



Tree species and microhabitat influence the population structure of the epiphytic lichen *Lobaria pulmonaria*



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ABSTRACT

Detailed knowledge of the habitat requirements of species is required because habitat greatly affects the persistence of species. We investigated the effects of tree species and microhabitat heterogeneity on the population of the locally threatened lichen *Lobaria pulmonaria*. We studied four *L. pulmonaria* populations in Central Spain and collected microhabitat data for individuals growing on beech and oak. The microhabitat affected the life stages of *L. pulmonaria*; being a phorophyte species the location of the lichen was the most important factor generating different patterns of establishment, abundance, thallus size and reproductive capacity. Although oak forests favoured the establishment and recruitment of new *L. pulmonaria* individuals, they apparently provided adverse environmental conditions for lichen growth, thus affecting the reproductive capacity since this is size-dependent. By contrast, beech forests offered a more favourable microclimate, because *L. pulmonaria* individuals reached larger sizes in these forests. In conclusion, our results indicate that habitats hosting large populations, with high rates of establishment and recruitment do not necessarily favour other life-cycle stages.

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1. Introduction

In conservation biology, the first step toward conserving a species is to identify the underlying mechanisms that determine its distribution patterns and abundance (Fonseca and Benson, 2003). Thus, it is necessary to identify the habitat characteristics of a species at the spatial scale at which they influence species abundance and performance.

Several plant studies have shown that fine scale microhabitat heterogeneity may affect the plant demography by influencing the plant size, population size, and/or genetic structure (e.g. Albert et al., 2001; Milla et al., 2009). The microhabitat operates at the individual level and indirectly influences population-level responses such as size structure. Predictions of population persistence require an understanding of how population structure and performance vary depending on microhabitat heterogeneity. However, this information is lacking for lichens despite the fact that this group of organisms is one of the few fungal groups with visible and distinct specimens, thus allowing investigation of population

sizes and dynamics. Although there are several fungal population studies (e.g. Brasier, 1999; Worrall, 1999; Stenlid, 2008), the mycelial nature of fungi together with species-specific characteristics complicate studies of population dynamics (Worrall, 1999). Lichen population studies can thus help us to understand other fungal responses at a population level.

Moreover, lichens represent a major part of the species diversity in many forest ecosystems (Sillett et al., 2000; Ellis, 2012); they are sensitive indicators of environmental changes (e.g. Belinchón et al., 2009; Juriado et al., 2012) and play important roles in ecosystem functioning (Ellis, 2012; Concostrina et al., 2014; Matos et al., 2015). Specifically, epiphytic lichens are functional components of forest ecosystems, contributing to nutrient cycles and providing food and habitats for animals (Sillett et al., 2000; Edman et al., 2008; Ellis, 2012). Yet, there is a need to increase the knowledge about factors influencing lichen populations and thus improve the understanding of lichens' occurrence, ecology and functioning.

Most lichen studies define the habitat quality based on the environmental factors that determine the presence or abundance of a species (Scheidegger and Werth, 2009; Belinchón et al., 2011). Less is known about the habitat requirements for individual establishment, growth, and reproduction (see Hilmo et al., 2011a; Martínez et al., 2012, 2014; Merinero et al., 2014, 2015). Lichens,

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especially those species confined to old forests, are sensitive to habitat changes (Belinchón et al., 2009, 2011; Otálora et al., 2011) and respond to minor differences in the habitat structure or to specialized microhabitats (Jüriado et al., 2011, 2012). Thus, finer resolution habitat studies are required to understand the habitat components that affect the selection of sites, as well as habitat-specific establishment, growth, and reproductive capacity.

Lobaria pulmonaria is a widespread epiphytic lichen frequently used as a model organism in ecological studies (e.g. Gu et al., 2001; Werth et al., 2007; Belinchón et al., 2009; Jüriado et al., 2012; Merinero et al., 2015). It is susceptible to changes in forest structure (e.g. Gauslaa et al., 2006; Edman et al., 2008) and has been described as an indicator species of long ecological continuity forests (Rose, 1976). *L. pulmonaria* is declining and is considered vulnerable or near threatened in many parts of Europe (e.g. Wirth et al., 1996; Scheidegger et al., 2002; Martínez et al., 2003; Gårdenfors, 2010).

Previous studies have shown that forest type and tree characteristics affect the presence and cover of *L. pulmonaria* (Snäll et al., 2004; Belinchón et al., 2009, 2011; Hilmo et al., 2011a). These and other studies suggest that this lichen species is more limited by the habitat quality than by low dispersal ability (Gu et al., 2001; Öckinger et al., 2005; Werth et al., 2007; Belinchón et al., 2009).

However, we do not know which factors affect various life stages of *L. pulmonaria* and which stages limit population development as a possible bottleneck (Sillett et al., 2000). Here, we evaluated the microhabitat characteristics for important life stages of *L. pulmonaria* in four Mediterranean forests. Our general hypothesis was that the tree species where *L. pulmonaria* grows (hereafter the phorophyte species), its characteristics and lichen position on it could be the main factors regulating *L. pulmonaria*. We hypothesized that *L. pulmonaria* individuals had phorophyte-specific patterns of establishment, growth and reproductive capacity. Our specific objectives were to: (1) compare the abundance and probability of occurrence of *L. pulmonaria* on *Fagus* and *Quercus* trunks; (2) evaluate the effects of phorophyte species on the structure of *L. pulmonaria* populations; and (3) identify the microhabitat factors affecting the reproductive capacity of *L. pulmonaria* individuals.

