*Journal of Vegetation Science* ▮▮ (2017)

# Phylogenetic and functional structure of lichen communities under contrasting environmental conditions

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**Keywords**
Competition; CWM; Facilitation; Functional traits; Habitat filtering; NRI; NTI; Phylogenetic signal; Phylogeny

**Nomenclature**
Mycobank: http://www.mycobank.org

Received 1 February 2016
Accepted 7 April 2017
Co-ordinating Editor: Francesco de Bello

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## Abstract

**Question:** In order to identify the factors and assembly rules which potentially shape natural lichen communities we asked whether these communities are phylogenetically and functionally structured along an environmental gradient in beech forests in the Iberian Peninsula.

**Location:** A climatic gradient in the Iberian Peninsula.

**Methods:** We used species inventories, trait data and a molecular dated phylogeny to calculate phylogenetic and functional community metrics. We examined the phylogenetic and functional diversity of epiphytic lichen assemblages in nine beech forests along an environmental gradient.

**Results:** We found a significant pattern in the average phylogenetic and functional diversity across sites. Species at northern sites were less closely related than expected by chance (phylogenetic and functional overdispersion), suggesting that these communities could be structured by species interactions limiting the similarity among them (e.g. by competition and facilitation). In contrast, species occurring in the southern distributional limit of the host tree were phylogenetically and functionally clustered, implying that these communities could be primarily structured by environmental filtering, driven by the reduction of summer rainfall. Lower precipitation areas favoured fruticulose and squamulose species and a larger proportion of species with green algal photobionts and asexual reproduction.

**Conclusions:** Our results suggest that environmental filtering and species interactions regulate lichen communities differently under contrasting environmental conditions in beech forests in the Iberian Peninsula. These processes are reflected by the presence of key lichen traits that are phylogenetically conserved and can provide advantages for competition or adaptation to the environment.

## Introduction

One of the oldest challenges in ecology is to understand the co-existence of species and the search for mechanisms and rules which explain the composition of communities (Gleason 1926; Gee & Giller 1987; Pavoine & Bonsall 2011). The co-occurrence of species is a product of chance, speciation and migration processes, dispersal, and abiotic and biotic factors (Götzenberger et al. 2012), which can be reflected in the phylogeny and functional structure of communities. Thus, the phylogenetic and functional patterns of communities may help to understand the processes controlling the assemblage of their species (Petchey & Gaston 2002; Hardy & Senterre 2007).

The action of the ecological processes depends on the phenotypes of organisms, and thus patterns of evolved functional similarity (phylogenetically conserved or convergent traits) will influence the resulting phylogenetic community structure. In lichens, traits can play a paramount role in the assemblage of communities since these organisms are very sensitive to environmental changes. Thus it is reasonable to test whether variation in both traits and evolutionary origins of co-existing species is different from that expected by chance and depending on

Doi: 10.1111/jvs.12544

phylogenetic signal of traits considered (Kraft et al. 2007). When traits are conserved, communities of closely related species (phylogenetically clustered) and with similar functional traits (functionally clustered) may represent the effects of environmental filtering (Weiher & Keddy 1999; Cornwell et al. 2006; Kraft et al. 2007) and communities of distantly related species (phylogenetically overdispersed) and functionally different (functional overdispersion) may represent the effects of competition and biotic interactions in a broad sense (Kraft et al. 2007; Mayfield & Levine 2010; Pausas & Verdú 2010).

Although phylogenetic and functional methods have allowed us to understand the structure of communities of organisms from different kingdoms and of different trophic levels (Pausas & Verdú 2010), there are few studies on symbiotic organisms or lichenized fungi (Peay et al. 2010; Rincón et al. 2014; Liu et al. 2015; Montesinos-Navarro et al. 2015; Geedicke et al. 2016). So far in lichens, community ecology has relied on "traditional" measures of diversity, i.e. community traits such as richness and diversity, and how these metrics are affected by forest disturbance, latitudinal or altitudinal gradients, phorophyte species identity, land use, pollution or tree age (e.g. McCune et al. 2000; Belinchón et al. 2007; Johansson et al. 2007; Aragón et al. 2010a, b, 2012; Gjerde et al. 2012; Lamit et al. 2015; Suija & Liira 2017).

