Environmental factors that drive the distribution and abundance of a threatened cyanolichen in Southern Europe: A multi-scale approach[1]

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- *Premise of the study:* High-quality information about threatened species is required to prevent current global biodiversity losses. Lichens are important components of forest biodiversity and help to maintain ecosystem functioning. The epiphytic cyanolichen *Lobarina scrobiculata* is red-listed in Europe and North America, but knowledge of its ecology and distribution in Southern Europe is scarce.
- *Methods:* We used a multispatial scale design to investigate the effects of macroclimate, forest structure, tree features, and microhabitat on the occurrence, abundance, spatial distribution, and performance of *Lobarina scrobiculata* in the Iberian Peninsula at plot and tree scales. Generalized linear models and mixed models were used for analysis.
- *Key results:* We recorded ca 14 000 individuals of the threatened species *Lobarina scrobiculata* from 22 populations in the Iberian Peninsula. Our results suggest that *L. scrobiculata* thrives mainly in oak forests with highly variable annual precipitation levels. At the plot scale, the *L. scrobiculata* abundance increased with annual precipitation and tree density (habitat quantity). At the tree scale, our models highlighted the importance of tree size and bark roughness (habitat quality) as the main drivers of species occurrence and abundance. We detected a marked spatial pattern on tree trunks, i.e., *L. scrobiculata* occurred preferentially on north-facing surfaces and close to the ground where humidity is higher.
- *Conclusions:* By integrating multiscale modeling, we analyzed a unique large dataset and these results are essential for understanding the ecology of this threatened cyanolichen. There is an urgent need to preserve the forests that this species currently inhabits as well as potential colonization sites.

Key words: Atlantic forest; conservation status; epiphytic lichens; *Lobaria scrobiculata*; *Lobarina scrobiculata*; Mediterranean forest; occupation rate; population size; precipitation.

The reduction of current biodiversity is one of the major challenges faced by society in the current century and it is the role of scientists to design conservation plans with a special focus on threatened species (Balmford et al., 2005). Effective conservation strategies rely on a thorough knowledge of the life processes and ecology of threatened species (Hilmo and Ott, 2002; Iriondo et al., 2009; Scheidegger and Werth, 2009). The viability of a population depends on two main factors: (1) population size; and (2) individual performance, which are usually associated with the habitat quality (Soulé, 1987; Hilmo and Ott, 2002; Iriondo et al., 2009; Belinchón et al., 2011). At a large scale, climatic conditions may influence the life cycle and performance of species, thereby shifting the species habitat quality requirements at finer scales (Scheidegger and Werth, 2009). Therefore, it is essential to identify the environmental factors that determine the occurrence, abundance, and performance of threatened species in a wide range of suitable habitats and at different spatial scales.

Few previous studies of lichens have used extensive quantitative and demographic datasets over a wide geographical range to obtain critical information about the habitat requirements, performance, and main threats for a species (but see, for example, Scheidegger and Werth, 2009; Hilmo et al., 2011a; Schei et al., 2012). Based on this type of study, however, two lichen species were included as Critically Endangered in the International Union for the Conservation of Nature's World Red List of Threatened Species (www.iucnredlist.org) because of their limited distribution and declining populations, i.e., the epiphyte cyanolichen *Erioderma pedicellatum* (Hue) P. M. Jørg and the terrestrial *Cladonia perforata* A. Evans (Scheidegger, 2003; Yahr, 2003). For example, the accurate population analysis, demographic monitoring, and identification of the causes of the decline of *E. pedicellatum* (commercial forestry and acid rain) (Cameron et al., 2013; Stehn et al., 2013) led to the implementation of conservation strategies to facilitate its recovery and maintenance in Canada, including the avoidance of forestry in occupied and potential suitable habitats (Environment Canada, 2007). Similarly, detailed knowledge of the environmental requirements of the endemic species *C. perforata* also led to the

establishment of habitat protection measures and reintroductions (Yahr, 2003).

Lichens represent an important component of the terrestrial biodiversity, especially in forests where they are among the dominant epiphytic organisms (Wein and Speer, 1975; Aragón et al., 2010), and they have critical roles in ecosystem functioning, i.e., water and mineral cycles, shelter for microfauna, and food webs (reviewed by Ellis, 2012). Lichens are poikilohydric organisms, i.e., they lack specialized mechanisms for regulating their water content, which is controlled passively by the water potential of the environment (Nash, 2008). Thus, the distribution and performance of lichens are determined greatly by the macro- and microclimate conditions, especially water and light availability, and their ranges of tolerance for these conditions, as well as other factors (i.e., suitable habitat availability, nutrient availability, and/or air pollution) (Nash, 2008; Ellis et al., 2009; Ellis, 2012; Marini et al., 2011). Therefore, changes in microclimate conditions, such as those induced by forest management, affect the diversity of epiphytic lichens, especially cyanolichens (i.e., lichens with cyanobacteria as the main photobiont) (Gauslaa et al., 2001; Aragón et al., 2010; Ellis, 2012). Cyanolichens are particularly sensitive to humidity because they require liquid water to activate photosynthesis (Lange et al., 1986), thus their distribution is generally controlled by the annual precipitation (see Marini et al., 2011). Cyanolichens play significant roles in the nutrient cycles in forests because they fix atmospheric nitrogen (Nash, 2008; Ellis, 2012). Thus, given the importance of cyanolichens for ecosystem functioning, species-specific studies are required to better understand their functioning and distribution at different spatial scales in the regions where they occur. These studies need to address different spatial scales because ecological processes are scale-dependent and they may generate different patterns at different spatial scales, which may explain the distribution, abundance, and assembly of species (Wiens, 1989; McGill, 2010; Nascimbene et al., 2013).

In the current study, we focused on the cyanolichen species *Lobarina scrobiculata*, which is generally associated with late successional epiphytic communities, traditionally referred as to *Lobarion* (Barkman, 1958; James et al., 1977; Burgaz et al., 1994). In general, *L. scrobiculata* has an incomplete circumboreal distribution, where it is more frequent on the west and east coasts of North America and Europe (http://data.gbif.org). However, a wider distribution does not necessarily correlate with its local abundance because this species has declined greatly in the United States in recent decades, and similar declines are likely in Europe (mean estimates of 10–30% based on the loss of locations) (Sérusiaux, 1989; NatureServe, 2014). The main causes of these declines are air pollution and habitat loss (Hallingbäck, 1989; Sérusiaux, 1989; Nimis, 1993; Smith et al., 2009). According to previous studies, *L. scrobiculata* is now a rare species in Europe and in some parts of North America. A growing awareness of its ongoing decline and increasing rareness has resulted in the inclusion of *L. scrobiculata* in numerous American and European Red Lists in different threatened categories, ranging from vulnerable to extinct (e.g., Sérusiaux, 1989; Randlane et al., 2008; Gärdenfors, 2010; NatureServe, 2014), based mainly on the loss of locations and/or occupancy area contraction. In Mediterranean Spain, Burgaz et al. (1994) suggested that it should be classified as "endangered" based on the persistence of the main threats to this species, i.e., forestry and agriculture practices. Based on the IUCN criteria, Martínez et al. (2003) classified it as "vulnerable" at a smaller regional scale (Central Spain). However, there is still a lack of exhaustive demographic data for this species, such as its population size and/or population structure, thereby suggesting that there is a need for new evidence to reassess the conservation status of this species in its current geographic range.

As a consequence of its rarity and ecological importance, *Lobarina scrobiculata* has been a target species in many ecological and population studies in boreal forests (e.g., Hallingbäck, 1989; Hilmo, 2002; Hilmo et al., 2011a, 2011b; Asplund et al., 2010; Larsson and Gauslaa, 2011). However, the macroenvironmental conditions and forest history in North America and Northern Europe differ from those in Southern Europe, where the ecology and habitat requirements of this species are poorly characterized. Thus, the main aim of the current study was to elucidate the environmental factors that modulate the occurrence, abundance, spatial distribution, and performance of *L. scrobiculata* in the Iberian Peninsula at multiple scales. We examined representative *L. scrobiculata* populations throughout the Iberian Peninsula to identify differences in the performance of this species between the Atlantic and Mediterranean biogeographical regions, with a specific focus on the latter. In the Mediterranean Basin, the climatic conditions may be particularly harsh for *L. scrobiculata* due to the physiological stress caused by low humidity during the long summer drought (Valladares et al., 2004), and these conditions might become even more extreme as a consequence of global warming (Giménez-Benavides et al., 2007). We hypothesized that the abundance of *L. scrobiculata* would increase with annual precipitation, which is consistent with the requirements of cyanolichens. Therefore, we also expected that *L. scrobiculata* would perform better in the Atlantic region in terms of abundance and occupation rate because, in addition to the higher macroenvironmental humidity, the forests are older and better preserved (Blanco et al., 2005), thereby providing a more suitable environment for this old-forest cyanolichen. We also discuss the implications of our results for the conservation status of *L. scrobiculata* in the study region.

