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Epiphytic lichen diversity along elevational gradients: biological traits reveal a complex response to water and energy

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ABSTRACT

Aim Patterns of epiphytic lichen diversity along elevational gradients covering the range of Norway spruce forests were analysed. The roles of water and energy variables in shaping the observed species–elevation relationship were tested, as well as how growth form and photobiont type distribution varied along the gradient.

Location South Tyrol, northern Italy.

Methods Eight sites were selected spanning the elevational range of spruce forests (900–1900 m a.s.l.) and the regional rainfall gradient. At each site, a pair of forest stands (one mature even-aged and one multilayered) was selected at three elevation steps. Epiphytic lichens were surveyed according to European guidelines for lichen diversity monitoring. Explanatory variables indicative of both forest structure and climate were included in the models.

Results A positive relationship was found between number of species and elevation. This reflected the physiological response of epiphytic lichens to the main climatic factors, trait selection being the mechanism that determined the response at community level. Nonlinear species–temperature and trait–temperature relationships predicted that major changes may be expected in the intermediate part of the gradient. Lichens with a *Trentepohlia* algal partner were more frequent at lower elevations and proved to be sensitive to environmental factors indicative of forest structure. Lichen growth forms had contrasting patterns related to temperature, crustose species richness being enhanced by increasing values, and alectorioid and foliose lichens by decreasing values. Alectorioid lichens were also negatively influenced by rainfall.

Main conclusions In a climate change scenario, lichen diversity in alpine regions will probably not benefit from an increase in air temperature in the same way as flowering plants. Monitoring variations in the proportions of growth form and photobiont type may represent a tool for detecting the effects of climate change on lichen species.

Keywords

Alpine spruce forests, climate change, elevational diversity gradient, energy, forest structure, Italy, lichen growth form, photobiont type, species richness, trait selection.

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INTRODUCTION

Elevational gradients are a suitable model template for predicting the potential effect of temperature warming on plant and animal communities because they encompass several clines in climatic factors over a relatively short distance

(Lomolino, 2001; Körner, 2007). Regarding the predictive power of climate effect on plant diversity (Hawkins *et al.*, 2003), the water–energy dynamics theory has shown the potential to become a possible unifying theory (O'Brien, 1993, 2006; Vetaas, 2006), at least for modelling tree species richness (Bhattarai & Vetaas, 2003; Field *et al.*, 2005). The

interaction between energy and water is known to be an important driver of diversity patterns of several taxonomic groups (Whittaker *et al.*, 2007), their effects being dependent on latitude, i.e. at higher latitudes energy is the key limiting component of the interaction, whereas at lower latitudes water is the key limiting component (Hawkins *et al.*, 2003). Mountain environments provide interesting study areas for exploring the relationship between water variables, energy variables and species diversity along vertical (elevational) gradients (Bhattarai & Vetaas, 2003, 2006; Banya *et al.*, 2010; Marini *et al.*, 2011a), which might be expected to resemble the broader latitudinal gradient.

Epiphytic lichens are among the most climate-sensitive organisms, and evaluation of their diversity patterns along elevational gradients may provide early warning signs regarding loss of forest diversity and ecosystem functions as a result of climate change. There is mounting evidence that changes in temperature and rainfall can severely affect the structure of epiphytic communities, leading to the local extinction of several species (e.g. Aragón *et al.*, 2012). The poikylhydric nature of lichens provides the basis for their different sensitivity to both water and energy compared with vascular plants. Both factors directly control relevant ecophysiological processes influencing growth rates and species distribution (Insarov & Schroeter, 2002). In particular, their physiology is closely coupled with ambient temperature and moisture conditions (Green *et al.*, 2008), which influence thallus water saturation and desiccation. Increasing ambient temperature may negatively affect lichens because of increased respiratory carbon losses (Schroeter *et al.*, 2000), especially when it does not reflect water availability. Despite these predicted effects, the relationship between climatic factors and species richness along elevational gradients is still poorly known for lichens compared with vascular plants and animals.

The response of lichen communities to climatic factors is likely to be mediated by different functional traits (e.g. photobiont type and growth form) that determine the performance of the species under given environmental conditions (Diaz & Cabido, 2001; Giordani *et al.*, 2012; Rapai *et al.*, 2012). Photobiont type and thallus growth forms are among the most responsive traits that account for large-scale patterns of lichen diversity (Ellis & Coppins, 2006, 2010; Marini *et al.*, 2011b); for example, lichens with a

Trentepohlia algal partner are enhanced by increasing temperatures (van Herk *et al.*, 2002; Aptroot & van Herk, 2007), lichens with a crustose growth form are expected to resist drought events because of desiccation tolerance, while those with a fruticose–filamentose growth form (i.e. alectorioid lichens) suffer from excessive rewetting that depresses net assimilation (Coxson & Coyle, 2003; Stevenson & Coxson, 2007).

