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Functional traits of epiphytic lichens as potential indicators of environmental conditions in forest ecosystems

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ABSTRACT

Several experimental studies support the effectiveness of lichen diversity as an indicator of environmental change. On the contrary, the potential of functional trait values of epiphytic lichens as indicators of environmental conditions is still poorly documented. Comparisons of lichen diversity across diverse regions may be problematic due to high levels of floristic variation related to differences in environmental conditions (e.g. climate and substrate availability and types). Species' functional traits may prove to be a user-friendly tool for large-scale and long-term ecological monitoring. This paper explores the use of functional traits of epiphytic lichen species as indicators of environmental conditions: we tested the susceptibility of the three easily discernible functional traits (growth form, reproductive strategy, and photobiont type) to environmental factors related to climate, human disturbance, and stand structure. Lichen diversity and associated species traits were recorded in 14 plots within the Italian ForestBiota network representing the four main forest types of Italy. For each plot, several predictors of forest structure, climatic features, and human-related disturbances were recorded. A forward variable selection method, based on permutations and parametric tests, was used to evaluate the response of lichen diversity and functional traits. Of the three species traits, growth form was the most responsive and was a reliable indicator for evaluating and comparing the responses of epiphytic lichens to climate, human disturbance, and stand structure-related conditions in forest ecosystems across diverse regions. However, further research is needed to better clarify the potential of lichen traits in bioindication.

1. Introduction

In the last few decades, national and European monitoring programmes have been established to assess the ecological and economic value of forest ecosystems and to evaluate the risks posed by human-related factors to ecosystem function and biodiversity conservation (e.g. Granke et al., 2009). The Italian National Forest Inventory consists of an ad hoc network of plots for the intensive monitoring of forest ecosystems (Petriccione and Pompei, 2002). This monitoring program aims at detecting long-term ecological processes and at evaluating the effects of human-related stressors. It is based on an integrated and combined evaluation of forest structure, atmospheric deposition, crown condition, climatic parameters, and biodiversity (Ferretti, 2002).

At the European level, some interdisciplinary monitoring programmes (e.g. the ForestBiota project, Fischer et al., 2009) have recently included diversity assessments for many organisms strictly dependent on forest dynamics, such as epiphytic lichens (Stofer et al., 2003; Giordani et al., 2006). The loss of lichen diversity in response to environmental conditions is widely used as an indicator for several complex phenomena, including air pollution (Cislaghi and Nimis, 1997; Giordani, 2007; Rose and Hawksworth, 1981), climate conditions (Jovan and McCune, 2004; Geiser and Neitlich, 2007; Giordani and Incerti, 2008), and forest structure and dynamics (Hedenås and Ericson, 2000; Johansson, 2008; Nascimbene et al., 2010).

The evaluation of observed patterns of lichen diversity in terms of species traits is a recent, promising approach, which is, however, in need of further research (Ellis and Coppins, 2006; Johansson et al., 2007). Species traits (e.g. photobiont type, growth form, reproductive strategy) could be indicative of lichen community adaptation to environmental conditions (Diaz and Cabido, 2001), therefore providing relevant ecological information. For example, different reproductive strategies could be responsible for species' spatial patterns in fragmented landscapes (Löbel et al., 2006), while the algal partner and growth form may control the community structure,

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which is responsible for large-scale patterns of diversity (Ellis and Coppins, 2006, 2010; Ellis et al., 2007; Marini et al., 2011).

In general, independently of species richness and composition, functional traits of species are expected to directly link to environmental factors (Webb et al., 2010; Ricotta and Bacaro, 2010), allowing comparisons among different ecosystems and across regions. Several experimental studies support the effectiveness of lichen diversity as an indicator of environmental change, based on its sensitiveness to both climatic and anthropogenic factors (Nimis et al., 2002; Dettki and Esseen, 2003; Hauck, 2009; Mayer et al., 2009; Svoboda et al., 2010). However, the influence of environmental conditions on lichen functional traits is poorly documented (e.g. Ellis and Coppins, 2006; Marini et al., 2011), hindering their use in environmental monitoring.

