre y en continuo crecimiento (*http://biodiversos.org/epidiversity-lichens-fagus-europe/*) que pueda ser utilizada no sólo por liquenólogos sino por distintos investigadores ya que representa una fuente de información digital especializada, organizada y accesible para los lectores de diversas áreas.

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9 | REFERENCIAS

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Capítulos / Chapters

Capítulo 1

Critical predictors of functional, phylogenetic and taxonomic diversity are geographically structured in lichen epiphytic communities

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ABSTRACT

1. Assessing the response of biological communities to contrasting environmental conditions is crucial to predict the effects of global change drivers. The influence of multiple environmental factors may differ depending on the diversity facet considered, which emphasizes the need to simultaneously evaluate the functional (FD), phylogenetic (PD) and taxonomic (TD) diversity.
2. To examine how these facets of biodiversity respond to environmental changes, we studied lichen epiphytic communities across 47 beech forest fragments from two biogeographic regions. We applied structural equation modelling to relate habitat fragmentation, climate and habitat quality with FD, PD and TD. We compared the community response to contrasting climatic conditions by analysing independently Atlantic and Mediterranean communities.
3. We found different major drivers of biodiversity patterns across biogeographic regions. Habitat fragmentation performed the highest effect on lichen communities, with a reduction of FD, PD and TD at both regions. However, the influence of climate was stronger in the Atlantic region than in the Mediterranean region, where the effect of habitat quality was superior. The effect of the environmental predictors over PD and TD was both direct and indirect through the different components of FD, and their intensity and sign differed across regions. Changes in PD were not related to changes in TD.
4. *Synthesis*. Our results evidenced that the major environmental drivers affecting epiphytic communities were geographically structured. These drivers modified the diversity of the epiphytic community directly but also indirectly through changes in FD, which emerged as a causal but not unique determinant of PD and TD. Our findings also showed the difficulty for inferring TD through PD. These results emphasize the essential role of FD predicting part of the response of lichen communities to global change drivers but also highlight the importance of considering multiple biodiversity facets to understand the effects of environmental change on community structure.

Key words

Biogeographic regions, environmental drivers, forest fragmentation, functional diversity, lichens, phylogenetic diversity, structural equation modelling, taxonomic diversity.

1 | INTRODUCTION

Understanding the factors that determine the patterns of biodiversity is still a challenge in community ecology (Gaston 2000, Peters et al. 2016). Traditionally, the study of biodiversity has been based on species composition and richness (Garnier et al. 2016). However, this taxonomic approach is hampered by the unrealistic assumption that all species are ecologically equivalent (Swenson 2011). To overcome this limitation, two new facets of biodiversity have emerged to complete the information provided by the former: the functional (FD) and phylogenetic diversity (PD) dimensions. The FD reflects the variety of

morphological, physiological and ecological traits found in the community (Petchey & Gaston 2006) and quantifies the role and function of species in the ecosystems (Díaz et al. 2007, Lavorel et al. 2011, Shipley et al. 2016), while the PD reflects the evolutionary history of a community (Srivastava et al. 2012, Webb et al. 2002).

The studies that integrate taxonomic diversity (TD), FD and PD address differences in the response of the three diversity facets to environment and in relation with the different scales considered (Arnan et al. 2015, Devictor et al. 2010, Gonçalves-Souza et al. 2015, Mouillot et al. 2011, Purschke et al. 2013). Furthermore, they confirm the plural nature of biodiversity and the limited value of using one facet as a surrogate of the others (Devictor et al. 2010). Therefore, using an integrative approach more effectively unveils the patterns of change in biodiversity in biological communities and its response to environment (Arnan et al. 2016, Devictor et al. 2010, Meynard et al. 2011). A theoretical framework that simultaneously explores the response of the three diversity facets under different scenarios and biological groups will provide a more comprehensive understanding of the distribution of biodiversity. For instance, under stressful conditions, the number of species in observed assemblages should drop. In parallel, the number of functional traits and their variability should also diminish (i.e. functional convergence), at least when environmental filters rule the community assembly (Grime 2006, Keddy 1992, Weiher et al. 1998). Moreover, the decline on FD will entail a reduction of the relatedness of the species if the functional structure of the community has a strong phylogenetic signal (see Dehling et al. 2014). However, the extent of these predictions under variable environmental conditions or in different biogeographical contexts remains almost unexplored. Even more, the extension of these predictions to other biological assemblages, different of vascular plants or animals, is really scarce (see Prieto et al. 2017).

Forest ecosystems represent 30.6% of land surface (FAO 2016) and constitute a key source of ecosystem services (Hanski 2005), being vulnerable to one of the major drivers of global change: habitat fragmentation (Fahrig 2003, Tylianakis et al. 2008). Most forest surveys are focused on trees but less often on inconspicuous organisms such as cryptogams in spite of the fact that they have an important contribution to certain ecosystem functions. Epiphytic lichens are particularly important determinants of ecosystem functioning in the temperate biome (Cornelissen et al. 2007). For instance, lichens are involved in nutrient cycling since they are able to uptake limiting nutrients (e.g. nitrogen) from the atmosphere and increase the flux rate of these nutrients into the system (Asplund & Wardle 2016, Ellis 2012). Furthermore, they are involved in the invertebrate community assembly because a

diverse set of these organisms such as gastropods, mites and beetles use lichens as shelter or forage (Asplund & Wardle 2016, Ellis 2012). In addition, the utility of lichens as an ecological model system is twofold. Firstly, lichens are tightly dependent on environmental conditions as they are highly sensitive to climate and anthropogenic disturbance (Aragón et al. 2010a, Aragón et al. 2010b, Matos et al. 2015, Mayer et al. 2009, Nimis et al. 2002, Svoboda et al. 2010), making them excellent indicators of environmental changes (Benítez et al. 2018, Giordani et al. 2012). Secondly, lichens have some easily noticeable traits such as growth form, type of photobiont and reproductive strategy (Giordani et al. 2012, Matos et al. 2015, Prieto et al. 2017) that affect ecosystem functioning and whose diversity depends on environmental factors (Benítez et al. 2018, Concostrina-Zubiri et al. 2014, Ellis 2012, Matos et al. 2015, Prieto et al. 2017). In this way, we know that an increase in forest fragmentation, usually coupled with decreasing habitat quality, results in diminishing TD of lichen epiphytic communities (Aragón et al. 2010b, Cardós et al. 2016); however, the response of FD and PD is still unexplored.

We aimed to evaluate the strength and direction of the effect of forest fragmentation, climate and habitat quality on the diversity of lichen epiphytic communities across biogeographic regions. More specifically, we proposed and tested a theoretical causal framework that conceptualizes the structure of relationships between these environmental predictors and the three facets of biodiversity (Fig. 1). As environmental variables and disturbance do not occur isolated (Mouillot et al. 2013), we evaluated the response of the lichen communities considering simultaneously the effect of multiple predictors. In agreement with the emergent trait-based postulates (see Escudero & Valladares 2016), we expected that mechanisms influencing the presence and abundance of species in realized communities may be primarily mediated by species functional trait values (Le Bagousse-Pinguet et al. 2017). However, FD may not account for all the variation in PD and TD due to the fact that some critical functional traits were not included in the FD characterization but also due to the incidence of some neutral demographic processes and the so-called stochastic dynamics related, for instance, with immigration (Chacón-Labella et al. 2016, Hubbell 2001, Loranger et al. 2018). To provide general clues to the relationships hypothesized and tested, we evaluated the robustness of the results under two contrasting climatic scenarios with a partially shared biodiversity pool: the Mediterranean and the Atlantic regions in the Iberian Peninsula. To do so, we selected 47 beech forests (*Fagus sylvatica* L.) encompassing a wide variety of climatic conditions, from the favourable climate in the Atlantic region to the stressful conditions in the Mediterranean distribution edge.

Based on the proposed causal model, we hypothesize that: (a) the main environmental factors shaping FD, PD and TD may differ depending on the biogeographic region since environmental heterogeneity varies between them; (b) increases in environmental stress reduce the FD of the lichen communities (Götzenberger et al. 2012, Schoener 1970, Weiher & Keddy 1999). Under niche conservatism, we expect that the decline in FD may be reflected in a reduction of species but also in clades presenting these trait values (i.e. lower PD and TD). Thus, decreasing forest size and declining of habitat quality may result in diminishing FD, PD and TD. Specifically, changes in the microclimatic conditions within the forest remnants may reduce the heterogeneity and availability of suitable habitats, diminishing the diversity in lichen functional traits linked to moisture and light availability gradients (e.g. growth form, type of photobiont, antiherbivore defence compounds), and also in traits related to establishment and colonization (e.g. reproductive strategy); (c) direct effects of environmental factors over the TD and PD may be found given that FD may not account for all the variation in TD and PD; and (d) increases in PD are also expected to be associated with increased TD since the presence of more lineages should mean the presence of more species (Losos 2008).

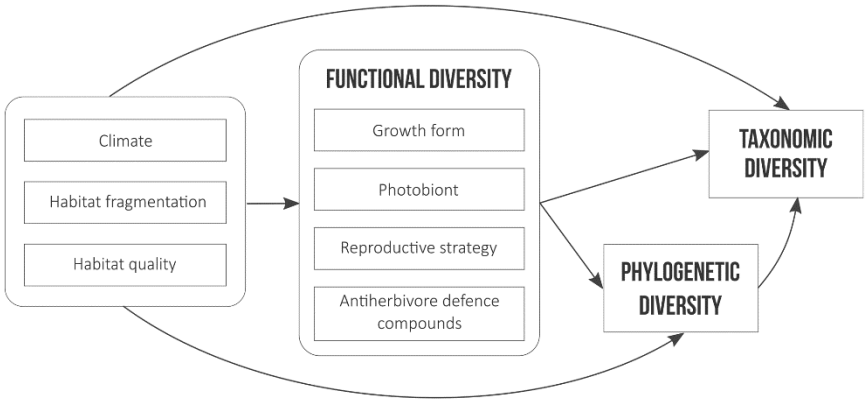

Figure 1. *A priori* conceptual metamodel of the relationships between the environment and the biodiversity facets in lichen epiphytic communities. Solid lines denote hypothesized causal relationships; arrows represent the direction of causality.

2 | MATERIALS AND METHODS

2.1. Study area

The study was carried out in the Iberian Peninsula, comprising two areas located in two different biogeographic regions: Cantabrian Range in the Atlantic region and Central Range in the Mediterranean region (Fig. 2). The Cantabrian Range is a temperate mountain characterized by a very rainy climate, with precipitation evenly distributed throughout the

year and without water shortage during the summer (mean annual precipitation = 1608 mm, summer precipitation = 204–252 mm, mean annual temperature = 10°C; Sánchez-Palomares et al. 1999). The Central Range constitutes one of the southernmost distribution limits for *F. sylvatica* and it is characterized by an intense summer drought and extreme temperatures (mean annual precipitation = 1104 mm, summer precipitation = 95–159 mm, mean annual temperature = 7.1°C, Sánchez-Palomares et al. 1999). Climatic conditions in the Atlantic region are optimal for beeches (Costa et al. 1997), whereas in the Mediterranean region, beech forest remnants are relict stands thriving in very adverse and stressful conditions. They are close to their range limits and, under these climatic conditions, beech forests are smaller and more isolated than in the Atlantic region (Fig. 2) (Aragón et al. 2012).

Lichen communities occurring in 22 beech forest remnants within the Atlantic region (Fig. 2a) and 25 beech remnants in the Mediterranean region (Fig. 2b) were studied. Mature and well-preserved pure forest stands of European beech with different sizes, shapes and surrounding matrices (Appendix S1) were selected. All the stands had a canopy cover > 65%, were not subjected to tree cutting during the last 50 years and had the lichen species *Lobaria pulmonaria* (L.) Hoffm. as indicator of maturity, quality and well preservation of forests.

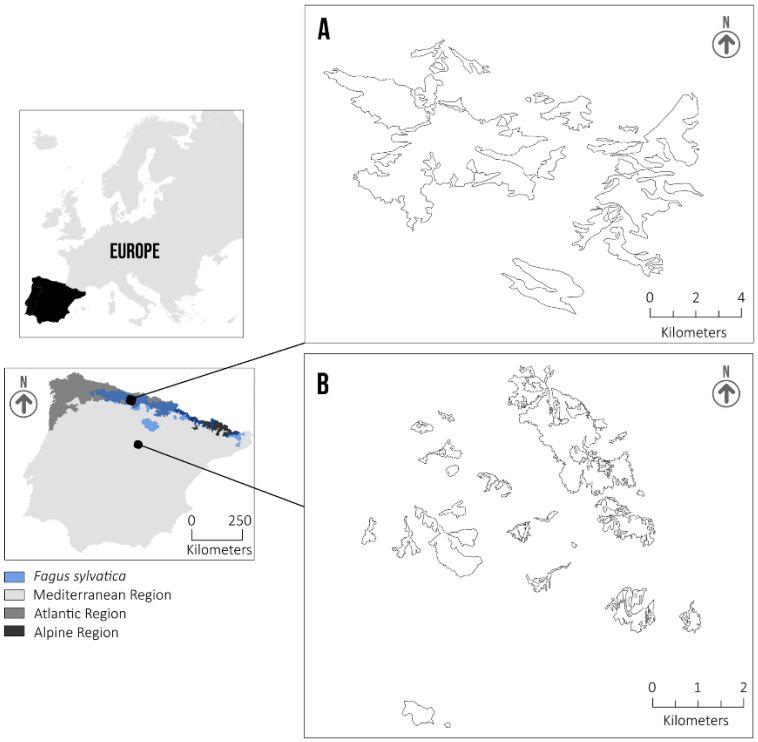

Figure 2. Map of the study area showing the biogeographic regions (European Environment Agency 2016; www.eea.europa.eu) and the natural distribution area of *Fagus sylvatica* in the Iberian Peninsula (EUROFORGEN 2009; www.eufor gen.org). **(a)** Sampling sites in the Atlantic region (Cantabrian Mountains) and **(b)** in the Mediterranean region (Central System).

2.2. Sampling design

Sampling was performed after spring leaf budding, between June and September 2015 in the Atlantic region and between June and July 2012 in the Mediterranean region. Lichen epiphytic communities were sampled following a standard protocol to record, at least, the 90% of the species occurring in each forest fragment (see Cardós et al. 2016). Within each fragment, four to eight 10 × 10 m plots were randomly established depending on the fragment size: four plots in fragments < 100 ha, six plots in fragments between 100 and 200 ha and eight plots in fragments > 200 ha. All plots were established at least 100 m away from the forest edge. Within each plot, four trees were selected: the trees with the greatest and the lowest diameter at breast height (DBH), and two trees with the DBH closest to the mean diameter of the trees within the plot. Only trees with DBH ≥ 25 cm were considered. In each tree, four 20 × 30 cm grids were placed, at two different aspects (north and south) and heights (breast and tree base). The cover (%) of all lichen species found within each grid was recorded. Lichen identification followed Smith et al. (2009). In total, data from 3808 sample units were collected: 1920 in the Atlantic region and 1888 in the Mediterranean region. Based on lichen cover estimated at grid level, the mean lichen cover (%) at plot level was calculated, for 120 plots in the Atlantic region and 118 plots in the Mediterranean region.

2.3. Environmental predictors

Twenty-five environmental variables were considered as surrogates of landscape structure, climate and habitat quality (Appendix S2). Climatic variables were calculated at plot level using the software CLIMOEST, an interpolating climate tool with a high spatial resolution and specifically designed for the Iberian Peninsula (Sánchez-Palomares et al. 1999). Variables related to landscape structure and habitat quality were measured in the field.

The correlation between the 25 environmental variables was analysed and all highly correlated predictors (Spearman rho > 0.7, $P < 0.05$) were removed. Large-scale (i.e. fragment size and summer precipitation) and small-scale (i.e. tree DBH) environmental variables were selected as surrogates of habitat fragmentation, climate and habitat quality respectively. For lichen epiphytic communities, tree diameter is a measure of the habitat quality that represents the amount of space and time available for colonization (Belinchón et al. 2009, Riiali et al. 2001).

2.4. Taxonomic, functional and phylogenetic diversity

To characterize the diversity of the epiphytic communities, TD, FD and PD indices were estimated at plot level (see Aragón et al. 2010b). Regarding TD, two metrics were computed: species richness and Inverse Simpson index. Species richness was calculated as the total number of species within each plot, while Inverse Simpson was quantified as $1/\Sigma_i^S \text{sum} p_i^2$ where *pi* is the proportional abundance of species *i,* and *S* is the species richness (Jost 2007). The higher the value of these metrics, the greater the TD.

The FD of the communities was summarized using the Rao's quadratic entropy index (hereafter 'Rao'; Rao 1982). This index is an indicator of functional dissimilarity highly correlated with another metrics such as functional variance and functional dispersion. It reflects the property of several indices with the advantage of including the relative abundance of species in the quantification of species dissimilarity (de Bello et al. 2010). Rao indices for four functional traits known to be related to key aspects of ecological strategies of lichens (see Prieto et al. 2017 and Appendix S3 for further explanations) were calculated: growth form, type of photobiont, reproductive strategy and presence or absence of antiherbivore defence compounds. The function melodic (de Bello et al. 2016) in r ver. 3.3.2 (R Core Team 2016) was used, which computes Rao as the sum of trait dissimilarity distances between each pair of species (*dij*) weighted by species cover at plot level (*pi* and *pj*) according to:

$$Rao = \sum_{i=1}^{s} \sum_{j=1}^{s} p_i p_j d_{ij}$$

To calculate trait dissimilarity distances (*dij*), a Gower distance matrix was used. The values of *dij* ranged from 0, when species were functionally equivalent, to 1 when species were completely dissimilar (Pavoine et al. 2009). The higher the value of Rao, the higher is the dissimilarity and the FD in the community.

Given that Rao can be computed with species dissimilarity (*dij*) based on trait and phylogenetic data, it is a key metric to compare FD and PD (de Bello et al. 2010). To estimate the PD, a Rao was calculated in the same way as for FD. In this case, *dij* represented the phylogenetic distance (i.e. difference in base pairs) between each pair of species calculated with the function *cophenetic* in the *picante* package (Kembel et al. 2010). To quantify the phylogenetic distances among pairs of species, a phylogenetic tree (Appendix S4) was built using a combined matrix of four molecular markers (nuITS, nuLSU, mtSSU and RPB1) for all the lichen species found in the communities. The sequences were downloaded from

GenBank or produced in the laboratory according to protocols by Prieto and Wedin (2013) (Appendix S5). For each molecular marker, MAFFT ver. 7 (Katoh & Standley 2013) was used to align the consensus sequences. The alignment was manually adjusted and the ambiguous regions and introns were excluded using MacClade ver. 4.0.1 (Sinauer, Sunderland, MA). Each individual gene region was analysed using maximum likelihood-based inference (ML) as implemented in RAxML ver. 8.2.10 (Stamatakis 2014) with a GTRGAMMA model for tree inference. Bootstraping was performed with a GTRCAT model and 1000 replicates. In order to check for gene-tree incongruence, maximum likelihood bootstrap values (ML-BS) between the individual gene trees were compared considering a conflict among clades when a supported clade (bootstrap support ≥ 70%) for one marker was contradicted with significant support by another. Because no supported nodes were in conflict, the individual gene regions were combined into a single concatenated matrix. The combined maximum likelihood (ML) analysis was run with five distinct partitions (nuITS, nuLSU, mtSSU, first and second codon positions of RPB1 and the third codon position of the RPB1), using a GTRGAMMA model of molecular evolution and rate heterogeneity with unlinked parameters and 1000 bootstrap replicates. All analyses were run on the CIPRES Science Gateway ver. 3.1 (Miller et al. 2010).

Using the multigene phylogenetic tree and the trait information, the phylogenetic signal for the four categorical traits was tested with the function *phylo.signal.disc* developed by Enrico Rezende in the *ape* package (Paradis et al. 2004). Based on the Maddison and Slatkin (1991) method, this function compares the minimum number of evolutionary transitions in a given trait with the median of a randomized distribution of trait changes derived from a null model. The null model was built randomizing the tips of the phylogeny 1000 times. Significant phylogenetic signal ($P < 0.05$) was detected when the observed trait change rates were lower than the expected by chance.

2.5. Structural equation modelling

The relationships between the three environmental predictors selected and the three diversity estimates were analysed using a structural equation modelling (SEM) approach. This is a causal inference tool (Shipley 2004) specially indicated to investigate the complex networks settled in natural ecosystems since multiple influences and responses can be analysed simultaneously (Grace 2006, Grace et al. 2010). SEM resolves complex multivariate relationships in a context of correlated causal factors (Grace 2008, Lefcheck 2015). This statistical approach has the advantage of separate direct and indirect effects making

quantitative predictions to infer causes from observational data (Shipley 2004) but also has some limitations. On the one hand, different alternative models can fit the data meaning that our model just represents one possible hypothesis explaining the covariance structure of the data (Grace 2006). On the other hand, some major influences not included in the tested model can reduce the predictive power or bias the estimated coefficients (Grace 2008).

A theoretical model including a complete set of direct and indirect causal relationships was proposed (Fig. 1). All the environmental variables (i.e. related to habitat fragmentation, climate and habitat quality) can first affect the FD of the epiphytic lichen community and, afterwards, the PD and TD. As already explained, we expected that environmental predictors may modify the PD and TD not only indirectly through the four categorical traits studied but also directly. Besides, a causal framework relating PD and TD was also proposed.

The causal metamodel was independently tested in the Atlantic (n = 120) and in the Mediterranean region (n = 118) because the climatic conditions are very different in these two biogeographic regions. Given that environmental predictors can affect both the number and the abundance of species, the models were fitted with richness and Inverse Simpson as surrogates of TD. When necessary, logarithmic transformations of variables to meet the assumption of normality were applied (fragment size, mean tree DBH, richness, Inverse Simpson and PD). In addition, variation inflation factors for each predictor variable were calculated to test for collinearity among them. The path coefficients were obtained with the maximum likelihood algorithm. The overall fit of the models was assessed by the likelihood chi-square value (χ^2) (Iriondo et al. 2003). Since this test has some limitations with large sample sizes and data deviation from normality, the fit of the models was also tested by the Goodness of Fit Index (GFI) and the Root Mean Square Error of Approximation (RMSEA). P-values χ^2 above 0.05, GFI values above 0.9 and RMSEA values below 0.05 indicate a good fit of the model meaning that the discrepancies among the variance/covariance matrices predicted and observed are very low (Byrne 2010). The software AMOS ver. 18 (Arbuckle 2006) was used to perform these analyses.

3 | RESULTS

Atlantic lichen communities were significantly more diverse in terms of FD, PD and TD than Mediterranean communities (Fig. 3). Richness in the Atlantic beech forests ranged from 7 to 47 species per plot (Fig. 3), with a total of 131 epiphytic lichen species in the 22 forest fragments studied. In the Mediterranean region, the richness per plot ranged from 12 to 33

(Fig. 3), with a total of 78 species in the 25 forest fragments studied. Both regions shared 64 species (Appendix S6). Regarding the FD, Atlantic communities exhibited higher values of Rao for all traits, except for antiherbivore defence compounds (Fig. 3).

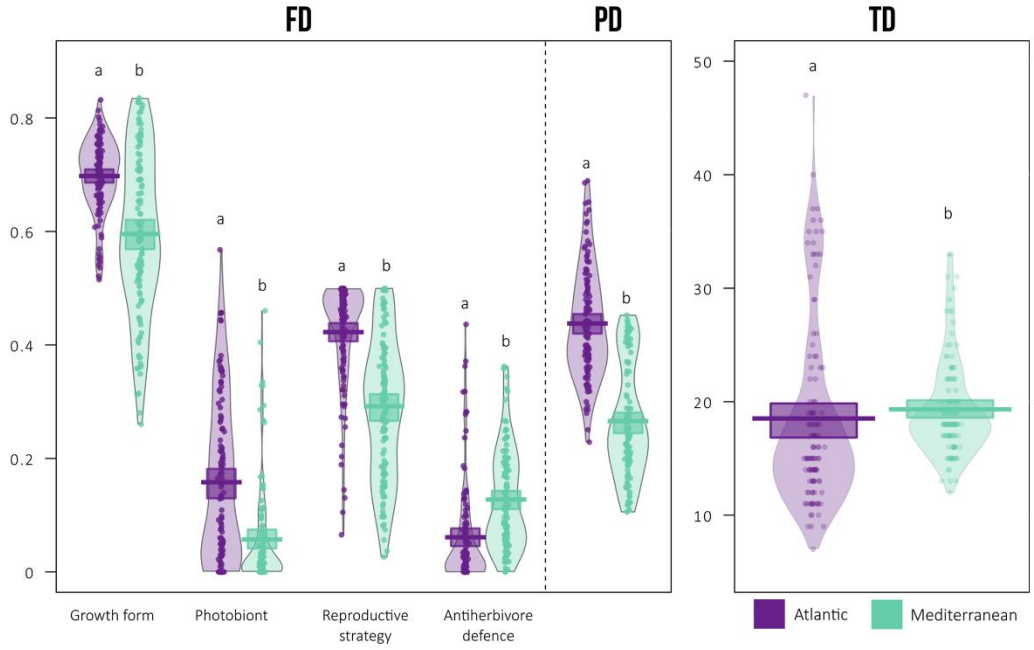

Figure 3. Representation of diversity values and the means per region. FD and PD were estimated through a Rao's quadratic entropy index and TD was calculated as the total species richness per plot. Points representing raw data have been randomly jittered horizontally in order to improve the visualization. Coloured shapes illustrate smoothed densities. Horizontal lines represent the mean. Boxes are the 95% Bayesian highest density intervals of the mean of each group. Different letters indicate significant differences between biogeographic regions ($P < 0.05$, based on one-way ANOVA): purple = Atlantic region ($n = 120$), light blue = Mediterranean region ($n = 118$). Abbreviations: FD, functional diversity; PD, phylogenetic diversity; TD, taxonomic diversity.

The proposed model (Fig. 1) showed an excellent and better fit in both biogeographic regions when species richness was used as surrogate of TD (Fig. 4) instead of using Inverse Simpson (Appendix S7). In the Atlantic region, the environmental variables included in the model accounted for 75% and 53% of the variance in PD and TD respectively (Fig. 4a). In the Mediterranean region, the explained variance reached 90% for PD and 37% for TD (Fig. 4b). As expected, abiotic variables differently affected the three components of biodiversity in the two biogeographic regions. First, fragment size was the most important abiotic variable showing a positive effect on FD, PD and TD in both regions (Fig. 4 and 5), and directly modifying PD and TD. Larger forest fragments harboured more diverse lichen communities. Second, higher values of summer precipitation were associated to less diverse communities

(lower FD, PD and TD values) in the Atlantic region. However, higher values of summer precipitation in the Mediterranean region increased FD and TD, but decreased PD (Fig. 4 and 5). Third, mean DBH modified biodiversity only in Mediterranean communities where bigger trees hosted communities with higher diversity of photobiont types, PD and TD values (Fig. 4 and 5). Overall patterns of relationships were consistent when we repeated the analyses using Inverse Simpson as surrogate of TD (Appendix S7 includes the significant paths of the SEM results, and a synthesis of the direct, indirect and total effects of environmental variables over PD and Inverse Simpson). Given that the fit of the models was also very similar, for simplicity, we focus on the results obtained with species richness as a surrogate of TD.

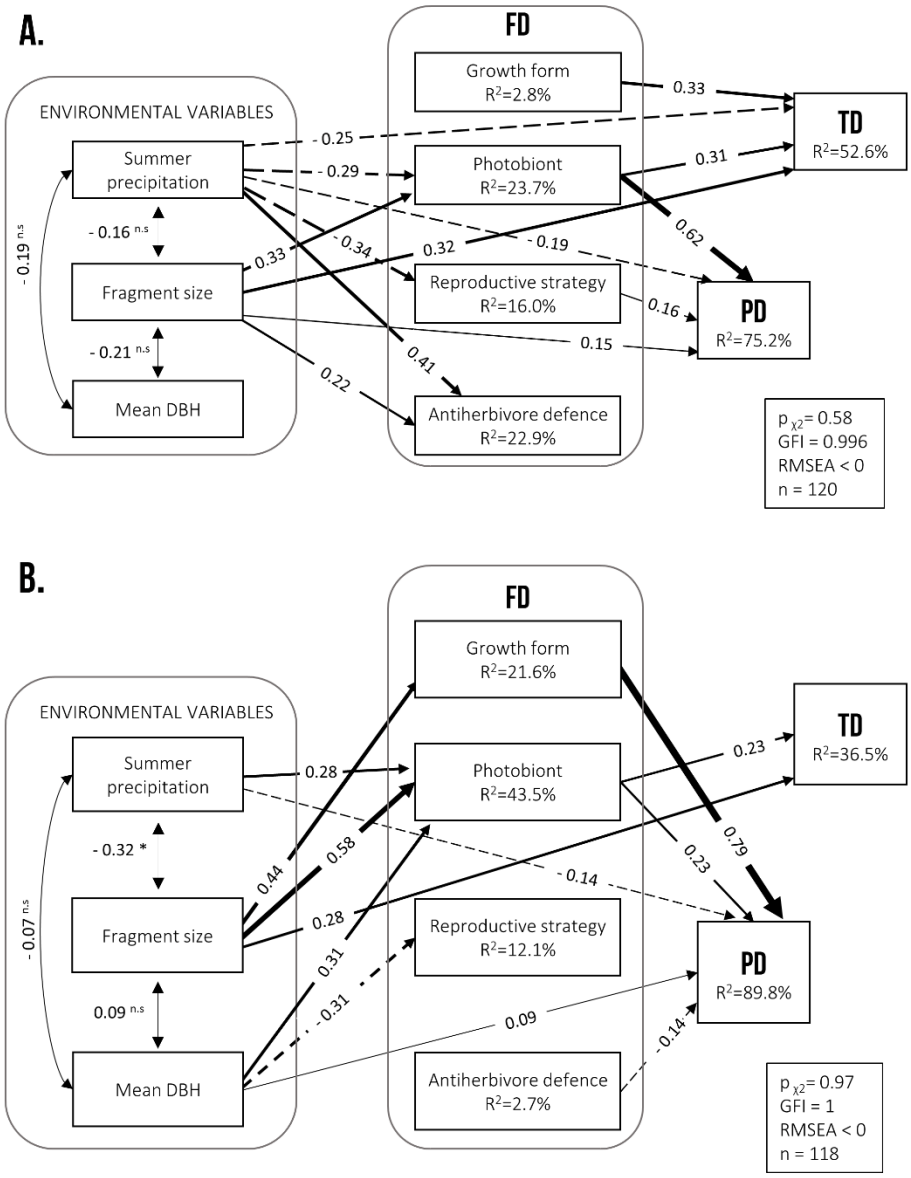

Figure 4. Significant causal paths of the SEM analyses showing the relationships between environmental variables and biodiversity metrics in the Atlantic region (a) and in the Mediterranean

region (b). Solid arrows represent positive relationships (→) and broken arrows (- ->) represent negative effects. Arrow width is proportional to the standardized coefficient of the path (indicated by numbers on the lines). Double-headed arrows (↔) represent correlation between exogenous variables (n.s. = non-significant; $*P < 0.05$). R^2 denotes the proportion of variance explained and appears below every response variable in the model. Abbreviations: FD, functional diversity; PD, phylogenetic diversity; TD, taxonomic diversity

Figure 5. Synthesis of direct, indirect and total effects of environmental variables over PD and TD obtained by SEM analyses in the Atlantic and Mediterranean regions. Path coefficients represent the standardized coefficient of the significant paths. Direct effects represent the standardized coefficient of the path when two variables are only connected through a single significant path (Grace 2006). Indirect effects were calculated as the product of the coefficients along the compound significant paths that involve multiple arrows (Grace 2006). Total effect of one variable on another was calculated as the sum of its direct and indirect effects taking into account all the significant pathways connecting these two variables (Grace 2006). Abbreviations: PD, phylogenetic diversity; TD, taxonomic diversity

Our field data were in agreement with the causal hypotheses proposed in which environmental drivers modify PD and TD indirectly through FD but also directly. The strength of direct and indirect effects varied in the two biogeographic regions. While indirect effects through the FD had more influence on PD and TD in the Mediterranean region, direct effects were comparatively stronger in the Atlantic region (Fig. 4 and 5). In both biogeographic regions, FD had strong positive relationships with PD and TD implying that communities with higher values of FD tend to have higher values of PD and TD (Fig. 4). The indirect effects of the environmental variables were mediated through three components of FD: the diversity of growth form, photobiont type and reproductive strategy (Fig. 4). The

four functional traits studied had significant phylogenetic signals (Table 1). However, only growth form and type of photobiont performed a primary role on the variation in PD and TD with a lower effect of the reproductive strategy. The most influencing traits over PD differed between regions. Meanwhile in the Atlantic region, the most related trait to PD was the type of photobiont, in the Mediterranean region, it was the growth form.

Table 1. Phylogenetic signal of the four categorical traits studied (growth form, type of photobiont, reproductive strategy and antiherbivore defence compounds)

Trait	Nº of Levels	Observed Transitions	Median Null Model (*p*-value)
Growth form	12	21	91***
Type of photobiont	3	12	34***
Reproductive strategy	2	33	48***
Antiherbivore-defence compounds	2	8	16***

Notes: No. of levels: number of categories for a given categorical trait; Observed transitions: number of observed evolutionary transitions; Median Null Model: median of expected evolutionary transitions under a null model in which the tips of the phylogeny were randomized 1000 times; p-value based on the comparison of observed and expected evolutionary transitions (***$P < 0.001$).

Finally, and contrary to the theoretical framework proposed (Fig. 1), TD was not significantly modified by PD either in the Atlantic region (Fig. 4a) or in the Mediterranean region (Fig. 4b).

4 | DISCUSSION

Our model evidenced a tight link between the three environmental predictors and the biodiversity facets of lichen epiphytic communities. It is remarkable that different critical predictors affected the diversity facets of lichen communities depending on the biogeographic region. The major changes in FD, PD and TD were related with differences in fragment size. However, climate performed a strong influence in the Atlantic region meanwhile habitat quality dominated in the Mediterranean. The observed relationships were congruent with a causal pattern in which changes in FD led to changes in PD and TD, but did not support the postulated relationship between PD and TD. Moreover, the effect of the environmental predictors over PD and TD was both direct and indirect through the different components of FD, and their intensity and sign differed across biogeographic regions (Fig. 6).

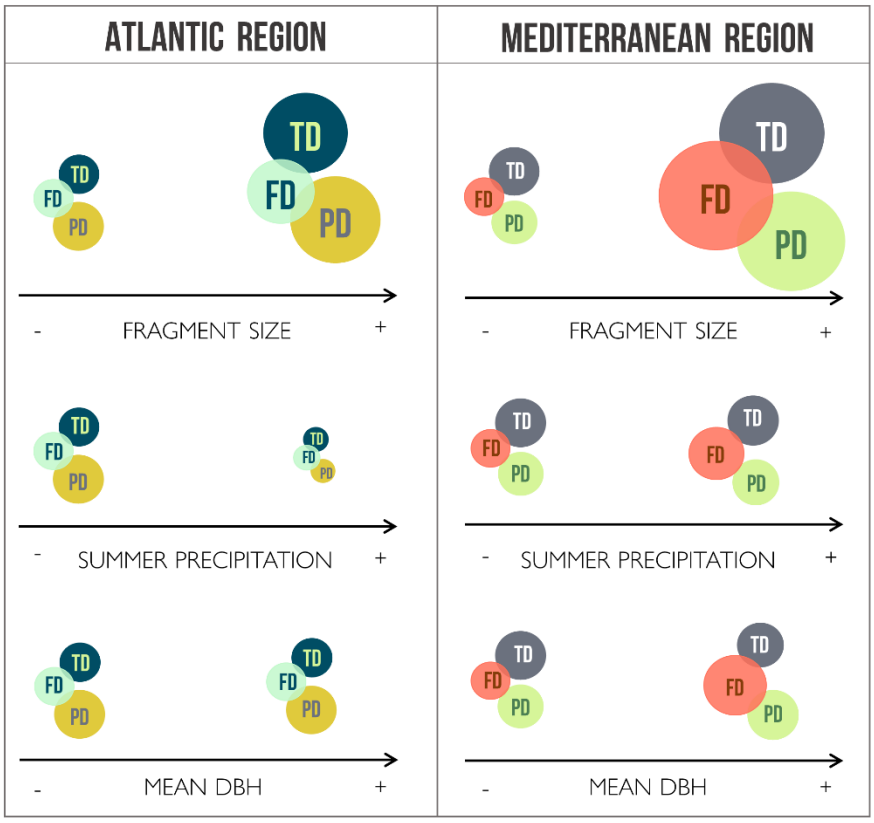

Figure 6. Conceptual diagram summarizing the main results of the study. Response of functional (FD), phylogenetic (PD) and taxonomic diversity (TD) of lichen epiphytic communities to three environmental variables (fragment size, summer precipitation and mean tree DBH) in two biogeographic regions, Atlantic and Mediterranean. Bubbles represent the three diversity facets (FD, PD and TD) of a certain community and their size is proportional to the diversity metric value: fragment size had the strongest effect on biodiversity in both regions, followed by summer precipitation and mean DBH in the Atlantic and Mediterranean regions respectively. The overlap between the bubbles represents the causal relationships between FD, PD and TD: changes in FD produced changes in PD and TD, but changes in PD did not modify TD.

4.1. Environmental factors shaping FD, PD and TD differed depending on the biogeographic region

Our results provide evidence that fragment size, summer precipitation and mean DBH drove the FD, PD and TD in lichen epiphytic communities. The relative importance of these drivers differed across biogeographic regions, with fragment size performing the largest influence on biodiversity, followed by summer precipitation in the Atlantic region, and mean DBH in the Mediterranean region. These results indicate that environmental factors acting at larger scales were better predictors of lichen diversity in the Atlantic region, where beech trees thrive under optimal and more benign climate conditions (Costa et al. 1997). In contrast, under the more stressful Mediterranean conditions, beech forest remnants are

smaller and more isolated (Costa et al. 1997). This implies that areas with genuine interior forest conditions are smaller, and, consequently, the availability of different microhabitats for epiphytic lichens is more limited (Cardós et al. 2016), which may explain why epiphytic communities were less diverse in this biogeographic region. Small-scale factors linked to the tree size performed a higher impact on lichen communities occurring under a strong environmental constraint, likely as a consequence of the increase in the surface and heterogeneity of microhabitats available for colonization (Aragón et al. 2012).

4.2. Increases in environmental stress reduce the FD of the lichen communities and affect PD and TD

Considering the fragment size, smaller forests harboured less diverse epiphytic communities in the three diversity facets regardless of the biogeographic region. As a consequence of the reduction in the forest core area (Brunialti et al. 2013, Cardós et al. 2016, Gignac & Dale 2005), fewer suitable habitats were available for those species that require interior forest microhabitats characterized by low irradiance and high air humidity levels (Cardós et al. 2016, Crouzeilles et al. 2014, Harrison & Bruna 1999). In the Atlantic region, this limitation reduced the diversity of photobiont types, with a decline in the number of species with cyanobacteria or *Trentepohlia* as photobiont (Appendix S8). These results are consistent with previous studies, which found an association of cyanolichens to moister habitats (Jovan & McCune 2004), and lichens with *Trentepohlia* to shaded and warm-moist sites (Marini et al. 2011). In the Mediterranean region, communities occurring in smaller forest remnants hosted a low number of cyanolichens and were dominated by broad-lobed foliose lichens (Appendix S8), which have been related to high solar radiation and aridity (Giordani et al. 2014, Matos et al. 2015). Habitat fragmentation narrowed the range of photobiont types and growth forms within the communities, leading to a decline in the number of species and the clades presenting these trait values (i.e. lower TD and PD). It can be argued that our results point to a filtering process of those species with traits helping to survive under higher light exposure and lower water availability conditions.

As discussed in the Section 4.1, the critical predictors of diversity were different between the two studied regions, and thus, we observed that factors as climate and habitat quality affected differently the diversity dimensions. Regarding climate, summer precipitation performed opposite effects in both biogeographic regions. In the Atlantic region, increases in summer precipitation resulted in lower FD, PD and TD. The number of species with *Trentepohlia* and sexual reproduction diminished (Appendix S8), which is somehow

unexpected since rainy and warm climatic conditions favour these organisms (Marini et al. 2011). However, equivalent findings were obtained by Reed et al. (2012) for similar organisms as the bryophyte *Syntrichia caninervis*, for which increases in the frequency of summer rainfall increased its mortality. Lichens, as mosses, are poikilohydric organisms that remain physiologically inactive under dry environmental conditions, and only become active when they are hydrated (Green et al. 2011). Thus, the decline of lichens with *Trentepohlia* could be reflecting a threshold in which increases in summer precipitation are not advantageous due to high rates of respiration and negative carbon balance (Reed et al. 2012). Further experimental research should be undertaken to investigate to what extent the timing of rainfall events is more important than the total summer precipitation in the survival of these lichens. In addition, given that lichens with *Trentepohlia* are sensitive to low temperatures (Nimis & Tetriach 1995), this unexpected result could be also due to the fact that sites with high summer precipitation where located at higher elevations where the temperatures were lower (Appendix S1). Conversely, in the Mediterranean region, the increase in precipitation during summer drought resulted in communities with a higher TD and higher diversity of photobiont types. The reduction of water stress during the summer drought allowed the entrance of species that need liquid water to activate photosynthesis (i.e. cyanolichens, Lange et al. 1986) in the communities previously dominated by drought-tolerant chlorolichens.

Habitat quality, measured as mean DBH, only modified the lichen communities in the Mediterranean region, where bigger trees hosted communities with higher PD and TD. The microclimatic changes related to the presence of bigger trees likely increased the heterogeneity of microhabitats and the availability of niches with lower irradiance and higher humidity (Belinchón et al. 2011, Ranius et al. 2008). As a consequence, epiphytic communities dominated by chlorolichens became more diverse with the entrance of cyanolichens (Appendix S8), suggesting that small-scale factors performed a high influence shaping the lichen communities under less favourable environmental conditions.

Overall, and linked with our first hypothesis, our results suggest that the keystone functional traits shaping the diversity of the communities vary across regions. In the Atlantic region, abiotic and biotic processes mainly operated through the type of photobiont while, in the Mediterranean region, through the growth form. In agreement with previous studies, the diversity of photobiont types varied according to climate (Marini et al. 2011, Nascimbene & Marini 2015) and water availability (Giordani et al. 2014, Lange et al. 1986, Merinero et al. 2014), which could explain the high explicative power of fragment size and summer precipitation in the Atlantic region. In turn, growth form has been related with water uptake

and loss (Büdel & Scheidegger 2008, Lange et al. 1986, Larson & Kershaw 1976), temperature (Nascimbene & Marini 2015) and light availability (Giordani et al. 2012), which may explain the importance of small-scale factors related to humidity and light availability in the Mediterranean region.

4.3. FD emerged as a causal but not unique determinant of PD and TD: direct effects of environmental factors over TD and PD and relationship between PD and TD

The relationships between the three facets of biodiversity have been explored previously (e.g. Arnan et al. 2016, Devictor et al. 2010), showing complex patterns and partial congruence between PD, TD and FD depending on data, area and scale considered. It has also been suggested that environment may strongly condition the relationship between different diversity components (Hermant et al. 2012, Safi et al. 2011). In accordance with these results, here we observe a high variability of the relationships between the environment and the three facets of biodiversity, with differences depending on the region and the environmental factor considered. First, we observed indirect effects mediated by functional traits. On the one hand, the strong positive causal relation between FD and PD reinforced the paradigmatic idea that close relatives tend to share similar trait values (Chave et al. 2006, Moles et al. 2005, Swenson & Enquist 2007, Wiens & Graham 2005). On the other hand, the positive causal relation between FD and TD suggests that a higher number of lichen species could represent a wider range of traits values as a consequence of functional complementarity (Petchey & Gaston 2002). Therefore, FD emerged as a keystone facet of biodiversity capable to predict changes in other diversity facets (similar to Purschke et al. 2013). Second, we also observed direct effects of the environment over PD and TD suggesting that FD is not the only predictor for the rest of diversity facets. This could be explained by some other relevant traits not included in our study or by some stochastic variation in immigration, survival or reproduction unrelated to the functional attributes of the species (Loranger et al. 2018). Thus, other mechanisms related to dispersal or biotic interactions could be involved, and further experimental approaches would be necessary to explore the mechanisms underpinning the observed relationships (Cadotte & Tucker 2017). It is important to underline that the strength of direct and indirect effects varied in the two biogeographic regions, with indirect effects being comparatively stronger in the Mediterranean lichen communities. Although we do not have evidence demonstrating the factors behind, this result suggests that a more intense filtering process may be acting in the Mediterranean region in comparison to the Atlantic region. Finally, TD was not determined by the phylogenetic structure of the

community, which implies that these two facets provided different information. For instance, contrasted phylogenetic or biogeographic histories reflected by the PD (Davis & Buckley 2011, Gerhold et al. 2015) may explain that different communities with the same number of species differed in their PD.

5 | CONCLUSIONS

We found that the environmental drivers modifying the lichen epiphytic diversity were geographically structured across biogeographic regions. Habitat fragmentation was a major driver of diversity impoverishment in Atlantic and Mediterranean lichen communities. Together with habitat fragmentation, communities located under stressful climatic conditions responded to drivers operating at small scale, while large-scale drivers were more important under favourable climatic conditions. The way in which environmental predictors modified the diversity facets emphasizes the crucial role of FD but also stresses the need for using multiple biodiversity facets to disentangle the response of the communities to environmental changes. Here, we propose a plausible model of relationships between environment and biodiversity based on observational data. Future works using experimental approaches and including the biotic interactions will help us to unveil the precise mechanisms underlying the observed patterns of relationships.

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7 | AUTHORS' CONTRIBUTIONS

IM, MP, GA and PH conceived the ideas and designed methodology; PH, MP, IM and GA collected the data; PH, AE and MP analysed the data; PH led the writing of the manuscript and all authors provided critical reviews. All authors gave approval for submission of the final manuscript.

8 | DATA ACCESSIBILITY

Data are available at https ://doi.org/10.6084/m9.figsh are.7907693 (Hurtado et al. 2019).

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10 | SUPPORTING INFORMATION

10.1. Appendix S1

Environmental variables related to landscape structure (fragment size, shape index, and perimeter), climate (annual mean temperature, total annual precipitation, and total summer precipitation), and habitat quality (mean tree DBH) of forest fragments studied in the Atlantic and Mediterranean regions.

Fragment	Size (ha)	Shape index (SI)	Perimeter (%)			Annual mean temperature (°C)	Total annual precipitation (mm)	Total summer precipitation (mm)	Mean tree DBH (m)
			Shrubland-grassland	Oak	Pine				
Atlantic Region									
1	7.65	1.69	100.00	0.00	0.00	9.7	1643	231	0.62
2	88.05	1.79	81.62	18.38	0.00	10.0	1618	228	0.54
3	15.06	2.14	90.85	0.00	9.15	9.5	1682	236	0.60
4	67.13	1.69	64.82	35.18	0.00	9.1	1749	243	0.57
5	100.17	1.87	50.82	49.18	0.00	9.7	1645	231	0.72
6	110.91	1.92	84.73	15.27	0.00	11.6	1409	206	0.45
7	177.60	3.43	81.87	18.13	0.00	9.9	1618	227	0.51
8	203.90	3.32	96.33	3.67	0.00	8.9	1773	244	0.38
9	757.70	1.74	72.56	27.44	0.00	10.4	1527	218	0.51
10	40.31	2.51	90.65	9.35	0.00	11.8	1397	204	0.61
11	2612.35	3.85	83.90	16.10	0.00	10.7	1509	216	0.49
12	61.57	2.63	83.08	16.92	0.00	11.7	1407	207	0.50
13	44.58	2.12	93.81	6.19	0.00	11.7	1400	204	0.49
14	460.32	2.27	71.33	28.67	0.00	8.5	1827	250	0.34
15	215.46	2.22	84.50	15.50	0.00	9.7	1647	232	0.48
16	20.76	1.66	91.44	8.56	0.00	9.0	1732	242	0.50
17	4.90	1.10	100.00	0.00	0.00	8.5	1826	252	0.53
18	8.67	1.11	90.88	9.12	0.00	9.4	1678	235	0.48
19	630.87	2.69	82.97	5.39	11.64	10.3	1583	225	0.50
20	54.80	1.25	79.34	20.66	0.00	9.6	1667	233	0.43
21	567.64	2.80	71.79	28.21	0.00	10.1	1599	225	0.54
22	29.67	1.71	70.34	29.66	0.00	11.7	1402	205	0.49

Appendix S1 (continued)

Fragment	Size (ha)	Shape index (SI)	Perimeter (%)			Annual mean temperature (°C)	Total annual precipitation (mm)	Total summer precipitation (mm)	Mean tree DBH (m)
			Shrubland-grassland	Oak	Pine				
Mediterranean Region									
23	35.02	5.50	85.13	5.61	9.25	6.9	944	112	0.18
24	209.80	6.96	60.00	30.00	10.00	7.2	1136	110	0.39
25	2.40	2.83	0.00	100.00	0.00	7.7	1025	105	0.37
26	1.27	1.38	52.00	1.20	46.80	7.1	1192	143	0.21
27	7.52	4.25	88.19	0.24	11.57	6.8	1102	147	0.25
28	10.12	4.43	92.29	0.00	7.71	7.2	1066	141	0.41
29	45.06	5.44	98.24	0.00	1.76	6.6	1030	115	0.29
30	12.96	3.40	67.93	32.97	0.00	6.9	1062	112	0.27
31	7.86	2.00	75.06	16.50	8.45	7.5	1192	137	0.35
32	12.73	3.17	54.37	0.49	45.14	6.8	1276	147	0.30
33	59.86	2.21	79.17	21.83	0.00	6.4	1212	154	0.39
34	8.65	1.94	71.88	28.12	0.00	6.7	998	149	0.17
35	4.58	1.27	67.33	32.67	0.00	6.3	1312	156	0.26
36	11.32	3.18	77.95	22.05	0.00	7.1	1136	143	0.27
37	6.76	2.33	44.76	55.24	0.00	7.0	1165	145	0.30
38	2.55	2.51	85.10	14.90	0.00	6.1	1350	159	0.27
39	49.81	4.84	59.67	8.58	31.75	7.0	1014	111	0.16
40	5.68	2.71	100.00	0.00	0.00	6.7	1211	149	0.25
41	2.84	2.65	88.35	0.00	11.66	6.9	1165	146	0.26
42	0.85	1.79	100.00	0.00	0.00	7.1	1121	142	0.29
43	3.08	2.34	33.72	46.07	20.21	7.1	1144	144	0.36
44	0.75	1.35	0.00	85.35	14.65	6.9	1034	112	0.32
45	34.41	1.03	10.00	85.00	5.00	9.4	836	95	0.35
46	5.15	1.26	5.00	80.00	15.00	9.4	830	95	0.29
47	13.71	1.45	19.19	20.81	0.00	6.5	1258	152	0.19

10.2. Appendix S2

List of the environmental variables recorded at Atlantic and Mediterranean regions. The three variables selected as surrogates of landscape structure, climate, and habitat quality and included in the structural equation modelling analyses are marked with an asterisk (*).

Landscape structure	Fragment size (ha) *
	Fragment perimeter (Km)
	Fragment shape index (SI) $SI = P/(200[\pi TA)^{0.5}])$ where P = perimeter, TA = total area
	Shrubland-grassland perimeter (%)
	Oak forest perimeter (%)
	Pine perimeter (%)
Climate	Annual mean precipitation (mm)
	Spring precipitation (mm)
	Summer precipitation (mm) *
	Autumn precipitation (mm)
	Winter precipitation (mm)
	Precipitation of wettest month (mm)
	Precipitation of driest month (mm)
	Annual mean temperature (°C)
	Mean temperature of max temperatures of warmest month (°C)
	Mean temperature of min temperatures of coldest month (°C)
	Temperature seasonality
Habitat quality	Altitude (m a.s.l.)
	Aspect (rad)
	Slope (degrees)
	Shrubland cover (%)
	Grassland cover (%)
	Number of trees per plot
	Mean DBH (m) *
	Mean canopy openness

10.3. Appendix S3

We classified growth form in twelve categories according to Aragón et al. (2016) (crustose conspicuous, crustose inconspicuous, leprose, gelatinous, foliose broad-lobed, foliose narrow-lobed, foliose placodiomorph, big foliose, squamulose, fruticose cylindrical, fruticose dorsiventral, and mixt). Growth form is related with some properties of the lichen (i.e. nutrient status, shelter for invertebrates, structural complexity, and water uptake and retention) with ecological consequences on decomposition, invertebrate community assembly, and rainfall and nutrient interception (Asplund & Wardle 2016). Growth form has been previously related to water uptake and loss (Larson & Kershaw 1976, Lange et al. 1986, Büdel & Scheidegger 2008), temperature (Nascimbene & Marini 2015), and light availability (Giordani et al. 2012).

We distinguished three categories of type of photobiont (green algae, *Trentepohlia,* and cyanobacteria) (Nimis & Martellos 2017) related to the ability of nitrogen fixation (Asplund & Wardle 2016), climatic conditions (Marini et al. 2011, Nascimbene & Marini 2015), and water balance (Lange et al. 1986, Giordani et al. 2014, Merinero et al. 2014).

In the case of reproductive strategy (sexual or asexual; Nimis & Martellos 2017) for those species which could have the two types of strategies, the categorization was based on the main reproductive strategy present in the study area. Reproductive strategy provides information about an ecological trade-off between potential colonization distance and successful local establishment (Ellis & Coppins 2006, Ellis 2012, Rapai et al. 2012, Nelson et al. 2015).

Finally, for the presence or absence of antiherbivore-defence compounds, we looked for information about the secondary metabolites present in every lichen species (Culberson 1969, CNALH 2017, Rambold 2018). After that, according to Molnár & Farkas (2010) and Huneck (1999) we related the presence of certain secondary compounds (usnic acid, pulvinic acid, caperatic acid, methyl beta-oricolcarboxylate, ethyl hematommate, 5-chlorohematommate, 3-hydroxyphysodic acid) to the antiherbivore-defence ability. The defence capability of thallus tissue is related to the consumption rate by invertebrates (Asplund & Wardle 2016).