We analysed patterns of lichen diversity along steep elevational gradients covering the range of managed spruce-dominated forests. To test the water–energy dynamics theory on lichen diversity, along with a temperature gradient we also accounted for a regional gradient of rainfall to obtain orthogonal gradients in rainfall and temperature. Our hypothesis was that temperature is one of the main drivers of lichen diversity and trait distribution along the elevational gradient. Indeed, because of their poikylhydric nature, lichens are expected to be particularly sensitive to high temperatures, which influence the process of rewetting and thallus water content, inducing frequent and severe desiccation events. On this basis, a positive species–elevation relationship was expected. Moreover, water availability is expected to interact with energy, i.e. the negative effect of high temperatures on species richness may be stronger in relatively arid areas than in wetter areas (a modified conjecture of Hawkins *et al.*, 2003; see also Bhattarai & Vetaas, 2003; McCain, 2007). We also tested whether growth form and photobiont type modified the species–elevation relationship. Firstly, a variety of responses to water and energy are expected for the different growth forms; crustose species are more resistant to high temperatures because of their capacity to withstand drought events, whereas foliose and alectorioid/fruticose growth forms are more desiccation-sensitive. Secondly, lichens with a *Trentepohlia* algal partner are expected to be more frequent in the lower part of the elevational gradient, being favoured by higher temperatures.

MATERIALS AND METHODS

Study area

The study was conducted in the alpine region of South Tyrol (northern Italy), which extends over 740,000 ha (Fig. 1a). The

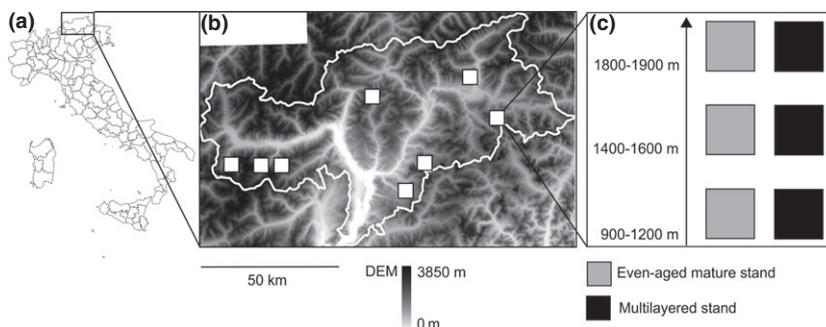


Figure 1 (a) Study area, (b) distribution of the elevational gradients, and (c) scheme of the sampling design used to investigate epiphytic lichen diversity along elevational gradients in the South Tyrol, northern Italy. DEM, digital elevation model.

climate is largely influenced by elevation, ranging from temperate conditions in the Adige Valley area, with a mean annual temperature of 11–12 °C, to alpine tundra conditions above 1700 m above sea level (a.s.l.), with a mean annual temperature of 2–3 °C. Precipitation varies across the region, ranging from < 600 to 1400 mm yr⁻¹ according to both elevation and a geographical gradient. Conditions are driest in the east–west orientated Venosta Valley in the western part of the study area, and wettest in the central northern and eastern parts of the study area. Given the high geological diversity of the study area, the bedrock varies from hard siliceous to metamorphic, porphyric and carbonatic rocks, while soils are usually podsoles and rendzinas (on calcareous bedrock).

Between 600 and 2100 m a.s.l. the landscape is dominated by forests that cover an area of 370,000 ha, of which 52% are spruce forests that are all managed for timber production in even-aged or multilayered, uneven-aged, stands. In both cases, management is based on progressive thinning and harvesting (1.6 m³ ha⁻¹ yr⁻¹) of mature trees.

Sampling design

Eight sites were selected (Fig. 1b) on the basis of the regional forest database, matching the requirement of containing spruce-dominated forests within the whole elevation range of this forest type (900–1900 m a.s.l.). The site selection spanned the entire regional rainfall gradient (c. 600–1200 mm yr⁻¹).