2. Materials and methods

2.1. Study area and data collection

The study area was in the Sistema Central Range of the Iberian Peninsula (Southern Europe), including the Sierra de Ayllón and Sierra del Rincón (Fig. S1). The climate is Mediterranean characterized by a drought period in the summer (an average of 1.8 months). Two habitats were studied: *Fagus sylvatica* and *Quercus pyrenaica* forests. *F. sylvatica* (beech) is a deciduous tree that is widespread throughout Western Europe and the study area is near its southernmost distribution limit. *Q. pyrenaica*, virtually endemic in the Iberian Peninsula, is a semi-deciduous oak retaining its dead leaves until the following spring. In this study, “beech forests” were designated as forests with >60% *F. sylvatica* trees, accompanied mainly by *Q. pyrenaica* and (<10%) other woody plants such as *Ilex aquifolium*, *Crataegus monogyna*, or *Sorbus aucuparia* “Oak forests” had mainly *Q. pyrenaica* trees, and <10% cover of other trees and bushes such as *C. monogyna* or *Prunus* spp.

Four square plots were established in a relatively small area (Table 1; Fig. S1). Locations were based on our previous knowledge of larger and denser *L. pulmonaria* populations, and included both main phorophyte species in Central Spain. Plot 1 was 1 ha, plots 2 and 3 were 0.25 ha and plot 4, 0.65 ha. Plots 1 and 4 were larger because data will be used for spatial analysis in another study and because the population was scattered, respectively (Table 1). All

oaks (840; 57%) and all beeches (475; 32%) present in the four plots were included; other tree species (<10%) were excluded because they supported <2.3% of the *L. pulmonaria* individuals. Variables at tree and *L. pulmonaria* individual levels were recorded. At a tree level, the following were recorded: the phorophyte species (the ‘host’ tree species, Kirk et al., 2008); the diameter of the trunk measured at the base and at 1.3 m; the roughness of the bark (the deepest crack measured with a digital caliper at 50 cm above the ground); the cover of bryophytes (%) on the trunk split at two height levels, i.e., from the ground to 1 m (lower strip) and from 1 m to 2 m (upper strip) (Table 2).

At a lichen specimen level, the following were recorded: the largest diameter of the thallus (± 0.1 mm) in the desiccated state (an estimate of individual size); the presence of sexual reproductive structures (apothecia); and the presence and abundance of asexual diaspores (soredia and isidia) estimated as % cover of total upper thallus surface done by one person. Both isidioid soredia (following Scheidegger et al., 1995) and coralloid isidia were present; here both were considered as isidia. Juvenile individuals are those lacking reproductive structures. It is not trivial to define an individual in lichen species like *L. pulmonaria*, as one thallus may be formed by merging lobes (lawn-shaped specimens). Following different authors (Hilmo et al., 2011b; Martínez et al., 2012; Scheidegger et al., 2012; Merinero et al., 2014), an individual was considered to be a thallus that was spatially separated from other thalli. Three variables were recorded to specify the individual microhabitat: the height (± 1 cm) from the ground (from 0 to 200 cm); aspect on the trunk ($0-359^\circ$; $\pm 1^\circ$); and the type of growth substrate or attachment site of the thallus, i.e., naked bark, bryophytes, or other lichens (Table 2). Height, exposure and attachment site were measured in the centre of each thallus. Whether an individual thallus was (a) decorticated and bleached, (b) fragmented, and/or had (c) lichenicolous fungi (e.g. *Plectocarpon lichenum*) was also recorded.

2.2. Data analysis

Variables with correlation values >0.7 were excluded to avoid problems of multicollinearity (Table 2). Mean \pm SE values are given for measured variables.

2.2.1. Global models

The individual size was used as a response variable to test the influence of environmental variables. Size was also an explanatory predictor for the presence/abundance of reproductive structures. The variables affecting the *L. pulmonaria* status was identified by fitting generalized linear mixed models (GLMM) using the SAS Macro program, which iteratively calls the SAS Procedure MIXED until convergence (GLIMMIX ver. 8 for SAS/STAT; available at <http://ftp.sas.com/techsup/download/stat/>). This modelling approach was used because our data had an unbalanced and hierarchical structure; individuals were nested within trees and trees were nested within plots. A hierarchical data structure implies a correlation between data points at different scales. This correlation inflates the degrees of freedom, thereby increasing the risk for type I error. To overcome these problems, the data were analysed using a multi-level approach with trees and plots as random factors, and mixed modelling was applied (Verbeke and Molenberghs, 1997). The occurrence and abundance of *L. pulmonaria* was modelled, as well as the abundance of juveniles and reproductive individuals per tree. The explanatory variables were: phorophyte species, diameter at breast height, the interaction between both variables, bark roughness, bryophyte cover on the lower and upper strip, respectively (Table 2). Second, the size, the presence of apothecia, and the presence and abundance of soredia and isidia were modelled. In

Table 1

Characteristics of the studied plots with *Lobaria pulmonaria* in Central Spain. T: annual mean temperature; P: total precipitation; DBH: mean tree diameter. Precipitation and temperature data source: Ninyerola et al. (2005).

