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Water-energy relationships shape the phylogenetic diversity of terricolous lichen communities in Mediterranean mountains: Implications for conservation in a climate change scenario

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1 **Water-energy relationships shape phylogenetic diversity of terricolous lichen communities in**
2 **Mediterranean mountains: implications for conservation in a climate change scenario**

3 Chiara Vallese^{1*}, Michele Di Musciano^{1,2*}, Lucia Muggia³, Paolo Giordani^{4**}, Luana Francesconi¹,
4 Renato Benesperi⁵, Alessandro Chiarucci¹, Valter Di Cecco⁶, Luciano Di Martino⁶, Luca Di
5 Nuzzo⁵, Gabriele Gheza¹, Piero Zannini¹, Juri Nascimbene¹

6

7 ¹ BIOME Lab, Department of Biological, Geological and Environmental Sciences, Alma Mater
8 Studiorum University of Bologna, via Irnerio 42, 40126 Bologna, Italy

9 ² University of L'Aquila, Department of Life, Health and Environmental Sciences, Piazzale
10 Salvatore Tommasi 1, 67100 L'Aquila

11 ³ Department of Life Sciences, University of Trieste, 34121 Trieste, Italy

12 ⁴ Università di Genova, Dipartimento di Farmacia, viale Cembrano, 4, 16148, Genova, Italia

13 ⁵ Università di Firenze, Dipartimento di Biologia, Via la Pira 4, 50121 Firenze, Italia

14 ⁶ Parco Nazionale della Maiella, Via Badia, 28, 67039 Sulmona, Italia

15

16 * These authors contributed equally

17 ** Corresponding author: Paolo Giordani, e-mail: giordani@difar.it

18

19 **Abstract**

20 Lichens are symbiotic organisms sensitive to climate change and susceptible to a severe decline in
21 diversity, especially in high elevation environments that are already threatened. In this study, we
22 focused on water-energy relationships derived from climatic variables and phylogenetic diversity
23 indices of terricolous lichen communities occurring on a representative Mediterranean mountain.
24 We hypothesized that the variation of precipitation and temperature and their interaction along the
25 altitudinal gradient will shape the phylogenetic diversity and structure of lichen communities. Our
26 results reveal that dry and arid conditions lead to a strong loss in phylogenetic diversity with
27 consequent impoverishment of high elevation lichen communities under a climate change scenario.
28 The interaction between variables, reflecting water-energy relationships with phylogenetic and
29 community diversity patterns, suggests that in a future climate change scenario, the novel climatic
30 conditions may reduce the capability of the species to survive harsher conditions, and
31 Mediterranean mountains may face a severe loss of genetic diversity in a climate change scenario.

32 **Keywords**

33 Altitudinal Gradient; Climate Change; High Elevation Environments; Maiella massif;
34 Mediterranean Mountains; Phylogenetic diversity; structure; Terricolous Lichens; Water-energy
35 hypothesis

36

37 **1 INTRODUCTION**

38 Organisms of high elevation environments are among the most threatened by climate change
39 (Mountain Research Initiative EDW Working Group, 2015) that is already causing an upward shift
40 of treelines and the decline of highly sensitive, cold-adapted species with an increase of more
41 generalist and competitive species (Alexander et al., 2018; Futschik et al., 2020; Parmesan, 2006).
42 These dynamics alter community assembly patterns, and are exacerbated in range-edge areas, as in
43 the case of the mountains of the Mediterranean basin (Giorgi and Lionello, 2008), where species
44 may be susceptible to extreme warming and drought effects (Giménez-Benavides et al., 2018;
45 Gottfried et al., 2012).

46 While most studies have traditionally focused on multiple aspects of taxonomic and functional
47 diversity, a relatively novel approach to effects of climate change, that is being increasingly
48 explored, is that of genetic diversity influencing the community phylogenetic structure at the local
49 scale (Zhou et al., 2018). Species in a community may be more closely related (clustering) due to
50 adaptation to specific ecological conditions. In contrast, under less stressful conditions species may
51 be distantly related (overdispersion) as a result of biotic interactions that hinder similarity and
52 promote between-species competition (Cavender-Bares et al., 2009; Mazel et al., 2016; Webb et al.,
53 2002). Recent studies in high elevation environments (Kluge and Kessler, 2011; Li et al., 2015;
54 Zhou et al., 2018) revealed that communities may experience a strong decrease in phylogenetic
55 diversity due to climate change. However, these studies were mainly focused on plant communities
56 while information is almost lacking for neglected taxa, as in the case of lichens (see e.g. Hurtado et
57 al., 2019, 2020a; Prieto et al., 2017 for arid-temperate areas), that are symbiotic organisms sensitive
58 to climate change and susceptible to severe species loss (Ellis et al., 2007; Sancho et al., 2019),
59 especially in high elevation environments (Allen and Lendemer, 2016; Nascimbene and Spitale,
60 2017). Due to their poikilohydric nature, the lichen metabolic activity depends on thallus water
61 content, which is in equilibrium with the surrounding environment (Green et al., 2011). Thus,
62 lichens are exposed to rapid hydration/dehydration cycles, and this implies that differences in

63 temperature and precipitation and their relative interactions can affect lichen communities by
64 filtering the species based on their water management strategies (Allen and Lendemer, 2016; Marini
65 et al., 2011; Vallese et al., 2021).