MATERIALS AND METHODS

Target species—Lobarina scrobiculata (Scop.) Nyl. ex Cromb. (Lobariaceae) was long considered to belong to the genus *Lobaria* but recent phylogenetic analyses have placed it clearly in the smaller genus *Lobarina* (Moncada et al., 2013). However, in the current study we refer to *Lobaria* sensu lato for convenience to place our results in a broader ecological context.

Lobarina scrobiculata is a foliose cyanolichen, which contains the cyanobacterium *Nostoc* as its main photobiont. This species occurs in the Northern Hemisphere and in oceanic areas of South America, Australia, New Zealand, and Africa (Smith et al., 2009; Nimis, 1993). In the Iberian Peninsula, it usually inhabits forests in mountain areas and it is relatively frequent in Central Spain, common in oceanic areas of the northwest, and increasingly rarer elsewhere, because it only occurs in forests with high relative air humidity (Burgaz and Martínez, 1999). This species is preferentially epiphytic and grows mainly on deciduous trees, but sometimes on mossy siliceous rocks (Hallingbäck, 1989; Burgaz and Martínez, 1999). The most frequent mode of reproduction is asexual via soredia (asexual diaspores that contain both symbionts), whereas sexual reproduction via apothecia (containing fungal spores) is rather infrequent (Burgaz and Martínez, 1999; Smith et al., 2009). The size of the individual appears to be the main factor that drives the onset of asexual reproduction in boreal forests (see e.g., Larsson and Gauslaa, 2011), but the factors that promote sexual reproduction are not known yet, although they may include other species-specific and/or environmental factors.

*Study area—*We selected 22 populations distributed throughout the Iberian Peninsula, which were representative of the habitats and regions where *Lobarina*

scrobiculata occurs (Fig. 1; see Burgaz and Martínez, 1999). We defined a population as at least 10 individuals inhabiting a forest. The latitudinal gradient where *L. scrobiculata* occurs in the Iberian Peninsula includes two biogeographical regions with very different climatic conditions: (1) the Atlantic region (northern fringe of the Iberian Peninsula) with an oceanic climate; and (2) the Mediterranean region (the rest of the Iberian Peninsula), which is characterized by a summer drought period that can be quite variable in length (European Environment Agency, 2009) (Fig. 1; Table 1). This latitudinal gradient and the topography result in high environmental heterogeneity, thereby leading to high forest diversity. In the Atlantic region, the forests are dominated by broad-leaved and deciduous species (e.g., *Fagus sylvatica* L., *Quercus petraea* (Matt.) Lieb., and *Q. robur* L.), whereas perennial or semideciduous species (e.g., *Q. ilex* L. and *Q. pyrenaica* Willd.) are the dominant forest species in the Mediterranean region (Blanco et al., 2005) (Fig. 1). Iberian forests have been managed for centuries, especially in the Mediterranean region (i.e., for timber, firewood extraction, and livestock) (Valladares et al., 2004; Blanco et al., 2005). Our study plots within the Mediterranean region exhibited different signs of low intensity management in the past and current livestock activity. However, the plots sampled in the Atlantic region had not been subjected to any forestry practices for more than 50 years.

***Experimental design and sampling*—**The field data were collected between October 2009 and July 2012. We approached this study using a multiscale design, i.e., plot and tree scales. We established a random 3000 m^2 plot inside a forest where the target species was detected. We investigated all living trees present in this area and recorded the occurrence and number of *Lobarina scrobiculata* individuals at a height of up to 2 m on the tree trunks, because *L. scrobiculata* occurs rarely above this height on the trunks and branches in the study region (e.g., Belinchón et al., 2009, 2011; S. Merinero et al., personal observation). We considered "individuals" to be all spatially distinguishable lichen entities that were easily differentiated from others. This definition is also used elsewhere (e.g., Hilmo et al., 2011a; Schei et al., 2012).

At the plot scale, we considered the following climatic variables (Table 1): (1) annual precipitation (mm); (2) winter precipitation (mm); (3) summer precipitation (mm); and (4) mean annual temperature (°C), which were derived using the climate simulation model CLIMOEST (developed for the Iberian Peninsula) by inputting the altitude, geographic coordinates, and hydrographic basin (Sánchez-Palomares et al., 1999). The longitude, latitude, and altitude were recorded in situ using a GPS device (GPSmap 60CSx, Garmin GPS; Garmin, Ltd., Olathe, Kansas, USA). We also measured the following forest structure variables: (1) the forest type based on the dominant tree species (oak, beech, or mixed); (2) the number of trees per plot (i.e., tree density); and (3) the mean tree diameter at breast height based on all trees within the plot (DBH, cm) (Table 2). At the tree scale, we recorded the tree species, DBH (cm), bark roughness (mm), which was measured using digital calipers as the depth of a representative crevice

Fig. 1. Locations of the 22 populations of *Lobarina scrobiculata* sampled throughout the Iberian Peninsula. The biogeographical regions are shown according to the European Environment Agency (2009). The details of the corresponding localities and plots are shown in Table 1. Triangles: Oak forests; circles: Beech forests; squares: Mixed species forests.

at approximately 50 cm above ground, and the trunk slope respect to the horizontal (°), which was measured using a clinometer. We also measured the position of each *Lobarina scrobiculata* individual on the trunk in terms of the height above ground (cm) and orientation (°).

***Statistical analyses*—**To avoid problems of multicollinearity, only uncorrelated variables (Pearson's correlation coefficient < 0.7 and $P > 0.05$) were included in the models. For two correlated variables, the models included the variable that had a stronger biological influence on the response of the lichen because it explained more variation. Thus, from the original 14 explanatory variables, only four were used in the models to examine their effects on the response variables at the two scales. The plot-scale explanatory variables were annual precipitation and tree density, whereas the tree-scale variables were DBH and bark roughness. The response variables at the plot scale were the abundance of *Lobarina scrobiculata* and the proportion of occupied trees (i.e., occupation rate), while the response variables at the tree scale were the probability of occurrence and the abundance of *L. scrobiculata*.

To test the effects of annual precipitation and tree density on the abundance and occupation rate of *Lobarina scrobiculata* at the plot scale we fitted generalized linear models (GLMs) (McCullagh and Nelder, 1989), where Poisson and binomial errors were applied, respectively. At the tree scale, the effects of the explanatory variables on the occurrence and abundance of *L. scrobiculata* were modeled by fitting generalized linear mixed models (GLMMs) with a Laplace approximation (Zuur et al., 2009). Binomial and Poisson errors were applied to the occurrence and abundance models, respectively. We selected this approach because our data had an unbalanced and hierarchical structure with trees nested within the plots. This data hierarchy suggests that there was a correlation between the data at the two scales, thereby inflating the error in the degrees of freedom and increasing the possibility of Type I errors. To overcome this problem, the data were analyzed using a multilevel approach, where we considered the variable "plot" as a random factor in the tree-scale model and the explanatory variables at the plot and tree scales were introduced as fixed factors (i.e., annual precipitation, tree density, DBH, and bark roughness) (Zuur et al., 2009). Further details of the GLM and mixed effects modeling approaches can be found in Zuur et al. (2009). The fixed factors were examined using Wald Z-statistic tests. Significant values with both procedures were estimated using a deviance test (Guisan et al., 2002) and variables were excluded if $P > 0.05$. Models using the complete data set, i.e., gathered data from the Atlantic and Mediterranean regions, are referred to as global/scale models.

