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Large-scale patterns of epiphytic lichen species richness: Photobiont-dependent response to climate and forest structure

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ABSTRACT

Lichens are composite organisms consisting of a symbiotic association of a fungus with a photosynthetic partner. Although the photobiont type is a key life-history trait, tests of the potential differential role of the main photobiont types in shaping large-scale patterns of lichen species richness are still absent. The aim of the study was to test the influences of forest structure and climate on epiphytic lichen species richness across Italy and to see whether these relationships change for groups of species sharing different photobiont types. Regional species richness of epiphytic lichens divided into three main photobiont types (i.e. chlorococcoid green algae, cyanobacteria, and *Trentepohlia* algae) was retrieved for each of the 20 administrative regions. Multiple linear regression was used to quantify the effect of climate and forest structure, and their potential interaction, on the regional species richness for the three photobiont types, accounting also for the effect of regional area. Regional species richness was associated with both climate and forest structure variables but the relationships with both factors were largely photobiont dependent. Regional area and precipitation were the only predictors included in all the models, confirming the strong dependence of lichens on atmospheric water supply, irrespective of the photobiont type. Number of species with chlorococcoid green algae were further positively associated with cover of high forest, whilst lichens with *Trentepohlia* were further enhanced by warm temperatures. Cyanolichen species richness was only related to area and precipitation. Our study shed light on the relative importance of climate and forest structure on lichen species richness patterns at the macroscale, showing a differential response of the photobiont types to various environmental determinants. This differential response suggested that the current and future impacts of global change on lichens cannot be generalized and that species richness response will be likely dependent on the photobiont type.
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1. Introduction

The composition of epiphytic lichen communities depends on factors that operate at multiple spatial and temporal scales. At the local scale, epiphytic lichen composition is mainly related to microclimatic and substrate factors associated with forest structure and continuity (Ellis and Coppins, 2007; Aragón et al., 2010a, 2010b; Nascimbene and Marini, 2010), while at broader scales climate and dispersal limitations are further important drivers (Werth et al., 2005; Giordani, 2006).

Lichen physiology is closely coupled to ambient moisture and temperature conditions (Green et al., 2008) so that their geographical distribution is expected to be associated with climatic gradients (Jovan and McCune, 2004; Goward and Spribille, 2005; Geiser and Neitlich, 2007; Giordani and Incerti, 2008). Previous biogeographical research on several taxonomic groups (Whittaker et al., 2007) has indicated that water-related variables usually represent the strongest control of species richness in 'warm' areas (low latitude), whereas energy variables gain importance in 'cold' areas (high latitude) ('conjecture' of Hawkins et al., 2003). The interaction between water and energy variables, however, has seldom been tested on species richness patterns of lichens (but see van Herk et al., 2002).

Along with climate, forest management, (i.e. modifying the availability and the diversity of substrates) is clearly a key direct control of epiphytic lichen species richness at the stand scale (e.g. Johansson et al., 2007; Nascimbene et al., 2007, 2009; Caruso et al., 2008; Aragón et al., 2010a, 2010b). Forest age is also known to be a key factor influencing epiphytic lichen communities by increasing substrate stability (Moning et al., 2009). Forest management and age have also an indirect effect through the alteration of microclimatic conditions, i.e. inside old, undisturbed and multi-layered forests the microclimate tends to be more buffered and more humid than the prevailing climate, favouring the growth of humidity-loving species (Werth et al., 2005; Ellis et al., 2009).

This template predicts that where climate is favourable for most of the species (e.g. high atmospheric moisture), relatively large lichen

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species richness can be found even where forest habitat quality is relatively 'low' (e.g. disturbed and young stands), whilst when climate is generally unsuitable, the influence of forest quality should gain importance (Ellis and Coppins, 2007). This interaction between forest structure and climate has been demonstrated at the local scale but it is still unclear if this pattern is also evident at the biogeographical scale.

As lichens possess a wide range of optima with regard to moisture, temperature, substrate quality and stability, and nutrient inputs, various life-history traits are expected to modify the lichen response to various environmental factors. Lichens are composite organisms consisting of a symbiotic association of a fungus (the mycobiont) with a photosynthetic partner (the photobiont). Although the type of photobiont partner has been demonstrated to be a key trait potentially mediating the response of lichens to both climate (Ellis and Coppins, 2006; Aptroot and van Herk, 2007) and land use (Stofer et al., 2006; Hedenås et al., 2007), large-scale tests of the potential role of photobiont type in shaping biogeographical patterns of species richness are still absent.