At each site, a pair of forest stands was selected at three different elevation steps (900–1200 m a.s.l., 1400–1600 m

a.s.l. and 1800–1900 m a.s.l.), comprising one even-aged mature stand and one multilayered stand that included mature trees, making a total of six stands at each site (Fig. 1c). In each forest stand, a 13-m radius plot was set out randomly, within which the species identity and diameter at breast height (d.b.h.) of all living trees (diameter > 15 cm) were recorded, as well as geographical position, elevation, aspect and slope (Table 1). In each plot, five mature spruce (*Picea abies* (L.) H.Karst.) trees were selected randomly for the lichen survey, for a total of 240. The lichen survey was conducted according to the European guidelines for lichen monitoring (Asta *et al.*, 2002). Lichen diversity was sampled using four standard frames of 10 cm × 50 cm as sampling grids, subdivided into five 10 cm × 10 cm quadrats, which were attached to the tree trunk at the cardinal points, with the shorter lower side at 100 cm from the ground. Two additional standard frames were placed at the base of the trunk on north- and south-facing sides. All lichen species inside the frames, including sterile crustose lichens, were listed and their frequency was computed as the number of 10 cm × 10 cm quadrats in which they occurred. The exhaustiveness of the sampling was tested for each elevation step using sample-based accumulation curves (Gotelli & Colwell, 2001).

Species identification

When possible, lichens were identified in the field. However, in most cases species identification was based on the study

Table 1 General overview of the main topographic features of the study plots and variability and range of the explanatory variables (forest structure and climate) used to investigate epiphytic lichen diversity along elevational gradients in South Tyrol, northern Italy. For the variables indicative of forest structure, the general mean values are reported as well as those related to the two types of stands (even-aged and multilayered).

	Variable	Mean ± SD	Range
Topography	Elevation (m a.s.l.)	1488 ± 312.5	900–1900
	Aspect (°)	215.5 ± 137	5–360
	Slope (°)	25.2 ± 9.8	5–44
Forest structure	Mean circumference of the plot (cm)	143.2 ± 24.7	100–216
	Even-aged stands	159 ± 20.8	131–216
	Multilayered stands	127.4 ± 17.2	100–157
	Circumference of sampled trees (cm)	185 ± 32	110–270
	Even-aged stands	189.7 ± 20.7	158–236
	Multilayered stands	180.6 ± 23.2	147–232
	Age of sampled trees (years)	144 ± 41	65–235
	Even-aged stands	141.2 ± 42	65–234
	Multilayered stands	146.5 ± 40	81–235
	Basal area (m ² ha ⁻¹)	66.9 ± 18.2	27.2–108.5
	Even-aged stands	65.4 ± 17	35–103
	Multilayered stands	68.5 ± 17	27.2–108.5
	% canopy closure	74.8 ± 3.9	66.3–82.9
Even-aged stands	75.5 ± 3.5	69–82.9	
Multilayered stands	74.3 ± 4	66.3–82	
	Stand type	–	Even-aged versus multilayered
Climate	Mean annual temperature (°C)	4.9 ± 1.9	2–9.1
	Mean annual precipitation (mm)	795.8 ± 180.6	563–1182
	Annual solar radiation (kWh m ⁻²)	992.8 ± 289.5	602.2–1777.2

of specimens (*c.* 800) collected and stored in the personal herbarium of J.N. and in the herbarium of the Natural Sciences Museum of South Tyrol (Bolzano, Italy). In particular, crustose lichens were identified in the laboratory using a dissecting and a biological microscope. Routine chemical spot tests were performed for most specimens. The identification of sterile crustose lichens (including all *Lepraria* species, *c.* 150 specimens) was based on standardized thin-layer chromatography (TLC) analyses following the protocols of White & James (1985) and Orange *et al.* (2001). Nomenclature of lichen species mainly follows Nimis & Martellos (2008).

Explanatory variables

Forest structure

We focused on the response of lichen richness to climate factors but we also took into account the variability of the forest habitat quality, which may be indicative of the effects of forest management. According to our sampling design, each plot was assigned to one of the two types of forest structure: even-aged mature stands or multilayered stands that included mature trees (categorical variable), the number of plots for each forest type being equal. Canopy closure was estimated using a spherical densitometer, by averaging 20 measurements recorded at the four cardinal points of each tree selected for the lichen survey. Mean tree circumference was calculated by averaging the circumference of all the trees recorded within each plot. Basal area, an indicator of both substrate amount and forest density, was calculated on the basis of the circumference measurements of all the trees within each plot. For each tree selected for the lichen inventory, the circumference was measured and its age determined by extracting cores using a Pressler-type increment borer at a height of 1.30 m. Because the effect of climate-related factors was the main interest, plots placed in the three elevation steps were chosen for comparable forest structure variables. However, by keeping tree diameter uncorrelated with elevation, tree age covaried with elevation as a result of different tree growth rates along the elevational gradient.

