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## Loss of epiphytic diversity along a latitudinal gradient in southern Europe

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## ABSTRACT

Latitudinal gradients that involve macroclimatic changes can affect the diversity of several groups of plants and animals. Here we examined the effect of a latitudinal gradient on epiphytic communities on a single host species (*Fagus sylvatica*) to test the core–periphery theory. The latitudinal span considered, covering two biogeographic regions, is associated with major changes in rainfall during the dry season. Because bryophytes and lichens are poikilohydric, we hypothesized that their species richness and composition might vary at different latitudes. We also speculated how epiphytic communities may respond to future climate change. The present study was carried out in Spain, and three latitudes that cover the distributional range of *F. sylvatica* were selected. The presence/absence and coverage of epiphytic lichens and bryophytes were identified on 540 trees (180 in each zone). We found consistent south to north change in the total richness and in the richness of bryophytes and of lichens separately, all of which tend to increase at higher latitudes due to the presence of several hygrophytic species. Epiphytic composition also differed significantly among the three latitudes, and the similarity decreased when the latitudinal span was greater. In addition, high species turnover was driven by the increased rainfall at higher latitudes. We conclude that epiphytic communities have a similar pattern to the predictors of the core–periphery theory from populations, and they suffer a great impoverishment in species richness at lower latitudes, coincident with the southern boundary of the *F. sylvatica* distribution.

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## 1. Introduction

Species richness and turnover profoundly vary across the earth from the larger scale of latitude patterning to the smaller scale of microsite heterogeneity (Gaston, 2000; Hillebrand, 2004). A huge research effort has been focused on dissecting this topic, more specifically on elucidating the mechanisms and processes that control such variability (Koleff et al., 2003; Davidar et al., 2007). At large scales, a latitudinal gradient in species diversity is the most familiar of these patterns (Koleff et al., 2003; Gaston et al., 2007; Qian et al., 2009), and the underlying mechanisms are related to differences in climate, topography and dispersal limitations of the species (Condit et al., 2002; Leigh et al., 2004; Davidar et al., 2007).

As a general latitudinal pattern, species diversity tends to decline from low to high latitudes (Koleff et al., 2003; Gaston et al., 2007; Qian et al., 2009). However, there are some discrepancies because many reports support this conclusion while others have found no relationships (Mourelle and Ezcurra, 1997) or even opposite patterns (Andrew and Hughes, 2005; Qian and Ricklefs, 2007; Giordani et al., 2012). This variation might be related to differences in the taxa examined, the latitudinal span considered or the biogeographical regions involved (Koleff et al., 2003).

To advance our knowledge on this topic, we think that co-occurring processes need to be considered at contrasting spatial scales:

1. Obvious shifts in primary productivity can result from profound changes in the enveloping bioclimate, despite a small span in latitude. The sharp climatic transition between the Eurosiberian/temperate world of central Europe and the Mediterranean biogeographical region encompasses abrupt changes in diversity.
2. In the context of population ecology, the species richness at the community level can be thought to be subject to a pattern rather similar to that predicted by the core–periphery theory at the species level (Gaston, 2003). That is, communities at the center of their environmental envelopes should be more complex and diverse than those at the periphery where stressful conditions may limit their diversity and complexity. For instance, we would expect diversity and complexity in some communities in mild oceanic conditions to decrease sharply in a southerly direction, resulting in an “unexpected” impoverishment the more southern the latitude.
3. Finally, studying small scale variation that would be driven by stochasticity and assemblage processes operating at such scales would be very relevant (Ellis and Coppins, 2010). We would expect variation at such scales to be higher in those communities located at the center of their range distribution and lower at the edge.

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To evaluate how mechanisms that operate at these relatively smaller scales may be affected by variation in latitude, we have modeled the diversity response of a community of epiphytic lichens and bryophytes. Lichens and bryophytes are the most important epiphytic organisms in the forests of southern Europe, and the diversity and composition of the communities depend on numerous factors that operate at diverse spatial and temporal scales (Gignac and Dale, 2005; Ellis and Coppins, 2007). At a local level, epiphytic composition is related to microclimatic factors associated with forest structure (tree age, canopy cover, management intensity) and landscape, including the surrounding matrix and historical factors (Ellis and Coppins, 2007; Belinchón et al., 2009; Moning et al., 2009; Aragón et al., 2010a; 2010b). At a broader level, macroclimatic and orographic differences and dispersal limitations are important explanatory factors (Werth et al., 2005; Hauck and Spribille, 2005; Turner et al., 2006; Giordani and Incerti, 2008).

The physiologies of lichens and bryophytes are strongly coupled to ambient moisture and temperature conditions (Gignac, 2001; Green et al., 2008) so that their distributions are expected to be associated with climatic gradients (Gignac, 2001; Giordani and Incerti, 2008; Marini et al., 2011). Annual rainfall and its seasonality are important determinants of species richness and diversity in areas with seasonal climates, because dry season is an important constraint for many of these poikilohydric organisms (Gignac, 2001; Turner et al., 2006; Aragón et al., 2010b; Marini et al., 2011). Recently, Marini et al. (2011) found that epiphytic richness declined as seasonal drought increased across a latitudinal gradient in the Italian Peninsula (Marini et al., 2011). Similar results were obtained in other areas with water deficits; the species richness of bryophytes and liverworts was positively related to the amount of rain during the driest month (Turner et al., 2006). However, Giordani et al. (2012) found that lichen species richness was negatively correlated with latitude, regardless of forest type, with high values at southern sites. A comparison of species richness and species composition among regions with different climates could provide insights into the mechanisms that regulate richness and composition.

