Edge effects on epiphytic communities in a Mediterranean *Quercus pyrenaica* forest

Belinchón, Rocío[1]**; Martínez, I.**[1*]**; Escudero, A.**[1]**; Aragón, G.**[1] **& Valladares, F.**[1,2]

[1]*Biodiversity and Conservation Area, Higher School of Experimental Sciences and Technology, Rey Juan Carlos University, C/Tulipán s/n, Móstoles, E-28933, Madrid, Spain;*
[2]*CSIC, Environmental Sciences Center, C/ Serrano 115 bis, E-28006, Madrid, Spain;*
E-mails rocio.belinchon@urjc.es; adrian.escudero@urjc.es; gregorio.aragon@urjc.es; ebvfv87@ccma.csic.es;
[*]Corresponding author; Fax +34 916647490; E-mail isabel.martinez@urjc.es

Abstract

Question: What are the edge effect responses of epiphytic lichen communities in Mediterranean *Quercus pyrenaica* forest?
Location: Central Spain.
Methods: We established ten transects perpendicular to a road dissecting a well conserved remnant of *Q. pyrenaica* forest into two sections. Transects extended from the forest/road edge to 100 m into the forest. Data were collected from seven plots in each transect at different distances from the edge. Variables were grouped into stand scale variables (distance to edge, number of trees per plot, mean diameter per plot, irradiance) and tree scale variables (diameter and height of sampled trees, aspect of the sampled square and relative height of the square). We used General Mixed Linear Models and constrained ordination techniques to test the hypothesis that the spatio-temporal heterogeneity of light and water controls the occurrence of lichens and bryophytes along the edge-interior gradient in the *Q. pyrenaica* forest.
Results: Microclimatic parameters vary in a non-linear way; edge and interior stands showed the most divergent and extreme values. Although the micro-environment within Mediterranean forests is heterogeneous, interior conditions are apparently suitable for the performance of some specific forest epiphytes. Consequently, species richness does not show significant differences along the gradient. Total epiphytic cover increases towards the forest interior, but distance to the edge together with other predictors at the tree scale (aspect and height of the square) are the most relevant predictors for the composition and structure of these communities.
Conclusions: Composition and structure of epiphytic communities in a Mediterranean semi-deciduous forest are affected by the edge between the forest and the road constructed. Since some extremely rare lichens only occur at interior stands, the conservation of these threatened elements requires urgent conservation measures because well preserved and unmanaged forests in the Mediterranean region are very rare.

Keywords: Conservation; Edge-interior gradient; Forest management; Fragmentation; Lichen; Spain.

Nomenclature: Hafellner & Türk (2001); Bisby & Rostov (2005).

Abbreviations: GLMM = General Mixed Linear Model; GSF = Global site factor; TVE = Total variation explained.

Introduction

Fragmentation represents one of the major global threats to biodiversity conservation (Santos & Tellería 1998; Hedenås & Ericson 2000). As a consequence, the amount of forest edge habitat is currently increasing worldwide (Murcia 1995; Kivistö & Kuusinen 2000). When continuous forest cover is converted into scattered forest remnants varying in size and isolation, ecological processes change (Rheault et al. 2003). Fragmentation decreases climatic homeostasis and produces changes in biotic and abiotic conditions (Murcia 1995; Santos & Tellería 1998). As a general rule, edge zones present more extreme conditions (temperature, humidity, light) which may become unsuitable for organisms adapted to forest interior conditions (Renhorn et al. 1997; Rheault et al. 2003). Since one of the conservation priorities is to formulate adequate guidelines for sustainable forest management and biodiversity conservation, knowledge of the effect of fragmentation on each component of any type of forest system is needed (e.g. Gibbs 1998; Kivistö & Kuusinen 2000; Meiners et al. 2002).

As lichens are poikilohydric, they are not very efficient in controlling their water content or light capture efficiency and are, therefore, very sensitive to changes in microclimate (Esseen & Renhorn 1996; Renhorn et al. 1997; Esseen & Renhorn 1998; Kivistö & Kuusinen 2000; Rheault et al. 2003). This makes them well suited organisms for an assessment of forest edge and fragmentation effects. Lichen abundance in forests is controlled by environmental conditions (Liu et al. 2000; Rheault et al. 2003), which exhibit high spatial and temporal variation both at the stand scale, due to changes in tree species composition and density (Arsenau et al. 1997; Chen et al. 1999; Liu et al. 2000), and at the tree scale, due to the influence of tree traits such as diameter, height and architecture on microhabitat conditions. Will-Wolf et al. (2006) and Giordani (2006), working at larger scales (regional), recently found that factors such as location, topography, climate, pollution, vegetation structure and

composition affected lichen communities. Aspects such as type of dispersion may also influence lichen diversity (Löbel et al. 2006).

Few studies deal with edge effect on lichen diversity, and most of these studies have concentrated on boreal environments in northern Europe (Renhorn et al. 1997; Esseen & Renhorn 1998; Kivistö & Kuusinen 2000) or in North America (Sillett 1994; Rheault et al. 2003). To our knowledge no studies have been carried out on edge effects in Mediterranean forest systems although these ecosystems are one of the most threatened forest systems in the world (Scarascia-Mugnozza et al. 2000). Extrapolation from northern epiphytic communities to Mediterranean forests should be conducted with caution because specific and distinctive factors operating in these forests such as severe water deficit during the growing season and high environmental heterogeneity, can lead to significantly different ecological scenarios (Marañón et al. 2004; Gómez-Aparicio et al. 2005).

Forest edge effects on lichens include a complex array of issues such as the disappearance of some epiphytic species (Jørgensen 1978; Sjöberg & Ericson 1992) or a decline in their populations as indicated by decreases in size, growth and biomass of lichens found at forest edges (Sillet 1994; Renhorn et al. 1997; Esseen & Renhorn 1998; Rheault et al. 2003). Some landscape scale processes have also been explored, such as the influence of patch size (Moen & Jonsson 2003) or the quality and isolation of remnant patches on the distribution and abundance of epiphytic lichens (Gu et al. 2001; Johansson & Ehrlén 2003). However, none of these studies have explored edge effect at the community level, except Kivistö & Kuusinen (2000), who studied edge effects on the entire epiphytic lichen flora in a boreal forest at a regional scale.

Our main goal was to quantify edge effect responses of epiphytic communities dominated by lichens in a well conserved Mediterranean *Quercus pyrenaica* forest in central Spain. We hypothesized that light and water, specifically their spatio-temporal variability, control the presence and abundance of lichens along the edge-interior gradient. We tested the complementary hypothesis that a complex set of predictors may modulate this gradient exacerbating or mitigating differences along this primary gradient. These factors act at different spatial scales (i.e. stand and tree scales), and exhibit high variability within the forest (Murcia 1995; Chen et al. 1999). Our specific objectives are: (1) to identify and quantify edge effects on epiphytic lichen communities in an old-growth Mediterranean forest; (2) to determine the most relevant predictors of edge effects on these organisms at the stand scale and at the tree scale; (3) to identify the most important factors that control the structure and composition of the epiphytic community.