Concerning functional traits, several studies have analysed their relation with colonization, land use, forest structure, tree age, succession or climate in epiphytic lichens (Ellis & Coppins 2006; Stofer et al. 2006; Johansson et al. 2007, 2012; Marini et al. 2011; Giordani et al. 2012; Koch et al. 2013; Matos et al. 2015; Nelson et al. 2015; Bässler et al. 2016; Rubio-Salcedo et al. 2017). Further studies have focused on terricolous and saxicolous communities and the influence of micro- and macro- environmental variables on lichen traits (Giordani et al. 2013; Concostrina-Zubiri et al. 2014). Based on these studies, we can highlight several traits (e.g. growth form, type of photobiont and the reproductive strategy) having functional attributes as they have been related to climate, human disturbance and stand structure (e.g. Giordani et al. 2012).

In this study, we examine the phylogenetic and functional structure of lichen communities along an environmental gradient in beech forests in the Iberian Peninsula in order to study the assembly rules shaping these communities. Our hypotheses are that (1) epiphytic communities under adverse conditions may be phylogenetically and functionally clustered, as would be expected if traits are conserved and only closely related species of a subset of lineages possess the traits that allow them to survive; and (2) communities under favourable conditions may be phylogenetically and functionally overdispersed, as would be expected if competitive exclusion is shaping the composition of local communities.

## Methods

To study the phylogenetic and functional structure of lichen communities under different environments, we surveyed the species composition in Iberian beech forests, measured micro- and macro-environmental variables, collected trait data of lichens and built its phylogenetic tree, as explained below.

### Data collection

The study was carried out in beech forests along an environmental gradient in the Iberian Peninsula covering two contrasting biogeographic regions. Three areas were sampled from south to north (Appendix S1): (1) Central System (area 1), situated in the southern distributional limit of *Fagus sylvatica* in the Iberian Peninsula; (2) Iberian System (area 2), being an intermediate area between 1 and 3, representing the transition zone between Mediterranean and Atlantic regions; and (3) Cantabrian Mountains (area 3), the northernmost area. Areas 1 and 2 belong to the Mediterranean region (with a mediterranean climate characterized by a summer dry season), while area 3 belongs to the Atlantic region (with an oceanic climate characterized by the absence of a summer drought period). Area 3 is considered to offer the most favourable environmental conditions for the host tree and the associated lichens, while area 1 presents harsh environmental conditions. Area 2 is a transitional zone with less harsh conditions than those in area 1.

Field sampling followed Aragón et al. (2012). Three forests per area and five plots within each forest were selected. Within each plot, 12 trees were randomly selected and four 20 cm × 30 cm grids per tree were sampled (see Appendix S2 for further details).

### Environmental data

Tree DBH of all trees was measured. A neighbourhood index at tree level was used as an indirect measurement of forest density. Climatic variables at forest level (mean annual temperature, annual, winter and summer rainfall), tree diameter and neighbourhood index are available in Aragón et al. (2012).

### Phylogenetic analyses

In order to calculate the phylogenetic diversity indices, we constructed a phylogenetic tree with four molecular markers and all taxa found in the communities. The phylogenetic tree was calibrated based on dates previously obtained by Prieto & Wedin (2013) in order to construct a chronogram (Appendices S3 and S4). Details of the genetic markers used and the phylogenetic analysis are explained in Appendix S3.

### Trait data

Based on previous studies we selected three lichen traits that could mediate the response to environmental factors, thus playing a functional role. Growth form (crustose, fruticulose, foliose, squamulose or mixed forms) has been previously related to water uptake and loss (Larson & Kershaw 1976; Lange et al. 1986; Büdel & Scheidegger 2008), temperature (Nascimbene & Marini 2015) and to light availability (Giordani et al. 2012). Type of photobiont (cyanobacteria, green algae and *Trentepohlia*) is also related to water uptake (Lange et al. 1986; Giordani et al. 2013; Merinero et al. 2014) and climate (Marini et al. 2011; Nascimbene & Marini 2015). Furthermore, reproductive strategy (sexual or asexual) may represent an ecological trade-off between long-distance colonization and successful local establishment and could be related to environmental gradients (Ellis & Coppins 2006; Ellis 2012; Rapai et al. 2012; Nelson et al. 2015).

Phylogenetic signal or trait conservatism is recognized when closely related species tend to be more similar between them than expected by chance. We tested the phylogenetic conservatism of the growth form and type of photobiont. Since the reproductive strategy studied here is the state in which the species are present in the Iberian *Fagus* forests, and not the biological capacity of the species, the phylogenetic signal of this trait has not been studied. To test the phylogenetic signal of these multi-state traits we used Pagel's lambda approach with the help of the function 'fitDiscrete' in the Geiger package for R (Harmon et al. 2008; R Foundation for Statistical Computing, Vienna, AT). A lambda of 1 is indicative of phylogenetic signal in the trait under a Brownian motion model, while lambda of 0 indicates no signal. This method compares the likelihood of an evolutionary model with the observed lambda against that of a model where lambda is fixed to zero.