Increases in temperature and changes in precipitation are important determinants of bryophyte and lichen distributions (Gignac, 2001; Giordani and Incerti, 2008). Ecological responses of both flora and fauna to recent climate change are clearly visible (Walther et al., 2002); shifts in their distribution poleward in latitude or in elevation are one of the most documented processes (Walther et al., 2002; Root et al., 2003; Giménez-Benavides et al., 2011). Rapid climate change can alter community composition and therefore the interaction among organisms as well as between an organism and its abiotic environment (Walther et al., 2002). Understanding how the structure of current communities varies along a latitudinal gradient will be an important predictive tool for assessing how these communities will respond to climatic changes in the future.

We analyzed the response of epiphytic communities (lichen and bryophytes) on a single host tree species (*Fagus sylvatica*) along a latitudinal gradient. The latitudinal span considered covers two biogeographic regions: the Atlantic region with optimal macroclimatic conditions for the development of the host tree, and the Mediterranean region where beech has its southern distributional limit. By comparing epiphytes on a single host species, we were able to control for habitat differences, other than climate, as much as possible. We hypothesized that differences in species richness and species composition under similar forest structures would be due to differences in climatic conditions linked to a latitudinal gradient. Specifically, we aimed to address the following questions: Do species richness and species turnover decrease at lower latitudes concurring with the periphery of the distribution of *F. sylvatica*? Can the stressful conditions of the periphery influence the most demanding species of bryophytes and lichens? Are macroclimatic conditions the main factor controlling epiphytic communities along a latitudinal gradient?

## 2. Materials and methods

### 2.1. Sampling design and data collection

*F. sylvatica* was selected as the focal host tree species because it has an extensive latitudinal range extending from central to northern Spain (Costa et al., 2001). Beech forests are mainly distributed in central and northern Europe, and central Spain constitutes the southern distributional limit in Europe (Costa et al., 2001). Although the selected latitudinal span is not very large (500 km), it covers two biogeographic regions that differ greatly in climate: the Atlantic region, with an oceanic climate characterized by the absence of a summer drought period, and the Mediterranean region, with a Mediterranean climate, with a dry season that is quite variable in length (EEA, 2009). Macroclimatic conditions of the Spanish Atlantic region are similar to those described for the core distribution of *F. sylvatica*.

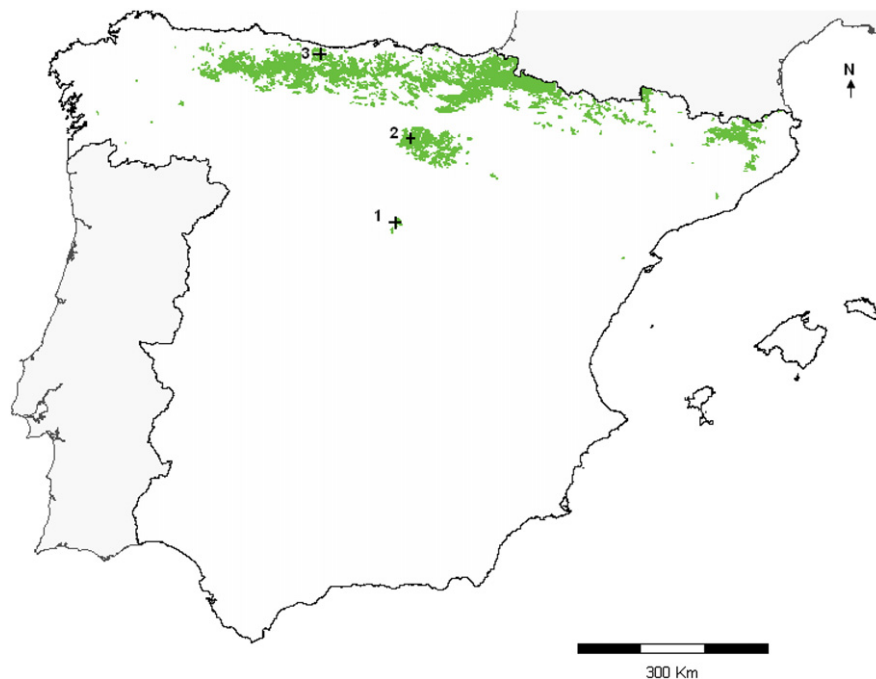
Three zones were selected to span almost the entire distributional range of *F. sylvatica* (Fig. 1), from south to north: Central System (Zone 1) (41° 13' N), Iberian System (Zone 2) (42° 15' N) and Cantabrian Mountains (Zone 3) (43° 10' N) (Fig. 1). The substrate of zones 1 and 2 is composed of siliceous slates, and the substrate of zone 3 is composed of limestone and sandstones. Within each zone, three replicate beech forests were selected. These forests have not been subjected to any forest practices (firewood, timber extraction, livestock) for more than 50 years, and they are mostly within protected areas. In addition, the selected forests were similar in tree density and tree diameter to partially avoid any effect of forest stand on the epiphytic species (Moning et al., 2009; Aragón et al., 2010b). The distance between forests within a zone was over 1 km. Five plots (200×200 m) at different altitudes and orientations were selected within each forest, and 12 trees were sampled within five plots. Only mature trees (diameter at breast height up to 32.5 cm) that supported communities of *Lobarion pulmonariae* (Burgaz et al., 1994a), an indicator of a well-preserved forest, were selected (Coppins and Coppins, 2002). Additionally, a neighborhood index at tree level was obtained as an indirect measurement of forest density (Ramírez, 2006). This index was calculated as the average ratio between the distance and diameter of the four nearest trees in the four exposure orientations (N, S, E, W) from the sample tree.