Hence, the main aim of this study was to test a potential differential response to climate and forest structure of species richness of epiphytic lichens sharing different photobiont types. We tested this prediction using a large-scale dataset on the distribution of epiphytic lichens in a Mediterranean country. Our hypotheses were that (i) species richness of lichens should be primarily enhanced by high precipitation whilst temperature should have a contrasting response; i.e. a positive effect in wet regions and a negative effect in dry regions (modified 'water–energy conjecture' of Hawkins et al., 2003); (ii) the presence of high forests rather than young coppice forests should increase epiphytic lichen species richness due to less intensive management and greater forest continuity; (iii) we expected a compensatory effect of the availability of high forests in regions with unsuitable climatic conditions (warm and dry), i.e. an interaction between forest structure and climate; and finally (iv) we expected a differential response to these environmental determinants of lichen species sharing different photobiont types (DePriest, 2004; Friedel and Büdel, 2008). As air pollution is considered an important driver of lichen communities (Geiser and Neitlich, 2007) we also tested the effect of this factor along with our climate and forest variables.

2. Methods

2.1. Study area

The study area included the entire territory of Italy, divided into 20 administrative regions. Forests covered c. 105,000 km^2, only 36% of which are high forest types (mainly coniferous forests). The rest were managed by coppicing. Coppicing is the traditional method of management applied to broad-leaf forests in Italy (INFC, 2005). Several species such as oaks, beech, and chestnut are often intensively coppiced for wood fuel production. In several regions coppice forest amounted up to ~75% of the total cover, replacing potential high forests. Since 1870 the forest cover has increased by c. 30%, mostly replacing extensively managed grasslands and traditional agricultural cultures. However, the proportion of forest managed by coppicing also increased, particularly in the central and southern part of the peninsula where high forest management was less frequent. Due to the relatively wide latitudinal range, the presence of the Alps in the north, and that of the Apennines along the peninsula, the climate of Italy is extremely heterogeneous. Together with a latitudinal gradient between the north and south, a strong climatic longitudinal gradient can be found across the peninsula.

2.2. Lichen data

In recent years, data on the distribution of epiphytic lichens in Italy has reached a comparable level of knowledge across regions. The use of epiphytic lichens in nation-wide monitoring projects made this group of lichens the best known. The number of species of epiphytic lichens for each of the 20 Italian administrative regions was retrieved from the most updated version of ITALIC, the on-line database of Italian lichens (available at: http://dbiodbs.univ.trieste.it/; Nimis and Martellos, 2008). All species which are known to occur on bark and/or wood were considered, excluding non-lichenised and lichenicolous fungi. We also excluded lichen species which are exclusively lignicolous, but included those which are both lignicolous and epiphytic. The whole data set was split in three non-overlapping species richness groups according to the different types of photobiont: (i) lichens with chlorococcoid green algae, mainly including trebouxioid species, (ii) lichens with cyanobacteria (cyanolichens), and (iii) lichens with *Trentepohlia*. Tripartite species [e.g. *Lobaria pulmonaria* L. (Hoffm.)] were assigned to only one of these groups according to their main photobiont type.

2.3. Explanatory variables

A set of parameters indicative of climatic conditions (both precipitation and temperature) and forest structure, along with other factors that were potentially important at our spatial scale, were selected as explanatory variables (Table 1). We included as predictors only variables that were expected to play an important role in shaping lichen species richness patterns according to current scientific knowledge. Normal mean annual temperature was derived from the WorldClim database (Hijmans et al., 2005; 1×1 km grid resolution; average over 1960–1990 period). Annual precipitation was derived from a national raster map (L'Abate and Costantini, 2005; 3×3 km grid resolution; average over 1960–1990 period). Up-to-date information on regional forest structure: dead wood biomass, basal area, forest composition and management (high vs. coppice forest) were retrieved from the National Forest Inventory (INFC, 2005). We used the regional statistics provided by the inventory which are based on data from 300,000 1-km^2 sampling cell covering the entire national territory. We contrasted coppice vs. high forests as these are the most common silvicultural systems applied in Italy. Coppice forests are normally young and degraded broadleaved forests for wood fuel production, in which young tree stems are repeatedly cut down to near ground level with short rotation cycles. After harvest, new shoots will emerge and, after a number of years, the coppiced tree is ready to be harvested again. High forests are woodlands where regeneration is usually of seedling origin, either natural or artificial (or a combination of both), and where the rotation cycles are generally long.