### Diversity indices

The maximum clade credibility tree (i.e. final chronogram; Appendix S4) was used to calculate the mean phylogenetic distance of taxa (MPD) and the mean distance to the nearest taxon (MNTD) at tree level (Webb et al. 2002; Hardy 2008). The phylogenetic distance between species pairs was computed with the function cophenetic in the picante R package (Kembel et al. 2010). Functional dissimilarity between species was computed with the Gower distance (Lepš et al. 2006). Calculation of MNTD and its standardized index NTI (known as Nearest Taxon Index) was performed in the picante R package (Kembel et al. 2010), and MPD and its standardized index NRI (known as Net Relatedness Index) using the melodic function (de Bello et al. 2016). NRI and NTI were calculated based on the phylogeny (phylogenetic NRI and NTI, NRI-P and NTI-P) and on the functional traits (functional NRI and NTI, NRI-F and NTI-F).

When species abundance is not phylogenetically structured, both MPD and MNTD combined with a null model randomizing species abundances within samples and maintaining richness have very good statistical power to detect community structure patterns (Hardy 2008; Götzenberger et al. 2016). In our case, species abundance was not phylogenetically structured according to Blomberg et al. (2003) (non-significant phylogenetic signal Blomberg's $K = 0.0007$, $P = 0.66$) and therefore we calculated the standardized MPD and standardized MNTD, with such a null model. Other randomization procedures to calculate NRI and NTI including taxon labels, frequency and independent swap were also tested.

We have used the average NRI and NTI over a set of sites (Areas), as proposed by Hardy (2008), and not the NRI and NTI within a site. This author also provides simulations on the statistical performance of these metrics under different null models. The combination of the metrics and null model we selected has a very good type I error rate when species abundances are not phylogenetically structured, as in our case. Values significantly higher than zero of NRI and NTI averaged across Areas indicate phylogenetic/functional overdispersion, while those lower than zero indicate phylogenetic/functional clustering.

To check the sensitivity of our results to the topological uncertainty of the phylogenetic tree, we used 100 randomly selected trees obtained with Beast (Drummond et al. 2012) and calculated one NRI and NTI for each tree (see Goberna et al. 2014 for a similar procedure). In all the analyses the conclusions were the same and therefore they are not shown.

Variations in functional trait composition have often been described quantitatively by trait averages over a community (de Bello et al. 2007), providing an indication of the most common traits in a community (Lepš et al. 2006). Thus, CWM, considering a continuous trait, represents the sum of each species trait value weighted by its relative abundance in the community (Lavorel et al. 2008). For multinomial traits, we calculated CWM at tree level as the sum of the cover of all species sharing a trait divided by the total species cover, representing the proportion of each individual trait category per community (i.e. mean trait values weighted with the abundance). Using species abundance will give more importance to dominant species, while a measure that considers only species occurrence (presence/absence data only) will give the same weight to all species (Kafer & Witte 2004).

Additionally, diversity (richness and Simpson index) and co-existence metrics (C-score) were calculated (Appendix S5).

### Data analysis

To test the effect of the gradient on the phylogenetic (NRI-P, NTI-P) and functional diversity (NRI-F and NTI-F) and on the CWM of communities we used a LMM for testing linear contrast using area as an ordered factor from north to south, with plots nested within forests and forests nested within areas as random factors. Significant linear contrasts with positive or negative *t*-values indicate, respectively, an increase or decrease of the dependent variable in response to the factor.

The effect of the climatic and the tree scale variables on the phylogenetic and functional structure (NRI-P, NRI-F, NTI-P, NTI-F) and on the CWM of communities was modelled using LMM. Elevation, mean annual temperature and summer rainfall were analysed with forests nested within areas in a first model at plot level. Tree diameter and neighbourhood index were added with forests nested within areas and plots nested within forests as random factors in a second model at tree level. Total and winter rainfall and elevation were not included in the models because they were highly correlated (setting the collinearity threshold to 0.7; Dormann et al. 2013) with summer rainfall (Pearson's correlation $r = 0.99$, $P < 0.001$; $r = 0.96$, $P < 0.001$; $r = -0.91$, $P < 0.001$). We carried out a selection of the best model explaining our data based on the AIC. We further calculated a marginal $R^2$ value for all models selected, providing an estimate of the variance explained by the fixed effects (Nakagawa & Schielzeth 2013). All statistical analyses were performed in R v 3.1.1, LMM were performed using lme function with nlme package, $R^2$ was calculated with MuMIn package, and post-hoc analyses of CWM were carried using Tukey's test.