Plot	Locality name	Coordinates X; Y (m)	Size (Ha)	Forest type	n trees	n beech	n oak	Altitude (m a.s.l.)	T (°C)	P (mm)	DBH (cm)
1	Montejo 1	4,555,119; 455,864	1	Beech	606	350	202	1320	9.5	954	27.84
2	Montejo 2	4,555,109; 458,677	0.25	Oak	159	0	123	1294	9.5	954	26.02
3	Cantalojas	4,564,030; 467,755	0.25	Beech	156	114	9	1580	8.6	1153	38.93
4	Santuy	4,549,449; 462,976	0.65	Oak	539	0	519	1410	8.9	744	14.59

Table 2

List of variables recorded at the tree and *Lobaria pulmonaria* individual level, with their respective codes. An asterisk (*) indicates a variable excluded from the models because of a high correlation level.

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

these models, the explanatory variables were: phorophyte species, thallus size (only for modelling reproductive structures), tree diameter, height above ground, the exposure aspect, bark roughness, the attachment site, bryophyte cover on the lower strip of the tree, and bryophyte cover on the upper strip (Table 2).

2.2.2. Specific models

The results of the global models indicated that the tree species was highly significant so data were analysed by differentiating between beech and oak models to detect the different responses of *L. pulmonaria* (Tables S3 and S4). For the presence of *L. pulmonaria*, GLMMs were fitted using a binomial distribution and the “logit” link function with “plot” as a random factor. Similarly, a mixed model was fitted to describe *L. pulmonaria* abundance, the abundance of juveniles, and the abundance of reproductive individuals. “Plot” was also selected as a random factor and the “log” link function with a Poisson distribution was used. For the “individual size” models, a log-transformation was performed for “size” because its distribution was biased strongly toward very small sizes. In the GLIMM, “tree” was nested in “plot” (random factors). Normal distribution and the link function “identity” were used. In the “apothecia presence” models, only data from plots 1, 2 and 3 were analysed, as no sexual individuals occurred in plot 4. The other models tested the factors influencing the presence and abundance of asexual reproductive structures (soredia and isidia). In all models, “tree” was nested in “plot” and both were random factors. In these models, the distribution of the response variables was “binomial” and the link function was “logit.” In the individual size model, as in the reproductive models, individuals larger than 1 m ($n = 23$ individuals) were eliminated from the analysis because they represent a bias of the total data distribution.

2.2.3. The relationship between size and the probability of reproduction

To estimate the probability curves for each reproductive structure relative to the individual size, generalized linear models (GENMOD SAS v. 9) were constructed. The probability for the three reproductive structures, i.e., apothecia, soredia, and isidia, was estimated. The significance of each predictor was estimated using a deviance test (Guisan et al., 2002). Binomial distribution and “logit” link function were applied. The relationship between the probability of being reproductive (p) and individual size can be quantified

using a logistic regression (Wesselingh et al., 1997), according to the formula $P = 1/(1 + e^{-(\mu + \alpha x)})$, where the parameters μ and α determine the intercept with the x-axis and the slope of the curve, respectively. They may be related to the threshold size for reproduction (Wesselingh et al., 1997; Méndez and Karlsson, 2004).

3. Results

3.1. Descriptive data

A total of 1315 oak and beech trees were recorded in the four plots, with 10,918 *L. pulmonaria* individuals growing on oak and 2760 on beech, although the percentage of occupied trees was higher for beech (Table S1). On both tree species, larger tree diameter, greater bark roughness, and a higher abundance of bryophytes favoured the presence of *L. pulmonaria* (Table S1). The mean size of *L. pulmonaria* thalli was 107.2 ± 1.2 mm, with a range of 2–990 mm, although there were 23 more extremely large thalli some of them reaching 2220 mm in diameter. A comparison between the phorophyte species showed that the mean individual thallus size was significantly larger on beech (Table S2). More than 50% of the individuals were juvenile in both phorophytes, with a slightly higher proportion on beech (Table S2). Most reproductive individuals had asexual reproduction only. Soredia occurred in similar proportions in the two phorophytes, but isidia were more frequent on oak (Table S2). Few thalli reproduced sexually (less than 10%), but apothecia were slightly more common on oaks (Table S2). The number of thalli with *P. lichenum* galls was very similar in both phorophytes (Table S2). However, the percentage of fragmented thalli was higher in beech trees, while the proportion of decorticated thalli was higher on oak (Table S2). The populations of *L. pulmonaria* on both phorophytes were skewed toward small individuals (Fig. 1), although this bias was stronger on oaks. Large individuals occurred on both phorophytes, but represented a greater proportion of the populations on beech.

3.2. Global models

Mixed models explaining the presence and the abundance of *L. pulmonaria*, as well as the abundance of juvenile and reproductive individuals, showed that the phorophyte species and the interaction between the phorophyte species and tree diameter