Material and Methods

Study site

The study was conducted in 'La Herrería', a well preserved forest of ca. 500 ha located in the Sierra de Guadarrama in the vicinity of Madrid, central Spain (40°34' N, 4°8' W, altitude 985 m a.s.l.). The climate is subhumid continental mediterranean with a mean annual temperature of 13 ℃ and an annual precipitation of 739 mm; there is a very pronounced drought season during summer (mean values for the last 44 years from the nearby weather station 'San Lorenzo de El Escorial', 1028 m a.s.l.). Tree species composition was dominated by *Quercus pyrenaica*, with *Fraxinus angustifolia* as subdominant (< 5% canopy cover). *Quercus pyrenaica* is a semi-deciduous oak mainly occurring in the Iberian Peninsula with some isolated populations in northern Morocco and on the southwest tip of France.

The study site consisted of one of the few unmanaged *Quercus pyrenaica* forests in Mediterranean Spain and is characterized by its good state of conservation (Izco 1984; Blanco et al. 1998) and high lichen diversity (pers. obs.). This area became a royal property in 1562 under King Felipe II and it was closed to the public for centuries. It probably constitutes the largest (>100 ha) old-growth unmanaged *Quercus pyrenaica* forest in Spain. The forest was divided in two (230 ha and 258 ha) by the construction of a road (M-505) 40 years ago. The road is 20 m wide and its length within the forest is ca. 3 km. These two unmanaged forest fragments have not been disturbed since the construction of the road, so we expect epiphytic lichen communities to have become relatively stable over this period. Traffic intensity is moderate, ca. 2500 vehicles per day (Service of Publications of Transport, Community of Madrid) and no signs of physical damage have been observed in the vegetation.

Sampling design and data collection

Field work was carried out in the western forest fragment between July 2003 and October 2004. We established ten transects perpendicular to the road in a flat area to minimize heterogeneity due to rough and extended terrain. Transects ran 100 m into the forest and were at least 15 m apart to avoid an overestimation of species with patchy distributions (Dauber & Wolters 2004). Data were collected from seven plots (5 m × 5 m) in each transect. Plots were placed at 5, 15, 25, 35, 45, 55 and 100 m from the beginning of each transect. Our design was based on the assumption that environmental conditions at 100 m from the edge should be typical of interior forests (Esseen & Renhorn 1998; Rheault et al. 2003; Esseen 2006).

Field sampling was based on the method of Esseen & Renhorn (1998) and all epiphytic lichens and bryophytes were included in the study, although bryophytes were not considered at species level. Within each plot, we measured DBH of all trees with a diameter > 5 cm. The number of trees in a plot was used as an estimate of tree density. Occurrence of epiphytic lichens and bryophytes was estimated on two trees per plot (for a total of 113 trees). The tree with the greatest diameter and the tree with a DBH closest to the mean DBH of the plot were selected in order to get a good representation of the most developed epiphytic community of the stand. A complete list of predictors and their characteristics is presented in App. 1. Based on our field experience in this type of community we used 20 cm × 20 cm squares as monitoring units. Four squares were located on the bark of each selected tree. These sampling units were located parallel to the edge which runs east-west at four locations on the bark of each tree: at breast height and at tree base and on the north and south aspects. Consequently, eight lichen squares were surveyed per plot. A digital photograph was taken of each sampling square at 50 cm from the tree bark. Cover estimates per species were calculated by means of an image analyzer (Micro-Image v. 4.5, Olympus, USA). In the field we also estimated the cover of all species in the square to avoid negligible crustose species being unnoticed in the image analysis.

Light availability at each microsite was estimated from hemispherical photographs. Photographs were taken at breast height and at ground level in the centre of each plot, using a horizontally levelled digital camera (Nikon Coolpix 4500, Nikon, Japan) aimed at the zenith, using a fish-eye lens of 180º field of view (FCE8, Nikon). Photographs were analysed using Hemiview canopy analysis software ver. 2.1 (1999, Delta-T Devices Ltd, Cambridge, UK). This software estimates several irradiance variables but we only used the global site factor (GSF) values in further analyses (Valladares 2003).

Both air temperature and relative humidity were measured with seven sensors (HOBO® H8 Pro Series, Onset USA) placed 1.60 m above the ground and located in each plot along one transect. Sensors were read every hour. The microclimate station recorded temperature and relative humidity continuously for 351 days (from 30 October 2003 to 15 October 2004). This information was not included in our statistical models as it was not replicated.

Numerical analyses

The effect of stand and tree scale variables (distance to edge, number of trees per plot, mean DBH per plot, irradiance/diameter and height of sampled trees, aspect of the sampling square and relative height of the square) on the community traits of richness, total cover, lichen cover and bryophyte cover was modelled by fitting generalised mixed linear models (GLMMs) (McCullagh & Nelder 1989). Our data on lichen occurrence and cover in the sampling squares had an unbalanced, hierarchical structure, with squares nested within plots and plots nested within transects. A hierarchical data structure implies correlation between data points at different scales, inflating the error degrees of freedom and increasing the chance of making a Type I error.

To overcome these problems, we analysed the data using a multilevel approach, considering plots and transects as random factors and applying mixed modelling. Predictors were included as explanatory variables (fixed factors) and transect and plot were included as random sources of variation. Because data were found to be overdispersed in some cases, we used the quasi-likelihood approach to overcome possible difficulties (Guisan et al. 2002). The significance of each predictor was estimated by means of an analysis of deviance (Guisan et al. 2002). For species richness and total cover we fitted the mixed models using a normal response and an 'identity' link function, setting the variance to '1'. For lichen cover we fitted the models using the gamma distribution. A 'log' link function was used, setting the variance to "mean". For bryophyte cover we used the Poisson response and a 'log' link function, setting the variance to 'mean'. We fitted each model using all applicable link functions and selected the one minimizing deviance of the model (Herrera 2000). Degrees of freedom were estimated by Satterwaite's method (Littell et al. 1996). All GLMM computations were performed using SAS Macro program GLIMMIX, which iteratively calls SAS Procedure Mixed until convergence (GLIMMIX ver. 8 for SAS/STAT; available at http://www.sas.com.techsup/download/stat/).