Further, correlations between diversity and co-existence metrics, including richness, Simpson index, C-score and NRI were carried (see Appendix S5).

## Results

A total of 70 lichen species were found in the nine forests (Appendix S6). Richness and C-score increased with latitude but Simpson index did not (Appendix S5). The maximum clade credibility tree used to calculate the phylogenetic community structure metrics is depicted in Appendix S4. The results obtained for different randomization procedures used to calculate NRI and NTI, for both phylogenetic and functional diversity, were highly correlated (Pearson's correlation $r > 0.85$); thus we only present here results obtained with the first model (richness). We found strong evidence for phylogenetic conservatism for the two traits studied: growth form and photobiont type. The growth form was evolutionarily conserved as shown by the significant phylogenetic signal ($\lambda = 1.00$, $P < 0.0001$; likelihood ratio test), and similar results were found for the type of photobiont ($\lambda = 0.97$, $P < 0.0001$; likelihood ratio test).

### Phylogenetic and functional community structure

Phylogenetic and functional net related index (NRI and NTI) increased with latitude (Fig. 1), as the significant results obtained in the linear contrast show (*t*-values = 5.79 (NRI-P) and 6.71 (NTI-P), $P < 0.001$; *t*-values = 2.45 (NRI-F) and 3.08 (NTI-F), $P < 0.05$). These results indicate that taxa in area 1 (Central System) were phylogenetically more clustered (negative NRI and NTI values; Fig. 1) showing that the species in these communities are more similar than expected by chance (*t*-value = −5.97 (NRI-P), −6.71 (NTI-P), $P < 0.001$), while areas 2 and 3 (Iberian System and Cantabrian Mountains) showed positive NRI and NTI values, meaning that taxa were phylogenetically overdispersed (*t*-values = 4.84 (NRI-P), 5.47 (NTI-P), $P < 0.001$ in area 2; *t*-values = 5.79 (NRI-P), 6.71 (NTI-P), $P < 0.001$ in area 3). On the other hand, communities had a clustered functional structure in areas 1 and 2, showing that the species in these communities are functionally more similar in the studied traits than expected by chance (*t*-value = −2.71 (NRI-F), −1.9 (NTI-F), $P < 0.05$ in area 1; *t*-value = −1.16 (NRI-F), −1.19 (NTI-F), $P < 0.05$ in area 2), while species were functionally overdispersed in the northernmost area 3 (*t*-value = 2.45 (NRI-F), 3.08 (NTI-F), $P < 0.05$).

Based on AIC we obtained a model in which only summer precipitation was included. Thus, area was not significant per se and summer precipitation was the most relevant predictor for the phylogenetic and functional diversity of the communities at regional scale by decreasing NRI and NTI values (lower phylogenetic and functional diversity) with lower summer rainfall (Table 1). The fixed factors of this model explained between 40–43% of the observed variance for NRI (NRI-P, $R^2 = 0.41$; NRI-F, $R^2 = 0.43$) and between 17–29% for NTI (NTI-P, $R^2 = 0.175$; NRI-F, $R^2 = 0.29$). Richness and C-score was positively correlated with NRI values but Simpson index did not (Appendix S5).

Regarding traits individually, significant differences were found in the three areas in growth form for all categories, except for mixed forms (crustose: $t = 3.98$,