66 In this study, we analysed the relationship between climatic variables and phylogenetic diversity of
67 terricolous lichen communities along an altitudinal gradient in the Maiella Massif (Central
68 Apennines, Abruzzo, Italy), the southernmost Mediterranean mountain massif with an alpine and
69 subalpine belt in Italy (Conti et al., 2019; Gheza et al., 2021). In this area, strong effects of climate
70 change were already evident in the taxonomic and functional diversity for plant and cryptogam
71 (thus including lichens) communities (Di Nuzzo et al., 2021; Stanisci et al., 2011). Along an
72 altitudinal gradient, climatic factors, such as precipitation and temperature, vary over a short
73 distance, thus providing a suitable observational perspective to evaluate the response of
74 communities to changing climatic conditions while constraining differences related to
75 biogeographic patterns and life history (McCain and Grytnes, 2010). Furthermore, altitudinal
76 gradients are particularly suitable to explicitly test potential interactions between temperature and
77 precipitation (water-energy hypothesis; Vetaas et al., 2019). Water-energy dynamics are crucial in
78 determining biodiversity patterns across biomes (O'Brien, 2006) and changing conditions may drive
79 biodiversity response to climate change influencing the future stability of ecosystem functioning. In
80 this context, our work aims at assessing the effect of climatic conditions on the patterns of genetic
81 diversity measured as phylogenetic difference and structure of high elevation terricolous lichen
82 communities. We hypothesize that the variation of precipitation and temperature and their
83 interaction along the altitudinal gradient can shape phylogenetic diversity and structure, leading to
84 different assembly mechanisms (overdispersion vs. clustering), based on the phylogenetic
85 relatedness of taxa.

86 **2 MATERIALS AND METHODS**

87 **2.1 Study Area and Study Design**

88 The study area is located in the Maiella National Park (MNP), in the Central-Apennines (Abruzzo,
89 Italy). The Maiella massif is NW–SE-oriented and consists of Mesozoic-Cenozoic limestones. Its
90 orogeny is rather recent, dating to the Pliocene and it is characterized by a very gentle summit
91 profile, due to the Quaternary glacial erosion. This process entailed the presence of an 11 km² large
92 area in the sub-alpine and alpine belt above 2500 m that forms a particular environment that is
93 unique in the Apennine landscape (Blasi et al., 2005). The weather station located in Campo
94 Imperatore (2132 m) indicates an average of 3.6 °C in annual mean temperature and 1613 mm in
95 annual precipitation (Palombo et al., 2013). The medium monthly winter temperatures drop below
96 zero and snowfalls are frequent above 1400 m. Sub-Mediterranean conditions prevail below 1000 m
97 (van Gils et al., 2012).

98 The area selected for our study lies along the massif ridge between 42°00'23" N (Blockhaus) and
99 42°09'41" N (Guado di Coccia). The sampling design consisted of an elevation transect that ran
100 along the ridge. The transect was 14 km long, 100 m wide and spanned 1000 m of elevation,
101 starting above the timberline (1800-1900 m a.s.l.) and reaching the highest altitude at Monte Amaro
102 (2793 m a.s.l.). We delimited 10 elevation belts, each one every 100 m of altitude; in these belts we
103 randomly selected 7 plots of 1 x 1 m using the software QGIS 3.10 (FIGURE 1). In two cases the
104 heterogeneous pattern of the mountain slope produced some disjunctions within the belts. In these
105 cases, more than 7 plots were selected. The final dataset contained therefore 154 plots in which we
106 recorded the occurrence of all terricolous lichens forming the local community (Appendix 1).
107 Sampling activities were performed between summer 2018 and summer 2019. Since the
108 identification of the species was almost impossible in the field partly due to poor development
109 conditions of the thalli, all the samples were identified in the laboratory using relevant literatures
110 (Nimis and Martellos, 2004; Wirth et al., 2013) and digital dichotomous keys available online on
111 the ITALIC website (Nimis and Martellos, 2020). When necessary, specimens were analysed with

112 dissecting and standard light microscopes, and chemical spots test (Orange et al., 2001).
113 Furthermore, we performed standardized thin-layer chromatography when needed (Orange et al.,
114 2001). Critical specimens were also sent to specialists to provide correct identification. The
115 nomenclature of the lichen species follows Nimis and Martellos (2021). For the statistical analysis,
116 we excluded 53 plots with less than 2 species due to poor robustness in the calculation procedure.