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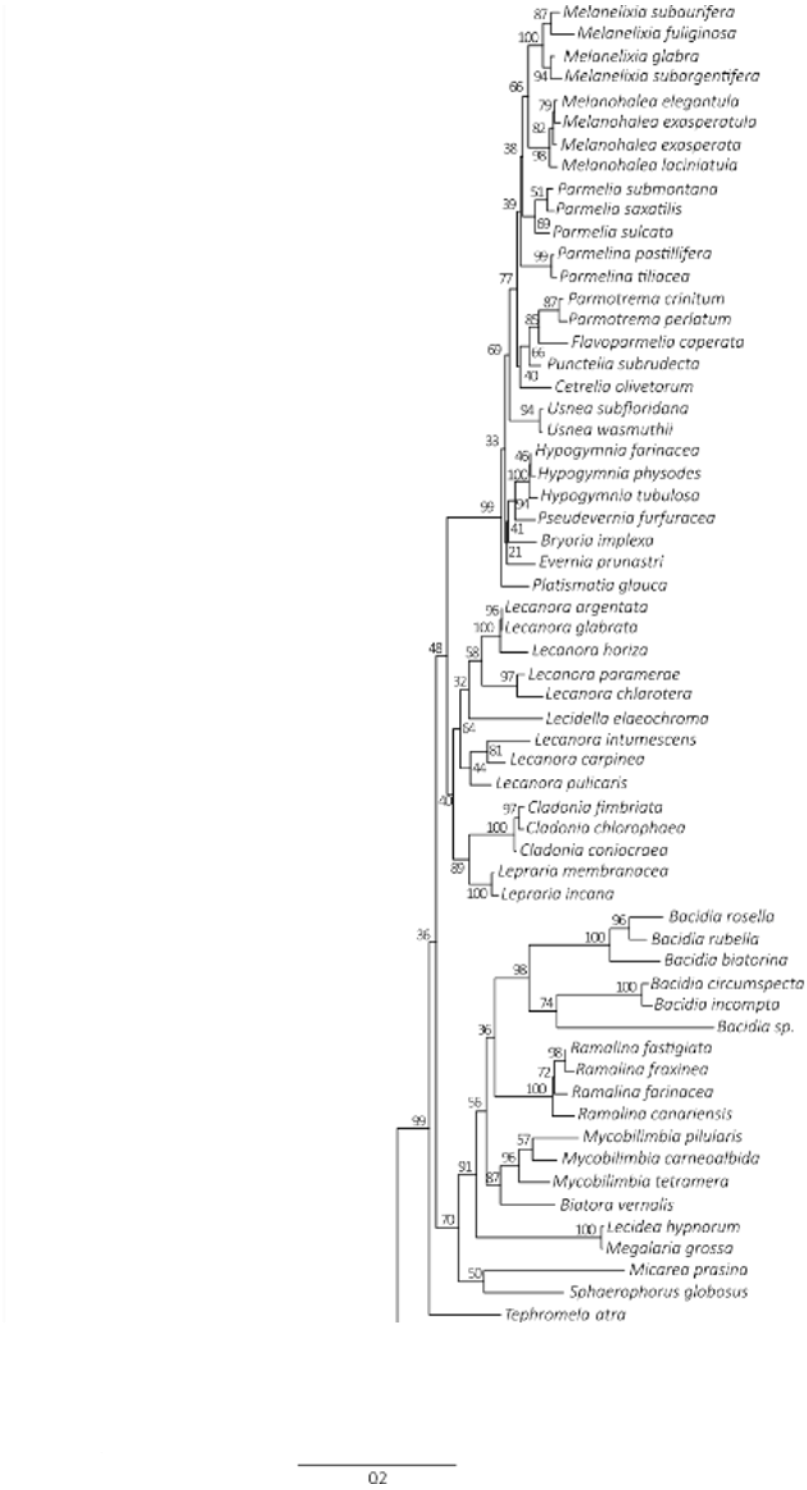
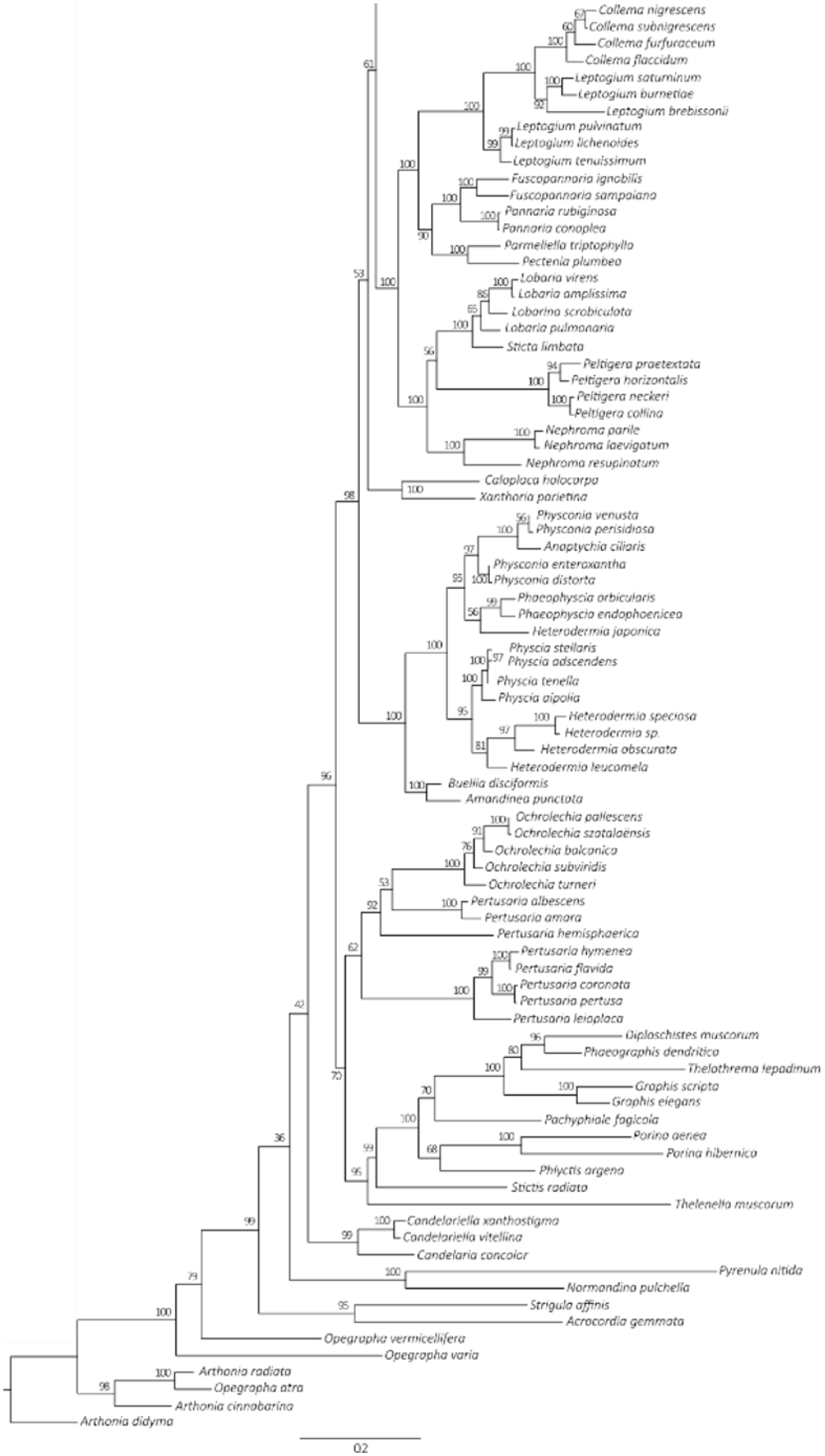
10.4. Appendix S4

Phylogenetic tree based on four molecular markers (nuITS, nuLSU, mtSSU and RPB1) including the lichen species found in the Atlantic and Mediterranean epiphytic communities. Numbers above nodes denote the bootstrap support (ML-BS) obtained with Maximum Likelihood in RAxML.



Appendix S4 (continued)



10.5. Appendix S5

GenBank accession numbers for the molecular markers used in the phylogenetic analyses. 'X' indicate sequences that have been produced for this study and sequences not available are marked with dashed lines.

Lichens	ITS	LSU	mtSSU	RPB1
Acrocordia gemmata (Ach.) A. Massal.	-	X	X	-
Amandinea punctata (Hoffm.) Coppins & Scheid	HQ650627	DQ986756	EU680860	KJ766906
Anaptychia ciliaris (L.) Körb.	AF389938	KX512894	EF582835	X
Arthonia cinnabarina (DC.) Wallr.	-	HQ454509	EU704046	X
Arthonia didyma Körb.	X	EU704083	EU704047	X
Arthonia radiata (Pers.) Ach.	-	-	EU704048	-
Bacidia biatorina (Körb.) Vain.	AF282079	X	X	-
Bacidia circumspecta (Norrl. & Nyl.) Malme	AF282124	AF282124	-	-
Bacidia incompta (Hook.) Anzi	AF282092	X	X	X
Bacidia rosella (Pers.) De Not.	AF282086	AY300829	AY300877	AY756412
Bacidia rubella (Hoffm.) A. Massal	HQ650644	DQ986793	AY567723	-
Bacidia sp. (*Bacidia aff. delicata*)	X	X	X	-
Biatora vernalis (L.) Fr.	AF282070	DQ838752	AM292711	-
Bryoria implexa (Hoffm.) Brodo & D.Hawksw.	KJ576721	X	KJ599561	X
Buellia disciformis (Fr.) Mudd	AF224349	AY340537	AY143401	X
Caloplaca holocarpa (Ach.) A.E. Wade	HM582157	X	X	X
Candelaria concolor (Dicks.) Stein	AF182075	DQ986791	EF436460	EF436462
Candelariella vitellina (Hoffm.) Müll.Arg.	AJ640085	AY853363	AY853315	-
Candelariella xanthostigma (Pers. ex Ach.) Lettau	EF535202	X	X	X
Cetrelia olivetorum (Nyl.) W.L. Culb. & C.F. Culb.	HQ671305	DQ923659	GU994638	GU994693
Cladonia chlorophaea (Flörke ex Sommerf.) Spreng.	DQ534460	EF489928	X	-
Cladonia coniocraea (Flörke) Spreng.	EU034663	X	X	X
Cladonia fimbriata (L.) Fr.	FJ756726	X	X	-
Collema flaccidum (Ach.) Ach.	-	AY424213	EU982578	X
Collema furfuraceum (Arnold) Du Rietz	GQ396263	EU982608	AY340488	GQ259048
Collema nigrescens (Huds.) DC.	-	EU982604	GQ259020	GQ259049
Collema subnigrescens Degel.	-	KJ766548	AY340489	X
Diploschistes muscorum (Scop.) R.Sant.	KC167008	KC167077	AY300886	KF688529
Evernia prunastri (L.) Ach.	EU266079	AF107562	AF351162	EF105428
Flavoparmelia caperata (L.) Hale	HQ650680	JN939607	AY584617	DQ883778

Appendix S5 (continued)

Lichens	ITS	LSU	mtSSU	RPB1
Fuscopannaria ignobilis (Anzi) M.Jørg.	HQ650673	DQ917417	KC608068	DQ986839
Fuscopannaria sampaiana (Tav.) P.M. Jørg.	KC618709	X	GU570030	KC608120
**Graphis elegans* (Borrer ex Sm.) Ach.	-	-	-	-
Graphis scripta (L.) Ach.	AF229195	AY640029	AY853322	DQ870947
Heterodermia sp. (Heterodermia aff. diademata)	X	X	X	X
Heterodermia japonica (M. Satô) Swinscow & Krog	DQ337322	X	KM397359	-
Heterodermia leucomela (L.) Poelt	AF540520	X	EF582790	X
Heterodermia obscurata (Nyl.) Trevis.	DQ337323	DQ337323	GU247185	-
Heterodermia speciosa (Wulfen) Trevis.	EU045439	JX000089	JX000125	-
Hypogymnia farinacea Zopf	GU300776	-	KJ766406	X
Hypogymnia physodes (L.) Nyl.	AF141368	JQ301600	AY756400	KJ766912
Hypogymnia tubulosa (Schaer.) Hav.	JF800095	X	HQ690160	X
Lecanora argentata (Ach.) Malme	X	X	X	-
Lecanora carpinea (L.) Vain.	AY541249	DQ787363	DQ787364	-
Lecanora chlarotera Nyl.	X	X	X	X
Lecanora glabrata (Ach.) Malme	-	DQ787359	DQ787360	-
Lecanora horiza (Ach.) Röhl.	AY541252	-	X	KT453903
Lecanora intumescens (Rebent.) Rabenh.	AY541253	AY300841	AY300892	AY756386
**Lecanora paramerae* I. Martínez, Aragón & Lumbsch	EF105413	-	EF105418	EF105431
Lecanora pulicaris (Pers.) Ach.	AY300892	DQ431915	KT630262	-
Lecidea hypnorum Lib.	X	X	X	X
Lecidella elaeochroma (Ach.) M. Choisy	HQ650605	DQ986747	DQ986719	DQ986818
Lepraria incana (L.) Ach.	JF739383	DQ986795	DQ986812	-
Lepraria membranacea (Dicks.) Vain.	DQ534473	-	KC183973	-
Leptogium brebissonii Mont.	-	EU982622	JX992943	-
Leptogium burnetiae C.W. Dodge	JF930694	EU982623	EU982584	-
Leptogium lichenoides (L.) Zahlbr.	DQ466041	EU166331	AY340498	DQ917414
Leptogium pulvinatum (L.) Zahlbr.	-	EU982629	EU982590	-
Leptogium saturninum (Dicks.) Nyl.	DQ466043	EU982610	AY340499	GQ259064
**Leptogium tenuissimum* (Hoffm.) Körb.	-	EU982593	X	-
Lobaria amplissima (Scop.) Forssell	AF524924	AY424206	EU558806	GQ259065
Lobaria pulmonaria (L.) Hoffm.	AF129285	AF183934	GU072912	DQ915597
Lobaria virens (With.) J.R.Laundon	KP941425	AY340553	AY340508	GQ259070

Appendix S5 (continued)

Lichens	ITS	LSU	mtSSU	RPB1
Lobarina scrobiculata (Scop.) P. Gaertn.	AF350297	AY424205	EU558816	DQ883736
Megalaria grossa (Pers. ex Nyl.) Hafellner	AF282074	AY756356	KJ766433	AY756419
Melanelixia fuliginosa (Fr. ex Duby) O. Blanco, A. Crespo, Divakar, Essl., D. Hawksw. & Lumbsch	HQ650599	DQ986803	AY611179	DQ986860
Melanelixia glabra (Schaer.) O. Blanco, A. Crespo, Divakar, Essl., D. Hawksw. & Lumbsch	EU761205	AJ421427	GU994651	EF092118
Melanelixia subargentifera (Nyl.) O. Blanco, et al.	EU761219	AJ421429	EU761238	EF092119
Melanelixia subaurifera (Nyl.) O. Blanco, et al.	AY611099	AJ421432	AY611156	EF092120
Melanohalea elegantula (Zahlbr.) O. Blanco, A. Crespo, Divakar, Essl., D. Hawksw. & Lumbsch	AY611094	JQ813007	AY611151	JQ813986
Melanohalea exasperata (De Not.) O. Blanco, A. Crespo, Divakar, Essl., D. Hawksw. & Lumbsch	AY611081	JQ813012	AY611138	EF092123
Melanohalea exasperatula (Nyl.) O. Blanco, A. Crespo, Divakar, Essl., D. Hawksw. & Lumbsch	JN943709	JQ813027	AY611147	JN987940
Melanohalea laciniatula (Flagey ex H. Olivier) O. Blanco, A. Crespo, Divakar, Essl., D. Hawksw. & Lumbsch	JQ813555	JQ813041	JQ813149	JQ814003
Micarea prasina Fr.	-	-	EF453669	-
Mycobilimbia carneoalbida (Müll.Arg.)	AJ247567	X	KJ766438	X
Mycobilimbia tetramera (De Not.) Vitik., Ahti, Kuusinen, Lommi & T. Ulvinen ex Hafellner & Türk	AJ247575	KJ766600	KF662403	KJ766915
Mycobilimbia pilularis (Körb.) Hafellner & Türk	AM292704	-	JQ922247	-
Nephroma laevigatum Ach.	AY124143	HQ394194	AY124182	-
Nephroma parile (Ach.) Ach.	DQ066708	HQ394196	AY584625	DQ973061
Nephroma resupinatum (L.) Ach.	DQ066710	AF286829	AY124168	-
Normandina pulchella (Borrer) Nyl.	-	GU121570	GU121607	GU121618
Ochrolechia balcanica Verseghy	AF329172	AF329171	AF329170	KC222183
Ochrolechia pallescens (L.) A. Massal.	-	DQ780310	DQ780277	DQ870960
Ochrolechia subviridis (Høeg) Erichsen	X	X	AY567980	X
Ochrolechia szatalaënsis Verseghy	X	AF274102	AY567981	X
Ochrolechia turneri (Sm.) Hasselrot	-	AY568002	AY567982	DQ870961
Opegrapha atra Pers.	-	-	EU704061	-
Opegrapha varia Pers.	AF138838	EU704103	EU704075	FJ772242
Opegrapha vermicellifera (Kunze) J.R. Laundon	-	EU704105	EU704077	-
Pachyphiale fagicola (Arnold) Zwackh,	X	X	HM244753	KC191663
Pannaria conoplea (Ach.) Bory	AF429281	AY424209	X	-
Pannaria rubiginosa (Ach.) Bory	GQ927267	AY340558	AY340513	GQ259073
Parmelia saxatilis (L.) Ach.	AF141370	JN939623	AY340514	DQ923695
Parmelia submontana Hale	JN609435	-	-	-
Parmelia sulcata Taylor	EU266084	JN939625	GU994669	GU994720

Appendix S5 (continued)

Lichens	ITS	LSU	mtSSU	RPB1
Parmeliella triptophylla (Ach.) Müll.Arg.	HM448804	GQ259008	GU570023	GQ259075
Parmelina pastillifera (Harm.) Hale	JX466460	JF757021	EU562697	-
Parmelina tiliacea (Hoffm.) Hale	EU266085	JN939631	AF351173	EF092137
Parmotrema crinitum (Ach.) M. Choisy	KP943761	KJ766620	KJ766454	GU994723
Parmotrema perlatum (Huds.) M. Choisy	AY586566	AY584838	AY586580	EF092146
Pectenia plumbea (Lightf.) P.M. Jørg., L. Lindblom, Wedin & S. Ekman	AF429264	DQ912347	AY340491	DQ912373
Peltigera collina (Ach.) Schrad.	FJ708926	AF286765	-	FJ709112
Peltigera horizontalis (Hudson) Baumg.	KC437645	KM005749	AY124163	FJ709130
Peltigera neckeri Müll.Arg.	AF350294	AY257964	-	FJ709230
Peltigera praetextata (Flörke ex Sommerf.) Zopf	DQ001296	AY257946	AY124167	FJ709246
Pertusaria albescens (Huds.) M. Choisy & Werner	AF329177	AF329176	AY568013	DQ870964
Pertusaria amara (Ach.) Nyl.	JN943621	AF356683	AY300900	DQ973048
Pertusaria coronata (Ach.) Th. Fr.	-	DQ780314	AY300902	DQ870968
Pertusaria flavida (DC.) J. R. Laundon	X	AY568003	X	X
Pertusaria hemisphaerica (Flörke) Erichsen	HQ650676	AF381556	AF381563	DQ902341
Pertusaria hymenea (Ach.) Schaer.	X	AF279297	AY567988	X
Pertusaria leioplaca DC.	AF332125	AY300852	AY568024	DQ870973
Pertusaria pertusa (L.) Tuck.	JN943618	AF279300	AF381565	KJ766877
Phaeographis dendritica (Ach.) Müll.Arg.	-	-	HQ639592	-
Phaeophyscia endophoenicea (Harm.) Moberg	AF224358	X	X	X
Phaeophyscia orbicularis (Neck.) Moberg	AF224356	DQ912343	GU247205	DQ912369
Phlyctis argena (Spreng.) Flot.	X	DQ986771	DQ986880	KJ766919
Physcia adscendens (Fr.) H.Olivier	FJ497044	-	EU682116	-
Physcia aipolia (Humb.) Fürnrh.	AY303132	DQ782904	EU682128	DQ782820
Physcia stellaris (L.) Nyl.	AF224408	AY773912	EU682115	-
Physcia tenella (Scop.) DC.	FJ497046	KX512869	EF582800	-
Physconia distorta (With.) J.R.Laundon	KX132933	AY773913	EF582813	-
Physconia enteroxantha (Nyl.) Poelt	AF224370	AY773909	EF582816	-
Physconia perisidiosa (Erichsen) Moberg	AJ421422	AY773911	EF582809	-
Physconia venusta (Ach.) Poelt	AY368147	X	EF582810	X
Platismatia glauca (L.) W.L.Culb. & C.F.Culb.	AF072231	DQ973032	AY756404	DQ912363
Porina aenea (Wallr.) Zahlbr.	-	X	DQ168411	KC191665
Porina hibernica P. James & Swinscow	X	X	X	X
Pseudevernia furfuracea (L.) Zopf	GU300783	KJ766637	GU300806	EF105435

Appendix S5 (continued)

Lichens	ITS	LSU	mtSSU	RPB1
Punctelia subrudecta (Nyl.) Krog	AY581089	JN939641	GU994674	-
Pyrenula nitida (Weigel) Ach.	X	AY607737	DQ328998	X
Ramalina canariensis J. Steiner	FJ871072	GU726340	X	-
Ramalina farinacea (L.) Ach.	JF923604	GU726354	X	KJ766831
Ramalina fastigiata (Pers.) Ach.	EU034669	GU726337	Y756375	AY756422
Ramalina fraxinea (L.) Ach.	JF923610	X	X	-
Sphaerophorus globosus (Huds.) Vain.	AY256775	DQ986767	AY256762	DQ986836
Sticta limbata (Sm.) Ach.	AB245118	AY424207	AY340531	KT281758
Strigula affinis (A. Massal.) R.C. Harris	X	JN887404	JN887416	-
Thelenella muscorum (Fries) Vain.	-	AY607731	AY607743	FJ941910
**Stictis radiata* (L.) Pers.	AY527309	AF356663	AY300914	AY641079
Thelothrema lepadinum (Ach.) Ach.	HQ650717	AY340576	AY340533	DQ973067
Tephromela atra Fée	DQ534487	DQ986766	AY300915	DQ986835
Usnea subfloridana Stirt.	JN086326	X	-	JN992586
Usnea wasmuthii Räsänen	JN086336	X	-	JN992579
Xanthoria parietina (L.) Th.Fr.	AF279888	AY340578	EU680868	JQ301734

*Species for which no sequences were obtained/available were substituted by close relatives (*Lecanora nemoralis* Makar. by *Lecanora paramerae* I. Martínez, Aragón & Lumbsch; *Leptogium aragonii* Otálora by *Leptogium tenuissimum* (Hoffm.) Körb. and *Thelopsis rubella* Nyl. by *Stictis radiata* (L.) Pers.)

10.6. Appendix S6

Location and functional trait values for all the species found in both biogeographic regions. Abbreviations: 1) Location: AT = Atlantic region, MD = Mediterranean region; 2) Growth form: CC=crustose conspicuous, CI=crustose inconspicuous, LEP=leprose, G=gelatinous, FBL=foliose broad-lobed, FNL=foliose narrow-lobed, FP=foliose placodiomorph, FB=big foliose, S=squamulose, FRC=fruticose cylindrical, FRD=fruticose dorsiventral and M=dimorphic thallus; 3) Type of photobiont: G=green algae, B=cyanobacteria, T=*Trentepohlia*; 4) Reproductive strategy: s=sexual, a=asexual; 5) Antiherbivore-defence compounds: A=absence, P=present. Nomenclature *sensu* Smith et al. (2009).

Species name	Location	Growth form	Type of photobiont	Reproductive strategy	Antiherbivore defence compounds
Acrocordia gemmata	AT	CI	G	s	A
Amandinea punctata	AT / MD	CI	G	s	A
Anaptychia ciliaris	AT / MD	FRD	G	s	A
Arthonia cinnabarina	AT	CI	G	s	A
Arthonia didyma	AT	CI	G	s	A
Arthonia radiata	AT / MD	CI	G	s	A
Bacidia biatorina	AT	CI	G	s	A
Bacidia circumspecta	AT	CI	G	s	A
Bacidia incompta	AT / MD	CI	G	s	A
Bacidia rosella	AT	CI	G	s	A
Bacidia rubella	AT / MD	CI	G	s	A
Bacidina aff. delicata	AT	CI	G	s	A
Biatora vernalis	AT / MD	CI	G	s	A
Bryoria implexa	MD	FRC	G	a	A
Buellia disciformis	AT / MD	CI	G	s	A
Caloplaca holocarpa	AT / MD	CI	G	s	A
Candelaria concolor	MD	FLE	G	a	P
Candelariella vitellina	MD	CI	G	s	P
Candelariella xanthostigma	AT	CI	G	a	P
Cetrelia oliaetorum	AT	FBL	G	a	A
Cladonia chlorophaea	AT / MD	M	G	a	A
Cladonia coniocraea	AT / MD	M	G	a	A
Cladonia fimbriata	AT / MD	M	G	a	A
Collema flaccidum	AT / MD	G	B	a	A
Collema furfuraceum	AT / MD	G	B	a	A
Collema nigrescens	AT / MD	G	B	a	A
Collema subnigrescens	AT / MD	G	B	s	A
Diploschistes muscorum	MD	CC	G	s	A
Evernia prunastri	AT / MD	FRD	G	a	P
Flavoparmelia caperata	AT	FBL	G	a	P
Fuscopannaria ignobilis	MD	S	B	s	A
Fuscopannaria sampaiana	AT	S	B	a	A

Appendix S6 (continued)

Species name	Location	Growth form	Type of photobiont	Reproductive strategy	Antiherbivore defence compounds
Graphis elegans	AT	CI	G	s	A
Graphis scripta	AT	CI	G	s	A
Heterodermia aff. diademata	AT	FNL	G	s	A
Heterodermia japonica	AT	FNL	G	a	A
Heterodermia leucomela	AT	FNL	G	a	A
Heterodermia obscurata	AT	FNL	G	a	A
Heterodermia speciosa	AT	FNL	G	a	A
Hypogymnia farinácea	AT / MD	FNL	G	a	P
Hypogymnia physodes	AT	FNL	G	a	P
Hypogymnia tubulosa	AT / MD	FNL	G	a	P
Lecanora argentata	AT / MD	CI	G	s	A
Lecanora carpinea	AT / MD	CI	G	s	A
Lecanora chlarotera	AT / MD	CI	G	s	A
Lecanora glabrata	AT / MD	CI	G	s	A
Lecanora horiza	AT	CI	G	s	A
Lecanora intumescens	AT / MD	CI	G	s	A
Lecanora nemoralis	AT	CI	G	s	A
Lecanora pulicaris	MD	CI	G	s	A
Lecidea hypnorum	AT	CI	G	s	A
Lecidella elaechroma	AT	CI	G	s	A
Lepraria incana	AT / MD	LEP	G	a	A
Lepraria membranacea	AT	LEP	G	a	A
Leptogium aragonii	AT / MD	G	B	s	A
Leptogium burnetiae	AT	G	B	a	A
Leptogium lichenoides	AT / MD	G	B	a	A
Leptogium pulvinatum	MD	G	B	s	A
Leptogium saturninum	AT / MD	G	B	a	A
Leptogium tenuissimum	AT	G	B	a	A
Lobaria amplissima	AT / MD	FG	G	s	A
Lobaria pulmonaria	AT / MD	FG	G	a	A
Lobaria virens	AT	FG	G	s	A
Lobarina scrobiculata	AT	FG	B	a	P
Megalaria grossa	AT	CI	G	s	A
Melanelixia fuliginosa	AT / MD	FBL	G	a	A
Melanelixia glabra	AT / MD	FBL	G	s	A
Melanelixia subargentifera	MD	FBL	G	a	A
Melanelixia subaurifera	MD	FBL	G	a	A
Melanohalea elegantula	AT	FBL	G	a	A
Melanohalea exasperata	MD	FBL	G	a	A
Melanohalea exasperatula	AT / MD	FBL	G	a	A
Melanohalea laciniatula	AT	FBL	G	s	A
Micarea prasina	AT	CI	G	s	A

Appendix S6 (continued)

Species name	Location	Growth form	Type of photobiont	Reproductive strategy	Antiherbivore defence compounds
Mycobilimbia carneoalbida	AT	CI	G	s	A
Mycobilimbia tetramera	MD	CI	G	s	A
Mycobilimbia pilularis	AT	CI	G	a	A
Nephroma laevigatum	AT / MD	FG	B	s	A
Nephroma parile	AT / MD	FG	B	a	A
Nephroma resupinatum	AT / MD	FG	B	s	A
Normandina pulchella	AT / MD	S	G	a	A
Ochrolechia balcanica	AT / MD	CC	G	s	A
Ochrolechia pallescens	AT / MD	CC	G	s	A
Ochrolechia subviridis	AT	CC	G	a	A
Ochrolechia szatalaënsis	AT	CC	G	s	A
Ochrolechia turneri	AT	CC	G	a	A
Opegrapha atra	AT	CI	T	s	A
Opegrapha varia	AT	CI	T	s	A
Opegrapha vermicellifera	AT	CI	T	s	A
Pachyphiale fagicola	AT	CI	T	s	A
Pannaria conoplea	AT	S	B	a	A
Pannaria rubiginosa	AT	S	B	s	A
Parmelia saxatilis	AT / MD	FBL	G	a	A
Parmelia submontana	MD	FBL	G	a	A
Parmelia sulcata	AT / MD	FBL	G	a	A
Parmeliella triptophylla	AT / MD	S	B	a	A
Parmelina pastillifera	AT	FBL	G	a	A
Parmelina tiliacea	AT / MD	FBL	G	a	A
Parmotrema crinitum	AT	FBL	G	a	A
Parmotrema perlatum	AT / MD	FBL	G	a	A
Pectenia plumbea	AT / MD	FP	B	s	A
Peltigera collina	AT / MD	FG	B	a	A
Peltigera horizontalis	AT	FG	B	s	A
Peltigera neckeri	AT / MD	FG	B	s	A
Peltigera praetextata	AT	FG	B	s	A
Pertusaria albescens	AT / MD	CC	G	a	A
Pertusaria amara	AT / MD	CC	G	a	A
Pertusaria coronata	AT / MD	CC	G	a	A
Pertusaria flavida	AT / MD	CC	G	a	A
Pertusaria hemisphaerica	AT / MD	CC	G	a	A
Pertusaria hymenea	AT	CC	G	s	A
Pertusaria leioplaca	AT / MD	CC	G	s	A
Pertusaria pertusa	AT	CC	G	s	A
Phaeographis dendritica	AT	CI	T	s	A
Phaeophyscia endophoenicea	AT	FNL	G	a	A

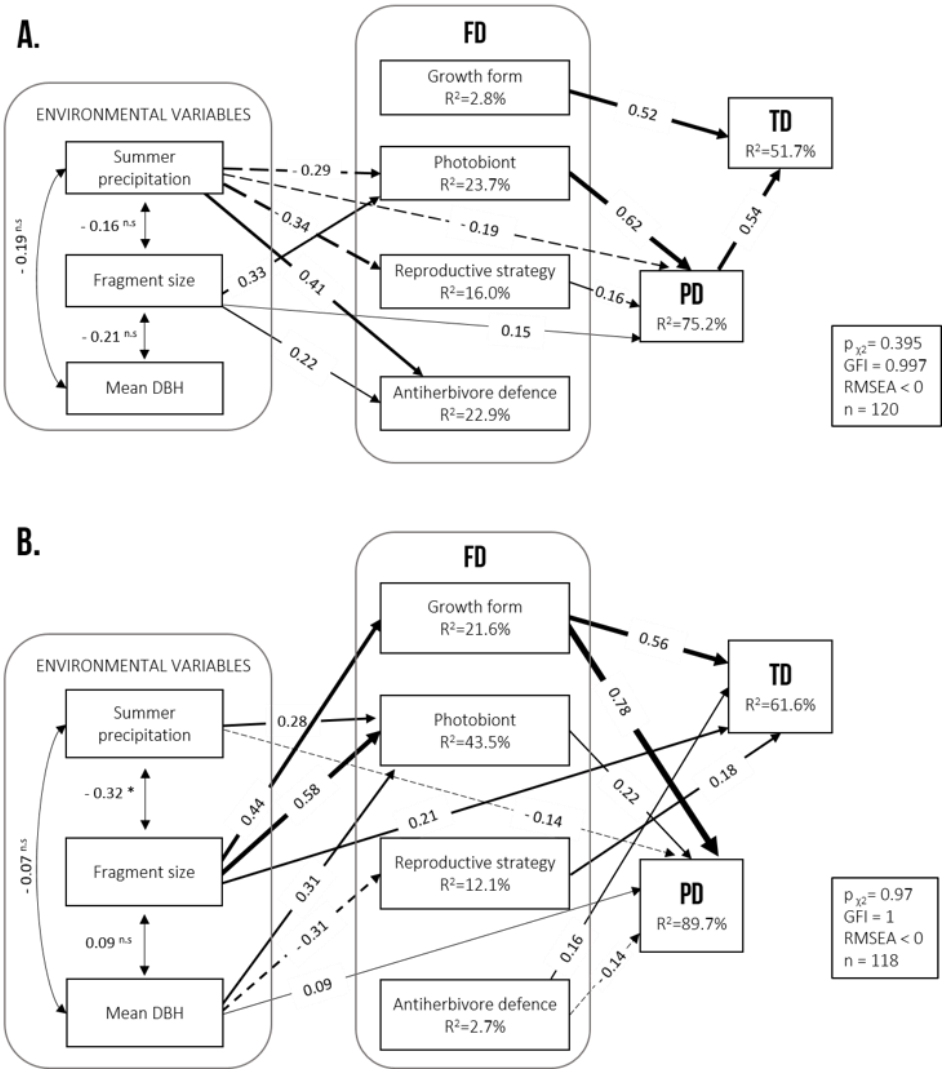
Appendix S6 (continued)

Species name	Location	Growth form	Type of photobiont	Reproductive strategy	Antiherbivore defence compounds
Phaeophyscia orbicularis	AT	FNL	G	a	A
Phlyctis argena	AT / MD	LEP	G	a	A
Physcia adscendens	MD	FNL	G	a	A
Physcia aipolia	MD	FNL	G	s	A
Physcia stellaris	AT	FNL	G	s	A
Physcia tenella	AT / MD	FNL	G	a	A
Physconia distorta	AT / MD	FNL	G	s	A
Physconia enteroxantha	AT / MD	FNL	G	a	A
Physconia perisidiosa	AT	FNL	G	a	A
Physconia venusta	AT / MD	FNL	G	s	A
Platismatia glauca	AT / MD	FBL	G	a	P
Porina aenea	AT	CI	T	s	A
Porina hibernica	AT	CI	T	s	A
Pseudevernia furfuracea	AT / MD	FRD	G	a	A
Punctelia subrudecta	AT	FBL	G	a	A
Pyrenula nitida	AT	CI	T	s	A
Ramalina canariensis	AT	FRD	G	a	P
Ramalina farinacea	AT / MD	FRD	G	a	P
Ramalina fastigiata	AT	FRD	G	s	P
Ramalina fraxinea	AT / MD	FRD	G	s	P
Sphaerophorus globosus	AT	FRC	G	s	A
Sticta limbata	AT	FG	B	a	A
Strigula affinis	AT	CI	T	s	A
Thelenella muscorum	AT / MD	CI	G	s	A
Thelopsis rubella	AT	CI	T	s	A
Thelotrema lepadinum	AT	CI	T	s	A
Tephromela atra	AT	CI	G	s	A
Usnea subfloridana	AT / MD	FRC	G	a	P
Usnea wasmuthii	AT	FRC	G	a	P
Xanthoria parietina	AT / MD	FNL	G	s	A

Smith, C.W., Aptroot, A., Coppins, B.J., Fletcher, A., Gilbert, O.L., James, P.W. & Wolseley, P.A. (2009). *The lichens of Great Britain and Ireland*. 2nd Ed, London: The British Lichen Society, Department of Botany, the Natural History Museum, Cromwell Road, London. England.

10.7. Appendix S7

In the figures A, B, and C we illustrate the SEM results of the relationships between environmental variables and biodiversity metrics, including Inverse Simpson index as surrogate of taxonomic diversity (TD). Similarly to the results obtained when richness was used as surrogate of TD, we identified that different critical predictors affected the diversity facets of lichen communities depending on the biogeographic region. Fragment size performed the largest influence on biodiversity, followed by summer precipitation in the Atlantic region, and mean DBH in the Mediterranean region. Habitat fragmentation declined the diversity of Atlantic and Mediterranean communities. In addition, increases in summer precipitation reduced the PD and TD in the Atlantic region. The overall patterns of relationships were similar when we used Inverse Simpson index and richness as surrogates of TD, with one exception: mean DBH performed a negative effect on Inverse Simpson index, and a positive effect on species richness.



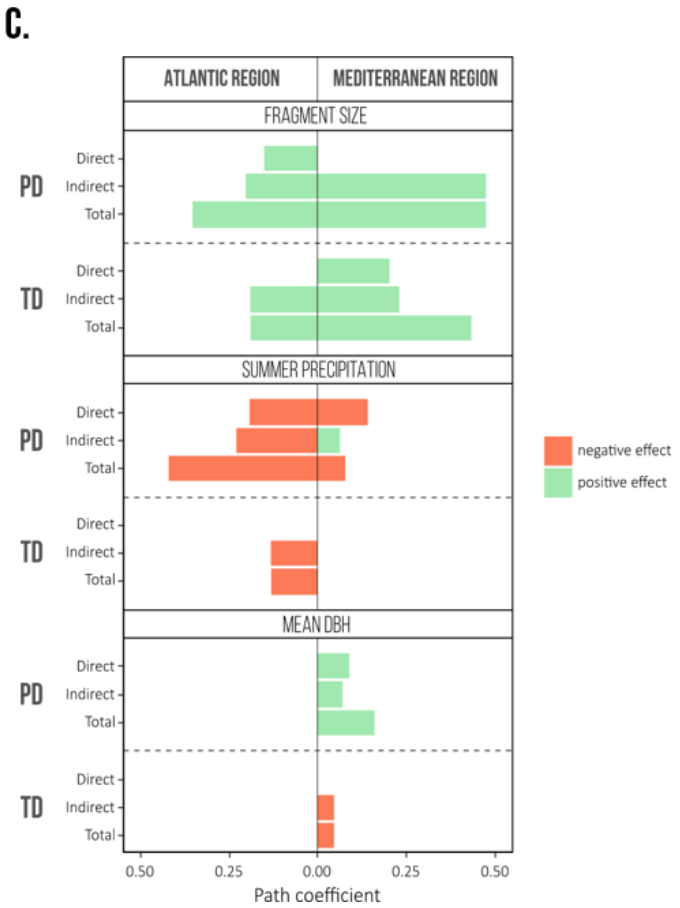
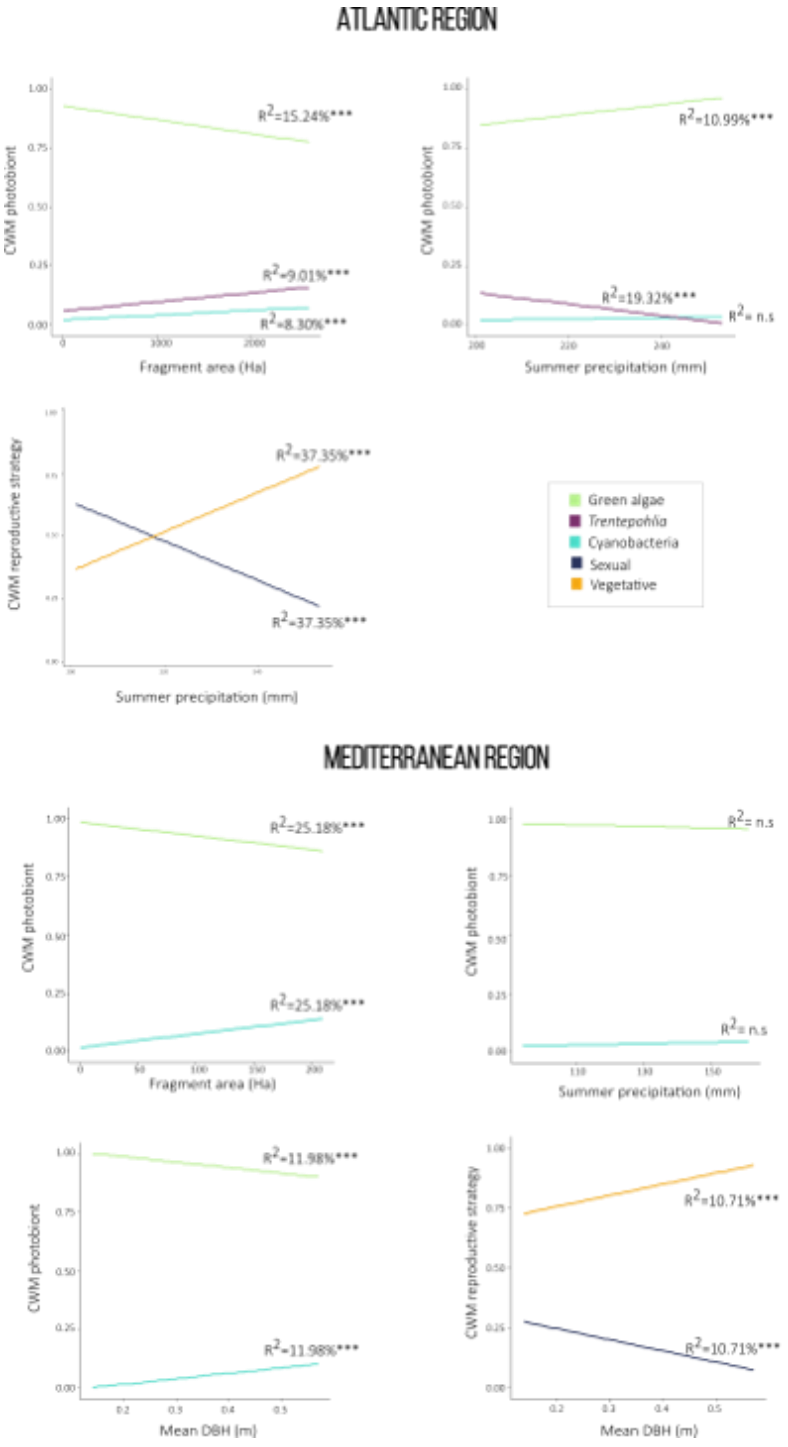


Figure S7. Results of the SEM analyses showing the relationships between environmental variables and biodiversity metrics. Significant causal paths obtained (A) in the Atlantic region, (B) in the Mediterranean region, and (C) synthesis of direct, indirect, and total effects. In A and B, solid arrows represent positive relationships (→) and broken arrows (- ->) represent negative effects. Arrow width is proportional to the standardized coefficient of the path (indicated by numbers on the lines). Double-headed arrows (↔) represent correlation between exogenous variables (n.s. = non-significant; * $P < 0.05$). R^2 denotes the proportion of variance explained and appears below every response variable in the model. In C, path coefficients represent the standardized coefficient of the significant paths. Direct effects represent the standardized coefficient of the path when two variables are only connected through a single significant path (Grace 2006). Indirect effects were calculated as the product of the coefficients along the compound significant paths which involve multiple arrows (Grace 2006). Total effect of one variable on another was calculated as the sum of its direct and indirect effects taking into account all the significant pathways connecting these two variables (Grace 2006). Abbreviations: FD, functional diversity; PD, phylogenetic diversity; TD, taxonomic diversity.

Grace, JB. (2006). *Structural Equation Modeling and Natural Systems.* Cambridge University Press, New York, NY.

10.8. Appendix S8

Results of linear regression models relating Community Weighted Mean (CWM) of functional traits and environmental variables in the Atlantic and Mediterranean regions. CWM were calculated at plot level (function *dbFD* of *FD* package) and represents the proportion of each individual trait category per community. R^2 represents the adjusted r-squared of linear regression models (function *lm* of *R stats* package). *** $P < 0.001$, n.s. = non- significant.



Capítulo 2

Contrasting climatic predictors determine patterns of taxonomic, functional and phylogenetic diversity in lichen communities along a European latitudinal gradient

Pilar Hurtado | María Prieto | Francesco de Bello | Gregorio Aragón | Paolo Giordani | Eva María Díaz-Peña | Rebeca Vicente | Alica Košuthová | Sonia Merinero | Renato Benesperi | Elisabetta Bianchi | Helmut Mayrhofer | Juri Nascimbene | Martin Grube | Mats Wedin | Martin Westberg | Isabel Martínez

En preparación

ABSTRACT

Assessing the ecological impacts of environmental change on natural communities requires knowledge of the factors driving the spatial patters of biodiversity along extensive environmental gradients. However, these patterns can differ substantially depending on the diversity facet considered (taxonomic, TD; functional, FD; and phylogenetic, PD), and a pluralistic approach integrating the response of all the three facets is needed. Here, we quantified the taxonomic, functional and phylogenetic diversity of lichen epiphytic communities in 23 beech forests along Europe (ca. 3000 km, from Sweden to Italy) to examine the patterns of biodiversity at a broad geographic scale. Regarding the FD, we selected three qualitative functional traits (i.e. growth form, type of photobiont and reproductive strategy) with a valuable role as indicators of climatic conditions in forest ecosystems. In addition, we quantified three physiological traits related to the water use strategy (i.e. specific thallus mass -STM- and water holding capacity -WHC-) and nutrient uptake (i.e. C/N). Our results show that spatial patterns of biodiversity in lichen communities were primarily determined by distinct environmental factors. The geographic variation of FD and PD responded to changes in annual temperature fluctuation, while patterns of TD were overall determined by precipitation of the wettest month. Throughout the latitudinal gradient, increases in FD were accompanied by increases in PD and decreases in TD, pointing out a strong phylogenetic signal and functional redundancy for the studied traits. Thus, FD appeared as a surrogate for PD and TD, but these two facets were not correlated. Interestingly, despite the partial congruence between the three facets of biodiversity, they were shaped by distinct critical predictors indicating than a multidimensional approach is needed to unveil the patterns of diversity. We also found that climate explained a large amount of spatial variation in the studied functional traits, which highlights their role as indicators of climatic changes and supports the assumption that species enter and persist in natural communities based on their functional trait values.

Key words

Beech forests, functional diversity, lichen, phylogenetic diversity, functional trait, taxonomic diversity, latitudinal gradient, climate.

1 | INTRODUCTION

Unveiling the factors that drive the heterogeneous distribution of biodiversity (Gaston 2000) at a broad-scale (geographical) is a primary goal to predict the response of natural communities in a changing environment. Community ecologists have largely evaluated how the spatial differences in biodiversity have been generated, identifying climate and primary productivity as some of the factors underpinning patterns such as the latitudinal diversity gradient (Mittelbach 2012). However, the knowledge on such biodiversity spatial patterns traditionally relied on species composition or richness, although the few studies that integrate taxonomic (TD), functional (FD) and phylogenetic (PD) diversity facets prove that they show different responses to environmental changes (Safi et al. 2011, Dainese et al. 2015,

Hurtado et al. 2019). These findings highlight the limitations of a purely taxon-based approach to assess the impact of environmental changes on the biodiversity (Stevens et al. 2003, Devictor et al. 2010, Davis & Cadotte 2011, Safi et al. 2011) and stress the need to also consider the response of FD and PD given that different species within the communities represent distinct functions and evolutionary histories (Swenson 2011). As a consequence, the spatial patterns of biodiversity shaped by the environmental conditions may differ depending on which species, traits or lineages within a community are affected (Díaz & Cabido 2001, Tilman 2001).

Since the biodiversity patterns can differ substantially depending on the facet considered (Purschke et al. 2013), an effective assessment of the response of communities requires knowledge of the relationships between TD, FD and PD. In this line, the extent to which these three facets are correlated along broad-scale gradients is still unclear. For example, it is expected that TD is positively correlated with FD and PD based on the assumption that a higher number of species would represent a higher range of trait values and lineages (Losos 2008). However, decreases in TD do not necessarily imply a decrease in FD and PD if functionally redundant species are removed (Cadotte et al. 2011, Fetzer et al. 2015) or if certain clades are overrepresented within the community (Forest et al. 2007, Tucker & Cadotte 2013). Furthermore, FD and PD might be correlated if the functional traits mediating the persistence of species within a community display a significative phylogenetic signal, meaning that close relatives exhibit more similar values for those traits than distant relatives (Harvey & Pagel 1991, Webb et al. 2002). Studies assessing the relationships between TD, FD and PD have found inconsistent results (Losos 2008, Mouquet et al. 2012, Purschke et al. 2013), which highlights the importance of disentangling the role of these diversity facets as surrogate for the others under contrasting environmental conditions.

The key to understand the spatial variation in TD, FD and PD for comprehending and predicting potential community changes, is unveiling the specific drivers shaping these dimensions of biological diversity along extensive gradients. In this regard, it has been shown that overall TD, FD and PD trends can be determined by different main predictors which modify different diversity dimensions in different ways (Leão-Pires et al. 2018). Thus, TD, FD and PD did not always respond similarly to environmental variables. For example, Chun & Lee (2017) found that climate was the main driver of PD in plant communities along an altitudinal gradient in East Asia, while FD was mainly determined by habitat heterogeneity. Safi et al. (2011) in a global scale study, obtained similar results in mammals, with PD

influenced by mean annual temperature and FD by seasonality. Thus, if these diversity dimensions are not always correlated and represent independent aspects of community structure, it is important to unveil which precise predictors modify them.

In the present study we address three questions. First, which are the main environmental drivers determining TD, FD and PD in natural communities along a wide latitudinal gradient? Second, which is the correlation between these three facets of biodiversity along the gradient? Third, is there a geographical configuration of the species composition and functional structure (i.e. the composition and diversity of functional traits) of the communities in response to the environmental conditions? To address these questions, we quantified the taxonomic, functional and phylogenetic diversity of lichen epiphytic communities in 23 beech forests from northern to southern Europe to examine the patterns of biodiversity in response to a continent-wide climatic and latitudinal gradient. We focused on epiphytic lichens since these organisms lack active mechanisms to regulate nutrient and water uptake and loss and, consequently, they are physiologically active only depending on the environmental conditions (Green et al. 2011). Therefore, they have been recognized as very sensitive indicators of environmental changes (Pinho et al. 2011, Matos et al. 2015). In particular, we selected three easily discernible functional traits (i.e. growth form, type of photobiont and reproductive strategy) considered valuable indicators of climatic conditions in forest ecosystems (Giordani et al. 2012). In addition, we quantified three physiological traits related to the water use strategy (i.e. specific thallus mass -STM- and water holding capacity -WHC-) and nutrient uptake (i.e. C/N). We hypothesise that: 1) spatial patterns of TD, FD and PD might be determined by distinct critical drivers; 2) FD might be correlated with TD and PD, but we do not expect a correlation between TD and PD (Hurtado et al. 2019); and 3) climatic drivers may determine the species composition and functional structure of lichen communities, with less diverse communities under stressful environmental conditions.

2 | MATERIALS AND METHODS

2.1. Study area and sampling design

The study area encompassed six European countries located along a latitudinal gradient from 57º in the north (Sweden) to 39º in the south (Italy). The gradient is characterized by strong climatic differences in mean annual temperature (from 3.9 to 11.9 ºC) and total annual rainfall (from 563 to 1644 mm), as well as in temperature and precipitation seasonality (Karger et al. 2017) (Table 1). Field data were collected between 2015 and 2016. Lichen epiphytic

communities were surveyed in twenty-three mature monospecific stands of European beech along a latitudinal gradient covering the entire range of *Fagus sylvatica* L. (Fig. 1). Forest stands had a tree cover over the 65%, were not subjected to tree cutting during the last 50 years and were separated, at least, 5 km among them. To minimize the effect of sampling communities in different successional stages, we only surveyed beech stands with the lichen species *Lobaria pulmonaria* (L.) Hoffm., which is an indicator of mature epiphytic communities (Rose 1988).

Table 1. Climatic variables of the study sites.

Country	Forest stands	Latitude	Temperature (ºC)		Precipitation (mm)	
			Mean annual	Seasonality	Total annual	Seasonality
Sweden	(22) Ramlaklitten i Skogsbo Naturreservat	57.076	7.46	6309	842	23.8
	(23) Ödegärdet Naturreservat	56.966	6.68	6502	914	22.0
	(21) Biskopstorps Naturreservat	56.800	6.96	6354	1069	23.0
	(20) Bjurkärrs Naturreservat	56.635	6.94	6489	658	22.0
Slovakia	(19) Rabia skala (Poloniny NP)	49.102	4.02	7484	1125	29.8
	(18) Cigánka-Muránsky hrad (Muránska planina NP)	48.762	6.20	7581	666	30.2
	(17) Klenovsý Vepor (Klenovské vrchy)	48.687	3.86	7439	1065	30.4
Austria	(16) Nationalpark Kalkalpen	47.816	6.78	7049	1031	31.4
	(14) Loibltal	46.461	6.16	7197	1644	22.2
	(15) Trögener Klamm	46.448	6.76	7247	1278	25.0
France	(8) Chadefour Valley Nature Reserve	45.540	6.12	5749	1032	12.2
	(9) Réserve naturelle nationale de Chastreix-Sancy	45.495	6.38	5769	1113	13.6
	(7) Picherande	45.468	6.82	5765	1354	13.0
Spain	(5) Parque Natural Saja-Besaya	43.114	11.12	4557	925	25.2
	(4) Parque Natural de Redes	43.105	8.70	4717	1174	30.6
	(6) La Selva de Irati	42.992	9.90	5343	1332	24.2
	(1) Sitio Natural de Interés Nacional del Hayedo de Montejo de la Sierra	41.227	9.42	6378	563	34.0
	(3) Parque Natural Sierra Norte de Guadalajara	41.218	7.10	6184	707	28.0
	(2) Hayedo La Pedrosa	41.112	8.00	6231	681	30.0
Italy	(13) Foresta del Cansiglio	46.074	6.96	6928	1427	20.4
	(12) Foresta Umbra (Parco Nazionale del Gargano)	41.810	11.92	5793	618	20.4
	(11) Parco Nazionale del Cilento e Valle de Diano	40.498	8.96	6055	942	41.0
	(10) Riserva Statale Serra Nicolino - Pian d'Albero	39.503	10.98	5657	1089	46.8

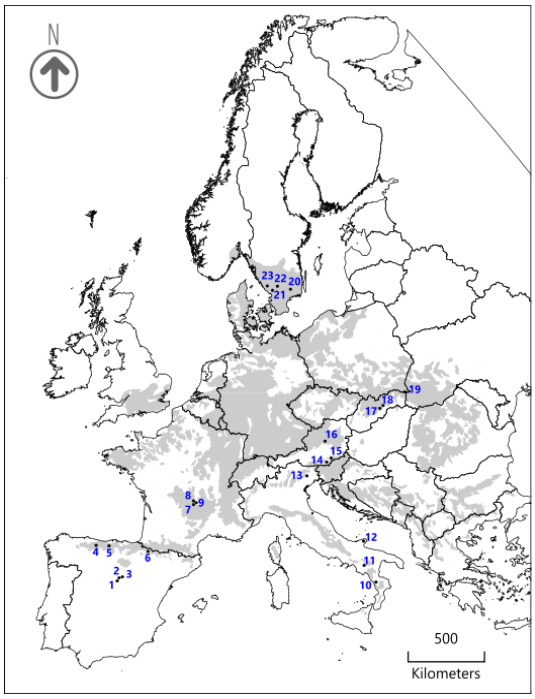


Figure 1. Map of the study area showing the distribution area of *Fagus sylvatica* (light grey) and the sampling sites (black dots). Name of sampling sites in Table 1.

We surveyed the composition of the lichen community following a standard protocol (see Aragón et al. 2012). Within each stand, we randomly stablished five 25 x 25 m plots with a minimum distance to forest edge of 100 m and a minimum distance of 500 m among plots. Within each plot, we selected 10 beech trees with a minimum diameter at breast height (dbh) > 25 cm and with a clear area on the trunk at the breast height without damage, decortication or branching. Within each tree, we stablished four 20 x 30 cm grids on the trunk, at two different aspects (north and south faces) and heights (breast and tree base). Within each grid, we estimated the cover (%) of all lichen species found, collecting the sample for later laboratory identification when it was needed. Lichen identification followed Smith et al. (2009) and Clauzade & Roux (1985). We collected data from 4600 grids and surveyed 1150 trees.

In addition to the estimation of the lichen cover and community composition, we collected a maximum of four thalli per forest of all macrolichen species found. Samples were air-dried and stored at -20ºC before the measurement of quantitative functional traits in the laboratory.

2.2. Trait data and phylogenetic tree

We categorized the 203 lichen species found according to three qualitative functional traits: growth form, type of photobiont and reproductive strategy (Appendix S1). These are easily discernible traits broadly used to differentiate lichen functional groups in relation to water

uptake and loss, response to climate, or colonization and establishment (Büdel & Scheidegger 2008, Giordani et al. 2014, Nascimbene & Marini 2015, Nelson et al. 2015, Prieto et al. 2017). We followed ITALIC database (Nimis & Martellos 2017) and Lias light database (Rambold et al. 2014) for trait classification. Growth form included seven categories (crustose, squamulose, leprose, foliose broad lobed, foliose narrow lobed, fruticose dorsiventral and fruticose filamentous) while both, type of photobiont (green algae, *Trentepohlia* and cyanobacteria) and reproductive strategy (sexual, asexual and both), included three categories.

Additionally, for the 58 species of macrolichens occurring along the latitudinal gradient, we measured three quantitative functional traits related to water use strategy (n = 1018 thalli) and nutrient uptake (n = 1179 thalli). Regarding water use strategy, we measured specific thallus mass (STM) and water holding capacity (WHC) according to Merinero et al. (2014). For nutrient uptake, we quantified thallus carbon-nitrogen ratio (C/N) using a PDZ Europa ANCA-GSL elemental analyser interfaced to a PDZ Europa 20-20 isotope ratio mass spectrometer (Sercon Ltd., Cheshire, UK) at UC Davis Stable Isotope Facility.

We built a phylogenetic tree including the 203 species found in the communities (Appendix S2). We used four molecular markers (nuITS, nuLSU, mtSSU and RPB1) to construct a combined phylogenetic tree using sequences from GenBank or generating the sequences following Prieto & Wedin (2013) for those species not available in this database (see Prieto et al. 2017 for further details about the phylogenetic analysis).

2.3. Diversity metrics

We used species composition and cover, trait and phylogenetic information to calculate taxonomic, functional and phylogenetic diversity indices at community level including the 23 forest stands surveyed. To do so, we merged all data within each forest stand, averaging species covers across all samples within a stand. Since we expected an effect of the environment not only in the presence but also in the abundance of the species conforming the communities, we calculated lichen species richness, Shannon and Inverse Simpson diversity indices for each forest stand.

