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# Small, fragmented native oak forests have better preserved epiphytic lichen communities than tree plantations in a temperate sub-oceanic Mediterranean climate region

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**ABSTRACT.** In increasingly fragmented landscapes tree plantations are thought to help maintain forest continuity among native patches. Epiphytic lichens are one of the most sensitive groups to change in forest conditions, but the effects of this management practice are still poorly studied in temperate regions. In this study we compared epiphytic lichen diversity among small patches of old, native oaks (*Quercus pyrenaica*) and young, planted chestnuts (*Castanea sativa*) and Monterey pines (*Pinus radiata*) in a major forestry area in northwestern Spain. Our results showed that the richness of epiphytic lichens was higher in *C. sativa* than *Q. pyrenaica*, but that the latter had more lichen species typical of mature forests, including macrocyanolichens. Overall, *C. sativa* plantations had more species typical of well-lit, dry environments than *Q. pyrenaica* or *P. radiata*, which is likely caused by the natural architecture of each tree species, and to differences in forest age and management. At the tree level, *Q. pyrenaica* had the highest total richness including all species of conservation interest, which were exclusively found on this species. On a corollary, this study shows that *Q. pyrenaica* forests had the best preserved epiphytic lichen communities but with marked signs of forest fragmentation. In this fragmented landscape, young plantations of *C. sativa* and *P. radiata* seem to be of limited help for providing connectivity to epiphytic lichens among old native forest patches.

**KEYWORDS.** Forest fragmentation, lichen diversity patterns, oak forests, traditional forest management, bioindicators.



Temperate deciduous forests support a valuable biodiversity but have experienced a long history of anthropogenic impacts. Since ancient times human populations have logged these forests as a source of wood and to create pastures and arable land (Costa et al. 2001; FAO 2010; Wade et al. 2003). Chestnut plantations have also been introduced to rural areas as additional source of food and wood (Conedera et al. 2004). The dominant forest practice is now the plantation of fast-growing species for timber production, including pines and eucalypts (Anonymous 2011; Paquette & Messier 2010); a tendency that has intensified due to land-use abandonment (San

Roman Sanz et al. 2013). As the situation is expected to worsen under current population models (Pinilla et al. 2008; Verburg et al. 2010), there is an urgent need to gain insight into how this mosaic of remnant native oaks, tree plantations and open areas affects forest diversity.

Habitat fragmentation is one of the major threats to forest diversity (Andrén 1997; Lindenmayer & Fischer 2013), and plantations could help provide connectivity among isolated patches (Brocknerhoff et al. 2008; Carnus et al. 2006). However, plantations typically have short rotation periods, resulting in too simplified forest structures and in a less suitable environment for forest interior species (Fedrowitz et al. 2014; Hartley 2002). Nonetheless, the situation may change with rural abandonment.

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The lack of thinning and understory clear out promote moist and shade environments (Nascimbene et al. 2013). However, tree species differ in their bark properties and canopy structure, which influences the species that grow on them, as well as the amount of water that reaches the soil and the light that penetrates (Barbier et al. 2008; Cáceres et al. 2007; Johansson & Ehrlén 2003; Király et al. 2013). Thus, both tree identity and management can affect forest species but especially sedentary taxa such as epiphytes.

Epiphytic lichens are a major component of forested ecosystems (Galloway 1992; Pike 1978; Porada et al. 2014) and a group of organisms most threatened by forest practices (Hauck et al. 2013). As a result of habitat fragmentation, populations of epiphytic lichens are more vulnerable to extinction, including threats such as the edge effect (Murcia 1995; Ries et al. 2004). This promotes species from disturbed, well-lit, dry environments (Aragón et al. 2015; Renhorn et al. 1997; Rheault et al. 2003) instead of those typical of mature, shaded and moist forests, including macrocyanolichens, most of them included in European Red Lists (e.g., Martínez et al. 2003; Nimis 2003; Randlane et al. 2008). If understory develops in small forest patches, this may buffer the edge effect and provide better forest interior conditions (see Aragón et al. 2010; Cardós et al. 2016). However, the lack of management also leads to an excessive canopy closure that is also detrimental for epiphytic lichens (Juriado et al. 2009; Nascimbene et al. 2013; Nordén et al. 2012).

