

FRAGMENT QUALITY AND MATRIX AFFECT EPIPHYTIC PERFORMANCE IN A MEDITERRANEAN FOREST LANDSCAPE¹

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Destruction and fragmentation of habitats represent one of the most important threats for biodiversity. Here, we examined the effects of fragmentation in Mediterranean forests on the epiphytic lichen *Lobaria pulmonaria* (Lobariaceae). We tested the hypothesis that not only the level of fragmentation affects *L. pulmonaria* populations, but also the quality of the habitat and the nature of the surrounding matrix affect them. The presence and abundance of the lichen was recorded on 2039 trees in a total of 31 stands. We recorded habitat quality and landscape variables at three hierarchical levels: tree, plot, and patch. We found that *L. pulmonaria* tends to occur in trees with larger diameters in two types of surveyed forests. In *Quercus pyrenaica* patches, the mean diameter of colonized trees was smaller, suggesting the importance of bark roughness. Factors affecting the presence and cover of the lichen in each type of forest were different. There was a strong positive influence of distance from a river in beech forests, whereas proximity to forest edge positively affected in oak forests. The influence of the surrounding matrix was also an important factor explaining the epiphytic lichen abundance.

Key words: epiphytic lichens; forest fragmentation; habitat quality; *Lobaria pulmonaria*; matrix; Mediterranean forests.

Habitat destruction and fragmentation pose major threats for biodiversity (Andrén, 1997; Debinski and Holt, 2000). For decades, large parts of forest ecosystems have been destroyed or degraded by human activities, resulting in fragmented landscapes (Primack and Rodrigues, 2001). Major changes in the distribution and abundance of species have occurred in response to human-induced modifications in ecosystems, particularly where original vegetation cover is lost or fragmented (Johansson and Ehrlén, 2003; Ries et al., 2004). Fragmentation reduces the amount of suitable habitat, increases isolation between patches, and produces changes in biotic and abiotic conditions (Fahrig, 2003). These changes subsequently affect forest biodiversity through the decline or disappearance of numerous species (Wilson, 1988; Forman, 1995; Gustafsson et al., 2004). Therefore, one priority for conservation ecologists is to identify how habitat loss and fragmentation of habitat may affect species distribution (Andrén et al., 1997; Dettki et al., 1998).

Historically, patch size and isolation have been shown to be the most critical factors for describing regional dynamics of species in fragmented landscapes (Hanski and Gaggiotti, 2004). Recently, some authors have also assessed the importance of habitat quality and other landscape features in fragmented systems (Moilanen and Hanski, 1998; Nielsen et al., 2006). Consequently, some species distribution models now incorporate spatiotemporal dynamics (Eriksson, 1996; Snäll et al., 2003),

landscape history (Cousins and Eriksson, 2001; Ellis and Coppins, 2007), or even the influence of the matrix surrounding the fragments on dispersal and pollen flux among patches (Cook et al., 2004; Williams et al., 2006). The nature of the matrix between suitable patches has a significant effect on connectivity in forest landscapes because the dispersal of organisms will either be facilitated or obstructed by the conditions therein (Lindenmayer and Franklin, 2002). It is known that the characteristics of fragments often vary with the nature of the surrounding matrix, and habitat quality depends on the type of matrix in which the fragments are embedded (Haynes and Cronin, 2004). Understanding fragmentation effects is complex because it requires knowledge of how the biota uses all landscape components, including the matrix (Lindenmayer and Franklin, 2002). The quality of the patch also may be crucial for the survival of different organisms (Johansson and Ehrlén, 2003; Haynes and Cronin, 2004; Nielsen et al., 2006). However, only a few papers dealing with fragmentation effects have explicitly considered field data on the nature of matrix and patch quality (Ricketts, 2001; Haynes and Cronin, 2004; Anderson et al., 2007).

The effects of habitat fragmentation on epiphytic organisms are poorly understood (Debinski and Holt, 2000; Belinchón et al., 2007). Most empirical studies about patch-occupancy distributions for both bryophytes and lichens point to dispersal limitations rather than unfavorable microclimatic regimes to explain species loss from fragments (Pharo and Zartman, 2007; Johansson, 2008). Furthermore, cryptogamic epiphytes are well documented to exert sharp declines when a continuous forest is converted to small fragments sheltered in the landscape (Sjöberg and Ericson, 1992; Snäll et al., 2004; Löbel et al., 2006). This species decline in fragmented systems is one of the more perplexing results of fragmentation studies considering the fact the cryptogams are considered to be relatively good dispersers.

Lobaria pulmonaria (L.) Hoffm. (Lobariaceae) is probably one of the best-known epiphytic lichens from an ecological point of view. In recent years, several studies have examined the spatial distribution and dynamics of *L. pulmonaria* populations related to different degrees of forest management and

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alteration (Gu et al., 2001; Kalwij et al., 2005; Snäll et al., 2005). However, nothing is known about this species in the Mediterranean Basin, where the environmental conditions are especially adverse due to high water and light stress related to frequent extreme summer drought (Valladares, 2004). The Mediterranean Basin is characterized by a long history of forest fragmentation, degradation, and deforestation that has affected structure and function in most of its forests. A history of forest degradation and destruction together with the climatic constraints make this region an interesting model system for studying the effects of forest fragmentation (Scarascia-Mugnozza et al., 2000). Further, these conditions may become even more extreme due to global warming (Giménez-Benavides et al., 2007). These stressful conditions make the Mediterranean, fragmented forest landscape exceptionally useful for testing the effects of patch quality and the surrounding matrix on the performance of *L. pulmonaria*.