Regarding the functional characterization of the epiphytic communities, we used individual species trait data to calculate two indices at community level: community weighted mean (hereafter 'CWM') and Rao's quadratic entropy index (hereafter 'Rao'). These two indices inform about different components of functional diversity: while CWM reflects the

dominant traits in a community, Rao is a multivariate form of the functional variance (de Bello et al. 2010). As an indicator of functional composition, we calculated the CWM index of every qualitative trait for each of the forests studied using the *functcomp* function implemented in the *FD* package (Laliberté & Legendre 2010). This index was computed as the mean trait value of each species in a community, weighted by the relative abundance of this species (Lavorel et al. 2008). The larger the relative abundance of one species, the more important contribution of its individual trait value to the global community average. For qualitative traits, the CWM reflects the percentage of a given category of the trait in a community. As an indicator of functional dissimilarity, we calculated a Rao index considering multiple qualitative and quantitative traits together (i.e. growth form, type of photobiont, reproductive strategy, STM, WHC and C/N). First, we calculated the species dissimilarity matrix using Gower distances and giving more weight to quantitative traits (w = 1) than qualitative traits (w = 0.5) since the latter usually show higher values of dissimilarity. Dissimilarity distances (d_{ij}) closer to 0 denote that species are functionally equivalent, while d_{ij} values closer to 1 reflect higher dissimilarity between species (Pavoine et al. 2009). Then, using the trait dissimilarity distances between each pair of coexisting species (d_{ij}) and the relative abundance of these species in a given forest (p_i and p_j), we computed the Rao index (Rao 1982) at forest level with the function *Rao* (de Bello et al. 2010):

$$Rao = \sum_{i=1}^{s} \sum_{j=1}^{s} p_i p_j d_{ij}$$

We finally applied the Jost correction (Jost 2007), to express the index in equivalent numbers. Higher values of Rao index denote higher community functional dissimilarity in a given forest. Some of the advantages of this metric are, the combination of functional richness and functional divergence (Mouchet et al. 2010), and the quantification of species dissimilarity including the relative abundance of species (de Bello et al. 2010).

Since Rao allows the measurement of species dissimilarity based on functional and phylogenetic data, it is a useful metric to compare these different diversity dimensions (i.e. FD and PD) (de Bello et al. 2010). Hence, we calculated a Rao index combining the species relative abundance with the phylogenetic tree as metric of PD. In this case, we used the function *cophenetic* implemented in the *picante* package (Kembel et al. 2010), to compute the phylogenetic distance between pairs of coexisting species (*dij*).

2.4. Environmental predictors

We used a set of variables related to forest structure and climate in order to assess the response of taxonomic, functional and phylogenetic community diversity to these environmental conditions. We measured the tree diameter at breast height (dbh) of the 50 trees sampled within each forest and we calculated the mean dbh as proxy of forest structure. Climatic information at forest level was retrieved from the high-resolution climate dataset CHELSA (Karger et al. 2017) including 19 bioclimatic variables related to annual values and seasonal ranges of temperature and precipitation (Appendix S3).

2.5. Data analyses

We applied Generalised Linear Models (GLMs) to evaluate the effect of environmental predictors in metrics describing the taxonomic, functional and phylogenetic diversity of communities including the 203 lichen species found along the gradient. We then assessed the correlation between these three diversity facets using Ordinary Least Square models (OLS). Finally, we performed constrained ordination analyses to assess the impact of climate on community species composition and trait values of the dominant species (CWM) using the qualitative traits available for all the 203 species. All statistical analyses were performed using R version 3.5.0 (R Core Team 2018), as explained below.

2.5.1. Effect of environmental predictors determining spatial patterns of TD, FD and PD along Europe

We evaluated the effect of environmental predictors on the community diversity metrics (i.e. TD, FD and PD indices) using Generalised Linear Models (GLM; McCullagh & Nelder 1989). To avoid multicollinearity and to reduce the number of explanatory variables, we excluded highly correlated predictors according to Pearson correlation coefficients ($r > 0.7$, $P < 0.05$). The resulting set of explanatory variables included in the models were: Mean Diurnal Range (BIO2), Max Temperature of Warmest Month (BIO5), Min Temperature of Coldest Month (BIO6), Mean Temperature of Wettest Quarter (BIO8), Precipitation of Wettest Month (BIO13), Precipitation of Driest Month (BIO14) and dbh.

We built separate models with each diversity index (richness, Shannon, Inverse Simpson, Rao FD and Rao PD) as dependent variables and the selected climatic and forest structure variables (BIO2, BIO5, BIO6, BIO8, BIO13, BIO14 and dbh) as independent variables. We used Gaussian family as error distribution and model selection based on the Akaike Information Criterion (AIC; Akaike 1973). Due to the small sample size, we

compared the second-order Akaike information criterion (AICc) of the alternative models with the AICc of the best candidate model (i.e. lowest AICc) and we selected all the models with ΔAICc < 2 (Burnham & Anderson 2002). In the case of Rao FD only one model was selected. R^2 values were calculated for each model in order to estimate the explanatory value. For the set of selected models, we estimated the Akaike weights (w_i) to quantify the relative likelihood of every model. No best model could be identified in any of the diversity index so we determined the model average for the equiprobable models and the estimates were averaged using the Akaike weights (Arnold 2010).

In all cases, we checked residual plots to assess model assumptions. Analyses were performed with *MASS* (Venables & Ripley 2002), *vegan* (Oksanen et al. 2010), *MuMIn* (Barton 2013) and *ape* (Paradis & Schliep 2018) packages.

To detect significant spatial autocorrelation, we analysed the residuals of each selected model using the Moran's Index (Diniz-Filho et al. 2003) with the function *Moran.I* ($P < 0.05$).

2.5.2. Relationship between TD, FD and PD along Europe

We used ordinary least square models (OLS) to analyze the relationship between TD with FD and PD, and between PD and FD. For each comparison, we conducted two models, one with the linear term and another also including the quadratic term given that the relationship between might be better described by a quadratic function. Based on the Akaike Information Criterion we selected the best model (ΔAICc < 2) and we visually check the best-model residuals in order to detect possible model bias.

2.5.3. Climatic predictors determining species composition and functional structure of lichen communities along Europe

We used constrained ordination analyses to evaluate the multivariate relationships between all the 19 climatic predictors and the changes in both, community species composition and CWM of growth form, type of photobiont and reproductive strategy (Legendre & Anderson 1999). To decide whether to apply linear or unimodal ordination methods, we first conducted a Detrended Correspondence Analysis (hereafter 'DCA'; Hill & Gauch 1980) with the species composition matrix and with the CWM matrix separately. We concluded that linear methods were suitable since the length of first DCA axis < 3 standard deviation units (Lepš & Smilauer 2003). For species composition and CWM, we performed two separate Redundancy Analysis (hereafter 'RDA') which is a constrained ordination method that

assumes linear responses of dependent variables with the extracted axes. We first tested the significance of the global models (including all the explanatory variables) with a Monte Carlo permutation test (999 permutations). Given that the global RDA models were significant (species composition: *F*-ratio statistics = 2.109, *P* = 0.03; CWM: *F*-ratio statistics = 4.499, *P* = 0.004), we applied a forward stepwise procedure to select a subset of explanatory variables maintaining the variation explained by them to maximum. We followed two different approaches to select the explanatory variables, one based on Monte Carlo permutation tests (function *ordistep* in *vegan* package) and the other based on adjusted R^2 (R^2_{adj}) (function *ordiR2step* in *vegan* package) (Blanchet et al. 2008). We finally conducted a RDA with the selected explanatory variables, BIO 3 and BIO15 for community species composition, and BIO1, BIO3, BIO12 and BIO18 for CWM of qualitative traits.

3 | RESULTS

3.1. Latitudinal patterns of TD, FD and PD respond to distinct environmental predictors

The three diversity facets (taxonomic, functional and phylogenetic) significantly responded to environmental predictors (Table 2) but the most important drivers behind this response differed between these facets (Fig. 2). While temperature variables significantly influenced all the three facets of biodiversity, TD and PD also responded to changes in precipitation and tree diameter variables, respectively (Table 2). In particular, Annual Mean Diurnal Range (BIO2) was the most important predictor of FD and PD (Fig. 2): these two diversity facets decreased with increasing temperature fluctuation over the year. Additionally, PD increased with increases in tree diameter and, to a lesser extent, with decreases in BIO6 and BIO5 (Fig. 2). Contrary to FD and PD, species richness was mainly determined by BIO6, BIO8 and BIO13, explaining the latter most of the variability in Shannon and Inverse Simpson (Table 2, Fig. 2). Therefore, oceanic sites (i.e. with higher values of min temperature of coldest month, mean temperature of wettest quarter and precipitation of wettest month) hosted communities with a higher number of species. Regarding Shannon and Inverse Simpson, communities with higher TD were associated to areas with higher values of precipitation of wettest month. Both species richness and Shannon were negatively related to BIO14, meaning that increases in precipitation during the driest month led to a reduction in the TD of lichen communities (Fig. 2).

None of the best-fit models showed a significant spatial autocorrelation according to the Moran's index quantification (Table 2), but in the model relating PD and BIO5. Although BIO5 is the less important predictor of this diversity facet (Fig. 2), this result suggests the existence of a spatial structure in the data not explained by the cited climatic variable.

Table 2. Ranking of generalized linear models of species richness, Shannon, Inverse Simpson, Rao FD (multitrait) and Rao PD following an AIC-based model selection procedure (ΔAICc ≤ 2). For each community diversity metric, the best model (i.e. lowest AICc value) is presented in the first row followed by the rest of models with ΔAICc ≤ 2. Columns represent environmental predictors related to forest structure (dbh) and climate (temperature and precipitation). Grey cells indicate environmental predictors included in a particular model. R^2, percentage of variance explained by a particular model; AICc, relative goodness of fit; ΔAICc, AIC differences; wi, Akaike weight; I_P, Moran index p-value. Abbreviations: TD, taxonomic diversity; FD, functional diversity; PD, phylogenetic diversity; dbh, tree diameter at breast height; BIO2, Annual Mean Diurnal Range; BIO5, Max Temperature of Warmest Month; BIO6, Min Temperature of Coldest Month; BIO8, Mean Temperature of Wettest Quarter; BIO13, Precipitation of Wettest Month; BIO14, Precipitation of Driest Month.

		Environmental predictors							R^2	AIC_c	ΔAIC_c	w_i	I_p
		dbh	TEMPERATURE				PRECIPITATION						
			BIO2	BIO5	BIO6	BIO8	BIO13	BIO14					
TD	Richness				■	■	■		0.59	168.2	0	0.67	0.82
					■	■	■	■	0.63	169.6	1.45	0.33	0.68
	Shannon						■		0.22	-3.7	0	0.38	0.61
				■			■		0.29	-2.8	0.9	0.24	0.96
					■		■		0.28	-2.6	1.08	0.22	0.73
							■	■	0.26	-1.9	1.79	0.15	0.78
	Inverse Simpson						■		0.13	105.6	0	0.46	0.57
				■			■		0.17	107.4	1.80	0.19	0.37
FD	Rao functional		■						0.27	-24.1	0	1	0.07
PD	Rao phylogenetic tree		■		■				0.25	-16.2	0	0.15	0.30
		■	■						0.24	-16.2	0.02	0.15	0.41
			■						0.14	-16.1	0.09	0.15	0.06
		■							0.13	-15.9	0.32	0.13	0.14
		■	■		■				0.33	-15.8	0.34	0.13	0.78
		■		■					0.21	-15.1	1.10	0.09	0.21
				■					0.09	-14.8	1.34	0.08	0.02*

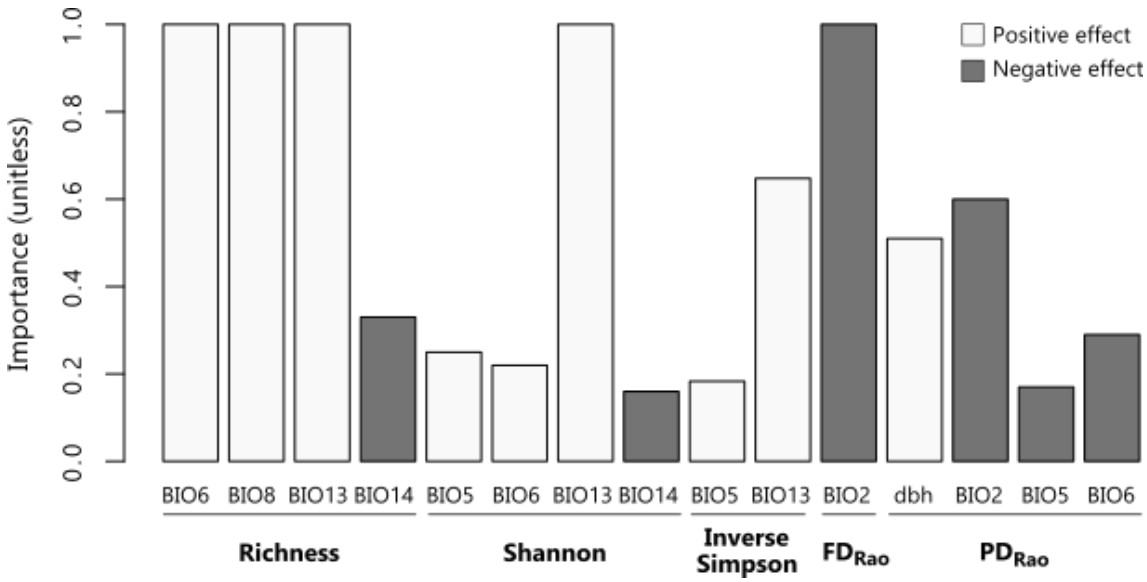


Figure 2. Relative importance of environmental predictors in generalized linear models of community diversity metrics. Bar height represents the relative importance of each predictor quantified as the sum of Akaike weights (w_i) of all models in which the predictor was selected and considering the number of models in which this predictor appears. Light and dark grey colour denote, respectively, positive or negative effects of each predictor on a given diversity metric and represent the model-averaged estimates of the best fit models. See Table 1 for abbreviations.

3.2. Relationship between TD, FD and PD along Europe

Both TD and PD were correlated with FD, but this correlation was negative with TD and positive with PD (Table 3). In addition, TD and PD were not related (Table 3). In all cases, the percentage of variance explained by the models were relatively low (between 19 and 25%) (Table 3).

Table 3. Results of OLS models used to analyse the relationship between TD, FD and PD. Only significant relationships ($P < 0.05$) are shown. R^2_{adj}, percentage of variance explained by a particular model; FD, functional diversity; PD, phylogenetic diversity.

	FD_{Rao}				PD_{Rao}			
	Estimate±SE	*F*	*P*	R^2_{adj}	Estimate±SE	*F*	*P*	R^2_{adj}
Richness	Ns	ns	ns	Ns	ns	ns	ns	ns
Shannon	-0.15±0.06	7.46	0.01	0.23	ns	ns	ns	ns
Inverse Simpson	-1.44±0.57	6.37	0.02	0.19	ns	ns	ns	ns
PD_{Rao}	0.09±0.03	8.46	0.01	0.25	-	-	-	-

3.3. Temperature and precipitation factors determined species composition and functional structure of lichen communities along Europe

The RDA models (Fig. 3) where significant both for species composition (*F-ratio* statistics = 4.046, $P = 0.001$) and CWM of growth form, type of photobiont and reproductive strategy (*F-ratio* statistics = 7.4002, $P = 0.001$). Both, species composition and functional structure of lichen communities were determined by different climatic variables. In the first case, RDA analysis suggested that most of the variability in the taxonomic composition of lichen communities along the gradient was explained by isothermality (BIO3: daily temperature range divided by the annual temperature range) and precipitation seasonality (BIO15) (Fig. 3a). In terms of species composition, lichen communities located in areas with higher temperature fluctuations within a month (France and Spain) were different from those located in Sweden, Slovakia, Austria and North Italy where temperature fluctuations were smaller (i.e. lower BIO3). We also identified a gradient in precipitation seasonality (BIO15) isolating lichen communities of France (with the lowest values of BIO15) from the others.

Concerning the functional structure of the communities, CWM of growth form, type of photobiont and reproductive strategy showed to be better predicted by temperature (BIO1 and BIO3) than by precipitation variables (BIO12 and BIO18) (Fig. 3b). Crustose and squamulose species, and those lichens with two types of reproductive strategies were mainly associated to sites with higher annual mean temperature (BIO1) (Fig. 3b). In addition, foliose broad lobed, fruticose filamentous and cyanolichens, thrived in sites with high values of isothermality (BIO3) and low values of precipitation during the warmest month (BIO18), which are climatic conditions characteristic from the southern forests (Fig. 3b).

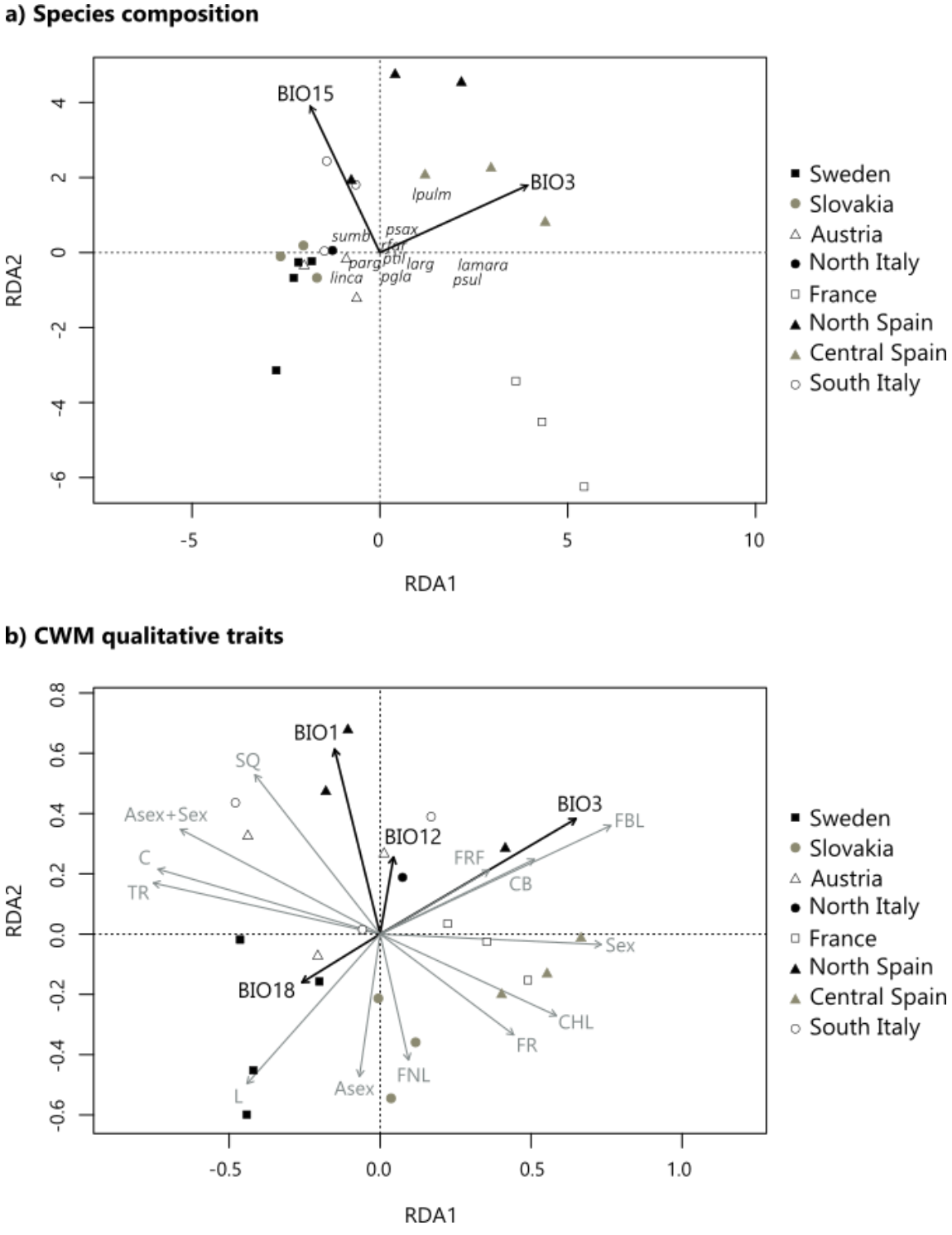


Figure 3. First two axes of the redundancy analysis ordinations (RDA) conducted with the climatic predictors as independent variables and a) species composition, and b) the CWM of qualitative traits (i.e. growth form, type of photobiont and reproductive strategy) as dependent variables. The first two RDA axes explained 28.81% of the variance found in the species composition of the community (a), and 62.19% of the variance found in the CWM of growth form, type of photobiont, and reproductive strategy (b). Only the climatic variables that significantly explained variability in lichen epiphytic community composition and CWM following the forward stepwise procedure are shown (black

arrows). (a) Each point represents the lichen community at a specific forest (n = 23) and the labels in italic denote the species with higher weight on the ordination axis. b) Each arrow represents the CWM of the qualitative trait categories. Arrows direction indicate the maximum change of that variable, and the length is proportional to the rate of change. Species: larg= *Lecanora argentata;* lamara = *Pertusaria amara;* linca = *Lepraria incana;* lpulm = *Lobaria pulmonaria;* psax = *Parmelia saxatilis;* psul = *Parmelia sulcata;* ptil = *Parmelina tiliacea;* parg = *Phylctis argena;* pgla = *Platismatia glauca;* rfar = *Ramalina farinacea;* sumb = *Scoliciosporum umbrinum*. Abbreviations: for growth form: C = crustose, SQ = squamulose, L = leprose, FBL = foliose broad lobed, FNL = foliose narrow lobed, FR = fruticose, FRF = fruticose filamentous, for photobiont: CB = cyanolichen, CHL = chlorolichen, TR = *Trentepohlia*, for reproduction: Asex = asexual reproduction, Sex = sexual reproduction, Asex+Sex = with asexual and sexual reproduction. Climatic variables: BIO1= Annual Mean Temperature; BIO3 = Isothermality; BIO12= Annual Precipitation; BIO15 = precipitation seasonality; BIO18= Precipitation of Warmest Quarter.

4 | DISCUSSION

The present study shows that spatial patterns of biodiversity in lichen communities along Europe were primarily determined by distinct environmental factors, depending on the diversity facet considered (i.e. TD, FD and PD). The geographic variation of FD and PD along this 3000 km latitudinal gradient responded to changes in annual temperature fluctuation, while patterns of TD were overall determined by precipitation of the wettest month. Throughout the gradient, increases in FD were accompanied by increases in PD and decreases in TD, pointing out a strong phylogenetic signal and functional redundancy for the studied traits. Thus, FD appeared as a surrogate for PD and TD, but these two facets were not correlated. Interestingly, despite the partial congruence between the three facets of biodiversity, they were shaped by distinct critical predictors indicating than a multidimensional approach is needed to unveil the patterns of diversity. We also found that climate explained a large amount of spatial variation in the studied functional traits, which highlights their role as indicators of climatic changes and supports the assumption that species enter and persist in natural communities based on their functional trait values.

In previous studies, all taxonomic, functional and phylogenetic diversity patterns have been shown to be affected by environmental gradients, but the precise major drivers shaping such patterns varied depending on the facet considered (Hurtado et al. 2019). Therefore, contrasting factors might act as abiotic filters of the different facets of lichen community diversity along Europe and these facets might provide complementary information about the response of the communities (Pavoine et al. 2013, Safi et al. 2011,

Arnan et al. 2015). On the one hand, increases in temperature fluctuation during the day resulted in a functional and phylogenetic homogenization of lichen communities, suggesting that only species with the range of functional traits that provide a better acclimation strategy to seasonal changes in temperature will persist. Under marked temperature fluctuations, assemblages were composed of close relative species with similar traits indicating a high trait redundancy under these conditions. Despite it would be expected a combined sensitivity to temperature and precipitation factors given the poikilohydric nature of epiphytic lichens, there was no variation in FD and PD, but changes in precipitation during the wettest month and temperature factors did shape patterns of TD. Oceanic sites, with warmer and more humid conditions, favoured an increase in the number of species, Shannon and Inverse Simpson within the communities. Apart from climatic factors, habitat quality indicators such as tree diameter (i.e. dbh) (Belinchón et al. 2009) only affected the PD, but not the FD and TD. In sites with bigger trees in which the amount of space and time available for colonization is larger (Riiali et al. 2001), there is a replacement of species with similar traits (i.e. TD and FD do not vary) but with distinct evolutionary or biogeographical histories (i.e. high PD). This result suggests a parallel evolution of traits within the communities, meaning that species with different origins share functional traits as it has been demonstrated in lichens (e.g. Tehler & Irestedt 2007).

We observed that patterns of TD, FD and PD were explained by distinct drivers even though we found that some of these diversity facets were related. According to previous studies (Devictor et al. 2010, Arnan et al. 2016, Hurtado et al. 2019), we identified a partial congruence between FD, PD and TD. First, the negative relationship between FD and TD suggests that lichen communities along the studied gradient display high functional redundancy, meaning that species within these communities do not have unique roles which makes them more resilient in the face of a changing environment (Fetzer et al. 2015). Surprisingly, Hurtado et al. (2019) found the opposite result, with a positive relationship between FD and TD in lichen communities located in two contrasting biogeographic regions, which points to the importance of the spatial scale and the specific environmental gradient considered when the relation of the different facets of diversity is evaluated (Safi et al 2011, Arnan et al. 2016, Ramm et al. 2018). Second, the positive relation between FD and PD might reflect the strong phylogenetic signal of the studied traits, meaning that distant relatives display different trait values (Swenson & Enquist 2007, Wiens & Graham 2005). Finally, the lack of relation between TD and PD might respond to the existence of

mechanisms selecting for clades of closely related species within the communities (Cadotte et al. 2010, Tucker & Cadotte 2013).

To better understand the observed patterns of biodiversity in response to climatic gradients, we analysed the changes on species composition and functional structure of the lichen communities. Regarding the species composition, we identified a geographical structuration of the epiphytic communities according to temperature and precipitation seasonality gradients. In both cases, the communities located in the extremes of these climatic gradients corresponded to the southernmost forests (i.e. France, Spain and Italy), which were clearly differentiated from those communities located in the northern sites. The climatic factors only accounted for the 29% of the variability found in the species composition of the study sites, whereas almost the 62% of the community-level variation of the selected traits were explained by climate. These results support the idea that the species thriving in natural communities respond to environmental changes through their functional traits (Weiher & Keddy 1995, Díaz et al. 1998, Shipley et al. 2016) and remark the value of this suite of easily discernible traits as ecological indicators (Giordani et al. 2012). As observed and congruent with patterns in FD, changes in CWMs of growth form, type of photobiont and reproductive strategy mainly responded to temperature rather than precipitation variables. These organisms are only intermittently active during certain seasonal cycles and can acclimate their physiological activity to light and temperature changes (MacKenzie et al. 2001). Therefore, our results indicate that, along the studied gradient, temperature fluctuations constrain the metabolic rates of lichen species rather than precipitation changes. Thus, the temperature variables act as filters selecting for certain traits which do perform better under these constraints (e.g. crustose and squamulose species at higher mean annual temperatures, fruticose and asexual species at low mean annual temperatures or cyanolichens at sites with high isothermic sites).

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6 | AUTHORS' CONTRIBUTIONS

IM, MP, GA and PH conceived the study. PH, MP, IM, GA, PG, RB, EB, JN, AK, HM, SM and EM-DP did the fieldwork PH, RV, EM-DP and SM did laboratory work. PH and FdB performed the data analyses. PH led the manuscript writing and all authors provided critical reviews. All authors gave approval for submission of the final manuscript.

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8 | SUPPORTING INFORMATION

8.1. Appendix S1

Functional trait values for the 203 lichen species found in the 23 studied beech forests along Europe. Mean values ± SE pf specific thallus mass (STM), water holding capacity (WHC) and carbon:nitrogen ratio (C/N) are provided for the 53 machrolichen species. Abbreviations: 1) Growth form: C=crustose, SQ=squamulose, L=leprose, FBL=foliose broad lobed, FNL=foliose narrow lobed, FR=fruticose dorsiventral, FRF=fruticose filamentous; 2) Reproductive strategy: ASEX=asexual; SEX=sexual; 3) Type of photobiont: CB=cyanobacteria, CHL=green algae, T=*Trentepohlia;* 4) STM=specific thallus mass; 5) WHC=water holding capacity.

Lichen species	Growth form	Reproductive strategy	Type of photobiont
Acrocordia cavata (Ach.) R.C. Harris	C	SEX	TR
Acrocordia gemmata (Ach.) A. Massal. var. *gemmata*	C	SEX	TR
Agonimia allobata (Stizenb.) P. James	C	ASEX+SEX	CHL
Agonimia octospora Coppins & P. James	SQ	SEX	CHL
Agonimia tristicula (Nyl.) Zahlbr.	SQ	SEX	CHL
Alyxoria varia (Pers.) Ertz & Tehler	C	SEX	TR
Amandinea punctata (Hoffm.) Coppins & Scheid.	C	SEX	CHL
Anaptychia ciliaris (L.) A. Massal.	FR	SEX	CHL
Anisomeridium biforme (Schaer.) R.C. Harris	C	SEX	TR
Anisomeridium polypori (Ellis & Everh.) M.E. Barr	C	SEX	TR
Arthonia atra (Pers.) A. Schneid.	C	SEX	TR
Arthonia didyma Körb.	C	SEX	TR
Arthonia punctiformis Ach.	C	SEX	TR
Arthonia radiata (Pers.) Ach.	C	SEX	TR
Arthonia sp.	C	SEX	TR
Arthonia spadicea Leight.	C	SEX	TR
Arthonia vinosa Leight.	C	SEX	TR
Bacidia circumspecta (Vain.) Malme	C	SEX	CHL
Bacidia incompta (Borrer) Anzi	C	SEX	CHL
Bacidia laurocerasi (Duby) Zahlbr.	C	SEX	CHL
Bacidia rosella (Pers.) De Not.	C	SEX	CHL
Bacidia rubella (Hoffm.) A. Massal.	C	SEX	CHL
Bacidia sp.	C	SEX	CHL
Bacidia subincompta (Nyl.) Arnold	C	ASEX+SEX	CHL
Bacidina arnoldiana (Körb.) V. Wirth & Vězda	C	ASEX+SEX	CHL
Bacidina delicata (Leight.) V. Wirth & Vězda	C	SEX	CHL
Biatora chrysantha (Zahlbr.) Printzen	C	ASEX+SEX	CHL
Biatora efflorescens (Hedl.) Räsänen	C	ASEX+SEX	CHL
Biatora vernalis (L.) Fr.	C	SEX	CHL
Blastenia herbidella (Hue) Servít	C	ASEX+SEX	CHL
Bryobilimbia hypnorum (Lib.) Fryday, Printzen & S. Ekman	C	SEX	CHL
Bryoria fuscescens (Gyeln.) Brodo & D. Hawksw.	FRF	ASEX	CHL
Buellia disciformis (Fr.) Mudd	C	SEX	CHL
Buellia griseovirens (Sm.) Almb.	C	ASEX	CHL
Calicium salicinum Pers.	C	SEX	CHL
Calicium viride Pers.	C	SEX	CHL
Caloplaca obscurella (J. Lahm) Th. Fr.	C	ASEX	CHL
Candelaria concolor (Dicks.) Stein	FNL	ASEX+SEX	CHL
Candelariella vitellina (Hoffm.) Müll. Arg.	C	SEX	CHL
Candelariella xanthostigma (Ach.) Lettau	C	ASEX+SEX	CHL
Carbonicola myrmecina (Ach.) Bendiksby & Timdal	SQ	ASEX+SEX	CHL
Catillaria nigroclavata (Nyl.) J. Steiner	C	SEX	CHL
Cetrelia olivetorum (Nyl.) W.L. Culb. & C.F. Culb.	FBL	ASEX+SEX	CHL
Chaenotheca furfuracea (L.) Tibell	C	SEX	CHL

Appendix S1 (continued)

Lichen species	Growth form	Reproductive strategy	Type of photobiont
Chrysothrix candelaris (L.) J.R. Laundon	L	ASEX+SEX	CHL
Cladonia chlorophaea (Sommerf.) Spreng.	FR	ASEX+SEX	CHL
Cladonia coniocraea (Flörke) Spreng.	FR	ASEX+SEX	CHL
Cladonia cornuta (L.) Hoffm.	FR	ASEX+SEX	CHL
Cladonia digitata (L.) Hoffm.	FR	ASEX+SEX	CHL
Cladonia fimbriata (L.) Fr.	FR	ASEX+SEX	CHL
Cladonia parasitica (Hoffm.) Hoffm.	FR	ASEX+SEX	CHL
Cladonia pyxidata (L.) Hoffm.	FR	ASEX+SEX	CHL
Coenogonium luteum (Dicks.) Kalb & Lücking	C	SEX	TR
Coenogonium pineti (Ach.) Lücking & Lumbsch	C	SEX	TR
Collema flaccidum (Ach.) Ach.	FBL	ASEX+SEX	CB
Collema furfuraceum Du Rietz	FBL	ASEX+SEX	CB
Collema nigrescens (Huds.) DC.	FBL	ASEX+SEX	CB
Collema subflaccidum Degel.	FBL	ASEX+SEX	CB
Collema subnigrescens Degel.	FBL	SEX	CB
Coniocarpon cinnabarinum DC.	C	SEX	TR
Enterographa crassa (DC.) Fée	C	SEX	TR
Evernia prunastri (L.) Ach.	FR	ASEX+SEX	CHL
Flavoparmelia caperata (L.) Hale	FBL	ASEX+SEX	CHL
Fuscidea stiriaca (A. Massal.) Hafellner	C	SEX	CHL
Fuscopannaria leucosticta (Tuck.) P.M. Jørg.	SQ	SEX	CB
Graphis elegans (Sm.) Ach.	C	SEX	TR
Graphis scripta (L.) Ach.	C	SEX	TR
Gyalecta carneola (Ach.) Hellb.	C	SEX	TR
Heterodermia japonica (M. Satô) Swinscow & Krog	FNL	ASEX	CHL
Heterodermia obscurata (Nyl.) Trevis.	FNL	ASEX+SEX	CHL
Heterodermia speciosa (Wulfen) Trevis.	FNL	ASEX+SEX	CHL
Hyperphyscia adglutinata (Flörke) H. Mayrhofer & Poelt	FNL	ASEX+SEX	CHL
Hypogymnia farinacea Zopf	FNL	ASEX+SEX	CHL
Hypogymnia physodes (L.) Nyl.	FNL	ASEX+SEX	CHL
Hypogymnia tubulosa (Schaer.) Hav.	FNL	ASEX+SEX	CHL
Lecania naegelii (Hepp) Diederich & van den Boom	C	SEX	CHL
Lecanora albella (Pers.) Ach.	C	SEX	CHL
Lecanora allophana (Ach.) Nyl. f. *allophana*	C	SEX	CHL
Lecanora argentata (Ach.) Malme	C	SEX	CHL
Lecanora carpinea (L.) Vain.	C	SEX	CHL
Lecanora chlarotera Nyl. subsp. *chlarotera*	C	SEX	CHL
Lecanora expallens Ach.	C	ASEX+SEX	CHL
Lecanora glabrata (Ach.) Nyl.	C	SEX	CHL
Lecanora horiza (Ach.) Linds.	C	SEX	CHL
Lecanora intumescens (Rebent.) Rabenh.	C	SEX	CHL
Lecanora leptyrodes (Nyl.) Degel.	C	SEX	CHL
Lecanora pulicaris (Pers.) Ach.	C	SEX	CHL
Lecidella elaeochroma (Ach.) M. Choisy var. *elaeochroma* f. *elaeochroma*	C	SEX	CHL
Lecidella sp.	C	SEX	CHL
Lepra albescens (Huds.) Hafellner	C	ASEX	CHL
Lepra amara (Ach.) Hafellner	C	ASEX	CHL
Lepra multipuncta (Turner) Hafellner	C	ASEX+SEX	CHL
Lepraria incana (L.) Ach.	L	ASEX	CHL
Lepraria membranacea (Dicks.) Vain.	L	ASEX	CHL
Leptogium saturninum (Dicks.) Nyl.	FBL	ASEX+SEX	CB
Lobaria pulmonaria (L.) Hoffm.	FBL	ASEX+SEX	CHL
Lobarina scrobiculata (Scop.) Nyl.	FBL	ASEX+SEX	CB
Loxospora elatina (Ach.) A. Massal.	C	ASEX	CHL
Melanelixia fuliginosa (Duby) O. Blanco, A. Crespo, Divakar, Essl., D. Hawksw. & Lumbsch	FNL	ASEX	CHL

Appendix S1 (continued)

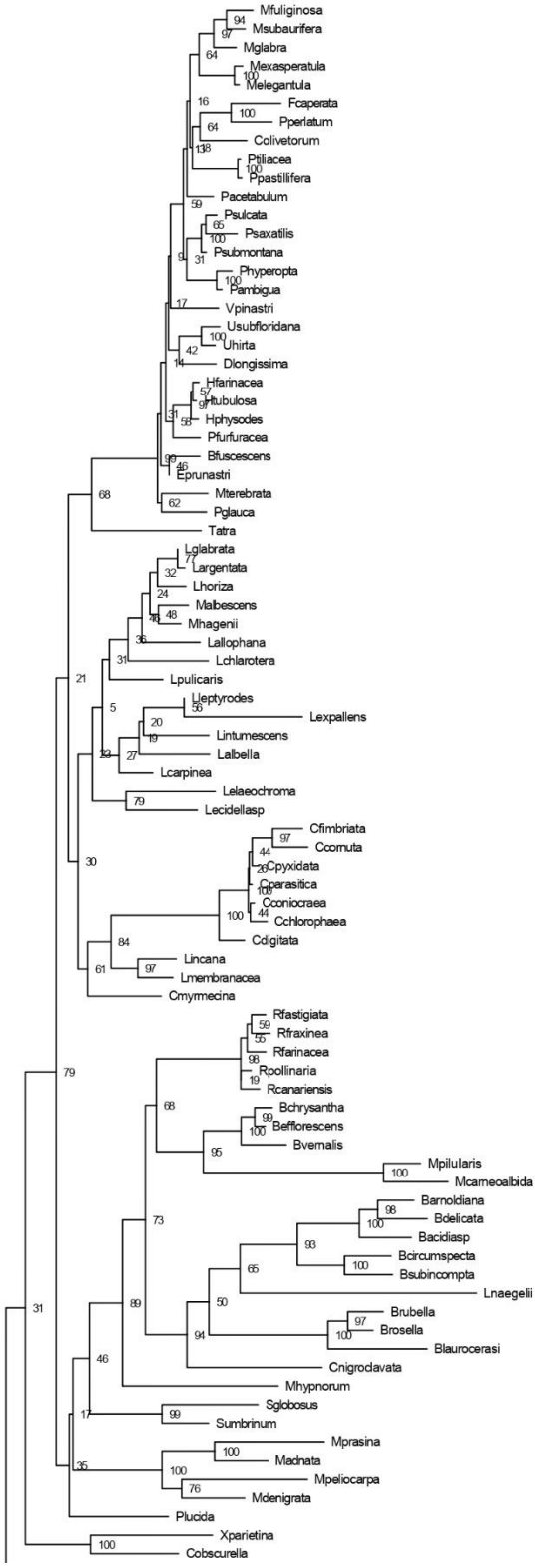
Lichen species	Growth form	Reproductive strategy	Type of photobiont
Melanelixia glabra (Schaer.) O. Blanco, A. Crespo, Divakar, Essl., D. Hawksw. & Lumbsch	FBL	SEX	CHL
Melanelixia subaurifera (Nyl.) O. Blanco, A. Crespo, Divakar, Essl., D. Hawksw. & Lumbsch	FBL	ASEX+SEX	CHL
Melanohalea elegantula (Zahlbr.) O. Blanco, A. Crespo, Divakar, Essl., D. Hawksw. & Lumbsch	FBL	ASEX+SEX	CHL
Melanohalea exasperatula (Nyl.) O. Blanco, A. Crespo, Divakar, Essl., D. Hawksw. & Lumbsch	FBL	ASEX+SEX	CHL
Menegazzia terebrata (Hoffm.) A. Massal.	FBL	ASEX+SEX	CHL
Micarea adnata Coppins	C	SEX	CHL
Micarea denigrata (Fr.) Hedl.	C	SEX	CHL
Micarea peliocarpa (Anzi) Coppins & R. Sant.	C	SEX	CHL
Micarea prasina Fr.	C	SEX	CHL
Mycobilimbia carneoalbida (Müll. Arg.) S. Ekman & Printzen	C	SEX	CHL
Mycobilimbia pilularis (Körb.) Hafellner & Türk	C	SEX	CHL
Myriolecis albescens (Hoffm.) Sliwa, Zhao Xin & Lumbsch	C	SEX	CHL
Myriolecis hagenii (Ach.) Sliwa, Zhao Xin & Lumbsch	C	SEX	CHL
Nephroma laevigatum Ach.	FBL	SEX	CB
Nephroma parile (Ach.) Ach.	FBL	ASEX+SEX	CB
Nephroma resupinatum (L.) Ach.	FBL	SEX	CB
Nevesia sampaiana (Tav.) P.M. Jørg., L. Lindblom, Wedin & S. Ekman	SQ	ASEX	CB
Normandina pulchella (Borrer) Nyl.	SQ	ASEX+SEX	CHL
Ochrolechia balcanica Verseghy	C	SEX	CHL
Ochrolechia pallescens (L.) A. Massal.	C	SEX	CHL
Ochrolechia subviridis (Høeg) Erichsen	C	ASEX	CHL
Ochrolechia szatalaensis Verseghy	C	SEX	CHL
Ochrolechia turneri (Sm.) Hasselrot	C	ASEX+SEX	CHL
Opegrapha sp.	C	SEX	TR
Opegrapha trochodes Coppins, F. Berger & Ertz	C	SEX	TR
Opegrapha vermicellifera (Kunze) J.R. Laundon	C	SEX	TR
Pannaria conoplea (Ach.) Bory	FNL	ASEX+SEX	CB
Pannaria rubiginosa (Ach.) Bory	FNL	SEX	CB
Pannaria tavaresii P.M. Jørg.	SQ	ASEX+SEX	CB
Parmelia saxatilis (L.) Ach.	FBL	ASEX+SEX	CHL
Parmelia submontana Hale	FBL	ASEX+SEX	CHL
Parmelia sulcata Taylor	FBL	ASEX+SEX	CHL
Parmeliella triptophylla (Ach.) Müll. Arg.	C	ASEX+SEX	CB
Parmelina pastillifera (Harm.) Hale	FBL	ASEX+SEX	CHL
Parmelina tiliacea (Hoffm.) Hale	FBL	ASEX+SEX	CHL
Parmeliopsis ambigua (Hoffm.) Nyl.	FNL	ASEX+SEX	CHL
Parmeliopsis hyperopta (Ach.) Arnold	FNL	ASEX+SEX	CHL
Parmotrema perlatum (Huds.) M. Choisy	FBL	ASEX+SEX	CHL
Pectenia plumbea (Lightf.) P.M. Jørg., L. Lindblom, Wedin & S. Ekman	FNL	SEX	CB
Peltigera collina (Ach.) Schrad.	FBL	ASEX+SEX	CB
Peltigera degenii Gyeln.	FBL	ASEX+SEX	CB
Peltigera horizontalis (Huds.) Baumg.	FBL	SEX	CB
Peltigera membranacea (Ach.) Nyl.	FBL	SEX	CB
Peltigera praetextata (Sommerf.) Zopf	FBL	ASEX+SEX	CB
Pertusaria coccodes (Ach.) Nyl.	C	ASEX+SEX	CHL
Pertusaria coronata (Ach.) Th. Fr.	C	ASEX+SEX	CHL
Pertusaria flavida (DC.) J.R. Laundon	C	ASEX	CHL
Pertusaria hymenea (Ach.) Schaer.	C	SEX	CHL
Pertusaria leioplaca (Ach.) DC.	C	SEX	CHL
Pertusaria pertusa (L.) Tuck. var. *pertusa*	C	SEX	CHL
Pertusaria pupillaris (Nyl.) Th. Fr.	C	ASEX+SEX	CHL

Appendix S1 (continued)

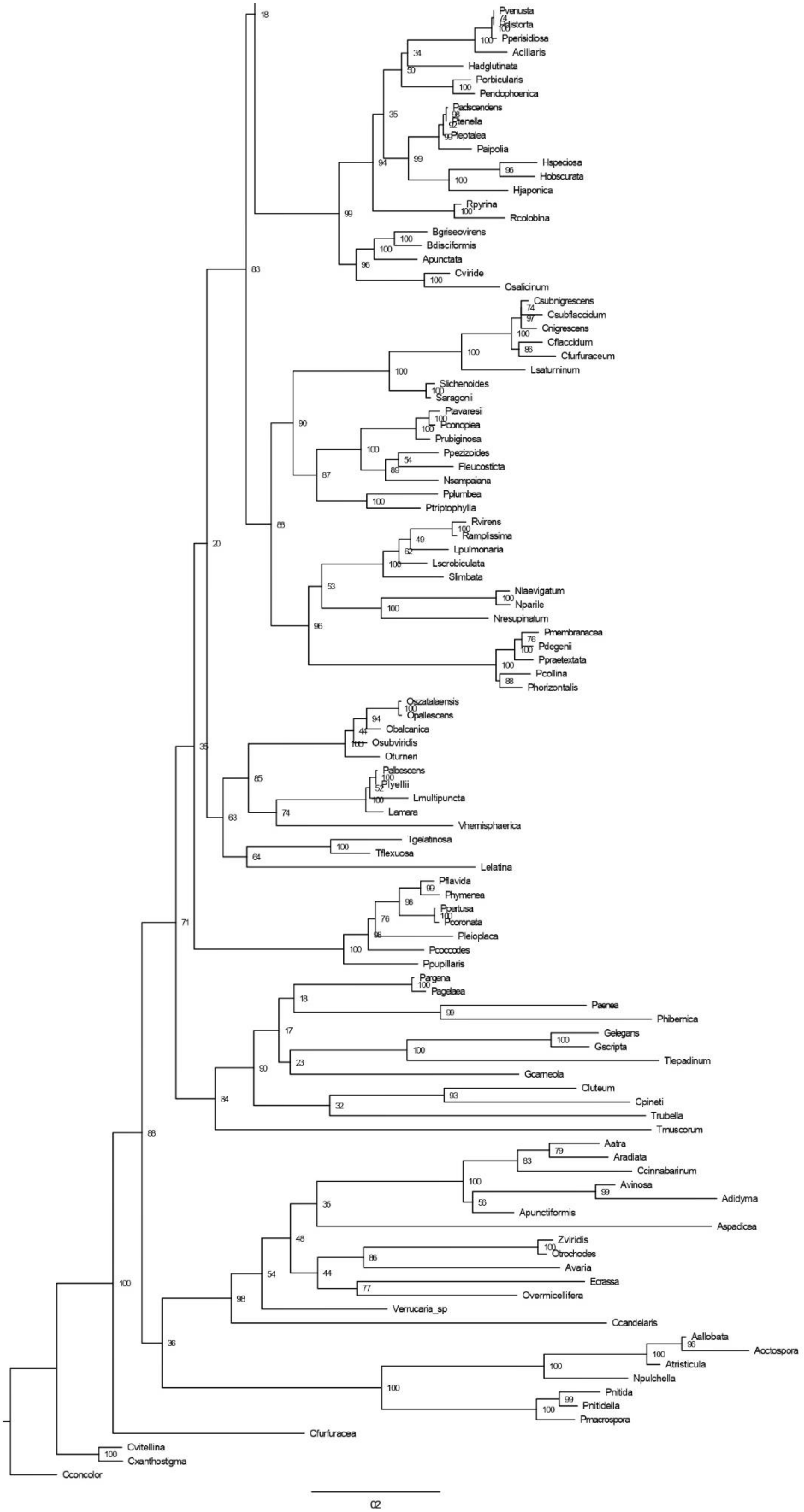
Lichen species	Growth form	Reproductive strategy	Type of photobiont
Phaeographis lyellii (Sm.) Zahlbr.	C	SEX	TR
Phaeophyscia endophoenicea (Harm.) Moberg	FNL	ASEX	CHL
Phaeophyscia orbicularis (Neck.) Moberg	FNL	ASEX+SEX	CHL
Phlyctis agelaea (Ach.) Flot.	C	ASEX+SEX	CHL
Phlyctis argena (Spreng.) Flot.	C	ASEX+SEX	CHL
Physcia adscendens H. Olivier	FNL	ASEX+SEX	CHL
Physcia aipolia (Humb.) Fürnr.	FNL	SEX	CHL
Physcia leptalea (Ach.) DC.	FNL	SEX	CHL
Physcia tenella (Scop.) DC.	FNL	ASEX+SEX	CHL
Physconia distorta (With.) J.R. Laundon	FNL	SEX	CHL
Physconia perisidiosa (Erichsen) Moberg	FNL	ASEX+SEX	CHL
Physconia venusta (Ach.) Poelt	FNL	SEX	CHL
Platismatia glauca (L.) W.L. Culb. & C.F. Culb.	FBL	ASEX+SEX	CHL
Pleurosticta acetabulum (Neck.) Elix & Lumbsch	FBL	SEX	CHL
Porina aenea (Wallr.) Zahlbr.	C	SEX	TR
Porina hibernica P. James & Swinscow	C	SEX	TR
Protopannaria pezizoides (Weber) P.M. Jørg. & S. Ekman	C	SEX	CB
Pseudevernia furfuracea (L.) Zopf var. *furfuracea*	FBL	ASEX+SEX	CHL
Psilolechia lucida (Ach.) M. Choisy	L	SEX	CHL
Psoroglaena stigonemoides (Orange) Henssen	C	ASEX+SEX	CHL
Pyrenula macrospora (Degel.) Coppins & P. James	C	SEX	TR
Pyrenula nitida (Weigel) Ach.	C	SEX	TR
Pyrenula nitidella (Schaer.) Müll. Arg.	C	SEX	TR
Pyrrhospora quernea (Dicks.) Körb.	C	ASEX+SEX	CHL
Ramalina canariensis J. Steiner	FR	ASEX+SEX	CHL
Ramalina farinacea (L.) Ach.	FR	ASEX+SEX	CHL
Ramalina fastigiata (Pers.) Ach.	FR	SEX	CHL
Ramalina fraxinea (L.) Ach.	FR	SEX	CHL
Ramalina pollinaria (Westr.) Ach.	FR	ASEX+SEX	CHL
Ricasolia amplissima (Scop.) De Not.	FBL	SEX	CHL
Ricasolia virens (With.) H.H. Blom. & Tønsberg	FBL	SEX	CHL
Rinodina colobina (Ach.) Th. Fr.	C	ASEX+SEX	CHL
Rinodina griseosoralifera Coppins	C	ASEX+SEX	CHL
Rinodina pyrina (Ach.) Arnold	C	SEX	CHL
Scoliciosporum umbrinum (Ach.) Arnold	C	SEX	CHL
Scytinium aragonii (Otálora) Otálora, P.M. Jørg. & Wedin	SQ	SEX	CB
Scytinium lichenoides (L.) Otálora, P.M. Jørg. & Wedin	SQ	ASEX+SEX	CB
Sorediate	C	ASEX	CHL
Sphaerophorus globosus (Huds.) Vain.	FR	SEX	CHL
Sticta limbata (Sm.) Ach.	FBL	ASEX+SEX	CB
Tephromela atra (Huds.) Hafellner var. *atra*	C	SEX	CHL
Thelenella muscorum (Th. Fr.) Vain. var. *muscorum*	C	SEX	CHL
Thelopsis rubella Nyl.	C	SEX	TR
Thelotrema lepadinum (Ach.) Ach.	C	SEX	TR
Trapeliopsis flexuosa (Fr.) Coppins & P. James	C	ASEX	CHL
Trapeliopsis gelatinosa (Flörke) Coppins & P. James	C	ASEX	CHL
Usnea hirta (L.) F.H. Wigg.	FRF	ASEX+SEX	CHL
Usnea longissima Ach.	FRF	ASEX+SEX	CHL
Usnea subfloridana Stirt.	FRF	ASEX+SEX	CHL
Varicellaria hemisphaerica (Flörke) I. Schmitt & Lumbsch	C	ASEX	CHL
Vulpicida pinastri (Scop.) J.-E. Mattsson & M.J. Lai	FBL	ASEX+SEX	CHL
Xanthoria parietina (L.) Th. Fr.	FBL	SEX	CHL
Zwackhia viridis (Ach.) Poetsch & Schied.	C	SEX	TR

8.2. Appendix S2

Phylogenetic tree based on four molecular markers (nuITS, nuLSU, mtSSU and RPB1) including the 203 lichen species found across Europe. Numbers above nodes denote the bootstrap support (ML-BS) obtained with Maximum Likelihood in RAxML.



Appendix S2 (continued)



8.3. Appendix S3

Environmental variables characterizing the 23 beech forests studied.