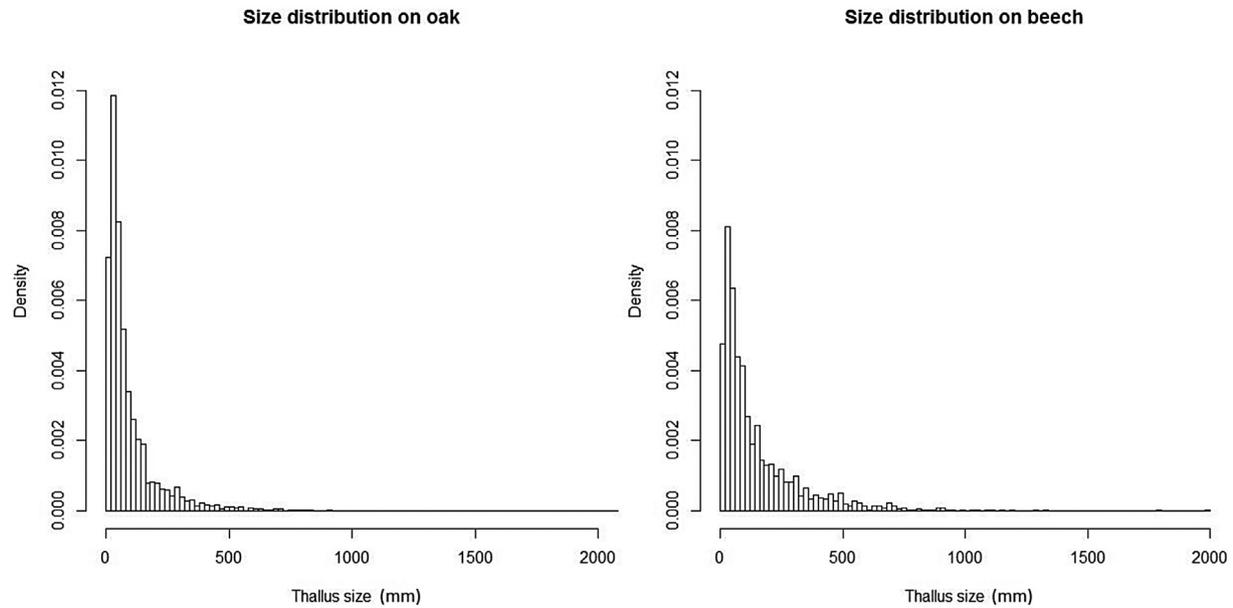


Fig. 1. Size distribution of *Lobaria pulmonaria* populations per phorophyte. X-axis: individual size as maximum diameter (mm), y-axis: density (0–1).

were significant in all cases (Table 3). Thus the probability of the presence of *L. pulmonaria* increased on larger trees. The abundance was influenced by the phorophyte species, the tree diameter, and the interaction of these two variables, as well as the bark roughness and the bryophyte cover on the lower strip of the tree (Table 3). The tree species and diameter (and their interaction) also positively correlated with the abundance of juvenile and reproductive individuals (Table 3). Furthermore, the abundance of juvenile individuals increased with bark roughness, whereas the abundance of reproductive individuals was larger in trees with a high bryophyte cover at the lower strip. The random variable plot was not significant in any model (data not shown). The phorophyte species was also a key factor that affected the individual size and the presence and abundance of reproductive structures (Tables S3 and S4). In these cases, the random variable plot also had no significant effect, whereas the random variable tree was significant in the models.

3.3. Phorophyte-specific models

The abundance of juveniles was greater on large trees with coarse bark, regardless of the tree species (Table 4). However, the abundance of reproductive individuals on beech positively depended on tree diameter only, while greater bark roughness and lower bryophyte cover at the lower strip also had a significant role in oaks (Table 4). The variables that affected the size of *L. pulmonaria* differed in the phorophyte-specific models (Table 5). In beech, large tree diameter and coarse bark were associated with large individual size, whereas the aspect of individuals on the tree and the microhabitat significantly influenced thallus size in oak (Table 5). In both phorophytes, individuals tended to be larger at northern exposure. The height on the trunk was only significant in beech; individuals were larger near the trunk base (Table 5). In addition, the substratum type also had effects in both tree species; there were more large individuals on naked bark (Table 5). Regarding the

Table 3

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

Occurrence of <i>Lobaria pulmonaria</i>					Abundance of <i>Lobaria pulmonaria</i>				
Fixed factors	DF	Estimator	F	P	Fixed factors	DF	Estimator	F	P
Sp	1308	-4.653	8.28	0.005	Sp	1305	-2.081	206.67	<0.001
DBH	1308	0.046	18.94	<0.001	DBH	1305	0.008	92.93	<0.001
					DBH*Sp	1305	0.009	18.93	<0.001
					Roughness	1305	0.029	11.86	<0.001
					BL	1305	0.004	5.04	0.024
Random factors		Estimator	Z	P	Random factors		Estimator	Z	P
Residual		2.367	0.092	<0.001	Residual		10.423	25.54	<0.001
Abundance of juveniles					Abundance of reproductive individuals				
Fixed factors	DF	Estimator	F	P	Fixed factors	DF	Estimator	F	P
Sp	1306	-2.046	135.57	<0.001	Sp	1305	-2.175	217.71	<0.001
DBH	1306	0.009	71.89	<0.001	DBH	1306	0.006	75.55	<0.001
DBH*Sp	1305	0.008	9.95	0.001	DBH*Sp	1305	0.013	28.41	<0.001
Roughness	1305	0.033	10.65	0.001	BL	1305	0.006	11.61	<0.001
Random factors		Estimator	Z	P	Random factors		Estimator	Z	P
Residual		9.052	25.54	<0.001	Residual		4.3787	25.54	<0.001

Notes: Only significant factors are shown. The data are the Wald-type F-statistic (F), Wald-Z statistic for random factors, degrees of freedom (DF), coefficient of the variable in the model (Estimator), and the significance value (P). See Table 2 for the abbreviations of the variables.