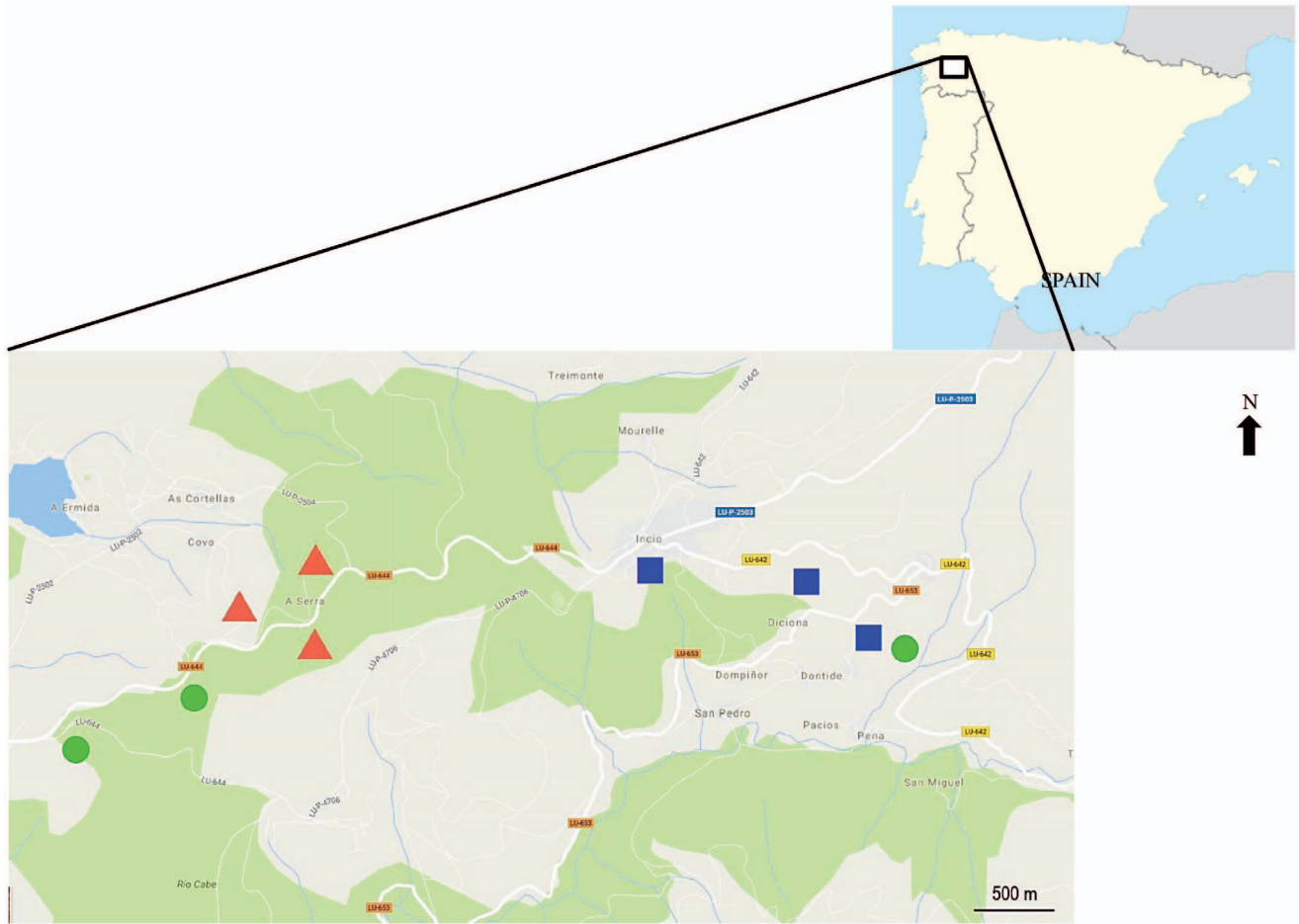
Many studies have examined the effects of forest management on epiphytic lichens (Bartels & Chen 2015; Johansson 2008; Lommi et al. 2010). However, their impact on temperate deciduous forests is less well understood (Nascimbene et al. 2013), especially in small forest patches. This is of particular concern in areas such as the Iberian Peninsula, a hotspot of biodiversity (Gómez & Lunt 2007) in which a matrix of small private properties is still the dominant landscape (Manuel & Gil 2002). The lack of management is expected to favor forest aging, which provides better habitat for epiphytes. Calviño-Cancela et al. (2013) found that epiphytic lichen communities on mature pines (*Pinus pinaster*) can be comparable to those of mature native oak (*Quercus robur*) forests of ca. 60 ha in terms of total richness but not in species composition. However, the role of smaller patches in epiphytic lichen conservation, where the edge effect is likely to

intensify, is unknown. Further, the suitability of other common forest species such as *Pinus radiata* and *Castanea sativa* as habitat for epiphytic lichens of native oaks has not yet been investigated.

The present study compares epiphytic lichen diversity among young *Castanea sativa* plantations with a rudimentary management at the understory level, and those of unmanaged young *Pinus radiata* and old native oaks (*Quercus pyrenaica*) in a major forestry area of Spain. Given natural structural factors, broad-leaved trees create more shadow and moister environments than those with needle-shaped leaves (Barbier et al. 2008). Therefore, regardless of differences in understory, we expect epiphytic lichen species richness and composition to be more similar among deciduous trees than with pines. For the deciduous trees, we also expect that most species of conservation interest would be on the trunks (Boch 2013; Fritz 2009). Finally, we predict a higher number of epiphytic lichen species typical from disturbed, well-lit, dry conditions on the pines and oaks from our study, contrary to what was found by Calviño-Cancela et al. (2013), because of a stronger edge effect.

## MATERIALS AND METHODS

**Study area.** This study was conducted nearby the Site of Community Importance ‘SCI ES1120016 Río Cabe’ in northwestern Spain (Habitats Directive 92/43/EEC, **Fig. 1**). Located in the municipality of O Incio (42°38′25″N, 7°21′49″E), the study area is sparsely populated (306 inhabitants), far from industries (>30 km), and the forest cover is increasing due to farming abandonment and little ranching (~80 cattle). The climate is temperate oceanic sub-Mediterranean (Rivas-Martinez et al. 2004); fog is frequent, precipitation is abundant (800–1800 mm annual) and mean temperature is moderate (16°C), but summers can be dry and warm (<60mm; >27°C). The landscape structure is made up of small private properties in which forest areas and open areas, including pastures and thicket (*Ulex europaeus*), alternate. Forests are dominated by oaks (*Quercus pyrenaica* and *Q. robur*) and the historically introduced chestnuts (*Castanea sativa*). Some recent private plantations, mostly of Monterey pine (*Pinus radiata*), red oak (*Q. rubra*), white poplar (*Populus alba*) and eucalyptus (*Eucalyptus* sp.), are also present in the area but to a lesser extent. Undergrowth consisted of herbs, shrubs (e.g., *Rubus*



**Figure 1.** Location of the sampling sites of *Quercus pyrenaica* (triangles), *Castanea sativa* (squares) and *Pinus radiata* (circles) in northwestern Spain.