As broad geographical gradients might be associated with large variations in both land use and climate, measures of environmental

Table 1
Variables included in the study and quantified in the 20 Italian regions.

Variables name and explanation		Unit	Mean	Min	Max
Area	Area of the region	km^2	15,059	3266	25,701
NO*x*	Average emission of nitrogen oxides (1990–2005)	mg yr^{-1}	77,481	6383	216,445
Climate					
Rain	Mean annual precipitation	mm	1010	769	1277
Rain-SD	Standard deviation of precipitation	mm	168.5	84.8	314.2
Temp	Mean annual temperature	°C	11.62	1.86	15.58
Temp-SD	Standard deviation of temperature	°C	0.729	0.278	1.116
Forest structure					
High	Proportion of forest area managed as high forest	%	37.37	11.11	76.43
Coppice	Proportion of forest area managed by coppicing	%	39.89	1.96	74.31
Basal	Mean basal area	m^2 ha^{-1}	19.82	12.60	31.30
Wood	Mean dead wood	m^3 ha^{-1}	6.95	1.40	16.50
For-Het	Shannon index of forest types	–	1.933	1.176	2.260

heterogeneity should be considered, particularly as the size of the sampling unit increases. Thus, as measure of climate heterogeneity we used the standard deviation of temperature and precipitation computed from the pixels falling within each region. Forest habitat heterogeneity was quantified using the Shannon–Wiener index (For-Het). The latter measure was computed using the national forest inventory data that defines 17 forest categories on the basis of the dominant tree species (INFC, 2005). The Shannon–Wiener index was computed as follow:

$$For - Het = -\sum p_i \log p_i,$$

where p_i is the relative abundance of the i forest type in each region.

As atmospheric pollution might be an important driver of lichen distribution across different spatial scales, we included the average annual emission of the main pollutants (SO*x*, NO*x*, and organic volatile compound) in each region across four periods (1990, 1995, 2000, and 2005) (ISPRA, 2005). The pollution data were estimated by using proxy variables such as the industrial, agricultural, and other anthropogenic activities and represent estimates of the cumulative production of pollutants at the regional scale. As SO*x*, NO*x*, and organic volatile compound were strongly correlated ($r>0.90$), we included in the analyses only the average NO*x* regional emissions across the four periods. We also computed the standard deviation of NO*x* emissions over the four years. However, the correlation between average and standard deviation of NO*x* was very high ($r>0.95$), and we therefore excluded the latter from further analyses.

2.4. Data analysis

Regional number of species per photobiont type in each Italian region was used as a response variable. Multiple regression was used to quantify the effects of regional area, climate, forest structure, and pollution on species richness. We verified the assumptions of linear regression by inspecting all the pairwise relationships between our response and explanatory variables and by inspecting model diagnostic plots (Q–Q plot of model residuals and plot of model residuals vs. fitted values). As the sampling unit (i.e. regions) differed in size, we first tested the effect of regional area in all models to account for the species–area relationship. If in these univariate analyses area was significant this factor was included in the model before testing the other explanatory variables. After testing all the linear terms, we also tested the interaction between temperature and precipitation ('conjecture' of Hawkins et al., 2003) and the interaction between proportion of high forest and precipitation. The analyses were performed for the three photobiont types, separately. The analysis was run using the lm(stats) function in R version 2.12 (R Development Core Team, 2011).

Due to the low number of replicates and the relatively large number of competing hypotheses we also evaluated our models by using a multi-model inference approach (Burnham and Anderson, 2002). Our information-theoretic approach compared the fit of all the possible candidate models obtained by the combination of our predictors using second-order Akaike's information criterion (AICc). The AICc is a measure of relative model fit, proportional to the likelihood of the model and the number of parameters used to build it. The best fitting model is the one with the lowest AICc. Amongst a set of n models, each model i can be ranked using its difference in AICc with the best fitting model ($\Delta AICc_i = AICc_i - AICc$ minimum). The difference in AICc values indicates the relative support for the different models. A model is usually considered plausible if its ΔAICc is below 2. The multi-model inference analyses were performed using the 'MuMIn' package (Barton, 2010) implemented in R version 2.12 (R Development Core Team, 2011).

3. Results

The total number of epiphytic lichen species known from Italy was 822, 625 of which had chlorococcoid green algae (76.0%), 61 had cyanobacteria (7.5%), and 136 had *Trentepohlia* (16.5%). Lichen species richness in the regions varied from a minimum of 167 to a maximum of 468, with a mean of 337. The three photobiont groups had different richness patterns across the 20 regions (Fig. 1).