Climate

Mean annual precipitation was considered as an indicator of water availability. Mean annual temperature and solar radiation, considered as a measure of potential light available for photosynthesis (Table 1), were used as a measure of available energy. Mean annual temperature (1980–2011), using ordinary kriging with external drift (Benavides *et al.*, 2007), was interpolated from 84 meteorological stations, evenly scattered throughout and outside the study area at elevations ranging from 200 to 2000 m a.s.l. (see Marini *et al.*, 2011a for more details). The fitted temperature was first estimated from a simple regression with elevation, and the residuals were then interpolated using ordinary kriging and the interpolated residuals summed with the fitted temperature from the

regression with elevation. Mean annual precipitation was interpolated using ordinary kriging from 88 meteorological stations evenly scattered throughout the study area. The geostatistical interpolations were computed using the Kriging Interpolator 3.2 extension for ARCVIEW 3.2 (ESRI, Redlands, CA, USA). For each plot, the annual potential solar radiation was calculated using the digital elevation model (DEM) of the study area with a resolution of 25 m employing ARCVIEW 3.2.

Statistical analyses

Species composition

As well as environmental factors, geographical position is very likely to affect local patterns of species composition (Borcard *et al.*, 1992). In order to elicit the spatial gradient, the potential spatial autocorrelation was taken into account using Moran's eigenvector map method (MEM; Dray *et al.*, 2006). Spatial eigenvector mapping is based on the premise that the spatial relationships among data points can be translated into explanatory variables, which capture spatial effects at different spatial scales (Dray *et al.*, 2006; Griffith & Peres-Neto, 2006). Eigenvectors from these connectivity matrices represent the decompositions of Moran's *I* statistic into all mutually orthogonal maps that can be generated from a given connectivity matrix (Griffith & Peres-Neto, 2006). There are several possibilities for building connectivity matrices, but the implementation suggested in Dray *et al.* (2006) and the procedure suggested by Eisenlohr (2014) were followed. The spatial weights were quantified using the minmax methods based on Kelejian & Prucha (2010) and the MEMs were computed using the scores.listw() function. A forward selection (Blanchet *et al.*, 2008) was performed separately for the environmental variables (elevation and management type) and MEMs ($P \leq 0.05$) to select significant predictors that accounted for most of the variation in species composition. The significant variables were then analysed further by means of a variation partitioning approach to determine the relative influence of environmental variables and spatial structure on species composition (Legendre *et al.*, 2012). The variation in species composition was decomposed using a series of (partial) redundancy analysis (RDA), implemented in the R package VEGAN (Oksanen *et al.*, 2013). All RDAs were tested for significance with a Monte Carlo permutation test (1000 runs). The total variation in species composition was divided into three components: the pure effect of abiotic environment, the pure effect of space, and their joint effect. For the species composition analysis the species by site, and not the species by tree, matrix was used, as trees within the same plot were too close to each other to perform the spatial analysis.

An indicator species analysis (ISA; Dufrêne & Legendre, 1997) was used to determine how strongly each species was associated with each elevation step and forest type. For each species, the indicator value (INDVAL) ranges from 0 (no

indication) to 100 (maximum indication). The statistical significance of INDVAL was tested by means of a Monte Carlo test, based on 10,000 randomizations. ISA and Monte Carlo tests were performed with PC-ORD (McCune & Mefford, 1999).

Determinants of species richness and traits incidence

A mixed model (Zurr *et al.*, 2009) was used to test the effect of climatic and forest structure on lichen species richness and trait distribution. Tree-level species richness and the incidence (% of species) of selected biological traits (Table 1) were considered as response variables that could be indicative of the adaptation to climatic conditions (Giordani *et al.*, 2012). Particular focus was placed on the photobiont type, analysing the incidence of lichens with a *Trentepohlia* algal partner (Aptroot & van Herk, 2007; Marini *et al.*, 2011b), and on thallus growth forms (Giordani *et al.*, 2012), analysing the incidence of crustose, alectorioid/fruticose and foliose lichens. Biological traits of the species were retrieved from Nimis & Martellos (2008). The various climatic and forest variables described in Table 1 were included as fixed effects, and plot within elevation step within gradient as a random factor, as follows (random intercept model): response variable, fixed effects: environmental variables, random effects: gradient/elevation step/plot.

The random structure accounted for the spatial dependence between trees in our hierarchical sampling design. The interaction between rainfall and temperature was included in order to test the conjecture of Hawkins *et al.* (2003), that the effect of rainfall will be stronger at lower (warmer) elevations, and a modified conjecture, that the negative effect of temperature will be stronger in the arid part of our sample area.