*ulmifolius*) and ferns (mostly *Pteridium aquilinum*), which have remained unmanaged for the last 25 years in most of our plots. The exceptions were *C. sativa* plantations in which a manual, annual clear out is carried out to collect the fruit. We are not aware of other forest management practices before our survey.

**Sampling design.** In August 2013, epiphytic lichen communities were sampled on trunks of native *Quercus pyrenaica* and the planted *Castanea sativa* and *Pinus radiata* (3 sampling sites/forest type), but also at the whole tree level for the deciduous trees. Sampling sites were selected on the basis of similar altitude (500–693 m.a.s.l.) and slope (lower than 10°), surrounding landscape (>65% open land), tree size, and the agreement of private owners. All sites represent typical small private properties (<1 ha), ranging between 590 and 649 m<sup>2</sup>, and were relatively close to each other to ensure similar macroclimate (e.g., rainfall, solar irradiation).

In each forest type, 15 trees were selected (5 trees/site) in the center of each plot (20 m from the edge), leaving a space of 20 m between trees. The number of sampled trees in each site represented 80% of the tree individuals in each sampling site. To minimize the tree size effect in the study design, individuals per tree species did not differ in trunk diameter between sampling sites (**Table 1**); trees of *P. radiata* and *C. sativa* were size-matched and homogeneously smaller than those of *Q. pyrenaica*. At each target tree, we sampled all lichen taxa present in a 10 × 60 cm rectangle all around the trunk at 1.5 m height. Additionally, we collected lichen samples from five branches (10 cm Ø and 60 cm length) and 25 twigs (≤1 cm Ø and 60 cm length) recently cut by owners to characterize crown lichens of each individual of *Q. pyrenaica* and *C. sativa*. For *P. radiata*, crown samples were unavailable as these plantations are not pruned but fully wiped out when trees fit the commercial requirements. At each site, the mean undergrowth height and cover was also

**Table 1.** Habitat features (mean  $\pm$  SE) of the sampling sites surveyed for studying the epiphytic lichen communities on three forest types (*Quercus pyrenaica*, *Castanea sativa* and *Pinus radiata*) in northwestern Spain. Letters (a,b,c) indicate values that are not significantly different at  $p \leq 0.05$  using ANOVA followed by TukeyHSD post-hoc test. DBH = tree diameter at breast height.

Forest types	Patch	Altitude (m)	DBH (m)	Mixed-age forest	Undergrowth (m)
<i>Quercus pyrenaica</i>	QP1	561	1.92 $\pm$ 0.21 <sup>b</sup>	Yes	0.71 $\pm$ 0.04 <sup>c</sup>
<i>Quercus pyrenaica</i>	QP2	615	1.92 $\pm$ 0.19 <sup>b</sup>	Yes	0.69 $\pm$ 0.02 <sup>c</sup>
<i>Quercus pyrenaica</i>	QP3	652	1.98 $\pm$ 0.19 <sup>b</sup>	Yes	0.67 $\pm$ 0.05 <sup>c</sup>
<i>Castanea sativa</i>	CS1	676	0.59 $\pm$ 0.01 <sup>a</sup>	No	0.20 $\pm$ 0.03 <sup>a</sup>
<i>Castanea sativa</i>	CS2	693	0.58 $\pm$ 0.01 <sup>a</sup>	No	0.23 $\pm$ 0.03 <sup>a</sup>
<i>Castanea sativa</i>	CS3	659	0.59 $\pm$ 0.01 <sup>a</sup>	No	0.30 $\pm$ 0.03 <sup>a</sup>
<i>Pinus radiata</i>	PR1	500	0.56 $\pm$ 0.02 <sup>a</sup>	No	0 $\pm$ 0 <sup>b</sup>
<i>Pinus radiata</i>	PR2	570	0.54 $\pm$ 0.02 <sup>a</sup>	No	0 $\pm$ 0 <sup>b</sup>
<i>Pinus radiata</i>	PR3	628	0.59 $\pm$ 0.02 <sup>a</sup>	No	0 $\pm$ 0 <sup>b</sup>

estimated based on 10 measures distributed on a 5 m grid.

#### Lichen identification and indicator metrics.

Lichen species were identified by the second author in the laboratory at the University of Barcelona under stereomicroscope and conventional light microscopy 100,  $\times 400$  or  $\times 1000$ , and using standard chemical spot tests (Orange et al. 2001). Species nomenclature (**Supplementary Table S1**) followed Nimis & Martellos (2008) and for those species not listed here, we adopted the standardized name provided in the Index Fungorum database (<http://www.indexfungorum.org/>). Presence/absence data were recorded because the presence of inconspicuous species can bias lichen cover data estimated based on pictures (personal observation). To determine the conservation value of small forest patches, we used the total taxonomic richness of lichens and the number of macrocyanolichens, a group that is in marked regression in Europe (e.g., Jørgensen et al. 1978; Martínez et al. 2003; Nimis 2003). We also ranked all lichen species according to their frequency of occurrence in each forest patch to better identify lichen-tree species associations. A similar analysis was also used to compare lichen communities between crowns and trunks in the two deciduous tree species.