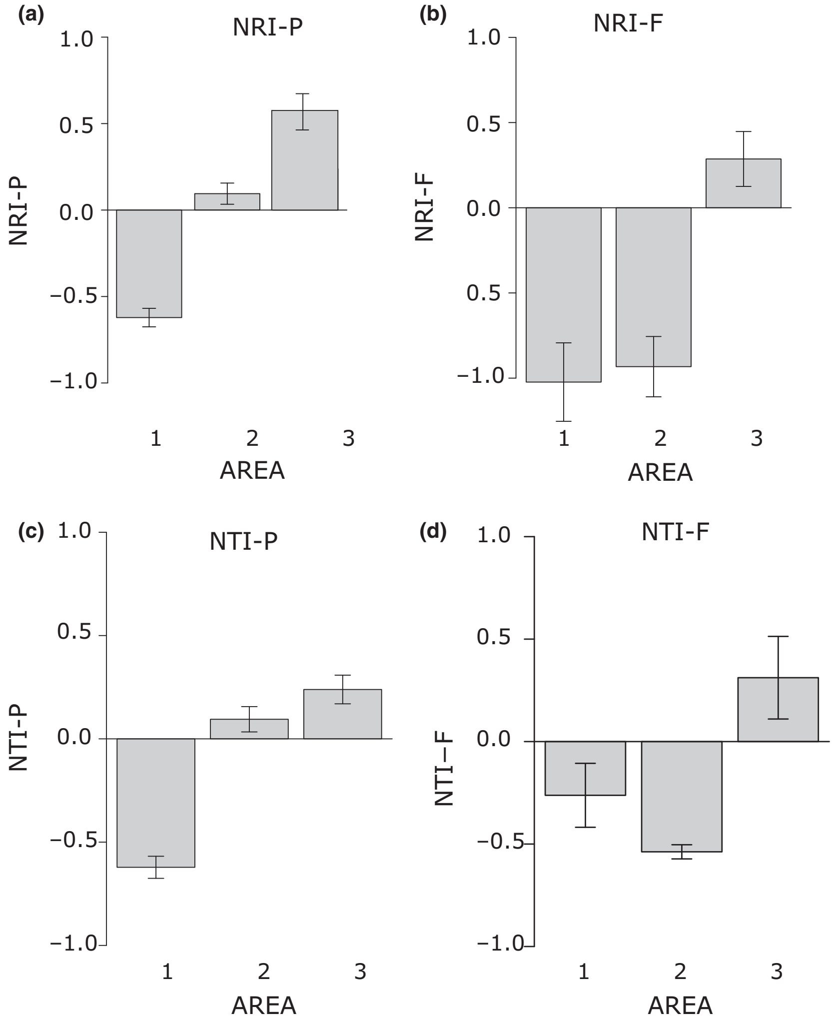

**Fig. 1.** Phylogenetic (**a**, **c**) and functional (**b**, **d**) community structure (mean NRI-P, NTI-P, NRI-F, NTI-F and SE (bars), *y*-axis) of each study area along a latitudinal gradient (Areas 1, 2 and 3). Negative values indicate phylogenetic or functional clustering, and positive values indicate phylogenetic or functional overdispersion.

$P < 0.001$; foliose: $t = -3.25$, $P < 0.05$; fruticulose: $t = -4.06$, $P < 0.001$; squamulose: $t = 2.71$, $P < 0.05$) in *Trentepohlia* and green photobiont except in cyanobacteria (*Trentepohlia:* $t = 7.66$, $P < 0.001$; green: $t = -2.67$, $P < 0.05$) and in the reproductive strategy ($t = -3.64$, $P < 0.05$; Fig. 2). We found a negative correlation of fruticulose species with summer rainfall and a positive relation between squamulose forms and summer rainfall (Table 1). For the type of photobiont, differences in species with *Trentepohlia* were positively related to summer rainfall, while those with green algae were inversely related to this latter factor (Table 1). Sexual reproduction strategy increased with higher values of summer rainfall and the asexual forms decreased (Table 1).

## Discussion

Our results show phylogenetically and functionally structured epiphytic communities along an environmental gradient including two distinct and contrasting biogeographic regions (i.e. Atlantic and Mediterranean) in the Iberian Peninsula. We found clustered communities in the distributional southern limit of the phorophyte species (*F. sylvatica*) and overdispersed communities in northern forests under more suitable environmental conditions (Table 2). Central communities are phylogenetically overdispersed but functionally clustered. This trend is related to an environmental gradient, and specifically with summer drought in the southern region, which is critical for these organisms (Pintado et al. 1997).