Our main goal was to understand the effects of fragmentation in Mediterranean forests on *L. pulmonaria* populations across different spatial scales. We hypothesized that not only the level of fragmentation (i.e., patch size, isolation) affects *L. pulmonaria* populations, but also the quality of habitat (understood as patch longevity and type of forest) and the nature of the matrix. Consequently, we expected that forest type may differentially affect the performance of our epiphyte model and that this effect may be reduced or exacerbated depending on the nature of the matrix. Our study was carried out in central Spain where *L. pulmonaria* occurs in two different types of forest fragments: semideciduous endemic oak (*Quercus pyrenaica*) and beech (*Fagus sylvatica*) forests. Our specific objectives were (1) to determine the influence of quantity, isolation, and habitat quality on the presence and abundance of *L. pulmonaria*; (2) to know whether forest type influences the presence and abundance of this species, and (3) to determine the effects of the surrounding matrix.

MATERIALS AND METHODS

Study area—The study site is comprised of ~5600 hectares in the Sierra de Ayllón, located in the easternmost tip of the Sistema Central Range in Spain (Fig. 1). At this location, *Fagus sylvatica* reaches its southern and western limit (41°13'N 3°21'W). The area located on the southern slope has been part of the Parque Natural Hayedo de Tejera Negra since 1978, whereas the northern slope is not currently protected. The climate is mediterranean with a mean annual temperature of 8.6°C and an annual rainfall of 1253 mm (climatic station Cerezo de Arriba, La Pinilla, 1500 m a.s.l), with a drought period from July to August mediated by summer storms. The study area consists of 31 isolated patches of two different forest types (23 *Fagus sylvatica* and 8 *Quercus pyrenaica* forest remnants) embedded in a matrix dominated by heathlands (*Erica arborea* and *E. australis*) and pine plantations (*Pinus sylvestris*). The fragments range from 0.75 ha to 209.80 ha, and the distances between patches range from 200 m to 8 km with a mean distance of 3.10 km (SD = 1.63). *Quercus pyrenaica* is a semideciduous oak almost entirely restricted to the Iberian Peninsula with some isolated populations in northern Morocco and on the southwestern tip of France. *Fagus sylvatica* is a deciduous tree widespread throughout western Europe.

Fragmentation in our study area is mainly due to logging activities in the past. During the 16th to 19th centuries some forests were turned into pasture and heathlands. Logging and charcoal production were mainly practiced on Mediterranean oaks but also in beech forests. Forest loss and fragmentation have been intense, with well-preserved forests restricted to areas of difficult access. From the 1960s onward, most forests were clear cut and converted to pine plantations (Hernández and Sainz, 1978). Beech forests have been less affected by firewood extraction, being the best well-preserved forests in areas of difficult access.



Fig. 1. Localization of the study area in the Sistema Central Range, Spain.

Study species—*Lobaria pulmonaria* is one of the most commonly used indicator species of unpolluted and undisturbed forest due to its assumedly limited dispersal ability (Werth et al., 2006) and its vulnerability to excessive light and/or high temperatures (Gauslaa and Solhaug, 2001). This lichen species is an epiphytic green-algae macrolichen with internal cephalodia containing *Nostoc*. It is widespread throughout the northern hemisphere, but their populations have declined considerably during the last century from forest management practices and air pollution (Rose, 1988; Purvis et al., 1992). In the Iberian Peninsula, it mainly occurs in the northern oceanic edge, although it does reach some mountainous places in the center and south. However, the species is currently declining in the Mediterranean region, where forests with mesic conditions are presently extremely rare for a variety of reasons such as wood extraction, grazing by cattle and meadow management (Martínez et al., 2003). Like many other lichens, *L. pulmonaria* can reproduce asexually in the form of relatively large vegetative soredia and/or isidia, and sexually by means of ascospores, which are formed in a later stage of thallus development (Denison, 2003).

Sampling—The field work was carried out between 2006 and 2008. Field data were collected in both *Fagus sylvatica* and *Quercus pyrenaica* fragments. We identified forests fragments with orthophotos taken in 2003 (provided by the SIGPAC service of the Ministry of Agriculture <http://www.mapa.es/es/sig/pags/sigpac/intro.htm>). The orthophotos were georeferenced using the program ArcGIS 9.0 (ESRI Inc, 1999-2005), a geographic information system (GIS). The landscape included 31 forest remnants, which were identified and georeferenced in the field. We assigned the forest type according to the dominant tree species (>90%). We considered two fragments different when there was at least 40 m of unsuitable habitat between them (Hanski et al., 1994) (Fig. 2A). For each fragment, we recorded a set of predictor variables, summarized in Table 1, using the program ArcView GIS version 3.1 (ESRI). To calculate geometric parameters, we used the X-Tools Extension in ArcView GIS 3.1 for Windows. The topographic parameters were derived from the digital elevation model of Sierra de Ayllón (100 m of pixel resolution). The connectivity of suitable patches was calculated following Hanski et al. (1994): $S_j = \sum \exp(-\alpha d_{ij}) \cdot A_j (i \neq j)$, where A_j is the area of patch j (ha), d_{ij} is the distance between centroids of patches i and j , and α is the parameter of the exponential distribution setting the influence of distance on connectivity. We used centroid-to-centroid distance because the study patches were relatively small compared to the scale of the landscape. The value of α was set to 1 because dispersal abilities were unknown (Johansson and Ehrlén, 2003). Additionally, given that the matrix may influence the dispersal of organisms as well as the quality of remnant patches, we categorized habitat between forest fragments into two categories: heathland and pine plantations. We also estimated the percentage of patch perimeter covered by pine or heathland.