To infer the environmental conditions of each forest type, we used indicators of environmental conditions based on lichen traits developed by Nimis & Martellos (2008). All lichen species on each tree trunk were ranked 1–5, where the highest score indicates the highest tolerance to a given environmental condition (eutrophication, pH, aridity and solar irradiation, **Supplementary Table S2**). As an additional indicator of moist conditions, we used the

total richness of particular taxa (macrocyanolichens and *Cladonia* spp.), as these require liquid water (not only fog) to be channelized through the trunk to survive (Lange et al. 1986, 1993). Finally, we included an indicator of habitat naturalness based on lichen traits ('poleophoby' in Nimis & Martellos 2008), which ranges from 1–4 with 4 indicating a strong preference of lichens for mature, undisturbed forests. For all indicators of environmental conditions based on lichen traits, we calculated the median for the epiphytic lichen community on each tree individual. To specifically test if our forest patches had species indicative of forest continuity, we calculated the Revised Index of Ecological Continuity (RIEC) (Coppins & Coppins 2002). This index ranges from 0–100 and values  $\leq 25$  indicate no ecological continuity.

**Statistical analyses.** All statistical analyses were performed in R 3.1.1 (R Development Core Team 2014). Mean tree diameter and undergrowth height and cover were compared among forest types using an analysis of variance (ANOVA) followed by the post-hoc Tukey's honest significant difference (HSD) test. For lichens, we used two richness estimators (Jackknife 1 and bootstrap methods, see Moreno 2004) to determine the completeness of our inventories and species detectability, estimated by the difference between observed and estimated species richness. At the trunk and crown levels, lichen richness was compared among forest types using generalized linear mixed models (GLMMs) with a quasipoisson error distribution followed by the post-hoc Tukey's HSD test. Site was included as a random effect to account for pseudo-replication. Tree diameter was included as co-variable but as it did not reach significance (All  $p > 0.16$ ) nor influ-



**Table 2.** Number of taxa and richness estimators (mean  $\pm$ SE) of epiphytic lichen species at the three tree levels (trunk, branches and twigs) in the three forest types (*Quercus pyrenaica*, *Castanea sativa* and *Pinus radiata*) surveyed in northwestern Spain. Detectability indicates the completeness of the lichen inventories (see methods).

Forest types	Observed richness		Estimated richness		Detectability
	Mean	Total	Jackknife1	Bootstrap	%
<i>Quercus pyrenaica</i>					
Trunk	10 $\pm$ 0.3	39	48 $\pm$ 1.3	44 $\pm$ 0.6	81–89
Branches	6 $\pm$ 0.3	27	36 $\pm$ 1.3	31 $\pm$ 0.6	75–87
Twigs	8 $\pm$ 0.7	29	36 $\pm$ 1	32 $\pm$ 0.6	81–91
Total	19 $\pm$ 0.7	60	75 $\pm$ 1.6	68 $\pm$ 1	80–88
<i>Castanea sativa</i>					
Trunk	11 $\pm$ 1.3	39	52 $\pm$ 2	45 $\pm$ 3	75–86
Branches	12 $\pm$ 1.3	27	29 $\pm$ 0.3	28 $\pm$ 0.3	93–96
Twigs	10 $\pm$ 1.3	29	36 $\pm$ 1	32 $\pm$ 0.6	81–91
Total	20 $\pm$ 1.3	52	65 $\pm$ 2	58 $\pm$ 1	80–90
<i>Pinus radiata</i>					
Trunk	5 $\pm$ 0.6	12	14 $\pm$ 0.3	13 $\pm$ 0.3	86–92

enced the significance of other factors, it was deleted for simplicity. The same analysis assuming a Gaussian distribution was carried out to examine variations in the median value of each environmental indicator (eutrophication, pH, aridity and solar irradiation) based on the lichen assembly of each tree. Factor effects in all models were assessed using a likelihood-ratio test. As environmental-based lichen indicators were ordinal variables and do not meet the requirements of parametric statistics, results from GLMMs were confirmed using the non-parametric Kruskal-Wallis test followed by Mann-Whitney tests for pair-wise comparisons (results not shown). In contrast to GLMMs, these tests do not control for pseudo-replication.

Differences in the taxonomic structure of epiphytic lichen communities among the three forest types and between the crowns of deciduous trees were examined using a permutational multivariate analysis of variance (PERMANOVA) using site as grouping factor. Bray-Curtis distance was employed

to determine the dissimilarity between lichen communities because it is equivalent to the Sørensen-distance when presence-absence data are used (Legendre & Legendre 2012). Significance was reached  $p \leq 0.05$  in all analyses.