In this study, we explore the use of the functional traits of epiphytic lichen species as indicators of environmental conditions. In particular, we tested the susceptibility of the three main functional traits (growth form, reproductive strategy, and photobiont type) to environmental factors related to climate, human disturbance, and forest stand structure.

2. Materials and methods

2.1. Study area

Twelve 50 m × 50 m plots included in the Italian ForestBiota network (Fischer et al., 2009), plus two additional plots of the same size of the Italian CON.ECO.FOR. network for which lichen data were available (Nascimbene, 2006; Giordani et al., 2006), were included in this study. Plots were distributed across Italy and belonged to four forest types (Fig. 1): (1) *Picea abies*-dominated forests (four plots), which were mainly restricted to the montane-subalpine belt of the northern regions; (2) *Fagus sylvatica*-dominated forests (three plots), which are distributed in the montane belt and can be found in all Italian regions, except for Sardinia; (3) deciduous *Quercus* spp.-dominated forests (three plots), distributed across Italy at lower altitudes than *Fagus sylvatica*-dominated forests; and (4) *Quercus ilex*-dominated evergreen forests (four plots), restricted to the coastal ranges of the Tyrrhenian and Adriatic sides of the peninsula and islands.

2.2. Lichen survey

Epiphytic lichens were surveyed according to the sampling protocol developed by Stofer et al. (2003) based on Asta et al. (2002). On each 50 m × 50 m plot, all trees above 50 cm circumference were divided into four groups based on size (two categories: diameter at breast height, DBH ≤ 36 cm and DBH > 36 cm) and bark pH (two categories: acidic bark, i.e. trees with bark pH ≤ 6, and neutral bark, for trees with bark pH > 6). Because our samples derived from a random selection among all trees with circumference > 50 cm, in each plot and in each forest type more than one tree species was selected (Tables 1 and 2). For each tree species, we considered average pH values obtained from the ICP Forests database. For each of the four categories, a number of trees was then randomly selected proportional to the relative occurrences of the four groups within the plot. In each plot, a minimum of 12 trees was selected for lichen survey. To minimize variability in the estimation of species richness within the plot for each of the four pre-categorized groups, additional trees were randomly selected until there were at least three trees per group. On each selected tree, epiphytic lichens were sampled by means of four 10 cm × 50 cm grids, each placed on one of the cardinal points (N, E, S and W) 100 cm above ground level (Asta et al., 2002). Further details of the lichen diversity assessment method

Fig. 1. Locations of the 14 plots included in this study. Plots belonging to different forest types are indicated by different symbols: ▲, *Picea abies*-dominated forests (four plots); ★, *Fagus sylvatica*-dominated forests (three plots); ●, deciduous *Quercus* spp.-dominated forests (three plots); *, *Quercus ilex*-dominated forests (four plots). Plots were named according to the standards of the CON.ECO.FOR., ICP Forests, and ForestBiota projects.

Modified from Petriccione and Pompei (2002).

are available in Giordani et al. (2006) and at www.forestbiota.org (Stofer et al., 2003).

2.3. Species identification and nomenclature

Most of the lichen species were identified in the field. Specimens of critical species were collected and identified in the laboratory on the basis of their macro-, micromorphological and chemical features. They were then stored in the herbaria of the Universities of Genova (GE), Siena (SI) and Turin (HUT). Nomenclature follows Nimis and Martellos (2008).

2.4. Environmental predictors

The descriptive statistics of 19 environmental predictors at the selected plots are presented in Table 1. Data were collected during periodic surveys carried out within the framework of the Italian network of forest ecosystems (CON.ECO.FOR.) and other National and International monitoring programmes (e.g. ICP Forests), with different temporal intervals depending on the expected variations of the parameters. Hereafter, the main sampling methods of three subsets of predictors are described (climatic and geomorphologic variables, atmospheric depositions, forest structure), although further details are available in the references cited for each subset.

2.4.1. Climatic and geomorphologic variables

Basic information about the geographical location of the selected plots was available in Petriccione and Pompei (2002). Meteorological monitoring instruments have been located in the open at each plot since 1997, and data for the observed parameters have been acquired continuously and stored in a database.

Table 1
Descriptive statistics: environmental predictors and response variables (forest type mean ± SD).