Because of the relatively low number of replicates and the relatively high number of potential predictors, multimodel inference within an information-theoretic framework was used to evaluate the role of the selected variables (Table 1) in explaining patterns of epiphytic lichen species richness and trait incidence (Burnham & Anderson, 2002). All selected variables corresponded to meaningful ecological predictors of lichen species richness patterns. Severe collinearity was absent in our dataset, the only two variables that were highly correlated ($r > 0.50$) being age and temperature (see Appendix S1 in Supporting Information). This correlation was unavoidable as trees were selected of comparable size along the elevational gradient. Both variables were included in the multimodel inference analysis as they were both expected to have an important effect on lichens. The fit of all the possible candidate models obtained by the combination of the predictors described above was compared using second-order Akaike's information criterion corrected for small samples (AICc). The AICc is a measure of relative model fit, proportional to the likelihood of the model and the number of parameters used to generate it; the best fitting model is the one with the lowest AICc. In a set of n models, each model can be ranked by using

its difference in AICc score with the best-fitting model ($\Delta\text{AICc}_i = \text{AICc}_i - \text{AICc minimum}$). 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 (Burnham & Anderson, 2002). For every model, an Akaike's weight (w_i) was also calculated, in order to determine whether the model would be selected as the best fitting model if the data were collected again under identical circumstances (Burnham & Anderson, 2002). Akaike's weight should be interpreted as a measure of model selection uncertainty. The multimodel inference analyses were performed using the MuMIn package (Barton, 2010) implemented in R (R Development Core Team, 2011).

To test the assumptions of our mixed models, the normality and variance homogeneity of model residuals were checked. The potential residual spatial autocorrelation was also tested using Moran's I and the correlog() function in the R package ncf (Bjornstad, 2013) on both geographical and ordination space distances (Diniz-Filho *et al.*, 2003). To obtain ordination space distances, detrended correspondence analysis (DCA) was used on a dataset based on the abundance of all species on the 240 trees sampled. Many shared species yielded high statistical dependence and vice versa, i.e. there was species ordination space autocorrelation. The location of sampling points in species ordination space will be almost as important as the geographical distance because this determines the statistical independence of species richness observations (Vetaas *et al.*, 2014). All model diagnostics were performed on the plausible models ($\Delta\text{AICc} < 2$) identified by the multimodel inference analysis (see Appendix S2).

RESULTS

General results

On 240 trees distributed in 48 plots, 124 lichen species (including five non-lichenized fungi) occurred (see Appendix S3) with a frequency ranging from 0.4% to 76%. Mean species richness was 13.2 ± 6.4 (range 2–28).

Sixty-three species were found at the lowest elevation step (900–1200 m a.s.l.), 89 at the intermediate (1400–1600 m a.s.l.) and 83 at the highest (1800–1900 m a.s.l.). Sample-based rarefaction curves indicated an equal exhaustiveness of the sampling among the three elevation steps (Fig. 2). The lowest elevation step shared 44 and 37 species with the intermediate and highest steps, respectively; the latter two steps shared 63 species.

Seventy-four species were crustose, 23 foliose and 27 fruticose, including 14 alectorioid species (i.e. with a fruticose–filamentose thallus) belonging to the genera *Bryoria*, *Evernia* and *Usnea*. The mean percentage of crustose species was 49.7 ± 25.7 (range 0–100), that of foliose species 34.3 ± 18.1 (range 0–86) and that of alectorioid species 8.5 ± 8.4 (range 0–50). One-hundred and eleven species had chlorococcoid green algae and eight species had a *Trentepohlia* algal partner. The mean percentage of species with a *Trentepohlia* algal

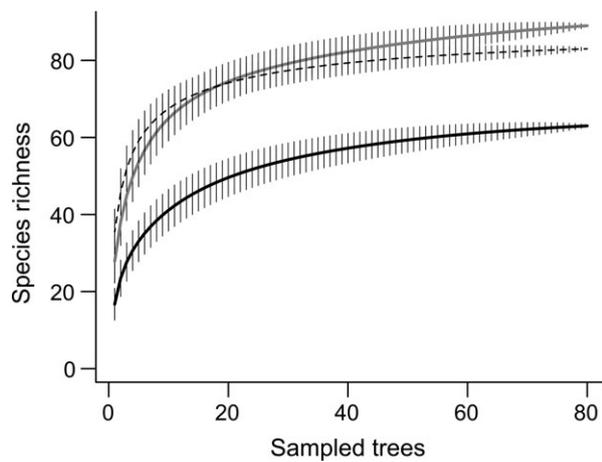


Figure 2 Sample-based (tree) rarefaction curves within each elevation step used to investigate epiphytic lichen diversity along elevational gradients in the South Tyrol, northern Italy. Black line, elevation step between 900 and 1200 m a.s.l.; grey line, elevation step between 1400 and 1600 m a.s.l.; dotted line, elevation step between 1800 and 1900 m a.s.l.

partner was 5.7 ± 9.3 (range 0–50). The main reproductive strategy was by vegetative propagules (65 sorediate and 8 isidiate species), followed by sexual reproduction by ascospores (50 species) and thallus fragmentation (one species).