Within each fragment, we randomly located 20 × 20 m² plots to survey the forest stand quality. The number of plots that we placed in each fragment depended on the size of the fragment and ranged from 1 to 14 (Appendix S1, see Supplemental Data with the online version of this article). We located plots at different altitudes, aspects, and forest structure to estimate variability within the

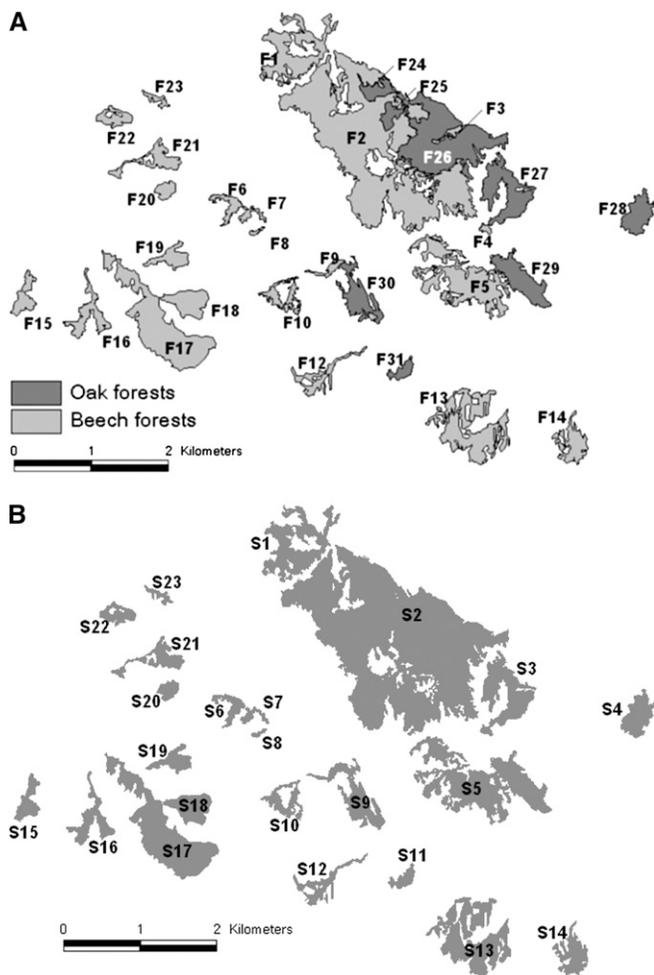


Fig. 2. Maps of the study area with the surveyed stands in the Sistema Central Range in Spain. (A) distribution of the 31 forests patches divided into *Fagus sylvatica* and *Quercus pyrenaica* forests; (B) distribution of the 23 patches of suitable substrate for *Lobaria pulmonaria* after combining oak and beech fragments that are in contact.

patch. On the basis of our field experience and on results of a project on the demography of *L. pulmonaria* along the Iberian Peninsula, we established a threshold size for each host tree species. This size was the minimum size in which we have found a lichen specimen: 7 cm for oaks and 9 cm for beeches. We counted the total number of trees and calculated the mean diameter at base height (dbh) for each plot. Variables such as distance to the fragment edge and distance to the nearest permanent water source of each plot were estimated using a geographic information system (ArcView GIS version 3.2 for Windows).

We also collected data on each tree in each plot for the following variables: diameter at tree base (dbb), dbh, tree species (oak or beech), and tree status (alive or dead). In each tree, presence of *L. pulmonaria* was recorded and the cover of the lichen species below 2 m height was measured in square centimeters because *L. pulmonaria* rarely grows above this height in the studied area (I. Martínez and G. Aragón, personal observations). Cover values were estimated by drawing *L. pulmonaria* thallus on transparent plastics in the field. *Lobaria pulmonaria* cover was then calculated by means of an image analyzer (ImageJ 1.36b, National Institutes of Health, Bethesda, Maryland, USA).

Twenty-seven environmental variables were derived from the different spatial levels. Only nine predictors were included in our models to predict the distribution of *L. pulmonaria*, because we excluded environmental predictors with correlations >0.7 to avoid multicollinearity problems (Table 1).