	Picea forests (n = 4)	*Fagus* forests (n = 3)	Deciduous *Quercus* sp. pl. forests (n = 3)	*Quercus ilex* forests (n = 4)
Predictors				
Climatic and geomorphologic variables[a]				
Latitude (range)	461,416–462,928	382,538–460,326	375,432–462,537	392,056–433,034
Longitude (range)	93,316–133,536	120,156–161,047	101,213–132,415	83,408–133,523
Elevation (m) (elev)	1381 ± 460	1233 ± 231	567 ± 370	267 ± 296
Rainfall (mm year^{-1}) (rain)	1142 ± 316	1567 ± 306	924 ± 239	838 ± 125
Temperature (°) (temp)	5.75 ± 1.71	8.33 ± 2.89	12.1 ± 0.81	14.9 ± 0.63
Atmospheric deposition[b,c]				
pH	5.19 ± 0.28	5.40 ± 0.21	5.54 ± 0.19	5.58 ± 0.23
H^+ (μequiv l^{-1})	7.50 ± 4.12	4.00 ± 1.73	2.50 ± 0.87	3.00 ± 1.15
NH_4^+ (μequiv l^{-1})	21.0 ± 3.2	32.3 ± 16.0	73.0 ± 54.7	69.00 ± 14.3
Ca^{2+} (μequiv l^{-1})	46.5 ± 11.9	82.0 ± 37.7	144 ± 111	121 ± 41.2
Mg^{2+} (μequiv l^{-1})	22.8 ± 7.8	43.7 ± 29.0	73.7 ± 54.0	156 ± 19.1
Na^+ (μequiv l^{-1})	18.5 ± 15.3	84.7 ± 82.9	118 ± 135	318 ± 77.3
K^+ (μequiv l^{-1})	34.5 ± 6.9	67.3 ± 33.4	101.7 ± 67.0	114 ± 22.0
SO_4^{2-} (μequiv l^{-1})	42.8 ± 18.1	63.7 ± 34.1	90.7 ± 45.1	150 ± 34.7
NO_3^- (μequiv l^{-1})	32.0 ± 11.2	27.7 ± 6.7	49.7 ± 28.8	68.0 ± 12.3
Cl^- (μequiv l^{-1})	17.0 ± 6.38	99.7 ± 95.1	142 ± 181	270 ± 163
Forest structure[a]				
Mean tree age (years) (age)	125 ± 52.0	113.3 ± 5.8	50.0 ± 20.0	43.8 ± 7.5
Basal area (m^2 ha^{-1}) (Bas)	48.9 ± 6.22	40.0 ± 0.10	25.0 ± 0.0	31.6 ± 6.85
Canopy depth (Can dep)	19.3 ± 2.36	11.7 ± 2.40	6.80 ± 0.00	6.65 ± 1.46
Leaf area index (LAI)	3.73 ± 0.58	4.51 ± 0.16	2.44 ± 0.00	4.30 ± 0.75
Number of sampled tree species	6	1	7	8
Response variables				
Growth form				
Crustose species (CRUST)	0.40 ± 0.18	0.67 ± 0.12	0.47 ± 0.12	0.85 ± 0.06
Fruticose species (FRUT)	0.18 ± 0.15	0.07 ± 0.06	0.13 ± 0.12	0.00 ± 0.00
Foliose species, narrow lobes (FOLN)	0.28 ± 0.15	0.00 ± 0.00	0.10 ± 0.10	0.08 ± 0.05
Foliose species, broad lobes (FOLB)	0.15 ± 0.13	0.27 ± 0.06	0.23 ± 0.06	0.05 ± 0.06
Photobiont				
Chlorococcoid algae (CHL)	0.98 ± 0.05	0.87 ± 0.12	1.00 ± 0.00	0.63 ± 0.15
Trentepohlia (TREN)	0.03 ± 0.05	0.10 ± 0.10	0.03 ± 0.06	0.38 ± 0.15
Reproductive strategy				
Sorediate species (SOR)	0.70 ± 0.14	0.47 ± 0.15	0.60 ± 0.10	0.48 ± 0.24
Isidiate species (ISI)	0.13 ± 0.13	0.13 ± 0.06	0.00 ± 0.00	0.00 ± 0.00
Sexual reproduction (SEX)	0.15 ± 0.10	0.43 ± 0.12	0.33 ± 0.06	0.53 ± 0.24
Lichen diversity				
Total number of species per FT (richness)	47	73	68	72
Average number of lichen species per tree (Avnsp)	5.9 ± 3.7	13.6 ± 7.0	10.8 ± 7.1	6.1 ± 2.6
Shannon index (H')	2.57 ± 0.79	3.50 ± 0.36	3.17 ± 0.68	3.17 ± 0.49
Simpson index (D)	0.90 ± 0.10	0.97 ± 0.01	0.95 ± 0.02	0.95 ± 0.02