We studied the relationships between the measured environmental variables and lichen composition across the 452 lichen squares by means of constrained ordinations. We conducted all the analyses with downweighting of rare species and log-transformation of cover. We first determined the main gradient structure of the data cover set with a Detrended Correspondence Analysis (DCA; Hill & Gauch 1980). Since the length of the first DCA axis was 5.8 standard deviation units, which is a relatively large gradient, we used a Canonical Correspondence Analysis (CCA; ter Braak 1986; Legendre & Anderson 1999). CCA was carried out to test the null hypothesis

that epiphytic cover is independent of the environmental variables. Variables were grouped in two different sets, the stand scale variables and the tree scale data set. Two CCAs were conducted with each environmental data set. The sum of all canonical eigenvalues or trace was used to build the F-ratio statistic (ter Braak 1990; Legendre & Anderson 1999), which was used to estimate the level of significance with a Monte Carlo process with 1000 randomizations. A forward stepwise procedure was conducted to select significant predictors. Variables were selected sequentially in order of their decreasing eigenvalues until the new variable was non-significant ($p > 0.05$). Improvement of the reduced model with each new selected variable was determined by a Monte Carlo permutation test (1000 permutations).

Partial CCA (ter Braak & Šmilauer 1997) was conducted to evaluate the relative importance of each constraining matrix after adjusting the variability of the other data set which was considered a covariable data set (Bocard & Legendre 1994; Legendre & Legendre 1998).

This was carried out to determine whether both data sets were concomitant. The tree scale matrix was the explanatory data set, whereas the stand scale data set (only significant variables) was considered the covariable data set. All the partial models were also tested using a Monte Carlo permutation approach.

Results

Tree density ranged between one and five trees per plot (25 m²). Mean tree diameter at breast height was 29.17 ± 6.45 cm and varied between 13.4 and 45.4 cm, while tree height oscillated between 9 m and 21 m (App. 1).

Distance of the plot to the edge was positively correlated with mean tree diameter per plot (Spearman correlation coefficient $r_S = 0.420$, $p < 0.001$) but negatively correlated with irradiance ($r_S = -0.164$, $p < 0.001$) which was estimated as the mean value between GSF at ground level and GSF at breast height. Number of trees per plot was significantly correlated with mean tree diameter per plot ($r_S = -0.225$, $p < 0.001$) and irradiance ($r_S = -0.185$, $p < 0.001$). However, no significant relationship was found between number of trees and distance to edge ($p = 0.179$) or between mean tree diameter per plot and irradiance ($p = 0.229$).

Microclimatic variation along the distance gradient for temperature, moisture and irradiance is shown in Fig. 1. Irradiance at breast height and at ground level did not present significant differences between the different distances to the edge (irradiance KW = 2.691, $df = 6$, $P = 0.84$) although light reached its minimum at the great-
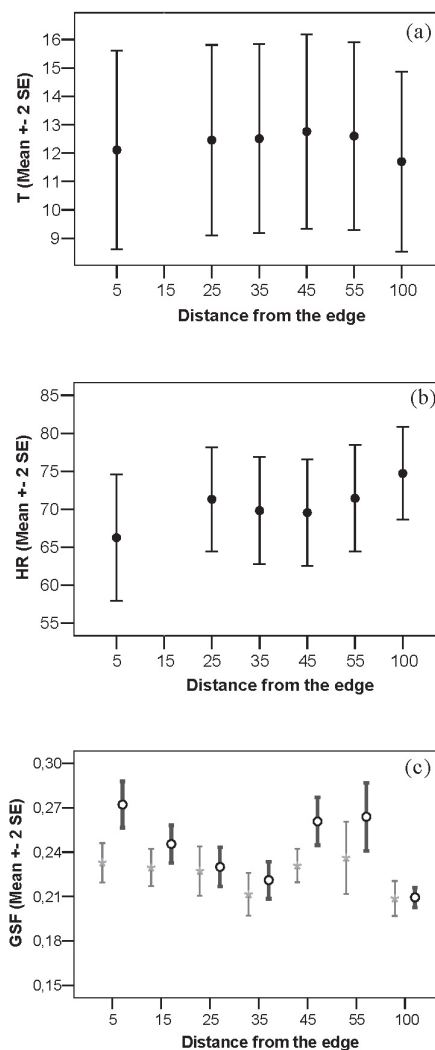

Fig. 1. Micro-environment effects as a function of distance from the edge. Changes in (**a**) temperature (ºC); (**b**) relative humidity (%) were measured from an open edge into the forest; (**c**) GSF was measured from an open edge into the forest at two different level: ground level (diamonds), DBH (circles). Distance between 55 m and 100 m are not proportional in our graphs.

est distance from the edge and a significant, but weak, relationship between distance and irradiance was found. Mean relative air humidity and temperature was higher in the interior of the forest while temperature reached a maximum at the edge. Nevertheless, our results suggest that variation for this microclimate parameter is not linear, even though edge and interior stands (5 m - 100 m) show the most divergent and extreme values. The variation coefficient of temperature remained constant along the edge-interior gradient whereas the variation coefficient of humidity increased from the interior to the edge (13.54 to 23.51 respectively).

Table 1. Results of the Generalized Mixed Linear Models on some community traits. Coeff.= coefficient of the variable in the model. The random variable transect was non-significant in all cases, while plot variable was significant: species richness (Z-value = 1.72, Prob. Z = 0.04), total cover (Z-value = 2.48, Prob. Z = 0.006), lichens cover (Z-value = 3.23, Prob. Z = <0.0001), bryophytes cover (Z-value = 2.54, Prob. Z = 0.005).

Species richness	Effect	Coeff.	*F*-value	*P*-value
Tree scale variables	Height of the square	−0.2108	1.06	0.3035
	Aspect of the square	−0.4435	4.85	0.0283
	Tree diameter	−0.0638	5.63	0.0183
	Tree height	0.1111	4.80	0.0301
Stand scale variables	Distance to edge	−0.0002	0.00	0.9743
	Number trees per plot	0.1148	0.76	0.3874
	Mean DBH per plot	−0.0190	0.53	0.4703
	Irradiance	−1.1635	0.21	0.6502
Total cover				
Tree scale variables	Height of the square	−17.6814	4.09	0.0438
	Aspect of the square	−60.5013	47.87	<0.0001
	Tree diameter	2.0552	3.07	0.0808
	Tree height	−1.1550	0.35	0.5564
Stand scale variables	Distance to edge	0.6493	7.82	0.0068
	Number trees per plot	2.1942	0.16	0.6895
	Mean DBH per plot	−1.1481	0.96	0.3311
	Irradiance	−56.3479	0.31	0.5792
Lichen cover				
Tree scale variables	Height of the square	−0.4797	115.88	<0.0001
	Aspect of the square	0.0062	0.02	0.8851
	Tree diameter	0.0076	1.44	0.2302
	Tree height	0.0251	4.41	0.0380
Stand scale variables	Distance to edge	0.0005	0.09	0.7671
	Number trees per plot	0.0386	1.11	0.2966
	Mean DBH per plot	−0.0126	2.87	0.0947
	Irradiance	−0.5333	0.69	0.4089
Bryophyte cover				
Tree scale variables	Height of the square	2.4793	144.32	<0.0001
	Aspect of the square	−1.0049	65.30	<0.0001
	Tree diameter	0.01455	0.94	0.3330
	Tree height	−0.0712	7.59	0.0075
Stand scale variables	Distance to edge	0.0072	3.98	0.0910
	Number trees per plot	−0.1548	3.64	0.0610
	Mean DBH per plot	0.0037	0.06	0.8088
	Irradiance	1.1112	0.53	0.4683

A total of 57 epiphytic lichen species were recorded in the 452 lichen squares (App. 2). Most lichens were foliose lichens (29 species) followed by 13 crustose, 7 fruticose, 6 squamulose and 2 *Cladonia* species (with squamulose primary thallus and podetia). The most common species were *Melanelia glabra, Physconia distorta, Parmelina tiliacea* and *Ramalina farinacea* which appeared in more than 200 squares, while others such as *Fuscopannaria ignobilis, Leptogium furfuraceum, Lobaria pulmonaria, Mycobilimbia berengeriana* and *Waynea adscendens* were rare. The species which had the highest cover were: *Melanelia glabra* and *Physconia distorta,* as well as the compound group 'bryophytes' (App. 2).