We performed similar GLMs and GLMMs separately for the Atlantic and the Mediterranean regions to compare the performance of the species between regions. The number of populations examined in each region reflected the area of each biogeographical region in the Iberian Peninsula, i.e., 5/22 populations were located in the Atlantic region and 17/22 in the Mediterranean region (Fig. 1). The lower sample size in the Atlantic region meant that we only included tree density as an explanatory variable for the GLMs at the plot level in this region because it explained more variation than the annual precipitation. Finally, all of the models were checked for residual patterns and nonlinear effects. The statistical analyses were performed using R version 2.15.2 (R Foundation for Statistical Computing, Vienna, Austria). We used the packages nlme (Pinheiro et al., 2008) and lme4 (Bates et al., 2013) for the mixed effect model analyses. The mean values ± SD (SD) are reported, unless stated otherwise.

RESULTS

***Population characteristics (plot scale)*—**Tables 1 and 2 summarize the environmental and forest structure variables for each plot. The study area comprised a wide range of different mountain systems and there was high environmental heterogeneity. There were very high variations in the altitude (290 to 1406 m a.s.l.), annual precipitation (621 to 2050 mm), and mean temperature (7.5° to 18°C) (Table 1). As the latitude decreased, the mean annual temperature increased and the summer precipitation declined (Table 1). However, the differences in the annual precipitation were not consistent with the latitudinal gradient because some southern populations received extremely high precipitation levels due to topographic factors (e.g., plots 21 and 22) (Table 1).

In the 22 study populations, a total of 14 tree species were recorded, which were distributed mainly among the following
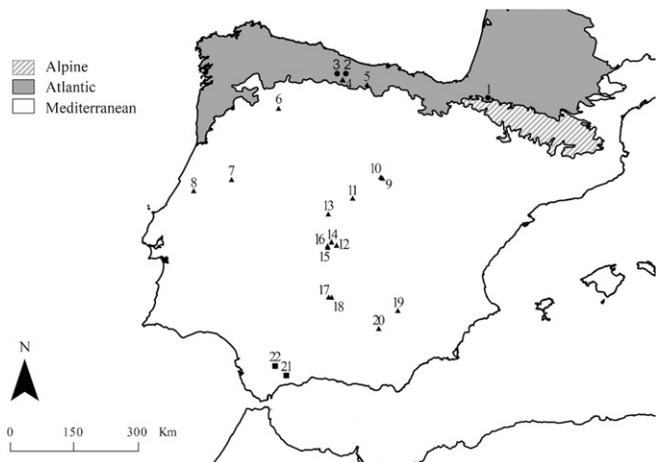
TABLE 1.   Summary of the geographic, topographic, and climatic variables in the areas of the study populations (plots). Atl = Atlantic Biogeographical Region; Medit = Mediterranean Biogeographical Region; Coord = coordinates in UTM WGS84; P = Precipitation; Mean T = Mean annual temperature.

Plot	Locality	Province	Region	Coord X (UTM)	Coord Y (UTM)	Altitude (m a.s.l.)	Annual P (mm)	Winter P (mm)	Summer P (mm)	Mean T (°C)
1	Irati	Navarra	Atl	30T654582	4761165	965	1615	589	149	8.9
2	Pontón	León	Atl	30T335853	4774195	1328	1721	552	229	7.8
3	Burón	León	Atl	30T321674	4771356	1353	1371	368	135	7.5
4	Riaño	León	Atl	30T335246	4758497	1150	1156	295	117	8.8
5	Brañosera	Palencia	Atl	30T394739	4754232	1260	946	326	131	8.1
6	Sanabria	Zamora	Medit	30T198543	4667428	950	1054	384	95	10.3
7	Estrela	Guarda	Medit	30T116951	4484577	978	2050	865	85	13.5
8	Sicó	Coimbra	Medit	30T133915	4442826	290	1178	612	41	18.0
9	Santuy	Guadalajara	Medit	30T462970	4549459	1235	801	252	92	9.7
10	Montejo	Madrid	Medit	30T458649	4551345	1263	818	258	92	9.5
11	Escorial	Madrid	Medit	30T402181	4491369	1066	796	272	85	11.2
12	San Pablo	Toledo	Medit	30T381950	4377721	908	621	239	48	12.8
13	San Vicente	Toledo	Medit	30T352060	4445771	1239	947	334	68	10.5
14	Risco Paradas	Ciudad Real	Medit	30T369194	4382836	1165	756	286	54	11.2
15	Cigüeñelas	Ciudad Real	Medit	30T361629	4372486	797	638	246	45	13.6
16	Gargantilla	Ciudad Real	Medit	30T362757	4369364	749	656	235	42	13.8
17	Fuencaliente	Ciudad Real	Medit	30T389768	4256034	881	729	224	49	13.9
18	Robledo Hoyas	Ciudad Real	Medit	30T382652	4255571	1030	777	248	54	13.2
19	Torca Malojos	Albacete	Medit	30T545875	4252003	1406	1023	396	77	11.6
20	Cazorla	Jaén	Medit	30T508204	4202997	738	790	254	42	15.6
21	Sierra Nieves	Málaga	Medit	30T314483	4059400	1064	1155	517	23	14.0
22	Grazalema	Cádiz	Medit	30T284707	4073443	775	1753	734	32	15.4

three forest types: 17 oak deciduous forests (*Quercus faginea* Lam., *Q. petraea*, and/or *Q. pyrenaica*), three beech forests (dominated by *Fagus sylvatica*), and two forests that comprised other mainly perennial species (i.e., *Quercus ilex* + *Abies pinsapo* Boiss. + *Phillyrea latifolia* L.) (Table 2). Minor proportions of other tree species were present in the three forest categories: *Abies alba* Mill. and *Ilex aquifolium* L. in beech forests; *Castanea sativa* Mill., *Corylus avellana* L., *Olea europaea* L., and

TABLE 2.   Summary of the forest structure variables and tree features at the plot scale. Absolute and mean ± SD values are shown for each plot, all plots, and each of the biogeographical region plots. Plots marked with asterisks (*) belong to the Atlantic Biogeographical Region, whereas the remainder belong to the Mediterranean region. Substrate: Soil type, C = calcareous; S = siliceous. Forest type: Main dominant species (*Fs* = *Fagus sylvatica*; *Aa* = *Abies alba*; *Qpet* = *Quercus petraea*; *Qpyr* = *Quercus pyrenaica*; *Qfag* = *Quercus faginea*; *Qilex* = *Quercus ilex*; *Apin* = *Abies pinsapo*; *Plat* = *Phillyrea latifolia*). No. tree: Tree density (number of trees per plot); DBH = Diameter at breast height; abundance = Number of *Lobarina scrobiculata* individuals; Occup rate = Proportion of colonized trees by *L. scrobiculata*.