Table 4

Summary of the generalized linear mixed models used to examine the effects of environmental factors on the abundance of juveniles and reproductive individuals of *L. pulmonaria* in separate models, depending on the phorophyte species, i.e., *Quercus pyrenaica* (oak) and *Fagus sylvatica* (beech).

Abundance of juveniles on oak					Abundance of juveniles on beech				
Fixed factors	DF	Estimator	F	P	Fixed factors	DF	Estimator	F	P
DBH	790	0.008	12.79	<0.001	DBH	22.9	0.020	65.40	<0.001
Roughness	789	0.033	9.60	0.002	Roughness	457	0.106	8.99	0.029
Random factors		Estimator	Z	P	Random factors		Estimator	Z	P
Residual		0.455	19.86	<0.001	Residual		7.481	15.12	<0.001

Abundance of reproductive individuals on oak					Abundance of reproductive individuals on beech				
Fixed factors	DF	Estimator	F	P	Fixed factors	DF	Estimator	F	P
DBH	789	0.006	9.90	0.001	DBH	181	0.020	42.73	<0.001
Roughness	789	0.021	6.25	0.012					
BL	789	−0.006	14.21	<0.001					
BH	789	0.007	5.98	0.014					
Random factors		Estimator	Z	P	Random factors		Estimator	Z	P
Residual		3.776	19.86	<0.001	Residual		6.159	15.12	<0.001

Notes: Only significant factors are shown. The data are the Wald-type F-statistic (F), Wald-Z statistic for random factors, degrees of freedom (DF), coefficient of the variable in the model (Estimator), and the significance value (P). See Table 2 for the abbreviations of the variables.

Table 5

Summary of the generalized linear mixed models used to examine the effects of environmental factors on *Lobaria pulmonaria* individual size in separate models for each phorophyte species, i.e., *Quercus pyrenaica* (oak) and *Fagus sylvatica* (beech).

Individual size on oak				
Fixed factors	DF	Estimator	F	P
Or	11,000	0.073	30.06	<0.001
EPI	11,000	C > B > L	126.67	<0.001
Random factors		Estimator	Z	P
Tree		0.099	8.59	<0.001
Residual		0.052	72.79	<0.001

Individual size on beech				
Fixed factors	DF	Estimator	F	P
DBH	179	0.003	6.72	0.010
Roughness	130	0.061	10.34	0.001
Height	2702	−0.001	13.94	<0.001
Or	2707	0.192	38.67	<0.001
EPI	2736	C > B > L	65.62	<0.001
Random factors		Estimator	Z	P
Tree		0.102	5.35	<0.001
Residual		0.051	35.85	<0.001

Notes: Only significant factors are shown. The data are the Wald-type F-statistic (F), Wald-Z statistic for random factors, degrees of freedom (DF), coefficient of the variable in the model (Estimator), and the significance value (P). See Table 2 for the abbreviations of the variables.

reproductive capacity, similar variables influenced the presence and abundance of reproductive structures in both phorophyte species (Tables 6 and 7). Large thalli were often reproductive (sexual and asexual) (Tables 6 and 7). Furthermore, microhabitat variables affected the development of reproductive structures. On both phorophytes, individuals with apothecia were more frequent at the tree base, whereas the presence and abundance of isidia increased with height on the trunks (Tables 6 and 7). Northern exposure boosted the presence and abundance of reproductive structures, especially in beech (Tables 6 and 7). The random variable tree significantly influenced the individual size and the presence of reproductive structures (Tables 5–7), suggesting that additional and not measured factors at the tree level were also responsible for the differences in the modelled variables. However, the random variable plot did not show any significant effect.

3.4. Relationships between size and the probability of reproduction

All logistic models used to analyse the relationships between individual size and reproductive capacity showed a high positive

correlation ($P < 0.001$). The phorophyte species was also a key factor for reproduction in *L. pulmonaria*. The probability of occurrence of reproductive structures depended on individual size (Fig. 2). The probability curves were different for oak and beech because although size-dependence pattern was common, the threshold size for the development of all types of reproductive structures was smaller for individuals on oak (Fig. 2). For example, an individual of 350 mm had a 50% probability of developing apothecia on oak, whereas it needed to be almost twice as large (690 mm) to reach 50% probability on beech (Table S5).

4. Discussion

Our results indicated that the structure of *L. pulmonaria* populations depended on the phorophyte species and the microhabitat heterogeneity in studied Mediterranean forests. We detected different patterns of establishment, abundance, thallus size and reproductive capacity on the two phorophytes. We found larger populations on oaks with a higher number of small individuals, and individuals became reproductive at smaller sizes than in beech forests. These differences may indicate that oaks provide a more favourable habitat for colonization and recruitment of new individuals, whereas beech with larger *L. pulmonaria* individuals represented a more favourable habitat for growth.