Forest	Latitude	Longitude	Altitude	DBH	BIO1	BIO2	BIO3	BIO4	BIO5	BIO6	BIO7	BIO8	BIO9	BIO10	BIO11	BIO12	BIO13	BIO14	BIO15	BIO16	BIO17	BIO18	BIO19
at_kalk	47.82	14.45	757.6	0.66	6.8	80.0	284.6	7048.8	21.2	-6.9	28.1	15.9	-2.3	16.3	-2.8	1030.8	144.4	57.6	31.4	415.6	183.2	370.4	208.6
at_loib	46.46	14.27	1118.4	0.93	6.2	83.6	285.6	7196.6	21.1	-8.1	29.3	10.7	-3.1	15.9	-3.7	1643.6	178.8	83.2	22.2	514.2	255.8	495.4	292.2
at_trogener	46.45	14.48	855.8	0.66	6.8	84.0	284.8	7247.2	21.8	-7.6	29.4	16.5	-2.6	16.5	-3.2	1278.0	145.2	62.8	25.0	428.4	194.4	428.4	207.6
ce_cantaloias	41.23	-3.38	1541.6	0.64	7.1	95.0	341.0	6184.0	23.2	-4.5	27.8	0.8	16.5	16.5	-0.6	707.0	80.0	27.0	28.0	228.0	82.0	82.0	202.0
ce_monteio	41.11	-3.49	1335.2	0.54	9.4	95.0	334.4	6378.4	25.9	-2.5	28.4	2.9	19.2	19.2	1.5	563.0	70.6	17.2	34.0	200.6	53.6	53.6	168.2
ce_pedrosa	41.22	-3.41	1604.4	0.64	8.0	95.0	340.0	6231.0	24.2	-3.7	27.9	1.6	17.5	17.5	0.2	681.0	78.0	24.0	30.0	222.0	72.0	72.0	200.0
fr_chadefour	45.54	2.85	1181.8	0.80	6.1	77.0	315.0	5749.2	19.9	-4.5	24.3	7.3	1.1	14.5	-1.2	1032.4	105.8	67.4	12.2	291.2	211.0	264.2	250.8
fr_pavin	45.50	2.89	1272.6	0.88	6.4	77.0	314.2	5768.8	20.2	-4.3	24.4	7.5	1.3	14.7	-1.0	1113.4	117.4	73.0	13.6	322.4	231.4	262.6	277.8
fr_picherande	45.47	2.78	1200.2	1.14	6.8	77.0	314.2	5764.6	20.6	-3.8	24.4	0.9	4.4	15.2	-0.5	1353.6	136.8	94.2	13.0	396.2	290.0	317.0	358.2
in_cansiglio	46.07	12.41	1080.2	0.84	7.0	81.0	286.0	6928.4	21.5	-6.9	28.4	7.8	-1.9	16.5	-2.4	1427.4	151.2	77.8	20.4	437.6	235.6	393.2	264.4
is_alburni	40.50	15.37	1213.0	0.88	9.0	84.4	321.4	6055.2	23.3	-2.9	26.2	3.5	17.0	17.9	1.2	942.0	126.8	27.2	41.0	370.0	89.4	96.4	276.4
is_calabre	39.50	16.05	1077.6	1.13	11.0	49.0	230.0	5657.4	22.6	1.4	21.2	8.4	18.4	19.5	3.8	1089.0	152.0	24.8	46.8	440.6	85.6	96.4	354.4
is_umbra	41.81	15.98	750.2	0.47	11.9	43.4	207.4	5793.2	23.1	2.3	20.8	10.4	19.7	20.6	4.6	618.2	71.4	36.6	20.4	203.8	116.4	117.8	148.0
ne_irati	42.99	-1.16	855.8	1.28	9.9	85.6	355.0	5343.0	23.2	-0.9	24.1	4.4	17.5	17.7	3.0	1332.2	152.2	65.0	24.2	450.4	209.4	209.4	402.0
ne_redes	43.11	-5.29	1237.4	1.17	8.7	78.6	364.8	4716.8	20.7	-0.8	21.5	4.0	15.7	15.7	2.7	1174.0	145.6	46.6	30.6	403.6	145.4	145.4	367.4
ne_saja	43.11	-4.28	866.2	0.88	11.1	69.0	344.6	4557.4	22.2	2.2	20.1	6.7	17.9	17.9	5.4	925.0	109.2	43.6	25.2	308.4	142.4	142.4	277.6
sk_kv	48.69	19.76	1233.4	0.59	3.9	76.0	264.4	7438.8	18.8	-9.9	28.6	11.2	-5.9	13.8	-6.3	1065.0	145.8	56.0	30.4	404.2	174.0	341.8	185.8
sk_mp	48.76	20.06	900.2	0.34	6.2	75.2	260.8	7581.2	21.2	-7.7	29.0	13.8	-3.7	16.3	-4.1	665.6	86.8	31.6	30.2	249.6	100.8	201.4	106.2
sk_rabia	49.10	22.45	1151.4	0.68	4.0	73.0	259.0	7483.6	18.7	-9.6	28.3	13.7	-6.0	13.9	-6.2	1124.6	144.4	60.2	29.8	430.4	181.8	368.2	212.8
sw_bisk	56.80	12.88	141.6	0.65	7.0	57.0	236.0	6353.6	20.0	-4.1	24.1	4.8	4.0	15.9	-1.4	1069.4	117.4	57.4	23.0	335.4	188.2	327.8	203.2
sw_biur	56.64	14.67	161.0	0.40	6.9	62.0	248.0	6488.6	20.8	-4.4	25.2	15.8	3.1	16.1	-1.5	657.6	76.4	36.6	22.0	211.2	115.4	203.2	124.6
sw_oder	56.97	13.53	197.0	0.57	6.7	65.0	255.0	6501.6	20.6	-4.9	25.5	4.3	3.8	15.8	-1.8	914.4	94.8	50.4	22.0	281.4	162.2	265.8	179.2
sw_ramlak	57.08	12.56	107.8	0.50	7.5	49.6	213.8	6309.0	20.0	-3.2	23.2	5.4	4.4	16.4	-0.8	842.0	90.2	44.0	23.8	267.0	148.2	251.2	156.4

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

Capítulo 3

Intraspecific variability drives functional changes in lichen epiphytic communities along Europe

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En Preparación

ABSTRACT

Traditional approaches in trait-based community ecology typically expect that trait filtering along broad environmental gradients is largely due to replacement of species, rather than intraspecific trait adjustments. Recently, the role of intraspecific trait variability has been largely highlighted as an important contributor mediating community-level trait variation, particularly along limited environmental gradients, and the ability of the communities to persist under changing conditions. Several studies on plant communities have found that intraspecific trait variability do contribute to functional variation, but species turnover tends to have a considerably greater relative contribution over large environmental variations. Unfortunately, few studies quantify the relative importance of species turnover versus intraspecific variability mediating the response of communities different to vascular plants. Here, we studied the functional changes in lichen communities within 23 beech forests along large latitudinal (ca. 3000 km) and environmental gradients in Europe to quantify the relative contribution of species turnover and intraspecific variability and the role of climate controlling community-level trait changes. We focused on a set of ten quantitative functional traits potentially affected by climatic conditions and related to photosynthetic performance (n = 1184 thalli), water use strategy (n = 1017 thalli) and nutrient uptake (n = 1179 thalli). Our results showed that intraspecific trait variability explained most of the functional changes in lichen communities in response to the latitudinal gradient. Moreover, different climatic predictors explained functional variation due to both intraspecific trait variability and species turnover. We propose that lichen communities cope with contrasting climatic conditions by adjusting the functional traits values of the most abundant species within the communities rather than by the replacement of the species. Consequently, intraspecific variability should be explicitly incorporated to better understand the effect of environmental changes on lichen communities. Our results challenge the universality of the hypothesis that species turnover chiefly drives functional trait changes across large environmental gradients and call for a wider test of such important assumptions in trait-ecology in different organism types and ecosystems.

Key words

Beech forests, climate, community ecology, functional ecology, functional trait variation, intraspecific variability, latitudinal gradient, lichen, species turnover.

1 | INTRODUCTION

Understanding the patterns of biodiversity along environmental gradients is a primary goal to predict the potential response of communities in a global change context (Díaz & Cabido 2001, Lavorel & Garnier 2002, Safi et al. 2011, de Bello et al. 2013). In this way, functional traits provide a link for assessing not only the performance of communities under different environmental scenarios (Webb et al. 2010), but also the impact of such contrasting conditions on ecosystem functioning (de Bello et al. 2010). Most studies, so far, have assessed changes in community trait structure neglecting the possible effect of intraspecific trait

adjustments. Particularly, over broad environmental gradients it is expected that the effect of intraspecific trait adjustments should be negligible (Auger & Shipley 2013).

Overall, the functional variation in natural communities along different gradients is determined by species turnover and intraspecific trait variability, and their covariation (Lepš et al. 2011). While existing tests of the importance of these sources of trait variation are rather limited, it should be noticed that the relative contribution of these drivers may differ across sites and biological groups. A great number of studies relied on the assumption that differences in functional traits are larger among than within species (Grime et al. 1988, Garnier 2001), which justifies why intraspecific trait variability has been largely ignored (Shipley 2016). In the case of vascular plants, intraspecific trait variability do contribute to functional variation (Albert et al. 2010, Jung et al. 2010), but species turnover tends to have a considerably greater relative contribution (Kichenin et al. 2013, Siefert et al. 2015). Until now, the importance of intraspecific trait variability has been largely explored in plant communities, and to a lesser extent in mosses (Lett et al. 2017), but much less is known about the sources and extent of functional variability in different organisms such as animals (Moretti et al. 2017) or lichens (Asplund & Wardle 2014). For instance, Griffiths et al. (2016) found that interspecific differences explained the majority of functional variation in dung beetle communities. Conversely, intraspecific variability emerged as the main contributor to functional trait variation in response to environmental changes in lichen communities (Asplund & Wardle 2014), which supports the importance of intraspecific variation as adaptation to changing environmental conditions (Björklund et al. 2009). This finding challenges the generalization of the trends found in vascular plants and suggests that the inclusion of intraspecific variability might better predict the response of communities by better approaching the ability of species to cope with environmental changes (Violle 2012, Kichenin et al. 2013, Crawford et al. 2018). However, as far as we know, only Asplund & Wardle (2014) have sought to acknowledge the importance of species turnover and intraspecific variability in lichen communities and more studies including a wider suite of traits and environmental conditions are needed to elucidate general patterns.

Lichens are amongst the most sensitive organisms to environmental changes (Matos et al. 2015) and represent a valuable ecological system to anticipate and model the response of other less sensitive organisms present in the ecosystems (Pinho et al. 2011). They are poikilohydric organisms particularly sensitive to precipitation and temperature factors since their physiology is tightly linked to cycles of hydration and dehydration and they lack mechanisms to control their water and nutrient content (Prentice et al. 1992). Therefore, they

have been largely recognized as meaningful ecological indicators of environmental factors such as climate and nutrient deposition (Giordani et al. 2012, Matos et al. 2015). The lichen functional traits typically used as response traits (*sensu* Belluau & Shipley 2018) are growth form, type of photobiont and reproductive strategy, which are easily recognizable morpho-anatomical attributes ('soft traits') that inform about different aspects related with the physiology and activity of lichens. On the other hand, and as in vascular plants, a different set of functional traits inform about specific functions of these organisms (Cornelissen et al. 2007) such as photosynthetic performance (i.e. chlorophyll content), water use strategy (i.e. specific thallus mass -STM- and water holding capacity -WHC-) and resource uptake and retention (i.e. thallus nutrient concentration and isotopic ratios). Despite these traits capture precise functions with consequences for the ecosystem functioning (e.g. water and nutrient cycling, litter decomposition and food webs), they are time consuming and expensive to measure and, subsequently, they are rarely studied in lichenized organisms. Thus, meanwhile the specific leaf area has been largely used and probed to successfully reflect distinct responses to environmental gradients in vascular plants (Wright et al. 2004, Dwyer et al. 2014), very few studies have characterized the variation of the analogous lichen functional trait (i.e. STM) occurring in natural communities along wide environmental gradients (Gauslaa & Coxson 2011, Asplund & Wardle 2014).

In the present study, we quantify the relative contribution of species turnover and intraspecific variability determining the functional variation in lichen communities. We also assess the role of climate controlling the species turnover, intraspecific variability and total variation in the community-level trait measures. To address these questions, we studied lichen epiphytic communities in 23 beech forests along a latitudinal gradient in Europe comprising the entire distribution range of *Fagus sylvatica* L. We focused on a set of ten quantitative functional traits potentially affected by climatic conditions and related to photosynthetic performance, water use strategy and nutrient uptake. Based on previous studies on lichens (Asplund & Wardle 2014) and contrary to the findings for vascular plants (Kichenin et al. 2013, Siefert et al. 2015), we hypothesize that functional changes at community level along the latitudinal gradient will be influenced by both species turnover and intraspecific variability, with a higher relative contribution of the intraspecific variability. Furthermore, we expect that climatic factors will be the main drivers behind both species turnover and intraspecific variability in lichen communities given the inherent limitations of these poikilohydric organisms to actively buffer contrasting climatic conditions.

2 | MATERIALS AND METHODS

2.1. Sampling design

The study was carried out along a latitudinal gradient in Europe comprising more than 3000 km from southern Sweden to southern Italy. The latitudinal gradient reflects a climatic gradient in temperature and precipitation both, in annual values and seasonality, with differences of 7ºC in mean annual temperature and 1080 mm in total annual precipitation (Appendix S1). We surveyed lichen epiphytic communities in 23 mature and well-conserved monospecific stands of European beech with a tree cover > 65% and without tree cutting during the last 50 years (Fig. 1). In all cases, the lichen species *Lobaria pulmonaria* (L.) Hoffm. was present in order to sample communities in the same successional stage.

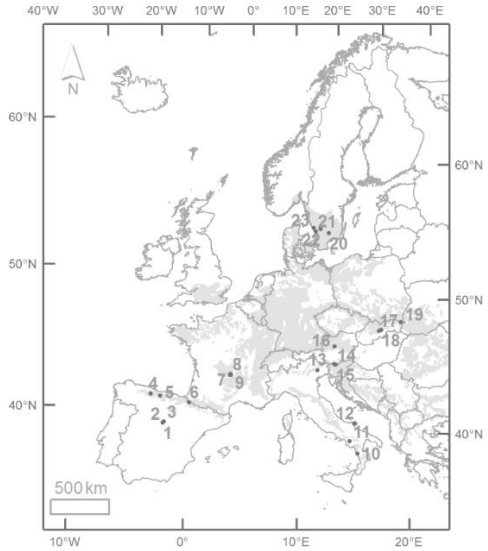

Figure 1. Map of the study area showing the distribution area of *Fagus sylvatica* (light grey) and the 23 sampling sites (black dots). Full name of the sampling sites in Appendix 1.

We followed the protocol of Aragón et al. (2012) to record the composition of the lichen community accounting more than a 90% of the species present in each stand. Within each stand, we randomly selected five 25 x 25 m plots, 100 m apart from forest edge and 500 m among plots. Within each plot, we selected 10 beech trees (dbh > 25 cm) and placed four 20 x 30 cm grids on each trunk, in the north and south faces and at breast height and tree base. Within each grid, we estimated the cover (%) of all lichen species found following Smith et al. (2009) and Clauzade & Roux (1985) for species identification. In total, we surveyed 1150 trees and collected data from 4600 sample units (grids).

In addition, we collected four thalli in each forest, whenever possible, of all macrolichen species found along the gradient for the measurement of quantitative functional

traits in the laboratory. All the samples were air-dried and frozen (-20 ºC), as it is recommended for later physiological studies in lichens (Honegger 2003).

2.2. Trait data

A total of 58 species of macrolichens were found across the latitudinal gradient. For these species we measured ten quantitative functional traits related to photosynthetic performance (n = 1184 thalli), water use strategy (n = 1018 thalli) and nutrient uptake (n = 1179 thalli). Regarding photosynthetic performance, we quantified chlorophyll a content (Chla), chlorophyll b content (Chlb) and normalized phaeophytinization index (NPQI) following Barnes et al. (1992) and equations given by Wellburn (1994). In relation to water use strategy, we measured specific thallus mass (STM) and water holding capacity (WHC) according to Merinero et al. (2014). For the nutrient uptake, we quantified thallus carbon content (%C), thallus nitrogen content (%N), carbon-nitrogen ratio (C/N), carbon isotopic ratio ($\delta^{13}C$) and nitrogen isotopic ratio ($\delta^{15}N$) using a PDZ Europa ANCA-GSL elemental analyser interfaced to a PDZ Europa 20-20 isotope ratio mass spectrometer (Sercon Ltd., Cheshire, UK) at UC Davis Stable Isotope Facility.

2.3. Climatic predictors

We used a suite of 19 climatic variables in order to assess the contribution of these climatic conditions to explain the species turnover and intraspecific trait variability of the lichen communities along the gradient. Climatic information at forest level was retrieved from the high-resolution climate dataset CHELSA (Karger et al. 2017) including variables related to annual values and seasonal ranges of temperature and precipitation (Appendix S1).

2.4. Data analysis

We performed a variance partitioning analysis to unveil the drivers behind the variability of the quantitative traits measured in macrolichen communities along the gradient and their response to the climatic conditions. All statistical analyses were performed using R version 3.5.0 (R Core Team 2018), as explained below.

We tested whether the variation of community weighted mean indices (CWM) along the gradient for the ten quantitative traits studied was caused by species turnover, intraspecific trait variability or their covariation following the method proposed by Lepš et al. (2011). This method is the only existing that allows the assesement of trait variation along gradients and the quantification of the relative effect caused by species turnover, intraspecific trait variability or their covariation (Siefert et al. 2015). For each quantitative trait the

approach is based on computing three community parameters, the specific CWM (CWMs), the fixed CWM (CWMf) and the difference between them. We calculated the first two with the *functcomp* function implemented in the *FD* package (Laliberté & Legendre 2010). The CWMs was computed with the trait values measured in each of the 23 forest stands (i.e. mean value at a given site for each species). Variations across the forest in CWMs inform about the total functional variation across forest stands, which can be due to both species turnover and intraspecific trait variability. The CWMf was computed using the same trait value for a given species irrespectively of where it is growing (i.e. the overall mean value across all sites). The CWMf informs about the species turnover only, as it is used the same trait value for species in all sites. The difference between CWMs and CWMf accounts exclusively for the effect of intraspecific trait variability. Thus, CWMs, CWMf and their difference were used to quantify the amount of variability explained by species turnover or intraspecific trait variability by using a sum of squares decomposition procedure through the function *trait.flex.anova* (see Lepš et al. 2011 for further details about the procedure). The method provides also a measure of covariation between turnover and intraspecific effects. When the covariation is positive (i.e. the sum of variance due to turnover and intraspecific trait variability is below 100%) it indicates that turnover and intraspecific trait variability have a similar effect, for example, in those conditions where smaller species are favoured, smaller individuals within those species are favoured. When the sum of the variance explained by species turnover and intraspecific trait variability is larger than 100%, there is a negative covariation between them. A negative covariation suggests that the variation in traits along the studied gradient due to species turnover counterbalances each other (i.e. the changes in trait values have the different sign, for example in those conditions where smaller species are favoured, bigger individuals within those species are favoured).

Besides determining the relative contribution of species turnover and intraspecific trait variability across the 23 forest stands in Europe, we also investigated the direct influence of climatic predictors in such variation. Among the set of all environmental variables, we selected four main climatic predictors, two related to temperature (BIO3, Isothermality and BIO9, Mean Temperature of Driest Quarter) and two related to precipitation (BIO17, Precipitation of Driest Quarter and BIO19, Precipitation of Coldest Quarter). These predictors were not significantly correlated (Spearman rho < 0.7, $P > 0.05$) and showed high load in the axes of the Principal Components Analysis performed with the 19 climatic variables available (Appendix S2). We repeated the procedure explained above for each of the ten quantitative traits (dependent variables) using as explanatory variables BIO3, BIO9,

BIO17 and BIO19. We used the function *trait.flex.anova* with Anova type II for quantifying the relative contribution of each predictor explaining the trait variability and the significance of the testable effects.

3 | RESULTS

Decomposition of total variability indicated that the relative contribution of intraspecific trait variability and species turnover differed in the ten quantitative traits studied (Fig. 2). In six of the measured traits (Chla, NPQI, STM, WHC, %C and $\delta^{13}C$), the intraspecific trait variability was the main determinant of functional trait variations, meaning that changes in dominant trait values along the gradient derived from the variation of the trait values within given species, rather than changes in the species pool conforming the macrolichen communities in each forest stand. In contrast, only in %N, the species turnover showed the highest contribution to the total variability. Another suite of three traits (Chlb, C/N and $\delta^{15}N$) had a similar relative contribution of intraspecific trait variability and species turnover, but the intraspecific variability was always higher than the species turnover. The covariation found between intraspecific trait variability and species turnover was positive in the case of three traits (Chlb, %C, C/N and $\delta^{15}N$), but negative in six traits (Chla, NPQI, STM, WHC, %N and $\delta^{13}C$; Fig. 2).

Figure 2. Relative contribution of intraspecific trait variability and species turnover to community trait variation along the gradient. Yellow and dark green denote the contribution of intraspecific trait variability and species turnover, respectively. The covariation between intraspecific trait variability and species turnover is represented through the space between the column and the black line (total

variance). When the column goes beyond the black line there is a negative covariation, and when the column does not reach the black line, the covariation is positive. Abbreviations: Chla, chlorophyll a content; Chlb, chlorophyll b content; NPQI, normalized phaeophytinization index; STM, specific thallus mass; WHC, water holding capacity; %C, thallus carbon content; %N, nitrogen thallus content; C/N, carbon/nitrogen ratio; $\delta^{13}C$, carbon isotopic ratio; $\delta^{15}N$, nitrogen isotopic ratio.

Changes in community-weighted trait values due to species turnover and intraspecific trait variability responded to climatic predictors (Table 1). Both total trait variation and variation due to intraspecific trait variability were better explained by climatic predictors than functional variation due to species turnover. Overall, temperature variables showed a greater contribution than precipitation variables explaining the observed functional variation. In particular, functional variation linked to species turnover was only explained by temperature variables: isothermality (temperature fluctuations within a month relative to the year) and mean temperature of driest quarter were the main drivers determining changes in Chla, Chlb and STM due to species turnover, whereas WHC, $\delta^{13}C$ and $\delta^{15}N$ were only affected by mean temperature of driest quarter (Table 1). Regarding functional variation linked to intraspecific trait variability, both temperature and precipitation variables contributed: changes in Chla, NPQI, STM, WHC, %C, %N and $\delta^{13}C$ responded to mean temperature of the driest quarter, with isothermality also affecting STM and WHC, and precipitation of the coldest quarter explaining NPQI, STM, %C, %N and $\delta^{13}C$ (Table 1). Finally, the total variation at community level in four of the studied traits (Chlb, NPQI, %C and C/N), were explained by mean temperature of the driest quarter. NPQI also responded to isothermality and precipitation of the coldest quarter, while STM and %C were affected by the latter (Table 1).

Table 1. Relative contribution (%) of climatic factors to species turnover, intraspecific trait variability and total variation of functional traits along the gradient. Only significant relationships are shown. Abbreviations as in Fig. 2.

	SPECIES TURNOVER				INTRASPECIFIC TRAIT VARIABILITY				TOTAL VARIATION			
	BIO3	BIO9	BIO17	BIO19	BIO3	BIO9	BIO17	BIO19	BIO3	BIO9	BIO17	BIO19
Chla	1.54	1.89	-	-	-	23.88	-	-	-	-	-	-
Chlb	4.55	8.21	-	-	-	-	-	-	-	22.05	-	-
NPQI	-	-	-	-	-	30.64	-	17.97	15.24	15.18	-	11.92
STM	4.36	4.57	-	-	15.55	-	-	12.15	-	-	-	18.38
WHC	-	5.61	-	-	23.63	17.28	-	-	-	-	-	-
%C	-	-	-	-	-	21.06	-	14.34	-	19.66	-	15.64
%N	-	-	-	-	-	22.09	-	12.08	-	-	-	-
C/N	-	-	-	-	-	-	-	-	-	17.06	-	-
$\delta^{13}C$	-	3.40	-	-	-	28.25	-	14.24	-	-	-	-
$\delta^{15}N$	-	9.22	-	-	-	-	-	-	-	-	-	-

4 | DISCUSSION

Our results showed that intraspecific trait variability explained most of the functional changes in lichen communities in response to a latitudinal gradient, in contrast to the broad trends typically expected in plant communities (Auger & Shipley 2013, Siefert et al. 2015). Therefore, intraspecific trait variability was as important, if not more important, than species turnover, in determining functional trait changes along broad environmental gradients. Another important finding was that such functional changes at community level were determined by the covariation between intraspecific trait variability and species turnover, which varied in sign depending on the trait considered. In the majority of studies, a positive covariation was found (Siefert et al. 2015) while, in our case, there was the double of cases showing negative, rather than positive covariation. Finally, functional variation due to both intraspecific trait variability and species turnover, was explained by different climatic predictors. Whereas intraspecific trait variability and total trait variation in lichen communities along the gradient responded to temperature and precipitation variables, species turnover was only explained by temperature (Fig. 3). We discuss below these three main findings of the study.

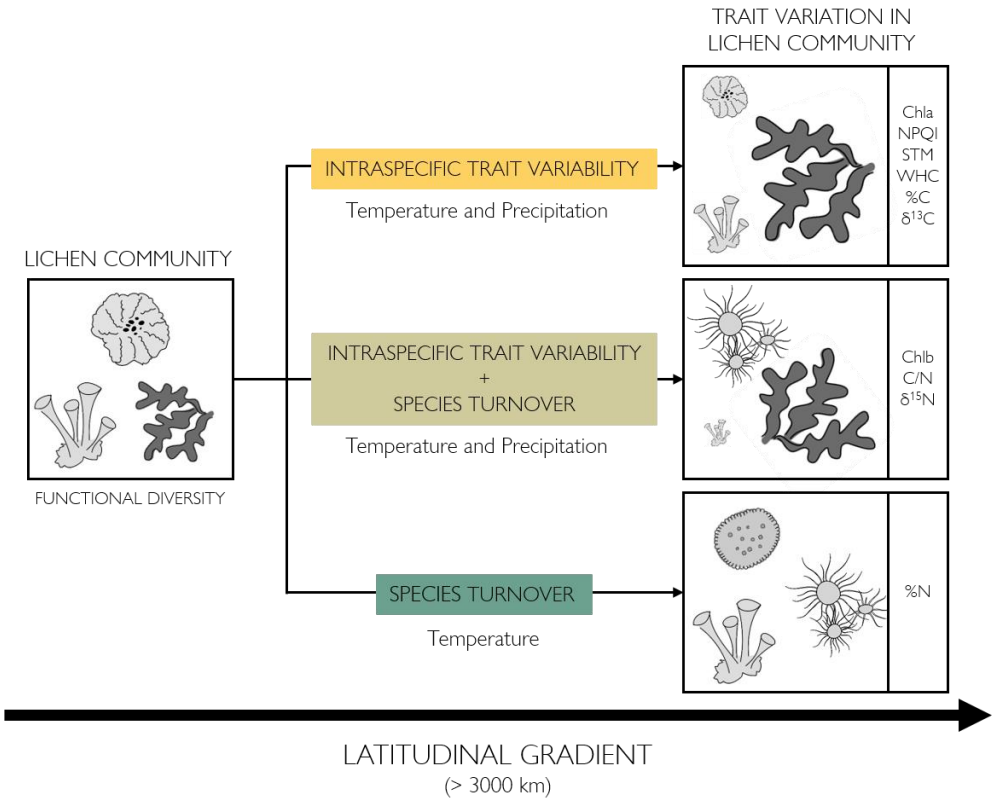

Figure 3. Summary of the main results. Intraspecific trait variability explained most of the functional changes in lichen communities in response to a latitudinal gradient along Europe. We identified three patterns of functional variation at community level with: 1) Intraspecific trait variability performing

the highest relative contribution in Chla, NPQI, STM, WHC, %C and $\delta^{13}C$; 2) intraspecific trait variability having the highest relative contribution, but species turnover showing a similar relative contribution in Chlb, C/N and $\delta^{15}N$; 3) species turnover showing the highest contribution to variability in %N. Total trait variation and functional variation due to intraspecific trait variability responded to temperature and precipitation variables, whereas functional variation linked to species turnover was only explained by temperature. Abbreviations as in Fig. 2.

Overall, intraspecific variability performed the highest contribution explaining the variation of lichen functional traits at community level. This finding entails a disrupt with respect to vascular plants in which interspecific variation tends to be larger than intraspecific variation at community level (e.g. Lepš et al. 2011, Auger & Shipley 2013, Kirchein et al. 2013, Siefert et al. 2015). Similarly to Asplund & Wardle (2014), we identified a much greater contribution of intraspecific variability than species turnover in six of the functional traits studied (Chla, NPQI, STM, WHC, %C and $\delta^{13}C$), meaning that the response of lichen communities to environmental changes are influenced by the high phenotypic plasticity, or selection of heritable genetic variation that the most abundant species across the communities considered (Fridley & Grime 2010), and not by the replacement of the species alone. Therefore, traits related to photosynthetic performance, water use strategy and carbon allocation showed large differences within lichen species and resulted highly sensitive to the environmental conditions, pointing out that intraspecific variation of this suite of traits cannot be safely ignored along the studied latitudinal gradient (Shipley et al. 2016). However, Chlb and traits related with nitrogen allocation showed a different pattern, with an increasing relative importance of species turnover. Exclusively for the thallus nitrogen content, species turnover was considerably more important than intraspecific trait variability. Interestingly, those traits with an important contribution of species turnover were related to the main photosynthetic partner in the lichen symbiosis (i.e. green algae or cyanobacteria), suggesting that these traits are genetically constrained, varying mostly at the interspecific level (Marks 2007). As such, cyanolichens are known to lack of Chlb (Palmqvist & Sundberg 2000) and to possess the ability for fixing atmospheric nitrogen (Palmqvist et al. 1998). Thus, changes in the abundance of chloro- and cyanolichens within the communities along the gradient could be underpinning the high contribution of species turnover to the trait variation.

For all studied traits, intraspecific trait variability and species turnover covaried but the 'directionality' of such covariation differed. We found a positive covariation in those traits with a similar relative contribution of intraspecific variability and species turnover, meaning that the same drivers favoured both the abundance of species with higher values of

Chlb, C/N and $\delta^{15}N$, and the increase of these trait values within individuals of the same species. In turn, we found the opposite result when intraspecific trait variability or species turnover displayed a much larger relative contribution than the other. As such, the same factor explained the decrease of the relative abundance of species with high levels of Chla, NPQI, STM, WHC, %N and $\delta^{13}C$, together to the accompanying intraspecific increase in these trait values in response to the gradient. Surprisingly, even for the same biological group (i.e. lichens), our results are not completely consistent with those obtained by Asplund & Wardle (2014) along a soil fertility gradient, who found a positive covariation for %N. This contrasting result emphasizes the importance of the precise environmental gradient considered (Kichenin et al. 2013) and prevents establishing general patterns of covariation between intraspecific variability and species turnover. One possible reason explaining why a high thallus nitrogen content within species is not accompanied by an increase of the abundance of species with higher %N, could be related with differences in the factors determining both determinants of functional variation. Nutrient content in lichens is tightly determined by the amount of atmospheric nutrients (Johansson et al. 2010) and, consequently, high levels of atmospheric nitrogen may increase the %N in lichens without nitrogen fixing photobionts. However, the increase of the relative abundance of cyanolichens, with nitrogen fixation ability and higher %N, may depend on the availability of compatible photobionts (Cardós et al. 2019) rather than on the atmospheric nutrient deposition.

We observed contrasting climatic factors affecting the species turnover and intraspecific trait variability of lichen communities along the latitudinal gradient. Regarding the species turnover, the amount of variation explained was relatively low (i.e. 1.5-9.2%), which may be partially explained by the low relative contribution of species turnover to the community-level variation in most studied traits. Furthermore, those traits with a relatively high contribution of species turnover are related with the type of photobiont and the atmospheric nutrient availability, suggesting that factors such as the availability of compatible photobionts, the level of specificity for the photobiont and the nitrogen deposition affect species turnover more than climate do (Johansson et al. 2010, Cardós et al. 2019). Also, the species turnover may respond to biotic interactions of competition and facilitation, and to the dispersal capacity and effective local establishment of different species due to their reproductive strategy (Nelson et al. 2015). Nonetheless, isothermality and temperature of the driest quarter were the main climatic factors driving species turnover in lichen communities, suggesting that temperature rather than precipitation was the constraining factor determining

changes in community composition along the latitudinal gradient. Conversely, community-level responses linked to intraspecific trait variability responded to both temperature and precipitation factors, reflecting the combined sensitivity of these poikilohydric organisms (Matos et al. 2015), which are physiologically active according to cycles of hydration and dehydration. In particular, isothermality, temperature of the driest quarter and precipitation of the coldest quarter mediated intraspecific changes in traits related to photosynthetic performance, water use strategy and nutrient allocation, pinpointing that precise physiological changes at individual level may shape lichen community responses to climate. Surprisingly, when considering the total trait variation, five traits were not affected by climate (Chla, WHC, %N, $\delta^{13}C$ and $\delta^{15}N$) and, for the other five traits (Chlb, NPQI, STM, %C and C/N) the climatic factors accounted for less than ca. 40% of the total variation. This relatively low impact of the large-scale climatic drivers considered, suggests that these traits linked to precise physiological functions could play an important role to better understand the effects of environmental changes on ecosystem functioning rather than as ecological indicators. However, species may respond to finer-scale changes in environmental variables that cannot be predicted using climate averages (Kimball et al. 2010).

5 | CONCLUSIONS

Disentangling the relative contribution of inter- and intraspecific trait variability and the environmental drivers underpinning the responses of natural communities is critical in community ecology for gaining insight into the effects of the ongoing global change. Indeed, unveiling whether the replacement of species or the adjustment of traits values as the climate changes mediate the response of communities along environmental gradients will improve our understanding on the ability of the communities to persist under changing conditions. We found that the relative contribution of intraspecific trait variability and species turnover mediating the response of lichen communities to a latitudinal gradient differed among traits, but intraspecific trait variability was larger than interspecific variation. Therefore, intraspecific variability likely has significant ecological consequences and should be explicitly incorporated to better understand the effect of environmental changes on lichen communities. In particular, traits related to photosynthetic performance, water use strategy and carbon allocation varied mostly at the intraspecific level showing up their high sensitivity to the environment and suggesting that this suite of traits allow lichen species to respond to environmental changes. Conversely, traits tightly linked to the main photosynthetic partner in the lichen symbiosis were more conserved and varied mostly at the interspecific level.

More generally, our findings highlight the need to avoid average values for the studied traits and the measurement of trait values at the level of individuals for assessing community-level responses. In plant communities, integrating intraspecific trait variability in community ecology may strengthen understanding of processes operating at community and ecosystem levels (Siefert et al. 2015), but in lichen communities it becomes essential since intraspecific trait variability performed the highest contribution mediating these community-level functional responses in a wide set of traits.

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7 | AUTHORS' CONTRIBUTIONS

IM, MP, GA and PH conceived the study; PH, MP, IM and GA did the fieldwork; PH did laboratory work; PH and FdB performed the data analyses; PH led the manuscript writing and all authors provided critical reviews. All authors gave approval for submission of the final manuscript.

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9 | SUPPORTING INFORMATION

9.1. Appendix S1

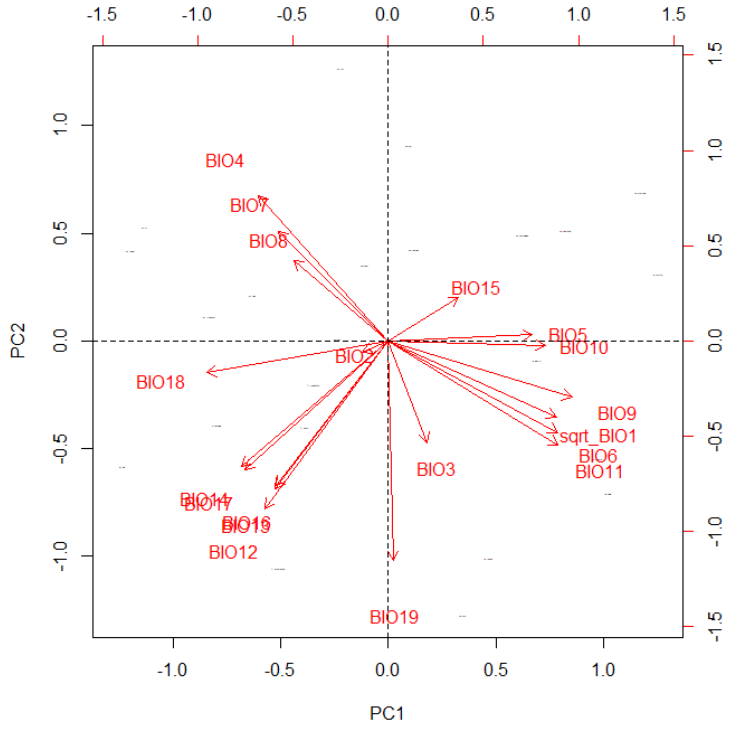
Table 1. Location and climatic variables of the study sites.

Forest stands	Forest abbreviation	X	Y	CLIMATIC VARIABLES (BIO)																	
				1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19
Ramlakliten i Skogsbo Natureservat	sw_ramlak	12.6	57.1	7.5	49.6	214	6309	20.0	-3.2	23.2	5.4	4.4	16.4	-0.8	842	90.2	44.0	23.8	267.0	148.2	251.2	156.4
Ödegårdet Natureservat	sw_oder	13.5	57.0	6.7	65.0	255	6502	20.6	-4.9	25.5	4.3	3.8	15.8	-1.8	914	94.8	50.4	22.0	281.4	162.2	265.8	179.2
Biskopstorps Natureservat	sw_bisk	12.9	56.8	7.0	57.0	236	6354	20.0	-4.1	24.1	4.8	4.0	15.9	-1.4	1069	117.4	57.4	23.0	335.4	188.2	327.8	203.2
Bjurkärrs Natureservat	sw_bjur	14.7	56.6	6.9	62.0	248	6489	20.8	-4.4	25.2	15.8	3.1	16.1	-1.5	658	76.4	36.6	22.0	211.2	115.4	203.2	124.6
Rabia skala (Poloniny NP)	sk_rabia	22.5	49.10	4.0	73.0	259	7484	18.7	-9.6	28.3	13.7	-6.0	13.9	-6.2	1125	144.4	60.2	29.8	430.4	181.8	368.2	212.8
Čigánka-Muránský hrad (Muránska planina NP)	sk_mp	20.1	48.76	6.2	75.2	261	7581	21.2	-7.7	29.0	13.8	-3.7	16.3	-4.1	666	86.8	31.6	30.2	249.6	100.8	201.4	106.2
Klenovský Vepor (Klenovské vrchy)	sk_kv	19.8	48.69	3.9	76.0	264	7439	18.8	-9.9	28.6	11.2	-5.9	13.8	-6.3	1065	145.8	56.0	30.4	404.2	174.0	341.8	185.8
Nationalpark Kalkalpen	at_kalk	14.5	47.82	6.8	80.0	285	7049	21.2	-6.9	28.1	15.9	-2.3	16.3	-2.8	1031	144.4	57.6	31.4	415.6	183.2	370.4	208.6
Loibtal	at_loib	14.3	46.46	6.2	83.6	286	7197	21.1	-8.1	29.3	10.7	-3.1	15.9	-3.7	1644	178.8	83.2	22.2	514.2	255.8	495.4	292.2
Trogener Klamm	at_trogener	14.5	46.45	6.8	84.0	285	7247	21.8	-7.6	29.4	16.5	-2.6	16.5	-3.2	1278	145.2	62.8	25.0	428.4	194.4	428.4	207.6
Chadefour Valley Nature Reserve	fr_chadefour	2.9	45.54	6.1	77.0	315	5749	19.9	-4.5	24.3	7.3	1.1	14.5	-1.2	1032	105.8	67.4	12.2	291.2	211.0	264.2	250.8
Réserve naturelle nationale de Chastreix-Sancy	fr_pavin	2.8	45.50	6.4	77.0	314	5769	20.2	-4.3	24.4	7.5	1.3	14.7	-1.0	1113	117.4	73.0	13.6	322.4	231.4	262.6	277.8
Picherande	fr_picherande	2.8	45.47	6.8	77.0	314	5765	20.6	-3.8	24.4	0.9	4.4	15.2	-0.5	1354	136.8	94.2	13.0	396.2	290.0	317.0	358.2
Parque Natural Saja-Besaya	se_saja	-4.3	43.11	11.1	69.0	345	4557	22.2	2.2	20.1	6.7	17.9	17.9	5.4	925	109.2	43.6	25.2	308.4	142.4	142.4	277.6
Parque Natural de Redes	se_redes	-5.2	43.11	8.7	78.6	365	4717	20.7	-0.8	21.5	4.0	15.7	15.7	2.7	1174	145.6	46.6	30.6	403.6	145.4	145.4	367.4
La Selva de Irati	se_irati	-1.1	42.99	9.9	85.6	355	5343	23.2	-0.9	24.1	4.4	17.5	17.7	3.0	1332	152.2	65.0	24.2	450.4	209.4	209.4	402.0
Parque Natural Sierra Norte de Guadalajara	ce_cantalojas	-3.4	41.23	7.1	95.0	341	6184	23.2	-4.5	27.8	0.8	16.5	16.5	-0.6	707	80.0	27.0	28.0	228.0	82.0	82.0	202.0
Hayedo La Pedrosa	ce_pedrosa	-3.4	41.22	8.0	95.0	340	6231	24.2	-3.7	27.9	1.6	17.5	17.5	0.2	681	78.0	24.0	30.0	222.0	72.0	72.0	200.0
Sitio Natural de Interés Nacional del Hayedo de Montejo de la Sierra	ce_montejo	-3.5	41.11	9.4	95.0	334	6378	25.9	-2.5	28.4	2.9	19.2	19.2	1.5	563	70.6	17.2	34.0	200.6	53.6	53.6	168.2
Foresta del Cansiglio	in_cansiglio	12.4	46.07	7.0	81.0	286	6928	21.5	-6.9	28.4	7.8	-1.9	16.5	-2.4	1427	151.2	77.8	20.4	437.6	235.6	393.2	264.4
Foresta Umbra (Pauco Nazionale del Gargano)	is_umbra	16.0	41.81	11.9	43.4	207	5793	23.1	2.3	20.8	10.4	19.7	20.6	4.6	618	71.4	36.6	20.4	203.8	116.4	117.8	148.0
Parco Nazionale del Cilento e Valle de Diano	is_alburni	15.4	40.50	9.0	84.4	321	6055	23.3	-2.9	26.2	3.5	17.0	17.9	1.2	942	126.8	27.2	41.0	370.0	89.4	96.4	276.4
Riserva Statale Serra Nicolino - Pian d'Albero	is_calabre	16.1	39.50	11.0	49.0	230	5657	22.6	1.4	21.2	8.4	18.4	19.5	3.8	1089	152.0	24.8	46.8	440.6	85.6	96.4	354.4

Longitude (X), Latitude (Y), Annual Mean Temperature (BIO1), Mean Diurnal Range (BIO2), Isothermality (BIO3), Temperature Seasonality (BIO4), Max Temperature of Warmest Month (BIO5), Min Temperature of Coldest Month (BIO6), Temperature Annual Range (BIO7), Mean Temperature of Wettest Quarter (BIO8), Mean Temperature of Driest Quarter (BIO9), Mean Temperature of Warmest Quarter (BIO10), Mean Temperature of Coldest Quarter (BIO11), Annual Precipitation (BIO12), Precipitation of Wettest Month (BIO13), Precipitation of Driest Month (BIO14), Precipitation Seasonality (BIO15), Precipitation of Wettest Quarter (BIO16), Precipitation of Driest Quarter (BIO17), Precipitation of Warmest Quarter (BIO18) and Precipitation of Coldest Quarter (BIO19). Temperature variables in °C and precipitation variables in mm.

9.2. Appendix S2

Principal component analysis (PCA) summarizing climatic variables at the forest level. First and second axis explained the 68.11% of the variance explained. Specifically, axis 1 explained 45.2% of the variance and axis 2 explained 22.91% of the variance. Annual mean temperature (BIO1) were square-rooted transformed to satisfy the normality assumptions. Climatic variables: Annual Mean Temperature, BIO1; Annual Mean Diurnal Range, BIO2; Isothermality, BIO3; Temperature Seasonality, BIO4; Max Temperature of Warmest Month, BIO5; Min Temperature of Coldest Month, BIO6; Annual Temperature Range, BIO7; Mean Temperature of Wettest Quarter, BIO8; Mean Temperature od Driest Quarter, BIO9; Mean Temperature of Warmest Quarter, BIO10; Mean Temperature of Coldest Quarter, BIO11; Annual Precipitation, BIO12; Precipitation of Wettest Month, BIO13; Precipitation of Driest Month, BIO14; Precipitation Seasonality, BIO15; Precipitation of Wettest Quarter, BIO16; Precipitation of Driest Quarter, BIO17; Precipitation of Warmest Quarter, BIO18 and Precipitation of Coldest Quarter, BIO 19.



Capítulo 4

Disentangling functional trait variation and covariation in epiphytic lichens along a continent-wide latitudinal gradient

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ABSTRACT

Characterizing functional trait variation, drivers behind such variation and patterns of trait covariation, is critical to understand the response of species to a changing environment. Evolutionary and environmental factors determine how traits vary among and within species at multiple scales. However, disentangling their relative contribution is challenging and it is necessary to apply a comparative framework integrating the functional and phylogenetic approaches. We investigated the functional variation in a suite of traits related to photosynthetic performance, water use and nutrient acquisition applying phylogenetic comparative analyses in lichen epiphytic communities across Europe. These poikilohydric organisms offer an outstanding model due to their inherent limitations to buffer contrasting environmental conditions. Evolutionary processes (i.e. phylogenetic history) largely determined trait variation, although the intraspecific component was non-negligible. Climatic factors related to seasonality, rather than mean values, also had an impact on trait variation leading to shifts from resource-conservative to resource-acquisitive traits in more seasonal environments. The inconsistency of trait covariation among and within species prevented establishing major resource-use strategies in lichens. However, we did identify a general pattern related to the water-use strategy. Thus, to robustly unveil lichen responses under different climatic scenarios, it is necessary to incorporate both among and within-species trait variation and covariation.

Key words

Climate seasonality, functional traits, latitudinal gradient, lichens, phylogenetic comparative analysis.

1 | INTRODUCTION

Understanding how functional traits vary along environmental gradients is crucial to disentangle the response of species to environmental drivers under the current global change context. Functional traits exhibit a range of values that vary among and within species and across environmental gradients (Violle et al. 2007), and potentially affect the performance of individuals (Reich et al. 2003). The patterns of functional trait variation not only inform about the impact of environmental changes on communities (Webb et al. 2010), but also are useful for assessing the effect of community changes on ecosystem processes (de Bello et al. 2010).

The variation of functional traits within species is constrained by genetic differentiation and phenotypic plasticity (Albert et al. 2010b) reflecting the evolutionary history and the adaptation of species to environmental conditions (Díaz & Cabido 2001). Given the complexity of the sources of functional variation, it is important to adopt a pluralistic framework integrating the phylogenetic dimension of biodiversity and the trait-based approach (i.e. phylogenetic comparative analysis) (Felsenstein 1985, Martins & Hansen

1997). Beyond the species level, some aspects of trait variation may differ at different scales (e.g. family, species, population, and tree) (Messier et al. 2010, Vilà-Cabrera et al. 2015). Thus, exploring the distribution of functional variation across scales would improve our understanding on the distinct responses of species under different environmental scenarios and the implications for ecosystem functioning (Violle et al. 2014). Several studies have assessed the extent of functional variation among and within species, and the trait-environment relationships (Wright et al. 2005). However, the specific drivers determining trait variation and the scales at which such variation occurs are not well known (Anderegg et al. 2018).

Plant ecologists have gone one step forward in the study of functional variation on the basis of the idea that functional traits covary (Grime et al. 1997). Consistent patterns of covariation between functional traits are valuable tools to define general ecological strategies (Reich et al. 2003). For instance, the pattern of covariation between leaf traits (e.g. leaf economic spectrum) has been related with rapid resource acquisition versus resource conservation strategies (Wright et al. 2004). Thus, functional traits are useful proxies to identify ecological strategies in vascular plants (e.g. Wright et al. 2004), but the ecological link between traits and ecological strategies in other organisms such as epiphytic lichens remains almost unexplored. Lichens are excellent study organisms to address ecological questions about environmental changes, traits, and ecosystem processes for two main reasons. First, lichen physiology (e.g. photosynthetic performance, water use, and nutrient acquisition) strictly depends on environmental conditions (Nimis et al. 2002), because they lack mechanisms to regulate water and nutrient uptake and loss. Second, their life-history traits respond to environmental changes (Prieto et al. 2017, Hurtado et al. 2019) and directly impact on ecosystem functioning (Ellis 2012, Benítez et al. 2018). For example, they contribute to forest ecosystem processes including nutrient cycling, soil fertility, water regulation and purification, and primary production (see Ellis 2012 for review, Asplund & Wardle 2017).

Most studies reporting environmental impacts on lichens using a trait-based approach typically use 'soft' traits (*sensu* Belluau & Shipley 2018) since they provide integrative information about many physiological functions and are easy to obtain. It is well recognized that certain lichen traits such as type of photobiont and growth form are indicators of environmental changes (Giordani et al. 2012, Matos et al. 2015). However, the link of these traits with specific functions is weak. Thus, more information is needed about the variation of specific physiological traits (i.e. 'hard' traits) in a wide set of species under contrasting environments. There is some evidence that traits related to photosynthetic

performance, water use, and nutrient acquisition differ according to environmental drivers. For instance, in certain species, environmental conditions determine the photosynthetic performance (e.g. chlorophyll content, degradation or fluorescence) (Gauslaa et al. 2006), the specific thallus mass (STM, Asplund et al. 2012), the water storage capacity (WHC, Pérez-Ortega et al. 2012) and the nutrient content (Cornelissen et al. 2007). Therefore, traits such as chlorophyll content, STM, WHC, nutrient content (e.g. nitrogen and carbon content; %N and %C), and isotopic ratios may provide valuable information to explore species responses to environmental changes and to identify general ecological strategies in lichens. For example, species with resource-conservative traits such as low nitrogen content, and high chlorophyll and STM (i.e. the equivalent to specific leaf area in vascular plants) may be favoured in stressful environments (Adler et al. 2013).

Here, we analysed the functional response of epiphytic lichens from beech forests (*Fagus sylvatica* L.) across its latitudinal distribution range in Europe covering a broad range of climatic conditions (i.e. temperature, precipitation, and seasonality). We used a comparative approach integrating phylogenetic relatedness and a trait-based approach to decouple the effect of phylogeny and environment on lichen functional variation among 52 species. First, we assessed the scale (i.e. order, species, and population) that better explained the observed trait variation to unravel to what extent among *versus* within species variation control functional variation. Second, we analysed the response of each functional trait to different climatic drivers. Third, we calculated the covariation of functional traits along the gradient to unveil the existence of trade-offs between the studied traits and to evaluate to what extent this covariation is consistent among and within species.

We hypothesised that: 1) evolutionary and environmental drivers would determine functional variation of anatomical and physiological traits with a more important contribution of inter- than intraspecific variability and with a key role of environment on traits related with photosynthetic performance, water use, and nutrient acquisition; 2) under stressful environmental conditions, species with a conservative strategy will be favoured over those with an acquisitive strategy; and 3) correlation of traits related with general ecological strategies may not vary among and within species. For example, the positive correlations STM-WHC (Merinero et al. 2014, Esseen et al. 2015) and Chla-%N (Palmqvist et al. 2002), for the water use strategy and the photosynthetic performance, respectively.

2 | MATERIALS AND METHODS

2.1. Collection sites and lichen sampling

The present study was carried out in 23 beech forests located in six European countries (Sweden, Slovakia, Austria, Italy, France, and Spain) covering the whole latitudinal range of *F. sylvatica* (from southern Sweden to southern Italy). To reduce habitat differences, we selected mature and well-preserved forests at least 5 km away from each other, with a tree cover over 65 %, and without tree cutting during the last 50 years. All forests harboured the lichen species *Lobaria pulmonaria* (L.) Hoffm. to ensure the survey of mature epiphytic communities in the same successional stage (Rose 1988), thus minimizing the differences related to the community development. The latitudinal gradient represented a large climatic gradient with mean annual temperature ranging from 3.9 to 11.9 ºC and total annual precipitation ranging from 563 to 1644 mm (Karger et al. 2017) (Table S1). By studying epiphytes on this single host species, we were able to: 1) control as much as possible the habitat differences not related with climate and 2) measure functional traits on individuals located both, at the extremes and at the core area of distribution of the host tree species.

Within each forest we collected four thalli, whenever possible, of all macrolichen species found (i.e. large and conspicuous lichens). After collection and before measurements, samples were air-dried, cleaned from debris, and stored at -20 ºC (Honegger 2003). Because not all species were present in the 23 forests surveyed, we selected for analyses the 52 species present in at least three forests (1486 thalli belonging to three taxonomic orders with 5-80 thalli sampled per species) (Table S2) (see 'Data analyses' section).

2.2. Climatic drivers

Climatic variables for each forest were obtained from the high-resolution climate dataset CHELSA (Karger et al. 2017) including 19 bioclimatic variables related to temperature and precipitation. To reduce the number of climatic drivers we performed a Principal Components Analysis (PCA) (Fig.S1) and we selected orthogonal variables with high loading in the first four PCA axes. As a result, the climatic variables selected were Annual Mean Temperature (BIO1), Annual Precipitation (BIO12), Temperature Seasonality (BIO4; standard deviation of the mean monthly temperature), and Precipitation Seasonality (BIO15; coefficient of variation).

2.3. Functional traits measurement

We classified each species by two categorical functional traits: type of photobiont and growth form (Table S3). We considered whether the lichens have cyanobacteria (cyanolichens, CB) or chlorococcoid algae (chlorolichens, CHL) as the main photobiont (Nimis & Martellos 2017). We classified growth form in five categories (foliose broad-lobed, FB; foliose narrow-lobed, FN; fruticose dorsiventral, FR; fruticose cylindrical, FRC and squamulose, SQ) (Aragón et al. 2016).

In addition, we measured nine quantitative functional traits on the sampled thalli (mean values in Table S3) related with photosynthetic performance (Chla, Chlb, and normalized phaeophytinization index, NPQI), water use (STM and WHC) and nutrient acquisition (%C and %N; carbon and nitrogen isotopic ratio, $\delta^{13}C$ and $\delta^{15}N$). The number of measures varied depending on the species and functional trait considered (Table S4).

To quantify Chla, Chlb, and NPQI we followed Barnes et al. (1992) with some modifications. Since chlorophyll content may vary within a thallus (Valladares et al. 1996), we selected 20 mg of clean lichen material including inner, outer, and medium portions of the lichen thallus. Lichen material was subjected to six 10-minutes washes with $CaCO_3$ saturated 100% acetone to remove lichen secondary compounds. After 24 h of acetone evaporation, chlorophyll was extracted using 5 ml of 2.5 mg/ml polyvinylpolypyrrolidone (PVP_i) in dimethylsulphoxide (DMSO). We incubated the tubes in a hot water bath with continuous stirring for 40 min, at 65 ºC in the dark. Extracts were cooled in ambient temperature during one hour to measure the absorbance at 750, 665, 648, 435 and 415 nm. Concentrations of Chla and Chlb, and NPQI were calculated following the equations in Wellburn (1994).

We quantified STM and WHC following Merinero et al. (2014). To standardize the samples of the different species, we selected thalli of c. 120 mg. We hydrated the thalli until full saturation with deionised water, scanned them and recorded the thallus area (A) analysing the images in Adobe Photoshop CS6 Extended (Adobe Systems, San Jose). Immediately after, thalli were fully hydrated and gently blotted with filter paper before measuring wet mass (WM) to the nearest mg. Then, thalli were oven-dried (60 ºC for 72 h) and we quantified dry mass (DM) in mg. Specific thallus mass was calculated as STM (mg DM/cm^2) = DM/A, and water-holding capacity as WHC (mg H_2O/cm^2) = (WM − DM)/A.

To quantify %C, %N, $\delta^{13}C$, and $\delta^{15}N$ lichen samples from the marginal and central parts within each thallus were oven-dried (60 ºC, 72 h), milled (Precellys 24-DUAL) and encapsulated in tin capsules for analysis at UC Davis Stable Isotope Facility. Analyses were done using a PDZ Europa ANCA-GSL elemental analyser interfaced to a PDZ Europa 20-20 isotope ratio mass spectrometer (Sercon Ltd., Cheshire).

2.4. Phylogenetic analyses

We constructed a phylogenetic tree for the 52 species using four molecular markers (nuITS, nuLSU, mtSSU, and RPB1). For those species absent in GenBank, we generated the sequences following Prieto et al. (2013) (23 newly produced sequences for 14 species, Table S5). For each molecular marker, we aligned the consensus sequences (MAFFT ver.7) and manually excluded the ambiguous regions and introns using MacClade ver.4.0.1 (Sinauer, Sunderland). We analyzed each individual gene region with a maximum likelihood approach implemented in RAxML ver.8.2.10 using a GTRGAMMA model of evolution and 1000 bootstrap replicates. Since we did not find supported nodes in conflict, we combined the individual gene regions and run a combined maximum likelihood (ML) analysis. We run a RAxML analysis with five distinct partitions (nuITS, nuLSU, mtSSU, first and second codon positions of RPB1 and the third codon position of the RPB1) and the same settings as the individual gene analyses. RAxML analyses were run on the CIPRES Science Gateway ver.3.1.

2.5. Data analyses

First, we calculated the phylogenetic signal of the quantitative functional traits and assessed the trait variation within different functional groups using Phylogenetic Generalized Least Squares linear models (PGLS). Second, we did a variance component analysis for each trait using three nested scales (i.e. order, species, and population) to disentangle the main determinants of the functional variation observed along the latitudinal gradient. After, we focused on the effect of the climatic drivers on each quantitative trait using Phylogenetic Generalized Linear Mixed Models (PGLMM). Finally, we evaluated the covariation between pairs of functional traits calculating the correlation with a phylogenetically informed comparative analysis.

We used R version 3.4.0 (R Core Team 2018) for data analyses. We included in the analyses the 52 species present in at least three forests, and we $\log_e$-transformed the traits Chla, Chlb, STM, WHC, %C, and %N to meet normality.

2.5.1. Physiological and anatomical trait variation within functional groups

We calculated the phylogenetic signal for the quantitative traits with Pagel's Lambda (λ) using *phylosig* function in the package *phytools* (Revell 2012). Given the non-independence of the trait data due to phylogenetic relationships among species and the high phylogenetic signal obtained for the studied functional traits (λ close to 1, see Table S6), we used Phylogenetic Generalized Least Squares linear models (PGLS) to assess trait differences between species with different types of photobiont and growth forms. We controlled the lack of independence of species with shared ancestry (Felsenstein 1985) and optimized the branch length transformation using maximum likelihood to find the best value of lambda transformation considering the data and the model (Freckleton et al. 2002). We performed the PGLS linear models using the function *pgls* in the *caper* package (Orme 2013). When significant differences were observed, we performed pairwise comparisons to unveil differences between groups.

2.5.2. Trait variation and variance decomposition

We quantified the variation of each functional trait using the quartile coefficient of dispersion (QDC) calculated as the ratio between half the interquartile range ((Q3-Q1)/2) and the average of the quartiles ((Q1+Q3)/2) (Table S7). To assess the scale at which trait variation occurs, we conducted a variance component analysis for each trait calculating their variance partitioning across order, species, and population with the *lme* function in *nlme* package (Pinheiro et al. 2018). We used linear mixed effects models with a fixed intercept and nested scales as random factors and we compared the magnitude of the random factors variance parameters across orders, species, populations (i.e. all thalli of a given species collected in different forests) and within populations (i.e. residual variance).