Species composition

In the RDA analysis, the separated forward selection procedure resulted in two MEMs among the spatial variables, while only elevation was selected among the environmental variables ($P \leq 0.05$), i.e. the species composition changed significantly with elevation but also included some spatial autocorrelation. The variation partitioning analysis indicated that the pure effects of space and elevation were 2% and 18%, respectively, while the joint contribution was 5%. The ISA revealed that 51% of the lichens were over-represented in one of the three elevation steps (Appendix S3), with 33, 20 and 11 species associated with higher, intermediate and lower elevations, respectively.

Determinants of species richness and incidence of traits along the entire elevational gradient

Lichen species richness showed a linear positive relationship with elevation (Fig. 3a) and no support for an interaction between rainfall and temperature could be detected; multi-model inference analyses are therefore presented without this interaction (Table 2). Along the whole elevational gradient, species richness was significantly explained by temperature, with a negative nonlinear effect resulting in a peak close to the lower end of the temperature gradient (Fig. 3b). A linear positive effect of solar radiation was also found, but no significant interaction could be detected between temperature and rainfall, nor any pure effect of rainfall (Table 2). Conversely, the

effect of temperature on lichens with a *Trentepohlia* algal partner revealed that these species were more frequent at lower elevations (Fig. 3c), also because of their sensitivity to environmental factors indicative of forest structure, being enhanced by increasing basal area and more competitive on young trees (a negative relationship with tree age).

Lichen growth forms had contrasting patterns in relation to temperature, the incidence of crustose species being enhanced by increasing values and that of alectorioid/fruticose and foliose lichens by decreasing values (Fig. 3d,e,f, Table 2). Relationships for foliose and crustose lichens were nonlinear with a significant quadratic term. Alectorioid/fruticose lichens were also negatively influenced by rainfall. Factors indicative of forest structure had only weak effects on the incidence of different lichen growth forms (Table 2).

No autocorrelation in the mixed model residuals considering both the geographical and ordination space (DCA scores) distances were detected, indicating that our models could explain the spatial and compositional autocorrelation of our response variables.

DISCUSSION

Patterns of epiphytic lichen diversity along steep elevational gradients in managed alpine spruce forests indicated that the influence of water and energy on poikylhydroic organisms may result in species–elevation relationships that differ from those of vascular plants and many other organisms (e.g. Rahbek, 1995; Marini *et al.*, 2011a) where species richness declines with elevation or presents a hump-shaped relationship (cf. Banya *et al.*, 2010). In contrast, a linear positive species–elevation relationship was found, perhaps reflecting the fact that only a partial gradient (Nogués-Bravo *et al.*, 2008), avoiding both low and high elevation, was considered. However, the nonlinear relationship between lichen diversity, trait composition and temperature (i.e. the most meaningful climatic factor varying with elevation) indicated that the response of lichen species richness to temperature was relatively non-intense up to a certain level (5–6 °C in our study) and then became very strong, i.e. even a slight temperature increase resulted in a reduction of species richness. This relationship may imply that, under climate warming scenarios, major changes could be expected in the intermediate part of the elevational gradient. This corroborates the hypothesis that many lichens will probably not benefit from an increase in air temperature in the same way as flowering plants (Inсарov & Schroeter, 2002) and that several lichen species may be locally threatened by climate change (e.g. Ellis *et al.*, 2007; Aragón *et al.*, 2012).

The pattern of species richness and trait composition along the elevational gradient corresponded with a turnover in species composition occurring between the lower and the higher elevations. An increase in lichen diversity with elevation, associated with a substantial species turnover, has also been found in other geographical and environmental conditions (e.g. Dietrich & Scheidegger, 1997; McCune *et al.*,