Climatic variables (mean annual temperature, annual rainfall and summer rainfall) at forest level were generated using CLIMOEST (Sánchez-Palomares et al., 1999). We assumed that these variables are the most important climatic variables affecting the distribution of lichens and bryophytes (Turner et al., 2006; Aragón et al., 2010b; Marini et al., 2011). Additionally, a xeric index (Lang aridity index) was calculated as the ratio between annual rainfall and mean annual temperature. The average measurements for each zone are in Table 1.

We determined the species richness and composition of epiphytic lichens and bryophytes on 540 trees (180 in each zone). Following the method of Belinchón et al. (2007), we established four 20×30 cm grids on the bark of each selected tree: at breast height, at the tree base, and on the northern and southern aspects. We used the means of five data sets (lichen composition, total species richness, lichens, bryophytes and cyanolichens' richness) for a given sample position. The total species richness was defined as the total number of species found in the four grids per tree. For the lichen composition, we calculated the mean estimated cover of each species (% of the grid area) for the four sample grids. We calculated the total species cover per tree (as percentage of the grids) using the same methods.

### 2.2. Data analyses

The effect of climatic variables (mean annual temperature and summer rainfall) and tree scale variables (tree diameter and neighborhood index) on the community traits at the tree level was



**Fig. 1.** Distribution of *Fagus sylvatica* in the Iberian Peninsula. Study area showing the three zones. 1+: Zone 1 (Central System); 2+: Zone 2 (Iberian System); 3+: Zone 3 (Cantabrian Mountains).

modeled by fitting Generalized Linear Mixed Models (GLMMs) (McCullagh and Nelder, 1989). The community traits were the total species richness, and separately the richness of lichens, bryophytes and cyanolichens. This modeling approach was chosen because our data had a hierarchical structure with trees nested within plots, plots nested within forests and forests nested within zones. We analyzed the data using a multilevel approach and, when necessary, considered plots and forests as random factors and applied mixed modeling (Verbeke and Molenberghs, 1997). Zone was also initially included in the models, but none of the response variables were significantly related to it, so it was removed from the models to be as parsimonious as possible. Predictors were included as explanatory variables (fixed factors), and plot and forest were included as random sources of variation. Effects of random factors were tested using the Wald Z-statistic test. All GLMM computations were performed using SAS Macro program GLIMMIX, which iteratively calls SAS Procedure Mixed until convergence (GLIMMIX ver. 8 for SAS/STAT). In order to prevent multi-collinearity problems some climate variables (xeric index and annual rainfall) were not included in the models because they showed high correlations with summer rainfall and mean annual temperature.

Epiphytic composition among zones was compared using version 6.1.11 of the PRIMER multivariate statistical analysis software (Anderson et al., 2008). In this analysis, the experimental design

included three factors: zone (three levels, fixed factor), forest (three levels, random factor nested within zone), and plot (five levels, random factor nested within forest) with 12 replicate trees for each plot. The cover data (percentage cover by each lichen per tree) were  $\log_{10}(x + 1)$ -transformed to account for contributions by both rare and abundant taxa. We used the Bray–Curtis distance measure.

To test whether the three zones had significantly different compositions of epiphytic species and to detect the effects of forest and plot variability, we performed a three-factor permutational multivariate analysis of variance (PERMANOVA) on the cover data (Anderson et al., 2008). To assess species similarity among the different zones, we performed additional pairwise PERMANOVA tests (Anderson et al., 2008). We also calculated the Bray–Curtis dissimilarity within zones as a measure of species turnover. For all tests, we allowed 9999 random permutations under the reduced model.

### 3. Results

#### 3.1. Characterization of the patches

Environmental variables are summarized in Table 1. We found no significant differences among the three zones in relation to their forestry variables (neighborhood index and tree diameter). However, environmental variables (summer precipitation, total precipitation, average temperature, xeric index) differed significantly (Table 1). In addition, the selected latitudinal range corresponded to a climatic range.