**Table 1.** Results from the LMM on net relatedness index and nearest taxon index (NRI-P, NTI-P, NRI-F and NTI-F) and CWM values. The data comprise the coefficient of variation in the model (Coef), SE of the estimator, *t*-statistic (*t*-value) and significance (*P*-value <0.05 in bold).

| | Summer Rainfall | | *P*-value |
|---|---|---|---|
| | Coef. (SE) | *t*-value | |
| NRI-P | 0.006 (0.001) | 2.95 | **0.005** |
| NRI-F | 0.011 (0.003) | 3.15 | **0.01** |
| NTI-P | 0.006 (0.001) | 3.78 | **0.01** |
| NTI-F | 0.004 (0.001) | 2.59 | **0.00** |
| Crustose | 0.001 (0.001) | 1.10 | 0.27 |
| Foliose | −0.001 (0.000) | −0.91 | 0.37 |
| Fruticulose | −0.0003 (0.000) | −3.55 | **0.001** |
| Squamulose | 0.000 (0.000) | 3.06 | **0.004** |
| Green Photobiont | −0.001 (0.000) | −3.34 | **0.000** |
| *Trentepohlia* | 0.001 (0.0001) | 9.94 | **0.000** |
| Asexual Reproduction | −0.003 (0.000) | −3.90 | **0.000** |
| Sexual Reproduction | 0.003 (0.000) | 3.90 | **0.000** |

Based on both phylogenetic and functional structure, and taking into account that the studied traits are phylogenetically conserved (see Kraft et al. 2007), our results suggest that epiphytic lichen communities are subjected to environmental filtering on trait selection under harsh environmental conditions (i.e. drought), promoting coexistence among species with successful strategies and favouring co-occurrence of closely related species at its Iberian southern limit. On the other hand, under less stressful conditions, in the northern communities (area 3), distantly related lichens tend to co-exist, suggesting that these communities are probably structured by processes such limiting similarity, possibly caused by the effect of biotic interactions like competition and facilitation.

However, convergence of traits may also reflect competitive interactions (Mayfield & Levine 2010). Biotic filtering is the process through which large clades are out-competed when competitive superiority is phylogenetically conserved, resulting in a phylogenetically and functionally clustered community structure (Mayfield & Levine 2010). These authors, among others, proposed including this biotic filtering together with the classical abiotic (habitat) filtering under the wider term "environmental filtering". The relative role of abiotic and biotic filtering in the organization of communities should depend on the role of the traits in the community and their relation with niche differentiation or competitive ability of shared resources (Herben & Goldberg 2014). Thus the traits studied here (growth form, type of photobiont and reproductive strategy) may be linked to acquisition of resources, being indicative of competitive exclusion, or may be related to physiological tolerances to local environmental conditions, being more indicative of an abiotic filter (Garnier et al. 2016).

In this context, thallus morphology is optimized for water uptake and loss and photosynthetic capacity (Larson & Kershaw 1976; Lange et al. 1986; Büdel & Scheidegger 2008). In the southern forests of the gradient, foliose and fruticulose forms were dominant while crustose forms dominated in the intermediate and northern forests. Several studies (e.g. Ellis & Coppins 2006; Ravera et al. 2006; Giordani et al. 2012; Matos et al. 2015; Nascimbene & Marini 2015) have found a similar pattern in different type of forests, with foliose and fruticulose lichens being more common in drier situations and crustose forms more abundant in humid situations. Fruticulose and foliose lichens have a high surface area to mass ratio (Larson & Kershaw 1976), so they can rehydrate very rapidly, providing an advantage to these growth forms to live in drier areas. However, this would result in supra-saturation in humid areas limiting the ecological success of these forms under higher precipitation (Green et al. 2008). In this respect, crustose lichens repel water by creating a hydrophobic layer in the medulla (Lakatos et al. 2006). Additionally, photobiont type interacts with growth form in controlling water relation strategies and photosynthetic capacity. The observed dominance of lichens with green photobionts in southern forests is congruent with the fact that under drier conditions maximum photosynthesis and re-activation may be achieved by green algal lichens at lower thallus water content (Lange 1988) and from water vapour alone (Lange et al. 1986). This supports better performance of green algal lichens in drier conditions, and even better when combined with foliose and fruticulose growth forms (also suggested by Nelson et al. 2015).

Lichens with *Trentepohlia* increased in northern forests, enhanced by rainy and warm climates, due to their photosynthetic optimum in shaded–warm and humid situations and their sensitivity to freezing (Kappen 1993; Nimis & Tetriach 1995). Marini et al. (2011) and Matos et al. (2015) found these results in Italy and along a gradient of aridity in the Iberian Peninsula, respectively, where lichens with *Trentepohlia* were more abundant in rainy regions or in areas exposed to a maritime influence, while they decreased in continental areas. Finally, the absence of differences in cyanobacterial lichens in the three areas could be related to different performance of these lichens, i.e. requirement for liquid water (Lange et al. 1986) for photosynthesis but a higher water-holding capacity than green algal species (Gauslaa & Coxson 2011). Furthermore, cyanolichens belong to different lineages of Ascomycota comprising a variety of growth forms and cyanobionts and thus inhabiting different environments ranging from humid and old growth forests to drylands (Jovan & McCune 2004; Zedda et al. 2011).