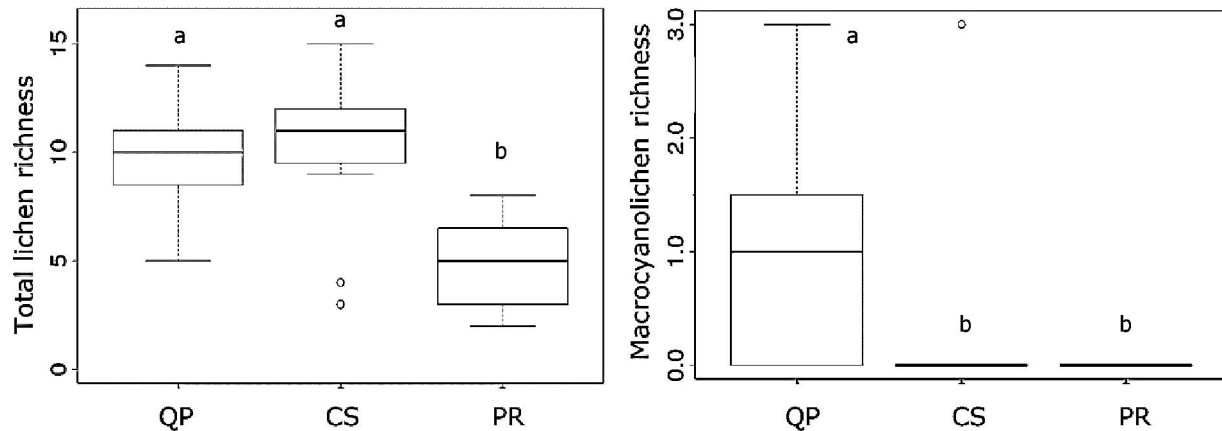
## RESULTS

A total of 81 epiphytic lichen species were recorded in oaks (*Quercus pyrenaica*), chestnuts (*Castanea sativa*) and Monterey pines (*Pinus radiata*) with all samples combined (**Supplementary Table S2**). At the trunk level, mean lichen species richness varied with forest type (**Table 3**), with the lowest values in *P. radiata* (**Fig. 2**). Richness estimators indicated that 75–92% of species present have been detected, supporting the lowest species richness found in the pines (**Table 2**). In the deciduous trees, richness patterns in the trunks reflected well those in the crowns, with the highest lichen richness on *C. sativa* (**Table 2**). However, at the tree level, the total richness was higher on *Q. pyrenaica* than on *C. sativa* (**Table 2**). *Quercus pyrenaica* had a larger trunk diameter at breast height than *C. sativa*, whereas *C. sativa* trunks were size-matched with those of *P. radiata*. *Quercus pyrenaica* plots also had the best-developed understory, followed by *C. sativa* and *P. radiata* sites (**Table 1**).

Differences in species richness between forest types were reflected in their lichen species composition (PERMANOVA:  $F=18.04$ ,  $p < 0.01$ ). Thirty percent of lichen species were exclusive to *Quercus pyrenaica*, exceeding the number found on *Castanea sativa* (26%) and *Pinus radiata* (5%, **Supplementary Table S1**). Overall, the epiphytic lichen community of *Q. pyrenaica* and *C. sativa* had more representatives of mature forests (*Lobarina scrobiculata*, *Pannaria conoplea*, *Peltigera collina*, *Rinodina isidioides* and *Sticta limbata*), even though the RIEC index did not show evidence of forest continuity in any forest type (*Q. pyrenaica* = 25 and *C. sativa* = 20). Of particular interest is the high macrocyano-

**Table 3.** GLMM outputs for the comparison of mean epiphytic lichen richness, and the number of macrocyanolichens on *Quercus pyrenaica* (QP), *Castanea sativa* (CS) and *Pinus radiata* trees in northwestern Spain. Bold values indicate significance at  $P \leq 0.05$ . df = degrees of freedom; np = not present.

Response variable	Trunk			Crowns (only for QP and CS)		
	$\chi^2$	df	P-value	$\chi^2$	df	P-value
Total species richness	21.58	2	<b>&lt;0.01</b>	21.38	1	<b>&lt;0.01</b>
Number of macrocyanolichens	6.00	2	<b>0.04</b>	Np	np	np



**Figure 2.** Changes in total epiphytic lichen richness and macrocyanolichen richness on trunks of *Quercus pyrenaica* (QP), *Castanea sativa* (CS) and *Pinus radiata* (PR). Letters group forest types homogeneous at  $p > 0.05$  (TukeyHSD posthoc test).

lichen richness on *Q. pyrenaica* compared to *C. sativa* and *P. radiata* (Fig. 2). Further, the most frequently recorded epiphytic lichen species on trunks also varied among *Q. pyrenaica* (e.g., *Cladonia pyxidata*, *Flavoparmelia caperata* and *Pertusaria hemisphaerica*), *P. radiata* (e.g., *Hypogymnia physodes*, *Lecanora strobilina* and *L. pulicaris*) and *C. sativa* (e.g., *Ramalina subgeniculata*, *Buellia disciformis* and *L. hybocarpa*; Table 4). Likewise, the most frequent species on crowns differed between *Q. pyrenaica* (e.g., *Evernia prunastri*, *H. physodes* and *Hypotrachyna revoluta*) and *C. sativa* trees (e.g., *B. disciformis*, *Melanohalea exasperata* and *Usnea hirta*; PERMANOVA:  $F=23.18$ ,  $p < 0.01$ ). Interestingly, the trunks and crowns of *C. sativa* had more species in common than those of *Q. pyrenaica* (Table 4).