4.1. Species occurrence and abundance

Phorophyte species and the tree diameter were main factors driving the occurrence and abundance of *L. pulmonaria* individuals. Occupied oaks had a greater abundance of *L. pulmonaria* than beech, but smaller individuals, suggesting higher colonization and establishment rates on oak, probably because of its coarser bark. Short-distance dispersing propagules (asexual symbiotic ones) are likely retained in cracks of rough oak bark. Although the occurrence and abundance of *L. pulmonaria* depended on a large tree diameter in both phorophyte species, it required thicker trunks of beech than of oak, probably because beech needs to reach a larger size to provide coarse bark facilitating establishment and subsequent growth of propagules. These results are consistent with previous studies at the landscape scale, and emphasize the importance of habitat quality for this species (e.g. Öckinger et al., 2005; Werth et al., 2007; Belinchón et al., 2009, 2011; Juriado et al., 2011, 2012). Many studies have shown that the tree diameter is an important predictor of *L. pulmonaria* occupancy, because large trees have long been available for colonization, and also provide

Table 6
Summary of the generalized linear mixed models used to examine the effects of individual size and microhabitat factors on the presence and abundance of reproductive structures of *Lobaria pulmonaria* on *Fagus sylvatica* (beech).

Apothecia presence				
Fixed factors	DF	Estimator	F	P
Size	2725	2.335	404.93	<0.001
Height	2719	-0.012	48.81	<0.001
Or	2733	0.804	36.49	<0.001
Random factors				
Tree	Estimator	Z	F	P
Tree		3.804	7.08	<0.001
Residual		0.426	35.58	<0.001

Soredia presence					Soredia abundance				
Fixed factors	DF	Estimator	F	P	Fixed factors	DF	Estimator	F	P
Size	2733	2.247	502.92	<0.001	Size	2727	11.600	828.52	<0.001
Or	2526	0.317	8.82	0.003	Or	2647	3.001	20.29	<0.001
EPI	2610	C > L > B	5.99	0.002	EPI	2720	C > L > B	13.68	<0.001
Random factors					Random factors				
Tree	Estimator	Z	P		Tree	Estimator	Z	P	
Tree		0.649	3.71	<0.001	Tree		77.927	5.76	<0.001
Residual		1.234	35.55	<0.001	Residual		106.49	35.21	<0.001

Isidia presence					Isidia abundance				
Fixed factors	DF	Estimator	F	P	Fixed factors	DF	Estimator	F	P
Size	2713	1.484	373.91	<0.001	Size	2722	10.112	601.33	<0.001
Height	1856	0.003	11.28	<0.001	Height	2736	0.007	15.82	0.0218
Or	2640	0.346	12.17	<0.001	Or	2751	2.933	13.09	<0.001
EPI	2741	C > L > B	6.35	0.001	EPI	2745	L > C > B	5.89	<0.001
Random factors					Random factors				
Tree	Estimator	Z	P		Tree	Estimator	Z	P	
Tree		1.558	5.94	<0.001	Tree		11.335	7.04	<0.001
Residual		0.661	35.51	<0.001	Residual		0.033	22.18	<0.001

Notes: Only significant factors are shown. The data are the Wald-type F-statistic (F), Wald-Z statistic for random factors, degrees of freedom (DF), coefficient of the variable in the model (Estimator), and the significance value (P). See Table 2 for the abbreviations of the variables.

variation in bark roughness, moisture, and nutrient conditions (Gu et al., 2001; Öckinger et al., 2005; Snäll et al., 2003, 2005; Edman et al., 2008; Belinchón et al., 2009, 2011). Furthermore, Gustafsson and Eriksson (1995) indicated that the bark chemistry of large, old trees often differs from that of younger and smaller trees,

which may influence lichen establishment. Öckinger et al. (2005) found that *L. pulmonaria* occupied trees with a cover of bryophytes. In agreement, our results showed that the bryophyte cover appeared to be a favourable habitat for colonization by new individuals. This might reflect one of two possible phenomena: (1)

Table 7
Summary of the generalized linear mixed models used to examine the effects of individual size and microhabitat factors on the presence and abundance of reproductive structures of *Lobaria pulmonaria* on *Quercus pyrenaica* (oak).

Apothecia presence				
Fixed factors	DF	Estimator	F	P
Size	9580	2.137	1173.98	<0.001
Height	1400	-0.003	11.57	<0.001
EPI	1400	L > C > B	4.16	0.005
Random factors				
Tree	Estimator	Z	F	P
Tree		0.536	5.53	<0.001
Residual		1.089	72.50	<0.001

Soredia presence					Soredia abundance				
Fixed factors	DF	Estimator	F	P	Fixed factors	DF	Estimator	F	P
Size	11,300	2.103	2340.41	<0.001	Size	11,300	10.827	2323.01	<0.001
Or	11,300	0.206	24.44	<0.001	Or	11,300	1.779	31.29	<0.001
EPI	11,300	C > L > B	39.77	<0.001	EPI	11,300	C > L > B	39.37	<0.001
					BL	282	0.007310	4.37	0.037
					BH	290	-0.144	9.98	0.001
Random factors					Random factors				
Tree	Estimator	Z	P		Tree	Estimator	Z	P	
Tree		0.773	7.99	<0.001	Tree		76.873	9.66	<0.001
Residual		0.986	72.74	<0.001	Residual		115.96	72.82	<0.001

Isidia presence					Isidia abundance				
Fixed factors	DF	Estimator	F	P	Fixed factors	DF	Estimator	F	P
Size	11,300	1.440	1714.12	<0.001	Size	11,300	4.853	1134.86	<0.001
Height	11,300	0.003	38.95	<0.001	Height	11,300	0.020	48.43	<0.001
EPI	11,300	C > B > L	33.79	<0.001	EPI	11,300	C > B > L	18.56	<0.001
Random factors					Random factors				
Tree	Estimator	Z	P		Tree	Estimator	Z	P	
Tree		1.014	8.33	<0.001	Tree		16.358	8.34	<0.001
Residual		0.853	72.71	<0.001	Residual		48.318	72.85	<0.001

Notes: Only significant factors are shown. The data are the Wald-type F-statistic (F), Wald-Z statistic for random factors, degrees of freedom (DF), coefficient of the variable in the model (Estimator), and the significance value (P). See Table 2 for the abbreviations of the variables.