[a] CONECOFOR project (Cutini, 2002; Fabbio and Amorini, 2002; Petriccione et al., 2002).
[b] Mosello et al. (2002).
[c] Marchetti et al. (2002).

2.4.2. Atmospheric deposition

We based our analysis on data of volume weighted mean concentrations in through-fall deposition at the selected plots, collected by Mosello et al. (2002) and Marchetti et al. (2002) (Table 1). At each plot, through-fall deposition was collected with 16 evenly distributed collectors. Precipitation samples were collected weekly from continuously exposed collectors consisting of a 2-l graduated polyethylene bottle with a 19.5 cm diameter funnel. A polyethylene net in the funnel prevented the collection of coarse debris, insects and leaves. The volume of water collected was 30 ml per millimetre of precipitation. Sample volumes were measured separately, then pooled together and an aliquot sent to the laboratory for analysis.

2.4.3. Forest structure

Data on forest structure at the selected plots have been collected during several surveys since 1998. For the purposes of this study, we used the dataset provided by Fabbio and Amorini (2002) and Cutini (2002).

Leaf area index (LAI) data were collected systematically at 12 locations within each plot, using a LAI-2000 Plant Canopy Analyser (Li-Cor, Lincoln, NE, USA). DBH of all living trees above the thresholds of 3 and 5 cm, in coppices and high forests respectively, were measured in order to calculate the basal area at plot level. Canopy depth was calculated on randomly selected trees as a function of tree height and height to crown base. Stand age was estimated and past radial stem growth assessed by core sampling in the upper tree storey (i.e. dominant and co-dominant trees).

2.5. Data analysis

Lichen diversity was evaluated using the following parameters: (1) species composition, (2) mean number of species per tree (Avnsp), (3) number of species in each plot (hereafter simply “species richness”), (4) Shannon index (H'), and (5) Simpson's index of diversity ($1 - D$).

Table 2
Tree species sampled within the forest types. Information on the total number of lichen species occurring on different tree species and on the average number of species per tree are also reported.

Forest type tree species	No. of sampled trees	Tot number of lichen species per tree species	Av n sp per tree ± st. dev.
***Picea* forests**	**45**	**47**	**5.9 ± 3.7**
Picea abies	37	41	6.4 ± 4.3
Abies alba	3	13	5.0 ± 2.0
Larix decidua	2	10	6.0 ± 1.4
Acer pseudoplatanus	1	4	4.0
Fraxinus excelsior	1	3	3.0
Pinus cembra	1	5	5.0
***Fagus* forests**	**33**	**73**	**13.6 ± 7.0**
Fagus sylvatica	33	73	13.6 ± 7.0
Deciduous *Quercus* sp. pl. forests	**43**	**68**	**10.8 ± 7.1**
Quercus cerris	19	61	15.2 ± 8.2
Quercus pubescens	12	26	8.5 ± 2.4
Quercus petraea	8	11	5.4 ± 1.6
Abies alba	1	16	16.0
Acer campestre	1	6	6.0
Carpinus betulus	1	13	13.0
Tilia platyphyllos	1	13	13.0
***Quercus ilex* forests**	**53**	**72**	**6.1 ± 2.6**
Quercus ilex	43	62	6.7 ± 3.4
Quercus pubescens	3	6	2.3 ± 1.5
Arbutus unedo	2	3	2.0 ± 0.0
Acer monspessulanum	1	5	5.0
Fraxinus ornus	1	13	13.0
Malus domestica	1	2	2.0
Quercus cerris	1	1	1.0
Ulmus minor	1	1	1.0

Functional traits of the observed species were retrieved from Nimis and Martellos (2008). We considered four growth forms: crustose (CRUST), fruticose (FRUT), narrowly lobed foliose (FOLN), and broadly lobed foliose (FOLB); three types of photobiont: chlorococcoid green algae (CHL), *Trentepohlia* (TREN) and cyanobacteria (CYAN); and three types of reproductive strategy: by soredia (SOR), by isidia (ISI), and by sexual reproduction (SEX).