117 **2.2 Phylogenetic analyses**

118 To calculate the phylogenetic diversity and structure of the lichen communities, we firstly retrieved
119 from GenBank (<http://www.ncbi.nlm.nih.gov/>) the sequences available corresponding to each
120 identified species. Six fungal genetic markers were used: the nuclear ribosomal RNA small subunit
121 18S gene (nucSSU), the ribosomal large subunit 28S gene (nucLSU), the partial ITS1-5.8S and
122 ITS2 (ITS) regions, the first and the second large subunits of RNA polymerase II (RPB1 and RPB2,
123 respectively), and the small mitochondrial ribosomal subunit 12S gene (mtSSU). Sequences were
124 aligned in multiple sequence alignments individually for each genetic marker using the function
125 ClustalW Multiple alignment run in the software BioEdit v7.2.5 (Hall, 1999). To improve the final
126 alignment, sequences were also adjusted manually. Ambiguous regions and introns were delimited
127 manually and excluded from phylogenetic analyses. We finally used the SequenceMatrix software
128 (Vaidya et al., 2011) to assemble multilocus datasets, the first combining three markers (ITS,
129 mtSSU, and nucLSU) and the second combining all the six markers.

130 The 3-gene (3G) and the 6-gene (6G) multilocus datasets were used to construct the phylogenetic
131 trees. The best phylogenetic inference for our species dataset was selected by comparing the tree
132 topologies obtained from the 3-gene (3G) and the 6-gene (6G) datasets. Both datasets were analysed
133 with the Maximum Likelihood (ML) and the Bayesian approaches. The ML approach was run in the
134 program RAxML v8.2. (Stamatakis, 2014), applying the GTRGAMMA model and running 1000
135 bootstrap replicates. Two runs of four simultaneous Markov chains were run for 2,000,000
136 generations and trees were sampled every 100th generation. A MCMC heated chain was set with a
137 “temperature” value of 0.15. The distribution of log-likelihood scores was examined using the

138 program Tracer v1.5 (Rambaut et al., 2018) to determine that the stationary phase for each search
139 was reached and chains had achieved convergence. The first 25% of the sampled topologies were
140 discarded as part of a burn-in procedure, while the remaining trees were used for calculating the
141 posterior probabilities in the majority rule consensus tree. The convergence of the chains was also
142 confirmed by the convergent diagnostic of the Potential Scale Reduction Factor (PSRF), which
143 approached 1 (Ronquist et al., 2011). The phylogenetic trees were visualized in TreeView v1.6.6
144 (Page, 1996). In either analysis, the outgroup taxa were represented by the species in our dataset
145 belonging to the order *Verrucariales*, i.e. *Agonimia tristicula*, *Catapyrenium cinereum*, *C.*
146 *daedaleum*, *Placidium lachneum* and *P. squamulosum*.

147 **2.3 Diversity and Structure indices**

148 We calculated four phylogenetic indices. The Faith's phylogenetic diversity (PD; Faith, 1992) was
149 calculated using the 'pd' function in R package 'picante' (Kembel et al., 2010) and was used to
150 quantify the phylogenetic diversity within each plot. The PD index represents the total phylogenetic
151 branch length spanned by all species in a community (Faith, 1992).

152 The phylogenetic structure was evaluated using the Net Relatedness Index (NRI), and the Nearest
153 Taxon Index (NTI) (Webb, 2000; Webb et al., 2002) that represent respectively the standardised
154 effect size of Mean Phylogenetic Distance of taxa (MPD) and Mean distance to the nearest taxon
155 (MNTD) (Webb, 2000; Webb et al., 2002). NRI and NTI reflect phylogenetic structures in different
156 parts of the phylogeny. NRI is based on the mean phylogenetic distance (MPD) of an assemblage.
157 In contrast, NTI is based on the mean nearest neighbour distance (MNND), within the assemblage
158 and its nearest neighbour in the assemblage phylogeny. NTI is therefore most sensitive to clustering
159 or overdispersion near the tips of the pool phylogeny. Negative values indicate phylogenetic
160 overdispersion (i.e., species are more distantly related than expected by chance), positive values
161 indicate phylogenetic clustering (i.e., species are more closely related than expected by chance).
162 NRI and NTI were calculated using the 'ses.mpd' and the 'ses.mntd' functions in the 'picante' R
163 package (Kembel et al., 2010) and multiplying by -1 the resulting values. We used a null model

164 with 999 randomizations that shuffles the species occurrences randomly within plots, thereby
165 maintaining species richness.

166 We conducted correlation analyses to assess the relationship between each phylogenetic metric and
167 the species richness. Pearson's correlation was calculated, using the function 'rcorr' in the R
168 package 'Hmisc' (Harrell, 2019). Correlations were considered significant when $P < 0.05$
169 (Appendix 2).