Results of the mixed models mainly showed the influence of tree scale variables on all community traits studied (Table 1). The most relevant predictors of the epiphytic communities were aspect and relative height of the square on the tree followed by tree height, tree diameter and distance to edge. The random variable transect had no significant effect in any case, while plot exerted a significant influence in all cases (Table 1). Species richness was higher on tall trees with a small diameter and northern orientation. Total lichen and bryophyte cover had opposite behaviours as lichens increased their cover at breast height on tall trees, while bryophytes preferred northern exposures on the lower part of trunks and, surprisingly, on low trees. Finally, the highest cover values were found in the forest interior at breast height and northern exposures (Table 1).

CCA models indicated that both data sets explain significant ($p < 0.05$) parts of the composition and cover distribution of the different species at our study site (Table 2). However, total variation explained was

Table 2. CCA models obtained using the species cover matrix and two environmental data sets as constraining matrices (stand and tree variables) and a forward stepwise procedure using the two environmental data sets to select a reduced model including only significant variables. Constraining matrix indicates data set used to build models. λ_1, λ_2 and λ_3 are the eigenvalues of the corresponding extracted axes. λ is the eigenvalue of the corresponding variable. Σcons is the sum of all constrained axes. ICA = sum of all eigenvalues. TVE = total variation explained (in %). F-ratio statistic was computed using the trace or sum of all eigenvalues. P is the level of significance of the model (1000 randomizations).

	Stand scale variables					Tree scale variables				
		λ	F-ratio	p			λ	F-ratio	p	
Step 1	Distance from edge	0.06	10.54	0.001	Step 1	Height of square	0.15	27.86	0.001	
Step 2	GSF	0.01	2.51	0.006	Step 2	Aspect square	0.10	18.22	0.001	
Step 3	Mean diameter	0.01	1.99	0.015	Step 3	Diameter tree	0.03	6.07	0.001	
					Step 4	Height tree	0.02	2.95	0.001	

Constraining matrix	λ_1	λ_2	λ_3	Σ cons	ICA	TVE	Monte Carlo test F-ratio	p
Stand scale (reduced model)	0.062	0.017	0.009	0.093	2.64	3.25	10.70	0.001
Tree scale (reduced model)	0.219	0.045	0.027	0.300	2.647	11.33	40.14	0.001

rather low: 11.3% for the tree scale variables and 3.25% for the stand scale data set. A complete model with all the predictors together explained 14.07% of TVE (total variation explained).

In the CCA forward stepwise selection procedure applied to determine which environmental parameters were the best predictors of the cover data set, all variables of the two environmental data sets were selected, except number of trees ($p = 0.1808$) (Table 2).

Partial CCA was used to study patterns in floristic composition, explained exclusively for each environmental matrix. The two environmental data sets (tree scale and stand scale) explained a fraction of TVE once the information explained by the covariable data set was previously partialled out (Fig. 2).

As shown in Fig. 3a, edge distance was a strong determinant of axis 1 when the stand scale predictors were used. The second axis was correlated with irradiance and mean tree diameter per plot. Although the species did
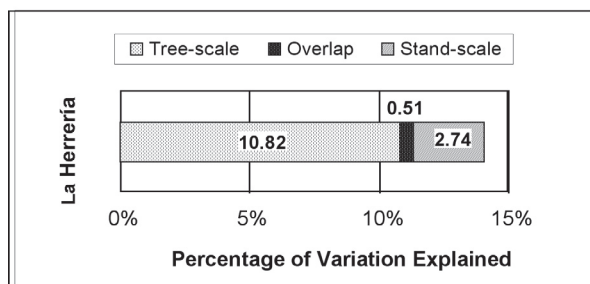

Fig. 2. Graphic summary of partial CCA performed to quantify the amount of variation in the species cover matrix explained by the fractions defined by the constraining matrices (represented by bars). The numbers located in each bar indicate the amount of variation in the species cover matrix explained by each fraction. All individual fractions of variation were significant ($P = 0.001$).
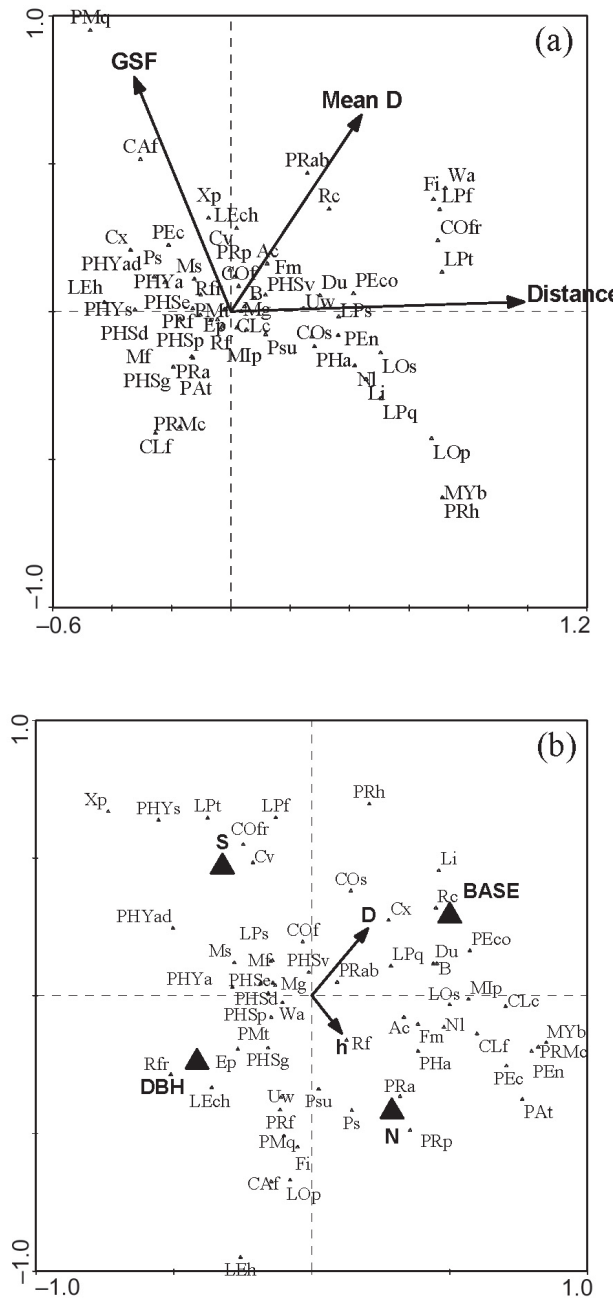
not form well defined groups, some species located their cover centroids in the extreme values of the environmental vectors (see ter Braak 1983). For example, one group of species was found at long distance from the edge (*Collema fragrans, Fuscopannaria ignobilis, Leptogium furfuraceum, L. teretiusculum, Lobaria pulmonaria, Mycobilimbia berengeriana* and *Pertusaria hemisphaerica*) while another group was negatively correlated with distance to the edge (e.g. *Candelariella xanthostigma, Caloplaca ferruginea, Parmelina quercina* and *Physcia adscendens)*. Likewise, there was a group of species related to lower values of irradiance (e.g. *Leptogium quercicola, Lobaria pulmonaria, Mycobilimbia berengeriana* and *Pertusaria hemisphaerica*) and a group with preference for exposed, highly illuminated sites (e.g. *Caloplaca ferruginea, Lecanora chlarotera* and *Xanthoria parietina*). In addition, species such as *Fuscopannaria ignobilis, Leptogium furfuraceum, Ramalina calicaris* and *Waynea adscendens* were found to be associated with plots with a high mean tree size (DBH) (Fig. 3a).