2.5.3. Functional trait variation in response to climatic drivers

We fitted Phylogenetic Generalized Linear Mixed Models (PGLMM) to explore the relationships between traits and climate accounting for the phylogenetic covariances among species (Ives 2018). We used each functional trait as dependent variables and BIO1, BIO4, BIO12, and BIO15 as independent variables. We included species, forest, and phylogenetic covariance as random factors on the intercept. Before fitting the models, we checked potential multicollinearity among independent variables using variance inflation factors (Fox 2015). Models were fitted using the *communityPGLMM* function in the package *phyr* (https://github.com/daijiang/phyr), with Gaussian family as error distribution for modelling and likelihood-ratio test to assess the significance of fixed effects.

2.5.4. Functional trait correlation networks

To assess the correlation between pairs of functional traits across the 52 species, we used a phylogenetically informed comparative analysis (Swenson 2014). To do so, we calculated a covariance matrix among the traits including the phylogenetic relatedness using the function *phyl.vcv* in the package *phytools* (Revell 2012). This covariance matrix was used to compute the correlation matrix with the function *cov2cor* in *phytools* package (Revell 2012). We also performed Pearson correlations within species for each of the 16 most common species, all sampled in at least ten forests (*rcorr* function in *Hmisc* package; Harrell 2017). All significant correlations ($P < 0.05$) were illustrated as networks where nodes represented traits and lines the correlations between pairs of functional traits (*igraph* package; Csardi & Nepusz 2006). In addition, we quantified centrality of each trait with two measures: the degree (D) (i.e. the number of edges incident upon a node) and the weighted degree (Dw) (i.e. the sum of significant coefficients of correlation incident upon a node) (Rosas et al. 2019).

3 | RESULTS

3.1. Physiological and anatomical trait variation within functional groups

Phylogenetically controlled tests showed that type of photobiont and growth form accounted for differences in four of the nine quantitative physiological and anatomical traits (Fig. 1a, b). Regarding the type of photobiont, cyanolichens had higher levels of %N, $\delta^{13}C$, and $\delta^{15}N$, but lower Chlb content than chlorolichens (Fig. 1a). In relation to growth form, we found significant differences in $\delta^{15}N$ (Fig. 1b). Foliose broad-lobed and squamulose lichens had the highest levels of $\delta^{15}N$, narrow-lobed lichens intermediate $\delta^{15}N$, and fruticose lichens (dorsiventral and cylindrical) the lowest $\delta^{15}N$.

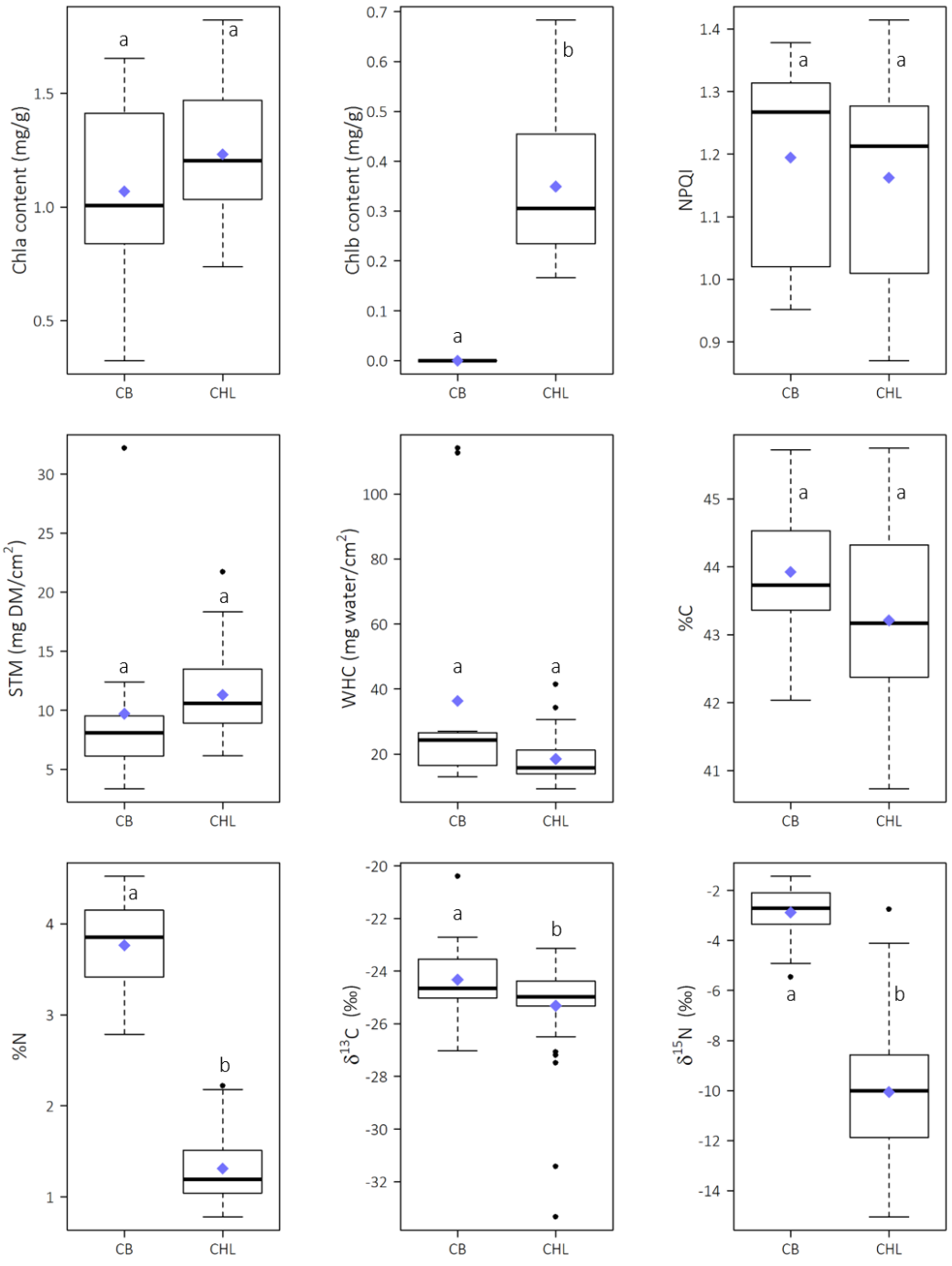

Figure 1a. Boxplots of the functional trait values for different types of photobiont. The horizontal lines within boxes represent the median, and the limits of the boxes the first and third quartiles. Blue diamonds represent mean trait values. Different letter(s) above the error bars denote significant differences of mean functional traits values between types of photobiont accounting for the phylogeny (PGLS). Sample size (number of species): CHL = 37, CB = 15. Abbreviations: Chla, chlorophyll a content; Chlb, chlorophyll b content; NPQI, normalized phaeophytinization index; STM, specific thallus mass; WHC, water-holding capacity; %C, thallus carbon content; %N, nitrogen thallus content; $\delta^{13}C$, carbon isotopic ratio; $\delta^{15}N$, nitrogen isotopic ratio; CB, cyanobacteria; CHL, chlorococcoid algae.

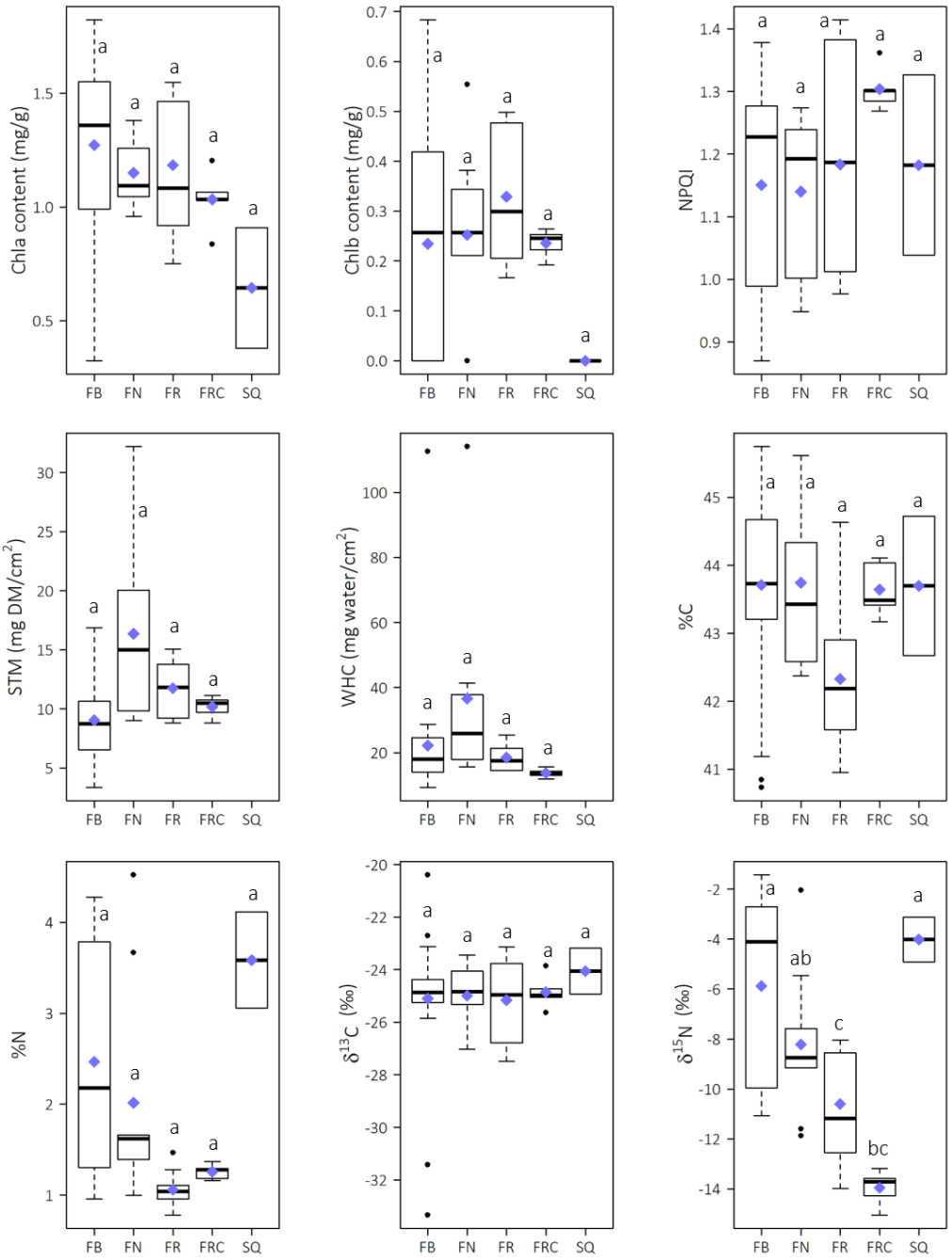

Figure 1b. Boxplots of the functional trait values for different growth forms. The horizontal lines within boxes represent the median, and the limits of the boxes the first and third quartiles. Blue diamonds represent mean trait values. Different letter(s) above the error bars denote significant differences of mean functional traits values among growth forms accounting for the phylogeny (PGLS). Sample size (number of species): FB = 25, FN = 9; FR = 11, FRC = 5, and SQ = 2. Abbreviations: Chla, chlorophyll a content; Chlb, chlorophyll b content; NPQI, normalized phaeophytinization index; STM, specific thallus mass; WHC, water-holding capacity; %C, thallus carbon content; %N, nitrogen thallus content; $\delta^{13}C$, carbon isotopic ratio; $\delta^{15}N$, nitrogen isotopic ratio; FB, foliose broad-lobed; FN, foliose narrow-lobed; FR, fruticose dorsiventral; FRC, fruticose cylindrical and SQ, squamulose.

3.2. Trait variation and variance decomposition

The total amount of variation (Fig. 2a) and the scales at which such variation occurs (Fig. 2b) differed among the studied traits. In all cases, excepting Chla and %C, order and species levels (among species variation) explained most of the variance, while population and residual levels (within species variation) accounted for lower variation (Fig. 2b). Most trait variation occurred at order level (Caliciales, Lecanorales, and Peltigerales) in the most variable traits (Chlb, %N, and $\delta^{15}N$; Fig. 2a), while species level was the largest contributor to overall variation for Chla, NPQI, STM, WHC, and $\delta^{13}C$ (Fig. 2b).

Variation among species ranged from 71.54% in NPQI to 79.09% in %N, while variation within species ranged from 20.91% to 28.46% (Fig. 2b). However, %C showed an opposite pattern, with intraspecific variability accounting for 84.94% of total variation (Fig. 2b). For Chla, variation was approximately equally distributed within (53.21%) and among species (46.79%) (Fig. 2b).

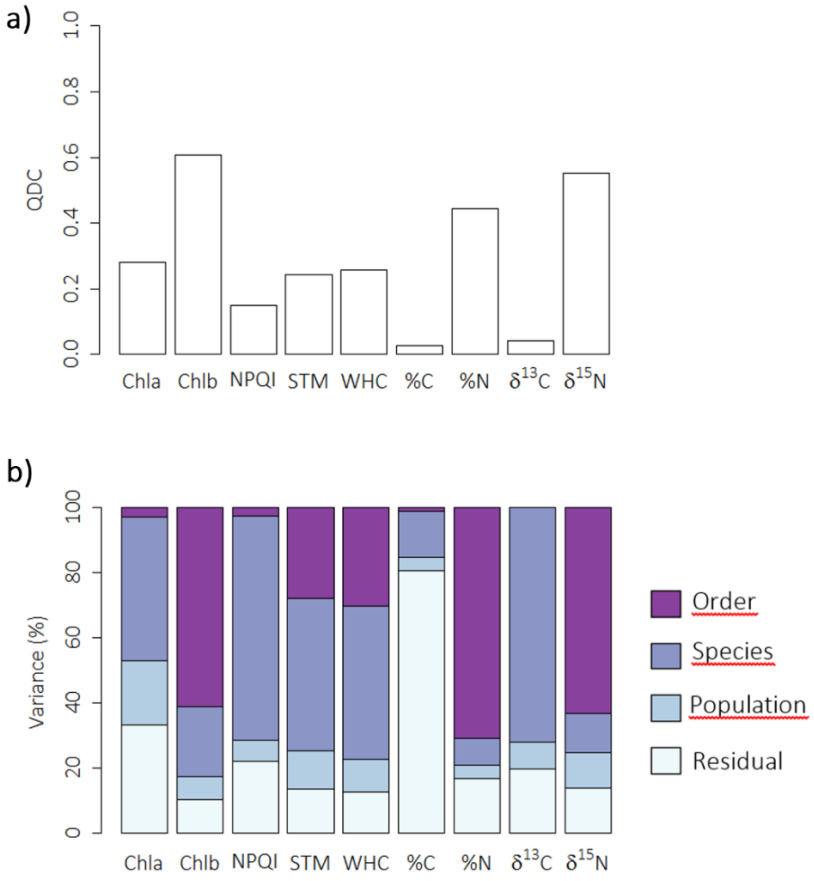

Figure 2. (a) Quartile coefficient of dispersion (QDC) and (b) variance partitioning across different scales for each functional trait. 'Residual' indicates the variance not explained by order, species, and population (i.e. the variance among thalli collected in the same population). Abbreviations: Chla,

chlorophyll a content; Chlb, chlorophyll b content; NPQI, normalized phaeophytinization index; STM, specific thallus mass; WHC, water-holding capacity; %C, thallus carbon content; %N, nitrogen thallus content; $\delta^{13}C$, carbon isotopic ratio; $\delta^{15}N$, nitrogen isotopic ratio.

3.3. Functional trait variation in response to climatic drivers

After analysing trait-environment relationships, we found significant effects of climatic drivers on most functional traits. However, these drivers explained a small amount of trait variation (Fig. 3; Table S8). Chla, Chlb, STM, %N, and $\delta^{13}C$ responded to temperature-associated variables, whereas Chla, %C, and $\delta^{15}N$ responded to variables related to precipitation. Lichens with lower Chlb and higher $\delta^{13}C$ were associated to forests with higher annual mean temperature. Temperature seasonality (i.e. temperature change over the course of the year) showed a positive effect in Chla, Chlb, and %N, and a negative effect on STM. Thus, lichens with high STM, low Chla and Chlb content, and low %N were associated to forests with low temperature seasonality. Increases in annual precipitation reduced Chla. Precipitation seasonality (i.e. precipitation variability throughout the year) also had a significant effect on %C and $\delta^{15}N$: lichens with low %C and high $\delta^{15}N$ were favoured in forests with high precipitation seasonality. Climatic variables did not affect NPQI and WHC.

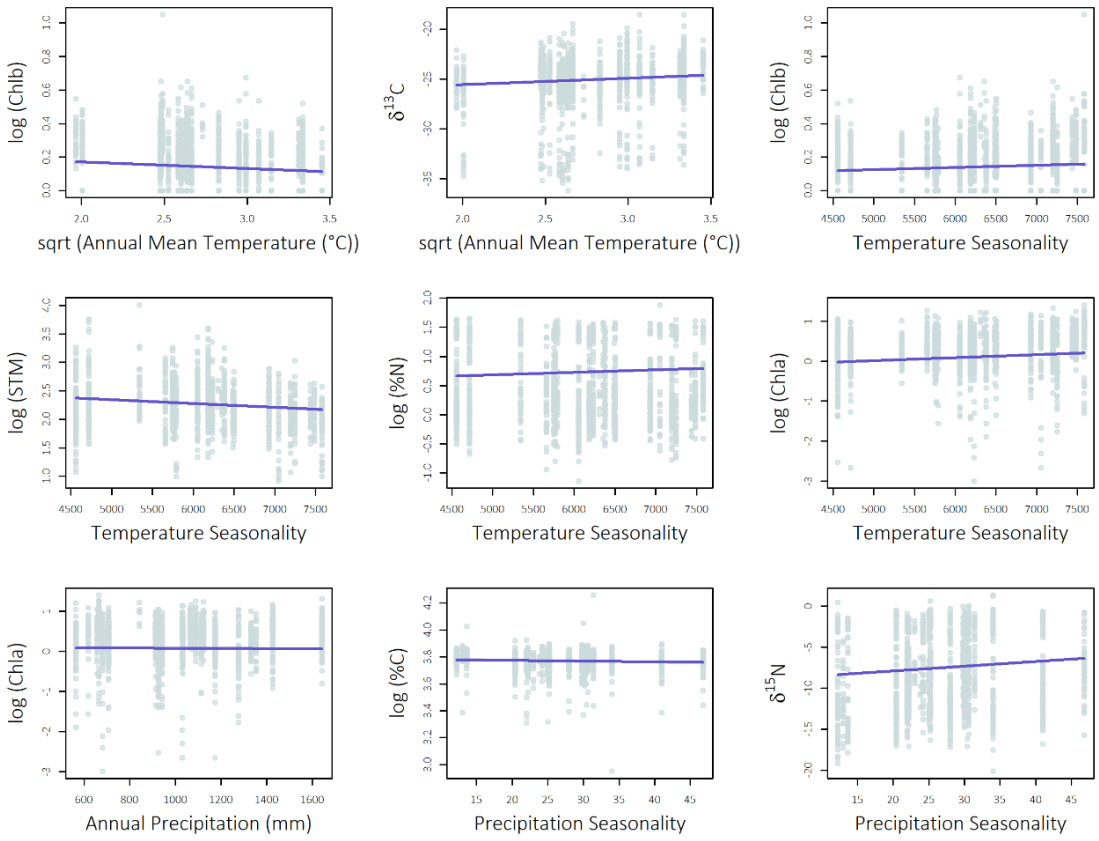

Figure 3. Response of lichen functional traits to temperature and precipitation factors. Blue lines represent predicted regression lines of significant relationships ($P < 0.05$) between functional traits

and climatic variables based on PGLMM (see Appendix S9). Light blue points illustrate raw data. Abbreviations as in Fig. 2.

3.4. Functional trait correlation networks

We found different patterns of trait correlation when the 52 species were analysed together and when species were considered separately, implying that trait-trait covariation differed among and within species (Fig. 4; Table S9). Only the positive correlation between STM and WHC was consistent among and within species (Fig. 4). Thus, we did not identify trade-offs apart from the one related to the water use strategy: rapid moisture-uptake versus conservative water-storage. In addition, traits with high centrality (measured as weighted degree) also differed among and within species (Table S10). Among species, STM showed the highest weighted degree while Chla, Chlb, STM, WHC, and $\delta^{15}N$ were the most central traits depending on the species (Fig. 4).

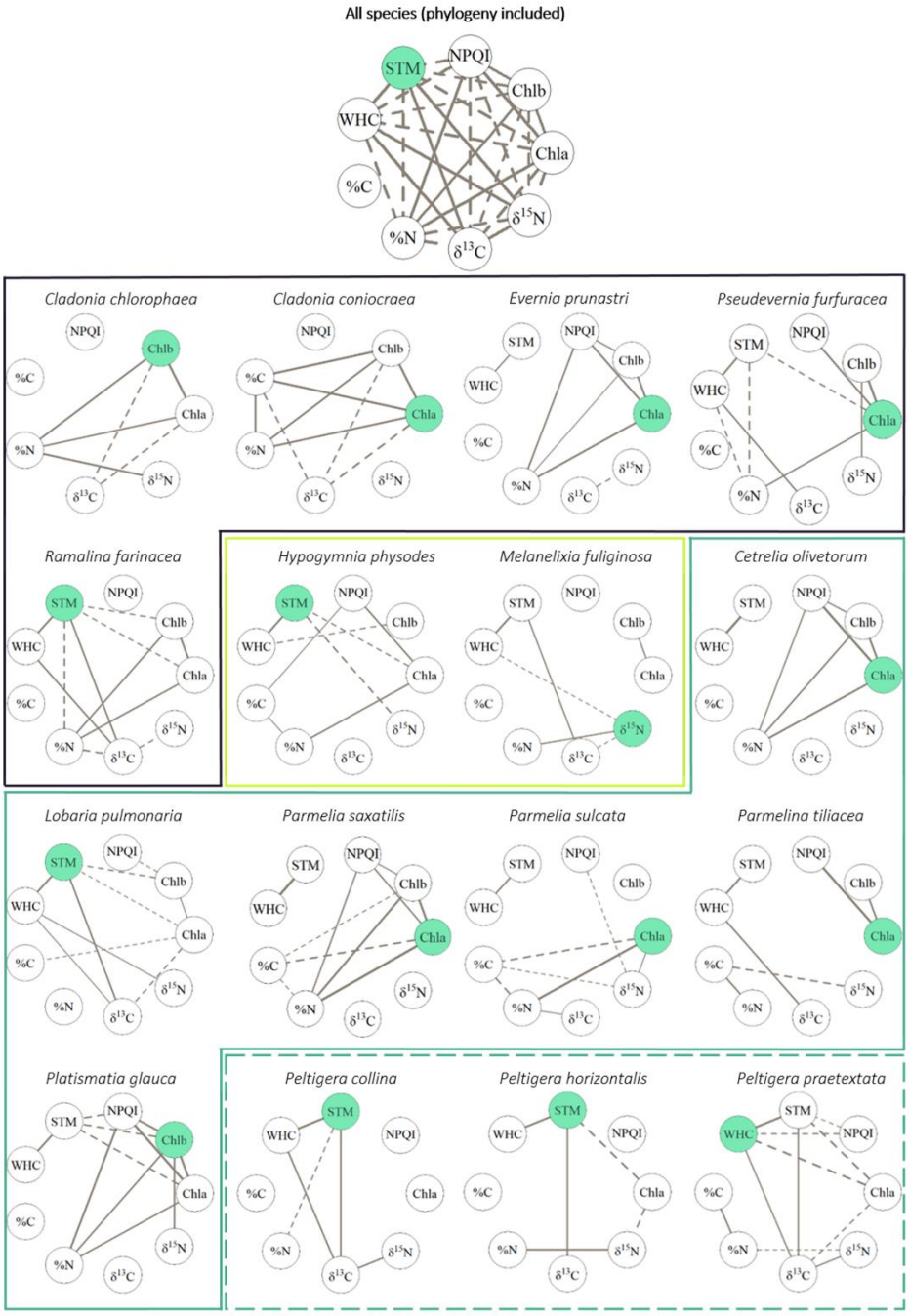

Figure 4. Covariation networks for all the species (n = 52 for all traits excepting STM and WHC, n = 44) accounting for phylogenetic relatedness, and for each of the 16 most common species separately. Solid grey lines denote significant positive correlations and dashed grey lines denote negative significant correlations ($P < 0.05$). Lines width is proportional to the strength of the correlation. Turquoise nodes represent the traits with the highest centrality measured as weighted degree. Boxes encompass lichens with different types of photobiont or growth forms: solid line boxes encompass chlorolichens while dashed line box encompasses cyanolichens. Dark blue colour denotes fruticose lichen, light green, foliose narrow-lobed and light blue, foliose broad-lobed. Abbreviations as in Fig. 2.

4 | DISCUSSION

In this study, we investigated the variation of nine functional traits of 52 lichen species along an environmental gradient throughout Europe. According to our initial hypothesis, functional variation was distributed across scales, with order and species having the highest contribution to the overall variation. Although functional variation was higher among than within species, intraspecific variability (particularly within populations) substantially contributed to overall trait variation mostly in %C. Climatic variables related to temperature and precipitation seasonality drove such variation along the gradient, and functional traits differently responded to these drivers, although explained variance was low. Based on the patterns of trait covariation, we identified a positive correlation related with the water-use strategies (STM-WHC) that was consistent among and within species. After controlling for the non-independence of the species because of shared ancestry, we found that 'soft' traits broadly used to characterize lichen functional groups (i.e. type of photobiont and growth form) accounted for differences of certain 'hard' traits (e.g. Chla, NPQI, STM, WHC, and %C) (Fig. 5).

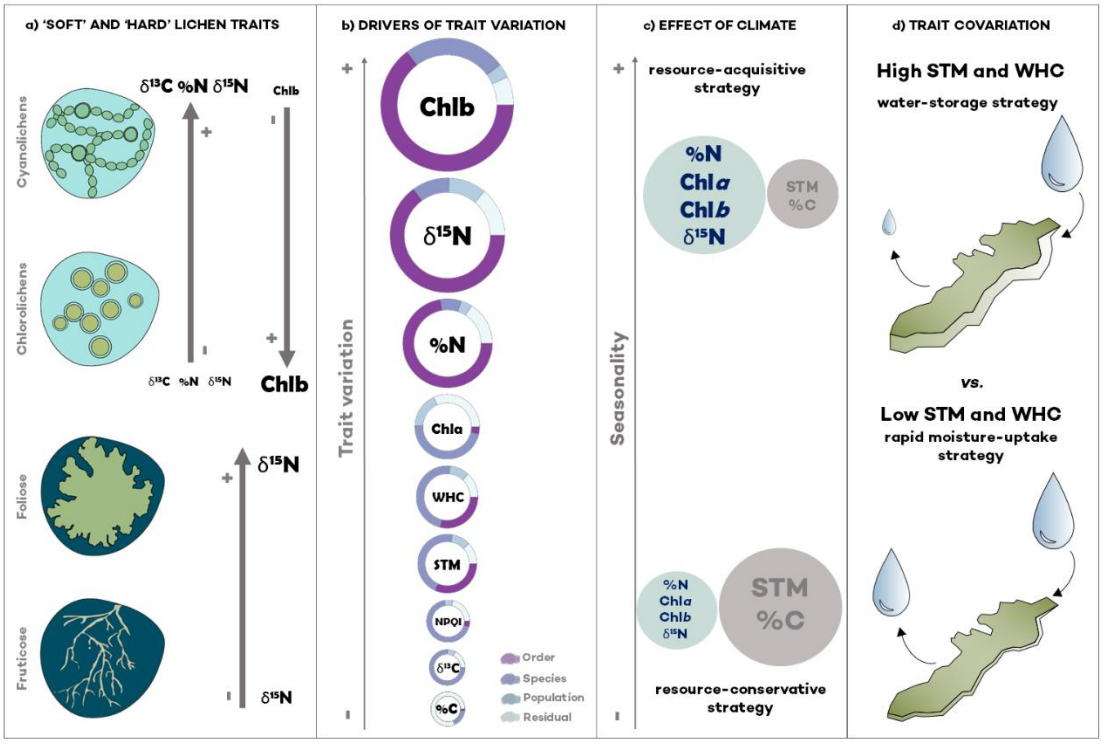

Figure 5. Summary of the main results. a) 'Soft' functional traits (type of photobiont and growth form) accounted for differences in Chlb, $\delta^{13}C$, %N, and $\delta^{15}N$. b) Amount and drivers behind functional trait variation. Circle size is proportional to the amount of trait variation and colours denote the contribution of different drivers to the overall variation accounted for each trait. c) Sites

with high temperature or precipitation seasonality harbour lichens with functional traits linked to a rapid resource-acquisitive strategy while a resource-conservative strategy predominate when seasonality is low. d) The positive covariation related with water-use strategies between STM and WHC was consistent among and within species. Abbreviations as in Fig. 2.

4.1. 'Soft' traits captured the variation of certain 'hard' physiological traits in epiphytic lichens

Our PGLS results corroborate that mean values of Chlb, %N, $\delta^{15}N$, and $\delta^{13}C$ differed with photobiont type while $\delta^{15}N$ also varied according to growth form, and these associations were not the result of phylogenetic relatedness. Previous studies have identified type of photobiont and growth form as easily noticeable traits with effects on nitrogen fixation and lichen nutrient status (Asplund & Wardle 2017).

Cyanolichens showed higher values of %N and $\delta^{15}N$ than chlorolichens due to the ability of cyanobionts to fix atmospheric nitrogen (Palmqvist et al. 1998). In addition, cyano- and chlorolichens also differed in their Chlb content and $\delta^{13}C$, likely as consequence of the photosynthetic activity of the photobiont. While the chloroplasts of the green algae contain Chla and Chlb pigments, the thylakoids of cyanobacteria, where photosynthesis occurs, lack Chlb (Palmqvist & Sundberg 2000). On the other hand, higher values of $\delta^{13}C$ in cyanolichens could reflect the presence of a carbon-concentrating mechanism, reducing the CO_2 limitation during the fixation and allowing the accumulation of inorganic carbon (Lakatos et al. 2007).

Surprisingly, the expected relationship between WHC and type of photobiont (i.e. higher WHC in cyanolichens than in chlorolichens) (Gauslaa et al. 2014, Merinero et al. 2014) was not detected. In turn, when we did not consider the phylogenetic relatedness among the species, this relationship was found (results not shown). This result highlights the importance of considering trait phylogenetic signal when functional variation is assessed (Cantalapiedra et al. 2014) and suggests that may be other attributes related with the photobiont (e.g. thickness of the photobiont layer) or with the mycobiont partner (e.g. development of cortex or rhizines) underpinning the water storage capability in lichens.

The growth form may influence the lichen interception of elements from the atmosphere (Branquinho 2001). Thus, fruticose lichens exhibited lower $\delta^{15}N$ than foliose broad-lobed and squamulose lichens. The low $\delta^{15}N$ may be related with the high surface-volume ratio in fruticose lichens (Branquinho 2001) providing a high number of cation exchange sites which help to take up high amounts of ammonium from the atmosphere (Hauck 2010).

Given that type of photobiont and growth form did not capture the differences in certain of the studied 'hard' traits, we stress the need for extending the lichen trait collection incorporating specific measurements of photosynthetic (i.e. Chla and NPQI), water use (i.e. STM and WHC) and nutrient acquisition (i.e. %C) traits along with type of photobiont and growth form traits.

4.2. Most functional trait variation occurred between orders and species

Our findings, together with previous studies on vascular plants (Messier et al. 2010; Vilà-Cabrera et al. 2015), suggest that trait variation drivers act at different scales. Most trait variation occurred at order and species level (i.e. among species), which point out a strong phylogenetic control shaping the variation of the studied traits. On the contrary, the population scale (i.e. within species) explained the lowest amount of variation, suggesting that the environmental conditions, or other factors such as genetic differences within species, had a low contribution to overall trait variation. Chlb, %N, and $\delta^{15}N$ showed consistent patterns of variance partitioning with variation mostly accounted among orders, which reflects the high conservatism of the photobiont partner within the three studied orders: Caliciales and Lecanorales with green algae versus Peltigerales with cyanobacteria (nitrogen-fixing without Chlb). Conversely, variation in Chla, NPQI, STM, WHC, and $\delta^{13}C$ was mainly observed at the species level, suggesting that the species-level quantification becomes necessary in these traits, which is particularly important in the case of STM and WHC since, so far, most studies have focused on differences within species or individuals.

Intraspecific variability (i.e. population level and residual) also accounted for a substantial and variable amount of trait variation, mainly in Chla and %C. Inter- and intraspecific variability had similar contribution to the overall variation in Chla, while %C variation was mostly distributed within populations. Consequently, our results support the general assumption that functional variation is higher among than within species, but also highlight the need to include the intraspecific variability as an important component of functional trait variation (Albert et al. 2010a).

4.3. Functional trait variation along environmental gradients responded to temperature and precipitation factors

Even though climatic drivers explained a low amount of the overall trait variation, seven of the nine lichen functional traits responded to temperature and precipitation factors. This result bears out the combined sensitivity of epiphytic lichens, which are poikilohydric organisms (without vascular tissues) tightly linked to atmospheric moisture conditions and

temperature (Prentice et al. 1992). In agreement with the modelled response for 26 species along the British Islands (Ellis et al. 2007), functional trait variation mainly responded to changes in temperature and precipitation seasonality rather than to total or average climatic values. These seasonal climatic effects may determine lichen physiological processes such as photosynthesis (Palmqvist & Sundberg 2000) or nitrogen-fixation (MacFarlane & Kershaw 1977). We found that increases in seasonality led to a shift from resource-conservative (e.g. high STM and %C) to resource-acquisitive strategies (e.g. high Chla, Chlb, %N, and $\delta^{15}N$). In this line, high seasonality may be related to longer periods in which lichens remain metabolically inactive leading to a reduction of photosynthetic capacity and, consequently, of net carbon gain (Palmqvist & Sundberg 2000). However, further research should be undertaken to investigate to what extent the lack of in-site climatic data may explain the observed small contribution of climatic drivers to the overall functional trait variation.

4.4. Patterns of trait covariation differed among and within species

According to our initial hypothesis, lichen functional traits covaried. Furthermore, we found that the patterns of covariation varied among and within species (Anderegg et al. 2018), with the exception of the consistent positive correlation observed between STM and WHC, showing a trade-off related with water use strategies. On the other hand, it was not possible to identify axes of variation reflecting different lichen ecological strategies in relation to photosynthetic performance and nutrient acquisition. Our study including 52 species and a wide environmental gradient, confirmed that lichens with thicker thallus tend to hold more water per unit area, both among and within species (Merinero et al. 2014, Esseen et al. 2015), implying a trade-off between rapid moisture-uptake (low STM and WHC) and conservative water-storage strategy (high STM and WHC) (Asplund & Wardle 2017). Besides, the key traits shaping the functional correlation networks differed among and within species, supporting that different constraints determine the functional correlation networks for the studied set of traits and species.

Our results did not show evidence of strong and consistent trait covariation defining overall resource use strategies. Further research including a wider set of functional traits and species, and integrating among and within-species trait comparisons, is needed to show the extent to which covariation between lichen traits can be used to identify major resource use strategies in lichens, as exemplified in vascular plants by the leaf economics spectrum.

5 | ACKNOWLEDGEMENTS

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6 | AUTHORS' CONTRIBUTIONS

IM, MP, GA and PH conceived the study. Fieldwork was done by PH, MP, IM, GA, PG, RB, EB, JN, AK, HM, SM and E-MD-P. Laboratory work was done by PH, E-MD-P and SM. Data were analysed by PH, JL-A and JM-V. Manuscript writing was led by PH and all authors provided critical reviews. All authors gave approval for submission of the final manuscript.

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8 | SUPPORTING INFORMATION

8.1. Appendix 1

Table S1. Environmental drivers for each surveyed forest.

Country	Forest	Longitude	Latitude	Altitude (m)	BIO1 (°C)	BIO4	BIO12 (mm)	BIO15	DBH (m)
Sweden	Biskopstorps Naturreservat	12.882	56.800	142	6.96	6354	1069	23.0	0.48
	Bjurkärrs Naturreservat	14.668	56.635	161	6.94	6489	658	22.0	0.52
	Ödegärdet Naturreservatet	13.530	56.966	197	6.68	6502	914	22.0	0.45
	Ramlaklitten i Skogsbo Naturreservat	12.558	57.076	108	7.46	6309	842	23.8	0.43
Slovakia	Klenovský Vepor	19.764	48.687	1233	3.86	7439	1065	30.4	0.58
	Národný park Muránska planina	20.061	48.762	900	6.20	7581	666	30.2	0.56
	Riaba Skala	22.449	49.102	1151	4.02	7484	1125	29.8	0.41
Austria	Nationalpark Kalkalpen	14.453	47.816	758	6.78	7049	1031	31.4	0.59
	Loibltal	14.268	46.461	1118	6.16	7197	1644	22.2	0.55
	Trögener Klamm	14.478	46.448	856	6.76	7247	1278	25.0	0.51
France	Chadefour Valley Nature Reserve	2.854	45.540	1182	6.12	5749	1032	12.2	0.54
	Réserve naturelle nationale de Chastreix-Sancy	2.886	45.495	1273	6.38	5769	1113	13.6	0.41
	Picherande	2.780	45.468	1200	6.82	5765	1354	13.0	0.38
Spain	La Selva de Irati	-1.163	42.992	856	9.90	5343	1332	24.2	0.52
	Parque Natural de Redes	-5.288	43.105	1237	8.70	4717	1174	30.6	0.62
	Parque Natural Saja-Besaya	-4.284	43.114	866	11.12	4557	925	25.2	0.45
	Sitio Natural de Interés Nacional del Hayedo de Montejo de la Sierra	-3.385	41.227	1542	9.42	6378	563	34.0	0.45
	Hayedo La Pedrosa	-3.493	41.112	1335	8.00	6231	681	30.0	0.42
	Parque Natural Sierra Norte de Guadalajara	-3.410	41.218	1604	7.10	6184	707	28.0	0.42
Italy	Parco Nazionale del Cilento e Valle de Diano	15.372	40.498	1213	8.96	6055	942	41.0	0.53
	Riserva Statale Serra Nicolino - Pian d'Albero	16.050	39.503	1078	10.98	5657	1089	46.8	0.47
	Foresta Umbra (Parco Nazionale del Gargano)	15.984	41.810	750	11.92	5793	618	20.4	0.61
	Foresta del Cansiglio	12.410	46.074	1080	6.96	6928	1427	20.4	0.50

Abbreviations: BIO1, Annual Mean Temperature; BIO4, Temperature Seasonality; BIO12, Annual Precipitation; BIO15, Precipitation Seasonality; DBH, mean diameter at breast height.

8.2. Appendix 2

Table S2. Lichen species found along the environmental gradient, with the total number of thalli collected per species and the number of forests where each species appeared.

Species	Number of thalli	Number of forests
Anaptychia ciliaris (L.) Körb.	17	6
Cetrelia olivetorum (Nyl.) W.L. Culb. & C.F. Culb.	46	12
Cladonia chlorophaea (Flörke ex Sommerf.) Spreng.	22	10
Cladonia coniocraea (Flörke) Spreng.	32	10
Cladonia fimbriata (L.) Fr.	18	8
Cladonia pyxidata (L.) Hoffm.	32	9
Collema flaccidum (Ach.) Ach.	39	7
Collema subnigrescens Degel.	11	4
Evernia prunastri (L.) Ach.	71	19
Heterodermia speciosa (Wulfen) Trevis.	5	3
Hypogymnia physodes (L.) Nyl.	50	17
Hypogymnia tubulosa (Schaer.) Hav.	16	5
Leptogium saturninum (Dicks.) Nyl.	10	5
Lobaria pulmonaria (L.) Hoffm.	80	20
Lobarina scrobiculata (Scop.) P. Gaertn.	25	7
Melanelixia fuliginosa (Fr. ex Duby) O. Blanco, A. Crespo, Divakar, Essl., D. Hawksw. & Lumbsch	65	19
Melanelixia subaurifera (Nyl.) O. Blanco, et al.	10	4
Melanohalea elegantula (Zahlbr.) O. Blanco, A. Crespo, Divakar, Essl., D. Hawksw. & Lumbsch	9	3
Melanohalea exasperatula (Nyl.) O. Blanco, A. Crespo, Divakar, Essl., D. Hawksw. & Lumbsch	6	3
Menegazzia terebrata (Hoffm.) A. Massal./ *Menegazzia subsimilis* (H. Magn.) R. Sant.*	19	4
Nephroma laevigatum Ach.	30	8
Nephroma parile (Ach.) Ach.	11	7
Nephroma resupinatum (L.) Ach.	30	7
Pannaria conoplea (Ach.) Bory	7	4
Parmelia saxatilis (L.) Ach.	78	20
Parmelia submontana Hale	18	3
Parmelia sulcata Taylor	75	19
Parmeliella triptophylla (Ach.) Müll.Arg.	27	8
Parmelina pastillifera (Harm.) Hale	5	3
Parmelina tiliacea (Hoffm.) Hale	46	11
Parmotrema perlatum (Huds.) M. Choisy	18	3
Pectenia plumbea (Lightf.) P.M. Jørg., L. Lindblom, Wedin & S. Ekman	10	4
Peltigera collina (Ach.) Schrad.	30	10
Peltigera horizontalis (Hudson) Baumg.	22	10
Peltigera membranacea (Ach.) Nyl.	15	7
Peltigera praetextata (Flörke ex Sommerf.) Zopf	70	19

Table S2 (continued)

Species	Number of thalli	Number of forests
Physconia distorta (With.) J.R.Laundon	30	6
Physconia perisidiosa (Erichsen) Moberg	10	6
Physconia venusta (Ach.) Poelt	13	6
Platismatia glauca (L.) W.L.Culb. & C.F.Culb.	70	13
Pseudevernia furfuracea (L.) Zopf	54	14
Ramalina farinacea (L.) Ach.	71	18
Ramalina fastigiata (Pers.) Ach.	18	8
Ramalina fraxinea (L.) Ach.	23	8
Ricasolia amplissima (Scop.) De Not.	24	7
Scytinium lichenoides (L.) Otálora, P.M. Jørg. & Wedin	13	5
Sphaerophorus globosus (Huds.) Vain.	20	6
Usnea dasopoga (Ach.) Nyl.	9	3
Usnea florida (L.) F.H. Wigg.	10	5
Usnea glabrescens (Vain.) Räsänen var. glabrescens	11	7
Usnea subfloridana Stirt.	26	9
Usnea wasmuthii Räsänen	9	3
Total	1486	23

* Most samples were *M.terebrata* but some samples showed intermediate characteristics between *M.terebrata* and *M.subsimilis.*

Notes: Grey colour denotes those species found, at least, in ten of the 23 beech forests surveyed. Nomenclature *sensu* Smith et al. (2009).

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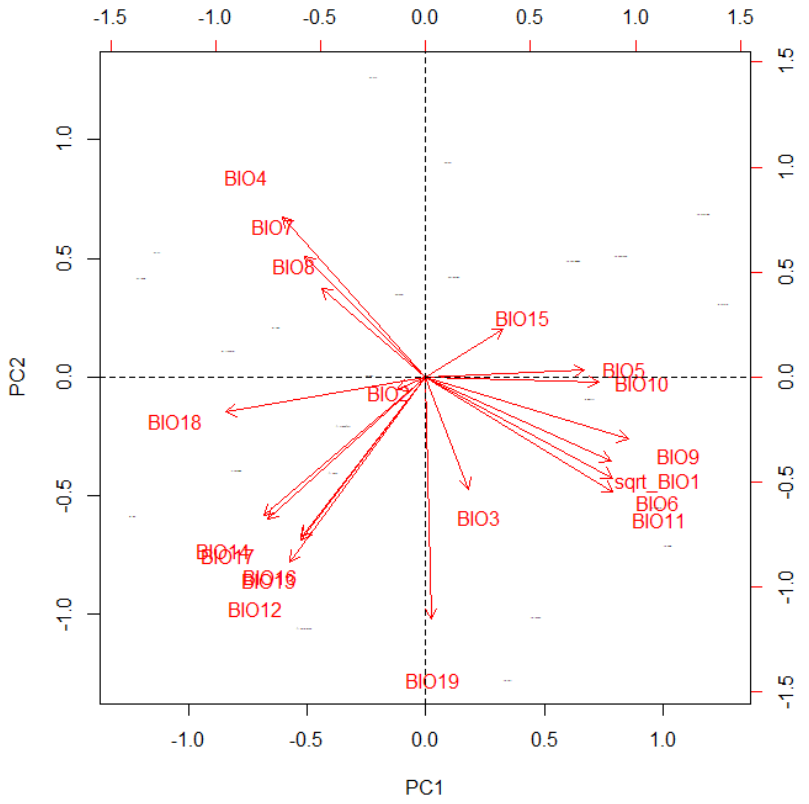
8.3. Appendix 3

Figure S1. Principal component analysis (PCA) summarizing climatic variables at the forest level. First and second axis explained the 68.11% of the variance explained. Specifically, axis 1 explained 45.2% of the variance and axis 2 explained 22.91% of the variance. Annual mean temperature (BIO1) were square-rooted transformed to satisfy the normality assumptions. Climatic variables: Annual Mean Temperature, BIO1; Annual Mean Diurnal Range, BIO2; Isothermality, BIO3; Temperature Seasonality, BIO4; Max Temperature of Warmest Month, BIO5; Min Temperature of Coldest Month, BIO6; Annual Temperature Range, BIO7; Mean Temperature of Wettest Quarter, BIO8; Mean Temperature od Driest Quarter, BIO9; Mean Temperature of Warmest Quarter, BIO10; Mean Temperature of Coldest Quarter, BIO11; Annual Precipitation, BIO12; Precipitation of Wettest Month, BIO13; Precipitation of Driest Month, BIO14; Precipitation Seasonality, BIO15; Precipitation of Wettest Quarter, BIO16; Precipitation of Driest Quarter, BIO17; Precipitation of Warmest Quarter, BIO18 and Precipitation of Coldest Quarter, BIO 19.



8.4. Appendix 4

Table S3. Functional traits values (category in categorical traits and mean in quantitative traits) for the 52 species found in the 23 forests surveyed.

Species	Photobiont	Growth form	Chla	Chlb	NPQI	STM	WHC	%C	%N	$\delta^{13}C$	$\delta^{15}N$
Anaptychia ciliaris	CHL	FR	0.90	0.19	1.41	12.18	19.29	42.71	0.88	-24.96	-12.94
Cetrelia olivetorum	CHL	FB	1.61	0.40	1.09	6.52	10.79	44.67	1.19	-25.04	-8.69
Cladonia chlorophaea	CHL	FR	1.45	0.48	0.98	-	-	41.79	1.05	-27.48	-8.49
Cladonia coniocraea	CHL	FR	1.46	0.48	1.02	-	-	41.20	1.04	-27.07	-8.21
Cladonia fimbriata	CHL	FR	1.47	0.50	0.99	-	-	41.37	0.99	-27.19	-8.05
Cladonia pyxidata	CHL	FR	1.47	0.50	1.01	-	-	40.95	0.92	-26.50	-8.68
Collema flaccidum	CB	FB	0.78	0.00	0.97	3.36	14.36	43.61	4.28	-23.12	-1.48
Collema subnigrescens	CB	FB	0.32	0.00	0.99	9.49	112.58	42.04	3.13	-22.71	-3.28
Evernia prunastri	CHL	FR	1.05	0.23	1.03	9.23	14.52	43.09	1.02	-24.05	-13.99
Heterodermia speciosa	CHL	FN	1.38	0.30	0.95	16.46	21.20	45.32	1.66	-26.47	-8.81
Hypogymnia physodes	CHL	FN	1.09	0.38	0.99	9.59	17.30	42.55	1.00	-25.13	-11.60
Hypogymnia tubulosa	CHL	FN	1.26	0.34	1.12	10.05	18.49	44.10	1.03	-24.69	-11.87
Leptogium saturninum	CB	FB	0.59	0.00	0.95	5.73	26.97	43.73	4.17	-20.40	-2.30
Lobaria pulmonaria	CHL	FB	1.36	0.31	1.31	11.95	21.06	44.32	2.22	-33.33	-4.12
Lobarina scrobiculata	CB	FB	0.89	0.00	1.29	12.39	25.45	45.01	2.78	-24.38	-2.70
Melanelixia fuliginosa	CHL	FN	1.29	0.55	1.23	9.00	15.62	42.38	1.65	-25.33	-8.74
Melanelixia subaurifera	CHL	FB	1.58	0.68	1.23	10.67	17.93	43.01	1.50	-25.25	-11.06
Melanohalea elegantula	CHL	FB	0.94	0.39	1.27	9.77	14.40	40.73	1.11	-24.41	-7.98
Melanohalea exasperatula	CHL	FB	1.48	0.65	1.28	7.78	15.77	41.19	1.95	-24.62	-7.91
Menegazzia terebrata/ Menegazzia subsimilis	CHL	FB	0.74	0.26	0.92	13.45	25.10	40.85	0.95	-25.33	-10.88
Nephroma laevigatum	CB	FB	1.46	0.00	1.33	5.70	12.95	43.95	3.24	-25.01	-3.87
Nephroma parile	CB	FB	1.60	0.00	1.30	6.53	14.83	45.72	3.91	-25.82	-2.15
Nephroma resupinatum	CB	FB	1.65	0.00	1.27	6.49	18.03	43.21	3.59	-24.11	-3.43
Pannaria conoplea	CB	FN	0.96	0.00	1.00	-	-	45.61	3.67	-27.03	-5.46
Parmelia saxatilis	CHL	FB	1.43	0.45	0.89	13.92	21.20	45.33	1.15	-25.27	-10.06
Parmelia submontana	CHL	FB	1.52	0.48	0.88	8.75	13.33	44.36	1.51	-24.66	-10.00
Parmelia sulcata	CHL	FB	1.20	0.45	0.87	10.93	17.47	44.83	1.04	-24.87	-10.32
Parmeliella triptophylla	CB	SQ	0.91	0.00	1.04	-	-	44.72	4.11	-24.93	-3.12
Parmelina pastillifera	CHL	FB	1.55	0.42	1.11	9.55	14.02	44.57	1.92	-23.93	-6.86
Parmelina tiliacea	CHL	FB	1.66	0.40	1.10	8.13	13.11	45.75	1.56	-25.11	-9.95
Parmotrema perlatum	CHL	FB	1.82	0.50	1.18	6.17	9.31	45.55	1.30	-25.19	-8.58
Pectenia plumbea	CB	FN	1.01	0.00	1.19	32.18	114.05	44.34	4.52	-23.92	-2.05
Peltigera collina	CB	FB	1.36	0.00	1.27	8.07	21.83	44.03	3.79	-24.70	-1.44
Peltigera horizontalis	CB	FB	1.31	0.00	1.25	8.13	23.95	43.44	3.85	-25.85	-2.83
Peltigera membranacea	CB	FB	1.30	0.00	1.37	9.59	26.13	43.51	4.12	-24.66	-2.18
Peltigera praetextata	CB	FB	1.51	0.00	1.38	8.88	24.49	43.29	4.23	-25.04	-1.94
Physconia distorta	CHL	FN	1.04	0.21	1.24	21.72	41.37	43.42	1.39	-23.45	-7.59
Physconia perisidiosa	CHL	FN	1.23	0.26	1.27	13.54	30.66	42.58	1.59	-24.84	-9.15

Table S3 (continued)

Species	Photobiont	Growth form	Chla	Chlb	NPQI	STM	WHC	%C	%N	$\delta^{13}C$	$\delta^{15}N$
Physconia venusta	CHL	FN	1.09	0.22	1.27	18.35	34.17	43.41	1.62	-24.07	-8.68
Platismatia glauca	CHL	FB	1.14	0.26	0.99	7.13	11.56	43.23	1.01	-23.32	-10.24
Pseudevernia furfuracea	CHL	FR	1.55	0.38	1.19	8.81	14.46	44.63	1.47	-25.24	-11.35
Ramalina farinacea	CHL	FR	0.91	0.22	1.21	11.46	15.68	42.38	1.28	-24.38	-11.19
Ramalina fastigiata	CHL	FR	1.08	0.30	1.40	13.77	21.31	43.10	1.14	-23.49	-12.68
Ramalina fraxinea	CHL	FR	0.93	0.17	1.41	15.07	25.40	42.19	1.07	-23.14	-12.42
Ricasolia amplissima	CHL	FB	0.99	0.21	1.28	16.87	28.61	42.84	2.18	-31.42	-2.76
Scytinium lichenoides	CB	SQ	0.38	0.00	1.33	-	-	42.67	3.06	-23.18	-4.92
Sphaerophorus globosus	CHL	FR	0.75	0.17	1.36	-	-	42.17	0.78	-23.28	-8.62
Usnea dasopoga	CHL	FRC	1.03	0.26	1.30	8.81	11.91	43.17	1.18	-25.64	-13.18
Usnea florida	CHL	FRC	0.84	0.19	1.30	9.70	13.04	43.49	1.16	-25.06	-13.71
Usnea glabrescens	CHL	FRC	1.20	0.25	1.36	10.76	14.27	43.42	1.28	-24.74	-14.27
Usnea subfloridana	CHL	FRC	1.07	0.25	1.27	11.12	15.57	44.04	1.37	-24.98	-13.58
Usnea wasmuthii	CHL	FRC	1.03	0.22	1.28	10.48	13.67	44.11	1.29	-23.86	-15.04

Abbreviations: 1) Type of photobiont: CB, cyanobacteria; CHL, chlorococcoid algae; 2) Growth form: FB, foliose broad-lobed; FN, foliose narrow-lobed; FR, fruticose; FRC, fruticose cylindrical and SQ, squamulose; 3) Quantitative traits: Chla, chlorophyll a content; Chlb, chlorophyll b content; NPQI, normalized phaeophytinization index; STM, specific thallus mass; WHC, water-holding capacity; %C, thallus carbon content; %N, nitrogen thallus content; $\delta^{13}C$, carbon isotopic ratio; $\delta^{15}N$, nitrogen isotopic ratio. Grey colour denotes those species found, at least, in ten of the 23 beech forests surveyed.

8.5. Appendix 5

Table S4. Sample size for each species and functional trait studied.

Species	Chla	Chlb	NPQI	STM	WHC	%C	%N	$\delta^{13}C$	$\delta^{15}N$
Anaptychia ciliaris	17	17	17	17	17	17	17	17	17
Cetrelia olivetorum	46	46	46	46	46	46	46	46	46
Cladonia chlorophaea	22	22	22	0	0	22	22	22	22
Cladonia coniocraea	32	32	32	0	0	32	32	32	32
Cladonia fimbriata	18	18	18	0	0	18	18	18	18
Cladonia pyxidata	32	32	32	0	0	32	32	32	32
Collema flaccidum	39	39	39	39	39	39	39	39	39
Collema subnigrescens	11	11	11	11	11	10	11	11	11
Evernia prunastri	71	71	71	71	71	71	71	71	71
Heterodermia speciosa	5	5	5	5	5	4	5	5	5
Hypogymnia physodes	50	50	50	50	50	50	50	50	50
Hypogymnia tubulosa	16	16	16	16	16	16	16	16	16
Leptogium saturninum	10	10	10	10	10	10	10	10	10
Lobaria pulmonaria	80	80	80	80	80	80	80	80	80
Lobarina scrobiculata	25	25	25	25	25	25	25	25	25
Melanelixia fuliginosa	65	65	65	65	65	64	65	65	65
Melanelixia subaurifera	10	10	10	10	10	10	10	10	10
Melanohalea elegantula	9	9	9	9	9	9	9	9	9
Melanohalea exasperatula	6	6	6	6	6	6	6	6	6
Menegazzia terebrata/ Menegazzia subsimilis	19	19	19	19	19	19	19	19	19
Nephroma laevigatum	30	30	30	30	30	30	30	30	30
Nephroma parile	11	11	11	11	11	11	11	11	11
Nephroma resupinatum	30	30	30	30	30	30	30	30	30
Pannaria conoplea	7	7	7	0	0	7	7	7	7
Parmelia saxatilis	78	78	78	78	78	77	77	77	77
Parmelia submontana	18	18	18	18	18	18	18	18	18
Parmelia sulcata	75	75	75	75	75	75	75	75	75
Parmeliella triptophylla	27	27	27	0	0	27	27	27	27
Parmelina pastillifera	5	5	5	5	5	5	5	5	5
Parmelina tiliacea	46	46	46	46	46	46	46	46	46
Parmotrema perlatum	18	18	18	18	18	18	18	18	18
Pectenia plumbea	10	10	10	10	10	10	10	10	9
Peltigera collina	30	30	30	30	30	30	30	30	30
Peltigera horizontalis	22	22	22	22	22	21	20	21	21
Peltigera membranacea	15	15	15	15	15	15	15	15	15
Peltigera praetextata	70	70	70	70	70	69	70	70	70
Physconia distorta	30	30	30	30	30	29	29	30	30
Physconia perisidiosa	10	10	10	9	9	10	10	10	10
Physconia venusta	13	13	13	13	13	13	13	13	13
Platismatia glauca	70	70	70	70	70	70	70	70	70
Pseudevernia furfuracea	54	54	54	54	54	54	54	54	54
Ramalina farinacea	71	71	71	71	71	71	70	71	71

Table S4 (continued)

Species	Chla	Chlb	NPQI	STM	WHC	%C	%N	$\delta^{13}C$	$\delta^{15}N$
Ramalina fastigiata	18	18	18	18	18	18	18	18	18
Ramalina fraxinea	23	23	23	23	23	23	23	23	23
Ricasolia amplissima	24	24	24	23	23	24	24	24	24
Scytinium lichenoides	13	13	13	0	0	13	13	13	13
Sphaerophorus globosus	20	20	20	0	0	20	20	20	20
Usnea dasopoga	9	9	9	9	9	9	9	9	9
Usnea florida	10	10	10	10	10	10	10	10	10
Usnea glabrescens	11	11	11	11	11	11	11	11	11
Usnea subfloridana	26	26	26	26	26	26	26	26	26
Usnea wasmuthii	9	9	9	9	9	9	9	9	9
Total	1486	1486	1486	1313	1313	1479	1481	1484	1483

Abbreviations: Chla, chlorophyll a content; Chlb, chlorophyll b content; NPQI, normalized phaeophytinization index; STM, specific thallus mass; WHC, water-holding capacity; %C, thallus carbon content; %N, nitrogen thallus content; $\delta^{13}C$, carbon isotopic ratio; $\delta^{15}N$, nitrogen isotopic ratio. Grey colour denotes those species found, at least, in ten of the 23 beech forests surveyed.