The pattern found in the reproductive strategy is somewhat confusing since it is related to dispersal ability and

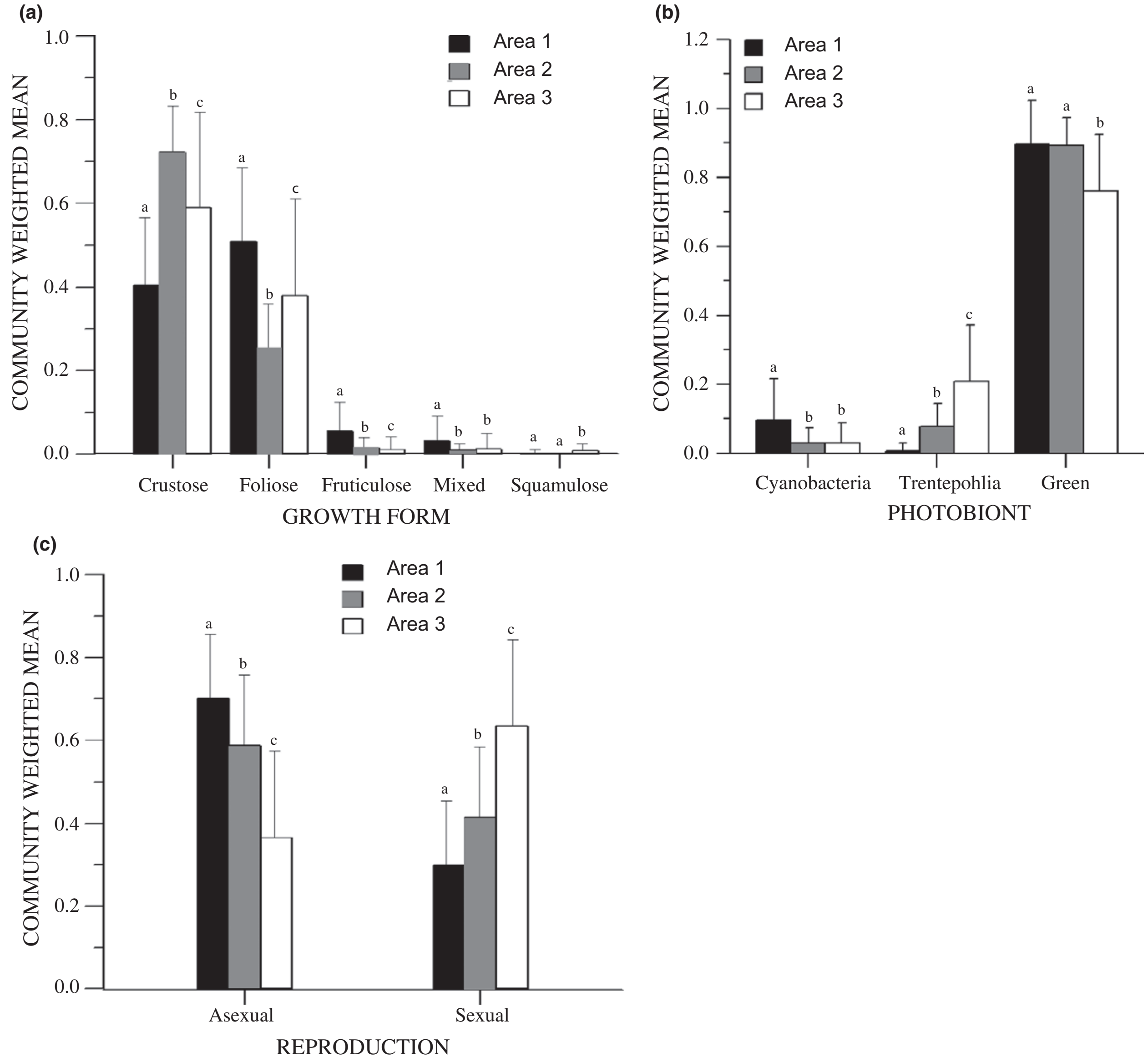

**Fig. 2.** Relative abundance of each trait category per area (CWM values with SE bars in the *y*-axis) for: (**a**) Growth form, (**b**) Type of photobiont and (**c**) Reproduction. Different letters above bars indicate significant differences between areas at $P < 0.05$ based on Tukey's test.