In the case of the tree scale data set (Fig. 3b), the first gradient was correlated to the position of the plot on trunks, whereas aspect was determinant of the second axis. Among the species with optima close to north exposures and also on taller trees, we found *Ramalina farinacea, Parmelia sulcata, Pertusaria amara* and *Pertusaria pertusa*. We also found a complete set of lichens in south exposures and on shorter trees (e.g. *Candelariella vitellina, Leptogim teretiusculum, Physcia semipinnata* and *Xanthoria parietina*). Species associated with the lower part of the trunks on trees with larger diameters included bryophytes and the lichens *Dendriscocaulon umhausense, Lepraria incana, Peltigera collina, Pertusaria hemisphaerica* and *Ramalina calicaris* (Fig. 3b).

Fig. 3. Species-environment biplots Axis 1 and 2. (**a**) stand scale variables; (**b**) tree scale variables. Variables in the model were BASE and S but DBH and N were also included as passive variables. Only variables selected by the forward stepwise procedure were included. Dummy variables were represented by their centroids. GSF = Global site factor indicated the total amount of light under canopy; Mean D = Mean diameter per plot; D = tree diameter; h = tree height; N = north aspect; BASE = trunk base position. Species abbreviations are shown in App. 2.

Discussion

Our results show that microclimate is to some extent related to the edge-interior gradient in our Mediterranean *Q. pyrenaica* forest, although stand heterogeneity is very high along the gradient. The marked differences found between edge and interior stands suggest that the edges of a road line may produce edge-interior gradients similar to those described for isolated forest fragments (Murcia 1995). Despite some methodological and macro-environmental differences between study areas, this edge-interior gradient is similar to those reported in other temperate forests (Cadenasso et al. 1997). In agreement with other studies, both air temperature and irradiance in our *Q. pyrenaica forest* present the highest values in the edge zone, whereas air humidity shows the opposite pattern (Cadenasso et al. 1997; Renhorn et al. 1997). Some authors have pointed out that edge dynamics are very complex and linear environmental responses are unlikely to be obtained (Murcia 1995; Esseen & Renhorn 1998). In fact, several factors acting at the stand scale can influence microclimatic conditions apart from the inherent variation of measured variables (Murcia 1995; Chen et al. 1999). Nevertheless, this endogenous environmental heterogeneity is not great enough to completely mask the prevalence of edge-interior variation. It is known that the environmental heterogeneity of Mediterranean forests is higher than that of northern forests where light, and not water, is the main limiting ecological factor (Marañón et al. 2004). This fact may also have determined the relatively small differences found along the edge-interior gradient.

Species richness does not present significant variation along the edge-interior gradient. Many studies have shown that forest edge represents an unfavourable habitat for the establishment and survival of many epiphytic organisms (e.g. Sillet 1994; Esseen & Renhorn 1998; Moen & Jonsson 2003) favouring a set of species with a broad tolerance and an opportunistic strategy (Barreno & Pérez-Ortega 2003). Although we do not know what the conditions of the forest were like before road construction 40 years ago, our findings suggest that forest fragmentation has implied a replacement of epiphytic species. In this sense we found that most of the edge species of our study have their optimum at the edge or even out of our forest environmental envelope (Martínez et al. in prep.). On the other hand, a direct chemical or physical effect of cars on the epiphytic communities is also possible. However, the level of traffic is considerably low and we have not observed any physical damage in the thalli of lichens.

We also found that total cover increased with distance to the edge, although the number of species remained constant. Moreover, the total cover peaks found at north-

ern aspects and at the trunk base suggest that sunnier and drier conditions limit lichen growth (Rheault et al. 2003). Additionally, distance to the edge is the main predictor. This reinforces the importance of water for the performance of lichens on *Q. pyrenaica* bark.

It is known that differences in species composition and lichen performance along the edge-interior gradient are related to environmental variation at different scales both in Mediterranean forests (Burgaz et al. 1994) and in boreal forests (Renhorn et al. 1997; Kivistö & Kuusinen 2000; Will-Wolf et al. 2006). Most studies emphasise the importance of tree scale variation in humidity, light, temperature and bark properties (Arsenau et al. 1997) while predictors at higher scales are of secondary importance. In agreement with this, we found species richness, total cover, lichen and bryophyte cover to be mainly determined by variables at the tree scale. In fact, tree predictors explained a significantly higher fraction of variation in CCAs than the stand scale variables. Besides, we identified different lichen groups in relation to the characteristics and position on the tree. These differences have been pointed out by different authors (Burgaz et al. 1994; Esseen & Renhorn 1996; Johansson & Ehrlén 2003).