170 **2.4 Climatic variables**

171 We downloaded 19 bioclimatic variables representative of the period 1979-2010 from CHELSA
172 database website (<http://chelsa-climate.org/>). The variables have a 1 km² spatial resolution and were
173 consequently downscaled to a 20 m resolution. Thus, all the variables were downscaled to a
174 resolution suitable for our study. We downscaled the temperature-related variables by fitting a
175 generalized linear model (GLM) as covariate, and altitude and northness as independent
176 variables, this latter were extracted from 20 m resolution Digital Elevation Model (DEM). In this
177 way, we re-projected each temperature variable to 20 m/pixel resolution. In the case of
178 precipitation-related variables, since they did not have a clear relationship with topographic
179 variables, we used linear interpolation of CHELSA rasters to obtain a 20 m/pixel resolution. To
180 reduce the collinearity, we performed a pairwise Pearson correlation between bioclimatic
181 predictors. We retained those variables that were not highly correlated (pairwise Pearson correlation
182 $< |0.75|$), always considering the ecology of the taxa considered. Therefore, we selected four
183 variables: BIO1-Annual Mean Temperature, BIO7-Temperature Annual Range (BIO5-Max
184 Temperature – BIO6-Min Temperature), BIO12-Annual Precipitation, and BIO17-Precipitation of
185 the Driest Quarter.

186 **2.5 Data analysis**

187 The effects of bioclimatic variables on phylogenetic diversity were investigated using generalized
188 additive models (GAMs). All possible combinations of linear and smoothed terms were evaluated.
189 For each phylogenetic index, we selected the formula that maximized the amount of deviance

190 accounted (D-squared) and minimized the Akaike Information Criterion (AIC). In addition, the
191 interactions between BIO1 with BIO12, and between BIO1 with BIO17 were included in the model.
192 The importance of each variable was estimated using the ‘varImp’ function in ‘caret’ package
193 (Kuhn, 2008). Response curves of the single climatic variables were performed with ‘inflated
194 response curves’(Zurell et al., 2012), modified for quantitative response variables. The response
195 curves for interaction variables were calculated without using the inflate approach, and the fixed
196 variables have been set to their mean value.

197 All statistical analyses were performed in R version 4.0.3 (R Core Team, 2021) using the following
198 packages ‘tidyverse’(Wickham et al., 2019), ‘ggpubr’(Kassambara, 2020), ‘modEvA’(Barbosa et
199 al., 2020), ‘gam’(Hastie and Tibshirani, 2017), and ‘ggeffects’ (Lüdecke, 2017).

200

201 **3 RESULTS**

202 Species richness of local communities included in our plots ranged from 0 to 18 species per plot,
203 with a mean value of 3.3. We included in the analyses 60 lichen species both according to the
204 sequences retrieved from GenBank and 101 plots in which more than two species were recorded
205 (Appendix 1). The final sequences dataset contained a large amount of missing data (44%). The
206 best supported phylogenetic tree was obtained from the 3-gene (3G) datasets. A comparison with
207 literature (Nimis and Martellos, 2021) then revealed that the 3G-tree topology that fits better with
208 our dataset was obtained by the Bayesian approaches and consisted of 60 ingroups and 54 internal
209 nodes, with no polytomies (Appendix 3).

210 The best-fitting GAMs for each phylogenetic index showed an explained deviance ranging from
211 0.27 to 0.42 (TABLE 1). Annual Precipitation (BIO12) was the most important variable for all the
212 indices, except for NRI in which Annual Mean Temperature (BIO1) was the variable with the
213 highest value of importance (Appendix 4).

214 **3.1 Climatic drivers of phylogenetic indices**

215 Phylogenetic diversity (PD) was positively related with annual precipitation (BIO12) while the
216 phylogenetic structure indices (NRI and NTI) were negatively affected by increasing values of
217 BIO12. Low values of BIO12 led to positive values only for NRI (FIGURE 2). In the case of PD,
218 we also found a slightly positively correlation with the Precipitation of the Driest Quarter (BIO17)
219 (Appendix 5a). In contrast, NRI and NTI were negatively correlated with BIO17 (Appendix 5b).
220 Variation in annual temperature (BIO1) did not affect PD except for a negative effect at very low
221 temperature (Appendix 5a).
222 Annual temperature and precipitation had an interactive effect. At low temperatures, PD increased
223 with annual precipitation. Conversely, at higher temperatures, PD slightly decreased with increasing
224 precipitation. PD reached the highest values at medium-low temperature and high precipitation
225 values (FIGURE 3).
226 Variation in BIO1 also affected the phylogenetic structure indices that showed quite similar
227 patterns. In general, both NRI and NTI had negative values at medium-low temperature, the fitted
228 response curve assumed a hump shape in the case of NRI. Higher temperature led to positive values
229 for both NRI and NTI (FIGURE 4A). The difference between the Maximum and Minimum
230 Temperature (BIO7) also appeared to be an important variable influencing phylogenetic structure
231 indices with positive values for both NRI and NTI at higher values of BIO7 and negative at very
232 low values for NTI (FIGURE 4B).