Data analysis—The effect of the nine environmental predictors at each hierarchical spatial scale (patch, plot, and tree) for the occurrence and abundance

of *L. pulmonaria* on each tree were modeled by fitting a generalized linear mixed model (GLMM) (McCullagh and Nelder, 1989). Similarly, we modeled the percentage of trees colonized and the cover of this lichen at the plot level. This modeling approach was chosen because our data had an unbalanced and hierarchical structure with trees nested within plots and plots nested within patches. A hierarchical data structure implies a correlation between data points at different scales, inflating the error degrees of freedom and increasing the chance of making a type I error. To overcome these problems, we analyzed the data using a multilevel approach and, when necessary, considered plots and patches as random factors and applied mixed modeling (Verbeke and Molenberghs, 1997). Predictors were included as explanatory variables (fixed factors), and patch and plot were included as random sources of variation. Because the data tended to be overdispersed in some cases, we used the quasi-likelihood approach to overcome possible difficulties (Guisan et al., 2002). The significance of each predictor was estimated by means of an analysis of deviance (Guisan et al., 2002). For the presence and number of trees with *L. pulmonaria*, we fitted the mixed models using the binomial estimation, a “logit” link function, and setting the variance to “1-mean”. For *L. pulmonaria* cover, we used a Poisson distribution, with a “log” link function and setting the variance to “mean”. Effects of random factors were tested using the Wald Z-statistic test.

We tested two different model extensions given that both beech and oak are suitable host trees for *L. pulmonaria*. First, we mapped the spatial distribution of suitable forest fragments as the sum of both beech and oaks fragments when they were in contact (23 fragments) (Fig. 2B). We tested whether spatial distribution of suitable forests stands, irrespective of whether they were beeches or oaks, improved model fit. Second, we analyzed the behavior of *L. pulmonaria* in both beech and oak forests separately. We tested which variables gave the best model fit on each type of forest. Furthermore, we determined the most relevant predictors of the presence and cover of *L. pulmonaria* at two different scales, at plot and tree level.

All GLMM computations were performed using SAS Macro program GLIMMIX, which iteratively calls SAS Procedure Mixed until convergence (GLIMMIX ver. 8 for SAS/STAT; available at <http://www.sas.com.techsup/download/stat/>).

TABLE 1. List of the environmental variables recorded at the patch, plot, and tree level at the study area in the Sistema Central Range, Spain. The nine variables included in the model analysis are marked with an asterisk.

Patch level	Plot level	Tree level
Perimeter (m)	Distance from edge (m) *	Dbh (cm) *
Area (ha) *	Distance from river (m) *	Dbb (cm)
Perimeter/Area	Altitude (m)	State (alive, dead)
Maximum aspect (degrees)	Slope (degrees)	Tree species *
Minimum aspect (degrees)	Mean dbh (cm)	(beech, oak)
Mean aspect (degrees)	Mean dbb (cm)	
Maximum slope (degrees)	Number of trees *	
Minimum slope (degrees)		
Mean slope (degrees)		
Maximum altitude (m a.s.l.)		
Minimum altitude (m a.s.l.)		
Mean altitude (m a.s.l.)		
Altitudinal range (m)		
Connectivity *		
Pine perimeter (%) *		
Heath perimeter (%) *		

RESULTS

Lobaria pulmonaria occupied 562 of the 2039 sampled trees, having a strong preference for oak trees ($n = 569$; 42% colonized) compared to beech ($n = 1470$; 22% colonized) (randomization test with 5000 permutations; $p = 0.0032$). Because *L. pulmonaria* tended to occur on trees with larger diameters, its preference for oaks should be even greater because oaks are significantly smaller than beeches in our study area (Table 2, Fig. 3A).

TABLE 2. Mean dbh \pm SE of trees with and without *Lobaria pulmonaria* in study area in the Sistema Central Range, Spain. All comparisons are significantly different (randomization test with 5000 permutations; $p < 0.05$). n = total number of trees

Variable	With <i>L. pulmonaria</i> (n)	Without <i>L. pulmonaria</i> (n)
All trees	29.56 \pm 0.78 (562)	20.39 \pm 0.29 (1477)
Beech forests	36.52 \pm 1.08 (322)	21.83 \pm 0.35 (1148)
Oak forests	20.21 \pm 0.81 (240)	15.40 \pm 0.31 (329)

Most of the environmental variables did not differ significantly between both types of forests (Table 3). However, it is worth noting that some of the differences were relevant. For instance, beech patches were located at higher altitudes and in areas with steeper slopes. They were also more connected than oak fragments, and they were more often surrounded by heathland areas. Moreover, the plots in oak forests presented a higher tree density (Table 3).

When we considered suitable forest fragments for *L. pulmonaria* as the sum of both beech and oak fragments, the results of mixed models at tree level showed that tree diameter is the most important variable explaining the occurrence and cover of this lichen, although distance to a river and surrounding matrix of pine plantations were also important predictors (Table 4). In addition, the occurrence of *L. pulmonaria* was influenced by the interaction between tree species and dbh. The percentage of occupied trees and the cover of the species at the plot level were significantly affected by the interaction between the number of trees per plot and the tree species (Table 4, Fig. 3B).

On the other hand, the major factors that determined the occurrence and cover of *L. pulmonaria* differed between the two forest types (Table 5). In the case of beech forests, the proximity to a river and large tree diameters were the main factors that increased the occurrence and cover of *L. pulmonaria* at tree level. However, at plot level, no variables accounted for the variation in the data (Table 5). In oak forests, *L. pulmonaria* had a higher cover and probability of occurrence in larger diameter trees and near the edge of the patches at both tree and plot level. Moreover, *L. pulmonaria* cover decreased significantly when the percentage of heathland around the oak patch was higher at the tree level (Table 5). Furthermore, surrounding heathland showed a weak effect on the occurrence of *L. pulmonaria* as well as on the percentage of occupied trees.