Differences in species composition at the trunk level led to major changes in median values of most indicators of environment conditions based on lichen traits (Table 5; Supplementary Table S2). In particular, *Castanea sativa* had more lichen species typical of well-lit and dry environments than *Quercus pyrenaica* and *Pinus radiata* (Fig. 3). However, *Q. pyrenaica* trees had the highest richness of water-liquid dependent taxa (all macrocyanolichens, Fig. 2). Lichen traits showed that *Q. pyrenaica* and *C. sativa* were rather similar in terms of tolerance to pH and eutrophication when compared to *P. radiata*, which had the most acidophilous and least eutrophy-tolerant taxa (Fig. 3). Only marginally significant differences in the lichen trait values related to poleophoby were observed across forest types (Table 4), with the lowest values found in *P. radiata* (Fig. 3).

## DISCUSSION

Our study shows that small, old, native oak forests (*Quercus pyrenaica*) had the highest total richness of epiphytic lichens, including many forest-interior species, compared to small, young plantations of chestnuts (*Castanea sativa*) and Monterey pines (*Pinus radiata*). *Quercus pyrenaica* and *C. sativa* shared the highest number of lichen species, but we still found major differences in species composition and lichen traits. Of particular conservation interest is that macrocyanolichens which are all in marked regression in Europe (e.g., Jørgensen et al. 1978; Martínez et al. 2003; Nimis 2003) were mostly found on *Q. pyrenaica* trunks. There was evidence of forest fragmentation in all the epiphytic lichen communities we sampled according to the Revised Index of Ecological Continuity.

As expected, epiphytic lichen communities on *Quercus pyrenaica* and *Castanea sativa* were more similar to each other than with pines, and we used indicators of environmental conditions based on lichen traits to infer the causes, as reported elsewhere (e.g., Calviño-Cancela et al. 2013; Pinho et al. 2012). Since all sampling sites were located in a relatively narrow area, our results cannot be attributed to differences in macroclimate but in the structure of forest patches, bark properties, tree age and microclimate. *Q. pyrenaica* forest was expected to provide, at the trunk level, more stable microclimate than pines, because tree architecture and broad-leaves are better at reducing light penetration and condensing water than needle-shape leaves (Barbier et al. 2008). On the other hand, lichen trait values of *Q. pyrenaica* and *Pinus radiata* from our study indicated similar values of

**Table 4.** Ten most frequently recorded epiphytic lichen species on trunks and crowns of *Quercus pyrenaica* (QP) and *Castanea sativa* (CS) in northwestern Spain. Only trunks of *P. radiata* (PR) were surveyed.

Trunks		
QP	CS	PR
<i>Parmelia sulcata</i>	<i>Evernia prunastri</i>	<i>Melanelixia subaurifera</i>
<i>Cladonia pyxidata</i>	<i>Parmelia sulcata</i>	<i>Hypogymnia physodes</i>
<i>Flavoparmelia caperata</i>	<i>Ramalina subgeniculata</i>	<i>Lecanora strobilina</i>
<i>Pertusaria hemisphaerica</i>	<i>Buellia disciformis</i>	<i>Evernia prunastri</i>
<i>Ramalina farinácea</i>	<i>Lecanora hybocarpa</i>	<i>Lecanora pulicaris</i>
<i>Pertusaria albescens</i>	<i>Melanelixia subaurifera</i>	<i>Parmelia sulcata</i>
<i>Normandina pulchella</i>	<i>Lecidella elaeochroma</i>	<i>Ramalina farinácea</i>
<i>Parmotrema perlatum</i>	<i>Ramalina farinácea</i>	<i>Chrysothrix candelaris</i>
<i>Phlyctis argena</i>	<i>Lecanora intumescens</i>	<i>Scoliciosporum umbrinum</i>
<i>Pertusaria amara</i>	<i>Lecanora carpinea</i>	<i>Fuscidea lightfootii</i>
Crowns		
QP	CS	
<i>Parmelia sulcata</i>	<i>Evernia prunastri</i>	
<i>Evernia prunastri</i>	<i>Lecanora hybocarpa</i>	
<i>Melanelixia subaurifera</i>	<i>Melanelixia subaurifera</i>	
<i>Parmotrema perlatum</i>	<i>Buellia disciformis</i>	
<i>Hypogymnia physodes</i>	<i>Melanohalea exasperata</i>	
<i>Ramalina farinácea</i>	<i>Parmelia sulcata</i>	
<i>Hypotrachyna revoluta</i>	<i>Normandina pulchella</i>	
<i>Flavoparmelia caperata</i>	<i>Ramalina farinácea</i>	
<i>Pertusaria amara</i>	<i>Usnea hirta</i>	
<i>Lecanora hybocarpa</i>	<i>Lecanora carpinea</i>	

aridity and solar irradiation. The most plausible explanation for these results is the different tree density, as pines were more clustered (<2 m between trees) than oaks (>4 m between trees). However, in our study, *Q. pyrenaica* had the highest richness of macrocyanolichens, a lichen group that is highly liquid-water dependent (Lange et al. 1986) and typical of shadow forests (Nimis & Martellos 2008). This is likely to be attributed to the fact that oaks have more efficient canopies than pines to collect and channel rain water towards trunks (Oerlemans 2010), and that species other than macrocyanolichens can survive with only fog (Lange et al. 1986, 1993).