A forward variable selection method, based upon permutations and parametric tests (Blanchet et al., 2008; but see Gioria et al. (2010) for an application of the method), was used for evaluating the response of lichen communities in terms of diversity and abundance of functional traits to environmental parameters indicative of climate, atmospheric deposition, and forest structure. Classic forward selection of ecological variables has two well-known problems: (1) an inflated rate of Type I error and (2) an overestimation of the amount of variance explained. The forward procedure proposed by Blanchet et al. (2008) and adopted here overcomes these problems, because the selection of predictors is done by applying a permutation of residuals under reduced models. This allows the selection of a minimal adequate (parsimonious) model, avoiding multicollinearity among selected predictors.

The forward selection was carried out using two stopping criteria, as suggested by Blanchet et al. (2008): (1) that the adjusted coefficient of multiple determination (R^2_{Adj}) calculated for any submodel (comprising a subset of predictors) must not exceed that of the full model (all predictors included), and (2) that the alpha significance level = 0.05. When forward selection identified a variable that caused one of these two quantities to exceed its threshold, that variable was rejected and the procedure stopped. The detailed procedure was as follows: to prevent inflation of Type I errors, a global test (with all the explanatory variables used to model the response variable) was carried out prior to forward selection. Once the global test was significant and a global R^2_{Adj} had been computed, the first stopping criterion was used to avoid a nonsense submodel, that is, one whose R^2_{Adj} was higher than the R^2_{Adj} of the full model. By combining the first and the second stopping criteria, the possibility of including useless variables in the model was greatly reduced in comparison to classic forward selection; this is certainly the biggest advantage in using this method. Moreover, this method is more conservative than classic forward selection, allowing the selection of a fewer and ecologically meaningful variables (for other practical applications of this method, please see: Gioria et al., 2010, 2011; Santi et al., 2010; Chiarucci et al., 2011). We performed 10,000 permutations. All regression analyses were carried out with R software (R Core Development Team, 2009) and its “packfor” package (version 0.0–7).

3. Results

3.1. Lichen diversity

One hundred and seventy-seven epiphytic lichen species were observed in the 14 plots. The total number of species in each forest type (Tables 1 and 2) ranged from 47 (*Picea*-forest plots) to 73 (*Fagus*-forest plots).

In all forest types, the dominant species accounted for the highest number of sampled trees and hosted the highest number of lichen species (41 on *Picea* trees of a total 47 species in *Picea* forests; 61 on *Quercus cerris* of 68 in deciduous *Quercus spp.* forests, 62 on *Q. ilex* of 72 in *Q. ilex* forests). Only *Fagus* trees were sampled in *Fagus* forests. In general, the non-dominant tree species contributed little to lichen diversity.

One-way ANOVA analysis with post-hoc Tukey’s HSD test showed non-significant differences ($p > 0.05$) among forest types for all lichen diversity indices considered. The models for diversity descriptors included environmental parameters indicative of climate, atmospheric deposition and forest structure (Table 3). In general, lichen species richness was mainly associated with

Table 3
Parsimonious models after forward selection for response variables of species composition (multivariate), diversity and functional traits.