CCA results showed that predictors at both spatial scales (stand and tree scales) do not overlap and consequently explain significant and complementary fractions of variation. Changes in the environment of the forest at the two scales along the edge-interior gradient have direct consequences for the composition of the epiphytic communities. Results at the stand scale suggest that environmental conditions near the margin were not necessarily unfavourable for establishment and development of certain species. The most outstanding species among those with preference for the forest interior are *Collema fragrans, Fuscopannaria ignobilis, Leptogium furfuraceum, Leptogium teretiusculum, Lobaria pulmonaria, Mycobilimbia berengeriana, Pertusaria hemisphaerica* and *Waynea adscendens*. Some of these species contain cyanobacteria as a photosynthetic partner, so they need some degree of shade for their development and stability in humid conditions (Richardson & Cameron 2004). Cyanobacterial lichens are very sensitive to alterations of environmental conditions (Hilmo & Såstad 2001) and most of them are included in European red lists because their populations show important declines (Randlane 1998; Thor & Arvidsson 1999; Nimis 2003; Martínez et al. 2003). Cyanobacterial lichens are positively correlated with moisture availability (Sillet 1994), and they indicate both a high level of spatial and temporal environmental continuity and high forest conservation value (Gu et al. 2001). They are also favoured by certain microhabitat structures, such as deeply rough barks or mossy barks (Aragón et al. 2005) and present a moderate

level of photoinhibition when they are exposed to high irradiance values (Kivistö & Kuusinen 2000). Presence of these lichens in well-preserved Mediterranean forests suggests that interior conditions are really mesic despite extreme summer droughts and more heterogeneous light conditions than in temperate and boreal forests. Unfortunately, there are very few mature forest stands with such conditions in the Mediterranean Iberian Peninsula where coppice is the dominating forest type (see Martínez et al. 2003). The conservation of these forest specialists requires undisturbed mature forest stands, not coppice, with at least an edge buffer of 100 m. Consequently, most of these species are probably on the verge of extinction in Mediterranean Spain and they are included in several regional Red Lists of the Iberian Peninsula (Martínez et al. 2003; Atienza & Segarra 2000).

References

Aragón, G., Belinchón, R. & Martínez, I. 2005. *Programa de conservación de líquenes amenazados y bioindicadores en quejigares, rebollares y alcornocales en Castilla-La Mancha- Final Report*. Consejería de Medio Ambiente, Junta de Comunidades de Castilla-La Mancha, ES.

Arsenau, M.J., Sirois, L. & Ouellet, J.P. 1997. Effects of altitude and tree height on the distribution and biomass of fruticose arboreal lichens in an old growth balsam fir forest. *Ecoscience* 4: 206-213.

Atienza, V. & Segarra, J.G. 2000. Preliminary Red List of the lichens of the Valencia Community (eastern Spain). *For. Snow Landscape Res.* 75: 391-400.

Barreno, E. & Pérez-Ortega, S. 2003. *Líquenes de la Reserva Natural Integral de Muniellos, Asturias*. KRK ediciones, Asturias, ES.

Bisby, F.A. & Rostov, Y.R. 2005. *Species 2000 Baseline documents: Standard dataset, version 3.2*. http://www.sp2000.org/

Blanco, E. et al. 1998. *Los bosques ibéricos. Una interpretación geobotánica*. Editorial Planeta, Barcelona, ES.

Bocard, D. & Legendre, P. 1994. Environmental control and spatial structure in ecological communities: an example using oribatid mites (*Acari, Oribatei*). *Environ. Ecol. Stat.* 1: 470-479.

Burgaz, A.R., Fuertes, E. & Escudero, A. 1994. Ecology of cryptogamic epiphytes and their communities in deciduous forests in mediterranean Spain. *Vegetatio* 112: 73-86.

Cadenasso, M.L., Traynor, M.M. & Pickett, S.T.A. 1997.

Functional location of forest edges: gradients of multiple physical factors. *Can. J. For. Res.* 27: 774-782.

Chen, J., Saunders, S.C., Crow, T.R., Naiman, R.J., Brosofske, K.D., Mroz, G.D., Brookshire, B.L. & Franklin, J.F. 1999. Microclimate in forest ecosystem and landscape ecology. Variations in local climate can be used to monitor and compare the effects of different management regimes. *BioScience* 49: 288-297.

Dauber, J. & Wolters, V. 2004. Edge effects on ant community structure and species richness in an agricultural landscape. *Biodivers. Conserv.* 13: 901-915.

Esseen, P.A. 2006. Edge influence on the old-growth forest indicator lichen *Alectoria sarmentosa* in natural ecotones. *J. Veg. Sci.* 17: 185-194.

Esseen, P.A. & Renhorn, K.E. 1996. Epiphytic lichen biomass in managed and old-growth boreal forests: effect of branch quality. *Ecol. Appl.* 6: 228-238.

Esseen, P.A. & Renhorn, K.E. 1998. Edge effects on an epiphytic lichen in fragmented forests. *Conserv. Biol.* 12: 1307-1317.

Gibbs, J.P. 1998. Distribution of woodland amphibians along a forest fragmentation gradient. *Landscape Ecol.* 13: 263-268.

Giordani, P. 2006. Variables influencing the distribution of epiphytic lichens in heterogeneous areas: A case study for Liguria, NW Italy. *J. Veg. Sci.* 17: 195-206.

Gómez-Aparicio, L., Valladares, F., Zamora, R. & Quero, J.L. 2005. Response of tree seedlings to the abiotic heterogeneity generated by nurse shrubs: an experimental approach at different scales. *Ecography* 28: 1-12.

Gu, W.-D., Kuusinen, M., Konttinen, T. & Hanski, I. 2001. Spatial pattern in the occurrence of the lichen *Lobaria pulmonaria* in managed and virgin boreal forests. *Ecography* 24: 139-150.

Guisan, A., Edwards, T.C. & Hastie, T. 2002. Generalized linear and generalized additive models in studies of species distributions: setting the scene. *Ecol. Model.* 157: 89-100.

Hafellner, J. & Türk, R. 2001. Die lichenisierten Pilze Österreichs – eine Checkliste der bisher nachgewiesenen Arten mit Verbreitungsangaben. *Stafia* 76: 3-167.

Hedenås, H. & Ericson, L. 2000. Epiphytic macrolichens as conservation indicators: successional sequence in *Populus tremula* stands. *Biol. Conserv.* 93: 43-53.

Herrera, C. 2000. Flower-to-seedling consequences of different pollination regimes in an insect-pollinated shrub. *Ecology* 81: 15-29.

Hill, M.O. & Gauch, H.G. 1980. Detrended Correspondence Analysis: an improved ordination technique. *Vegetatio* 42: 47-58.

Hilmo, O. & Såstad, S.M. 2001. Colonization of old-forest lichens in a young and an old boreal *Picea abies* forest: an experimental approach. *Biol. Conserv.* 102: 251-259.

Izco, J. 1984. *Madrid Verde*. IEAPA-Consejería de Agricultura de la Comunidad de Madrid, Madrid, ES.

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

Jørgensen, P.M. 1978. The lichen family Pannariaceae in Europe. *Opera Bot.* 45: 1-124.

Kivistö, L. & Kuusinen, M. 2000. Edge effects on the epiphytic lichen flora of *Picea abies* in middle boreal Finland. *Lichenologist* 32: 387-398.

Legendre, P. & Anderson, M.J. 1999. Distance-based redundancy analysis: testing multispecies responses in multifactorial ecological experiments. *Ecol. Monogr.* 69: 1-24.