DISCUSSION

Our results suggest that in fragmented landscapes, the habitat quality (i.e., tree species and stand structure) and the nature of the surrounding matrix exert an influence at different scales than other features considered critical in the behavior of species in fragmented landscapes, such as patch size and isolation. Our study suggests that *L. pulmonaria* is sensitive to a decrease in habitat quality linked to habitat fragmentation. Patch longevity (represented in our case as the mean diameter of the trees) is more important than distance between patches as in other studies (Keymer et al., 2000). However, Gu et al. (2001) pointed out that remnant populations of a lichen species might reflect the delay between habitat fragmentation and the extinction of local populations. Tree size seemed to be the most important predictor for the maintenance of populations of *L. pulmonaria* in each type of forest. Furthermore, forest structure, proximity

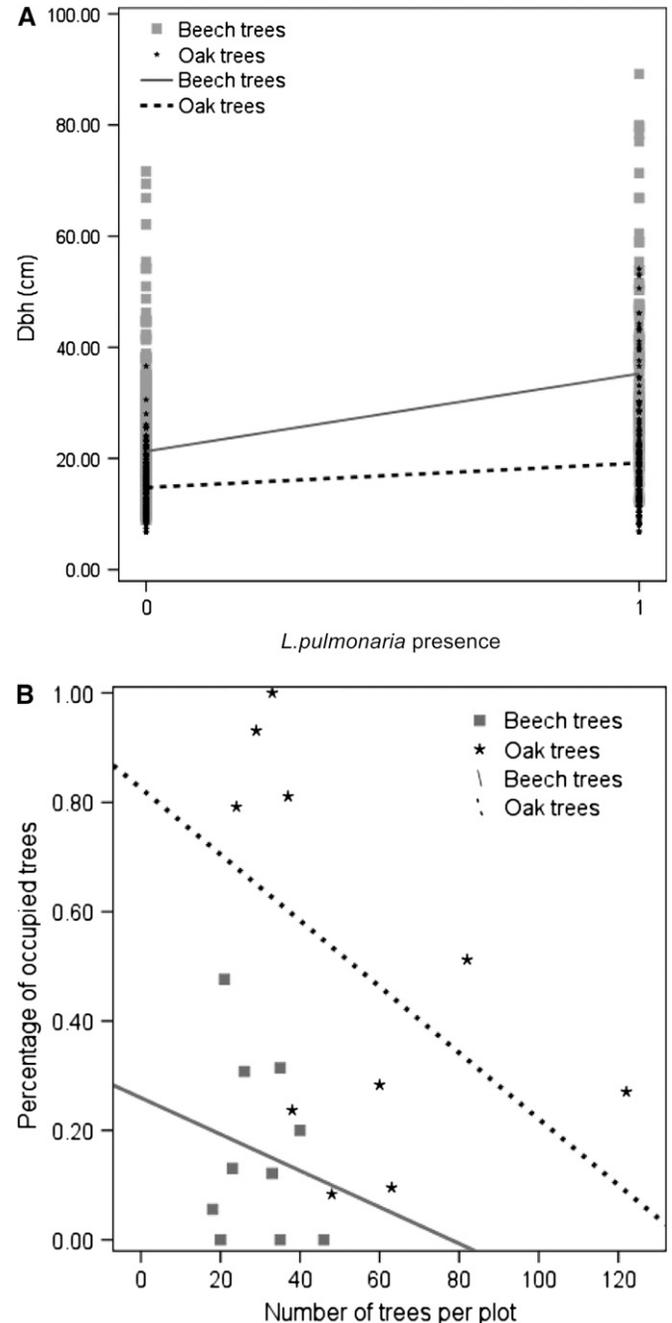


Fig. 3. Relationship of the presence of *Lobaria pulmonaria* and the percentage of occupied trees per plot between oak and beech trees in the Sistema Central Range in Spain. Data represent (A) dbh values for each sort of forest and (B) percentage of occupied trees in relation to the number of trees per plot in each sort of forest. The mean dbh and the percentage of occupied trees differed significantly between beech and oak forests (randomization test with 5000 permutations; $p < 0.05$).

to a permanent water source, as well as distance to the edge were important characteristics at the plot level to ensure the development of the species. We found that the distribution of *L. pulmonaria* differed between tree host species, which has been shown for other lichen epiphytes (McCune, 1993; Snäll et al., 2004). In fact, responses of lichen species to habitat fragmentation

TABLE 3. Mean values and standard deviations of each environmental variable measured at each of three levels (A–C) for both oak and beech forests in the study area in the Sistema Central Range, Spain. Boldfaced values denote significant differences (randomization test with 5000 permutations; $p < 0.05$).