	Lichen diversity					Functional traits								
	Multivariate	Avnsp	Richness	*H′*	*D*	CRUST	FRUT	FOLN	FOLB	CHL	TREN	SOR	ISI	SEX
Climate and geomorphology														
Longitude	ns	0.289* (+)	ns	0.167* (+)	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns
Latitude	0.141** (+)	ns	0.537** (−)	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns
Elevation	ns	0.230** (+)	ns	ns	ns	0.069* (+)	0.398* (+)	ns	ns	ns	ns	ns	0.419** (+)	ns
Rainfall	ns	ns	ns	ns	ns	0.301*** (+)	ns	0.264** (−)	ns	ns	ns	ns	ns	ns
Temperature	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns
Atmospheric deposition														
pH	ns	0.365** (+)	ns	ns	ns	0.037* (+)	ns	ns	0.045* (+)	ns	ns	0.399* (+)	ns	ns
H^+	ns	ns	ns	0.464* (−)	0.558* (−)	ns	ns	0.560* (−)	0.377** (−)	ns	ns	ns	ns	ns
$NH_4{}^+$	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns
Ca^{2+}	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns
Mg^{2+}	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns
Na^+	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns
K	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns
$SO_4{}^{2-}$	ns	ns	ns	ns	ns	ns	ns	0.073* (−)	ns	ns	ns	ns	ns	ns
$NO_3{}^-$	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns
Cl^-	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns
Forest type and structure														
Q. ilex forests[a]	0.137*** (+)	ns	ns	ns	ns	0.546** (+)	ns	ns	0.424** (+)	0.694*** (+)	0.728*** (+)	ns	ns	ns
Deciduous *Quercus* forests[a]	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns
Fagus forests[a]	ns	ns	ns	ns	ns	0.016* (+)	ns	ns	ns	ns	ns	ns	ns	ns
Picea forests[a]	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	0.449*** (+)
Age, year	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns
Basal area	ns	ns	ns	ns	ns	0.018* (−)	ns	ns	ns	ns	ns	ns	ns	ns
Canopy depth	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns
LAI	ns	ns	ns	ns	ns	ns	0.217* (−)	ns	0.079*(−)	ns	ns	ns	ns	ns
Total explained variance (R^2_{Adj} cumulated)	0.148	0.850	0.498	0.565	0.522	0.980	0.546	0.868	0.895	0.669	0.705	0.349	0.371	0.403
No. retained predictors	2	3	1	2	1	6	2	3	4	1	1	1	1	1

ns, not significant.
[a] Dummy variables derived from forest type categorization. Within cells are the R^2 values for each variable. (+) and (−) symbols denote positive or negative trend, respectively.
* <0.05.
** <0.01.
*** <0.001.

geographic predictors. The model for multivariate species composition, influenced both by longitude and *Q. ilex* forests, was not very informative ($R^2_{Adj} = 0.148$). Of the lichen diversity indices, Avnsp accounted for the highest total explained variance ($R^2_{Adj} = 0.850$) and was significantly correlated with three predictors: longitude, elevation and the pH of through-fall deposition at plot level.

Species richness was negatively correlated with latitude, with very high values at southern sites, regardless of forest-type. Both Shannon and Simpson indices were associated mainly with decreasing H^+ concentration ($R^2_{Adj} = 0.464$, and $R^2_{Adj} = 0.558$, respectively).

3.2. Functional traits

Models for functional traits (Table 3) also included predictors indicative of climate, atmospheric deposition, and forest structure (bivariate correlations among predictors are reported in Appendix A). Growth form was the most responsive trait and associated with two to six predictors across the three categories. Photobiont type and reproductive strategy were less responsive; each was associated with only one predictor. Crustose and foliose forms were both significantly associated with rainfall but with opposite gradients, the former being generally more common, but specifically associated with plots with higher precipitation.

The presence of both fruticose and isidiate species was heavily influenced by elevation. The presence of fruticose lichens was also negatively correlated with shady forests.

Both narrowly lobed and broadly lobed foliose lichens were negatively affected by acidic deposition. Narrowly lobed species were also negatively influenced by increasing concentrations of $SO_4{}^{2-}$.

As far as forest type was concerned, several traits (FOLB, CHL, TREN) were positively associated with *Q. ilex*-forest plots. In particular, this habitat was the only significant predictor associated with the occurrence of lichens with chlorococcoid green algae and with *Trentepohlia* photobionts. Finally, in *Picea*-forest plots, we found the highest percentage of species with sexual reproduction.