A complementary explanation for our results is that barks of oaks are more stable than those of conifers, creating suitable conditions for the establishment of epiphytes (Barkman 1958; Fengel & Wegned 1983), even though macrocyanolichens often grow on mosses, and this substrate is more

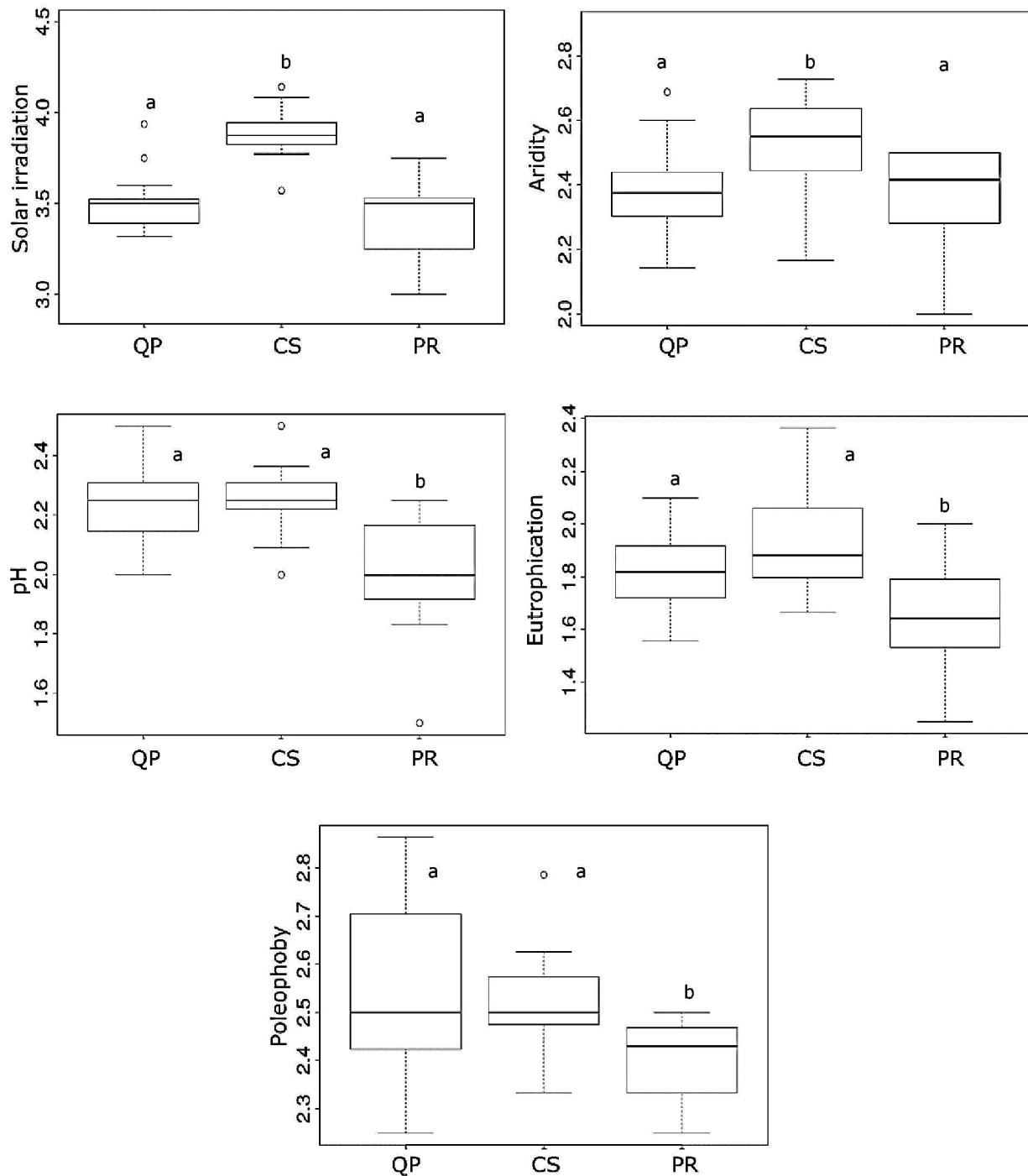
**Table 5.** GLMM outputs for the differences in lichen trait median values calculated for the trunks of the three forest species (*Quercus pyrenaica*, *Castanea sativa* and *Pinus radiata*) surveyed in northwestern Spain. Bold p-values indicate significance at  $p \leq 0.05$ .

	$\chi^2$	Df	p-value
Solar irradiation	32.23	2	<0.001
Aridity	10.20	2	0.01
pH	18.34	2	<0.001
Eutrophication	8.79	2	0.01
Poleophoby	5.90	2	0.05

unstable than pine bark (personal observation, second author). As macrocyanolichens are typically found in mature forests (Nimis & Martellos 2008), their presence in our oak patches may have also been favored by the larger diameter and architecture of the older *Quercus pyrenaica* trees (centripetal crown, Barkman, 1958). *Quercus pyrenaica* and *Castanea sativa* trunks showed similar lichen richness but major differences in their diameter, a factor that has been shown to be positively related to lichen species richness (Fritz et al. 2008; Lie et al. 2009). *Pinus radiata* and *C. sativa* trees were size-matched but the latter had the highest lichen species richness, suggesting that differences in tree size or age, which positively correlates with tree size, were of minor importance in our study, and factors such as bark type or pH may be more important. *Castanea sativa* trees have a smoother bark than pines and this is expected to favor epiphytic lichen establishment (Barkman 1958). Pine bark is slightly more acid and less eutrophic than those of *C. sativa*, as shown by a predominance of species that are favored by this type of bark (*Chrysothrix candelaris*, *Lecanora strobilina* and *Tromera resiniae*), which supports that these two factors affect the lichen community composition (Van Herk 2001).