Variable	Beech stands	Oak stands	<i>p</i>
A) Patch level			
Area, ha	22.40 ± 44.14	21.64 ± 22.53	0.267
Perimeter, m	5.45 ± 8.30	5.22 ± 4.55	0.832
Perimeter/Area	0.38 ± 0.16	0.27 ± 0.12	0.076
Maximum slope, degrees	42.94 ± 16.30	25.67 ± 5.83	0.012
Minimum slope, degrees	14.34 ± 14.78	8.00 ± 6.64	0.173
Mean slope, degrees	29.45 ± 13.96	16.11 ± 3.83	0.065
Maximum aspect, degrees	276.02 ± 82.93	282.23 ± 94.99	0.003
Minimum aspect, degrees	89.00 ± 107.78	96.94 ± 110.12	0.195
Mean aspect, degrees	195.39 ± 85.25	184.49 ± 90.96	0.003
Maximum altitude, m a.s.l.	1725.35 ± 93.37	1639.25 ± 97.25	0.003
Minimum altitude, m a.s.l.	1528.04 ± 93.00	1504.13 ± 97.44	0.003
Mean altitude m a.s.l.	1626.54 ± 78.89	1562.69 ± 95.62	0.002
Connectivity	67.93 ± 36.65	108.57 ± 66.17	0.045
Pine perimeter	10.08 ± 16.61	44.30 ± 39.07	0.758
Heath perimeter	72.92 ± 27.53	22.20 ± 19.15	0.008
B) Plot level			
Distance from edge, m	45.56 ± 45.48	23.89 ± 17.89	0.141
Distance from river, m	661.51 ± 501.55	310.46 ± 447.84	0.061
Altitude, m	1606.31 ± 91.50	1582.50 ± 125.36	0.002
Slope, degrees	18.33 ± 6.53	17.23 ± 5.00	0.009
Number of trees	29.35 ± 14.60	53.60 ± 29.95	0.042
C) Tree level			
Dbh, cm	25.13 ± 15.34	16.64 ± 7.35	0.004

may differ between life-history traits, forest type, cutting intensity, and regions (McCune, 1993; Coxson and Stevenson, 2005).

Classical metapopulation theory assumes that patch size and connectivity are important in determining species distribution (Hanski and Gaggiotti, 2004). However, habitat fragmentation, estimated by patch size and connectivity, did not account for a substantial amount of the variation in the distribution of *L. pulmonaria*. In our study, larger patches did not support larger populations of this lichen nor imply a higher number of potential host trees. In fact, for many specialized lichen species, the lack of suitable substrate probably affects their local presence and abundance (Uliczka and Angelstam, 1999). In recent epiphyte studies, connectivity is a common predictor of species presence, which has been related to a supposedly limited capability of these organisms to disperse at the regional and local scales (Gu et al., 2001; Snäll et al., 2005; Löbel et al., 2006). Our results showed that connectivity among patches was not correlated with *L. pulmonaria* distribution, suggesting that the landscape configuration may not influence the dispersal of this species. This lack of importance of connectivity in lichen dynamic is in agreement with Eriksson (1996), which suggests that time is more important than spatial factors in the dispersal process for slowly growing species.

Although the present landscape structure may not be an important factor affecting *L. pulmonaria* performance, the surrounding matrix is an important factor for explaining the abundance of this epiphytic lichen. Few studies have focused on the matrix, although changes in the structure of the landscape matrix are known to affect habitat quality (Haynes and Cronin, 2004). In our study, coniferous matrix habitats exerted a negative influence on *L. pulmonaria* cover (Table 4). Coniferous forest was previously shown to be a filter for dispersing propagules, affecting the presence of two other epiphytic

lichens (Johansson and Ehrlén, 2003). In addition, heathlands surrounding oak patches also negatively affected the cover of *L. pulmonaria*. Changes in microclimatic conditions within a patch may be associated with exposure to the differing conditions of the surrounding matrix and are likely to depend on the type of matrix (Ries et al., 2004). Oak forests are located in drier conditions than beeches, and a matrix dominated by heaths may imply greater insolation exposure and more intense drying during the limiting summer season. This hardening of the environmental conditions might not only affect the growth of *L. pulmonaria*, but also prevent development in the early stages after the arrival of the propagules. Johansson (2008) makes a literature review of the consequences of different disturbances on epiphytic lichens in boreal forests. In relation to edge effects, he pointed out that the influence of the edge on the epiphytic lichen species depend on the edge conditions. A heath matrix may be considered a “hard” edge because oak patches are exposed to open ground, changing the microclimate and irradiance levels of the oak patch, which can affect the metabolic activity of the lichens (Palmqvist and Sundberg, 2000).

Another measure of the habitat quality was the tree diameter, which reflects how long the tree has been available for colonization (Riialti et al., 2001). Many epiphytic lichens and bryophytes need old trees for their persistence, because the colonization process is slow (Kuusinen, 1996; Snäll et al., 2003). Although *L. pulmonaria* was related to large tree diameter in both tree species, beech trees needed a greater diameter than oak trees to favor the colonization of the species as suggested by the significant interaction between tree species and dbh (Table 4). Beech trees have very smooth bark with some crevices when they are very old, whereas oak trees have rough bark even when young. Dispersing propagules are more likely to get caught in the cracks and crevices of trees with rough bark than in trees with smooth bark (Barkman, 1958; Gu et al., 2001).