Plot	Substrate	Forest type	No. tree	Mean DBH (cm)	Mean Bark (mm)	Mean Slope (°)	Abundance	Occup rate (%)
1*	C	*Fs + Aa*	197	28.2 ± 13.7	1.5 ± 1.3	85.1 ± 5.4	129	6.6
2*	C	*Fs*	176	21.6 ± 10.9	1.4 ± 0.7	74.6 ± 15.4	201	21.6
3*	C	*Fs + Qpet*	245	18.7 ± 21.5	1.5 ± 2.0	74.1 ± 14.3	988	6.1
4*	C	*Qpet*	170	20.2 ± 12.8	4.3 ± 2.5	77.6 ± 10.5	1487	19.4
5*	S	*Qpet+Qpyr*	251	22.7 ± 14.0	5.3 ± 3.7	78.5 ± 10	587	8.0
6	S	*Qpyr*	375	17.0 ± 9.8	6.1 ± 2.3	81.3 ± 8.8	1091	8.0
7	S	*Qpyr*	385	12.1 ± 4.8	5.0 ± 2.7	80.7 ± 10.2	4063	55.1
8	S	*Qfag*	137	18.0 ± 13.4	6.3 ± 2.9	75.2 ± 10.9	158	24.8
9	S	*Qpyr*	355	14.2 ± 7.9	6.0 ± 2.4	84.7 ± 4.9	220	16.9
10	S	*Qpyr*	207	23.2 ± 12.8	7.2 ± 5.0	81.8 ± 9.0	491	2.4
11	S	*Qpyr*	299	14.2 ± 7.4	8.3 ± 3.1	79.9 ± 9.0	1758	70.2
12	S	*Qpyr*	245	18.8 ± 10.3	9.3 ± 2.3	82.7 ± 4.3	11	2.9
13	S	*Qpyr*	135	24.4 ± 11.0	9.9 ± 2.3	84.3 ± 6.8	273	40.0
14	S	*Qpyr*	390	10.3 ± 4.5	9.7 ± 2.2	79.4 ± 7.4	169	17.9
15	S	*Qpyr*	197	18.8 ± 12.2	7.6 ± 3.5	83.2 ± 4.9	510	65.5
16	S	*Qpyr*	224	16.1 ± 6.6	9.6 ± 2.2	84.4 ± 4.1	203	37.5
17	S	*Qpyr*	169	13.8 ± 7.7	7.6 ± 2.7	83.4 ± 4.6	725	63.3
18	S	*Qpyr*	76	21.1 ± 12.4	11.9 ± 4.9	84.8 ± 4.3	491	86.8
19	C	*Qpyr*	46	49.1 ± 19.7	13.1 ± 1.5	84.8 ± 1.8	49	41.3
20	C	*Qfag*	144	25.0 ± 11.3	9.2 ± 4.8	77.8 ± 8.8	20	4.9
21	C	*Qilex*	275	12.5 ± 5.5	4.0 ± 1.5	76.3 ± 9.9	82	10.2
22	S	*Qfag + Apin + Plat+ Qilex*	265	14.6 ± 16.8	3.2 ± 2.3	74.8 ± 15.7	102	15.5
Atlantic			1039	22.2 ± 15.8	2.8 ± 2.9	77.9 ± 12.3	3392	11.4
Mediterranean			3924	16.3 ± 11.1	7.9 ± 3.0	81.8 ± 7.0	10416	29.6
Total			4963	17.5 ± 12.5	6.3 ± 3.9	80.2 ± 9.9	13 808	25.8

Sorbus sp. in oak forests; and *Crataegus monogyna* Jacq. in oak and other forests (Table 2).

In addition to the tree species heterogeneity, all of the forests differed greatly in structure where the tree density varied from 46 to 390 trees per plot (Table 2). This variable had a strong negative correlation with the mean DBH (Pearson's correlation coefficient = –0.7, *P* < 0.001), thus a higher tree density indicated a greater number of thinner trees. The mean DBH was 17.5 cm, but it was highly variable among plots (Table 2). Plot 14 had the thinnest trees, whereas plot 19 contained four times the number of larger trees (Table 2). In the Mediterranean region, the mean DBH was significantly less than that in the Atlantic region (Table 2; Kruskal-Wallis, χ^2 = 164.95, df = 1, *P* < 0.0001). The bark roughness was also highly variable among plots (Table 2), where it was significantly lower in beech forests and higher in oak forests (Kruskal-Wallis, χ^2 = 1805.906, df = 2, *P* < 0.0001).

Among the 22 populations, we recorded 13 808 *Lobarina scrobiculata* individuals on 1282 trees (from 4963 trees sampled). The abundance was highly variable, i.e., from 11 to 4063 individuals per plot. *L. scrobiculata* was found mainly in oak forests, which had the largest populations (≥ 1000 individuals) (Table 2). The occupation rate varied from 2.4 to 86.8% but it was not significantly correlated with abundance (Table 2). The occupation rate was >50% in five populations and >70% in two (Table 2). There were clear differences in the *L. scrobiculata* abundance and occupation rates between the two biogeographical regions (Table 2). The mean population size was similar in both regions (Mann-Whitney *W* = 54, df = 1, *P* = 0.38), although the variability was much higher in the Mediterranean region (612.7 ± 997.3 vs. 678.4 ± 567.4 individuals in the Atlantic region). The mean occupation rate was significantly higher in the Mediterranean region than the Atlantic region (Table 2; Mann-Whitney *W* = 25, df = 1, *P* < 0.01).

The global GLMs showed that the species abundance was higher with increasing annual precipitation and with a greater tree density (i.e., thinner trees) (Table 3). By contrast, the occupation rate was independent of precipitation but it was significantly higher in plots with a lower tree density. According to the regional GLMs, in the Mediterranean region the species abundance increased with tree density, whereas in the Atlantic region tree density did not affect abundance (Table 3). The occupation rate increased with the annual precipitation in the Mediterranean region only (Table 3).

***Occurrence, abundance, and performance of* Lobarina scrobiculata *(tree scale)*—*Lobarina scrobiculata* was common on oaks followed by beech and other tree species (1177,

59, and 46 trees, respectively, among the 1282 occupied trees) (Fig. 2). Its occurrence was lower on *Abies pinsapo*, *Phillyrea latifolia,* and *Crataegus monogyna* (Fig. 2). Only one *Castanea sativa* tree (n = 2) and one *Olea europaea* tree (*n* = 2) hosted *L. scrobiculata* individuals. No individuals were recorded on *Abies alba* (*n* = 51), *Ilex aquifolium* (*n* = 48), *Sorbus* sp. (n = 16), or *Corylus avellana* (*n* = 5). The bark roughness and DBH were not highly correlated when we evaluated all of the trees present in both regions, as well as trees from the Atlantic and Mediterranean regions separately, and the three more common tree species separately (deciduous *Quercus* sp., *Fagus sylvatica*, and *Q. ilex*) (Pearson's correlation coefficients < 0.3, *P* < 0.001).

The global GLMMs results (Table 4) showed that certain tree features, such as large trunks and rough bark, significantly favored the probability of *Lobarina scrobiculata* occurrence and its abundance. The tree density and annual precipitation did not enhance the occurrence or abundance of *L. scrobiculata* at the global scale (Table 4). According to the regional GLMMs, the pattern obtained for the global dataset was similar in the Mediterranean region, although only the bark roughness increased the probability of occurrence in this region, where larger trees were likely to host more *L. scrobiculata* individuals (Table 4). In the Atlantic region, the probability of occurrence was also increased by a reduced density of trees, while the abundance of *L. scrobiculata* per tree increased significantly with decreasing annual precipitation (Table 4).

We observed different distribution patterns of *Lobarina scrobiculata* individuals (13808) along the height and orientation ranges (Figs. 3 and 4). The abundance of individuals decreased gradually with increasing height from the ground (Fig. 3). More than half of the individuals grew at <60 cm and <5% at >150 cm. This trend was much stronger in the Mediterranean region where nearly 40% of the individuals were located at the base of the trunk and only 3.5% grew at >150 cm (Fig. 3). The pattern differed greatly in the Atlantic region, where <15% of the individuals grew at the base of the trunk and a higher proportion of individuals were found at >150 cm (10%). Almost 65% of the individuals in this region were located 30–120 cm from the ground (Fig. 3).

The distributions were also imbalanced in terms of their orientations (Fig. 4). Among all of the individuals, the largest portion (37%) had a northerly orientation, followed by westerly and easterly, whereas a much lower number had a southerly orientation (16%) (Fig. 4). This trend was most evident in the Mediterranean region plots, where half of the individuals had a northerly orientation but <7% had a southerly orientation. In contrast to the Mediterranean pattern, the proportion of individuals growing on each orientation was more balanced in the

TABLE 3. Results of the generalized linear models used to examine the effects of environmental variables on the abundance and occupation rate (%) at the plot scale (global data; *n* = 22) and by region (Atlantic, *n* = 5; Mediterranean, *n* = 17). P = Annual precipitation (mm). No. tree = Tree density (number of trees per plot). The data comprise the Wald-type χ^2-statistic (Z value), degrees of freedom (df), coefficient of the variable in the model (Estimator), standard error of the estimator (SE), and significance value (*P*).