233

234 **4 DISCUSSION**

235 Climate Change will affect the high elevation lichen communities of Mediterranean mountains both
236 in terms of taxonomic and functional diversity (Di Nuzzo et al. 2021) and in their phylogenetic
237 diversity. Our results reveal a non-random pattern of phylogenetic diversity correlated to climate
238 along elevation gradients, showing a higher diversity in high moisture and mid- to low-temperature
239 environments, and a lower phylogenetic diversity under dry-arid conditions. The progressive
240 dryness promotes an increasing change in climate, points to a general threat to phylogenetic

241 diversity and the associated pattern in community structure. Communities adapted to high elevation
242 and mostly those living in the southern mountains of our hemisphere will be most affected as the
243 conditions in which they specialize alter (Rehm et al. 2015). Water availability is expected to be the
244 main driver of phylogenetic diversity and structure. In this perspective, the forecasted reduction of
245 precipitation in the Mediterranean basin (Giorgi and Lionello, 2008) may negatively affect lichen
246 phylogenetic diversity. The interaction between precipitation and temperature, reflecting water-
247 energy effects on community diversity patterns, suggests that acclimation to novel climatic
248 conditions may depend on the capability of the species to track changing conditions and
249 combinations of both these factors. In particular, our results indicate that phylogenetic diversity is
250 maximized under intermediate-low temperature and high precipitation, that implies harsher
251 conditions of a warming-drought scenario. While several studies have already revealed the key role
252 of water availability in controlling both taxonomic and functional diversity of lichen communities
253 (Giordani et al., 2019; Hurtado et al., 2020b; Marini et al., 2011), reflecting the poikilohydric nature
254 of the lichen symbiosis, our findings provide support for a negative impact of drought that may
255 modify the genetic structure of the lichen community. This warns about the impact of climate
256 change on the variability of high elevation lichen communities leading to an increase of more
257 closely related taxa in sites where water availability is low, thus resulting in phylogenetic clustering
258 of lichen communities.

259 While the pattern is relatively clear, the exact mechanism need further clarification and may even
260 involve complex biotic interaction between the multiple components of the lichen symbiosis (Singh
261 et al., 2017). Terricolous lichen communities at the wettest-cold part of the gradient have the
262 highest values in terms of phylogenetic diversity including more distantly related taxa
263 (overdispersed phylogenetic structure). This may reflect the fact that community assembly was
264 related to evolutionary filtering of phylogenetically diverse species that have their main radiation
265 center in boreal to arctic-alpine regions, as in the case of *Nephromopsis nivalis* or *Lecanora*
266 *epibryon* (Nimis and Martellos, 2021). However, the relatively low diversity of these communities

267 when compared to their counterparts in the Alps and boreal-arctic regions (Nascimbene et al., 2017;
268 Nimis and Martellos, 2021) suggests that Mediterranean mountains may host already
269 phylogenetically depleted assemblages reflecting a baseline of less suitable climatic conditions for
270 this pool of cold-adapted species. Many species of these communities have a relictual distribution
271 pattern, being disjunct from their closest core populations in the Alps. This is for example the case
272 of *Cetraria madreporiformis* whose populations in the Maiella massif are the southernmost of the
273 boreal region in the northern hemisphere (Nimis and Martellos, 2021). This intrinsically extreme
274 situation may be exacerbated by changes in the water-energy dynamics, warning about the loss of
275 the genetically diverse pool of arctic-alpine species.

276 In the warmer-arid part of the gradient, phylogenetic diversity of terricolous lichen communities is
277 likely maintained by a diverse pool of drought-adapted species (Prieto et al., 2017), as in the case of
278 several crustose lichens (Nascimbene and Marini, 2015). With future warmer and drought
279 conditions, ecological processes are likely expected to generate further genetic diversity in these
280 communities triggering a thermophilization process even in high elevation ranges. However, in a
281 previous study (Di Nuzzo et al., 2021) we found support for a lack of species replacement in high
282 elevation ranges probably due to a simultaneous increase of competition with taller vascular plants
283 that may hinder lichen establishment and development. This would hamper the compensation of the
284 loss of phylogenetic diversity in the wettest and coldest part of the gradient, thus resulting in net-
285 loss of phylogenetic diversity of terricolous lichen communities in Mediterranean mountains.

286 Water-energy dynamics are crucial for poikilohydric organisms, and our study reveals their impact
287 on the evolutionary history of terricolous lichen communities warning of detrimental effects in the
288 Mediterranean mountains, where already depleted communities may face severe loss of genetic
289 diversity in a climate change scenario. However, our results are likely not exhaustive to depicting
290 the risks that lichens are facing in terms of phylogenetic diversity loss, especially in high elevation
291 ranges, and further research may test the consistency of our results expanding the focus to other
292 mountain systems along a latitudinal-macroclimatic gradient. More effort dedicated also to

293 population dynamics and biotic interactions in the lichen symbiosis may help to elucidate the
294 mechanisms behind the loss of phylogenetic diversity.