During model fitting we log-transformed species richness and regional area to improve model fit and increase the linearity of the relationships. After these transformations models met the assumptions of multiple linear regression.

The degree of collinearity between our predictors was generally low (Table 2). Except for NO*x* emissions and forest heterogeneity, no predictor had a significant correlation with regional area. The relatively high correlation between area and pollution reduced the possibility to evaluate the role of pollution in driving regional species richness. As there was a high correlation between coppice and high forests ($r_s = -0.90$), we tested only the latter in our models. We chose proportion of high forests as this variable generally presented a stronger relationship with lichen species richness. Due to the high correlation between basal area and mean quantity of deadwood, the basal area was not included in the forward selection.

A linear positive relationship was found between area and the number of species belonging to the three photobiont groups. The species–area relationship explained 27.4, 36.1 and 50.7% of the total variation in species richness of lichens with chlorococcoid green algae,

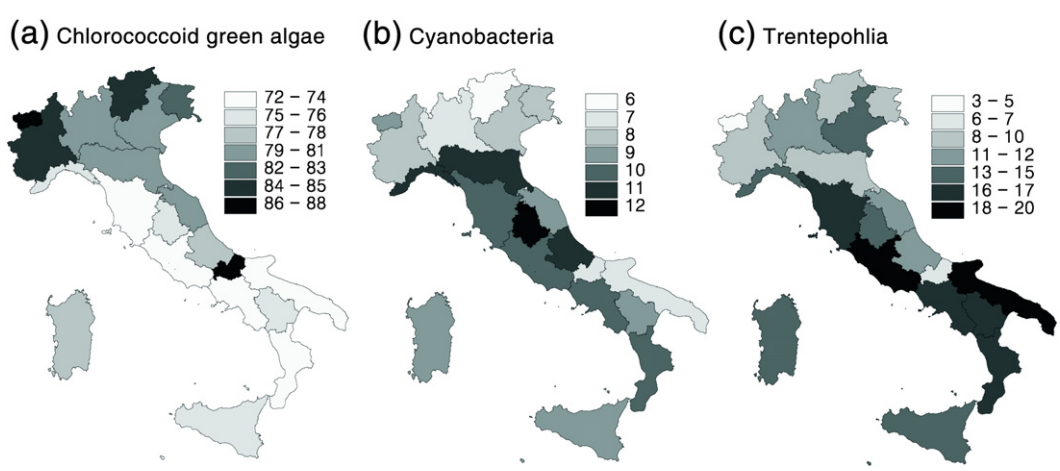

Fig. 1. Maps of the proportion (%) of lichen species in symbiosis with (a) chlorococcoid green algae, (b) cyanobacteria, and (c) *Trentepohlia* in the 20 regions of Italy.

Table 2
Pearson correlations between the predictors quantified in the 20 Italian regions. In the three lines at the bottom of the table the correlations with the species richness of the three photobiont types are also reported. Only significant correlations are shown (P<0.10). Variables inside of square brackets were excluded from further analyses due to large collinearity.

	Log(Area)	NO*x*	Rain	Temp	[Basal]	Wood	High	[Coppice]	Rain-SD	Temp-SD	For-Het
NO*x*	0.68										
Rain	–	–									
Temp	–	–	–								
[Basal]	–	–	0.57	–							
Wood	–	–	0.48	−0.60	0.75						
High	–	–	–	–	0.43	–					
[Coppice]	–	–	–	–	–	–	−0.90				
Rain-SD	–	–	–	–	–	–	–	–			
Temp-SD	–	–	–	–	–	–	–	–	–		
For-Het	0.43	0.64	–	–	–	–	–	–	–	0.42	
Log(Chloro)	0.60	0.45	0.46	–	0.57	0.55	0.38	–	–	0.50	–
Log(Cyano)	0.52	0.38	0.44	–	–	–	–	–	–	–	0.54
Log(Trente)	0.71	0.50	–	0.59	–	–	–	–	–	–	0.58

Log(Chlor), Log(Cyano), and Log(Trente) indicate log-transformed species richness of lichens with chlorococcoid green algae, cyanobacteria, and *Trentepohlia*, respectively.

cyanobacteria, and *Trentepohlia*, respectively. The final models were therefore built using a forward selection procedure (P<0.05) starting from a model already including area. The multiple regression model for lichen species with chlorococcoid green algae included, along with area, annual precipitation, and the proportion of high forest, both factors with a positive effect (Table 3). Including the proportion of coppice instead of high forest we would have obtained very similar models, but with a negative effect of the former factor. The model for cyanolichen species richness included area and annual precipitation. The model for lichens with *Trentepohlia* included area, temperature, and precipitation. All factors had a marginal positive influence on the number of species. Measures of environmental heterogeneity were never significant. No interactions were detected between climate factors and between forest and climate factors, i.e. at our spatial scale the effect of climate was independent from that of forest structure. No marginal effect of atmospheric pollution on lichen species richness was found for the three photobiont types.