Legendre, P. & Legendre, L. 1998. *Numerical ecology*. Elsevier, Amsterdam, NL.

Littell, R.C., Milliken, G.A., Stroup, W.W. & Wolfinger, R.D. 1996. *SAS System for Mixed Models*. SAS Institute Inc. NC, US.

Liu, C., Ilvesniemi, H. & Westman, C.J. 2000. Biomass of arboreal lichens and its vertical distribution in a boreal coniferous forest in central Finland. *Lichenologist* 32: 495-504.

Löbel, S., Snäll, T. & Rydin, H. 2006. Species richness patterns and metapopulation processes – evidence from epiphyte communities in boreo-nemoral forests. *Ecography* 29: 169-182.

Marañón, T., Camarero, J.J., Castro, J., Díaz, M., Espelta, J.M., Hampe, A., Jordano, P., Valladares, F., Verdú, M. & Zamora, R. 2004. Heterogeneidad ambiental y nicho de regeneración. In: Valladares, F. (ed.) *Ecología del bosque mediterráneo en un mundo cambiante*, pp. 69-100. Organismo Autónomo de Parques Nacionales, Ministerio de Medio Ambiente, Madrid, ES.

Martínez, I., Aragón, G., Sarrión, F.J., Escudero, A., Burgaz, A.R. & Coppins, B. 2003. Threatened lichens in central Spain. *Cryptog. Mycol.* 24: 73-97.

McCullagh, P. & Nelder, J.A. 1989. *Generalized Linear Models*, 2nd ed. Monographs on Statistics and Applied Probability 37. Chapman and Hall/CRC, New York, NY, US.

Meiners, S.J., Pickett, S.T.A. & Handel, S.N. 2002. Probability of tree seedling establishment changes across a forest-old field edge gradient. *Am. J. Bot.* 89: 466-471.

Moen, J. & Jonsson, B.G. 2003. Edge effects on Liverworts and lichens in forests patches in a mosaic of Boreal Forest and Wetland. *Conserv. Biol.* 17: 380-388.

Murcia, C. 1995. Edge effects in fragmented forests: implications for conservation. *Trends Ecol. Evol.* 10: 58-62.

Nimis, P.L. 2003. *Checklist of the lichens of Italy 3.0*. University of Trieste. http://dbiodbs.univ.trieste.it

Randlane, T. 1998. Red list of Estonian macrolichens. *Folia Cryptog. Est.* 32: 75-79.

Renhorn, K.E., Esseen, P.A., Palmqvist, K. & Sundberg, B. 1997. Growth and vitality of epiphytic lichens. I. Responses to microclimate along a forest edge-interior gradient. *Oecologia* 109: 1-9.

Rheault, H., Drapeau, P., Bergeron, Y. & Esseen, P.A. 2003. Edge effects on epiphytic lichen in managed black spruce forests of eastern North America. *Can. J. For. Res.* 33: 23-32.

Richardson, D.H.S. & Cameron, R.P. 2004. Cyanolichens: Their response to pollution and possible management strategies for their conservation in northeastern North America. *Northeast. Nat.* 11: 1-22.

Santos, T. & Tellería, J.L. 1998. *Efectos de la fragmentación de los bosques sobre los vertebrados en las mesetas ibéricas*. Organismo Autónomo de Parques Nacionales, Dirección

General de Conservación de la Naturaleza, Ministerio de Medio Ambiente, Madrid, ES.

Scarascia-Mugnozza, G., Oswald, H., Piussi, P. & Radoglou, K. 2000. Forests of the Mediterranean region: gaps in knowledge and research needs. *For. Ecol. Manage.* 132: 97-109.

Sillet, S.C. 1994. Growth rates of two epiphytic cyanolichen species at the edge and in the interior of a 700-Year-Old Douglas Fir Forest in the Western Cascades of Oregon. *Bryologist* 97: 321-324.

Sjöberg, K. & Ericson, L. 1992. Forested and open wetland complexes. In: Hansson, L. (ed.) *Ecological principles of nature conservation*, pp. 326-351. Elsevier, London, UK.

ter Braak, C.J.F. 1983. Principal components biplots and alpha and beta diversity. *Ecology* 64: 454-462.

ter Braak, C.J.F. 1986. Canonical correspondence analysis, a new eigenvector technique for multivariate direct gradient analysis. *Ecology* 67: 1167-1179.

ter Braak, C.J.F. 1990. *Update notes: CANOCO version 3.1.* Microcomputer Power, New York, NY, US.

ter Braak, C.J.F. & Šmilauer, P. 1997. *CANOCO. Reference manual and user's guide to CANOCO for Windows: Software for canonical community ordinations, Version 4.5.* Microcomputer Power, Ithaca, NY, US.

Thor, G. & Arvidsson, L. 1999. *Rödlistade lavar I Sverige-Artfakta.* [*Swedish Red Data Book of Lichens*]. Artdatabanken, SLU, Uppsala, SE.

Valladares, F. 2003. Light and the evolution of leaf morphology and physiology. *Curr. Top. Plant Biol.* 4: 47-61.

Will-Wolf, S., Geiser, L.H., Neitlich, P. & Reis, A.H. 2006. Forest lichen communities and environment – How consistent are relationships across scales? *J. Veg. Sci.* 17: 171-184.

For App. 1 and 2, see also JVS/AVS Electronic Archives; www.opuluspress.se/

App. 1. Environmental variables investigated. Data mean ± SD and range between parentheses.

Variable names	Data/categories	Explanation
Distance to edge	5, 15, 25, 35, 45, 55, 100 m	Distance in meters of the plot to the edge
N of trees per plot	2.82 ± 1.13 (1-6)	Number of trees in each plot
Mean dbh per plot	29.17 ± 6.45 (13.4-45.4) cm	Mean diameter at breast height (dbh) of all trees larger than 5 cm in each plot
Irradiance	0.23 ± 0.06 (0.1-0.41) mol.m^{-2}.d^{-1}	Light availability using the global site factor (GSF values)
Height of the square	2 point scale: 0=at tree base, 1= at breast height	Height on the tree where the square was located (at breast and at tree base)
Aspect of the square	2 point scale: 0 = south, 1 = north	The square was located at two orientations of the bark: north and south
Diameter of tree	33.94 ± 6.04 (22-43) cm	Diameter of the trees on the epiphytic data were taken
Height of tree	16.18 ± 3.52 (9-21) m	Height of the trees on the epiphytic data were taken

App. 2. Cover and appearance of species. Growth form (CO = thallus of two parts; CR = crustose; FO =foliose; FR = fruticose; SQ = squamulose). Data represent means ± standard error per plot and range (minimum and maximum cover in the plots where each species appeared) for all identified species. No. of squares indicates total number of squares where each species was found. Total number of squares was 452.