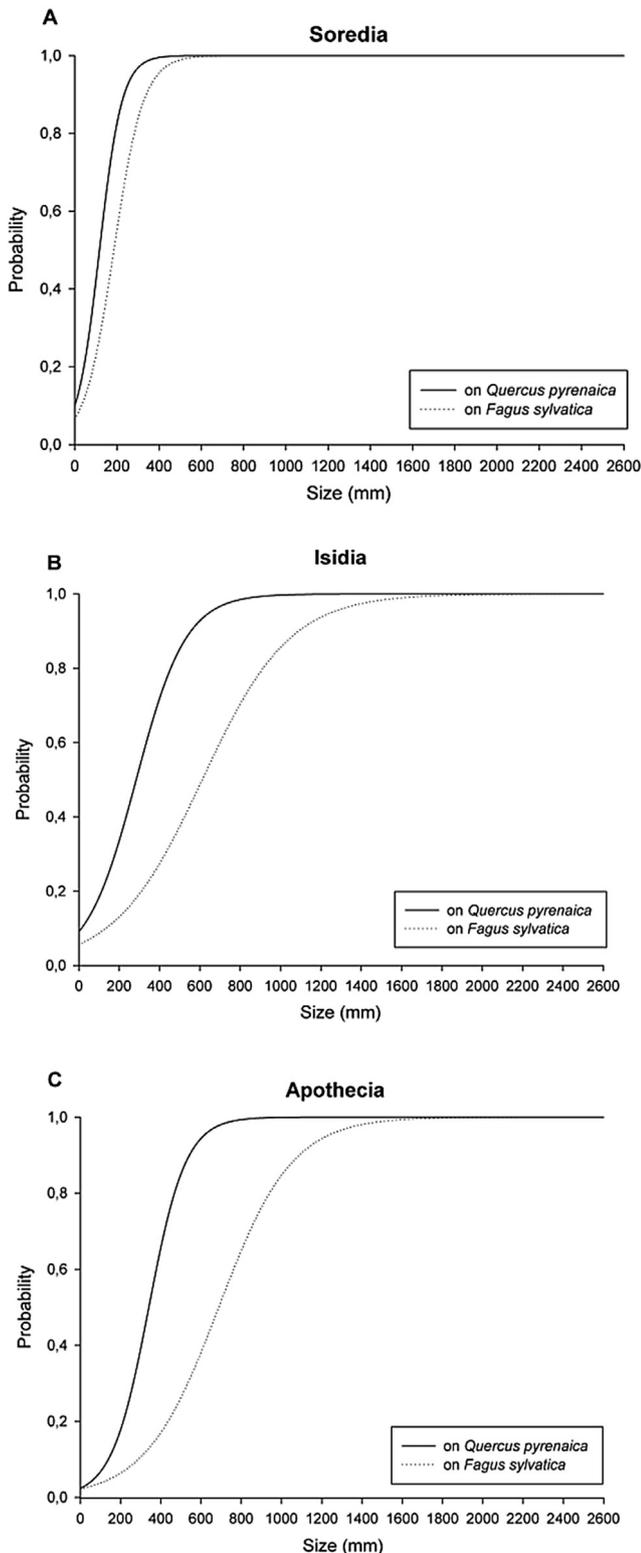


Fig. 2. Reproductive probability of *Lobaria pulmonaria* relative to individual size in each phorophyte (*Quercus pyrenaica* and *Fagus sylvatica*). A: Presence of soredia. x-axis: thallus size (mm); y-axis: asexual reproduction (by soredia) probability. B: Presence of isidia. x-axis: thallus size (mm);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

bryophytes facilitate the attachment and/or establishment of propagules and provide a more humid microenvironment because they can store water, accumulate nutrients, and form a spongy

surface (Colesie et al., 2012); and (2) *L. pulmonaria* and bryophytes require similar environments.

4.2. Individual size

On beech, we found larger individuals on large trees with coarse bark, at northerly exposure, and closer to the ground, conditions where water availability is presumably higher (Geiger, 1950; Merinero et al., 2014, 2015). However, on oak, the size depended only on the tree diameter. These results suggest that individuals growing on beech require a wider set of microhabitat conditions than on oak, probably to compensate the adverse effect of smooth bark. Larger size and presumably faster growth on beech may be related to the amount of light that lichens received while hydrated (Dahlman and Palmqvist, 2003). Hydration is frequent from autumn to early spring in the Mediterranean region. *F. sylvatica* is a deciduous tree with a fairly long leafless period, whereas *Q. pyrenaica* retains many dry leaves (Costa et al., 2001). This means that beech forests have a long period with a good combination of light and humidity, but little light in the dry summer when the intense light outside the canopy can damage *Lobaria*, which is high-light susceptible when dry (Gauslaa et al., 2012). This may enhance growth of *L. pulmonaria* on beech in a relatively dry Mediterranean climate. By contrast, oak forests retaining dry leaves in the canopy probably provide environment too dark for growth of *Lobaria* from late autumn to early spring. Oak is more light-demanding than beech, and excess light in summer is likely responsible for the high photoinhibition and high light avoidance symptoms of *L. pulmonaria* on oaks (I. Martínez per. obs.), like many thalli with curled margins and dark-brown colour (Gauslaa and Solhaug, 2001; Bártak et al., 2006).