**Table 2.** Summary of main results found in the three areas.

| | Area 1 | Area 2 | Area 3 |
|---|---|---|---|
| Phylogenetic Structure | Clustered | Overdispersed | Overdispersed |
| Functional Structure | Clustered | Clustered | Overdispersed |

establishment and also to habitat filtering and facilitation. Local dispersal limitation of individuals may be a mechanism underlying the observation of co-existence of closely related competitors rather than competitive exclusion (e.g. Hurtt & Pacala 1995; Tofts & Silvertown 2002). However, limited dispersal is unlikely because propagules of lichen-forming fungi are widely and effectively dispersed at both small and large spatial scales and populations are not structured at and below the landscape level (Muñoz et al. 2004; Buschbom 2007; Lättman et al. 2009; Otálora et al. 2010). In relation to environmental conditions, we found dominance of lichens with an asexual reproductive strategy in southern forests and related to lower summer rainfall (i.e. in more stressful situations). Some studies have found a direct relationship between vegetative reproduction and stress conditions and inverse in relationship with sexual reproduction (Monte 1993; Martínez et al. 2012; Matos et al. 2015). The presence of isidia could be related to the function of water storage and conduction developed by isidia and between isidia (Rikkinen 1997). Moreover, under more stressful conditions the dispersal of both symbionts together (in asexual reproduction) may represent an advantage to avoid the risk of reproductive failure.

Although the traits studied here are related to a limiting abiotic factor (i.e. summer precipitation), they are also related to both acquisition of resources and physiological tolerances of lichens. Moreover, it is possible that the effects of biotic and abiotic filters on the functional structure of communities can occur concomitantly (Goberna et al. 2014), thus being difficult to separate. However, phylogenetic and functional clustering found in in the southern Iberian communities suggests that environmental filtering is stronger than competitive exclusion in determining co-existence (Webb et al. 2002; Mayfield & Levine 2010). The pattern found in the species co-existence also supports this idea, with higher species co-occurrence (aggregation) in clustered southern communities, and lower species co-occurrence in overdispersed northern areas (segregation), where competition is more important than environmental filtering. The opposite pattern found between the functional and phylogenetic structure in central forests could be related to the low number of traits considered, and the possibility that the phylogenetic analysis is capturing a signal that is not observed in the studied phenotypes.

## Conclusion

The results of this study show that different drivers of community assembly could be acting at the same time along an environmental gradient. The phylogenetic and functional clustered pattern found indicate that environmental filtering is an important assembly process structuring lichen communities in extreme habitats. On the other hand, overdispersed communities are consistent with the notion that biotic interaction, including competition or facilitation processes, cause divergence among co-existing species in more favourable environments. Thus trait selection, promoting co-existence among species with successful strategies, is shaping these communities.

## Acknowledgements

This research was supported by the Spanish Ministry of Education and Science (project BIOFRAG, CGL2007-66066-C04-4/BOS), the Ministry of Science and Innovation (project EPICON, CGL2010-22049) and the Ministry of Economy and Competitiveness (ECOMETAS, CGL2014-53840-REDT). We thank Marcelino de la Cruz, Marcos Méndez, Rosa Viejo, Luis Cayuela and Sonia Merinero for help with analysis, graphics and comments on the manuscript. We also thank reviewers and the editor for helping to improve the manuscript.

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## Supporting Information

Additional Supporting Information may be found in the online version of this article:

**Appendix S1.** Distribution of *Fagus sylvativa* in the Iberian Peninsula.

**Appendix S2.** Sampling details.

**Appendix S3.** Phylogenetic analyses.

**Appendix S4.** Maximum clade credibility chronogram for the species found in the three areas of the study (Ascomycota).

**Appendix S5.** Diversity and co-existence indices.

**Appendix S6.** Species with GenBank accesion numbers for the molecular markers used in the phylogenetic analyses.

# Graphical Abstract

The contents of this page will be used as part of the graphical abstract of html only. It will not be published as part of main.

We examined the phylogenetic and functional diversity of epiphytic lichen communities along an environmental gradient in beech forests in the Iberian Peninsula. Our results show phylogenetic and functional overdispersion at northern sites but phylogenetically and functionally clustered communities in the southern distributional limit of the host tree. Environmental filtering and species interactions regulate lichen communities differently under contrasting environmental conditions.