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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.

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