The observed differences in lichen richness between *Quercus pyrenaica* and *Pinus radiata* contrasted with Calviño-Cancela et al. 2013, who found a similar total lichen richness in mature oaks (*Q. robur*) and pines (*P. pinaster*). A major reason for this result is likely to be the different size of forest patches, as ours were smaller (590–649 m<sup>2</sup>) than those (60 ha) of Calviño-Cancela et al. (2013). Smaller patches typically have a larger edge effect, which promotes epiphytic lichen species typical of well-lit, arid environments instead of those of mature forests (Aragón et al. 2015; Rheault et al.





**Figure 3.** Changes in lichen trait values used as indicators of the environmental conditions (solar irradiation, aridity, pH, eutrophication and poleophoby) in *Quercus pyrenaica* forests (QP), and *Castanea sativa* (CS) and *Pinus radiata* plantations (PR). Note differences in y-axis to facilitate comparisons of scores among forest types. Letters group forest types homogeneous at  $p > 0.05$  (TukeyHSD posthoc test).

2003). However, in our study, lichen traits of *Castanea sativa* patches had the highest values of aridity and solar irradiation, as opposed to *Q. pyrenaica* and *P. radiata* which were rather similar in these two lichen traits.

Management practices have most likely also contributed to the differences we observed in epiphytic lichen communities among all three forest types. Patches of *Quercus pyrenaica* and *Pinus radiata* were unmanaged and so likely to have

denser canopies, which reduce light penetration (Nascimbene et al. 2013). This may have undermined their potential to hold higher lichen species richness, even though canopies of *Castanea sativa* were also unmanaged and these trees had the highest mean richness in our study. Another possible explanation for our results is the different understory cover of forest patches, which affects local air humidity (Aragón et al. 2010; Brunialti et al. 2010). However, this was not clearly evident in the lichen traits because these suggested similar aridity values in *Q. pyrenaica* and *P. radiata*, and these two forest types had a very different understory cover.

Even though lichen species richness on trunks was similar between the two deciduous tree species, canopies of *Castanea sativa* had higher lichen species richness than those of *Quercus pyrenaica*. Since light is one of the main drivers of epiphyte diversity along the trees (Boch et al. 2013; Fritz 2009), the most plausible explanation for our result is that the older *Q. pyrenaica* had denser canopies than the younger *C. sativa* trees. This was evidenced in the lichen traits of the most frequently recorded lichen species on their canopies related to solar irradiation, with high extreme values for those on *C. sativa* (e.g., *M. exasperata* and *U. hirta*) compared to *Q. pyrenaica* (e.g., *H. physodes* and *H. revoluta*) (Nimis & Martellos 2008). Our comparison of epiphytic lichens between trunks and crowns also supports that the surveillance of trunks is sufficient to monitor epiphytic lichen communities (Boch et al. 2013; Fritz 2009). However, this inevitably ignores lichen diversity, as 28% of species were only found on crowns, even though none of them was of particular conservation concern, as reported by Fritz (2009) and Boch et al. (2013).

Overall, our results support the growing evidence that young plantations can reach lichen richness values similar to old native forests but have very different communities, including the number of macrocyanolichens (Calviño-Cancela et al. 2013; Nascimbene et al. 2013). This can have major implications for nutrient cycles since macrocyanolichens fix atmospheric N (Pike 1978; Porada et al. 2014), but also for taxa that use lichens as a resource such as birds and arthropods (Gunnarsson et al. 2004; Pettersson et al. 1995). Furthermore, our study highlights a major conservation concern, as lichen species experiencing marked regression, such as the macrocyanolichens *Pannaria conoplea* and *Protopannaria pezizoides* in central Spain (Martínez et al.

2003), were only found on the older *Quercus pyrenaica*. More worrisome is that their presence in small patches (590–649 m<sup>2</sup>) may be threatened by the low forest continuity, as indicated by the RIEC (Coppins & Coppins 2002). In this regard, young plantations embedded in a mosaic of small native old forests seems to be of limited help to maintain forest continuity, as the number of shared species between them was low, especially for pine plantations.

## CONCLUSIONS

In increasingly fragmented landscapes our study suggests that small patches of unmanaged, old *Quercus pyrenaica* forests have the potential to hold the typical epiphytic lichen community of temperate deciduous forests. However, all epiphytic lichen communities we surveyed had signs of being severely affected by forest fragmentation. Young plantations of managed *Castanea sativa* and unmanaged *Pinus radiata* do not appear to be suitable for providing connectivity among native forest patches, especially the pines which had the lowest number of shared species with *Q. pyrenaica* and no species of conservation interest. However, more studies are needed to determine the minimum patch size required for the conservation of lichen epiphytes, and the effect of management and forest age in fragmented landscapes.

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#### Supplementary documents online:

**Supplementary Table S1.** List of the 81 species recorded on the three tree species.

**Supplementary Figure S2.** Type of photobiont and median values of lichen traits for each epiphytic lichen species.