4. Discussion

Models for both lichen diversity and functional traits were effective in describing patterns of epiphytic lichen communities across a wide geographical and ecological range; the models explained a considerable amount of variation. Among species traits, three types of growth forms (crustose, narrowly lobed and broad-lobed foliose) were the best candidate indicators, being sensitive to factors in all three categories of predictors used. Reproductive strategy may also be a valuable indicator, although to a lesser extent, while photobiont type was scarcely informative.

Lichen species richness and species traits responded differently to climate and geomorphology-related factors. While lichen species richness was influenced, among other factors, by longitude and latitude, functional traits were more related to factors that may be independent of geographic position. This suggests that species richness comparisons across wide geographic ranges may be problematic (Pinho et al., 2004; Giordani, 2006; Giordani and Incerti, 2008), while comparisons based on the functional traits of species may be more consistent. Functional traits give detailed ecological information about the sampling sites, with elevation and rainfall among the most meaningful predictors of lichen patterns (Brunialti and Giordani, 2003; Ellis and Coppins, 2006; Giordani, 2006). In particular, rainfall determines whether crustose or narrowly lobed foliose species dominate communities, the former benefiting from abundant precipitation.

As for atmospheric deposition, pH and H^+ concentrations were the most influential variables in terms of both lichen diversity and species traits. Bark acidification is known to be an important driver of lichen patterns (Rose and Hawksworth, 1981), with both direct effects, altering the physiology of symbiosis (Farmer et al., 1991), and indirect effects, influencing substrate pH (Frati et al., 2008). In particular, we found evidence that foliose lichens were negatively affected by high H^+ concentrations, whereas crustose and fruticose lichens seem to be less sensitive to this factor. Crustose lichens are likely to be protected to some extent by having less surface exposed to the atmosphere, while fruticose species may be protected by less exposure to the bark (Kershaw, 1985; Sancho and Kappen, 1989; Tretiach and Brown, 1995; Lange and Green, 2008). Reproductive strategy seems to be affected by pH as well, with increasing pH favouring sorediate species. This pattern is in accordance with their well-known tolerance to high levels of anthropogenic eutrophication (Van Herk, 1999). Increasing sulphate ion concentrations negatively affected foliose lichens as well, confirming findings by Hesse (2002), who observed a decrease in the cover of the lichen *Hypogymnia physodes* with increasing $SO4^{2-}$ concentrations in the stemflow.

Forest type and light conditions had the greatest influence on lichen patterns; the latter was among the main factors shaping lichen communities (Humphrey et al., 2002; Moning et al., 2009). While growth form was indicative of both factors, reproductive strategy was, to a lesser extent, influenced by forest type alone. Fruticose lichens were clearly separated from other growth forms, requiring higher light availability (lower LAI). In many forest ecosystems, this growth form is known to be restricted to the higher part of the canopy or to open stands, which provide well-lit conditions (Barkman, 1958).

5. Conclusion

Lichen growth form type was the most responsive trait to factors in all the three categories of predictors. Thus, this easily identifiable trait could be valuable for evaluating and comparing the responses of epiphytic lichens to climate, human disturbance and stand structure-related conditions in forest ecosystems across diverse regions. According to Johansson et al. (2007), the use of lichen functional traits to gather ecological information is a promising approach. However, further research is needed to better clarify the potential of lichen traits for bioindication.

The evaluation of lichen patterns in term of species traits could also be useful for large scale comparisons when species-based evaluations (e.g. species richness descriptors) might be strongly affected by uneven levels of taxonomic knowledge (Giordani et al., 2009). Our results suggest that models describing the gradients of functional traits (1) minimize background noise with respect to interpretations based on species richness and composition and (2) are probably more consistent in detecting variation associated with the gradient of macro-environmental factors in forest ecosystems.

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Appendix A. Matrix of correlation coefficients (Pearson's product moment) for the set of variables used as predictors.