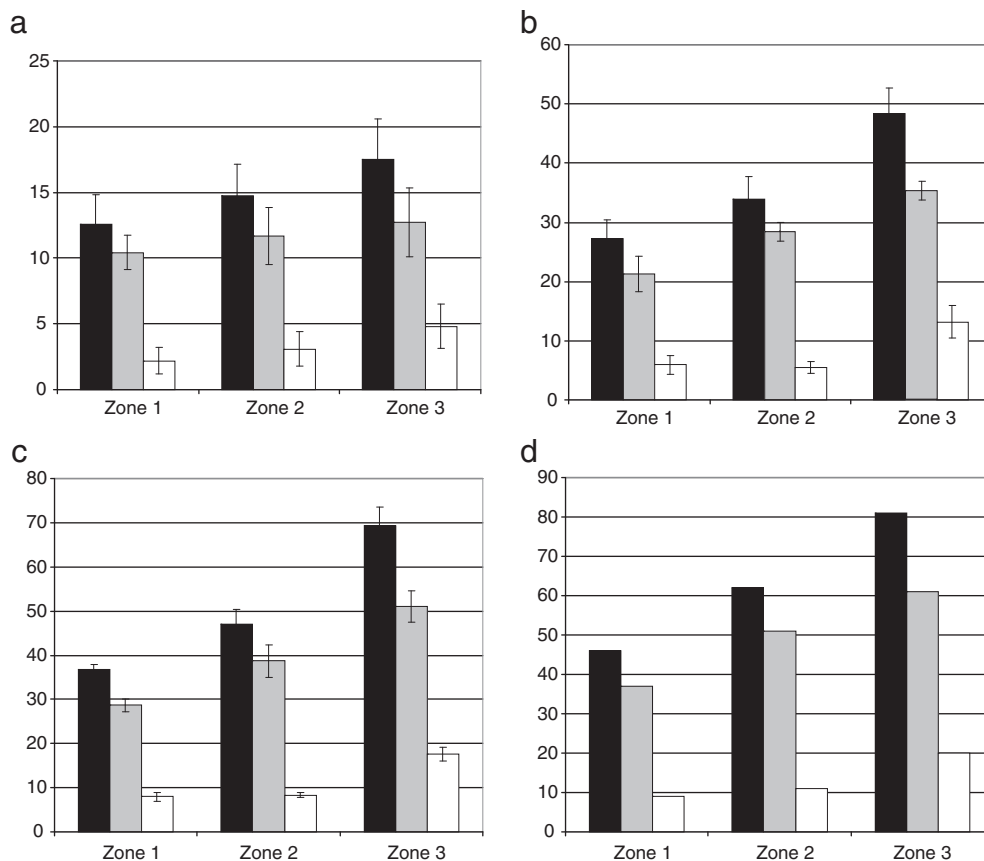
#### 3.2. Species diversity

A total of 95 epiphytic species (74 lichens and 21 bryophytes) were identified on the 540 trees (Appendix A). The total number of species at all levels (tree, plot, forest, zone) was higher when the latitude increased (Fig. 2). Similar trends were observed for lichens and bryophytes separately (Fig. 2). A total of 46 species were found in zone 1, 62 species in zone 2 and 81 species in zone 3. We found 29 exclusive species in zone 3, but only four exclusive species in zone 1 and zone 2 (Appendix A).

**Table 1**

Means  $\pm$  SD for the environmental variables grouped by the three zones considered. P: level of significance. Zone 1: Central System; Zone 2: Iberian System; Zone 3: Cantabrian Mountains.

	Zone 1	Zone 2	Zone 3	P
Elevation (masl)	1493.73 $\pm$ 117.96	1422.13 $\pm$ 16.18	873 $\pm$ 61.06	0.061
Mean annual temperature ( $^{\circ}$ C)	8.30 $\pm$ 0.68	7.4 $\pm$ 0.11	9.19 $\pm$ 0.13	0.039
Annual rainfall (mm)	967.13 $\pm$ 61.47	1097.2 $\pm$ 25.50	1499.8 $\pm$ 78.16	0.027
Summer rainfall (mm)	107.33 $\pm$ 8.13	145.33 $\pm$ 1.93	213.93 $\pm$ 9.37	0.027
Xeric index (mm/ $^{\circ}$ C)	117.78 $\pm$ 16.35	148.31 $\pm$ 4.45	163.31 $\pm$ 9.12	0.027
Tree diameter (cm)	43.64 $\pm$ 6.87	44.50 $\pm$ 6.20	45.66 $\pm$ 6.53	0.353
Neighborhood index	0.34 $\pm$ 0.23	0.40 $\pm$ 0.26	0.37 $\pm$ 0.20	0.430



**Fig. 2.** Total species richness (black color), lichen (gray color) and bryophyte species richness (white color) in the three zones at (a) tree level, (b) plot level, (c) forest level and (d) zone level. Values represent the means ( $\pm$ SD).

Results of the mixed models showed that the most relevant predictor of the epiphytic communities at regional scale was summer rainfall (Table 2). The random variable forest had no significant

effect in any case, while plot exerted a significant influence in all cases (Table 2).

**Table 2**

Results of the Generalized Linear Mixed Models on some community traits. Coef.: coefficient of the variable in the model. S.E.: standard error. The random variable forest was non-significant in all cases, while plot variable was significant: total species richness (Z-value = 2.36, Prob. Z = 0.011), lichen species richness (Z-value = 2.27, Prob. Z = 0.011), bryophyte species richness (Z-value = 2.09, Prob. Z = 0.018) and cyanolichen species richness (Z-value = 3.09, Prob. Z = 0.001). Tree diameter and the neighborhood index were at tree level, while summer rainfall and mean annual temperature were at forest level.