4.3. Reproductive capacity

Less than 50% of the individuals in our study area were reproductive. In boreal rain forests, only 14% of the *L. pulmonaria* individuals had reproductive structures (Hilmo et al., 2013). In the latter study, the population inhabited *Picea* branches, a finer and more short-lived habitat than tree trunks, probably reducing the frequency of large *L. pulmonaria* individuals and thus of reproductive individuals. In our Mediterranean forests, the abundance of reproductive individuals (asexual and sexual) on beech increased only with the tree diameter, whereas larger oak trees with coarser bark and less bryophyte cover hosted more reproductive individuals. Such patterns are not consistent with the positive effect of bryophytes on colonization rates.

Apothecia occurred in <10% of our individuals; the scarcity of fertile individuals seems to be a common trend in various geographic regions (Zoller et al., 1999; Denison, 2003; Walser et al., 2004; Hilmo et al., 2013). More specifically, in plot 4 we did not observe sexual reproduction, maybe because this population is small (<130 individuals), and sexual reproduction in *L. pulmonaria* may increase with the population size (e.g. Scheidegger et al., 1995; Edman et al., 2008; Öckinger and Nilsson, 2010). On beech, we found smaller populations and a lower proportion of fertile individuals than on oak. Because *L. pulmonaria* is a heterothallic species (Singh et al., 2012), a lower number of fertile individuals on beech may be a consequence of a scarcity of compatible mating types, as previously suggested (Zoller et al., 1999; Walser et al., 2004; Jüriado et al., 2011). This might also be the case for plot 4, the smallest population, where no fertile individuals occurred. Therefore, larger populations on oaks possibly contain more genets and thus have a higher probability of producing apothecia. The largest individuals had a higher probability of forming apothecia, but this size dependency was tuned by microhabitat conditions.

Individuals growing near the ground were larger and more likely had apothecia, whereas individuals growing higher on the trunks were smaller and produced more asexual structures, mainly isidia. These results are consistent with the higher growth rates of *L. pulmonaria* transplants at tree bases in the same study area (Merinero et al., 2015) and with the reproductive pattern described throughout the Iberian Peninsula (Martínez et al., 2012). Northerly exposure was also favourable, mainly on beech. The water retention capacity of bark is probably lower on beech trunks compared with oak. Thus, *L. pulmonaria* individuals growing on beech might require a greater amount of moisture that can be reached northerly, facilitating the development of apothecia.

An important result is that there was a relationship between a minimum threshold size and the development of reproductive structures, consistent with other studies (Larsson and Gauslaa, 2011; Martínez et al., 2012; Hilmo et al., 2013). *L. pulmonaria* develops reproductive structures in a size-dependent way, i.e., first soredia, followed by isidia and then apothecia (Denison, 2003; Martínez et al., 2012). Our results demonstrated that although a threshold size is required, this was habitat-dependent. The threshold size varied with the phorophyte species and with the microhabitat conditions.

Summarising, beech hosted larger juveniles than oak probably because the onset of reproduction started at larger sizes on beech. Based on these results, we hypothesized that *L. pulmonaria* grows faster on beech than on oak, likely because: (1) reproduction is regulated by thallus age; and a large thallus on beech is as old as a much smaller thallus on oak. This is consistent with previous studies (Eaton and Ellis, 2014); or (2) reproduction is induced by some environmental conditions or stress. Life-history theory predicts that plants in adverse environments initiate reproduction at smaller sizes to maximize their fitness during its short lifetime and vice versa (Stearns and Koella, 1986; Wesselingh et al., 1997). Because microclimatic conditions in oak forests seem to be more stressful than inside beech forests, we believe that smaller reproductive sizes are selected in oak forests, and larger reproductive sizes in beech forests.

5. Conclusions

Population characteristics and individual status of *L. pulmonaria* strongly depended on the phorophyte species and the microhabitat heterogeneity in the studied Mediterranean forests. Although oak forests favoured the establishment and recruitment of new *L. pulmonaria* individuals, they probably provided adverse environmental conditions for lichen growth and thus also affected the reproductive capacity because reproduction is size-dependent. The higher light incidence in oak forests in summer, together with the decoupling of moisture and light availability across an annual cycle, may shorten the generation time of *L. pulmonaria* on oaks. Adverse environmental conditions for lichen growth could be the reason why *L. pulmonaria* individuals reproduce at a smaller thallus size in oak. The next step to disentangle the mechanisms underlying the possible generation time differences between forests is to test whether *L. pulmonaria* growth rates in oaks are slower than in beech forests. This will contribute to the understanding that habitats hosting large species populations, with high rates of establishment and recruitment of new individuals, may not necessarily favour other life-cycle stages. This knowledge is of high relevance for management of the habitats where threatened species thrive, allowing the development of effective conservation strategies.

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Supplementary data

Supplementary data related to this article can be found at <http://dx.doi.org/10.1016/j.funeco.2015.08.002>.

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