Species	Species abbr.	Growth form	Mean cover ± SE	Range	Nº of squares
Bryophytes	B		0.126 ± 0.225	0.001-0.975	241
Anaptychia ciliaris (L.) Körb.	Ac	FR	< 0.001 ± 0.013	0.009-0.24	5
Caloplaca ferruginea (Huds.) Th. Fr.	CAf	CR	< 0.001	-	1
Candelariella vitellina (Hoffm.) Müll. Arg.	Cv	CR	< 0.001 ± 0,000	-	2
Candelariella xanthostigma (Ach.) Lettau	Cx	CR	< 0.001 ± 0.001	0.001-0.008	6
Cladonia chlorophaea (Flörke ex Sommerf.) Spreng.	CLc	CO	0.016 ± 0.055	0.001-0.494	102
Cladonia fimbriata (L.) Fr.	CLf	CO	< 0.001 ± 0,010	0.004-0.139	6
Collema fragrans (Sm.) Ach.	COfr	SQ	0.001 ± 0.016	0.014-0.324	6
Collema furfuraceum (Arnold) Du Rietz	COf	FO	0.011 ± 0,028	0.001-0.333	164
Collema subflaccidum Degel.	COs	FO	< 0.001 ± 0,005	0.012-0.055	7
Dendriscocaulon umhausense (Auersw.) Degel.	Du	FR	0.002 ± 0,012	0.003-0.116	36
Evernia prunastri (L.) Ach.	Ep	FR	0.017 ± 0,05	0.001-0.522	139
Fuscopannaria ignobilis (Anzi) P. M. Jørg.	Fi	SQ	< 0.001	-	1
Fuscopannaria mediterranea (Tav.) P. M. Jørg.	Fm	SQ	0.022 ± 0,066	0.002-0.735	139
Lecanora chlarotera Nyl.	LEch	CR	< 0.001 ± 0,000	0.001-0.005	6
Lecanora horiza (Ach.) Linds**.**	LEh	CR	0.001	-	1
Lepraria incana (L.) Ach.	Li	CR	< 0.001 ± 0,011	0.024-0.228	3
Leptogium furfuraceum (Harm.) Sierk	LPf	FO	< 0.001 ± 0,006	0.004-0.076	8
Leptogium quercicola Otálora Aragón I. Martínez and Molina	LPq	FO	0,001 ± 0,001	0.009-0.110	11
Leptogium subtile (Schrad.) Torss.	LPs	SQ	< 0.001 ± 0,007	0.005-0.136	6
Leptogium teretiusculum (Wallr.) Arnold	LPt	FO	< 0.001 ± 0,011	0.043-0.234	3
Lobaria pulmonaria (L.) Hoffm.	LOp	FO	< 0.001	-	1
Lobaria scrobiculata (Scop.) Cromb.	LOs	FO	0,004 ± 0,037	0.001-0.713	20
Melanelia fuliginosa (Fr. Duby) Essl.	Mf	FO	0,009 ± 0,034	0.002-0.227	83
Melanelia glabra (Schaer.) Essl.	Mg	FO	0,107 ± 0,156	0.001-0.748	312
Melanelia subaurifera (Nyl.) Essl.	Ms	FO	0,002 ± 0,013	0.002-0.140	32
Micarea prasina Fr.	MIp	CR	< 0.001 ± 0,001	0.004-0.027	4
Mycobilimbia berengeriana (A.Massal.) Hafellner and V. Wirth	MYb	CR	< 0.001	-	1
Nephroma laevigatum Ach.	Nl	FO	0,003 ± 0,026	0.006-0.338	13
Parmelia saxatilis (L.) Ach.	Ps	FO	< 0.001 ± 0,007	0.005-0.129	4
Parmelia sulcata Taylor	Psu	FO	0,017 ± 0,050	0.006-0.400	112
Parmeliella triptophylla (Ach.) Müll. Arg.	Pat	SQ	< 0.001 ± 0,002	0.006-0.029	3
Parmelina quercina (Willd.) Hale	PMq	FO	< 0.001	-	1
Parmelina tiliacea (Hoffm.) Hale	PMt	FO	0,042 ± 0,090	0.002-0.696	236
Parmotrema chinense (Osbeck) Hale and Ahti	PRMc	FO	< 0.001	-	1
Peltigera canina (L.) Willd.	PEc	FO	< 0.001	-	1
Peltigera collina (Ach.) Schrad.	PEco	FO	0,007 ± 0,041	0.003-0.486	26
Peltigera neckeri Hepp ex Müll. Arg.	PEn	FO	0,002 ± 0,021	0.036-0.247	5
Pertusaria albescens (Huds.) M. Choisy and Werner	PRab	CR	< 0.001 ± 0,016	0.007-0.329	5
Pertusaria amara (Ach.) Nyl.	PRa	CR	< 0.001 ± 0,008	0.003-0.140	7
Pertusaria flavida (DC.) J. R. Laundon	PRf	CR	< 0.001 ± 0,001	0.003-0.023	4
Pertusaria hemisphaerica (Flörke) Erichsen	PRh	CR	< 0.001	-	1
Pertusaria pertusa (Weigel) Tuck.	PRp	CR	< 0.001 ± 0,001	0.005-0.021	3
Phlyctis argena (Spreng.) Flot.	PHa	CR	0,004 ± 0,029	0.003-0.527	35
Physcia adscendens (Fr.) H. Olivier	PHYad	FO	0,005 ± 0,049	0.004-0.731	18
Physcia aipolia (Ehrh Humb.) Fürnr.	PHYa	FO	0,035 ± 0,060	0.003-0.560	219
Physcia semipinnata (J. F. Gmelin) Moberg	PHYs	FO	< 0.001 ± 0,006	0.011-0.127	3
Physconia distorta (With.) J. R. Laundon	PHSd	FO	0,064 ± 0,086	0.004-0.437	272
Physconia enteroxantha (Nyl.) Poelt	PHSe	FO	0,033 ± 0,064	0.004-0.514	193
Physconia grisea (Lamb.) Poelt	PHSg	FO	< 0.001 ± 0,009	0.016-0.118	5
Physconia perisidiosa (Erichsen) Moberg	PHSp	FO	0,012 ± 0,036	0.003-0.315	89
Physconia venusta (Ach.) Poelt	PHSv	FO	0,045 ± 0,088	0.004-0.449	171
Ramalina calicaris (L.) Fr.	Rc	FR	< 0.001 ± 0,011	0.012-0.175	3
Ramalina farinacea (L.) Ach.	Rf	FR	0,047 ± 0,096	0.002-0.601	223
Ramalina fraxinea (L.) Ach.	Rfr	FR	0,001 ± 0,011	0.015-0.156	8
Usnea wasmuthii Räsänen	Uw	FR	< 0.001 ± 0,004	0.001-0.057	10
Waynea adscendens Rico	Wa	SQ	< 0.001 ± 0,002	0.007-0.033	2
Xanthoria parietina (L.) Th. Fr.	Xp	FO	< 0.001 ± 0,000	0.0002-0.0004	3

OPULUSPRESS