Richness	Coef. (S.E.)	F-value	P-value
Total species			
Tree diameter	-0.027 (0.022)	1.58	0.210
Neighborhood index	-0.371 (0.810)	0.21	0.648
Summer rainfall	0.056 (0.011)	19.23	<b>0.002</b>
Mean annual temperature	0.261 (0.597)	0.190	0.676
Lichens			
Tree diameter	-0.031 (0.018)	2.96	0.086
Neighborhood index	-0.411 (0.660)	0.39	0.534
Summer rainfall	0.031 (0.010)	8.90	<b>0.024</b>
Mean annual temperature	0.021 (0.566)	0.00	0.972
Bryophytes			
Tree diameter	0.001 (0.003)	0.14	0.713
Neighborhood index	0.018 (0.093)	0.04	0.850
Summer rainfall	0.008 (0.003)	6.44	<b>0.040</b>
Mean annual temperature	-0.122 (0.159)	0.59	0.471
Cyanolichens			
Tree diameter	0.003 (0.003)	0.85	0.357
Neighborhood index	0.065 (0.126)	0.27	0.603
Summer rainfall	0.003 (0.006)	0.20	0.667
Mean annual temperature	-0.465 (0.197)	4.29	0.077

P-value < 0.05 (bold).

### 3.3. Species composition

Multivariate statistical analyses showed that epiphytic composition was structured according to the different spatial scales, and a large component of variation was associated with the spatial scale of the zones (Table 3). The subsequent pairwise test revealed significant differences in epiphytic composition between all three zones, and the dissimilarity between zones increased with an increase in the latitudinal span (Table 4). Results of the PERMANOVA test showed that the highest similarity values for species composition within a zone were associated with the lowest latitudes: zone 1 (55.59%), zone 2 (44.93%) and zone 3 (38.22%). Therefore, species turnover was greater at higher latitudes.

## 4. Discussion

Our results demonstrated changes in epiphytic communities along a latitudinal gradient on a single host tree species (*F. sylvatica*) within comparable habitat types. However, latitude is not the direct cause of

**Table 3**

Results of the three-factor PERMANOVA analysis by zone, forest and plot.

Source	df	MS	Pseudo-F	P	CV (%)
Zone	2	1.4278E5	4.699	0.0001	26.72
Forest (Zone)	6	30,656	6.709	0.0001	21.36
Plot (Forest (Zone))	37	4704.1	4.826	0.0001	17.86
Residual	494	974.76			31.22
Total	539				



**Table 4**

Results of pairwise PERMANOVA test between zones. Dissimilarity (%) (Bray–Curtis index) and level of significance.

Source	Dissimilarity (%)	P
Zone 1 vs Zone 2	62.40	0.0082
Zone 1 vs Zone 3	76.14	0.0002
Zone 2 vs Zone 3	66.26	0.0004

the pattern (only 2° of latitudinal span); latitude likely is a surrogate for another factor or set of factors affecting the biology and life forms of the organisms (Koleff et al., 2003). For lichens and bryophytes, the factors are related to solar radiation, temperature and water availability (Gignac, 2001; Hauck, 2011); the latitudinal span considered in this study is associated with major climate changes, particularly in water availability.

Differences in rainfall affect the host species as well as the lichens and bryophytes. Beech forests have an Atlantic distribution in Europe, and the southern fringe of this biogeographic region is situated in northern Spain, where the climate is optimal for beeches (Costa et al., 2001). Climatic conditions in more southern zones (Central Spain) are different, with lower annual and summer precipitation and a longer drought period. Under these climatic conditions, beech trees are closer to their range limits, and their populations tend to be smaller and more isolated (Hernández-Bermejo and Sáinz-Ollero, 1978; Belinchón et al., 2009). As we expected, epiphytic communities have a pattern similar to those of the predictors of the core–periphery theory for populations (Gaston, 2003), and they become impoverished at lower latitudes in concurrence with the range limit of the host tree species (*F. sylvatica*). The higher levels of similarity between epiphytic compositions at low latitudes also suggest either that the species are more dispersal-limited or that more stressful conditions at the periphery of their distribution may limit their diversity and complexity. These higher similarity values can also indicate that variables linked with the quality of the landscape, such as the distance between forest and the surrounding matrix, might limit or favor the dispersal of propagules of lichens and bryophytes (Snäll et al., 2005; Löbel et al., 2009).

Species richness increased with an increase in the rainfall in the dry season along the latitudinal gradient. Marini et al. (2011) noted that at the regional scale, variation in the duration and quantity of rainfall is an important correlate of species richness. Water stress during the dry season is probably a constraint for the more hygrophytic lichens and bryophytes and excludes drought-intolerant species (Gignac, 2001; Turner et al., 2006; Aragón et al., 2010b). In southern Europe, humidity is critical in these systems especially during the summer season when temperatures become high enough for efficient physiological activity in these poikilohydric organisms (Pintado et al., 1997). Although lichens and bryophytes are desiccation-tolerant, variations in their degree of tolerance are related to habitat (Proctor et al., 2007; Kranner et al., 2008). In this sense, species growing in moist habitats with more humid conditions tend to be less tolerant than those growing in more xeric sites (ref. in Kranner et al., 2008).