For all the three photobiont types the multi-model inference analysis indicated that only one plausible model was supported; i.e. all the possible alternative models had ΔAICc>2. The plausible models selected on the basis of AICc corresponded to those selected using the p-values of the regression coefficients (Table 3), indicating that model selection uncertainty was low within this dataset.

Table 3
Multiple regression models (n = 20) testing climate and forest variables vs. the log-transformed number of lichen species in symbiosis with (a) chlorococcoid green algae, (b) cyanobacteria, and (c) *Trentepohlia*. Log(Area) was tested first in all the models to account for the species–area relationship (refer to the data analysis section for more details).

	Regression coefficient	Standard error	t	P	R^2
(a) Chlorococcoid green algae					*0.90*
Intercept	1.0496	–	–	–	
Log(Area)	0.8808	0.0877	10.041	<0.01	
Rain	0.00076	0.0001227	6.26	<0.01	
High	1.7383	0.2811	6.18	<0.01	
(b) Cyanobacteria					*0.56*
Intercept	−0.5751	–	–	–	
Log(Area)	0.7571	0.2015	3.76	<0.01	
Rain	0.00095	0.00028	3.05	<0.01	
(c) Trentepohlia					*0.74*
Intercept	−4.2678	–	–	–	
Log(Area)	1.4805	0.3331	4.44	<0.01	
Rain	0.00127	0.0004292	2.95	<0.01	
Temp	0.0614	0.0255	2.40	0.03	

4. Discussion

In our Mediterranean country, the association of epiphytic regional lichen species richness with both climate and forest variables was largely photobiont dependent. According to our expectations regional area was one of the strongest predictor of lichen species richness. A positive species–area relationship is one of the most consistent biogeographical patterns in nature (Rosenzweig, 1995). Two often suggested mechanisms underpinning this positive relationship are the area per se and the habitat diversity hypotheses. The area per se predicts that the number of species in a region represents an area-mediated equilibrium between extinctions and colonizations, with higher extinction rates in smaller vs. larger areas (MacArthur and Wilson, 1967). The habitat diversity hypothesis assumes that larger areas are more likely to contain greater environmental heterogeneity and therefore more species as generally predicted by niche theory (Huston, 1979). Although we did not find any effect of pollution we cannot rule out this factor as a further potential driver of lichen species richness patterns because our ability to detect an effect of air pollution within the current data set was strongly diminished by its collinearity with area.

Concerning climate, precipitation was the dominant driver of lichen species richness irrespective of the photobiont type. All the photobiont types presented a positive association with annual precipitation, confirming that a rainy climate is a crucial factor for sustaining species-rich communities (Giordani and Incerti, 2008). Several authors have demonstrated the strong relationship between precipitation and lichen distribution, illustrating its crucial role in key metabolic processes such as gas exchange, nitrogen fixation, and photosynthesis (Nash, 2008). This suggests that in Mediterranean regions drier climates sustained less species than wetter ones probably because of less favourable conditions for key physiological processes. However, precipitation should not be considered as a direct control on lichens but more as a proxy for other forms of atmospheric moisture. For instance rainy regions are more likely to exhibit longer periods with large atmospheric humidity suitable for growth and reproduction. The climatic results confirmed only partially our first hypothesis, i.e. stronger effect of water-related variables in warm regions (Hawkins et al., 2003), as we did not find any interactive effect between temperature and precipitation. Temperature was positively related to the species richness of lichens in symbiosis with *Trentepohlia*, while for species with chlorococcoid green algae and cyanobacteria we did not find any significant association with this factor.

We did not find the expected interaction between forest structure and climate (e.g. Ellis and Coppins, 2007; Ellis et al., 2009), i.e. stronger effect of climate where forest quality was low for the large

majority of the species (coppice forests). This was probably caused by the coarse spatial grain of our data (i.e. regions) which might have masked this effect. As the response to both climate and forest structure was strongly dependent on the photobiont type, in the following sections, the specific response of the three photobiont groups will be discussed in more detail.