We also obtained some unexpected results related to the edge effect in oak fragments. The incidence, cover, and number of occupied trees by *L. pulmonaria* increased in plots closer to the edge. Oak forests in the studied area are mostly restricted to small patches but contain some scattered big trees with high cover of *L. pulmonaria* (I. Martínez and G. Aragón, personal observations). They probably originated in old dehesas, which are pasture habitats with some remaining trees. Abandonment of past management activities during the second half of the last century is associated with the recovery of these oak forests. These trees might behave as sources of propagules and may dilute the expected edge effect. Our results have shown that oak trees did not need to have a large diameter to maintain *L. pulmonaria* populations (online Appendix S2). In this sense, although the plot level was dominated by small oak trees, the presence of some trees that act as sources of propagules is critical for determining the total cover of *L. pulmonaria*. Several studies have shown negative consequences of edge effect on some lichen species, especially cyanolichens, which are particularly vulnerable because of their dependence on high moisture conditions and their intolerance to high light environments (Renhorn et al., 1997; Belinchón et al., 2007). However, less clear is how tripartite cyanolichens, such as *L. pulmonaria*, which is comprised of a fungal biont, a green-algal photobiont, and a cyanobacterium enclosed in cephalodia, respond to edge effects. The presence of a green-algal photobiont appears to give *L. pulmonaria* much greater flexibility in its ecological amplitude (Goward et al., 1994). This photobiont probably is responsible for its relatively plastic response to survival in increased light exposure and low

TABLE 4. Results from generalized linear mixed model examining *Lobaria pulmonaria* traits at the (A) tree and (B) plot levels in the Sistema Central Range in Spain. Oak and beech forests are considered as a suitable habitat. The tree species variable is related to the host tree and not with the dominant tree species in the fragment. df = degrees of freedom estimated using the formula $n - 1$; sign = sign of the coefficient of the variable in the model. Data represents the Wald-type F -statistic (Wald Z -statistic for random factors). Boldfaced values represent significant factors.

A) Tree variables								
Fixed factors	df	Cover of <i>L. pulmonaria</i>			Occurrence of <i>L. pulmonaria</i>			
		Sign	F	p	Sign	F	p	
Area	22	–	0.22	0.645	–	0.05	0.833	
Connectivity	22	+	0.01	0.941	+	1.06	0.315	
% Pine	22	–	5.22	0.032	–	2.62	0.112	
% Heathland	22	–	2.22	0.151	–	0.51	0.484	
Distance from edge	61	–	0.79	0.376	–	0.99	0.323	
Distance from river	61	–	6.55	0.013	–	4.84	0.031	
Number of trees	61	+	0.88	0.369	+	0.53	0.468	
Dbh	2038	+	85.76	<0.001	+	42.76	<0.001	
Tree species	1	+	25.63	0.124	+	15.25	0.159	
Dbh × tree species	2038	–	2.96	0.085	–	3.95	0.047	
Random factors			Z	p		Z	p	
Suitable patch			1.06	0.145		0.52	0.300	
Plot			3.51	<0.001		3.51	<0.001	
Residual (tree)			31.45	<0.001		31.31	<0.001	
B) Plot variables								
Fixed factors	df	Cover of <i>L. pulmonaria</i>			% Occupied trees			
		Sign	F	p	Sign	F	p	
Area	22	+	0.87	0.361	–	0.47	0.498	
Connectivity	22	+	1.32	0.263	+	0.09	0.766	
% Pine	22	–	2.87	0.104	–	2.68	0.116	
% Heathland	22	–	0.99	0.331	–	0.04	0.837	
Distance from edge	61	–	0.92	0.342	–	0.60	0.443	
Distance from river	61	–	3.04	0.086	–	2.42	0.125	
Number of trees	61	–	0.59	0.447	–	0.92	0.342	
Number of trees × tree species	61	+	5.99	0.017	+	6.65	0.012	
Random factors			Z	p		Z	p	
Suitable patch			1.68	0.047		1.51	0.066	
Residual (plot)			4.76	<0.001		4.39	<0.001	

humidity to a certain degree (Renhorn et al., 1997; Kalwij et al., 2005; Coxson and Stevenson, 2007). Although some studies have indicated that *L. pulmonaria* is very sensitive to habitat changes (Gauslaa et al., 2001), this lichen prefers semi-open environments and avoids dark and dense forests (Renhorn et al., 1997; Hazell and Gustafsson, 1999). It is worth noting that individual thalli may persist for decades (Gu et al., 2001), which would mean that once a lichen is established, a population may persist as long as the host tree continues to exist. In this sense, Coxson and Stevenson (2005) evaluated growth rate responses of large and small thalli of *L. pulmonaria* in transplant experiments in old-growth forest stands. Growth rates of large *L. pulmonaria* thalli increased near forest edges. Thus, although *L. pulmonaria* has been treated as an old growth forest associate (Kuusinen, 1996; Gu et al., 2001), it appears to be relatively plastic in its response to environmental change. Taken together, our results suggest that residual populations on old trees may be able to dilute this expected edge effect.