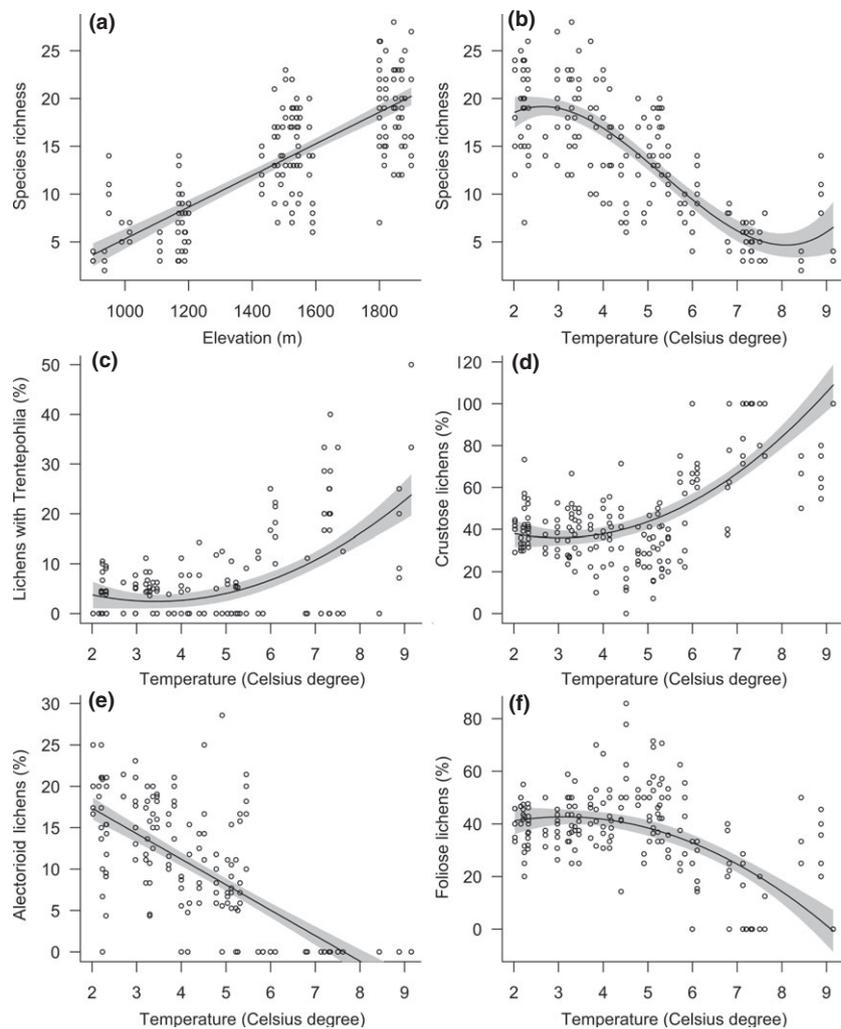


Figure 3 Scatterplots of the relationship between (a) elevation and lichen species richness, (b) mean annual temperature and lichen species richness, (c) mean annual temperature and the percentage of lichen species with *Trentepohlia* as algal partner, and (b–f) mean annual temperature and percentage of lichens with different growth forms, (d) crustose, (e) alectoroid (i.e. fruticose–filamentose) and (f) foliose, in the study of epiphytic lichen diversity along elevational gradients in the South Tyrol, northern Italy. Ninety-five per cent confidence intervals are shown.

1997; Cobanoglu & Sevgi, 2009), corroborating the hypothesis that the species–elevation relationship reflects the physiological response of these organisms to the main climatic factors. Our study supports this view, revealing that trait selection is the mechanism that determines the response at community level.

The climatic results only partially confirmed our hypothesis related to the conjecture of Hawkins *et al.* (2003), that the effect of rainfall should be stronger at lower (warmer) elevations, and to a modified conjecture, that the negative effect of temperature will be stronger in the arid part of our sample area, as no interactive effect between temperature and precipitation was found. The lack of a pure effect of precipitation on species richness patterns suggests that a larger rainfall gradient (e.g. Aragón *et al.*, 2012) should be spanned to test this hypothesis. The only signal of a relevance to the rainfall gradient derives from its negative influence on the incidence of alectoroid lichens, which fully reflects their particular ecophysiological requirements, being hindered by excessive wetting that depresses net assimilation (Stevenson & Coxson, 2007).

Temperature was the main driver of lichen diversity and trait selection along the elevational gradient. The negative

relationship with species richness reflects the negative effects of increasing temperature on key ecophysiological processes, such as an increase of respiratory carbon loss (Schroeter *et al.*, 2000) that may limit the distribution of many species. Moreover, an increase in temperature is usually associated with a decrease in relative air humidity, resulting in faster desiccation rates of poikylhydric organisms, which hinders photosynthetic activity (Insarov & Schroeter, 2002). The positive species–solar radiation relationship predicts that these effects are likely to be exacerbated by low solar radiation reducing the availability of light for photosynthetic activity.

The adaptation of lichen communities to a temperature regime is mediated by a trait selection that involves both the photobiont and thallus growth forms. Concerning the photobiont, lichens in symbiosis with *Trentepohlia* algae are more adapted to warm climates, confirming that the photobiont type can mediate the response to global warming (van Herk *et al.*, 2002; Aptroot & van Herk, 2007; Marini *et al.*, 2011b). However, the contribution of these lichens to community composition is not only determined by the temperature regime but also by some forest attributes. In particular, the positive relationship between the

Table 2 Sum of model weights (Σw_i) for each predictor used along the whole gradient for (a) all species and (b–e) the trait groups, separately (b, algal partner; c–e, thallus growth forms) in the investigation of epiphytic lichen diversity along elevational gradients in the South Tyrol, northern Italy. The sum can vary between 0 and 1. The variables that presented values close to 1 are those more supported by the multi-model inference analysis. Variables with sum > 0.65 are shown in bold.