295

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302

303 **Author contributions**

304 C.V., M.D.M., P.Z., A.C. and J.N. conceived the ideas; C.V., L.D.N., R.B., P.G., V.D.C., L.D.M.
305 and J.N. collected the data; L.D.N., C.V., G.G., and J.N. identified the lichens; M.D.M., L.M., L.F.
306 and C.V. analysed the data; L.M. created the trees; C.V. created the map; C.V., M.D.M., P.G., L.F.,
307 L.M., R.B. and J.N. contributed to write the draft; C.V., P.G. and J.N. lead the writing.

308

309

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FIGURE LEGENDS:

TABLE 1: GAMs model for each phylogenetic index, that maximized the deviance accounted (D-squared) and the Akaike Information Criterion (AIC). For each predictor, the smoothed term (s) was indicated when added.

FIGURE 1: Location of the study area and representation of the sampling design (A). The transect was divided into ten 100 m wide elevation belts (B). In each belt, 7 plots of 100x100 cm were randomly selected and samples of lichens were collected. The figure was produced using the open-source software QGIS 3.10.12 (QGIS.org, 2021) and assembled using Adobe Photoshop (2018). The contour line in (A) was calculated using Contour function available in QGIS 3.10 and using a 10 m resolution DTM freely available on INGV Pisa (Istituto nazionale di geofisica e vulcanologia – Sezione di Pisa) website: http://tinality.pi.ingv.it/Download_Area2.html. The picture was finally assembled using Adobe Photoshop CC 2018 and modified after Di Nuzzo et al. 2021.

FIGURE 2: Pattern in Faith's Phylogenetic Diversity (PD), Net Relatedness Index (NRI), and the Nearest Taxon Index (NTI) in response to Annual Precipitation (BIO12). Grey lines are the 100 inflated response curves, while the mean and the median value of the inflated curves are indicated with orange and blue lines respectively. Grey dots represent the observed values in each plot. Precipitation values are expressed in millimetres.

FIGURE 3: Interaction's response curve between mean annual temperature (BIO1) and annual precipitation (BIO12) on phylogenetic diversity (PD). Temperature is expressed in degrees Celsius ($^{\circ}\text{C}$) x 10. Precipitation in millimetres.

FIGURE 4: Pattern in Relatedness Index (NRI), and the Nearest Taxon Index (NTI) in response to Annual Mean Temperature (BIO1) and Temperature Annual Range (BIO7). Grey lines are the 100 inflated response curves, while the mean and the median value of the inflated curves are indicated with orange and blue lines, respectively. Grey dots represent the observed values in each plot. Precipitation values are expressed in millimetres.

TABLE 1

Index	Formula	D-squared	AIC
PD	$s(\text{BIO1}) + s(\text{BIO7}) + s(\text{BIO12}) + s(\text{BIO17}) + \text{BIO1}:\text{BIO12} + \text{BIO1}:\text{BIO17}$	0.42	64
NRI	$s(\text{BIO1}) + s(\text{BIO7}) + s(\text{BIO12}) + \text{BIO17} + \text{BIO1}:\text{BIO12} + \text{BIO1}:\text{BIO17}$	0.27	316
NTI	$s(\text{BIO1}) + s(\text{BIO7}) + s(\text{BIO12}) + s(\text{BIO17}) + \text{BIO1}:\text{BIO12} + \text{BIO1}:\text{BIO17}$	0.36	-513