Finally, *L. pulmonaria* was linked to high humidity stands near rivers, at least in the case of beech forests. The Mediterranean region is characterized by pronounced hot and dry summers (Scarascia-Mugnozza et al., 2000; Castro, 2002). Therefore, in Mediterranean forests, humidity, and not light, is the main factor affecting distribution of epiphytic lichens (Valladares, 2004; Belinchón et al., 2007). High levels of hu-

midity aid in the colonization and subsequent growth process therefore increasing the cover of epiphytes (Barkman, 1958; Snäll et al., 2004). The smooth bark of beech trees may be the reason *L. pulmonaria* was linked to high humidity areas in beech forests. Bryophyte cover increases in places with high humidity (i.e., near the river; I. Martínez and G. Aragón, personal observations), making better conditions for the attachment of propagules in trees with smooth bark. The relative importance of moisture on the colonization–extinction dynamics among trees within stands is, however, uncertain because a percentage of occupied trees was not related to moisture in the model. Colonization and growth conditions are favored near the river, but this might not guarantee that dispersed propagules reach suitable habitats.

A priority for biodiversity conservation is to develop criteria, tools, and strategies for proper forest management. Our results may provide useful information for managing forested areas and evaluating the effect of fragmentation on biodiversity conservation. Moreover, this type of study enriches our knowledge about the status of threatened lichens and can help in the development of conservation guidelines for “noncharismatic” organisms in the future. From a conservation point of view, our study shows that better knowledge about the performance of this species in each host forest at the landscape and local scales is needed to ensure the survival of this lichen. *Lobaria pulmonaria* appears to be positively affected by tree diameter in each

TABLE 5. Generalized mixed linear models (A–D) for *Lobaria pulmonaria* data in beech forests and oak forests in the Sistema Central Range in Spain. df = degrees of freedom estimated using the formula $n - 1$; sign = sign of the coefficient of the variable in the model. Data represent the Wald-type F -statistic (Wald Z -statistic for random factors). Boldfaced values represent significant factors.

Variables	Beech forests				Oak forests			
A) Cover of <i>L. pulmonaria</i> on a tree								
Fixed factors	df	Sign	F	p	df	Sign	F	p
Area	22	–	0.71	0.409	7	–	1.53	0.256
% Pine	22	–	1.44	0.242	7	+	2.05	0.195
% Heathland	22	+	0.05	0.818	7	–	6.87	0.034
Distance from edge	51	–	0.01	0.932	9	–	8.16	0.019
Distance from river	51	–	4.95	0.031	9	–	0.79	0.399
Number of trees per plot	51	+	0.01	0.930	9	+	0.06	0.805
Dbh	1476	+	75.91	<0.001	561	+	24.68	<0.001
Random factors			Z	p			Z	p
Patch			0.93	0.177			—	—
Plot			2.78	0.003			1.12	0.132
Residual (tree)			26.54	<0.002			15.90	<0.001
B) Occurrence of <i>L. pulmonaria</i> on a tree								
Fixed factors	df	Sign	F	p	df	Sign	F	p
Area	22	–	1.74	0.201	7	–	1.01	0.349
% Pine	22	–	0.17	0.687	7	+	2.17	0.185
% Heathland	22	+	0.19	0.670	7	–	4.15	0.081
Distance from edge	51	–	0.10	0.756	9	–	9.48	0.013
Distance from river	51	–	5.69	0.021	9	–	0.05	0.826
Number of trees per plot	51	+	0.25	0.622	9	+	0.01	0.915
Dbh	1476	+	106.00	<0.001	561	+	7.37	0.007
Random factors			Z	p			Z	p
Patch			0.74	0.231			0.42	0.336
Plot			2.88	0.002			0.20	0.420
Tree			26.45	<0.001			15.91	<0.001
C) Cover of <i>L. pulmonaria</i> in a plot								
Fixed factors	df	Sign	F	p	df	Sign	F	p
Area	22	–	0.73	0.404	7	+	0.08	0.785
% pine	22	–	0.78	0.386	7	+	0.04	0.847
% heathland	22	–	0.01	0.941	7	–	0.97	0.357
Distance from edge	51	–	0.68	0.414	9	+	2.97	0.119
Distance from river	51	–	1.09	0.300	9	–	0.64	0.446
Number of trees	51	+	0.92	0.342	9	–	69.37	<0.001
Random factors			Z	p			Z	p
Patch			2.10	0.018			—	—
Plot			3.83	<0.001			1.22	0.110
D) % Occupied trees in a plot								
Fixed factors	df	Sign	F	p	df	Sign	F	p
Area	22	–	1.34	0.259	7	–	1.63	0.243
% pine	22	–	0.16	0.688	7	+	1.10	0.328
% heathland	22	+	0.75	0.397	7	–	5.38	0.053
Distance from edge	51	–	0.08	0.775	9	–	7.69	0.022
Distance from river	51	–	2.81	0.099	9	–	0.01	0.924
Number of trees	51	–	0.33	0.566	9	+	0.11	0.747
Random factors			Z	p			Z	p
Patch			1.80	0.036			—	—
Plot			3.52	<0.002			1.22	0.110

forest type studied. However, not only do large trees guarantee the viability of this species, but habitat quality also needs to be controlled to ensure the colonization and development of *L. pulmonaria* in each forest stand. In beech forests, this lichen is favored by high moisture conditions. In oak forests, some edge effects may benefit *L. pulmonaria* on established thalli, but hard edges might adversely affect growth. However, the

most serious shortcoming in our understanding about the occurrence of *L. pulmonaria* in a fragmented forest landscape is a general lack of ecological knowledge about the dynamics of the lichen. Further studies are urgently needed about temporal processes, in particular the colonization process. Such information is needed to build a dynamic model to evaluate the fate of lichens under different ecological scenarios.

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