8.6. Appendix 6

Table S5. GenBank accession numbers for the molecular markers used in the phylogenetic analyses.

Lichens	**ITS**	**LSU**	**mtSSU**	**RPB1**
Anaptychia ciliaris	KJ027716	KX512894	EF582835	X
Cetrelia olivetorum	KU862940	DQ923659	GU994638	GU994693
Cladonia chlorophaea	DQ534460	EF489928	X	-
Cladonia coniocraea	KX132951	X	X	X
Cladonia fimbriata	FJ756726	X	X	-
Cladonia pyxidata	DQ534463	EF489926	X	-
Collema flaccidum	-	AY424213	EU982578	X
Collema subnigrescens	X	KJ766548	KJ766380	X
Evernia prunastri	EU266079	AF107562	KJ766390	KJ766909
Heterodermia speciosa	KX512927	KX512868	KX512975	-
Hypogymnia physodes	KX132937	JQ301600	AY756400	KJ766912
Hypogymnia tubulosa	KX132956	X	HQ690160	X
Leptogium saturninum	KJ409605	EU982610	AY340499	GQ259064
Lobaria pulmonaria	AF129285	AF183934	EU558813	DQ915597
Lobarina scrobiculata	AF350297	AY424205	EU558816	DQ883736
Melanelixia fuliginosa	KX132913	DQ986803	AY611173	DQ986860
Melanelixia subaurifera	KT695379	AJ421432	AY611156	JX126422
Melanohalea elegantula	AY611094	JQ813007	AY611151	JQ813986
Melanohalea exasperatula	JN943709	JQ813027	AY611147	JN987940
Menegazzia terebrata	KM250238	DQ899304	AY584624	DQ923694
Nephroma laevigatum	AY124143	HQ394194	AY124182	-
Nephroma parile	DQ066708	KX869862	AY124184	DQ973061
Nephroma resupinatum	DQ066710	AF286829	AY124168	-
Pannaria conoplea	FR799247	AY424209	X	-
Parmelia saxatilis	AF141370	JN939623	AY340514	DQ923695
Parmelia submontana	X	X	X	-
Parmelia sulcata	KX132926	JN939625	GU994669	GU994720
Parmeliella triptophylla	HM448804	GQ259008	GU570023	GQ259075
Parmelina pastillifera	JX466460	JN939630	EU562697	KR995501
Parmelina tiliacea	KX132912	JN939631	AF351173	KJ766917
Parmotrema perlatum	KX457691	AY584838	AY586580	EF092146
Pectenia plumbea	JX126708	DQ912347	AY340491	DQ912373
Peltigera collina	FJ708926	AF286765	-	FJ709112
Peltigera horizontalis	KX354708	KM005749	AY124163	FJ709130
Peltigera membranacea	FJ709033	KM005758	-	FJ709229
Peltigera praetextata	DQ001296	KM005766	AY124167	FJ709246
Physconia distorta	KX132933	AY773913	EF582813	-
Physconia perisidiosa	AJ421422	AY773911	EF582809	-
Physconia venusta	AY368147	X	EF582810	X
Platismatia glauca	AF072231	DQ973032	AY756404	DQ912363

Table S5 (continued)

Lichens	ITS	LSU	mtSSU	RPB1
Pseudevernia furfuracea	GU300783	KJ766637	GU300806	EF105435
Ramalina farinacea	JF923604	GU726354	KJ766480	KJ766831
Ramalina fastigiata	EU034669	GU726337	AY756375	KJ766832
Ramalina fraxinea	JF923610	X	X	-
Ricasolia amplissima	AF524924	AY424206	EU558806	GQ259065
Scytinium lichenoides	DQ466041	EU166331	AY340498	DQ917414
Sphaerophorus globosus	AY256775	DQ986767	AY256762	DQ986836
Usnea dasopoga	KJ947975	JN939699	-	JN992599
Usnea florida	FR799109	JN939703	-	JN992577
Usnea glabrescens	JN086308	KR995434	-	KU352036
Usnea subfloridana	JN086326	X	-	JN992586
Usnea wasmuthii	JN086336	X	-	JN992579

'X' indicate sequences that have been generated for this study and sequences not available are marked with dashed lines.

8.7. Appendix 7

Table S6. Summary of the PGLS linear models relating each functional trait with different types of photobionts or growth forms and phylogenetic signal for each trait (Pagel's Lambda).

		Chla	Chlb	NPQI	STM	WHC	%C	%N	$\delta^{13}C$	$\delta^{15}N$
Type of photobiont	*Lambda* (λ)	0.84	0.88	1	0.91	0.78	1	0.67	0.96	0.89
	F-value	0.92	10.14	0.004	0.35	1.06	0.99	26.87	26.68	4.75
	p-value	0.34	**0.002**	0.95	0.56	0.31	0.33	**$4 \cdot 10^{-6}$**	**$4 \cdot 10^{-6}$**	**0.03**
Growth form	*Lambda* (λ)	0.79	0.92	0.99	0.88	0.73	1	0.89	0.97	0.89
	F-value	1.26	1.34	1.32	0.82	1.41	0.07	0.68	0.06	6.35
	p-value	0.30	0.27	0.28	0.49	0.25	0.99	0.61	0.99	**$4 \cdot 10^{-4}$**
Pagel's Lambda		0.84	0.91	0.99	0.93	0.86	0.95	0.95	0.97	0.92

Lambda denote the strength of branch length transformation. Bold numbers indicate significant differences between groups ($P < 0.05$).

8.8. Appendix 8

Table S7. Summary of statistical descriptors for the functional traits.

	Chla	Chlb	NPQI	STM	WHC	%C	%N	$\delta^{13}C$	$\delta^{15}N$
Number of species	52	52	52	44	44	52	52	52	52
Sample size	1486	1486	1486	1313	1313	1479	1481	1484	1483
Mean	1.23	0.27	1.14	10.31	19.95	43.53	1.89	-25.33	-8.17
Min	0.05	0.00	0.33	2.50	6.60	19.11	0.32	-36.20	-20.15
Max	3.43	1.76	2.24	55.20	206.90	70.68	6.60	-18.53	1.35
Median	1.2	0.27	1.16	9.40	16.7	43.76	1.30	-24.88	-8.80
First Quartile	0.87	0.1	0.97	7.30	13.00	42.56	0.96	-25.96	-11.86
Third Quartile	1.55	0.41	1.31	12.00	22.00	45.03	2.50	-23.88	-3.43
QDC	0.28	0.61	0.15	0.24	0.26	0.03	0.45	0.04	0.55

Abbreviations: Chla, chlorophyll a content; Chlb, chlorophyll b content; NPQI, normalized phaeophytinization index; STM, specific thallus mass; WHC, water-holding capacity; %C, thallus carbon content; %N, nitrogen thallus content; $\delta^{13}C$, carbon isotopic ratio; $\delta^{15}N$, nitrogen isotopic ratio; QDC, quartile coefficient of dispersion.

8.9. Appendix 9

Table S8. Estimates from Phylogenetic Generalized Linear Mixed Models (PGLMMs) for 52 lichen species.

	BIO1		BIO4		BIO12		BIO15		lrtest
	Estimate	SD	Estimate	SD	Estimate	SD	Estimate	SD	
Chla	-	-	0.072	0.042	-	-	-	-	0.017*
Chla	-	-	-	-	-0.051	0.041	-	-	0.038*
Chlb	-0.014	0.005	-	-	-	-	-	-	0.009**
Chlb	-	-	0.015	0.006	-	-	-	-	0.016*
STM	-	-	-0.078	0.024	-	-	-	-	0.002**
%C	-	-	-	-	-	-	-0.004	0.002	0.036*
%N	-	-	0.047	0.020	-	-	-	-	0.026*
$\delta^{13}C$	0.220	0.091	-	-	-	-	-	-	0.020*
$\delta^{15}N$	-	-	-	-	-	-	0.531	0.208	0.015*

For each functional trait, climatic variables (BIO1, BIO12, BIO4, and BIO15) were used as fixed factors and species, forest, and phylogenetic covariance as random factors on the intercept. *lrtest* shows the results of likelihood-ratio tests used to assess the significance of fixed effects, $*P < 0.05$; $**P < 0.01$. We $\log_e$-transformed the traits Chla, Chlb, STM, WHC, %C, and %N to meet normality. Abbreviations: BIO1, Annual Mean Temperature; BIO4, Temperature Seasonality; BIO12, Annual Precipitation; BIO15, Precipitation Seasonality; Chla, chlorophyll a content; Chlb, chlorophyll b content; STM, specific thallus mass; %C, thallus carbon content; %N, nitrogen thallus content; $\delta^{13}C$, carbon isotopic ratio; $\delta^{15}N$, nitrogen isotopic ratio.

8.10. Appendix 10

Table S9. Trait-trait correlation matrices for all lichen species (n = 52, phylogenetically informed correlation analysis) and for the 16 most common species separately (Pearson correlation).

All species									
	Chla	**Chlb**	**NPQI**	**STM**	**WHC**	**%C**	**%N**	**$\delta^{13}C$**	**$\delta^{15}N$**
Chla	1.00	0.82*	0.94*	-0.96*	-0.96*	0.00	0.96*	-0.95*	-0.94*
Chlb	0.82*	1.00	0.78*	-0.80*	-0.79*	0.00	0.82*	-0.77*	-0.76*
NPQI	0.94*	0.78*	1.00	-0.98*	-0.98*	0.00	0.98*	-0.98*	-0.98*
STM	-0.96*	-0.80*	-0.98*	1.00	1.00*	0.00	-0.99*	0.99*	0.99*
WHC	-0.96*	-0.79*	-0.98*	1.00*	1.00	0.00	-0.99*	0.99*	0.99*
%C	0.00	0.00	0.00	0.00	0.00	1.00	0.00	0.00	0.00
%N	0.96*	0.82*	0.98*	-0.99*	-0.99*	0.00	1.00*	-0.99*	-0.99*
$\delta^{13}C$	-0.95*	-0.77*	-0.98*	0.99*	0.99*	0.00	-0.99*	1.00*	0.99*
$\delta^{15}N$	-0.94*	-0.76*	-0.98*	0.99*	0.99*	0.00	-0.99*	0.99*	1.00
Cladonia chlorophaea									
Chla	1.00	0.92*	0.22	-	-	0.15	0.66*	-0.64*	0.36
Chlb	0.92*	1.00	-0.02	-	-	0.29	0.85*	-0.64*	0.60
NPQI	0.22	-0.02	1.00	-	-	-0.42	-0.20	-0.43	-0.52
STM	-	-	-	-	-	-	-	-	-
WHC	-	-	-	-	-	-	-	-	-
%C	0.15	0.29	-0.42	-	-	1.00	0.48	-0.27	0.36
%N	0.66*	0.85*	-0.20	-	-	0.48	1.00	-0.59	0.82*
$\delta^{13}C$	-0.64*	-0.64*	-0.43	-	-	-0.27	-0.59	1.00	-0.20
$\delta^{15}N$	0.36	0.60	-0.52	-	-	0.36	0.82*	-0.20	1.00
Cladonia coniocraea									
Chla	1.00	0.95*	-0.35	-	-	0.90*	0.80*	-0.79*	0.13
Chlb	0.95*	1.00	-0.43	-	-	0.88*	0.82*	-0.73*	0.20
NPQI	-0.35	-0.43	1.00	-	-	-0.36	-0.53	0.19	-0.37
STM	-	-	-	-	-	-	-	-	-
WHC	-	-	-	-	-	-	-	-	-
%C	0.90*	0.88*	-0.36	-	-	1.00	0.86*	-0.69*	0.16
%N	0.80*	0.82*	-0.53	-	-	0.86*	1.00	-0.62	0.37
$\delta^{13}C$	-0.79*	-0.73*	0.19	-	-	-0.69*	-0.62	1.00	-0.31
$\delta^{15}N$	0.13	0.20	-0.37	-	-	0.16	0.37	-0.31	1.00

Table S9 (continued)

Evernia prunastri									
	Chla	**Chlb**	**NPQI**	**STM**	**WHC**	**%C**	**%N**	**$\delta^{13}C$**	**$\delta^{15}N$**
Chla	1.00	0.74*	0.85*	-0.30	0.14	0.10	0.83*	-0.01	-0.10
Chlb	0.74*	1.00	0.59*	-0.36	-0.07	0.00	0.51*	-0.21	0.32
NPQI	0.85*	0.59*	1.00	-0.36	0.10	0.23	0.72*	-0.10	-0.19
STM	-0.30	-0.36	-0.36	1.00	0.58*	-0.34	-0.30	0.18	-0.35
WHC	0.14	-0.07	0.10	0.58*	1.00	-0.02	0.00	-0.12	-0.03
%C	0.10	0.00	0.23	-0.34	-0.02	1.00	0.05	-0.38	0.11
%N	0.83*	0.51*	0.72*	-0.30	0.00	0.05	1.00	-0.09	-0.12
$\delta^{13}C$	-0.01	-0.21	-0.10	0.18	-0.12	-0.38	-0.09	1.00	-0.58*
$\delta^{15}N$	-0.10	0.32	-0.19	-0.35	-0.03	0.11	-0.12	-0.58*	1.00
Pseudevernia furfuracea									
Chla	1.00	0.82*	0.66*	-0.53*	-0.20	0.01	0.57*	-0.10	0.37
Chlb	0.82*	1.00	0.20	-0.49	-0.33	0.00	0.47	-0.21	0.56*
NPQI	0.66*	0.20	1.00	-0.30	-0.05	0.05	0.22	0.10	-0.17
STM	-0.53*	-0.49	-0.30	1.00	0.75*	0.21	-0.69*	0.45	-0.32
WHC	-0.20	-0.33	-0.05	0.75*	1.00	0.07	-0.53*	0.58*	0.02
%C	0.01	0.00	0.05	0.21	0.07	1.00	0.21	-0.20	-0.32
%N	0.57*	0.47	0.22	-0.69*	-0.53*	0.21	1.00	-0.49	0.13
$\delta^{13}C$	-0.10	-0.21	0.10	0.45	0.58*	-0.20	-0.49	1.00	-0.19
$\delta^{15}N$	0.37	0.56*	-0.17	-0.32	0.02	-0.32	0.13	-0.19	1.00
Ramalina farinacea									
Chla	1.00	0.84*	0.22	-0.51*	-0.27	-0.01	0.72*	-0.36	-0.09
Chlb	0.84*	1.00	-0.05	-0.59*	-0.36	0.15	0.70*	-0.45	0.10
NPQI	0.22	-0.05	1.00	-0.28	-0.12	-0.14	0.16	-0.22	0.30
STM	-0.51*	-0.59*	-0.28	1.00	0.82*	-0.11	-0.72*	0.69*	-0.29
WHC	-0.27	-0.36	-0.12	0.82*	1.00	-0.24	-0.47	0.72*	-0.28
%C	-0.01	0.15	-0.14	-0.11	-0.24	1.00	-0.18	-0.33	0.15
%N	0.72*	0.70*	0.16	-0.72*	-0.47	-0.18	1.00	-0.74*	0.13
$\delta^{13}C$	-0.36	-0.45	-0.22	0.69*	0.72*	-0.33	-0.74*	1.00	-0.52*
$\delta^{15}N$	-0.09	0.10	0.30	-0.29	-0.28	0.15	0.13	-0.52*	1.00
Hypogymnia physodes									
Chla	1.00	0.29	0.72*	-0.53*	-0.21	0.41	0.65*	0.05	0.36
Chlb	0.29	1.00	-0.03	-0.42	-0.53*	0.06	0.30	-0.34	0.08
NPQI	0.72*	-0.03	1.00	-0.32	-0.23	0.50*	0.46	-0.17	0.13
STM	-0.53*	-0.42	-0.32	1.00	0.84*	-0.42	-0.32	0.17	-0.64*
WHC	-0.21	-0.53*	-0.23	0.84*	1.00	-0.25	-0.13	0.41	-0.43
%C	0.41	0.06	0.50*	-0.42	-0.25	1.00	0.49*	0.15	0.24
%N	0.65*	0.30	0.46	-0.32	-0.13	0.49*	1.00	0.18	0.14
$\delta^{13}C$	0.05	-0.34	-0.17	0.17	0.41	0.15	0.18	1.00	0.40
$\delta^{15}N$	0.36	0.08	0.13	-0.64*	-0.43	0.24	0.14	0.40	1.00

Table S9 (continued)

Melanelixia fuliginosa									
	Chla	**Chlb**	**NPQI**	**STM**	**WHC**	**%C**	**%N**	**δ^{13}C**	**δ^{15}N**
Chla	1.00	0.56*	-0.23	-0.34	0.06	-0.08	0.42	-0.33	-0.02
Chlb	0.56*	1.00	-0.25	-0.22	0.02	-0.05	0.30	-0.18	0.06
NPQI	-0.23	-0.25	1.00	0.03	-0.34	0.17	0.17	0.18	0.31
STM	-0.34	-0.22	0.03	1.00	0.76*	-0.20	-0.26	0.51*	-0.28
WHC	0.06	0.02	-0.34	0.76*	1.00	-0.13	-0.21	0.26	-0.49*
%C	-0.08	-0.05	0.17	-0.20	-0.13	1.00	0.44	0.04	0.11
%N	0.42	0.30	0.17	-0.26	-0.21	0.44	1.00	-0.32	0.51*
δ^{13}C	-0.33	-0.18	0.18	0.51*	0.26	0.04	-0.32	1.00	-0.47*
δ^{15}N	-0.02	0.06	0.31	-0.28	-0.49*	0.11	0.51*	-0.47*	1.00
Cetrelia olivetorum									
Chla	1.00	0.82*	0.90*	-0.25	0.08	0.14	0.76*	-0.35	0.12
Chlb	0.82*	1.00	0.64*	0.08	0.34	0.43	0.67*	-0.07	-0.03
NPQI	0.90*	0.64*	1.00	-0.51	-0.22	0.03	0.62*	-0.55	-0.03
STM	-0.25	0.08	-0.51	1.00	0.92*	0.15	-0.05	0.53	-0.06
WHC	0.08	0.34	-0.22	0.92*	1.00	0.24	0.28	0.37	0.04
%C	0.14	0.43	0.03	0.15	0.24	1.00	0.42	0.25	-0.26
%N	0.76*	0.67*	0.62*	-0.05	0.28	0.42	1.00	-0.06	0.39
δ^{13}C	-0.35	-0.07	-0.55	0.53	0.37	0.25	-0.06	1.00	0.39
δ^{15}N	0.12	-0.03	-0.03	-0.06	0.04	-0.26	0.39	0.39	1.00
Lobaria pulmonaria									
Chla	1.00	0.47*	0.01	-0.50*	-0.18	-0.50*	0.09	-0.52*	0.33
Chlb	0.47*	1.00	-0.46*	-0.55*	-0.36	-0.05	-0.19	-0.35	-0.04
NPQI	0.01	-0.46*	1.00	0.36	0.10	0.04	0.39	0.23	-0.09
STM	-0.50*	-0.55*	0.36	1.00	0.85*	0.30	0.07	0.71*	0.18
WHC	-0.18	-0.36	0.10	0.85*	1.00	0.23	-0.06	0.46*	0.45*
%C	-0.50*	-0.05	0.04	0.30	0.23	1.00	0.07	0.29	-0.36
%N	0.09	-0.19	0.39	0.07	-0.06	0.07	1.00	-0.13	-0.17
δ^{13}C	-0.52*	-0.35	0.23	0.71*	0.46*	0.29	-0.13	1.00	0.04
δ^{15}N	0.33	-0.04	-0.09	0.18	0.45*	-0.36	-0.17	0.04	1.00
Parmelia saxatilis									
Chla	1.00	0.82*	0.61*	-0.09	0.10	-0.63*	0.89*	-0.27	-0.02
Chlb	0.82*	1.00	0.46*	-0.10	0.06	-0.49*	0.79*	-0.15	-0.04
NPQI	0.61*	0.46*	1.00	-0.40	-0.29	-0.41	0.54*	-0.15	-0.16
STM	-0.09	-0.10	-0.40	1.00	0.96*	-0.12	0.00	0.40	0.01
WHC	0.10	0.06	-0.29	0.96*	1.00	-0.25	0.16	0.36	0.06
%C	-0.63*	-0.49*	-0.41	-0.12	-0.25	1.00	-0.49*	0.01	-0.13
%N	0.89*	0.79*	0.54*	0.00	0.16	-0.49*	1.00	-0.01	0.00
δ^{13}C	-0.27	-0.15	-0.15	0.40	0.36	0.01	-0.01	1.00	0.05
δ^{15}N	-0.02	-0.04	-0.16	0.01	0.06	-0.13	0.00	0.05	1.00

Table S9 (continued)

Parmelia sulcata									
	Chla	**Chlb**	**NPQI**	**STM**	**WHC**	**%C**	**%N**	**$\delta^{13}C$**	**$\delta^{15}N$**
Chla	1.00	0.25	0.10	-0.39	-0.12	-0.67*	0.89*	0.33	0.48*
Chlb	0.25	1.00	0.05	0.16	0.36	-0.29	0.21	0.42	-0.03
NPQI	0.10	0.05	1.00	-0.35	-0.01	0.30	-0.01	-0.19	-0.48*
STM	-0.39	0.16	-0.35	1.00	0.67*	0.40	-0.26	0.24	-0.07
WHC	-0.12	0.36	-0.01	0.67*	1.00	0.31	-0.08	0.23	-0.05
%C	-0.67*	-0.29	0.30	0.40	0.31	1.00	-0.66*	-0.33	-0.48*
%N	0.89*	0.21	-0.01	-0.26	-0.08	-0.66*	1.00	0.48*	0.32
$\delta^{13}C$	0.33	0.42	-0.19	0.24	0.23	-0.33	0.48*	1.00	0.32
$\delta^{15}N$	0.48*	-0.03	-0.48*	-0.07	-0.05	-0.48*	0.32	0.32	1.00
Parmelina tiliacea									
Chla	1.00	0.68*	0.89*	-0.44	0.10	0.04	0.38	0.23	-0.07
Chlb	0.68*	1.00	0.47	-0.55	-0.35	0.14	0.37	-0.14	0.04
NPQI	0.89*	0.47	1.00	-0.38	0.13	-0.20	0.03	0.28	-0.08
STM	-0.44	-0.55	-0.38	1.00	0.80*	0.44	0.15	0.35	-0.29
WHC	0.10	-0.35	0.13	0.80*	1.00	0.43	0.36	0.70*	-0.40
%C	0.04	0.14	-0.20	0.44	0.43	1.00	0.68*	-0.10	-0.71*
%N	0.38	0.37	0.03	0.15	0.36	0.68*	1.00	0.19	-0.18
$\delta^{13}C$	0.23	-0.14	0.28	0.35	0.70*	-0.10	0.19	1.00	0.03
$\delta^{15}N$	-0.07	0.04	-0.08	-0.29	-0.40	-0.71*	-0.18	0.03	1.00
Platismatia glauca									
Chla	1.00	0.93*	0.88*	-0.64*	-0.37	0.09	0.72*	0.02	0.54
Chlb	0.93*	1.00	0.82*	-0.63*	-0.23	0.06	0.66*	-0.05	0.74*
NPQI	0.88*	0.82*	1.00	-0.63*	-0.39	0.17	0.78*	0.01	0.48
STM	-0.64*	-0.63*	-0.63*	1.00	0.77*	-0.06	-0.51	-0.20	-0.19
WHC	-0.37	-0.23	-0.39	0.77*	1.00	-0.29	-0.36	-0.30	0.33
%C	0.09	0.06	0.17	-0.06	-0.29	1.00	0.52	0.10	-0.10
%N	0.72*	0.66*	0.78*	-0.51	-0.36	0.52	1.00	-0.26	0.36
$\delta^{13}C$	0.02	-0.05	0.01	-0.20	-0.30	0.10	-0.26	1.00	-0.19
$\delta^{15}N$	0.54	0.74*	0.48	-0.19	0.33	-0.10	0.36	-0.19	1.00
Peltigera collina									
Chla	1.00	-	0.47	-0.61	-0.57	-0.04	0.56	-0.23	-0.52
Chlb	-	1.00	-	-	-	-	-	-	-
NPQI	0.47	-	1.00	-0.34	-0.39	0.16	0.09	-0.18	-0.17
STM	-0.61	-	-0.34	1.00	0.98*	-0.51	-0.62*	0.71*	0.54
WHC	-0.57	-	-0.39	0.98*	1.00	-0.48	-0.50	0.74*	0.52
%C	-0.04	-	0.16	-0.51	-0.48	1.00	0.54	-0.62	-0.19
%N	0.56	-	0.09	-0.62*	-0.50	0.54	1.00	-0.30	-0.12
$\delta^{13}C$	-0.23	-	-0.18	0.71*	0.74*	-0.62	-0.30	1.00	0.65*
$\delta^{15}N$	-0.52	-	-0.17	0.54	0.52	-0.19	-0.12	0.65*	1.00

Table S9 (continued)

Peltigera horizontalis									
	Chla	**Chlb**	**NPQI**	**STM**	**WHC**	**%C**	**%N**	**δ^{13}C**	**δ^{15}N**
Chla	1.00	-	0.18	-0.79*	-0.50	-0.18	0.28	-0.56	-0.64
Chlb	-	1.00	-	-	-	-	-	-	-
NPQI	0.18	-	1.00	0.01	0.03	0.01	0.64	0.39	-0.03
STM	-0.79*	-	0.01	1.00	0.76*	0.44	-0.27	0.74*	0.24
WHC	-0.50	-	0.03	0.76*	1.00	0.37	-0.33	0.43	-0.18
%C	-0.18	-	0.01	0.44	0.37	1.00	0.03	0.22	-0.24
%N	0.28	-	0.64	-0.27	-0.33	0.03	1.00	0.40	0.78*
δ^{13}C	-0.56	-	0.39	0.74*	0.43	0.22	0.40	1.00	0.35
δ^{15}N	-0.64*	-	-0.03	0.24	-0.18	-0.24	0.78*	0.35	1.00
Peltigera praetextata									
Chla	1.00	-	0.32	-0.81*	-0.75*	-0.10	0.12	-0.60*	-0.20
Chlb	-	1.00	-	-	-	-	-	-	-
NPQI	0.32	-	1.00	-0.48*	-0.57*	-0.44	-0.19	-0.14	0.08
STM	-0.81*	-	-0.48*	1.00	0.96*	0.30	-0.10	0.54*	0.09
WHC	-0.75*	-	-0.57*	0.96*	1.00	0.27	-0.07	0.51*	0.03
%C	-0.10	-	-0.44	0.30	0.27	1.00	0.70*	-0.17	-0.28
%N	0.12	-	-0.19	-0.10	-0.07	0.70*	1.00	-0.42	-0.49*
δ^{13}C	-0.60*	-	-0.14	0.54*	0.51*	-0.17	-0.42	1.00	0.57*
δ^{15}N	-0.20	-	0.08	0.09	0.03	-0.28	-0.49*	0.57*	1.00

Astherisks (*) denote significant correlations ($P < 0.05$). We $\log_e$-transformed the traits Chla, Chlb, STM, WHC, %C, and %N to meet normality. Abbreviations: Chla, chlorophyll a content; Chlb, chlorophyll b content; NPQI, normalized phaeophytinization index; STM, specific thallus mass; WHC, water-holding capacity; %C, thallus carbon content; %N, nitrogen thallus content; δ^{13}C, carbon isotopic ratio; δ^{15}N, nitrogen isotopic ratio.

8.11. Appendix 11

Table S10. Network descriptors across species (n = 52) including the phylogenetic relatedness among species and for each species separately.

	Descriptor	Chla	Chlb	NPQI	STM	WHC	%C	%N	$\delta^{13}C$	$\delta^{15}N$	Overall network
All species with phylogeny included	*Dw*	6.54	5.54	6.63	6.72	6.70	0	6.72	6.66	6.65	52.17
	D	7	7	7	7	7	0	7	7	7	56
Cetrelia olivetorum	*Dw*	2.47	2.13	2.16	0.92	0.92	0.00	2.05	0.00	0.00	10.66
	D	3	3	3	1	1	0	3	0	0	14
Cladonia chlorophaea	*Dw*	2.21	2.40	0.00	-	-	0.00	2.33	1.28	0.82	9.05
	D	3	3	0	-	-	0	3	2	1	12
Cladonia coniocraea	*Dw*	3.45	3.40	0.00	-	-	3.34	2.48	2.22	0.00	14.89
	D	4	4	0	-	-	4	3	3	0	18
Evernia prunastri	*Dw*	2.43	1.83	2.16	0.58	0.58	0.00	2.06	0.58	0.58	10.78
	D	3	3	3	1	1	0	3	1	1	16
Hypogymnia physodes	*Dw*	1.89	0.53	1.22	2.01	1.36	0.99	1.14	0.00	0.64	9.78
	D	3	1	2	3	2	2	2	0	1	16
Lobaria pulmonaria	*Dw*	1.98	1.48	0.46	2.61	1.76	0.50	0.00	1.69	0.45	10.93
	D	4	3	1	4	3	1	0	3	1	20
Melanelixia fuliginosa	*Dw*	0.56	0.56	0.00	1.27	1.25	0.00	0.51	0.98	1.47	6.61
	D	1	1	0	2	2	0	1	2	3	12
Parmelia saxatilis	*Dw*	2.95	2.56	1.62	0.96	0.96	1.61	2.71	0.00	0.00	13.37
	D	4	4	3	1	1	3	4	0	0	20
Parmelia sulcata	*Dw*	2.04	0	0.48	0.67	0.67	1.81	2.02	0.48	1.45	9.63
	D	3	0	1	1	1	3	3	1	3	16
Parmelina tiliacea	*Dw*	1.57	0.68	0.89	0.80	1.49	1.39	0.68	0.70	0.71	8.91
	D	2	1	1	1	2	2	1	1	1	12
Peltigera collina	*Dw*	0	-	0	2.31	1.72	0	0.62	2.09	0.65	7.39
	D	0	-	0	3	2	0	1	3	1	10
Peltigera horizontalis	*Dw*	1.43	-	0	2.29	0.76	0	0.78	0.74	1.42	7.41
	D	2	-	0	3	1	0	1	1	2	10
Peltigera praetextata	*Dw*	2.17	-	1.05	2.79	2.79	0.70	1.19	2.22	1.05	13.97
	D	3	-	2	4	4	1	2	4	2	22
Platismatia glauca	*Dw*	3.16	3.78	3.11	2.66	0.77	0.00	2.16	0.00	0.74	16.37
	D	4	5	4	4	1	0	3	0	1	22
Pseudevernia furfuracea	*Dw*	2.59	1.38	0.66	1.97	1.86	0.00	1.79	0.58	0.56	11.38
	D	4	2	1	3	3	0	3	1	1	18
Ramalina farinacea	*Dw*	2.08	2.13	0.00	3.32	1.54	0.00	2.88	2.67	0.52	15.14
	D	3	3	0	5	2	0	4	4	1	22

Abbreviations: Chla, chlorophyll a content; Chlb, chlorophyll b content; NPQI, normalized phaeophytinization index; STM, specific thallus mass; WHC, water-holding capacity; %C, thallus carbon content; %N, nitrogen thallus content; $\delta^{13}C$, carbon isotope ratio; $\delta^{15}N$, nitrogen isotope ratio; Dw, weighted degree; D, degree

Capítulo 5

Are functional, phylogenetic and taxonomic optimal climatic niches congruent along a continent-wide latitudinal gradient?

Pilar Hurtado | Paula Matos | Gregorio Aragón | Cristina Branquinho | María Prieto | Isabel Martínez

En Preparación

ABSTRACT

Aim

Identifying the optimal climatic conditions where lichen epiphytic communities maximize their functional, phylogenetic and taxonomic diversity to compare whether the optimal niches of the different facets of biodiversity are congruent or mismatch.

Location

Twenty-three beech forests comprising the whole distribution area of *Fagus sylvatica* L., from southern Sweden to southern Italy.

Time period

Present.

Major taxa studied

Fifty-eight epiphytic macrolichen species.

Methods

Using a wide climatic gradient along Europe we quantified the functional, phylogenetic and taxonomic diversity of lichen communities. We surveyed 23 beech forests and we ordinated 22 environmental variables. We then simultaneously illustrated non-parametric regressions of the diversity metrics against the climatic space using the 'hilltop plot' method to detect the climatic conditions in which the different diversity metrics peaked and to compare the congruency between the diversity facets.

Results

Functional diversity seemed to predict peaks of phylogenetic and taxonomic diversity, but phylogenetic and taxonomic hotspots did not overlap. Lichen communities maximized their functional and phylogenetic diversity in the southernmost forests, with the Mediterranean region appearing as a biodiversity hotspot. Regarding the specific traits studied, type of photobiont and growth form showed clearly defined optimal niches while the 'hard' traits and families' optimums did not show this pattern in response to the climatic conditions.

Main conclusions

All facets of biodiversity were not surrogates for the others highlighting the need of an integrative approach to assess the effect of environmental changes on communities. As functional traits mediated the response of lichen communities to climate, preserving high functional diversity might indirectly preserve high phylogenetic and taxonomic diversity. Relevant ecological indicators useful to develop rapid assessment methods to evaluate the effects of climatic changes include type of photobiont (with cyanolichens comprising three categories) and growth form. The lack of relation between 'hard' traits and climate call for further research to unveil their role as ecological indicators of small-scale variables or as effect traits.

Key words

Beech forests, climate, environmental gradient, functional diversity, functional traits, hotspot, lichens, optimal niches, phylogenetic diversity, taxonomic diversity.

1 | INTRODUCTION

Spatial variation in biodiversity provides critical information about the response of natural communities in a changing world, but biodiversity is a complex and multidimensional concept implying that a pluralistic approach is necessary to characterize its spatial variation (Swenson 2011, Stevens & Gavilanez 2015). Patterns of functional (Petchey & Gaston 2006) and phylogenetic diversity (Webb et al. 2002, Gerhold et al. 2015) can complement the commonly analysed patterns of taxonomic diversity (i.e. species richness) to give a more realistic picture of the communities' dynamic (Pavoine & Bonsall 2011). These three dimensions of biodiversity may respond to environmental gradients in different ways (Devictor et al. 2010, Purschke et al. 2013, Arnan et al. 2016, Hurtado et al. 2019), providing complementary information about the effect of environmental changes. Furthermore, communities that are taxonomic, functional or phylogenetically more diverse tend to maintain more ecosystem functions and to ensure more resilient ecosystems (Mouillot et al. 2013, Lefcheck et al. 2015). Therefore, exploring the patterns of taxonomic, functional and phylogenetic diversity along wide environmental gradients is crucial to unveil the optimal conditions where communities show their maximum values of diversity (i.e. biodiversity hotspots). These optimums may be important to assess the impacts of the environmental changes, to identify meaningful ecological indicators, and to propose effective management policies that minimize such impacts on the ecosystem functioning.

Many biotic and abiotic factors determine the distribution of species (Soberón 2007) being climate, among such factors, one of the major drivers shaping the species distributional ranges at large spatial scales (Thuiller et al. 2004). Based on the concept that ecological niches reflect the range of ecological conditions in which a certain species can establish populations (Grinnell 1924), the particular climatic conditions where communities maximize their diversity values could be considered as their taxonomic, functional and phylogenetic 'optimal niches'. The studies assessing the relationships between environment and communities integrating taxonomic, functional and phylogenetic approaches are mainly focused on vascular plants and animals (Devictor et al. 2010, Purschke et al. 2013, Arnan et al. 2016), but much less is known about other widely distributed organisms such as lichens. Lichens are poikilohydric organisms whose water content passively varies with surrounding environmental conditions, which also lacks mechanisms to control nutrient content or gas exchange (Nash 2008). These characteristics place them among the most sensitive organisms to environmental changes and as excellent early-warning ecological indicators for other less sensitive organisms thriving in the ecosystems (Pinho et al. 2014, Matos et al. 2015).

The use of functional traits has gain importance for evaluating the impact of environmental changes on communities (Webb et al. 2010) and for identifying general ecological strategies, at least in vascular plants (Reich et al. 2003, Wright et al. 2004). In lichens, the extent of studies analyzing functional traits and the suite of traits evaluated is scarcer. Most studies target on 'soft' traits, such as type of photobiont and growth form, since they respond to environmental conditions, are easy and quick to obtain, and provide integrative information about multiple functions (Giordani et al. 2012, Matos et al. 2015, Prieto et al. 2017). However, to obtain precise information about specific physiological functions such as photosynthetic performance, water use and nutrient acquisition it is necessary to measure 'hard' traits (e.g. chlorophyll content, specific thallus mass, water-holding capacity, nutrient thallus content). Given that measuring these 'hard' traits is difficult and expensive, we sought to assess to what extent 'soft' and 'hard' traits provide complementary or redundant information about the response of communities to environmental conditions and, thus, their role as meaningful ecological indicators. Furthermore, extending this framework to a phylogenetic-based approach could also provide guidance in the importance of obtaining very detailed phylogenetic information rather than less precise information based on taxonomical ranks (e.g. families). Thus, if there is congruence between community' phylogenetic diversity calculated with categorical information (i.e. taxonomical ranks) and with quantitative information based on a phylogenetic tree.

Here, we aimed to identify the climatic space where lichen epiphytic communities maximize their functional, phylogenetic and taxonomic diversity in order to detect biodiversity hotspots and their spatial congruence. Moreover, we focused on identifying the optimal niche for different lichen families and for functional 'soft' and 'hard' traits. To do so, we surveyed epiphytic lichen communities in 23 beech forests along Europe, covering a wide climatic gradient from southern Sweden to southern Italy. We hypothesized that: 1) functional hotspot will overlap with phylogenetic and taxonomic ones since the response of the communities to the climatic variables will be mediated through their functional traits (Weiher et al. 1998). However, as a consequence of contrasted phylogenetic or biogeographic histories of the species inhabiting different communities (Mazel et al. 2014, Hurtado et al. 2019), overlapping hotspots of phylogenetic and taxonomic diversity are not expected; 2) lichens with different types of photobiont, growth forms and hard traits values or belonging to different families will show clearly defined optimal niche patterns (i.e. niche differentiation) pointing out their role as ecological indicators. For instance, we expect that

lichens with high physiological tolerances such as chlorolichens and foliose broad lobed lichens will show wider optimal niches.

2 | MATERIALS AND METHODS

2.1. Study area and sampling design

We studied epiphytic lichen communities in 23 beech forest stands comprising the whole distribution area of *Fagus sylvatica* L., from its northern (Sweden) to its southern (Italy) distribution limits (Fig. 1; see Appendix 1 in Supporting Information). The study area represented a latitudinal gradient (>3000 km) with contrasting climatic conditions, both in temperature and precipitation. Mean annual temperature ranged from 3.9 to 11.9°C and total annual precipitation ranged from 563 to 1644 mm (Karger et al., 2017). Along this gradient, we selected mature and well-preserved beech forests with the lichen species *Lobaria pulmonaria* (L.) Hoffm. to ensure the survey of mature epiphytic lichen communities (Rose 1988).

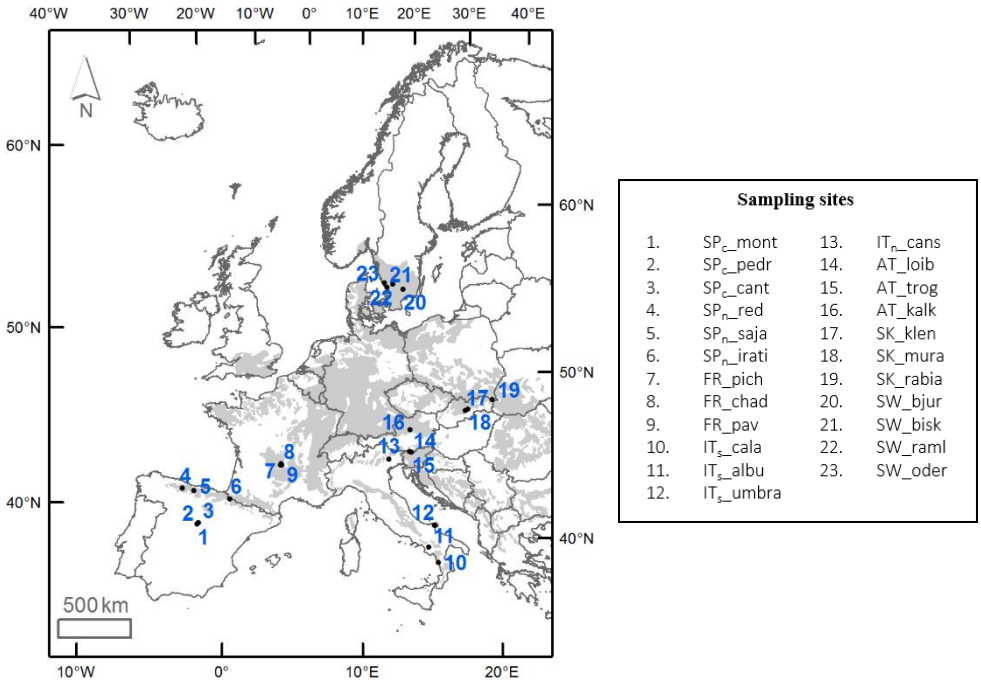


Figure 1. Map of the study area showing the distribution area of *Fagus sylvatica* (light grey) and the sampling sites (black points). Abbreviations of the countries: SP_c, Central Spain; SP_n, North Spain; FR, France; IT_s, South Italy; IT_n, North Italy; AT, Austria; SK, Slovakia; and SW, Sweden. Full name of the sampling sites in Appendix 1.

The sampling was carried out between 2015 and 2016, and the design followed Aragón et al. (2012) to capture the composition of epiphytic lichen communities accounting for more than 90% of the species thriving in each forest stand. At each stand, we sampled five 25 x 25 m plots located 100 m apart from forest edge and 500 m apart among them. Within each plot, we used four 20 x 30 cm grids in 10 beech trees with a minimum dbh > 25 cm. The grids were placed at two different aspects (north and south) and heights (breast and tree base) on a clear area of the trunk without damage, decortication or branching. Inside each grid, we recorded the cover in percentage of the lichen species found and we collected a sample when the identification *in situ* was not possible. Lichen identification followed Smith et al. (2009) and Clauzade & Roux (1985). We sampled a total of 23 forest stands, 115 plots, 1150 trees and 4600 sample units.

To quantify the functional diversity of the lichen communities studied, we collected a maximum of four thalli of all macrolichen species found in each forest stand. These samples were air-dried and stored at -20ºC (Honegger 2003) for posterior measurement of nine 'hard' functional traits in the laboratory. Finally, in relation to the phylogenetic diversity quantification, we collected a sample of all lichen species for which there was not information available in the Genbank database of the molecular markers nuITS, nuLSU, mtSSU and RPB1.

2.2. Climatic data

To characterize each of the forest stands surveyed, we obtained 19 climatic variables, two climatic indices and the altitude. All measurements were obtained at plot level and mean values were calculated at forest level. We recorded the altitude (m) in the field using a GPS. Potential evapotranspiration (mm) and aridity index were retrieved from the CGIAR-CSI Global-Aridity (Zomer et al. 2008) and Global-PET Database (Zomer et al. 2007) and represent the annual average for the 1950-2000 period. Climatic information was retrieved from the high-resolution climate dataset CHELSA (Karger et al. 2017). We obtained averaged values for the 1979-2013 period of 19 climatic variables: annual mean temperature (ºC), mean diurnal range (ºC), isothermality, temperature seasonality, max temperature of warmest month (ºC), min temperature of coldest month (ºC), temperature annual range (ºC), mean temperature of wettest quarter (ºC), mean temperature of driest quarter (ºC), mean temperature of warmest quarter (ºC), mean temperature of coldest quarter (ºC), annual precipitation (mm), precipitation of wettest month (mm), precipitation of driest month (mm), precipitation seasonality, precipitation of wettest quarter (mm), precipitation of driest

quarter (mm), precipitation of warmest quarter (mm) and precipitation of coldest quarter (mm).

2.3. Lichen diversity

We calculated taxonomic, functional and phylogenetic diversity metrics of the epiphytic macrolichen communities thriving in the 23 forest stands surveyed. We focused on macrolichen species and excluded microlichens (crustose and leprose lichens) because it was not possible to measure the 'hard' functional traits in this group. All diversity metrics were calculated at forest scale (n = 23), averaging species cover across all samples within a forest stand. We calculated lichen species richness, Shannon and Inverse Simpson taxonomic diversity indices for each forest.

For each of the 58 macrolichen species found along the gradient, we recorded two 'soft' traits and measured nine 'hard' traits in the laboratory. We selected two 'soft' traits as indicators of the response of lichens to the climatic conditions related to temperature, precipitation and aridity: type of photobiont and growth form (Nelson et al. 2015, Matos et al. 2015, Prieto et al. 2017). Following the ITALIC database (Nimis & Martellos 2017) and Lias light database (Rambold et al. 2014), we differentiated three categories of type of photobiont (green algae -chlorolichens-, cyanobacteria -cyanolichens- and both -cephalolichens-), and five categories of growth form (squamulose, fruticose, fruticose filamentous, foliose narrow lobed, and foliose broad lobed). Besides, we quantified nine 'hard' traits related to: 1) photosynthetic performance: chlorophyll a content (Chla), chlorophyll b content (Chlb) and normalized phaeophytinization index (NPQI); 2) water use strategy: specific thallus mass (STM) and water-holding capacity (WHC); and 3) nutrient uptake: thallus carbon content (%C), thallus nitrogen content (%N), carbon isotopic ratio ($\delta^{13}C$) and nitrogen isotopic ratio ($\delta^{15}N$). We measured Chla, Chlb and NPQI in 1524 thalli following Barnes et al. (1992) and Wellburn (1994), and STM and WHC in 1325 thalli following Merinero et al. (2014). Finally, %C, %N, $\delta^{13}C$ and $\delta^{15}N$ were quantified in 1520 thalli using a PDZ Europa ANCA-GSL elemental analyser interfaced to a PDZ Europa 20-20 isotope ratio mass spectrometer (Sercon Ltd., Cheshire, UK) at UC Davis Stable Isotope Facility.

We used individual species trait data to calculate two functional indices at community level for each forest stand: Rao's quadratic entropy index (hereafter 'Rao') reflected the functional diversity of the communities, whereas community weighted mean (CWM) informed about the functional structure. Rao multitrait including all the 'soft' and 'hard' traits

was selected as an indicator of functional variance (de Bello et al. 2010). We used Gower distances to compute the species dissimilarity matrix giving more weight to quantitative 'hard' (w=1) than qualitative 'soft' traits (w=0.5), because qualitative traits usually show higher values of dissimilarity. Trait dissimilarity distances between each pair of coexisting species (d_{ij}) and the relative abundance of these species in a given forest (p_i and p_j) were used to compute Rao with the function 'Rao' (de Bello et al. 2010) of CRAN software R (R Core Team 2018):

$$Rao = \sum_{i=1}^{s} \cdot \sum_{j=1}^{s} \cdot p_i p_j d_{ij}.$$

Higher values of Rao indicate higher functional dissimilarity of macrolichen communities in a given forest. To characterize the functional structure of communities, we calculated the CWM of every qualitative and quantitative trait for each of the forest stands studied. We used the function 'dbFD' in the 'FD' package (Laliberté & Legendre 2010) to compute the CWMs, which represent the mean trait value of each species in a community weighted by the relative abundance of the species having this trait value (Lavorel et al. 2008). This index reflects the percentage of a given category of a qualitative trait in a community or, in the case of quantitative traits, the trait value most frequently expected in a community.

Regarding phylogenetic diversity, we built a combined phylogenetic tree for the 58 macrolichen species using four molecular markers (nuITS, nuLSU, mtSSU and RPB1). We downloaded the sequences from GenBank and, when this information was not available, we generated the sequences in the laboratory following Prieto & Wedin (2013) (see Appendix S2 in Supporting Information) (more details about the phylogenetic analysis can be found in Prieto et al. 2017). We used the function 'Rao' (de Bello et al. 2010) to calculate a Rao index using the species relative abundance (p_i and p_j) and the phylogenetic distance between pairs of coexisting species (d_{ij}). The dissimilarity matrix was computed with the function 'cophenetic' in the 'picante' package (Kembel et al. 2010). Finally, we classified macrolichens by family (Cladoniaceae, Collemataceae, Lobariaceae, Nephromataceae, Pannariaceae, Parmeliaceae, Peltigeraceae, Physciaceae, Ramalinaceae and Sphaerophoaceae) and we calculated the CWM as explained before for qualitative functional traits.

2.4. Data analysis

We performed a non-metric multidimensional scaling (NMS) on a matrix of sampling sites by climatic variables to analyse the climatic space including the 22 variables recorded in the 23 beech stands studied. We used PC-ORD version 7.07 to conduct the statistical analyses.

To avoid negative values of climatic variables, we summed the most negative value to all the variables. In addition, we used a general relativization (McCune & Grace 2002) to standardize variables with different scales. For the NMS analysis, we used Euclidean distance and no penalty for ties in the distance matrix. We used a randomization test to evaluate whether the final stress was lower than expected by chance. The model with the lowest stress was chosen from 50 runs with real data, each run with a maximum of 500 iterations and starting with a random configuration. We calculated the coefficients of determination (r^2) for the correlations between final ordination distances and distances in the original matrix to assess the amount of variability explained by the ordination axes (McCune & Grace 2002). We also calculated the Spearman correlations (ϱ) between the climatic variables and the ordination axes to determine the main variables explaining the NMS axes. We used the function 'rcorr' in the R package 'Hmisc' (Harrell & Dupont 2017) to compute Spearman correlations that were considered significant when $P < 0.05$.

A second matrix including the diversity metrics was overlaid on the ordination using the 'hilltop plot' method (Nelson et al. 2015). For each overlaid variable, we used a flexibility value of 8.2, a contour fitting of 2.0 standard deviation, and 3% allowable missing values. The resulting plots show the maxima of many non-linear overlay variables on the climatic space. Diversity variables were overlaid by groups to prevent overcrowding and to facilitate results interpretation. We first overlaid richness, Shannon, Inverse Simpson, Rao phylogenetic and Rao functional in a single figure to address the position of the maximum values of these variables in the climatic space. After that, we overlaid separately the CWMs for each trait: type of photobiont, growth form, nine 'hard' traits and lichen families. These figures illustrate the optimal niche of the different functional traits and lichen families.

3 | RESULTS

The NMS ordination of the climatic variables (22 variables in 23 beech forest stands) suggested three axes with a final mean stress of 12.57 (randomization test, $P = 0.004$). Axis 1 explained 74.4% of the variability observed in the climatic space and represented a gradient of sites with higher temperatures in one extreme, and generally less arid sites with higher precipitation (e.g. in the warmest and driest quarters) in the other extreme (Table 1). In fact, the latter axis separated the forests located in the southernmost distribution limit (Southern Italy and Spain) from the rest of the forests. These southern forest stands showed high values of mean temperature during the driest quarter and low precipitation during the warmest quarter reflecting more stressful climatic conditions. Axis 2 explained less climatic variability

(15.1%) and was strongly related to a gradient in precipitation and temperature seasonality (Table 1). On opposite extremes of the axis, sites with higher values of temperature seasonality and lower precipitation (Sweden -SW_bjur and SW_raml-, Slovakia -SK_mura- and South Italy -ITs_umbra-) were separated from more humid sites and with lower values of temperature seasonality (North Spain - SPn_irati and SPn_saja-, France -FR_pich- and South Italy -ITs_cala-). Axis 3 was highly correlated with altitude (Table 1) but only explained 9% of the variability observed. Since the first and second axes together explained the 89.5% of the variability, axis 3 will be no further discussed.

Table 1. Spearman correlations (ϱ) between NMS axes and climatic variables (n = 23).

Environmental variable	Axis 1		Axis 2		Axis 3	
	ϱ	P	ϱ	P	ϱ	P
Potential evapotranspiration	0.35	0.100	0.18	0.404	-0.45	0.032*
Aridity index	-0.76	<0.001*	0.19	0.376	0.35	0.106
Altitude	0.08	0.705	0.16	0.478	-0.91	<0.001*
Annual mean temperature	0.86	<0.001*	0.12	0.587	0.21	0.335
Mean diurnal range	-0.06	0.774	0.13	0.549	-0.65	0.001*
Isothermality	0.18	0.414	0.38	0.077	-0.52	0.012*
Temperature seasonality	-0.68	<0.001*	-0.52	0.010*	-0.17	0.438
Max temperature of warmest month	0.62	0.002*	-0.04	0.840	-0.26	0.240
Min temperature of coldest month	0.88	<0.001*	0.23	0.282	0.27	0.215
Temperature annual range	-0.63	0.001*	-0.30	0.171	-0.53	0.010*
Mean temperature of wettest quarter	-0.51	0.013*	-0.13	0.556	0.26	0.239
Mean temperature of driest quarter	0.94	<0.001*	0.08	0.730	0.13	0.565
Mean temperature of warmest quarter	0.71	<0.001*	-0.09	0.678	0.09	0.672
Mean temperature of coldest quarter	0.89	<0.001*	0.28	0.198	0.14	0.526
Annual precipitation	-0.57	0.004*	0.84	<0.001*	0.03	0.893
Precipitation of wettest month	-0.48	0.021*	0.77	<0.001*	-0.02	0.934
Precipitation of driest month	-0.75	<0.001*	0.59	0.003*	0.26	0.232
Precipitation seasonality	0.28	0.190	-0.16	0.460	-0.47	0.022*
Precipitation of wettest quarter	-0.51	0.012*	0.74	0.000*	0.01	0.961
Precipitation of driest quarter	-0.73	<0.001*	0.60	0.003*	0.32	0.140
Precipitation of warmest quarter	-0.91	<0.001*	0.28	0.191	0.28	0.191
Precipitation of coldest quarter	-0.07	0.757	0.96	<0.001*	-0.08	0.717

Notes: Asterisks (*) represent significant correlations ($P < 0.05$).

Taxonomic (richness, Shannon and Inverse Simpson), phylogenetic (Rao phylogenetic) and functional (Rao multitrait) diversity indices, were overlaid on the NMS ordination (Fig. 2). Overall, we found that the most diverse lichen epiphytic communities were located in the extremes of the climatic space. Communities with maximum taxonomic

and phylogenetic diversity occupied different optimal niches, meaning that the highest values of taxonomic diversity did not occur in the same climatic niche as the highest values of phylogenetic diversity (Fig. 2). The southernmost forests (Central Spain and Southern Italy), with higher temperatures and more arid conditions, generally harboured the epiphytic communities with the highest phylogenetic diversity (Fig. 2). On the other hand, the forests characterized by warmer temperatures but more precipitation in the coldest quarter (Northern Spain) appeared as optimal niche maximizing species richness (Fig. 2). In the opposite extreme of the gradient, characterized by lower temperatures and higher precipitation during the driest and warmest quarter (Austria and Slovakia), the communities showed maximum values of Inverse Simpson and Shannon (Fig. 2). Whereas maximum values of phylogenetic and taxonomic diversity showed one clearly defined climatic niche, maximum values of functional diversity showed two optimal niches overlapping with the former niches (Fig. 2).