	Age	Circ_tree	Basal	Canopy	Circ_plot	Stand_type	Rad	Precip	Temp	Temp ²	Temp ³
(a) All species											
Σw_i	0.45	0.26	0.27	0.26	0.30	0.25	0.69	0.27	0.91	0.93	0.93
Averaged parameters	0.0053	0.0036	−0.0368	−0.0081	−0.0008	−2.542	0.0026	−0.0053	9.4765	−2.470	0.1533
(b) <i>Trentepohlia</i>											
Σw_i	0.79	0.54	0.69	0.26	0.33	0.48	0.28	0.39	0.43	0.52	0.71
Averaged parameters	−0.0332	0.02514	0.08534	0.0625	−0.0143	1.7930	0.00195	0.0084	−2.0809	−0.0475	0.0483
(c) Foliose											
Σw_i	0.25	0.36	0.28	0.29	0.36	0.38	0.60	0.31	0.83	0.89	0.86
Averaged parameters	−0.0030	0.0323	−0.0459	−0.2747	0.0663	−2.9809	−0.0119	−0.0085	56.5645	−10.634	0.6014
(d) Crustose											
Σw_i	0.27	0.50	0.37	0.28	0.40	0.28	0.62	0.50	0.87	0.92	0.89
Averaged parameters	−0.0161	−0.0492	0.1275	0.2848	−0.1046	0.5607	0.0159	0.0230	−80.230	15.2357	−0.853
(e) Alectoroid/fruticose											
Σw_i	0.25	0.40	0.46	0.51	0.28	0.26	0.27	0.97	0.67	0.66	0.70
Averaged parameters	0.0004	0.0048	0.0140	0.0806	0.0027	0.0118	0.0002	−0.0133	−3.1101	−0.3375	0.0394

Age, age of sampled trees (years); Circ_tree, circumference of sampled trees (cm); Basal, basal area (m² ha^{−1}); Canopy, % canopy closure; Circ_plot, mean circumference of the plot (cm); Stand type, even-aged mature stands versus multilayered stands; Rad, annual solar radiation (kWh m^{−2}); Precip, mean annual precipitation (mm); Temp, mean annual temperature (°C).

proportion of lichens with a *Trentepohlia* algal partner and forest basal area predicts that dense stands are able to fulfil better the habitat requirements of this group of species, which have their photosynthetic optimum in shaded, warm situations (Sipman & Harris, 1989; Nimis & Tretiach, 1995). Their preference for young trees (negative relationship with tree age) is likely to reflect the microhabitat requirements related to the crustose growth form of the trentepohlioid species included in our dataset. Crustose thalli develop undisturbed when the bark is smooth (i.e. on young trees) but undergo fragmentation and disintegration as the bark becomes wrinkled with increasing tree age and size.

Concerning the thallus growth form, our results indicate that crustose lichens are more resistant than foliose and fruticose–filamentose (i.e. alectoroid) species to increasing temperature (see Acharya *et al.*, 2011 for epiphytic orchids). Crustose lichens have a lower surface-to-volume ratio (i.e. less surface exposed to the atmosphere), resulting in a higher tolerance to desiccation, water loss being restricted to the upper exposed surface (Büdel & Scheidegger, 2008). In contrast, the contribution of foliose and fruticose–filamentose species to lichen diversity is higher in the lower part of the temperature gradient, reflecting their more rapid drying and wetting pattern that hinders these lichens surviving excessive evapotranspiration rates.

Our results add evidence to the sensitivity of epiphytic lichens to climate change (Insarov & Schroeter, 2002; Ellis

et al., 2007). This study found strong elevation dependence of epiphytic lichen diversity in spruce alpine forests that can be attributed to climatic factors controlling the main ecophysiological functions of these organisms. The mechanism of trait selection drives the response to environmental filtering, providing a tool for detecting major shifts in lichen communities that reflect changes in climatic conditions.

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SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article:

Appendix S1 Correlation matrix for the explanatory variables.

Appendix S2 Model diagnostics.

Appendix S3 List of the species recorded in this study.

BIOSKETCHES

Juri Nascimbene is an ecologist with a strong focus on conservation biology in terrestrial ecosystems. He investigates

the impact of local and climatic factors on lichen diversity in forest ecosystems. His research interests in biogeography include the study of lichen diversity patterns along wide environmental gradients.

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