4.1. Lichens with chlorococcoid green algae

The large majority of lichens were in symbiosis with chlorococcoid green algae. Besides with annual precipitation their species richness was positively associated with increasing availability of high forest. Conforming to our second hypothesis, the positive relationship between lichen species richness and indicators of forest continuity and extensive management indicated that forest structure was an important factor also at the macroscale (see also Will-Wolf et al., 2006). The positive relationship with the extent of high forests (and conversely the negative relationship with the proportion of young coppice forests) confirmed results obtained at the local scale (Will-Wolf et al., 2006; Moning et al., 2009; Aragón et al., 2010a). High forests provide more stable substrate availability, while the short rotation cycles such as those employed in coppice broadleaved forests were probably detrimental to the majority of the lichen species due to the high disturbance and low forest continuity.

4.2. Lichens with cyanobacteria

The occurrence of epiphytic lichens with cyanobacteria is expected to be strongly related to the amount of atmospheric moisture (Jovan and McCune, 2004; Goward and Spribille, 2005), because these photobionts need liquid water for activating photosynthesis (Lange et al., 1986, 1993). This results in a strong sensitivity of epiphytic cyanolichens to dry conditions (e.g. Gauslaa et al., 2007; Pinho et al., 2010). Accordingly, in Italy precipitation was the only factor explaining the richness pattern of cyanolichens, which were more numerous along the western side of the peninsula and, in northern Italy, in the rainiest areas of the Alps. Recent stand level studies indicated that in Italy these lichens are mainly restricted to humid and scarcely disturbed forests of the montane belt (Nascimbene et al., 2007, 2009), in which habitat features may compensate for sub-optimal climatic conditions (Ellis et al., 2009). Although cyanolichens are often found to be sensitive to forest management at the stand scale (Nascimbene et al., 2007; Moning et al., 2009; Aragón et al., 2010a), their regional distribution could not be explained in terms of forest structure. This could have been related to the rather low number of replicates, to the relatively short gradient in variation in the regional species richness and to the broad scale of our analyses which might have masked the local effect of forest management.

4.3. Lichens with Trentepohlia

Lichens with *Trentepohlia* proved to be sensitive only to climatic conditions, being enhanced by rainy and warm climates. This photobiont group was the only one responding to temperature. As lichens with *Trentepohlia* have their photosynthetic optimum in shaded-warm situations, with low moisture reducing their rates and efficiency of photosynthesis, epiphytic lichens with *Trentepohlia* are mainly found in subtropical-tropical (i.e. humid-warm) conditions (Sipman and Harris, 1989; Nimis and Tretiach, 1995). Moisture is also of critical importance for the reproduction of free-living *Trentepohlia* algae (Rindi and Guiry, 2002). According to Kappen (1993), these lichens are more sensitive to freezing than lichens with other types of photobiont. *Trentepohlia* algae, adapted to live under the canopy of tropical forests, require sheltered habitats and high air humidity. In Italy, these conditions can be fulfilled in rainy regions or in areas exposed to maritime influence, while the richness of lichens with *Trentepohlia* decreased in continental areas, being extremely low in the inner cold alpine regions. The sensitivity of these lichens to temperature was also confirmed by several authors (van Herk et al., 2002; Aptroot and van Herk, 2007), who stressed the key role of *Trentepohlia* photobiont in mediating the response of several taxonomically unrelated species to global warming.

5. Conclusions

Our study shed light on the relative importance of climate and forest structure on lichen species richness patterns at broad spatial scale, and demonstrated a photobiont-dependent response of lichen species richness to various environmental determinants. In our Mediterranean region, any possible future reduction in precipitation would probably impact the large majority of lichen species, irrespective of the photobiont type, whilst increasing temperature should not directly affect lichen species richness, negatively. Lichens with *Trentepohlia* are even expected to respond positively to global warming as already demonstrated in oceanic regions of Europe (van Herk et al., 2002; Aptroot and van Herk, 2007). Along with this climate effect, the current intensive forest management by coppicing applied in several Italian regions is causing severe impact on lichen species richness with chlorococcoid green algae, while, at our broad scale of analysis, a negative influence of intensive forest management was not apparent for lichens with *Trentepohlia* and cyanobacteria. This differential response suggests the current and future impacts of global change on lichens cannot be generalized and that species richness response will be likely dependent on the photobiont type.

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