Lichens with cyanobacteria are strongly dependent on the amount of atmospheric moisture (Jovan and McCune, 2004; Aragón et al., 2010b; Marini et al., 2011), because their photobionts need liquid water for activating photosynthesis (Lange et al., 1993). However, contrary to this expectation, we found no distinct south to north gradient in cyanolichen richness. Some authors have shown that not all cyanolichens have the same environmental requirements and respond differently to water stress (ref. in Kranner et al., 2008). Using a selective cutting experiment that affected evapotranspiration, irradiation and wind speed, Hedenås and Ericson (2003) showed different responses in the vitality, growth and damage of three cyanolichens. The thalli of *Collema* species grew slower and were fragmented as a consequence of their decreased size, while those of

*Leptogium saturninum* were less affected (Hedenås and Ericson, 2003). Recently, Aragón et al. (2010a; 2010b) showed that typical cyanolichens of forest environment may appear in open woodlands, but in the more favorable habitats (tree bases, northern slope of the tree trunks, or linked to bryophytes), where direct solar radiation is lower and the moisture retention is greater.

The similarity of the species composition between different zones decreases when the distance increases, and the high levels of species turnover (Bray Curtis similarity) along the latitudinal gradient are driven by an increase in rainfall during the dry season. Differences in rainfall will cause some species that have lower humidity requirements to be replaced by more hygrophytic species in a positive gradient of moisture (Jovan and McCune, 2004; Marini et al., 2011). In Mediterranean Spain, Burgaz et al. (1994a) found great differences in species composition on *Quercus* spp. in a latitudinal gradient, with a zone of inflection in the Central System. In our case, the differences between the three zones are due to the presence of more hygrophytic species in zones where the rainfall is higher (e.g. *Lobaria amplissima*, *Pannaria rubiginosa*, *Sphaerophorus globosus*, *Sticta limbata*, *Hypnum cupressiforme*, *Isothecium alopecurioides*, *Neckera complanata*). Additionally, we found another group of species with broad ecological requirements that increased their frequency at lower latitude (e.g. *Nephroma laevigatum*, *N. resupinatum*, *Peltigera collina*). Burgaz et al. (1994b) found that these species should be closest to its ecological optimum mainly associated to beech forests within the Mediterranean Iberian Peninsula (zones 1 and 2).

However, small-scale predictors (e.g. tree age and bark characteristics) may also exert an influence over species abundance at higher latitudes. *F. sylvatica* is a deciduous tree with a very smooth bark (Costa et al., 2001). Tree size is a major determinant of lichen dynamics, which is mainly related to the availability of different microhabitats, including bark crevices, porosity, roughness, the time available for colonization, and the increased surface area available with the tree growth (Ranius et al., 2008; Belinchón et al., 2011). In the case of *F. sylvatica*, tree growth may be slower under more xeric conditions (e.g. rocky hillsides and shallow soils at higher altitudes) (Costa et al., 2001) compared to optimum conditions in the North (e.g. deeper soils at lower altitudes) (Costa et al., 2001). Probably, the younger trees at higher latitude promote a more suitable habitat (smooth bark) for *Lecanora* species. On the contrary, *Antitrichia curtispindula* increased at lower latitudes, partly due to the bark roughness of the older trees.

Finally, an important part of the variability (found by ANOVA, PERMANOVA) was at the forest, plot and tree levels. At forest level, variability might be related to the size of forest patches, orographic situation, altitude or orientation (Gignac and Dale, 2005; Jürjado et al., 2009). The variability at plot level might be related to small changes in the canopy cover, orientation or inclination of the plots, because forest patches are heterogeneous in structure (Turner et al., 2006; Aragón et al., 2010b). At tree level, differences in size, roughness or slope of the trees might explain part of the variability (Fritz et al., 2008; Ranius et al., 2008). Epiphytic differences were also observed between tree base and tree breast height. Species on the tree bases (e.g. *Lepraria*, *Nephroma*, *Peltigera*, *Pterogonium*, *Zygodon*) are closely related with low solar radiation and high water availability, while photophytic species (e.g. *Flavoparmelia*, *Parmelia*, *Parmelina*) rather grow at breast height, in a drier microclimate conditions (Wirth et al., 2004).

#### 4.1. Potential impact of climate change on epiphytic communities

In southern Europe, climate models predict increases in temperature of 3–6 °C and decreases in precipitation up to 20% (IPCC, 2008). In the present work, richness and cover of the more hygrophytic species increased at higher latitudes, and 29 species were exclusive to the north. Most of these species grow inside forests under more humid conditions and tend to have very low tolerance to desiccation (Kranner et al., 2008). On the other hand, some of these species are

host-specific or, at less, grow mainly in beech forests. As the climate continues to warm, these species may potentially be the most vulnerable to local extinction and will be forced to shift their geographical range to higher latitudes in conjunction with their host species. Predictive response models for British lichens to climate change scenarios showed a loss of bioclimatic space for northern species (Ellis et al., 2007). Projections for northern-montane and northern-boreal species showed a decline in lichen incidence in response to increased temperature (e.g. warmer winters), in favor of more competitive and generalist species (Ellis et al., 2007). A similar conclusion might be reached for the most hygrophytic species (e.g. *Lobaria virens*, *Mycobilimbia pilularis*, *S. globosus*, *S. limbata*, *H. cupressiforme*, *I. alopecurioides*) that mainly grow inside beech forests of northern peninsular areas and are less tolerant to an increase in temperature linked to a decline in rainfall.

Alternatively, we think that species found in a broad range of latitude could be more resistant to a changing climate. Many of these species are cosmopolitan and may have the flexibility to move between hosts or to higher latitudes. In this sense, models developed by Ellis et al. (2007) predicted an increase in the bioclimatic span for the southern, widespread species, and similar trends were documented for the lichen flora of the Netherlands where tropical-warm species are increasing (van Herk et al., 2002). In our case, species such as *Parmelia serrana*, *P. collina*, *A. curtispindula* or *Pterogonium gracile* might have patterns similar to those shown by Ellis et al. (2007).