Response	Effect		Global				Atlantic Region				Mediterranean Region		
		df	Estimator (SE)	Z	P	df	Estimator (SE)	Z	P	df	Estimator (SE)	Z	P
Abundance	P	21	9×10^{-4} (1.77×10^{-5})	50.71	***					16	1.07×10^{-3} (1.98×10^{-5})	54.07	***
	No. tree	21	5.2×10^{-3} (9.60×10^{-5})	53.83	***	4	–0.32 (8.60)	0.41	n.s.	16	5.16×10^{-3} (1.18×10^{-4})	43.63	***
Occupation rate (%)	P	21	2.7×10^{-5} (7.70×10^{-5})	0.36	n.s.					16	4.64×10^{-4} (8.36×10^{-5})	5.55	***
	No. tree	21	-1.1×10^{-3} (3.70×10^{-4})	–2.99	**	4	–0.02 (3.30×10^{-3})	–5.07	***	16	-2.94×10^{-3} (3.99×10^{-4})	–7.36	***

Note: Significance of *P*-values: n.s. = nonsignificant, * *P* < 0.5, ** *P* < 0.01, and *** *P* < 0.001.
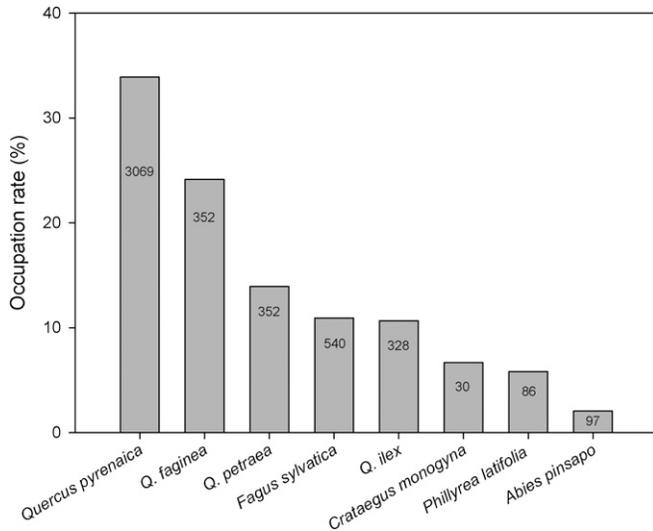
Fig. 2. Occupation rate (%) of *Lobarina scrobiculata* on the tree species where it occurred most frequently in the Iberian Peninsula. The total numbers of trees sampled from each species are shown inside the bars.

Atlantic plots (ca 25% for each cardinal aspect), with no major differences between north and south (Fig. 4).

DISCUSSION

The need to reduce current losses of biodiversity demands high-quality information on threatened species to facilitate their preservation. We performed the first multiscale evaluation of the distribution and population size of *Lobarina scrobiculata* in Southern Europe, and our results highlight key environmental factors that determine its occurrence, abundance, and performance at two different spatial scales in this heterogeneous region.

Plot-scale: Occurrence, distribution, and abundance— According to our results, *Lobarina scrobiculata* colonizes a wide range of localities, which differ greatly in terms of their annual precipitation, mean temperature, altitude, forest type, and host tree species. However, *L. scrobiculata* is not a frequent species in the Iberian Peninsula (Burgaz et al., 1994; Burgaz and Martínez, 1999), although it can be locally abundant in specific areas (e.g., plots 7 and 11). Thus, according to the rarity patterns described by Rabinowitz (1981), i.e., wide distribution with narrow habitat-specificity and sometimes locally abundant, *L. scrobiculata* can be classified as a rare species in our study area. The high differences in abundance among populations (up to two orders of magnitude) suggest that different factors and processes might operate at the macro- and microscales. Indeed, this situation may also have been affected by historical anthropogenic management, which has caused changes in the landscape configuration and forest structure.

Our results show that *Lobarina scrobiculata* tends to be more abundant in localities that receive more rain. A higher annual precipitation provides a humid environment, which is suitable for satisfying the liquid water demands of cyanolichens (Lange et al., 1986), thus humidity at the macroenvironmental scale facilitates the persistence and population development of this species. However, there was a surprisingly high frequency of *L. scrobiculata* in relatively dry locations (e.g., Central Spain, plots 9–18; Fig. 1). According to Burgaz and Martínez (1999), *L. scrobiculata* is generally considered to belong to the species of *Lobaria* s. l., which have greater tolerance of the xeric conditions in the Mediterranean climate. A plausible explanation for the occurrence of this cyanolichen in relatively dry forests is that the specific habitat features may compensate for suboptimal

TABLE 4. Summary of the generalized linear mixed models fit by a Laplace approximation, which were used to examine the effects of environmental factors on the occurrence and abundance of *Lobarina scrobiculata* at the tree scale in all of the plots sampled in the Iberian Peninsula (global), Atlantic regions plots, and Mediterranean region plots. P = Annual precipitation (mm); No. tree = Number of trees per plot (tree density); DBH = Tree diameter at breast height (cm); Bark = Bark roughness (mm). The data comprise the Wald-type Z-statistic value (Z), coefficient of the variable in the model (Estimator), standard error of the estimator (SE), significance value (P), and random effects standard deviation (SD).

Response		Global			Atlantic Region			Mediterranean Region		
		Estimator (SE)	Z	P	Estimator (SE)	Z	P	Estimator (SE)	Z	P
Occurrence	***Fixed effects***									
	P	0.005 (0.008)	0.64	n.s.	0.002 (0.009)	0.24	n.s.	0.009 (0.009)	0.90	n.s.
	No. tree	−0.001 (0.003)	−0.38	n.s.	−0.020 (0.007)	−2.80	**	−0.002 (0.003)	−0.66	n.s.
	DBH	0.051 (0.008)	6.41	***	0.051 (0.008)	6.41	***	−0.005 (0.005)	−1.09	n.s.
	Bark	0.136 (0.050)	2.69	***	0.136 (0.050)	2.69	***	1.161 (0.018)	9.02	***
	Random effects		SD			SD			SD	
	Plot		2.06			0.15			2.27	
	Residual		1.44			0.38			1.51	
Abundance	***Fixed effects***									
	P	0.006 (0.008)	0.73	n.s.	−0.022 (0.002)	−8.84	***	0.007 (0.009)	0.80	n.s.
	No. tree	0.002 (0.003)	0.78	n.s.	−0.028 (0.002)	−14.07	***	0.002 (0.003)	0.67	n.s.
	DBH	0.041 (0.006)	76.67	***	0.035 (0.001)	39.63	***	0.036 (0.001)	40.41	***
	Bark	0.067 (0.002)	35.21	***	1.199 (0.007)	28.00	***	0.056 (0.002)	25.41	***
	Random effects		SD			SD			SD	
	Plot		2.03			0.01			2.12	
	Residual		1.42			0.12			1.46	

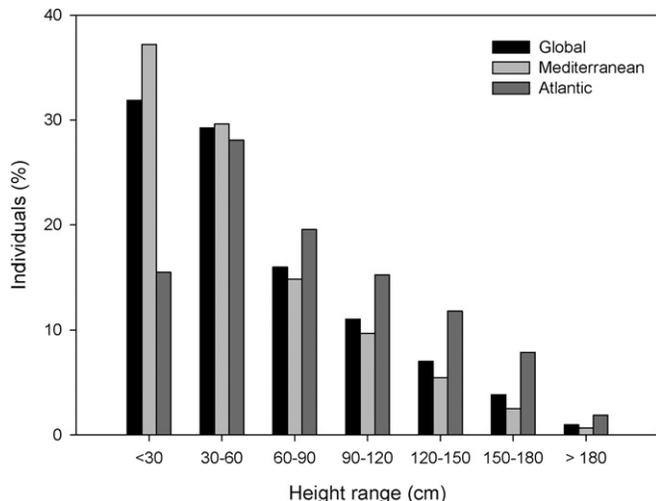Note: Significance of P-values: n.s. = nonsignificant, * P < 0.5, ** P < 0.01, and *** P < 0.001.