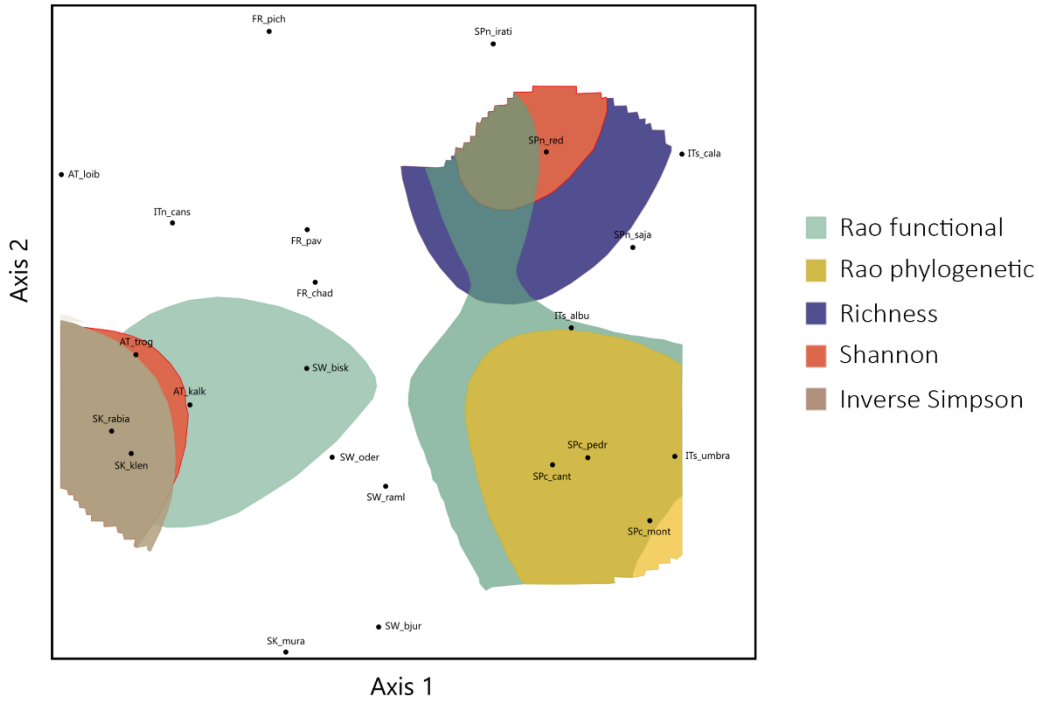


Figure 2. Hilltop plot of functional, phylogenetic and taxonomic diversity metrics of epiphytic lichen communities overlaid on the NMS ordination of environmental variables across 23 European beech forests. Coloured areas represent maximum values of diversity metrics in the environmental space. Points indicate the forests studied. Location of the sampling sites in Fig. 1.

The functional CWMs overlaid on the NMS ordination showed niche complementarity among cephalo-, chloro- and cyanolichens (see Appendix 3 in Supporting Information). The optimal niche of cephalolichens (i.e. maximum CWM values) was in the extreme of the climatic gradient characterized by higher temperatures and higher precipitation in the coldest quarter (Northern Spain). Cyanolichens exhibited three different optimums located in different areas of the climatic space (see Appendix 3). We were able to identify and separate these three different groups within the cyanolichens. Based on this result, we recoded the categorical trait 'type of photobiont' for five categories instead of three: cephalolichens, chlorolichens, cyanolichens, cyanolichens-Collemataceae and cyanolichens-Pannariaceae. The maximum of cyanolichens-Collemataceae appeared in sites with high precipitation of warmest quarter and low mean temperature of driest quarter (Austria and Slovakia), while the other groups of cyanolichens (cyanolichens-Pannariaceae and the rest of cyanolichens) had their maximum in the southernmost extreme (Fig. 3a). Those forests characterized by warmer temperatures but more precipitation in the coldest quarter arose as optimal niches of cyanolichens-Pannariaceae (Fig. 3a). Opposite to cephalo- and cyanolichens, having their optimal niche in the extremes of the gradient, chlorolichens optimal niche were in the middle of the climatic gradient, occupying the complementary space left by the former (see Appendix 3, Fig. 3a).

Regarding growth form, species with different growth forms had different climatic optimums and clearly defined optimal niches restricted to certain sites of the climatic space (Fig. 3b). Following axis 1, squamulose and fruticose filamentous lichens were associated to sites with higher temperatures and lower precipitation during the warmest and driest quarter; whereas fruticose and narrow lobed lichens dominated in areas with higher precipitation of warmest quarter and lower mean temperature of driest quarter (Fig. 3b). Following axis 2, the optimal niche of fruticose filamentous was different from fruticose, foliose narrow lobed and squamulose lichens optimal niche in sites with higher precipitation during the coldest quarter (Fig. 3b). The climatic optimum of foliose broad lobed comprised a large amount of the climatic space, occupying the complementary space left by the other growth forms (Fig. 3b).

Finally, regarding the 'hard' traits (Fig. 3c) and the family (Fig. 3d), results did not show a clear differentiation of the optimum for these traits in response to the climatic conditions.

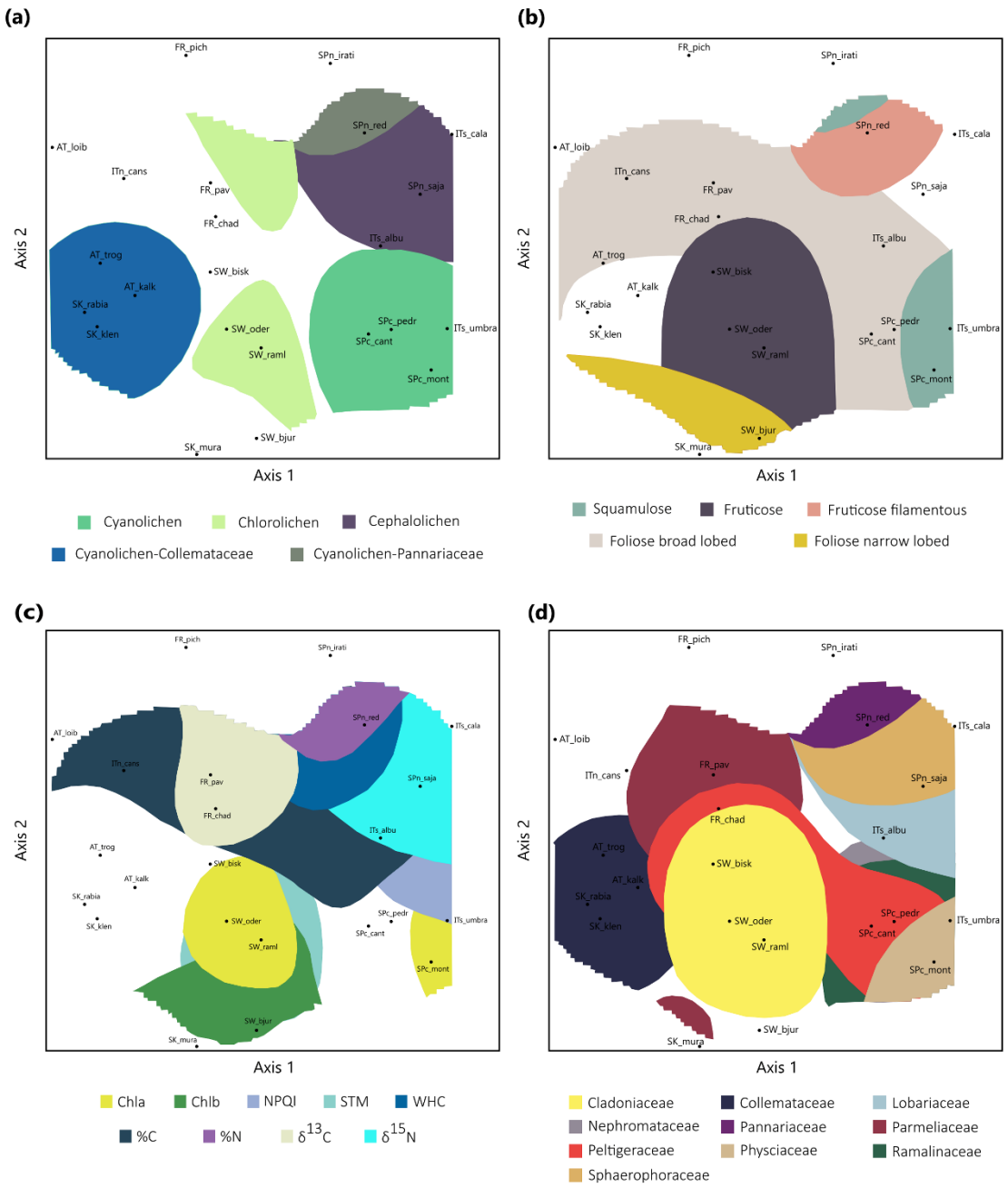


Figure 3. Hilltop plot of CWMs of the 'soft' and 'hard' functional traits, and the families of epiphytic lichen communities overlaid on the NMS ordination of environmental variables across 23 European beech forests: **(a)** type of photobiont recoded, **(b)** growth form, **(c)** 'hard' traits, and **(d)** lichen families. In (a), (b) and (c), coloured areas represent functional optimum for a given category of each functional trait (maximum values of CWM) in the environmental space. In (d), coloured areas represent the optimal niche of each lichen family. Points indicate the forests studied. Location of the sampling sites in Fig. 1.

4 | DISCUSSION

Epiphytic communities maximized their functional, phylogenetic and taxonomic diversity under different climatic conditions, which supports the idea that these facets provide complementary information about the spatial distribution of biodiversity (Pavoine et al. 2013, Dainese et al. 2015) and highlights the importance of considering that species are ecologically inequivalent and evolutionary dependent (Swenson 2011). The functional diversity peaked with phylogenetic and taxonomic maximums pointing out that functional traits might reflect the response of lichen communities to environmental conditions (Weiher et al. 1998, Shipley et al. 2016). Indeed, the congruence between functional and phylogenetic hotspots show that distant relatives display a wide range of trait values (phylogenetic conservatism; Webb et al. 2002, Pavoine & Bonsall 2011). In addition, correspondence between functional and taxonomic hotspots reflects that communities composed by a high number of species tended to have non-redundant functional traits (niche specialization; Petchey & Gaston 2002, Venail et al. 2015). It is important to note that phylogenetic and taxonomic diversity reached their maximums in different areas of the climatic space. Thus, richest communities did not correspond to communities with more distant lineages, which may reflect common phylogenetic or biogeographic histories (Davis & Buckley 2011, Gerhold et al. 2015).

Apart from the interplay between the different facets of biodiversity, unraveling the spatial heterogeneity of the distribution of biodiversity is a major challenge from both applied and theoretical approaches (Mazel et al. 2014). Interestingly, we found that communities maximized their diversity in the extremes of the climatic space. For instance, communities located in the southernmost forests characterized by a summer drought period and high temperatures had the highest functional and phylogenetic diversity. As found in other organisms such as ants (Arnan et al. 2016), the Mediterranean region appeared as a hotspot of functional and phylogenetic diversity in lichens. The high values of functional diversity in the Mediterranean region did not match with the highest values of species richness, which may reflect the existence of high functional complementarity in this region (Stuart-Smith et al. 2013). In turn, the high values of phylogenetic diversity may reflect the complex paleogeographic history of this region, with communities containing distant lineages.

Beyond the identification of biodiversity hotspots, pinpointing the specific traits meaningful as ecological indicators yield an opportunity to gain insight into the impact of climate change on biodiversity (Jørgensen et al. 2005). Therefore, functional traits may determine the shifts in lichen distribution due to environmental changes and niche

differentiation. We found clearly defined optimal niches for the 'soft' traits type of photobiont and growth form, which confirms that the climatic conditions determine the distribution of the species with different photobionts and growth forms.

Lichens with different photobionts showed complementary optimal climatic niches (Nelson et al. 2015), with cephalo- and cyanolichens occupying the extremes of the climatic space and chlorolichens dominating in the center of the space. According to the physiological constrains associated to the different photobionts, we expected wider optimal niches in cephalo- and chlorolichens, which are able to use several hydration sources, and narrower optimums in cyanolichens that require liquid water to initiate photosynthesis (Gauslaa 2014). In turn, we found that the optimal niche of cephalolichens was restricted to the warmest and most humid forests during the coldest quarter likely because warmer temperatures during the coldest quarter may help them avoid the strong photoinhibition that they suffer at low temperatures (Alam et al. 2015). Within the cyanolichens, we found three different groups with clearly differentiated optimal niches. The jelly lichens of the family Collemataceae had their optimal niche in sites with high precipitation during the warmest quarter and low mean temperature of driest quarter. This peak agrees with previous studies that associate cyanolichens with humid sites (Jovan & McCune 2004, Gauslaa 2014). However, and contrary to this expectation, cyanolichens-Pannariaceae and the rest of cyanolichens had their optimal niches associated to the drier southernmost forests. Different studies (Concostrina-Zubiri et al. 2014, Matos et al. 2015) suggest that cyanolichens comprise different groups of lichens with distinct physiological requirements and tolerances to certain environmental conditions such as high temperatures and irradiation. Finally, the peaks of chlorolichens in the complementary space left by the other functional groups may reflect their ability to use several water sources that cannot be used as water supply by the lichens with the other main photobionts. Interestingly, we identified two different groups of chlorolichens with optimal niches associated to diverse climatic conditions, but future research should be conducted to unveil the drivers underpinning these different responses.

Regarding growth form, fruticose filamentous lichens dominated in sites with high precipitation during the coldest quarter bringing up their efficiency to exploit water sources such as ephemeral snow (Nelson et al. 2015). In addition, this growth form was associated to warmer and drier sites during the warmest and driest quarters likely because they have a very high surface area/biomass ratio and, consequently, they are able to become physiologically active very fast (Lange et al. 1986, Gauslaa 2014). Likewise, squamulose lichens dominated in warm and dry sites perhaps because their small size better optimized

the use of the limited water sources than larger lichens in which the activation was less efficient since they require greater water availability (Merinero et al. 2014). Consequently, narrow lobed lichens were associated to more humid and colder sites, reflecting that they were more efficient with high water availability probably linked to the longer time needed to become hydrated (Lange et al. 1986, Gauslaa 2014). Fruticose occupied the central space between fruticose filamentous and narrow lobed lichens, showing that they were favoured in sites with intermediate values of temperature and precipitation during the year probably due to they become hydrated slower than fruticose filamentous but faster than narrow lobed. We observed that foliose broad lobed had the wider optimal niches, occupying the complementary space left by the other growth forms, which supports that they become hydrated in a wider range of climatic conditions. As suggested by Nelson et al. (2015), this could be the result of a wide range in the surface area/biomass ratio within the foliose broad lobed and their appressed morphology able to trap moisture between the thallus and the trunk.

Concerning the 'hard' traits, we did not identified patterns of clearly defined optimal niches, showing that these traits do not show clear differences depending on the climatic conditions. This finding points out the limited value of the set of studied 'hard' traits as ecological indicators for climate, but it may be interesting to study its relationship with other environmental factors such as pollution (e.g. nitrogen deposition). Furthermore, since our study lacks in-site climatic data, more studies are needed to find out whether these traits may respond to small-scale rather to large-scale climatic variables. Additionally, further research including the relationship of these traits with precise ecosystem functions and processes would unveil if they actually have a meaningful value as effect rather than as response traits (i.e. traits describing the effect of the species on ecosystem functioning rather than describing the response of the species to environmental changes; Lavorel & Garnier 2002). Similarly to 'hard' traits, when considering lichen families, we did not observed a clear niche differentiation in response to climatic factors. This finding suggests that families are not good surrogates of the evolutionary history in these communities.

From an applied perspective, conservation resources are scarce and intensive research efforts have been focused on identifying areas of high priority in which to allocate these resources (Brooks et al. 2006). Typically, conservation assessments relied on species richness (e.g. Myers et al. 2010) but several studies encourage the use of phylogenetic and functional facets to establish conservation priorities. For instance, Forest et al. (2007) proposed that maximizing phylogenetic diversity favours the response of species to

environmental change uncertainty while Cadotte et al. (2011) proposed that maximizing functional diversity prioritizes ecosystem function or stability. Our findings indicate that preserving communities with the highest functional diversity (i.e. numerous functions) might indirectly preserve high phylogenetic (i.e. distant lineages), and at certain level, high taxonomic diversity (i.e. many species). However, since functional and taxonomic optimums do not completely overlap, and taxonomic and phylogenetic optimums do not overlap at all, a multifaceted approach should be applied for establishing effective conservation policies. In addition, areas located in the climatic extremes, and particularly in the Mediterranean region (Myers et al. 2010, Devictor et al. 2010, Arnan et al. 2016), emerged as biodiversity hotspots that require special conservation attention.

In conclusion, the optimal functional niches overlapped with taxonomic and phylogenetic optimal niches indicating the key role of functional traits in the response of lichen communities in face of changing climatic scenarios. We showed that functional, phylogenetic and taxonomic hotspots were not necessarily congruent, meaning that not all the facets of biodiversity are good surrogates for the others. Therefore, we encourage the use of an integrative approach including functional, phylogenetic and taxonomic diversity metrics both, to assess the effect of climatic changes on communities and to select high priority areas in which develop conservation programs such as the Mediterranean region. We found that type of photobiont and growth form are valuable traits to evaluate the effects of large-scale climatic changes on the lichen communities' dynamic. Furthermore, we stress the need for including three different categories within the cyanolichens to assess the influence of climate since these functional groups respond in different ways to the climatic conditions. In contrast, further research is needed to unveil to what extent 'hard' physiological traits could respond to small-scale climatic variables or to other environmental factors and to what extent they are relevant to assess the effect of the communities' changes on the ecosystems functioning.

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6 | AUTHORS' CONTRIBUTIONS

IM, MP, GA and PH conceived the ideas and designed methodology; PH, MP, GA and IM collected the data; PH, PM and CB analysed the data; PH led the writing of the manuscript and all authors provided critical reviews.

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8 | SUPPORTING INFORMATION

8.1. Appendix S1

Table S1. Location of each beech forest surveyed.

Country	Forest stands	Abbreviation	Latitude	Longitude
Sweden	Ramlaklitten i Skogsbo Naturreservat	22) SW_raml	57.076	12.882
	Ödegärdet Naturreservat	23) SW_oder	56.966	14.668
	Biskopstorps Naturreservat	21) SW_bisk	56.800	13.530
	Bjurkärrs Naturreservat	20) SW_bjur	56.635	12.558
Slovakia	Rabia skala (Poloniny NP)	19) SK_rabia	49.102	19.764
	Cigánka-Muránsky hrad (Muránska planina NP)	18) SK_mura	48.762	20.061
	Klenovsý Vepor (Klenovské vrchy)	17) SK_klen	48.687	22.449
Austria	Nationalpark Kalkalpen	16) AT_kalk	47.816	14.453
	Loibltal	14) AT_loib	46.461	14.268
	Trögener Klamm	15) AT_trog	46.448	14.478
France	Chadefour Valley Nature Reserve	8) FR_chad	45.540	2.854
	Réserve naturelle nationale de Chastreix-Sancy	9) FR_pav	45.495	2.886
	Picherande	7) FR_pich	45.468	2.780
Spain	Parque Natural Saja-Besaya	5) SPn_saja	43.114	-1.163
	Parque Natural de Redes	4) SPn_red	43.105	-5.288
	La Selva de Irati	6) SPn_irati	42.992	-4.284
	Sitio Natural de Interés Nacional del Hayedo de Montejo de la Sierra	1) SPc_mont	41.227	-3.385
	Parque Natural Sierra Norte de Guadalajara	3) SPc_cant	41.218	-3.493
	Hayedo La Pedrosa	2) SPc_pedr	41.112	-3.410
Italy	Foresta del Cansiglio	13) ITn_cans	46.074	15.372
	Foresta Umbra (Parco Nazionale del Gargano)	12) ITs_umbra	41.810	16.050
	Parco Nazionale del Cilento e Valle de Diano	11) ITs_albu	40.498	15.984
	Riserva Statale Serra Nicolino - Pian d'Albero	10) ITs_cala	39.503	12.410

8.2. Appendix S2

Table S2.1. GenBank accession numbers for the molecular markers used in the phylogenetic analyses.

Lichens	ITS	LSU	mtSSU	RPB1
Anaptychia ciliaris (L.) Körb. ex A. Massal.	KJ027716	KX512894	EF582835	X
Bryoria fuscescens (Gyeln.) Brodo & D. Hawksw.	DQ534452	DQ534452	KJ599554	EF092101
Cetrelia olivetorum (Nyl.) W.L. Culb. & C.F. Culb.	KU862940	DQ923659	GU994638	GU994693
Cladonia chlorophaea (Flörke ex Sommerf.) Spreng.	DQ534460	EF489928	X	-
Cladonia coniocraea (Flörke) Spreng.	KX132951	X	X	X
Cladonia digitata (L.) Hoffm.	KX132950	AY756319	AY756366	AY756414
Cladonia fimbriata (L.) Fr.	FJ756726	X	X	-
Cladonia pyxidata (L.) Hoffm.	DQ534463	EF489926	X	-
Collema flaccidum (Ach.) Ach.	-	AY424213	EU982578	X
Collema furfuraceum (Schaer.) Du Rietz	GQ396263	EU982608	KJ766377	GQ259048
Collema subnigrescens Degel.	X	KJ766548	KJ766380	X
Evernia prunastri (L.) Ach.	EU266079	AF107562	KJ766390	KJ766909
Flavoparmelia caperata (L.) Hale	HQ650680	JN939607	AY584617	DQ883778
Heterodermia speciosa (Wulfen) Trevis.	KX512927	KX512868	KX512975	-
Hypogymnia physodes (L.) Nyl.	KX132937	JQ301600	AY756400	KJ766912
Hypogymnia tubulosa (Schaer.) Hav.	KX132956	X	HQ690160	X
Leptogium saturninum (Dicks.) Nyl.	KJ409605	EU982610	AY340499	GQ259064
Lobaria pulmonaria (L.) Hoffm.	AF129285	AF183934	EU558813	DQ915597
Lobarina scrobiculata (Scop.) P. Gaertn.	AF350297	AY424205	EU558816	DQ883736
Melanelixia fuliginosa (Fr. Ex Duby) O. Blanco.	KX132913	DQ986803	AY611173	DQ986860
Melanelixia glabra (Schaer.) O. Blanco.	KX132939	AJ421427	GU994651	EF092118
Melanelixia subaurifera (Nyl.) O. Blanco.	KT695379	AJ421432	AY611156	JX126422
Melanohalea elegantula (Zahlbr.) O. Blanco.	AY611094	JQ813007	AY611151	JQ813986
Melanohalea exasperatula (Nyl.) O. Blanco,	JN943709	JQ813027	AY611147	JN987940
Menegazzia terebrata (Hoffm.) A. Massal.	KM250238	DQ899304	AY584624	DQ923694
Nephroma laevigatum Ach.	AY124143	HQ394194	AY124182	-
Nephroma parile (Ach.) Ach.	DQ066708	KX869862	AY124184	DQ973061
Nephroma resupinatum (L.) Ach.	DQ066710	AF286829	AY124168	-
Nevesia sampaiana (Tav.) P.M. Jørg.	KC618709	X	GU570030	KC608120
Pannaria conoplea (Ach.) Bory	FR799247	AY424209	X	-
Parmelia saxatilis (L.) Ach.	AF141370	JN939623	AY340514	DQ923695
Parmelia submontana Nádv.	X	X	X	-
Parmelia sulcata Taylor	KX132926	JN939625	GU994669	GU994720
Parmeliella triptophylla (Ach.) Müll. Arg.	HM448804	GQ259008	GU570023	GQ259075
Parmelina pastillifera (Harm.) Hale	JX466460	JN939630	EU562697	KR995501
Parmelina tiliacea (Hoffm.) Hale	KX132912	JN939631	AF351173	KJ766917
Parmotrema perlatum (Huds.) M. Choisy	KX457691	AY584838	AY586580	EF092146
Pectenia plumbea (Lightf.) P.M. Jørg.	JX126708	DQ912347	AY340491	DQ912373
Peltigera collina (Ach.) Schrad.	FJ708926	AF286765	-	FJ709112

Lichens	ITS	LSU	mtSSU	RPB1
Peltigera degenii Gyeln.	JX195266	AY257905	AY584628	DQ782826
Peltigera horizontalis (Huds.) Baumg.	KX354708	KM005749	AY124163	FJ709130
Peltigera membranacea (Ach.) Nyl.	FJ709033	KM005758	-	FJ709229
Peltigera praetextata (Flörke ex Sommerf.) Zopf	DQ001296	KM005766	AY124167	FJ709246
Physconia distorta (With.) J. R. Laundon	KX132933	AY773913	EF582813	-
Physconia perisidiosa (Erichsen) Moberg	AJ421422	AY773911	EF582809	-
Physconia venusta (Ach.) Poelt	AY368147	X	EF582810	X
Platismatia glauca (L.) W.L. Culb. & C.F. Culb.	AF072231	DQ973032	AY756404	DQ912363
Pleurosticta acetabulum (Neck.) Elix & Lumbsch	KX132911	KJ766629	KJ766463	KJ766920
Pseudevernia furfuracea (L.) Zopf.	GU300783	KJ766637	GU300806	EF105435
Ramalina farinacea (L.) Ach.	JF923604	GU726354	KJ766480	KJ766831
Ramalina fastigiata (Pers.) Ach.	EU034669	GU726337	AY756375	KJ766832
Ramalina fraxinea (L.) Ach.	JF923610	X	X	-
Ricasolia amplissima (Scop.) De Not.	AF524924	AY424206	EU558806	GQ259065
Ricasolia virens (With.) H.H. Blom & T. Tonsberg.	KP941424	AY340553	AY340508	GQ259070
Scytinium lichenoides (L.) Otálora, P.M.	DQ466041	EU166331	AY340498	DQ917414
Sphaerophorus globosus (Huds.) Vain.	AY256775	DQ986767	AY256762	DQ986836
Sticta limbata (Sm.) Ach.	AB245118	AY424207	AY340531	KT281758
Usnea subfloridana (L.) F. H. Wigg.	JN086326	X	-	JN992586

'X' indicate sequences that have been generated for this study and sequences not available are marked with dashed lines.

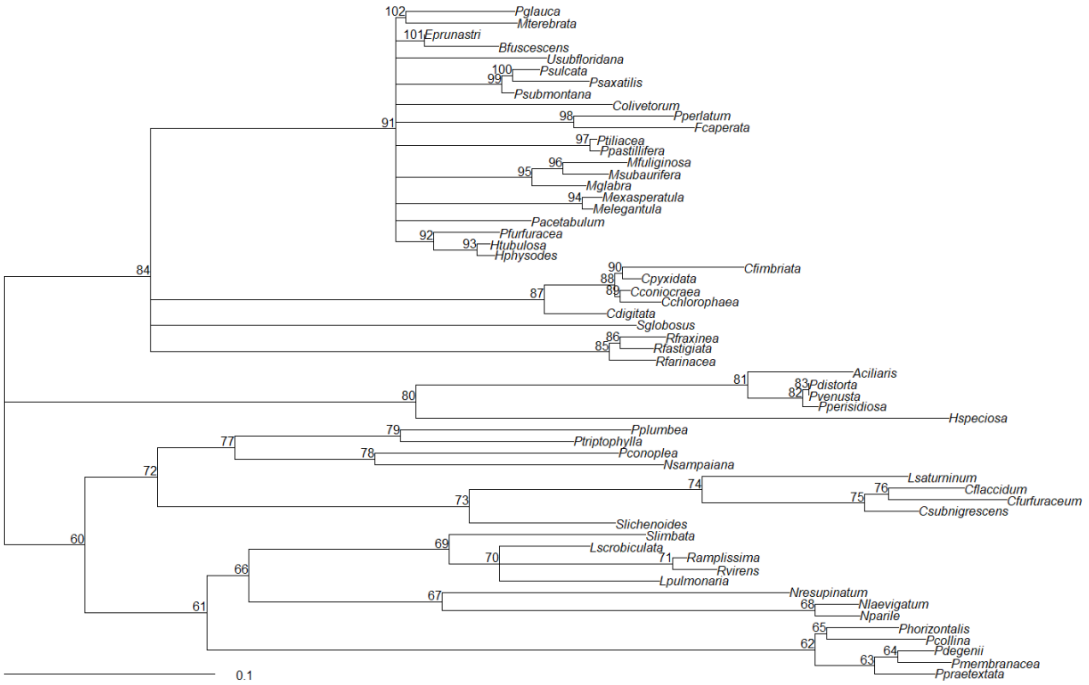

Figure S2.2. Phylogenetic tree based on four molecular markers (nuITS, nuLSU, mtSSU, and RPB1) including the 58 lichen species found in the 23 beech forests along Europe. Numbers above nodes denote the bootstrap support (ML-BS) obtained with Maximum Likelihood in RAxML.

8.3. Appendix S3

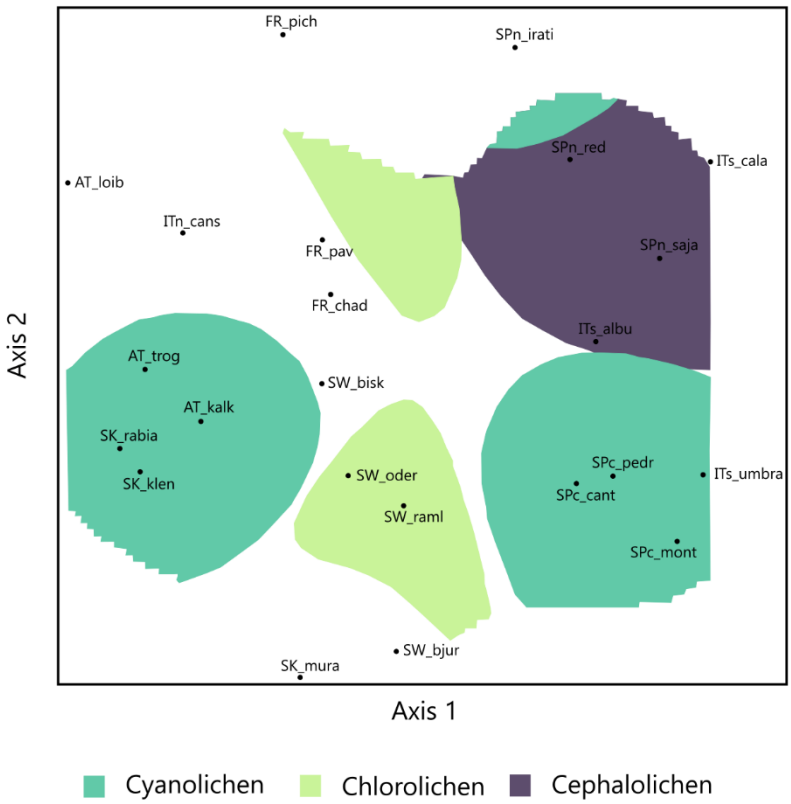

Figure S3.1. Hilltop plot of CWMs for 'type of photobiont' trait of epiphytic lichen communities overlaid on the NMS ordination of environmental variables across 23 European beech forests. Coloured areas represent functional optimum for a given category of each functional trait (maximum values of CWM) in the environmental space. Points indicate the forests studied. Location of the sampling sites in Fig. 1.

Capítulo 6

The epiphytic lichens on *Fagus sylvatica* in beech forests of Europe: towards an open and dynamic checklist

Pilar Hurtado | Gregorio Aragón | Isabel Martínez | Helmut Mayrhofer | María Prieto

En revisión en Herzogia

ABSTRACT

Beech forests are considered one of the most emblematic ecosystems in the temperate biome and host a wide variety of specialised cryptogamic organisms such as epiphytic lichens. This checklist is the first compilation focused on the epiphytic lichen diversity occurring on *Fagus sylvatica* trees along Europe. The checklist is based on a literature search encompassing 127 studies and includes data collected by our research group in Sweden, Slovakia, Austria, France, Italy and Spain. We report 674 lichen species differently distributed along 26 European countries. The richness of the lichen species ranged from one in Kosovo and Netherlands to 332 species in Ukraine. All information provided in this manuscript is available online (*http://biodiversos.org/epidiversity-lichens-fagus-europe/*) to facilitate the accessibility and updating of the data. Thus, we aim that this checklist becomes an open and dynamic database that continuously expands not only based on new lichenological studies, but also with the information retrieved by lichenologist in the past and the researches published in a diverse suite of languages.

Key words

Biodiversity, lichenised fungi, literature review, richness, taxonomy.

1 | INTRODUCTION

Beech forests represent one of the most emblematic ecosystems in the temperate broadleaf forest biome of the Northern Hemisphere. The current area of distribution of the European beech (*Fagus sylvatica* L.) comprises a large latitudinal gradient, from southern Sweden to southern Italy, exemplifying a unique case of expansion from a few isolated glacial refuge areas (Magri et al. 2006, whc.unesco.org). Among all beech species, the European beech is the most widely distributed one (Fang & Lechowicz 2006) and its continental distribution highlights its tolerance to a wide range of environmental conditions. However, human disturbances have resulted in fragmentation and simplification of some of these forests (Jones 1945, Bengtsson et al. 2000). As a consequence, primeval beech forests are really scarce and mainly occur as remnants in the Carpathians, Balkans and Alps (Parviainen 2005, Kaufmann et al. 2018). In this way, the anthropogenic disturbances also impact on the suite of epiphytic lichens species associated with these beech forests (Berg et al. 2002, Fritz et al. 2008, Hauck et al. 2013, Nascimbene et al. 2013), which in many cases are included in red lists (Arup et al. 1997, Gärdenfors 2005).

Lichenologists have done an intensive research effort investigating the lichen diversity along the whole distribution area of *Fagus sylvatica*. As a result, lichen diversity has been recorded in beech forests across different countries in Europe. The set of studies focused on lichens thriving in beech forests is diverse and comprises taxonomic (e.g. Tretiach 2014, Malíček et al. 2017), floristic (e.g. Gómez & Hladun 1981, Partl 2011, Roux et al. 2017), ecological (e.g. Dymytrova et al. 2014, Aragón et al. 2012) and applied approaches (e.g. Moning & Müller 2009, Brunialti et al. 2013, Ruete et al. 2017). Other studies are compilations and checklists of certain regions and provide records on a high number of species. For instance, Llop (2012-2013) reported 73 lichens on bark of *Fagus sylvatica* in La Garrotxa (Spain) and Malíček et al. (2018) 275 species in Uholka-Shyrokyi Luh (Ukraine). Despite a large amount of information is available, this information is not summarised in a single database. On top of this, the research effort is biased towards certain countries such as Poland, Italy or Germany, which stresses the need for the creation of an open checklist with the possibility of continuously updating, mainly in the case of the poorly-investigated areas. Therefore, having a database of the lichen species inhabiting beech forests would provide crucial information about the diversity in these ecosystems, providing a meaningful baseline for future theoretical and applied studies. On the one hand, this general overview favours biogeographic studies on the lichen species that, in many cases, cover a broad range of distribution (Nimis et al. 2018). On the other hand, it would provide insight to develop studies focused on effective conservation and management measures for coping with climate change and anthropogenic threats.

This is the first attempt to compile the lichen diversity of the beech forests, one of the most representative forests in temperate biomes. We aim to provide an open and dynamic checklist that could be updated online including information from new researches and from publications not retrieved in our literature search. To that end, together to the present manuscript, we have developed an online version to facilitate the accessibility and update of the data.

2 | METHODS

2.1. Literature search and selection of studies

We searched studies that reported the presence of lichen species on *Fagus sylvatica* trees. The search was done using two databases, Recent Literature on Lichens (Culberson et al. 2015) and Web of Science. The first database covered the period from 1536 to 2019, and the second, from 1900 to 2019. In both cases, we used the following combination of search

terms in English: 'lichen and Fagus'. As a result, we obtained 44 studies in Recent Literature on Lichens and 133 studies in Web of Science. Manuscripts published in non-indexed journals and several published in other languages than English did not appear in the literature search.

The studies were included in the checklist if they specified the country and reported the presence of lichen species on trunks of *Fagus sylvatica* as phorophyte. One hundred twenty-seven studies accomplished these criteria (Appendix S1) and were included on the final checklist. For species nomenclature, we followed Nimis (2016) and Nimis et al. (2018). We have maintained the old and well-established genera *Caloplaca s.lat* since many species are still awaiting a re-assignment to the new genera in which it was split.

Beyond the literature search, this compilation encompasses data collected by our research group in six European countries: Sweden, Slovakia, Austria, France, Italy and Spain. We surveyed the composition of epiphytic lichen communities across 23 well-conserved beech forests along a European latitudinal gradient: six forests in Spain, four forests in Sweden and Italy, and three forests in Slovakia, Austria and France. In total, we retrieved data from 4600 sample units in 1150 trees (see Hurtado et al. in prep.). In addition, we collected data of the epiphytic lichen species occurring in 22 beech forest remnants within the Atlantic region in northern Spain and 25 beech remnants in the Mediterranean region in Central Spain (see Hurtado et al. 2019).

3 | RESULTS AND DISCUSSION

The checklist included 674 lichen species differently distributed along 26 European countries (Table 1). Fifteen species appeared in more than ten countries and the most widespread species were: *Lecidella elaeochroma* and *Pertusaria pertusa* (21 countries), *Lepra amara* (20 countries), *Parmelia sulcata* (19 countries), and *Graphis scripta, Lecanora argentata* and *Lepra albescens* var. *albescens* (18 countries). Around one third of the species (231 species) were only reported in one country: 41 exclusive species from Poland, 39 species from Ukraine and 36 species from France. Our research group recorded 221 lichen species on beech trees along Sweden, Slovakia, Austria, France, Italy and Spain. The species richness broadly differed across the studied countries, with Ukraine, Poland and Slovakia hosting near the 50% of the total species retrieved from the literature search and Kosovo and Netherlands with only one species recorded. Since the literature search mainly yielded studies in English, the richness of epiphytic lichens in certain countries such as Spain and Italy, with a high literature production in another languages, may be underestimated. Moreover, these countries show a wide

environmental heterogeneity comprising different biogeographic regions (e.g. Atlantic and Mediterranean regions in Spain), which also points out an underestimation of the species richness. These issues highlight the need to create an open checklist where researches could continuously include their records. Thus, all information provided in this checklist is available online on (*http://biodiversos.org/epidiversity-lichens-fagus-europe/*). This is an open and dynamic database that could be updated by our research group and by different users, including new works and studies in different languages.

Table 1. Species richness recorded in the beech forests from 26 European countries.

COUNTRY	COUNTRY CODE	RICHNESS
Albania	AL	62
Austria	AT	160
Belgium	BE	5
Britain	GB	162
Bulgaria	BG	79
Croatia	HR	55
Czech Republic	CZ	143
Denmark	DK	80
France	FR	169
Germany	DE	88
Greece	GR	24
Italy	IT	212
Kosovo	RKS	1
Luxembourg	LU	52
North Macedonia	MK	54
Montenegro	ME	47
Netherlands	NL	1
Poland	PL	324
Romania	RO	118
Slovakia	SK	228
Slovenia	SI	171
Spain	ES	222
Sweden	SW	145
Switzerland	CH	5
Turkey	TR	8
Ukraine	UA	332

3.1. List of species

Lichen species recorded by our research group are in bold. The authors for the different species are available in the online database. Abbreviations of the countries as in Table 1.

SPECIES	COUNTRY CODE
Absconditella delutula	BE
Absconditella lignicola	FR, UA
Acarospora fuscata	UA
Acolium sessile	FR
Acrocordia cavata	AT, FR, IT, SK, ES, SW
Acrocordia conoidea	ES
Acrocordia gemmata	AL, AT, GB, DE, IT, MK, ME, PL, SK, SI, ES, SW, UA
Agonimia allobata	DE, SK, SW, UA
Agonimia borysthenica	UA
Agonimia flabelliformis	CZ, DE
Agonimia octospora	ES
Agonimia repleta	CZ, PL, SK, UA
Agonimia tristicula	AT, SK, ES, SW, UA
Alectoria sarmentosa	IT
Alyxoria culmigena	FR, PL, ES, UA
Alyxoria lichenoides	FR, ES
Alyxoria ochrocheila	GB, DK, FR, PL, SK, SW, UA
Alyxoria varia	AT, GB, BG, CZ, DK, FR, IT, MK, PL, RO, SK, SI, ES, SW, UA
Amandinea punctata	GB, CZ, DE, IT, PL, SK, ES, UA
Anaptychia ciliaris	AL, AT, HR, GR, IT, MK, ME, PL, RO, ES, UA
Anisomeridium biforme	DK, SW, UA
Anisomeridium macrocarpum	UA
Anisomeridium polypori	AT, CZ, DK, DE, PL, SK, ES, SW, UA
Arctomia fascicularis	FR
Arthonia apatetica	PL, UA
Arthonia atra	GB, BG, DK, FR, DE, IT, PL, ES, SW, UA
Arthonia didyma	AT, CZ, DK, FR, DE, IT, MK, PL, SK, ES, SW, UA
Arthonia dispersa	PL, ES, UA
Arthonia exilis[*1]	PL
Arthonia faginea	FR
Arthonia helvola	FR, SK
Arthonia mediella	CZ, FR, IT, PL, UA
Arthonia radiata	AT, GB, BG, HR, CZ, DK, FR, DE, IT, PL, RO, SK, SI, ES, SW, UA
Arthonia reniformis	FR
Arthonia ruana	DK, FR, PL, SK, UA
Arthonia spadicea	AT, GB, CZ, DK, DE, LU, PL, SK, SW, UA
Arthonia subastroidea	FR
Arthonia vinosa	CZ, PL, SK, SW, UA
Arthothelium spectabile	UA
Aspicilia faginea	PL

SPECIES	COUNTRY CODE
Aspicilia laevata	PL
Aspicilia verrucosa var. *mutabilis*	IT
Bacidia absistens	SW
Bacidia albogranulosa	UA
Bacidia arceutina	ES, UA
Bacidia biatorina	FR, SK, ES, SW
Bacidia caesiovirens	SI
Bacidia flavicans	FR
Bacidia fraxinea	IT, UA
Bacidia friesiana	GB
Bacidia igniarii	PL
Bacidia laurocerasi	CZ, FR, IT, PL, ES
Bacidia polychroa	PL, ES
Bacidia punica	ES
Bacidia rosella	DK, FR, IT, PL, SK, ES, SW, UA
Bacidia rubella	AT, CZ, DK, IT, PL, RO, SK, SI, ES, SW, UA
Bacidia trachona	SW
Bacidia viridifarinosa	SW
Bacidina adastra	GB
Bacidina arnoldiana[*2]	GB, DK, DE, IT, PL, SK, SW
Bacidina assulata	FR, PL
Bacidina chloroticula	AT, CZ
Bacidina delicata	GB, IT, SK, UA
Bacidina mendax	UA
Bacidina neosquamulosa	GB, BG
Bacidina phacodes	AT, CZ, DK, IT, MK, PL, SK, SW, UA
Bacidina sulphurella	DE, PL, SK, UA
Bellicidia incompta	BG, CZ, DK, PL, SK, ES, SW, UA
Biatora bacidioides	UA
Biatora beckhausii	PL, UA
Biatora chrysantha	AT, GB, CZ, FR, PL, RO, SK, SW, UA
Biatora efflorescens	AT, CZ, PL, RO, SK, SI, SW, UA
Biatora fallax	AT, CZ, RO
Biatora flavopunctata	SI
Biatora globulosa	MK, PL, SK, SI, SW, UA
Biatora helvola	AT, CZ, FR, PL, RO, SI
Biatora hemipolia	FR
Biatora longispora	UA
Biatora mendax	CZ, FR, SI, UA
Biatora ocelliformis	AT, CZ, RO, SK, SI, UA
Biatora pontica	AT, PL, SK, SI, UA
Biatora subduplex	SI
Biatora vernalis	AT, FR, SK, SI, ES, UA
Biatoridium monasteriense	AT, BG, CZ, PL, SK, SI, SW, UA

SPECIES	COUNTRY CODE
Bibbya vermifera	CZ, MK, UA
Bilimbia microcarpa	AT
Bilimbia sabuletorum	AT, PL, SK, UA
Brianaria bauschiana	GB
Bryobilimbia hypnorum	AT, IT, ES
Bryobilimbia sanguineoatra	AT, HR, CZ, SK
Bryoria bicolor	PL
Bryoria capillaris	IT, PL
Bryoria fuscescens	IT, PL, SK, SI, ES, UA
Bryoria implexa	PL, ES
Bryoria nadvornikiana	PL
Bryoria smithii	PL
Bryostigma muscigenum	CZ
Buellia disciformis	AT, GB, HR, CZ, FR, IT, LU, PL, RO, SK, SI, ES, SW, UA
Buellia erubescens	CZ, IT, SK, SI, UA
Buellia griseovirens	AT, GB, CZ, DK, DE, IT, LU, ME, PL, RO, SK, SI, SW, UA
Buellia schaereri	UA
Calicium abietinum	GB, BG, PL, UA
Calicium adspersum	PL
Calicium glaucellum	GB, PL, SK
Calicium quercinum	PL
Calicium salicinum	AT, GB, CZ, PL, SK, SI, SW, UA
Calicium viride	GB, CZ, PL, SW
Caloplaca alnetorum	ES
Caloplaca aurantia	IT
Caloplaca cerina	AL, HR, IT, MK, PL, UA
Caloplaca cerinella	CZ, IT, TR
Caloplaca cerinelloides	SK
Caloplaca chlorina	MK
Caloplaca ferruginea	IT, ES
Caloplaca herbidella	AT, HR, FR, IT, PL, RO, SK, SI, SW
Caloplaca holocarpa	DE, IT, PL, SK, ES
Caloplaca hungarica	ME
Caloplaca lucifuga	DE, ES
Caloplaca luteoalba	DK
Caloplaca monacensis	AT, RO, UA
Caloplaca obscurella	GB, SK, UA
Caloplaca pollinii	ES
Caloplaca pyracea	IT, SK, ES
Caloplaca sorocarpa	UA
Caloplaca stillicidiorum	UA
Caloplaca substerilis	MK, SK, UA
Caloplaca turkuensis	SK, UA
Caloplaca ulcerosa	GB
Candelaria concolor	AT, HR, IT, PL, RO, ES, SW, UA

SPECIES	COUNTRY CODE
Candelariella aurella	IT
Candelariella efflorescens	AT, CZ, DK, SK, UA
Candelariella faginea	AL
Candelariella reflexa	AT, GB, BG, DE, IT, LU, MK, ME, PL, RO, SK, SI
Candelariella vitellina	GB, FR, PL, SK, SI, ES, UA
Candelariella xanthostigma	AT, BG, CZ, DE, IT, PL, SK, SI, ES, UA
Carbonicola myrmecina	SW
Catapyrenium psoromoides	FR
Catillaria chalybeia	IT
Catillaria nigroclavata	DE, ES, SW, UA
Catillaria rugulosa	FR, PL
Catinaria atropurpurea	GB, UA
Catinaria montana	FR
Cetrelia cetrarioides	AL, AT, BG, CZ, DE, IT, ME, SK, SI, UA
Cetrelia chicitae	AT, RO, SI, UA
Cetrelia monachorum	AT, BG, CZ, DE, RO, SK, SI, UA
Cetrelia olivetorum	AT, BG, HR, FR, IT, PL, RO, SK, SI, ES, UA
Chaenotheca brachypoda	DK, IT, PL, SK, SW, UA
Chaenotheca brunneola	SK
Chaenotheca chlorella	CZ, SK, SW
Chaenotheca chrysocephala	GB, PL, SK
Chaenotheca ferruginea	GB, DE, PL
Chaenotheca furfuracea	DK, DE, IT, PL, SK, ES, SW, UA
Chaenotheca gracilenta	PL, UA
Chaenotheca phaeocephala	PL, UA
Chaenotheca stemonea	CZ, DE, PL, SK
Chaenotheca trichialis	GB, DK, DE, IT, PL, SK, UA
Chaenotheca xyloxena	IT, SK, UA
Cheiromycina flabelliformis	CZ
Chrysothrix candelaris	GB, BG, CZ, DK, IT, PL, SK
Chrysothrix chrysophthalma	GB
Circinaria caesiocinerea	UA
Circinaria gibbosa	PL
Cladonia caespiticia	PL
Cladonia cenotea	PL
Cladonia chlorophaea	AT, GB, BG, FR, IT, PL, SK, SI, ES, SW, UA
Cladonia coccifera	RO
Cladonia coniocraea	AT, GB, BG, HR, DE, IT, PL, RO, SK, SI, ES, SW, UA
Cladonia cornuta	GB, SK
Cladonia digitata	GB, BG, DE, PL, SK, SW
Cladonia fimbriata	AT, GB, FR, DE, IT, PL, RO, SK, SI, ES, SW, UA
Cladonia furcata	IT, RO, SI
Cladonia glauca	PL
Cladonia macilenta	GB, DE, PL, UA
Cladonia monomorpha	PL

SPECIES	COUNTRY CODE
Cladonia ochrochlora	GB, PL, UA
Cladonia parasitica	GB, IT, SW
Cladonia phyllophora	PL
Cladonia pleurota	SW
Cladonia polydactyla	GB, SK, SW
Cladonia portentosa	GB
Cladonia pyxidata	AT, HR, IT, PL, RO, SK, SI, ES, UA
Cladonia ramulosa	PL, SK
Cladonia squamosa var. *squamosa*	CZ, SW
Cladonia subulata	UA
Cliostomum griffithii	GB, DK, DE, PL, SW, UA
Coenogonium luteum	AT, FR, SK, SI, UA
Coenogonium pineti	AT, GB, DK, DE, IT, LU, PL, RO, SK, SW, UA
Collema flaccidum	AL, AT, BG, FR, IT, ME, PL, RO, SK, SI, ES, SW, UA
Collema furfuraceum	AL, SI, ES
Collema nigrescens	HR, FR, IT, MK, PL, SI, ES, UA
Collema subflaccidum	BG, HR, FR, IT, MK, SK, UA
Collema subnigrescens	FR, ES
Coniocarpon cinnabarinum	IT, PL, ES
Coniocarpon elegans	PL
Cratiria lauri-cassiae	ES
Cresponea premnea	GB
Dendrographa decolorans	GB, DK, ES
Dendrographa latebrarum	RO
Diploicia canescens	GB
Diploschistes muscorum	SI, ES, UA
Diplotomma alboatrum	IT, PL, ES
Diplotomma pharcidium	PL
Dolichousnea longissima	FR, PL, ES
Enterographa crassa	GB, IT, ES
Enterographa hutchinsiae	LU
Enterographa zonata	SW
Eopyrenula leucoplaca	PL, SK
Evernia divaricata	CZ, PL, RO
Evernia prunastri	AT, GB, BG, HR, DK, FR, DE, GR, IT, LU, PL, RO, SK, SI, ES, SW, UA
Felipes leucopellaeus	CZ, FR, PL
Fellhanera bouteillei	UA
Fellhanera gyrophorica	AT, FR, SK, CH, UA
Fellhaneropsis vezdae	GB, CZ, SW
Flavoparmelia caperata	AT, GB, BG, HR, IT, LU, PL, RO, SK, SI, ES, UA
Flavoparmelia soredians	GB, BG, ES
Flavopunctelia flaventior	PL
Frutidella furfuracea	CZ, PL, SK, UA
Fuscidea arboricola	CZ, PL, SK, SI, CH, UA

SPECIES	COUNTRY CODE
Fuscidea cyathoides	AL, HR, FR, IT, LU, ME, PL, SK, SI, SW, UA
Fuscidea lightfootii	GB, LU, ES
Fuscidea pusilla	PL
Fuscopannaria ignobilis	ES
Fuscopannaria leucosticta	AT
Fuscopannaria mediterranea	MK, ES
Gabura fascicularis	MK
Graphis betulina	FR
Graphis elegans	GB, FR, SK, ES
Graphis inustuloides	GB, RO
Graphis macrocarpa	FR
Graphis pulverulenta	FR, DE, SK
Graphis scripta	AT, GB, BG, HR, CZ, DK, FR, DE, GR, IT, ME, PL, RO, SK, SI, ES, SW, UA
Gyalecta arbuti	FR
Gyalecta carneola	DK, FR, IT, SK, SW, UA
Gyalecta derivata	AT, MK, PL, UA
Gyalecta fagicola	LU, MK, PL, ES
Gyalecta flotowii	AT, CZ, LU, PL, SK, SW, UA
Gyalecta herculina	PL, SK, SI, UA
Gyalecta ophiospora	PL
Gyalecta truncigena	IT, PL, SK, SI, ES, UA
Gyalecta ulmi	AT, PL, SW, UA
Gyalideopsis calabrica	IT
Gyalideopsis helvetica	UA
Gyalolechia flavorubescens var. *flavorubescens*	IT, ES
Haematomma ochroleucum	BG, DK, IT, PL, SK, SW, UA
Haematomma sorediatum	FR
Halecania viridescens	CZ, UA
Heterodermia obscurata	ES
Heterodermia speciosa	IT, PL, SI, ES, UA
Hyperphyscia adglutinata	GB, FR, DE, IT, SK, ES
Hypocenomyce scalaris	GB, HR, DE, PL, SK, UA
Hypogymnia bitteri	IT, PL
Hypogymnia farinacea	IT, PL, RO, SK, ES, UA
Hypogymnia physodes	AL, AT, GB, BG, CZ, DK, FR, DE, IT, PL, RO, SK, SI, ES, SW, UA
Hypogymnia tubulosa	AL, GB, DE, IT, ME, PL, RO, SK, SI, ES, UA
Hypogymnia vittata	PL, RO, SK, UA
Hypotrachyna afrorevoluta	AT, BE, BG, FR, LU, PL, UA
Hypotrachyna laevigata	IT
Hypotrachyna revoluta	AT, GB, BG, DK, IT, LU, PL, SK, SI, SW, UA
Imshaugia aleurites	PL, SK
Inoderma byssaceum	PL, UA
Jamesiella anastomosans	CZ, SW
Lathagrium auriforme	ME

SPECIES	COUNTRY CODE
Lecanactis abietina	GB, CZ, DK, PL, SW
Lecania chlorotiza	GB, LU
Lecania croatica	CZ, RO, SK, SI, UA
Lecania cyrtella	AT, CZ, DK, DE, MK, PL, SK, SW
Lecania cyrtellina	DK, SW, UA
Lecania erysibe	GB
Lecania naegelii	LU, PL, ES, SW, UA
Lecanographa amylacea	PL, SK
Lecanora albella	AT, BG, CZ, IT, LU, MK, PL, RO, SK, SI, UA
Lecanora albellula	GB, PL, ES, UA
Lecanora allophana	AL, AT, HR, DK, FR, IT, MK, PL, RO, SI, ES, SW, UA
Lecanora argentata	AL, AT, BG, HR, CZ, DK, FR, DE, GR, IT, MK, PL, RO, SK, SI, ES, SW, TR, UA
Lecanora carpinea	AL, AT, HR, CZ, DK, FR, DE, GR, IT, MK, PL, RO, SK, SI, ES, TR, UA
Lecanora cenisia	PL
Lecanora chlarotera	AL, AT, GB, BG, DK, FR, DE, GR, IT, MK, PL, RO, SK, SI, ES, SW, UA
Lecanora cinereofusca	GB, FR, RO, UA
Lecanora compallens	CZ
Lecanora conizaeoides	GB, DK, DE, LU, PL, RO, SK, SI, SW
Lecanora expallens	GB, BG, CZ, DK, DE, IT, PL, SK, SI, SW, UA
Lecanora expersa	UA
Lecanora glabrata	BG, HR, CZ, DK, FR, IT, MK, ME, PL, RO, SK, SI, ES, SW, UA
Lecanora horiza	AL, FR, IT, SI, ES
Lecanora hybocarpa	ES
Lecanora hypoptella	ES
Lecanora impudens	PL, UA
Lecanora intricata	UA
Lecanora intumescens	AL, AT, CZ, FR, DE, IT, LU, PL, RO, SK, SI, ES, SW, UA
Lecanora jamesii	AT, GB, LU
Lecanora leptyrodes	AL, FR, IT, ME, PL, SK, ES, UA
Lecanora paramerae	ES
Lecanora phaeostigma	UA
Lecanora polytropa	PL, UA
Lecanora pulicaris	AT, GB, CZ, DK, FR, DE, IT, PL, RO, SK, SI, ES, UA
Lecanora saligna	AL, HR, CZ, PL, SK, SI, UA
Lecanora stanislai	UA
Lecanora strobilina	PL, UA
Lecanora subcarpinea	HR, DE, LU, MK, ME, SK, SI
Lecanora subintricans	FR
Lecanora subintricata	SK, SI
Lecanora sublivescens	GB
Lecanora substerilis	CZ, RO, SK, UA
Lecanora symmicta	GB, IT, PL, SI, UA
Lecanora thysanophora	AT, CZ, DE, PL, RO, SK, SI, UA
Lecanora varia	PL, SK, SI, UA