	Age, year	Basal area	Ca^{2+}	Canopy depth	Cl^-	Elevation	H^+	K^+	LAI	Latitude	Longitude	Mg^{2+}	Na^+	NH_4^+	NO_3^-	pH	Rainfall	SO_4^{2-}	Temperature
Age, year	1.00	0.81	−0.50	0.84	−0.57	0.83	0.35	−0.62	0.06	0.31	0.35	−0.63	−0.61	−0.72	−0.78	−0.43	0.30	−0.70	−0.80
Basal area	0.81	1.00	−0.57	0.90	−0.52	0.73	0.66	−0.63	0.32	0.06	0.37	−0.53	−0.50	−0.63	−0.51	−0.63	0.34	−0.55	−0.79
Ca^{2+}	−0.50	−0.57	1.00	−0.60	0.83	−0.34	−0.47	0.95	−0.22	0.20	−0.80	0.70	0.69	0.31	0.13	0.67	−0.40	0.70	0.66
Canopy depth	0.84	0.90	−0.60	1.00	−0.63	0.78	0.65	−0.71	0.06	0.09	0.49	−0.68	−0.65	−0.69	−0.63	−0.67	0.29	−0.68	−0.87
Cl^-	−0.57	−0.52	0.83	−0.63	1.00	−0.52	−0.46	0.95	0.12	0.09	−0.84	0.95	0.97	0.31	0.36	0.63	−0.46	0.94	0.81
Elevation	0.83	0.73	−0.34	0.78	−0.52	1.00	0.31	−0.50	0.02	0.22	0.20	−0.65	−0.60	−0.70	−0.80	−0.34	0.28	−0.73	−0.81
H^+	0.35	0.66	−0.47	0.65	−0.46	0.31	1.00	−0.53	0.11	0.18	0.45	−0.45	−0.44	−0.36	−0.15	−0.93	0.40	−0.33	−0.65
K^+	−0.62	−0.63	0.95	−0.71	0.95	−0.50	−0.53	1.00	−0.05	0.13	−0.86	0.87	0.86	0.37	0.30	0.71	−0.47	0.85	0.82
LAI	0.06	0.32	−0.22	0.06	0.12	0.02	0.11	−0.05	1.00	−0.03	−0.07	0.15	0.21	−0.20	0.03	−0.08	0.37	0.13	0.01
Latitude	0.31	0.06	0.20	0.09	0.09	0.22	0.18	0.13	−0.03	1.00	−0.34	−0.10	−0.05	−0.38	−0.51	−0.20	0.36	−0.04	−0.15
Longitude	0.35	0.37	−0.80	0.49	−0.84	0.20	0.45	−0.86	−0.07	−0.34	1.00	−0.68	−0.72	−0.19	−0.07	−0.57	0.18	−0.70	−0.62
Mg^{2+}	−0.63	−0.53	0.70	−0.68	0.95	−0.65	−0.45	0.87	0.15	−0.10	−0.68	1.00	0.99	0.42	0.56	0.62	−0.57	0.96	0.87
Na^+	−0.61	−0.50	0.69	−0.65	0.97	−0.60	−0.44	0.86	0.21	−0.05	−0.72	0.99	1.00	0.35	0.50	0.59	−0.52	0.96	0.85
NH_4^+	−0.72	−0.63	0.31	−0.69	0.31	−0.70	−0.36	0.37	−0.20	−0.38	−0.19	0.42	0.35	1.00	0.86	0.45	−0.24	0.51	0.63
NO_3^-	−0.78	−0.51	0.13	−0.63	0.36	−0.80	−0.15	0.30	0.03	−0.51	−0.07	0.56	0.50	0.86	1.00	0.25	−0.33	0.62	0.65
pH	−0.43	−0.63	0.67	−0.67	0.63	−0.34	−0.93	0.71	−0.08	−0.20	−0.57	0.62	0.59	0.45	0.25	1.00	−0.48	0.50	0.73
Rainfall	0.30	0.34	−0.40	0.29	−0.46	0.28	0.40	−0.47	0.37	0.36	0.18	−0.57	−0.52	−0.24	−0.33	−0.48	1.00	−0.43	−0.53
SO_4^{2-}	−0.70	−0.55	0.70	−0.68	0.94	−0.73	−0.33	0.85	0.13	−0.04	−0.70	0.96	0.96	0.51	0.62	0.50	−0.43	1.00	0.86
Temperature	−0.80	−0.79	0.66	−0.87	0.81	−0.81	−0.65	0.82	0.01	−0.15	−0.62	0.87	0.85	0.63	0.65	0.73	−0.53	0.86	1.00

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