Fig. 3. Height distribution of *Lobarina scrobiculata* individuals (%) on the tree trunks based on the global data (all plots) (*n* = 13 808), Atlantic region plots (*n* = 3392), and Mediterranean region plots (*n* = 10 416). The height ranges were measured from the ground.

climatic conditions (e.g., Ellis et al., 2009). The deciduous forests canopies where *L. scrobiculata* is found mainly are relatively dense in late spring and summer, which probably maintains the humidity and provides the light conditions that this species requires. However, during the defoliated seasons, other species-specific traits may be more important for species persistence, i.e., *L. scrobiculata* has a high thallus water-holding capacity (Merinero et al., 2014) and it contains usnic acid, which is a sun-screening secondary compound (Culberson, 1969; McEvoy et al., 2007). Thus, the habitat conditions and these species-specific features may enhance the performance of this lichen in dry conditions. Indeed, Gauslaa et al. (2012) demonstrated that some old-forest cyanolichens (including *L. scrobiculata*) had better resistance to higher irradiance when desiccated
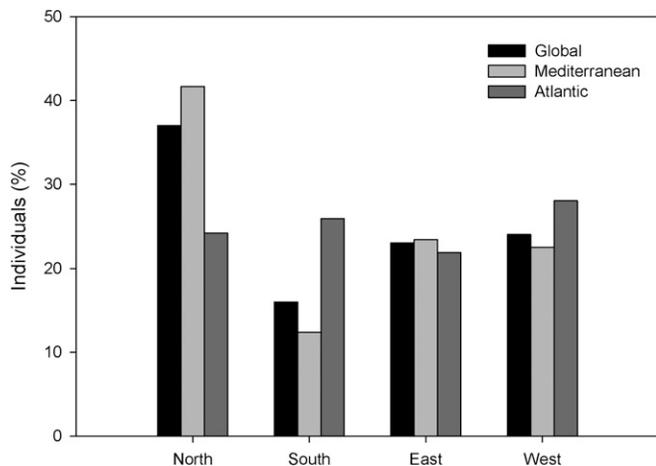

Fig. 4. Proportion of *Lobarina scrobiculata* individuals (%) distributed on the tree trunks in each orientation range: (1) north (311°–45°); (2) south (136°–225°); (3) east (46°–135°); and (4) west (226°–310°). The results are shown for the global data (all plots) (*n* = 13 808), Atlantic region plots (*n* = 3392), and Mediterranean region plots (*n* = 10 416).

compared with sympatric cephalo- and chlorolichens, thereby suggesting that cyanolichens might be better adapted to long hydration-desiccation cycles.

Lobarina scrobiculata was more abundant in forests with a high tree density and relatively thinner trees. In this forest structure, which is typical of relatively young/managed forests, there is probably more potential habitat available for lichen colonization and propagation at the plot scale. Thus, the higher frequency of *L. scrobiculata* in forests with relatively thin trees instead of large trees suggests that *L. scrobiculata* exhibits slightly different performance compared with *Lobaria pulmonaria* (L.) Hoffm. in our study area (e.g., Belinchón et al., 2009, 2011). Both are considered to be old-forest lichen species that are highly dependent on large trees and the microenvironments created by old-forest canopies (Barkman, 1958; James et al., 1977). However, recent studies in boreal forests also suggest that *L. scrobiculata* performs well in young forests, as well as old forests (Hilmo, 2002; Hilmo and Ott, 2002; Hilmo et al., 2011a, 2011b). Our results agree with these findings because *L. scrobiculata* was more abundant in the Mediterranean region, where the tree densities are generally higher but thinner trees are present, which is probably a consequence of the forest management history (Blanco et al., 2005).

This result was unexpected because the climatic conditions are more favorable in the Atlantic region (constant macroenvironmental high humidity), where the forests are also older and less intensively managed (Valladares et al., 2004; Blanco et al., 2005). However, the old-forest dependency may vary along ecological gradients (Scheidegger and Werth, 2009). Thus, *Lobarina scrobiculata* occurred in old forests but its abundance appeared to be enhanced in relatively young oak forests in the studied area. It is important to note that population size has been used as an indicator of environmental quality for threatened species (e.g., Carrascal and Seoane, 2009; Belinchón et al., 2011; Stehn et al., 2013). However, other factors such as the genetic diversity or population structure should be assessed to confirm this relationship in our case because a high abundance need not correlate with the optimum environmental conditions. For example, Larsson and Gauslaa (2011) suggested that lichens often experience suboptimal environmental field conditions even where the species are abundant. Nevertheless, the risk of local population extinction increases with decreasing population size (Soulé, 1987; Iriondo et al., 2009), thus special attention must be paid to very small populations (e.g., plots 12, 19, and 20; Table 2).

In addition to the population size, the spatial distribution of individuals within the plot, i.e., occupation rate, is a factor that may determine population persistence. The likelihood of local extinction is probably lower with a high occupation rate (Öckinger and Nilsson, 2010) because stochastic events (e.g., climatic extreme events, cattle activity, or tree falls) are less likely to cause major variations in the population size. The mean occupation rate in the study populations was close to 30%, but most of the populations had a strikingly low occupation rate (Table 2), thereby implying a highly aggregated spatial pattern, which may be a consequence of the following two factors. First, the populations might be young and a result of relatively recent colonization events, so these populations may expand over time (e.g., Kalwij et al., 2005). This may be consistent with our results, which showed that the occupation rate decreased with increasing tree density, and higher tree densities may be related to relatively young forests. Second, they could be declining populations that might become extinct (see Rolstad

et al., 2001; Belinchón et al., 2011; Schei et al., 2012). However, the fate of these populations is dependent on the colonization-extinction dynamics because the successful colonization of new trees relies on the dispersal of propagules and the success of establishment. This process is probably constrained by: (a) reproductive limitations due to the low production of diaspores (e.g., a lack of reproductive individuals) (Scheidegger, 1995); (b) unsuccessful establishment of new individuals due to the low availability of suitable microhabitats (Hedenås et al., 2003); or (c) the microenvironments are suitable for establishment but they limit the growth rate (Hilmo et al., 2011b).

The dispersal efficiency of lichens has been shown to be affected by the propagule size, which depends on the type of reproduction, where asexual symbiotic diaspores are much heavier and usually reach shorter distances than sexual fungal spores (Johansson and Ehrlén, 2003; Hedenås et al., 2003; but see Schei et al., 2012). According to Hedenås et al. (2003), asexual dispersal is efficient at a local scale (150 m × 150 m plots) where it results in a homogeneous distribution of epiphytes. Therefore, a high number of colonized trees may indicate effective dispersal within the plot (Johansson and Ehrlén, 2003; Schei et al., 2012). In the populations of *Lobarina scrobiculata* that we studied, soredia production did not appear to be a limitation (Burgaz and Martínez, 1999; S. Merinero et al., unpublished data). Thus, assuming that *L. scrobiculata* disperses effectively at the local scale (but not at the landscape scale; see Hilmo, 2002), we suggest that the high number of noncolonized trees we found might be explained by: (a) limited time for colonization and population expansion within the plot, and/or (b) the lack of a suitable quality microhabitat for the local establishment of *L. scrobiculata*. The latter reason agrees with other studies at a similar spatial scale, which reported the limited distribution and abundance of epiphytic lichens due to environmental filtering, usually in combination with limitations on local dispersal (Öckinger et al., 2005; Belinchón et al., 2011; Schei et al., 2012; Nascimbene et al., 2013). However, biotic interactions that operate at the tree scale (e.g., competition with other epiphytes) might also influence the distribution and abundance of *L. scrobiculata* at the plot scale.

Tree-scale: Occurrence, abundance, and distribution of individuals—The abundance of *Lobarina scrobiculata* was higher at the plot scale where the trees had a relatively thin DBH but, at this finer scale, both the probability of occurrence and abundance increased with the tree DBH. This result agrees with numerous studies (e.g., Hedenås et al., 2003; Ranius et al., 2008; Belinchón et al., 2011) because the tree diameter is generally correlated with tree age (Ranius et al., 2008; Öckinger and Nilsson, 2010) and larger trees have a greater surface area that has been available for colonization for a longer time, while they generally provide a more suitable microhabitat for propagule establishment (i.e., the bark chemistry and roughness may be more suitable) (Barkman, 1958; Belinchón et al., 2011). Our results also highlight the importance of bark roughness, independent of the tree size, as an essential microhabitat quality factor that increases the probability of occurrence and abundance for *L. scrobiculata*. Bark fissures with a greater depth and thickness enhance bark moisture retention (Barkman, 1958; Ranius et al., 2008), which may provide suitable conditions for lichen propagule establishment and development, especially in the dry macroclimatic conditions of the Mediterranean region (Barkman, 1958; Hilmo and Ott, 2002; Belinchón et al., 2009, 2011). The strong effect of bark roughness is probably due to

the fact that *L. scrobiculata* mostly colonizes oak trees, which have rough bark even when young (Fig. 2; Belinchón et al., 2009, 2011). In the Atlantic region, the probability of *L. scrobiculata* being abundant on each tree was also higher in forests that received less precipitation and with lower tree densities, which could have been related to the type of forest, because oak forests are found in slightly drier locations and they have a relatively more open canopy than beech forests.