We conclude that species richness and species turnover are driven by climate at a regional scale. The latitudinal gradient linked to the increased water availability in the dry season appears to drive the changes in epiphytic communities. The absence of the more hygrophytic species at low latitudes explains the impoverishment of the communities at the periphery of the distribution of the host tree species (*F. sylvatica*). Changes in rainfall and temperature can severely affect the structure of epiphytic communities and lead to the disappearance of species at local level.

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**Appendix A**

Number of trees on which each species appears in the three zones. Base = tree base; BH = tree breast height; +: cyanolichens. Zone 1: Central System; Zone 2: Iberian System; Zone 3: Cantabrian Mountains. \*: The species only occurs in one zone.

Species	Zone 1		Zone 2		Zone 3	
	Total	Base BH	Total	Base BH	Total	Base BH
<i>Lichens</i>						
<i>Anaptychia ciliaris</i> (L.) Körb.	11*		1	11		
<i>Arthonia cinnabarina</i> (DC.) Wallr.					24*	3 22
<i>Arthonia didyma</i> Körb.					19*	1 18

**Appendix A (continued)**

Species	Zone 1		Zone 2		Zone 3	
	Total	Base BH	Total	Base BH	Total	Base BH
<i>Lichens</i>						
<i>Arthonia radiata</i> (Pers.) Ach.	32	10	24	109	12	98 96 5 93
<i>Bacidia incompta</i> (Hook.) Anzi	2	0	2	1	0	1 3 0 3
<i>Bacidia rubella</i> (Hoffm.) A. Massal	27	11	20	24	18	8 51 36 41
<i>Biatora vernalis</i> (L.) Fr.				6	6	0 25 18 8
<i>Bryoria fuscescens</i> (Gyeln.) Brodo & D.Hawksw.	4	1	3	4	0	4 1 0 1
<i>Buellia disciformis</i> (Fr.) Mudd	41	9	38	56	8	49 34 9 26
<i>Chromatochlamis muscorum</i> (Fr.) H. Mayrhofer & Poelt						13 6 10
<i>Cladonia chlorophaea</i> (Flörke ex Sommerf.) Spreng.	58	54	9	23	19	6 7 7 0
<i>Cladonia fimbriata</i> (L.) Fr.				43	38	8 32 23 11
+ <i>Collema flaccidum</i> (Ach.) Ach.						5* 0 5
+ <i>Collema nigrescens</i> (Huds.) DC.	14	8	12	35	15	22 20 6 15
<i>Evernia prunastri</i> (L.) Ach.	14	1	14	22	7	17 1 0 1
<i>Flavoparmelia caperata</i> (L.) Hale				3	0	3 33 4 29
<i>Graphis elegans</i> (Sm.) Ach.				6	0	6 19 1 18
<i>Graphis scripta</i> (L.) Ach.				58	20	51 116 39 88
<i>Heterodermia obscurata</i> (Nyl.) Trevis.						37* 3 34
<i>Lecanora argentata</i> (Ach.) Malme	77	18	69	152	53	123 137 38 109
<i>Lecanora carpinea</i> (L.) Vain.	18	4	16	8	2	8
<i>Lecanora chlorotera</i> Nyl.	6	1	5	31	7	26 51 13 39
<i>Lecanora glabrata</i> (Ach.) Malme				123	35	91 37 7 32
<i>Lecanora intumescens</i> (Rebent.) Rabenh.	18	4	15	39	3	37 52 4 48
<i>Lecanora muralis</i> (Schreb.) Rabenh.				4	4	0 17 17 0
<i>Lecanora pulicaris</i> (Pers.) Ach.				4*	0	4
<i>Lecidea hypoptella</i>				5*	1	4
<i>Lepraria incana</i> (L.) Ach.	81	62	40	76	69	33 95 88 43
+ <i>Leptogium aragonii</i> Otálora				2	2	0 16 4 15
+ <i>Leptogium lichenoides</i> (L.) Zahlbr.	5	5	1	3	3	0
+ <i>Leptogium saturninum</i> (Dicks.) Nyl.	1	0	1	7	4	4 13 3 11
+ <i>Lobaria amplissima</i> (Scop.) Forssell				54	47	15 79 62 27
+ <i>Lobaria pulmonaria</i> (L.) Hoffm.	165	121	119	164	94	122 142 49 124
+ <i>Lobaria virens</i> (With.) J.R.Laundon						7* 1 6
<i>Melanelixia fuliginosa</i> (Fr. ex Duby) O. Blanco et al.	77	8	72	71	6	70 83 6 79
<i>Micarea prasina</i> Fr.						4* 4 0
<i>Mycobilimbia pilularis</i> Körb.) Hafellner & Türk						11* 8 3
<i>Nephroma laevigatum</i> Ach.	31	28	9	3	3	0
+ <i>Nephroma parile</i> (Ach.) Ach.	54	47	9	26	24	4 3 2 1
+ <i>Nephroma resupinatum</i> (L.) Ach.	55	48	16	51	44	18 10 7 3
<i>Normandina pulchella</i> (Borrer) Nyl.						24* 12 16
<i>Ochrolechia pallescens</i> (L.) A. Massal.	7	1	7	20	5	18 2 0 2
<i>Ochrolechia turneri</i> (Sm.) Hasselrot	15	9	8	33	14	21 17 5 14
<i>Opegrapha atra</i> Pers.						6* 3 4
<i>Opegrapha varia</i> Pers.						6* 0 6
+ <i>Pannaria conoplea</i> (Ach.) Bory						8* 3 7
+ <i>Pannaria rubiginosa</i> (Ach.) Bory						21* 7 17
<i>Parmelia saxatilis</i> (L.) Ach.				81	31	57 2 0 2
<i>Parmelia serrana</i> A. Crespo, M. C. Molina & D. Hawksw.	149	70	117	140	41	112 10 0 10
<i>Parmelina tiliacea</i> (Hoffm.) Hale	63	7	59	16	4	15
+ <i>Parmeliella triptophylla</i> (Ach.) Müll.Arg.	5	5	0			23 18 5
<i>Parmotrema perlatum</i> (Huds.) M. Choisy						124* 53 91
+ <i>Peltigera collina</i> (Ach.) Schrad.	80	71	17	30	28	4 3 3 0
+ <i>Peltigera neckeri</i> Müll.Arg.				3*	3	0
<i>Pertusaria albescens</i> (Huds.) M. Choisy & Werner	7	2	6	2	1	2 12 6 6
<i>Pertusaria amara</i> (Ach.) Nyl.	169	86	103	180	39	152 136 21 125