SPECIES	COUNTRY CODE
Lecidea albohyalina	CZ, PL, UA
Lecidea erythrophaea	PL, UA
Lecidea nylanderi	CZ, RO
Lecidea sphaerella	CZ
Lecidella albida	FR
Lecidella elaeochroma	AL, AT, GB, BG, HR, CZ, DK, FR, DE, GR, IT, MK, ME, PL, RO, SK, SI, ES, SW, TR, UA
Lecidella euphorea	AL, IT, SI, ES
Lecidella flavosorediata	PL, RO, SI, ES, UA
Lecidella pulveracea	FR
Lecidella stigmatea	GB
Lecidella subviridis	CZ
Leiorreuma lyellii	GB, FR, ES
Lepra albescens* var. *albescens	AL, AT, GB, BG, HR, DK, FR, DE, IT, MK, ME, PL, RO, SK, SI, ES, SW, UA
Lepra albescens var. *corallina*	GB, SI
Lepra amara	AL, AT, GB, BG, HR, CZ, DK, FR, DE, GR, IT, LU, ME, PL, RO, SK, SI, ES, SW, UA
Lepra borealis	RO
Lepra corallina	PL
Lepra dactylina	ES
Lepra graeca	FR
Lepra multipuncta	GB, DK, IT, PL, SW
Lepra ophthalmiza	FR, SI
Lepra pulvinata	GB
Lepra slesvicensis	IT
Lepra trachythallina	PL
Lepra waghornei	SK
Lepraria caesioalba	LU, ES
Lepraria celata	UA
Lepraria crassissima	LU
Lepraria eburnea	PL, SI, ES
Lepraria ecorticata	ES, UA
Lepraria elobata	PL, SI, UA
Lepraria finkii	AT, RO, ES, UA
Lepraria incana	AT, GB, BG, HR, DK, FR, DE, IT, PL, SK, SI, ES, SW, UA
Lepraria jackii	PL, ES
Lepraria lobificans [*3]	GB, BG, DK, DE, GR, IT, ME, PL, SK, SI, UA
Lepraria membranacea	FR, ES, SW, UA
Lepraria rigidula	CZ, DK, MK, PL, SK, SI, CH, UA
Lepraria umbricola	BE, GB
Lepraria vouauxii	PL, SI, UA
Leproplaca chrysodeta	CZ, UA
Leptogium brebissonii	ES
Leptogium burnetiae	ES
Leptogium cyanescens	BG, PL, RO, SK, ES, UA
Leptogium saturninum	AL, AT, FR, IT, PL, SI, ES, UA

SPECIES	COUNTRY CODE
Leucodermia leucomelos	GB, ES
Lichenomphalia umbellifera	SK
Lobaria pulmonaria	AL, AT, BG, HR, DK, FR, IT, ME, PL, RO, SK, SI, ES, SW, UA
Lobarina scrobiculata	FR, IT, PL, ES, SW
Lopadium disciforme	AT, BG, CZ, PL, SK, SI, SW, UA
Loxospora cismonica	AT
Loxospora elatina	GB, CZ, PL, SK, SI, UA
Maronea constans	PL
Megalaria grossa	BG, FR, ES
Megalaria laureri	BG, HR, FR, ME, PL, RO, SI, SW, UA
Megalaria pulverea	PL, SI
Megalospora pachycarpa	FR, PL
Melanelixia fuliginosa*[4]	AL, AT, GB, HR, FR, IT, PL, RO, SK, SI, ES, SW
Melanelixia glabra	AL, AT, FR, IT, MK, PL, SK, SI, ES, UA
Melanelixia glabratula	CZ, DK, DE, GR, IT, MK, PL, RO, SK, SI, ES, UA
Melanelixia subargentifera	GB, BG, IT, PL, ES, UA
Melanelixia subaurifera	AT, GB, BG, DE, IT, MK, PL, RO, SK, SI, ES, TR, UA
Melanohalea elegantula	DE, IT, PL, SK, SI, ES, UA
Melanohalea exasperata	AL, DE, IT, ME, PL, SK, SI, ES, UA
Melanohalea exasperatula	AL, AT, GB, DE, IT, PL, SK, ES, UA
Melanohalea laciniatula	FR, IT, PL, SI, ES
Menegazzia subsimilis	UA
Menegazzia terebrata	AT, BG, HR, CZ, FR, IT, PL, RO, SK, SI, SW, UA
Micarea adnata	CZ, IT, SW
Micarea botryoides	SK
Micarea cinerea	CZ, PL
Micarea denigrata	GB, CZ, FR, MK, PL, SK
Micarea globulosella	CZ, UA
Micarea lignaria	SI
Micarea melaena	GB
Micarea micrococca	CZ, UA
Micarea misella	UA
Micarea nitschkeana	PL
Micarea peliocarpa	AT, CZ, IT, PL, SK, SI, ES, SW, UA
Micarea prasina	AT, GB, CZ, DK, DE, LU, PL, SK, ES, SW, UA
Micarea pycnidiophora	FR, LU, PL
Micarea synotheoides	CZ
Multiclavula mucida	CZ, SK, UA
Mycobilimbia carneoalbida	AT, IT, PL, ES, SW, UA
Mycobilimbia epixanthoides	AT, PL, SW, UA
Mycobilimbia pilularis	CZ, FR, IT, PL, ES, SW, UA
Mycobilimbia tetramera	AT, PL, SK, ES, UA
Mycoblastus affinis	PL, RO
Mycoblastus sanguinarius	PL, RO
Myriolecis albescens	IT

SPECIES	COUNTRY CODE
Myriolecis dispersa	GB
Myriolecis hagenii	AT, BE, HR, DE, IT, PL, RO
Myriolecis persimilis	AL, AT, PL
Myriolecis sambuci	MK, UA
Nephroma bellum	FR, SK, SI
Nephroma helveticum	FR
Nephroma laevigatum	BG, FR, IT, PL, SK, ES
Nephroma parile	AL, AT, BG, HR, CZ, IT, ME, PL, RO, SK, SI, ES, SW, UA
Nephroma resupinatum	AL, AT, FR, IT, ME, PL, RO, SK, SI, ES, UA
Nephromopsis chlorophylla	PL, SK, UA
Nephromopsis laureri	UA
Nevesia sampaiana	FR, ES
Normandina acroglypta	SI, UA
Normandina pulchella	AT, GB, BG, FR, IT, PL, SK, SI, ES, SW, UA
Ochrolechia alboflavescens	UA
Ochrolechia androgyna	AL, GB, BG, CZ, LU, PL, RO, SK, SI, SW, UA
Ochrolechia arborea	AT, IT, PL, SI, UA
Ochrolechia bahusiensis	PL
Ochrolechia balcanica	IT, ME, ES
Ochrolechia microstictoides	CZ, PL
Ochrolechia pallescens	AT, FR, IT, ME, PL, SK, SI, ES, SW, UA
Ochrolechia subviridis	GB, DK, IT, PL, SK, SI, ES, SW
Ochrolechia szatalaensis	PL, SK, ES, UA
Ochrolechia trochophora	PL
Ochrolechia turneri	GB, IT, MK, ES, SW, UA
Opegrapha fumosa	UA
Opegrapha niveoatra	AT, GB, CZ, FR, PL, SK, ES, UA
Opegrapha phegospila	FR
Opegrapha trochodes	CZ, IT, SK, UA
Opegrapha vermicellifera	GB, BG, CZ, DK, LU, PL, SK, ES, SW, UA
Opegrapha vulgata	GB, BG, DK, DE, LU, MK, PL, RO, SK, SI, ES, SW, UA
Pachnolepia pruinata	IT, PL
Pannaria conoplea	FR, IT, PL, SI, ES, SW, UA
Pannaria rubiginosa	ES
Pannaria tavaresii	ES
Parmelia barrenoae	FR, MK
Parmelia ernstiae	AT, BG, DK, FR, MK, SW
Parmelia omphalodes	ES
Parmelia saxatilis	AL, AT, GB, HR, CZ, DK, FR, DE, IT, LU, PL, RO, SK, SI, ES, SW, UA
Parmelia serrana	ES
Parmelia submontana	AL, CZ, IT, MK, PL, RO, SK, SI, ES, UA
Parmelia sulcata	AL, AT, GB, BG, HR, CZ, DK, FR, DE, GR, IT, LU, PL, RO, SK, SI, ES, SW, UA
Parmeliella testacea	FR
Parmeliella triptophylla	AL, AT, BG, FR, LU, PL, SK, SI, ES, SW, UA

SPECIES	COUNTRY CODE
Parmelina carporrhizans	HR, RO, SI, ES, CH
Parmelina pastillifera	AL, AT, BG, HR, IT, MK, ME, PL, RO, SK, SI, ES, UA
Parmelina quercina	AL, HR, GR, IT, PL, SK, SI, CH
Parmelina tiliacea	AT, FR, DE, IT, PL, RO, SK, SI, ES, UA
Parmeliopsis ambigua	AT, GB, CZ, DE, IT, LU, PL, RO, SK, SI, SW, UA
Parmeliopsis hyperopta	AT, GB, CZ, GR, PL, SK, SW, UA
Parmotrema arnoldii	PL, SK, SI, UA
Parmotrema crinitum	AT, IT, PL, SI, ES, UA
Parmotrema perlatum	AT, GB, BG, HR, IT, ME, PL, RO, SK, SI, ES, UA
Parmotrema reticulatum	IT
Parmotrema stuppeum	PL
Pectenia atlantica	AL
Pectenia plumbea	IT, ME, SI, ES
Peltigera canina	SI, ES
Peltigera collina	AL, AT, GB, HR, FR, IT, ME, PL, RO, SI, ES, SW, UA
Peltigera degenii	AL, AT, CZ, RO, SK, SI, UA
Peltigera horizontalis	AT, GB, BG, HR, CZ, IT, ME, RO, SI, ES, SW, UA
Peltigera lactucifolia	BG
Peltigera membranacea	AL, AT, IT
Peltigera polydactylon	GR, IT, PL, UA
Peltigera praetextata	AL, AT, GB, BG, HR, CZ, FR, IT, LU, ME, PL, RO, SK, SI, ES, SW, UA
Peltigera rufescens	IT, ES
Pertusaria alpina	AT, FR, PL, SK, SI, ES
Pertusaria cinereocarneola	FR
Pertusaria coccodes	AL, AT, GB, HR, CZ, DK, FR, GR, IT, LU, PL, RO, SK, SI, ES, UA
Pertusaria constricta	AT, CZ, FR, PL, UA
Pertusaria coronata	AL, AT, BG, CZ, FR, DE, IT, MK, PL, RO, SK, SI, ES, SW, UA
Pertusaria deschatresii	FR
Pertusaria flavida	AL, AT, GB, HR, DK, FR, IT, LU, PL, SI, ES, SW, UA
Pertusaria hymenea	GB, BG, CZ, DK, FR, DE, IT, LU, PL, SK, SI, ES, SW
Pertusaria jurana	FR
Pertusaria laureri	FR
Pertusaria leioplaca	AT, BG, CZ, DK, FR, DE, GR, IT, MK, ME, PL, RO, SK, SI, ES, SW, UA
Pertusaria monogoniza	FR
Pertusaria pertusa	AL, AT, GB, BG, HR, CZ, DK, FR, DE, GR, IT, LU, ME, PL, RO, SK, SI, ES, SW, TR, UA
Pertusaria pulvereosulphurata	FR, PL
Pertusaria pupillaris	CZ, FR, LU, SW, UA
Pertusaria pustulata	GB, BG, PL, SK, ES, UA
Phaeographis dendritica	GB, FR, PL, SI, ES
Phaeographis inusta	FR
Phaeographis smithii	NL
Phaeophyscia ciliata	IT
Phaeophyscia endophoenicea	AL, AT, BG, CZ, IT, PL, SK, SI, ES, SW, UA

SPECIES	COUNTRY CODE
Phaeophyscia nigricans	PL, SK, UA
Phaeophyscia orbicularis	AL, GB, HR, CZ, DE, IT, PL, RO, SK, SI, ES, UA
Phaeophyscia pusilloides	FR, SK, ES
Phaeophyscia rubropulchra	RO
Phlyctis agelaea	AT, GB, BG, FR, IT, LU, PL, SK, SI, ES, SW, UA
Phlyctis argena	AT, GB, BG, CZ, DK, FR, DE, IT, LU, PL, RO, SK, SI, ES, SW, UA
Physcia adscendens	AT, GB, DE, GR, IT, LU, PL, RO, SK, SI, ES, TR, UA
Physcia aipolia	GB, IT, MK, RO, ES, UA
Physcia biziana var. *biziana*	IT
Physcia caesia	PL
Physcia clementei	ES
Physcia dubia	SK, UA
Physcia leptalea	DE, IT, RO, ES
Physcia stellaris	DE, IT, PL, RO, SI, ES, UA
Physcia tenella	GB, CZ, DK, DE, IT, PL, SK, SI, ES, SW, UA
Physcia tribacia	FR
Physciella chloantha	IT, SK, SI, ES, UA
Physconia detersa	AT, MK, UA
Physconia distorta	AL, AT, GB, IT, MK, PL, RO, ES, UA
Physconia enteroxantha	AT, GB, ES, UA
Physconia grisea	PL
Physconia muscigena	FR
Physconia perisidiosa	IT, PL, SK, ES, UA
Physconia servitii	IT
Physconia venusta	HR, FR, IT, ME, ES
Piccolia ochrophora	IT, SK, UA
Placynthiella dasaea	BG, CZ, MK, PL
Placynthiella icmalea	GB, BG, DE, PL, UA
Placynthiella oligotropha	PL
Placynthiella uliginosa	GB, PL
Platismatia glauca	AL, AT, GB, HR, CZ, FR, DE, IT, PL, RO, SK, SI, ES, SW, UA
Pleurosticta acetabulum	AL, HR, FR, GR, IT, ME, PL, RO, ES, UA
Polyblastidium subneglectum	FR, ES, UA
Polycauliona candelaria	GB, DE, PL, SI
Polycauliona polycarpa	GB, DK, DE, PL, SK, UA
Polycauliona ucrainica	DE
Porina aenea	AT, BG, CZ, DK, DE, IT, RKS, PL, SK, SI, ES, SW, UA
Porina borreri	FR, ES
Porina chlorotica	GB
Porina hibernica	AT, SI, ES, UA
Porina leptalea	GB, CZ, FR, PL, SK, UA
Porina pseudohibernica	AT, FR, IT, SI, UA
Porina rosei	FR
Porpidia macrocarpa	UA

SPECIES	COUNTRY CODE
Protopannaria pezizoides	AT, FR, SI, UA
Protoparmelia hypotremella	AT
Protoparmelia oleagina	PL
Protoparmeliopsis muralis	ES, UA
Pseudevernia furfuracea var. *ceratea*	GB, IT, ME, PL, ES
Pseudevernia furfuracea* var. *furfuracea	AL, HR, DE, IT, PL, RO, SK, SI, ES, UA
Pseudoschismatomma rufescens	AT, CZ, DK, FR, DE, IT, PL, SK, ES, SW, UA
Psilolechia lucida	SW
Psoroglaena abscondita	CZ
Psoroglaena dictyospora	CZ
Psoroglaena stigonemoides	SK, UA
Punctelia borreri	GB
Punctelia jeckeri	AT, GB, DE, PL, UA
Punctelia subrudecta	GB, HR, IT, PL, RO, SI, ES, UA
Puttea exsequens	FR
Pyrenula chlorospila	GB, RO, ES
Pyrenula coryli	UA
Pyrenula dermatodes	FR
Pyrenula laevigata	AT, CZ, FR, PL, UA
Pyrenula macrospora	IT, RO
Pyrenula nitida	AT, GB, BG, HR, CZ, FR, DE, IT, LU, ME, PL, RO, SK, SI, ES, SW, UA
Pyrenula nitidella	GB, FR, IT, PL, SI
Pyrenula occidentalis	GB
Pyrrhospora quernea	GB, DK, DE, PL, SW, UA
Ramalina baltica	PL
Ramalina calicaris	GR, IT, ME
Ramalina canariensis	AT, IT, RO, ES
Ramalina farinacea	AT, GB, BG, HR, DK, FR, DE, GR, IT, PL, RO, SK, SI, ES, SW, UA
Ramalina fastigiata	AL, AT, BG, HR, IT, ME, PL, SI, ES, UA
Ramalina fraxinea	AL, AT, GB, FR, GR, IT, MK, PL, RO, ES, UA
Ramalina obtusata	PL
Ramalina panizzei	IT
Ramalina pollinaria	IT, PL, RO, SK, SI, ES, UA
Ramalina thrausta	IT, PL
Ramonia luteola	SK, UA
Ramonia subsphaeroides	ES
Reichlingia leopoldii	SK, UA
Reichlingia zwackhii	FR
Rhizocarpon polycarpum	UA
Ricasolia amplissima	AL, AT, FR, IT, RO, ES, UA
Ricasolia virens	GB, FR, IT, ES, SW
Rinodina albana	AL, AT, MK, ME, UA
Rinodina archaea[*5]	UA

SPECIES	COUNTRY CODE
Rinodina capensis	CZ, IT, ME, PL, UA
Rinodina colobina	IT, SW
Rinodina conradii	UA
Rinodina efflorescens	BG, CZ, SW, UA
Rinodina exigua	AT, GB, IT, PL
Rinodina griseosoralifera	SK, UA
Rinodina oleae	GB
Rinodina orculata	UA
Rinodina pyrina	AT, IT, PL, UA
Rinodina roboris	GB
Rinodina sophodes	IT, ME, PL, SI, ES, UA
Rinodina subpariata	CZ, UA
Rinodina trevisanii	UA
Ropalospora viridis	CZ, DK, DE, LU, PL, RO, SK, SI, SW, UA
Sarcosagium campestre	SK
Schismatomma pericleum	FR, PL, SW
Schismatomma quercicola	GB, FR
Schismatomma ricasolii	IT
Sclerophora amabilis	CZ, SK, SW
Sclerophora farinacea	SK, UA
Sclerophora pallida	MK, PL, SK, UA
Sclerophora peronella	PL, SK, ES, SW
Scoliciosporum chlorococcum	GB, CZ, DK, DE, LU, PL, SK, SI, UA
Scoliciosporum gallurae	LU, ES
Scoliciosporum pruinosum	LU, SW, UA
Scoliciosporum sarothamni	GB, CZ, SK, UA
Scoliciosporum schadeanum	CZ, UA
Scoliciosporum umbrinum	AL, AT, FR, IT, MK, ME, SK, ES, UA
Scutula circumspecta	AT, BE, CZ, DK, FR, IT, MK, PL, SK, SI, ES, UA
Scutula effusa	FR, IT
Scytinium aragonii	AT, ES
Scytinium fragrans	FR
Scytinium gelatinosum	UA
Scytinium lichenoides	AL, AT, BG, IT, ME, SK, SI, ES, SW, UA
Scytinium pulvinatum	AT, UA
Scytinium tenuissimum	AT, ES
Scytinium teretiusculum	CZ, UA
Sphaerophorus globosus	IT, PL, ES, SW
Sticta fuliginosa	UA
Sticta limbata	IT, ES
Strangospora moriformis	SK
Strangospora pinicola	GB, UA
Strigula affinis	ES
Strigula glabra	FR
Strigula stigmatella	AT, BG, FR, ME, PL, RO, SK, SI, UA

SPECIES	COUNTRY CODE
Strigula thelopsidoides	FR
Strigula zizyphi	ES
Tephromela atra* var. *torulosa	AL, FR, IT, PL, ES, UA
Tephromela grumosa	LU
Tetramelas chloroleucus	SK, UA
Tetramelas insignis	UA
Thelenella muscorum	AT, ES, UA
Thelocarpon laureri	UA
Thelopsis flaveola	AT, FR, UA
Thelopsis rubella	AT, GB, CZ, FR, PL, SK, ES, SW, UA
Thelotrema lepadinum	AT, GB, BG, HR, CZ, DK, FR, IT, LU, PL, RO, SK, SI, ES, SW, UA
Thelotrema suecicum	AT
Toensbergia leucococca	UA
Toninia populorum	PL
Toniniopsis subincompta	AT, CZ, IT, MK, PL, RO, SK, SI, UA
Trapelia corticola	GB, CZ, PL, SK
Trapelia glebulosa	CZ
Trapeliopsis flexuosa	GB, DK, IT, PL, SK, UA
Trapeliopsis gelatinosa	AT, SK, SW
Trapeliopsis granulosa	GB, SK, SW
Trapeliopsis pseudogranulosa	GB, DK, PL, RO, SW, UA
Trapeliopsis viridescens	PL
Usnea articulata	IT
Usnea barbata	CZ, IT, PL, UA
Usnea cavernosa	PL
Usnea ceratina	GB, PL, UA
Usnea chaetophora	BG
Usnea cornuta	GB
Usnea dasopoga	FR, IT, MK, ME, PL, SK, SI, UA
Usnea florida	GB, PL, RO
Usnea glabrata	PL
Usnea glabrescens var. *glabrescens*	PL
Usnea glabrescens var. *fulvoreagens*	IT, PL
Usnea hirta	GR, IT, MK, PL, SI, UA
Usnea intermedia	AT, PL, RO, SI
Usnea perplexans	PL, UA
Usnea rubicunda	GB
Usnea silesiaca	PL
Usnea subfloridana	AT, GB, IT, PL, RO, SI, ES, UA
Usnea subscabrosa	IT
Usnea substerilis	MK, UA
Usnea wasmuthii	PL, ES, UA
Vahliella saubinetii	FR

SPECIES	COUNTRY CODE
Varicellaria hemisphaerica	AT, GB, BG, CZ, DK, FR, GR, IT, LU, PL, RO, SK, SI, ES, SW, UA
Varicellaria lactea	RO
Varicellaria velata	SW
Verrucaria corticola	CZ, UA
Verrucaria hegetschweileri	UA
Verrucaria viridigrana	AT, UA
Vezdaea aestivalis	CZ, PL, SK, SW
Violella fucata	GB, CZ, DK, LU, PL, RO, SK, SI, SW, UA
Vulpicida pinastri	AT, CZ, PL, SK, SI, UA
Wadeana dendrographa	UA
Xanthomendoza fallax[*6]	IT
Xanthomendoza fulva	AL, ME, UA
Xanthomendoza ulophyllodes[*6]	UA
Xanthoria parietina	AL, AT, GB, CZ, DK, DE, IT, PL, RO, SK, SI, ES, TR, UA
Xylopsora caradocensis	PL
Zwackhia prosodea	RO
Zwackhia sorediifera	DK, SW
Zwackhia viridis	AT, GB, BG, CZ, DK, FR, IT, LU, PL, SK, SI, ES, SW, UA

[*1] *Arthonia exilis* could be confounded with *Arthonia apatetica*
[*2] *Bacidina arnoldiana* could be confounded with *Bacidina sulphurella*
[*3] *Lepraria lobificans* could be confounded with *Lepraria finkii*
[*4] *Melanelixia fuliginosa* could be confounded with *Melanelixia glabratula*
[*5] *Rinodina archaea* could be confounded with *Rinodina trevisanii*
[*6] *Xanthomendoza fallax* and *X. ulophyllodes* could be confounded with *Xanthomendoza huculica*

4 | ACKNOWLEDGEMENTS

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5 | AUTHORS' CONTRIBUTIONS

MP, PH, IM and GA conceived the study; PH, MP, IM and GA collected the data; PH, MP and HM prepared the dataset; PH led the writing of the manuscript and all authors provided critical reviews.

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7 | SUPPORTING INFORMATION

7.1. Appendix S1

List of primary studies included in this review.

ADAMČÍK, S., AUDE, E., BÄSSLER, C., CHRISTENSEN, M., VAN DORT, K., FRITZ, Ö., GLEJDURA, S., HEILMANN-CLAUSEN, J., HOLEC, J., JANČOVIČOVÁ, S., KUNCA, V., LACKOVIČOVÁ, A., LÜTH, M. & ÓDOR, P. 2016. Fungi and lichens recorded during the Cryptogam Symposium on Natural Beech Forests, Slovakia 2011. – Czech Mycology **68**: 1–40.

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Discusión general

Entender cómo se distribuye la biodiversidad espacialmente y cuáles son los factores subyacentes ha sido una de las grandes preguntas en Ecología (Gleason 1926, Pavoine & Bonsall 2011). En la actualidad, el análisis de la incidencia de factores como la fragmentación del hábitat o el clima sobre la biodiversidad parece necesario para poder entender el impacto del cambio global en las comunidades y, potencialmente, poner freno a la actual pérdida de biodiversidad. Los resultados de esta tesis muestran que tanto la fragmentación como el clima afectan a los patrones de diversidad de las comunidades de líquenes epífitos, pero estos impactos difieren en función de la dimensión de la diversidad (taxonómica, funcional o filogenética) y de la escala espacial (Península Ibérica y Europa) consideradas. Si bien es cierto que este resultado revela que las conclusiones basadas en una única dimensión de la diversidad pueden proporcionar una visión parcial de la respuesta de las comunidades, comprobamos que el impacto de la fragmentación y el clima sobre la dimensión taxonómica y filogenética está mediado, al menos en parte, por los rasgos funcionales de las especies que conforman la comunidad.

Durante las últimas décadas, la importancia de la diversidad funcional ha sido reconocida llegando a formar parte de una disciplina propia, la llamada Ecología Funcional (Tilman et al. 1997, Cadotte et al. 2011, Garnier 2016). El desarrollo de esta disciplina se ha basado, principalmente apoyada en el estudio de plantas vasculares, sin embargo, en los líquenes este campo está mucho menos desarrollado y ciertas cuestiones bien conocidas en plantas continúan sin respuesta. Por ejemplo, cuáles son los rasgos clave que median la respuesta de las comunidades frente a distintos factores ambientales, cómo varían dichos rasgos a lo largo de extensos gradientes, o cuál es el papel que juega la variabilidad intraespecífica en esta variación son aspectos aún sin respuesta. En la presente tesis intentamos dar respuesta a estas preguntas para conocer de una manera más precisa el papel de los rasgos funcionales seleccionados y proporcionar pautas para su empleo en estudios ecológicos con líquenes. Nuestros resultados demuestran que los rasgos cualitativos de líquenes tales como la *forma de crecimiento*, el *tipo de fotobionte* y la *estrategia reproductiva* son buenos indicadores de los efectos de la fragmentación y de las variaciones climáticas. Por el contrario, los rasgos cuantitativos seleccionados, que son mucho más costosos de cuantificar, no responden a los cambios climáticos con la misma intensidad (al menos a la escala de bosque a la que hemos registrado las variables climáticas). Además, comprobamos que la variabilidad intraespecífica juega un papel muy importante, incluso más que el recambio de especies, a la hora de determinar los cambios funcionales en las comunidades de líquenes epífitos.

A lo largo de la tesis hemos aplicado una aproximación multidimensional del concepto de biodiversidad y, como tal, a parte de la dimensión funcional, ambas dimensiones, filogenética y taxonómica, han sido explícitamente consideradas. Asimismo, hemos querido poner en valor la importancia de conocer la diversidad de especies de líquenes en ecosistemas tan emblemáticos como son los hayedos. En un contexto en el que existen vacíos de conocimiento para ciertos grupos biológicos o para los rangos de distribución de las especies (Hortal et al. 2015), hemos creado una herramienta de acceso libre y dinámica que esperamos sea de utilidad no sólo para los liquenólogos sino también para investigadores de distintas áreas y gestores medioambientales.

1 | PATRONES DE DIVERSIDAD DE LAS COMUNIDADES DE LÍQUENES EPÍFITOS EN RESPUESTA A LA FRAGMENTACIÓN DEL HÁBITAT Y EL CLIMA

Los resultados obtenidos en diferentes capítulos de la tesis (1, 2 y 5) demuestran que la fragmentación del hábitat y el clima tienen un efecto en los patrones de diversidad de las comunidades de líquenes. Sin embargo, los factores concretos que determinan los patrones de diversidad taxonómica, funcional y filogenética varían en función de la dimensión de la diversidad y de la escala consideradas (capítulos 1 y 2).

En hayedos situados a lo largo de la Península Ibérica evaluamos la incidencia que el clima, la fragmentación y la calidad del hábitat (usando el tamaño del bosque, la precipitación de verano y el diámetro de los árboles respectivamente) podría ejercer sobre las tres dimensiones de la diversidad (capítulo 1). Los resultados mostraron que los efectos de estas variables dependían de la dimensión de la diversidad y la región considerada. Así, comprobamos que la fragmentación del hábitat ejercía el mayor efecto en las comunidades de líquenes epífitos, reduciendo las tres dimensiones de la diversidad. Sin embargo, el segundo determinante más importante difería en función de la región biogeográfica, siendo el clima en la región Atlántica y la calidad del hábitat en la región Mediterránea (capítulo 1). Estos resultados sugieren que, bajo condiciones climáticas en principio menos estresantes, los factores abióticos a mayor escala (variables climáticas a escala de bosque) tenían mayor incidencia en las comunidades mientras que, en condiciones menos favorables, las comunidades respondían a factores a una escala menor como, por ejemplo, el diámetro de los árboles (capítulo 1). En una segunda aproximación, ampliamos la escala geográfica de estudio y seleccionamos un gradiente latitudinal de aproximadamente 3000 km a lo largo y ancho de Europa representando un amplio gradiente climático (capítulo 2). Así, evaluando el efecto de un conjunto de 19 variables climáticas a escala de bosque (Karger et al. 2017) y

una variable a menor escala (diámetro de los árboles) pudimos dar un paso más y comprobar que distintas variables climáticas eran las que daban forma a los patrones de diversidad taxonómica, funcional y filogenética (capítulo 2) (Safi et al. 2011, Chun & Lee 2017). De esta forma, llegamos a la conclusión de que los patrones de diversidad funcional y filogenética estaban principalmente afectados por la fluctuación de la temperatura mientras que la diversidad taxonómica respondía, mayoritariamente, a la precipitación del mes más húmedo. En conjunto, sitios más oceánicos albergaban comunidades más ricas en especies y, ante menores fluctuaciones de temperatura a lo largo del año, las comunidades de líquenes eran también más diversas en cuanto a rasgos funcionales y linajes evolutivos (capítulo 2) (Pausas & Austin 2001). Por tanto, cabría pensar que las comunidades de líquenes epífitos más diversas están asociadas a sitios con condiciones de humedad y temperatura más estables y favorables. Por último, y, al igual que encontramos en el capítulo 1, el diámetro de los árboles afectó a la diversidad filogenética, pero en esta ocasión no afectó a la diversidad taxonómica. En ambos casos (capítulos 1 y 2), árboles más grandes albergaban comunidades formadas por especies con distintos orígenes evolutivos lo cual podría estar relacionado con el hecho de que el tamaño del árbol es un indicador no sólo del espacio sino también del tiempo disponible para la llegada y establecimiento de los organismos (Riiali et al. 2001, Belinchón et al. 2009). Sin embargo, este aumento de la diversidad de linajes en la región Mediterránea de la Península Ibérica respondía a la entrada de nuevas especies en las comunidades (aumento de la riqueza de especies; capítulo 1) mientras que en Europa se producía por un reemplazo de las especies existentes (la riqueza de especies no varía; capítulo 2). En cualquier caso, el incremento en la diversidad filogenética también podría deberse a factores bióticos, por ejemplo, de mayor intensidad de facilitación bajo condiciones climáticas menos favorables (Valiente-Banuet & Verdú, 2007). Estudios previos no han obtenido relaciones significativas entre el grosor de los árboles y la estructura filogenética de las comunidades liquénicas en gradientes ambientales (Prieto et al. 2017), pero si con la diversidad taxonómica (Belinchón et al. 2009).

Los determinantes climáticos de las diferentes dimensiones de la diversidad diferían en función de la dimensión considerada pero, además, las condiciones climáticas específicas donde se maximizaban las distintas dimensiones de la diversidad también resultaron ser diferentes al evaluar los patrones de diversidad en las comunidades de macrolíquenes (capítulo 5). Aquellos bosques más cálidos y húmedos tenían comunidades más ricas en relación al número de especies mientras que bosques más fríos y húmedos presentaban una mayor diversidad en la composición de las especies. Por otra parte, las comunidades de

macrolíquenes con mayor diversidad funcional y filogenética aparecían en áreas con mayor sequía estival y mayor temperatura lo cual también podría responder al hecho de que, bajo condiciones climáticas menos favorables, se produzca una mayor intensidad de facilitación que resulta en una mayor diversidad filogenética (Valiente-Banuet & Verdú, 2007). Teniendo en cuenta, además, la fuerte señal filogenética de los rasgos estudiados, este incremento en la presencia de especies más alejadas filogenéticamente estaría asociado a un incremento en el rango de rasgos representados en la comunidad (Cantalapiedra et al. 2014). Estos resultados contrastan con los obtenidos previamente por Prieto et al. 2017, en los que se encuentra una estructura filogenética y funcional dispersa en zonas más favorables mientras que en las zonas menos favorables las estructuras filogenética y funcional son agregadas. Al analizar en detalle las condiciones climáticas óptimas para los distintos rasgos evaluados encontramos que los rasgos gruesos presentaban una gran complementariedad de nicho en respuesta al clima mientras que no encontramos un patrón tan claro para los rasgos finos en los que el clima parecía tener una menor incidencia (capítulo 5). Un resultado similar fue obtenido en los capítulos 3 y 4, donde los diferentes factores climáticos mediaban la variación en estos rasgos finos (medidos sólo en macrolíquenes) pero el porcentaje de variabilidad que estos factores explicaban era bajo.

El hecho de que en varios capítulos de la tesis hayamos encontrado distintos factores determinando los patrones de las distintas dimensiones de la diversidad pone de manifiesto la necesidad de medir las tres dimensiones ya que nos están proporcionando una información complementaria de la dinámica de las comunidades frente a distintos factores abióticos y a distintas escalas (Devictor et al. 2010, Swenson 2011, Purschke et al. 2013).

2 | RELACIÓN ENTRE LAS TRES DIMENSIONES DE LA DIVERSIDAD: TAXONÓMICA, FUNCIONAL Y FILOGENÉTICA

Independientemente de la escala espacial (Península Ibérica vs. Europa), de la porción de la comunidad (total vs. macrolíquenes) y de la aproximación estadística utilizada, encontramos que, de forma consistente, la diversidad funcional está relacionada con la diversidad filogenética y taxonómica pero que estas dos dimensiones no están relacionadas entre sí (capítulos 1, 2 y 5). En todos los casos, encontramos una relación positiva entre la diversidad funcional y filogenética (capítulos 1, 2 y 5), mientras que la relación entre la dimensión funcional y taxonómica fue positiva en los capítulos 1 y 5, y negativa en el capítulo 2.

Respecto a la relación entre las dimensiones funcional y filogenética, comunidades con mayor diversidad de rasgos funcionales estaban constituidas por especies más alejadas filogenéticamente, congruente con la existencia de una señal filogenética de los rasgos gruesos seleccionados (forma de crecimiento, tipo de fotobionte, estrategia reproductiva y presencia de metabolitos antiherbivoría) por la cual especies más emparentadas son más similares en cuanto a los rasgos que poseen (Webb et al. 2002, Swenson & Enquist 2007, Wiens & Graham 2005). Según Devictor et al. (2010) cabría esperar que áreas de estudio más grandes representasen una mayor heterogeneidad de hábitats y de zonas biogeográficas de manera que las comunidades presentes en estas zonas podrían estar constituidas por especies con mayor diversidad de rasgos y/o historias evolutivas. Sin embargo, nuestros resultados son consistentes a una escala espacial más restringida (en dos regiones biogeográficas dentro de la Península Ibérica; capítulo 1) y a una escala espacial mayor (desde el sur de Suecia al sur de Italia; capítulo 2 y 5) sugiriendo que las especies que conforman las comunidades en los bosques estudiados proceden de un *pool* regional de especies con diferentes historias biogeográficas o evolutivas (Prinzing et al. 2008).

En cuanto a la relación entre la diversidad funcional y taxonómica, cabe esperar una relación positiva en un escenario de baja redundancia funcional (o alta complementariedad funcional; Petchey & Gaston 2002), es decir, cuando las especies que componen una comunidad desempeñen papeles funcionales únicos (tengan rasgos muy diferentes) (capítulos 1 y 5). En este caso, la pérdida de una especie puede tener un impacto negativo en el funcionamiento de los ecosistemas si dicha especie posee un rasgo único (Tilman et al. 1996, Fetzer et al. 2015). Por el contrario, una relación negativa apunta a la existencia de una alta redundancia funcional (baja complementariedad funcional; Petchey & Gaston 2002), haciendo que las comunidades sean más resilientes a los cambios ambientales ya que la pérdida de una especie es compensada por otra especie con una contribución similar al funcionamiento del ecosistema (Fetzer et al. 2015). Curiosamente, obtuvimos resultados opuestos en función del área de estudio de manera que dentro de la Península Ibérica (capítulo 1), comunidades con mayor riqueza de especies eran funcionalmente menos redundantes que a lo largo de Europa (capítulo 2) (de Bello et al. 2009, Cadotte et al. 2011). Este resultado podría estar indicando que a lo largo del gradiente latitudinal más extenso (capítulo 2) hay un alto grado de solapamiento de nicho probablemente debido a un filtrado abiótico sobre las comunidades de líquenes más acusado que en el gradiente ambiental representado en la Península Ibérica.

Por último, en ninguno de los capítulos encontramos una relación entre la diversidad taxonómica y la filogenética. Este resultado resulta contraintuitivo ya que cabría esperar que, por azar, al existir un mayor número de especies en una comunidad, mayor sería la probabilidad de tener una mayor variedad de linajes representados (Forest et al. 2007, Faith 2008, Meynard et al. 2011). Sin embargo, la falta de relación entre estas dimensiones podría deberse a que los factores que median la persistencia de las especies en una comunidad estuviesen seleccionando especies pertenecientes a clados muy emparentados filogenéticamente (Cadotte et al. 2010, Tucker & Cadotte 2013).

En el capítulo 5 identificamos los puntos calientes de diversidad de líquenes a lo largo del gradiente latitudinal europeo y comprobamos que las comunidades de líquenes maximizan su diversidad funcional bajo las mismas condiciones climáticas en las que alcanzan los máximos de diversidad filogenética o taxonómica pero los máximos de estas últimas no coinciden. Por tanto, identificar puntos calientes de diversidad funcional podría ayudar a conservar no sólo una mayor diversidad de rasgos funcionales sino también un mayor número de especies o de linajes evolutivos. Este resultado tiene especial interés ya que los líquenes son organismos clave en el funcionamiento de los bosques (Ellis 2012) y conservar estos puntos calientes no sólo ayudaría a conservar las especies más eficaces en su respuesta ante la incertidumbre de los cambios ambientales (Forest et al. 2007) sino también a mantener la estabilidad del ecosistema (Cadotte et al. 2011).

Tras evaluar la relación entre las tres dimensiones de la diversidad a lo largo de gradientes ambientales que abarcan distintas escalas espaciales comprobamos que la diversidad funcional juega un papel clave pudiendo incluso ser utilizado, al menos en parte, como subrogado de las otras dos dimensiones (Keddy 1992, Webb et al. 2002). Aun así, tal y como hemos visto también en el primer apartado de la discusión, es importante medir estas tres dimensiones ya que responden a distintos factores y proporcionan una información complementaria de la respuesta de las comunidades (Devictor et al. 2010, Swenson 2011, Purschke et al. 2013).

3 | EL VALOR DE LOS RASGOS FUNCIONALES EN LÍQUENES: rasgos gruesos vs. finos

La dimensión funcional aparece como un componente clave para evaluar la respuesta de las comunidades de líquenes epífitos ante cambios ambientales lo cual apoya la idea de que las comunidades responden a las presiones ambientales a través de los rasgos funcionales de las especies que las componen (Weiher & Keddy 1995, Díaz et al. 1998, Shipley et al.

2016). En este sentido, en los diferentes capítulos de la tesis hemos ido desvelando cuáles son los principales rasgos que se ven influidos por la fragmentación del hábitat (capítulo 1) y por el clima (capítulos 1-5). Los resultados del capítulo 1 muestran que los rasgos gruesos *tipo de fotobionte* y *forma de crecimiento* son los más adecuados para evaluar la incidencia de la fragmentación sobre las comunidades de líquenes epífitos. Tanto en la región Atlántica como en la Mediterránea un incremento en la fragmentación del hábitat condujo a una disminución en la diversidad de tipos de fotobionte que fue acompañada, sólo en la región Mediterránea, por una disminución en la diversidad de formas de crecimiento (capítulo 1). En cuanto al clima, encontramos que los rasgos gruesos se vieron muy afectados por los cambios climáticos a nivel de macroescala (capítulo 1, 2, 5) (Marini et al. 2011, Giordani et al. 2014, Matos et al. 2015), mientras que los rasgos finos no parecieron responder con tanta intensidad a las variaciones en el clima, al menos a la escala estudiada (capítulos 3, 4 y 5). La diversidad de los rasgos gruesos *tipo de fotobionte, forma de crecimiento* y *estrategia reproductiva* respondió, principalmente, a cambios en la precipitación de verano (capítulo 1) y a la fluctuación en las temperaturas (capítulo 2).

El *tipo de fotobionte* y la *forma de crecimiento* aparecen como los rasgos clave que median la respuesta de las comunidades de líquenes tanto a la fragmentación como al clima pero, además, aplicando el método comparado para tener en cuenta la falta de independencia de las especies debido a sus relaciones filogenéticas (capítulo 4), comprobamos que estos rasgos son capaces de recoger parte de la información proporcionada por los rasgos finos relacionados con funciones específicas tales como la actividad fotosintética, el balance hídrico y la adquisición de nutrientes. Estas características, junto al hecho de que son rasgos muy sencillos de obtener ya que no es necesario identificar las especies ni llevar a cabo procedimientos en el laboratorio, los señalan como indicadores ecológicos de gran valor para evaluar la incidencia de la fragmentación del hábitat y el clima (Marini et al. 2011, Giordani et al. 2012, Matos et al. 2015, Benítez et al. 2018). Por el contrario, no encontramos evidencia de que los rasgos finos cuantificados puedan ser utilizados como indicadores de cambios macroclimáticos. En este sentido, cabría esperar que estos rasgos, que dan información específica sobre funciones fisiológicas precisas (ver Fig. 1 en "Metodología general"), pudieran responder a factores ambientales a una escala mucho menor como, por ejemplo, a las condiciones microclimáticas que nosotros no recogemos en la presente tesis. Aún más, quizá estos rasgos tengan una mayor utilidad como "rasgos efecto" que informen sobre los impactos de los líquenes en las funciones de los ecosistemas y no como "rasgos respuesta" que nos permitan evaluar el efecto de los cambios ambientales sobre las comunidades de

líquenes. Por otra parte, y a diferencia de lo que ocurre en plantas con el *leaf economic spectrum* (Reich et al. 2003, Wright et al. 2004), sólo encontramos una tendencia general que permite identificar distintas estrategias ecológicas teniendo en cuenta la covariación de los rasgos (capítulo 4). En concreto, únicamente encontramos un patrón de covariación de los rasgos consistentes entre y dentro de especies el cual relaciona los rasgos de balance hídrico: talos con mayor masa específica (grandes y gruesos) son capaces de almacenar más cantidad de agua que talos con menor masa específica del talo (Gauslaa & Coxson 2011, Merinero et al. 2014).

Respecto al *tipo de fotobionte*, los resultados del capítulo 5 muestran que la clasificación clásica separando cloro- (con alga verde), cefalo- (con alga verde y cianobacteria) y cianolíquenes (con cianobacteria) (por ejemplo, Nimis & Martellos 2007), tendría que modificarse para poder evaluar la respuesta de los líquenes a variaciones climáticas. En este sentido, proponemos subdividir la categoría de los cianolíquenes en tres subgrupos: cianolíquenes-Collemataceae, cianolíquenes-Pannariaceae y resto de cianolíquenes ya que los tres grupos presentan óptimos diferentes.

En definitiva, por todo lo dicho anteriormente, el papel de los rasgos *tipo de fotobionte* y *forma de crecimiento* como indicadores ecológicos de alerta temprana sobre los efectos de la fragmentación del hábitat y el clima parece claro. Sin embargo, las variables climáticas a macroescala (escala de bosque) explican poco porcentaje de la variabilidad de los rasgos finos relacionados con la actividad fotosintética, el balance hídrico y la adquisición de nutrientes por lo que es necesario llevar a cabo más trabajos para desvelar de manera más precisa su respuesta a distintas variables en los estudios de ecología de comunidades que justifique el alto coste de recursos que requiere su empleo. En esta línea sería importante evaluar de manera concreta cómo responden a factores a microescala y cual es su relación con el funcionamiento de los ecosistemas.

4 | IMPORTANCIA DE LA VARIABILIDAD INTRA- E INTERESPECÍFICA EN LOS LÍQUENES

Tradicionalmente, los estudios sobre variabilidad de rasgos se centraban en cuantificar la variabilidad interespecífica basándose en la asunción de que las diferencias funcionales tienden a ser mayores entre especies que entre individuos de la misma especie (Grime et al. 1988, Garnier 2001). Sin embargo, últimamente ha habido un auge de estudios centrados en evaluar específicamente la contribución de la variabilidad intraespecífica para

así comprobar si esta asunción es consistente y bajo qué circunstancias la variabilidad intraespecífica puede ser desdeñada (Albert et al. 2010, Jung et al. 2010, Siefert et al. 2015, Shipley 2016). En este sentido, Auger & Shipley (2013) apuntaron que la variabilidad intraespecífica tiende a tener una mayor importancia a escalas geográficas pequeñas. De manera opuesta, nosotros encontramos que la variabilidad intraespecífica tiene una contribución muy importante, incluso mayor que el recambio de especies, para explicar los cambios de los rasgos funcionales finos en las comunidades de líquenes a escala continental (capítulo 3). Además observamos que, aunque la contribución del clima explicando estas variaciones funcionales no era muy grande, los cambios funcionales de la comunidad debidos a la variabilidad intraespecífica respondían mucho más al clima que los relacionados con el recambio de especies. Este resultado apunta a que las especies que conforman las comunidades son capaces de responder a los cambios climáticos modificando rasgos relacionados con su actividad fotosintética, balance hídrico y adquisición de nutrientes.

Una vez estudiada la variación funcional a escala de comunidad, evaluamos los patrones de variación de los rasgos a lo largo del gradiente controlando el efecto de las relaciones filogenéticas entre las especies (capítulo 4) y encontramos que la contribución de la variabilidad entre especies era muy elevada en aquellos rasgos relacionados con el *tipo de fotobionte*, es decir, aquellos relacionados con la capacidad de fijar nitrógeno atmosférico y con la presencia o ausencia de clorofila b. Además, nuestros resultados son consistentes con los obtenidos en los capítulos 3 y 5 de tal manera que las variables climáticas no afectaron a todos los rasgos finos cuantificados y, cuando lo hacían, el porcentaje de variabilidad explicada era bajo.

Tal y como hemos apuntado en los apartados anteriores, los resultados de los capítulos 3 y 4 demuestran que los rasgos relacionados con la actividad fotosintética, el balance hídrico y la adquisición de nutrientes no son buenos indicadores de los cambios climáticos en estos organismos. Cabe destacar que encontramos una mayor contribución relativa del recambio de especies en aquellos rasgos relacionados con el tipo de fotobionte principal en la simbiosis liquénica (capítulo 3). Este hallazgo, junto al hecho de que la variabilidad debido al recambio de especies explicada por el clima fuese muy baja tanto a escala de comunidad como de especies (capítulos 3 y 4), podría estar indicando que la entrada en las comunidades de especies con distintos tipos de fotobionte esté mediada por la disponibilidad del fotobionte o por el grado de especificidad por el fotobionte (Cardós et al. 2019) más que por un efecto directo de las condiciones ambientales.

5 | IMPORTANCIA DE LA DIVERSIDAD TAXONÓMICA

Es importante destacar que los objetos de estudio de esta tesis son, en última instancia, las especies, que se disponen y seleccionan de forma determinada para conformar las comunidades. Así hemos identificado un total de 203 especies de líquenes epífitos en los hayedos europeos estudiados y 145 especies en los muestreos en la Península Ibérica. Tal y como indican Hortal et al. (2015), existe un sesgo en los datos de biodiversidad disponibles que afectan a nuestra capacidad para entender, proteger y conservar la biodiversidad. Estos autores identifican diferentes vacíos de conocimiento relacionados, por ejemplo, con un sesgo en los grupos taxonómicos estudiados, la falta de información sobre los rangos de distribución de las especies o la falta de información sobre las interacciones bióticas. En este sentido los líquenes se incluyen dentro de lo que se conoce como "diversidad críptica" y están menos estudiados que otros grupos de organismos como las plantas vasculares, las aves o los mamíferos. Además, no tenemos conocimiento de la existencia de bases de datos especializadas en proporcionar información sobre la asociación de especies, en este caso, líquenes epífitos sobre haya. Por todo ello, reconociendo los vacíos de conocimiento señalados por Hortal et al. (2015) y siendo conscientes de la importancia del acceso a datos sobre diversidad, nos planteamos la necesidad de completar la información taxonómica recopilada por nosotros mismos durante los muestreos con la información publicada acerca de la presencia de especies de líquenes epífitos sobre haya a lo largo de Europa (capítulo 6).

6 | LIMITACIONES Y LÍNEAS DE INVESTIGACIÓN FUTURAS

A pesar de que hemos conseguido dar respuesta a las principales preguntas planteadas y conocer cómo la fragmentación del hábitat y el clima determinan los patrones de diversidad de las comunidades de líquenes epífitos, los resultados derivados de la presente tesis han puesto de manifiesto ciertas limitaciones y han abierto nuevas cuestiones que podrán ser evaluadas en el futuro. En primer lugar, sería necesario incorporar variables climáticas que ofrezcan una información más detallada de la intensidad y temporalidad de los cambios climáticos, por ejemplo, sobre cómo varía la temperatura y la humedad relativa a diferentes horas a lo largo de un mismo día. Además, la falta de información sobre factores abióticos a pequeña escala podría estar dificultando la evaluación del papel de los rasgos finos como indicadores ecológicos. Más allá, resultaría interesante analizar el impacto de las comunidades de líquenes estudiadas en el funcionamiento de los ecosistemas y evaluar el papel de los rasgos finos mediando estos impactos. Finalmente, incluir las interacciones biológicas, y no

sólo el efecto de las variables ambientales podría darnos una visión más amplia y realista de la dinámica de las comunidades.

Una de las principales cuestiones que merecen una mayor investigación está relacionada con el tipo de fotobionte principal presente en la simbiosis liquénica. En este sentido, y como ya hemos apuntado a lo largo de la discusión, es necesario obtener más información que permita evaluar si la presencia de especies con distintos tipos de fotobionte está más relacionada con la disponibilidad del fotobiontes en el ambiente, con el grado de especificidad del micobionte por el fotobionte, o por otros factores abióticos no considerados en esta tesis.

Por otra parte, aunque hemos encontrado tendencias generales semejantes en las dos escalas de estudio, al estudiar una escala geográfica más restringida (regiones biogeográficas dentro de la Península Ibérica) y una escala continental (Europa), hay pequeñas discrepancias, por ejemplo, en cómo las tres dimensiones de la diversidad se relacionan entre sí. Por tanto, parecería razonable hacer un estudio específico analizando la escala e incluyendo otros niveles como, por ejemplo, parcela y árbol (de las que disponemos de datos) o la escala global. En este sentido, además de incluir la diversidad α (con la que hemos trabajado a lo largo de la tesis), sería interesante evaluar la respuesta del recambio de especies (β-diversidad) a distintas escalas.

Por último, aunque algunas de las conclusiones de la tesis pueden ser utilizadas desde un punto de vista de la conservación como, por ejemplo, el reconocimiento de los rasgos débiles de fácil obtención como indicadores ecológicos de la fragmentación del hábitat y el clima (capítulo 1, 2 y 5), o la identificación de puntos calientes de biodiversidad a lo largo de Europa (capítulo 5), otros trabajos futuros deberían dirigirse de una manera más específica a aplicar los principales resultados de la tesis a la gestión y conservación de las comunidades de líquenes epífitos. En esta línea, con la información de la que disponemos, se podrían desarrollar modelos de predicción de cambio climático para evaluar los patrones de biodiversidad potenciales de las comundiades de líquenes epífitos bajo diferentes escenarios futuros.

7 | REFERENCIAS

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Conclusions

CONCLUSIONS

1. Different environmental drivers are the major predictors of functional, phylogenetic, and taxonomic diversity in lichen epiphytic communities. Thus, adopting an integrative approach and consider the response of the three biodiversity facets, functional (FD), phylogenetic (PD) and taxonomic (TD) diversity is necessary to disentangle the response of lichen communities to cope with habitat fragmentation and climate change.

2. The three facets of biodiversity provide complementary information about the dynamic of the communities, but FD emerge as a crucial component. The response of the communities to face the environmental changes is mediated through the functional traits of the species forming the community. Soft functional traits play a valuable role as ecological indicators, whereas hard traits are less responsive to macroclimatic factors.

3. Factors related to climatic fluctuations, in both temperature and precipitation, are the most important drivers of lichen community dynamics along a wide latitudinal gradient from Sweden to Italy. Increases in seasonality, reduce FD and PD in the communities. In addition, lichen species modify their ecological strategies according to seasonality gradients, with shifts from resource-conservative to resource-acquisitive strategies in more seasonal environments. Based on the global climate models' predictions, a future impoverishment of the FD and PD of the epiphytic communities and an increase of lichens with resource-acquisitive strategies are expected.

4. At community level, and contrary to the general pattern expected in vascular plants, intraspecific variability explained most of the functional trait variability. We encourage the consideration of the intraspecific variability to better understand the effect of environmental changes on lichen functional traits. When functional variation of hard traits is analysed at species-level, functional variation is higher among than within species, but intraspecific variability (particularly within populations) substantially contribute to overall trait variation. As a consequence, including within-species variation is essential to unveil the response of lichen species under different climatic scenarios even at broad environmental gradients.

5. Soft categorical traits such as type of photobiont and growth form are relevant ecological indicators useful to develop rapid assessment methods to evaluate the effects of macroclimatic changes. Furthermore, we stress the need for including three different categories within the cyanolichens to assess the influence of climate since these functional groups respond in different ways to the climatic conditions. Contrary to the categorical traits, further research is needed to unveil to what extent hard continuous traits could respond to small-scale environmental variables or are relevant to assess the effect of the communities on the ecosystems functioning.

6. Functional variation in continuous traits is distributed across scales, with order and species having the highest contribution to the overall variation. Evolutionary drivers highly contribute to overall functional variation, while the effect of environmental drivers is lower, highlighting the importance of combining the phylogenetic relatedness and the trait-based approach through the phylogenetic comparative analyses.

7. Lichen functional traits covary and, the patterns of covariation, vary among and within species, with the exception of a consistent correlation of traits related with water use strategies. Based on trait covariation, we identified a general ecological strategy of the water use strategy, but it was not possible to establish general strategies related to photosynthetic performance and nutrient acquisition. Nevertheless, we confirm that lichens with thicker thallus tend to hold more water per unit area, implying a trade-off between rapid moisture-uptake and conservative water-storage strategy.

8. Epiphytic communities maximize their functional, phylogenetic, and taxonomic diversity under different climatic conditions. Functional hotspots were congruent with phylogenetic and taxonomic maximums, which implies that preserving high functional diversity might indirectly preserve high phylogenetic and taxonomic diversity in lichen communities. However, since taxonomic and phylogenetic hotspots were not congruent, a multifaceted approach should be applied for identifying areas of high priority to allocate resources and to establish effective conservation policies.

9. Epiphytic communities maximize their diversity in the extremes of the climatic space studied, with Mediterranean region appearing as a hotspot of phylogenetic and functional diversity in lichens, that would require special conservation attention.

10. We have created an open checklist recording the lichen species present on *Fagus* trees along Europe. This is an online database where researches could continuously include their records (*http://biodiversos.org/epidiversity-lichens-fagus-europe/*). Thus, this is an open and dynamic database that could be updated by our research group and by different users, including new works and studies in different languages.

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