Therefore, our results suggest that the distribution of *Lobarina scrobiculata* throughout the Iberian Peninsula is highly dependent on the availability of suitable host trees in favorable oak forests. However, *L. scrobiculata* occurs on different types of broadleaf and coniferous species in other regions (Hallingbäck, 1989; Rolstad et al., 2001; Hilmo et al., 2011a; Smith et al., 2009; Schei et al., 2012).

Lobarina scrobiculata was more frequent on lower parts of the trunks with northerly orientation (Figs. 3 and 4). This suggests that its distribution is related to the gradients of light, temperature, and water availability along the trunk. The humidity increases with greater proximity to the ground (Geiger, 1950) and the light availability varies with the aspect on the tree (Gauslaa et al., 2001). Therefore, the pattern detected is consistent with a strong humidity demand at the microhabitat scale, which avoids extreme direct sunlight and wind exposure (i.e., higher desiccation). This trend was stronger in the Mediterranean region where the desiccation risk is higher. By contrast, the individual distribution was not orientation-dependent in the Atlantic region where all sides of the trunk appeared to be equally favorable for *L. scrobiculata* establishment and growth. In addition, it is interesting to note that the proportion of individuals growing close to the ground was much lower in this region compared with the Mediterranean region (Fig. 3). This could be attributable to factors other than humidity and light, which may influence the height distribution on the trunk. For example, we did not evaluate the effect of gastropod grazing but previous studies suggest that the proximity to the ground increases the risk and severity of herbivory for *L. scrobiculata* (Asplund et al., 2010). This factor is probably important in the Atlantic region, which is a very humid and generally calcareous habitat, thus the activity of gastropods may be favored (Gärdenfors et al., 1995).

Conclusions—This study contributes greatly to defining the ecological niche of the threatened species *Lobarina scrobiculata* in two contrasting biogeographical regions of the Iberian Peninsula. *L. scrobiculata* is a rare species in this area but it was locally abundant in rainy locations. However, the occurrence of *L. scrobiculata* in numerous forests with relatively low water availability might be explained by compensating factors, such as forest structural features and/or its high thallus water-holding capacity. Given the low occupation rates in most of the populations, we consider that the status of *L. scrobiculata* remains uncertain in the Iberian Peninsula because the extinction risk increases with a low occupation rate. Our hypothesis that *L. scrobiculata* would perform better in the Atlantic region was not supported because the abundance and occupation rates were generally lower than those in the Mediterranean region.

The abundance was higher in locations with more but thinner trees. Thus, although it is widely accepted that *Lobarina scrobiculata* belongs to mature epiphytic communities, relatively young and/or slightly managed forests hosted more abundant and vital populations of this species. Therefore, conservation

strategies should be directed toward the preservation of known populations, as well as uncolonized and nearby forests, which may be potential areas for population expansion.

Multiscale field measurements are required because environmental variables may affect the performance of a species in different ways depending on the scale (e.g., the differences in the importance of DBH or annual precipitation at the plot and tree scales). Our findings are important for extending the knowledge of the environmental requirements of *Lobarina scrobiculata*, which are critical for implementing conservation measures. Many questions are still unanswered but new hypotheses arise from these interesting results. For example, the fine-scale demographic population structure related to forest management, long-term population monitoring, and genetic population structure have not been determined but they are needed to assess the current conservation status of *L. scrobiculata* in this heterogeneous region.

LITERATURE CITED

Aragón, G., I. Martínez, P. Izquierdo, R. Belinchón, and A. Escudero. 2010. Effects of forest management on epiphytic lichen diversity in Mediterranean forests. *Applied Vegetation Science* 13: 183–194.

Asplund, J., P. Larsson, S. Vatne, and Y. Gauslaa. 2010. Gastropod grazing shapes the vertical distribution of epiphytic lichens in forest canopies. *Journal of Ecology* 98: 218–225.

Balmford, A., P. Crane, A. Dobson, R. E. Green, and G. M. Mace. 2005. The 2010 challenges: Data availability, information needs and extraterrestrial insights. *Philosophical Transactions of the Royal Society of London, B, Biological Sciences* 360: 221–228.

Barkman, J. J. 1958. Phytosociology and ecology of cryptogamic epiphytes. Koninklijke Van Gorcum & Comp. N.V., Assen, Netherlands.

Bates, D., M. Maechler, and B. Bolker. 2013. lme4: Linear mixed-effects models using S4 classes. R package version 0.999999-2. Website http://CRAN.R-project.org/package=lme4.

Belinchón, R., I. Martínez, G. Aragón, A. Escudero, and M. De la Cruz. 2011. Fine spatial pattern of an epiphytic lichen species is affected by habitat conditions in two forest types in the Iberian Mediterranean region. *Fungal Biology* 115: 1270–1278.

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

Blanco, E., M. A. Casado, M. Costa, R. Escribano, M. García, M. Génova, A. Gómez, et al. 2005. Los bosques ibéricos. Una interpretación geobotánica. Editorial Planeta, Barcelona, Spain.

Burgaz, A. R., E. Fuertes, and A. Escudero. 1994. Climax epiphytic communities in Mediterranean Spain. *Botanical Journal of the Linnean Society* 115: 35–47.

Burgaz, A. R., and I. Martínez. 1999. La familia Lobariaceae en la Península Ibérica. *Botanica Complutensis* 23: 59–90.

Cameron, R. P., T. Neily, and H. Clapp. 2013. Forest harvesting impacts on mortality of an endangered lichen at the landscape and stand scales. *Canadian Journal of Forest Research* 43: 507–511.

Carrascal, L. M., and J. Seoane. 2009. Linking density, productivity and trends of an endangered species: The Bonelli's eagle in Spain. *Acta Oecologica* 35: 341–348.

Culberson, C. F. 1969. Chemical studies in the genus *Lobaria* and the occurrence of a new tridepside, 4-O-methylgyrophoric acid. *Bryologist* 72: 19–27.

Ellis, C. J. 2012. Lichen epiphyte diversity: A species, community and trait-based review. *Perspectives in Plant Ecology, Evolution and Systematics* 14: 131–152.

Ellis, C. J., R. Yahr, and B. J. Coppins. 2009. Local extent of old-growth woodland modifies epiphyte response to climate change. *Journal of Biogeography* 36: 302–313.

Environment Canada. 2007. Recovery strategy for the boreal felt lichen (*Erioderma pedicellatum*), Atlantic population, in Canada. Species at Risk Act recovery strategy series, Environment Canada, Ottawa, Ontario, Canada.

European Environment Agency. 2009. Biogeographical regions in Europe. Website http://www.eea.europa.edu [Accessed 04 January 2014].

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

Gärdenfors, U., H. W. Waldén, and I. Wäreborn. 1995. Effects of soil acidification on forest land snails. *Ecological Bulletins* 44: 259–270.

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

Gauslaa, Y., M. Ohlson, K. A. Solhaug, W. Bilger, and L. Nybakken. 2001. Aspect-dependent high-irradiance damage in two transplanted foliose forest lichens, *Lobaria pulmonaria* and *Parmelia sulcata*. *Canadian Journal of Forest Research* 31: 1639–1649.

Geiger, R. 1950. The climate near the ground. Harvard University Press, Cambridge, Massachusetts, USA.

Giménez-Benavides, L., A. Escudero, and J. M. Iriondo. 2007. Reproductive limits of a late-flowering high-mountain Mediterranean plant along an elevational climate gradient. *New Phytologist* 173: 367–382.

Guisan, A., T. C. Edwards, and T. Hastie. 2002. Generalized linear and generalized additive models in studies of species distributions: Setting the scene. *Ecological Modelling* 157: 89–100.

Hallingbäck, T. 1989. Occurrence and ecology of the lichen *Lobaria scrobiculata* in Southern Sweden. *Lichenologist* 21: 331–341.