Appendix A (continued)

Species	Zone 1		Zone 2		Zone 3	
	Total	Base BH	Total	Base BH	Total	Base BH
<i>Lichens</i>						
<i>Pertusaria coronata</i> (Ach.) Th. Fr.	43*	20	31			
<i>Pertusaria flavida</i> (DC.) J. R. Laundon	41	19	36	21	2	19 13 0 13
<i>Pertusaria hemisphaerica</i> (Flörke) Erichsen	128	98	47	107	66	44 58 42 31
<i>Pertusaria hymenea</i> (Ach.) Schaer.						4* 3 1
<i>Pertusaria leioplaca</i> DC.	72	31	54	171	23	154 117 13 107
<i>Phaeographis dendritica</i> (Ach.) Müll.Arg.						8* 3 6
<i>Phyctis argema</i> (Spreng.) Flot.	66	27	50	31	9	24 18 5 14
<i>Physconia venusta</i> (Ach.) Poelt	41*	3	40			
<i>Platismatia glauca</i> (L.) W.L.Culb. & C.F.Culb.				8*	0	8
<i>Porina aenea</i> (Wallr.) Zahlbr.				7	2	7 22 6 18
<i>Pseudevernia furfuracea</i> (L.) Zopf	6	0	6	1	0	1 1 0 1
<i>Punctelia subrudecta</i> (Nyl.) Krog						4* 0 4
<i>Pyrenula nitida</i> (Weigel) Ach.				141	26	128 154 37 139
<i>Ramalina farinacea</i> (L.) Ach.	106	17	91	53	3	51 27 3 24
<i>Sphaerophorus globosus</i> (Huds.) Vain.						25* 18 13
<i>Sticta limbata</i> (Sm.) Ach.						27* 23 6
<i>Thelothrema lepadinum</i> (Ach.) Ach.				3	0	3 48 7 45
<i>Bryophytes</i>						
<i>Antitrichia curtipendula</i> Bridel	72	54	57	93	49	61 36 15 27
<i>Fruillania dilatata</i> (L.) Dumort.	53	38	26	60	37	35 114 73 75
<i>Habrodon perpusillus</i> Lindberg						9* 2 7
<i>Homalothecium sericeum</i> W. P. Schimper in B.S.G.				20	17	6 4 3 1
<i>Hypnum cupressiforme</i> Hedwig						32* 30 9
<i>Isoetecium alopecuroides</i> Isoviita						29* 12 21
<i>Leucodon sciuroides</i> Schwaegrichen	27	23	5	29	19	14 68 29 41
<i>Metzgeria furcata</i> (L.) Dumort.						58* 43 17
<i>Neckera complanata</i> Hübener						87* 46 53
<i>Orthotrichum affine</i> Schrader ex Bridel	31*	11	24			
<i>Orthotrichum lyellii</i> W. J. Hooker & Taylor	104	58	67	12	8	6 37 9 31
<i>Orthotrichum speciosum</i> Goffinet et al.						10* 2 8
<i>Orthotrichum stramineum</i> Hornschuch in Bridel						17* 1 16
<i>Porella platyphylla</i> (L.) Pfeiff.	61	47	34	6	3	4 50 43 22
<i>Pterogonium gracile</i> Smith	40	37	18	95	87	21 117 89 46
<i>Pterygynandrum filiforme</i> (Hedw) Timm	85	59	40	76	63	19 110 69 54
<i>Radula complanata</i> (L.) Dumort	6	6	2	5	5	0 55 21 38
<i>Thuidium tamariscinum</i> (Hedw.) Schimp.						13* 13 0
<i>Ulotia crista</i> Hornsch						22* 16 7
<i>Zygodon baumgarneri</i> Lorentz						57* 46 18
<i>Zygodon viridissimus</i> Lorentz.						49* 37 15

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