FIGURE 1

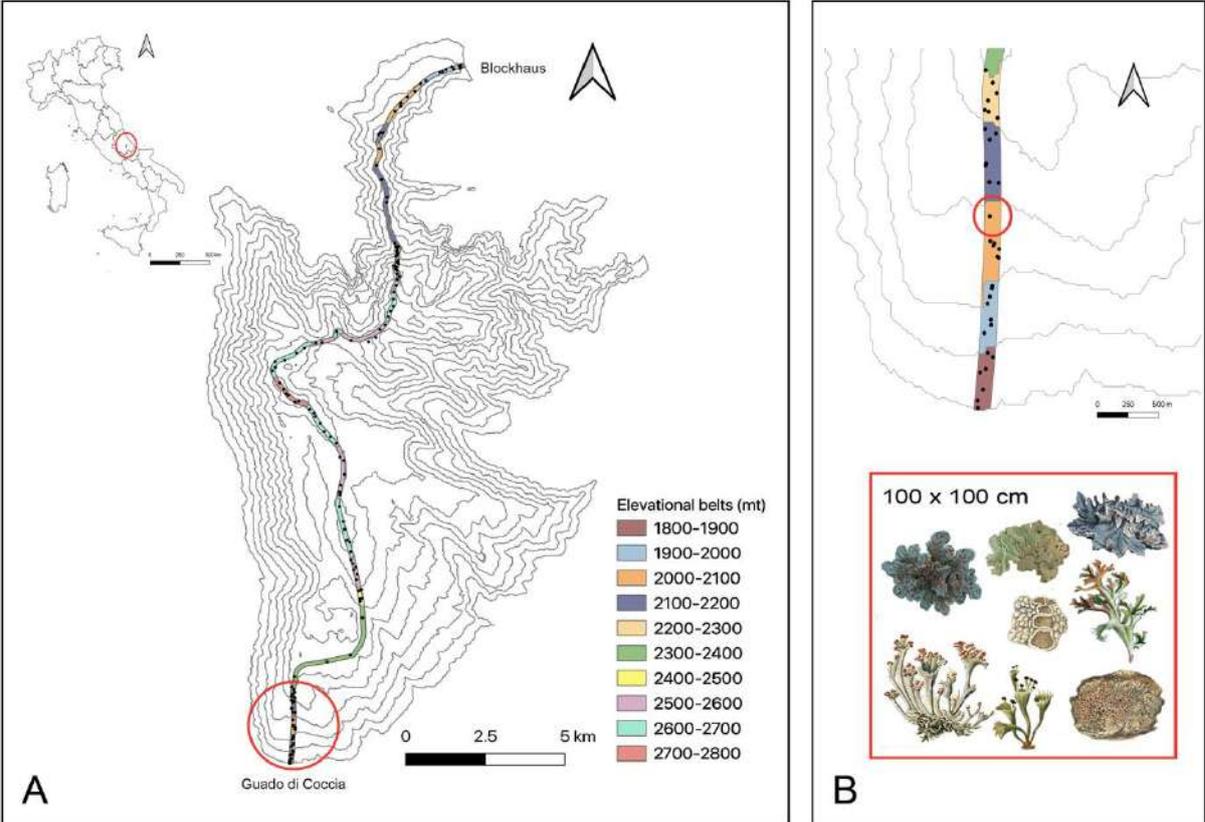


FIGURE 2

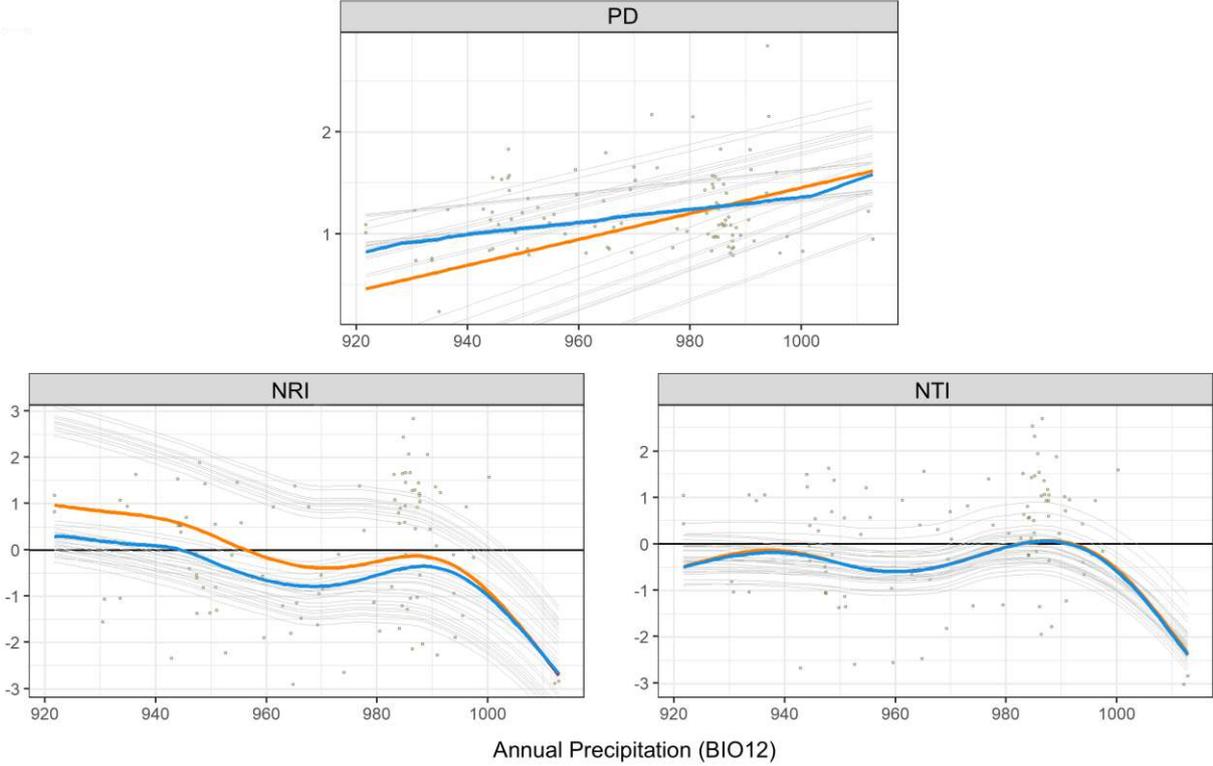


FIGURE 3

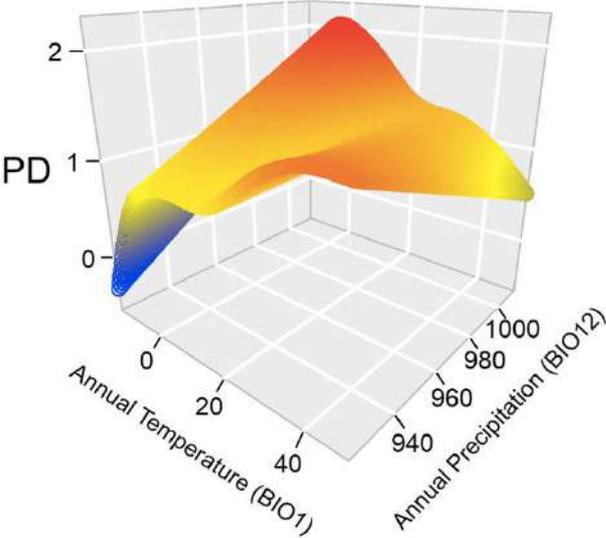
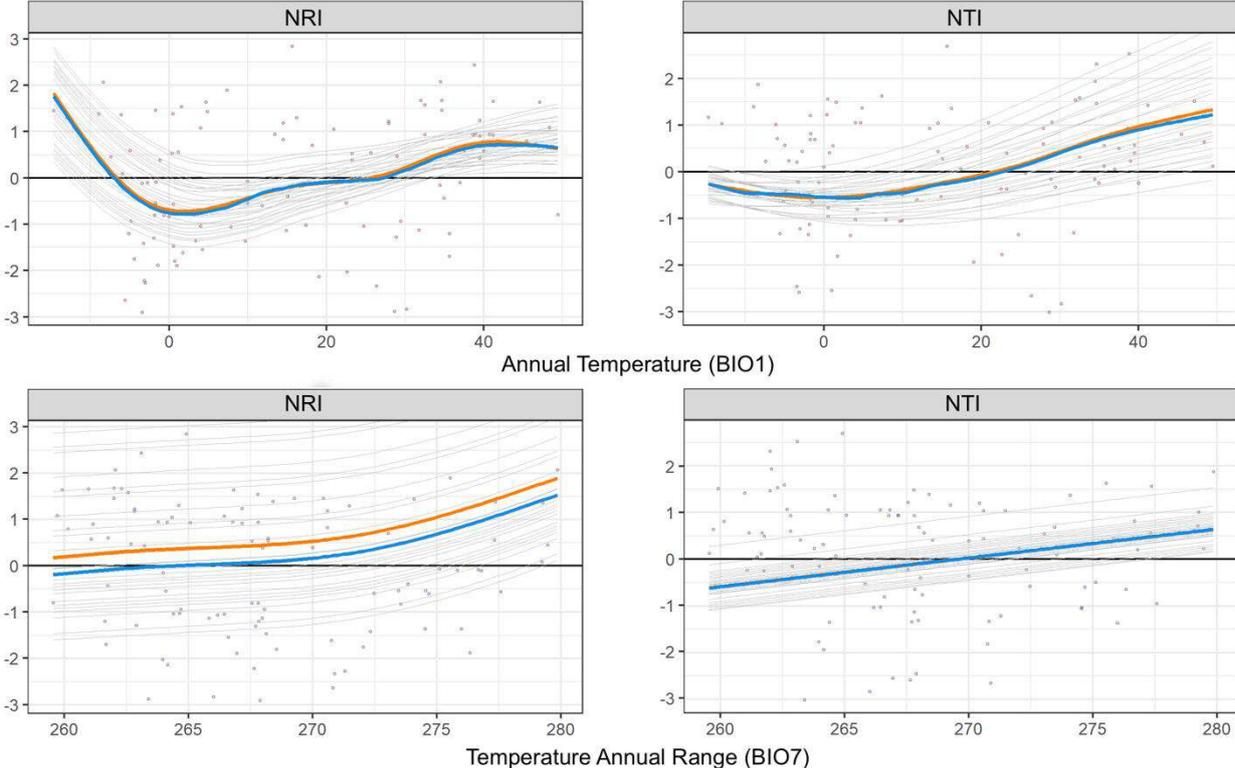
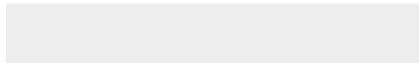
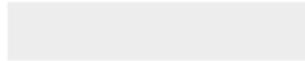


FIGURE 4





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Conflict of interest statement

The authors have no conflict of interest to declare.