Hedenås, H., V. O. Bolyukh, and B. G. Jonsson. 2003. Spatial distribution of epiphytes on *Populus tremula* in relation to dispersal mode. *Journal of Vegetation Science* 14: 233–242.

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

Hilmo, O., H. Ely-Aastrup, H. Hytteborn, and H. Holien. 2011a. Population characteristics of old forest associated epiphytic lichens in *Picea abies* plantations in the boreal rainforest of Central Norway. *Canadian Journal of Forest Research* 41: 1743–1753.

Hilmo, O., and S. Ott. 2002. Juvenile development of the cyanolichen *Lobaria scrobiculata* and the green algal lichens *Platismatia glauca* and *Platismatia norvegica* in a boreal *Picea abies* forest. *Plant Biology* 4: 273–280.

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

Iriondo, J. M., M. J. Albert, L. Giménez-Benavides, F. Domínguez-Lozano, and A. Escudero. [eds.]. 2009. Poblaciones en peligro: Viabilidad demográfica de la flora vascular amenazada de España. Dirección General de Medio Natural y Política Forestal (Ministerio de Medio Ambiente, y Medio Rural y Marino), Madrid, Spain.

James, P. W., D. I. Hawksworth, and F. Rose. 1977. Lichen communities in the British Isles: A preliminary conspectus. *In* M. R. D. S. Seaward [ed.], Lichen ecology, 295–413. Academic Press, London, UK.

Johansson, P., and J. Ehrlén. 2003. Influence of habitat quantity, quality and isolation on the distribution and abundance of two epiphytic lichens. *Journal of Ecology* 91: 213–221.

Kalwij, J. M., H. H. Wagner, and C. Scheidegger. 2005. Effects of stand-level disturbances on the spatial distribution of a lichen indicator. *Ecological Applications* 15: 2015–2024.

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

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

MARINI, L., J. NASCIMBENE, AND P. L. NIMIS. 2011. Large-scale patterns of epiphytic lichen species richness: Photobiont-dependent response to climate and forest structure. *Science of the Total Environment* 409: 4381–4386.

MARTÍNEZ, I., G. ARAGÓN, F. J. SARRIÓN, A. ESCUDERO, A. R. BURGAZ, AND B. J. COPPINS. 2003. Threatened lichens in central Spain (saxicolous excluded). *Cryptogamie. Mycologie* 24: 73–97.

MCCULLAGH, P., AND J. A. NELDER. 1989. Generalized linear models. Chapman and Hall, London, UK.

MCEVOY, M., K. A. SOLHAUG, AND Y. GAUSLAA. 2007. Solar radiation screening in usnic acid-containing coertices of the lichen *Nephroma arcticum. Symbiosis* 43: 143–150.

MCGILL, B. J. 2010. Matters of scale. *Science* 328: 575–576.

MERINERO, S., O. HILMO, AND Y. GAUSLAA. 2014. Size is a main driver for hydration traits in cyano-and cephalolichens of boreal rainforest canopies. *Fungal Ecology* 7: 59–66.

MONCADA, B., R. LÜCKING, AND L. BETANCOURT-MACUASE. 2013. Phylogeny of the *Lobariaceae* (lichenized Ascomycota: *Peltigerales*), with a reappraisal of the genus *Lobariella. Lichenologist* 45: 203–263.

NASCIMBENE, J., R. BENESPERI, G. BRUNIALTI, I. CATALANO, M. D. VEDOVE, M. GRILLO, D. ISOCRONO, ET AL. 2013. Patterns and drivers of β-diversity and similarity of *Lobaria pulmonaria* communities in Italian forests. *Journal of Ecology* 101: 493–505.

NASH, T. H. [ed.], 2008. Lichen biology. Cambridge University Press, Cambridge, UK.

NATURESERVE. 2014. NatureServe Explorer: An online encyclopedia of life [web application], version 7.1. NatureServe, Arlington, Virginia. Website http://explorer.natureserve.org [accessed 2 April 2014].

NIMIS, P. L. 1993. The lichens of Italy. An annotated catalogue. Museo Regionale di Scienze Naturali, Torino, Italy.

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

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

PINHEIRO, J. C., D. M. BATES, S. DEBROY, AND D. SARKAR. 2008. nlme: Linear and non-linear mixed effects models. R package version 3.1-87.

RABINOWITZ, D. 1981. Seven forms of rarity. *In* H. Synge [ed.], The biological aspects of rare plants conservation, 205–217. Wiley, New York, USA.

RANDLANE, T., I. JÜRIADO, A. SUIJA, P. LÕMUS, AND E. LEPPIK. 2008. Lichens in the new Red List of Estonia. *Folia Cryptogamica Estonica* 44: 113–120.

RANIUS, T., P. JOHANSSON, B. NICLAS, AND M. NIKLASSON. 2008. The influence of tree age and microhabitat quality on the occurrence of crustose lichens associated with old oaks. *Journal of Vegetation Science* 19: 653–662.

ROLSTAD, J., I. GJERDE, K. O. STORAUNET, AND E. ROLSTAD. 2001. Epiphytic lichens in Norwegian coastal spruce forest: Historic logging and present forest structure. *Ecological Applications* 11: 421–436.

SÁNCHEZ-PALOMARES, O., F. SÁNCHEZ-SERRANO, AND M. P. CARRETERO-CARRERO. 1999. Modelos y cartografía de estimaciones climáticas termopluviométricas para la España peninsular. Colección Fuera de Serie. INIA, Madrid, Spain.

SCHEI, F. H., H. H. BLOM, I. GJERDE, J. A. GRYTNES, E. HEEGAARD, AND M. SÆTERSDAL. 2012. Fine-scale distribution and abundance of epiphytic lichens: Environmental filtering or local dispersal dynamics? *Journal of Vegetation Science* 23: 459–470.

SCHEIDEGGER, C. 1995. Early development of transplanted isidioid soredia of *Lobaria pulmonaria* in an endangered population. *Lichenologist* 27: 361–374.

SCHEIDEGGER, C. 2003. *Erioderma pedicellatum.* 2008 IUCN Red List of threatened species. Website http://www.iucnredlist.org [accessed 14 January 2014].

SCHEIDEGGER, C., AND S. WERTH. 2009. Conservation strategies for lichens: Insights from population biology. *Fungal Biology Reviews* 23: 55–66.

SÉRUSIAUX, E. 1989. Liste Rouge des macrolichens dans la Communauté Européene. Centre de Recherchers sur les Lichens, Département de Botanique, Liége, Belgium.

SMITH, C. W., A. APTROOT, B. J. COPPINS, A. FLETCHER, O. L. GILBERT, P. W. JAMES, AND P. A. WOLSELEY. [eds.], 2009. The lichens of Great Britain and Ireland. British Lichen Society, London, UK.

SOULÉ, M. E. 1987. Viable populations for conservation. Cambridge University Press, Cambridge, UK.

STEHN, S. E., P. R. NELSON, C. A. ROLAND, AND J. R. JONES. 2013. Patterns in the occupancy and abundance of the globally rare lichen *Erioderma pedicellatum* in Denali National Park and Preserve, Alaska. *Bryologist* 116: 2–4.

VALLADARES, F., J. J. CAMARERO, F. PULIDO, AND E. GIL-PELEGRÍN. 2004. El bosque mediterráneo, un sistema humanizado y dinámico. *In* F. Valladares [ed.], Ecología del bosque mediterráneo en un mundo cambiante, 13–25. Ministerio de Medio Ambiente, Madrid, Spain.

WEIN, R. W., AND J. E. SPEER. 1975. Lichen biomass in Acadian and boreal forests of Cape Breton Island, Nova Scotia. *Bryologist* 78: 328–333.

WIENS, J. A. 1989. Spatial scaling in ecology. *Functional Ecology* 3: 385–397.

YAHR, R. 2003. *Cladonia perforata.* 2013 IUCN Red List of threatened species. Website http://www.iucnredlist.org [accessed 14 January 2014].

ZUUR, A. F., E. N. IENO, N. J. WALKER, A. A. SAVELIEV, AND G. M. SMITH. 2009. Mixed effects models and extensions in ecology with R. Springer Science+Business media, New York, New York, USA.