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Methodological Advances

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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ABSTRACT

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

1. Introduction

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

While most studies have traditionally focused on multiple aspects of taxonomic and functional diversity, a relatively novel approach to better understand the effects of climate change, that is being increasingly explored, is that of how genetic diversity influences community phylogenetic structure at the local scale (Zhou et al., 2018). Species in a community may be more closely related (clustering) due to adaptation to specific ecological conditions. In contrast, under less stressful conditions species may be distantly related (overdispersion) as a result of biotic interactions that hinder similarity and promote between-species competition (Cavender-Bares et al., 2009; Mazel et al., 2016; Webb et al., 2002). Recent studies in high elevation environments (Kluge and Kessler, 2011; Li et al., 2015; Zhou et al., 2018) revealed that communities may experience a strong decrease in phylogenetic diversity due to

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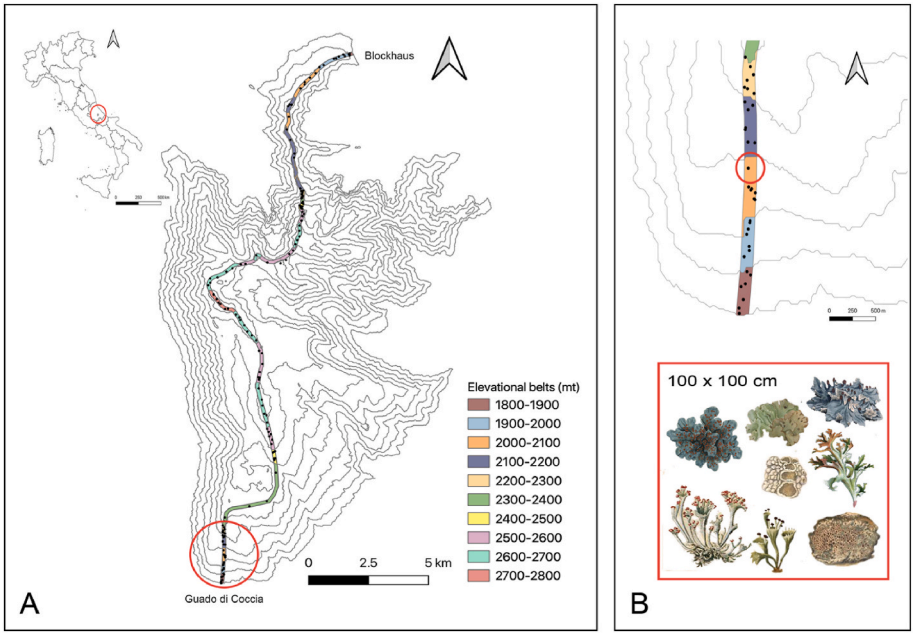

Fig. 1. Location of the study area and representation of the sampling design (A). The transect was divided into ten 100 m wide elevation belts (B). In each belt, 7 plots of 100 × 100 cm were randomly selected and samples of lichens were collected. The figure was produced using the open-source software 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://tinitaly.pi.ingv.it/Download_Area2.html. The picture was finally assembled using Adobe Photoshop CC 2018 and modified after Di Nuzzo et al., (2021).

climate change. However, these studies were mainly focused on plant communities while information is almost lacking for neglected taxa, as in the case of lichens (see e.g. Hurtado et al., 2019, 2020a; Prieto et al., 2017 for arid-temperate areas), that are symbiotic organisms sensitive to climate change and susceptible to severe species loss (Ellis et al., 2007; Sancho et al., 2019), especially in high elevation environments (Allen and Lendemer, 2016; Nascimbene and Spitale, 2017). Due to their poikilohydric nature, the lichen metabolic activity depends on thallus water content, which is in equilibrium with the surrounding environment (Green et al., 2011). Thus, lichens are exposed to rapid hydration/dehydration cycles, and this implies that differences in temperature and precipitation and their relative interactions can affect lichen communities by filtering the species based on their water management strategies (Allen and Lendemer, 2016; Marini et al., 2011; Vallese et al., 2021).

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

2. Materials and methods

2.1. Study area and study design

The study area is located in the Maiella National Park (MNP), in the Central-Apennines (Abruzzo, Italy). The Maiella massif is NW–SE-oriented and consists of Mesozoic-Cenozoic limestones. Its orogeny is rather recent, dating to the Pliocene and it is characterized by a very gentle summit profile, due to the Quaternary glacial erosion. This process entailed the presence of an 11 km^2 large area in the sub-alpine and alpine belt above 2500 m that forms a particular environment that is unique in the Apennine landscape (Blasi et al., 2005). The weather station located in Campo Imperatore (2132 m) indicates an average of 3.6 °C in annual mean temperature and 1613 mm in annual precipitation (Palombo et al., 2013). The medium monthly winter temperatures drop below zero and snowfalls are frequent above 1400 m. Sub-Mediterranean conditions prevail below 1000 m (van Gils et al., 2012).

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

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

2.2. Phylogenetic analyses

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

The 3-gene (3G) and the 6-gene (6G) multilocus datasets were used to construct the phylogenetic trees. The best phylogenetic inference for our species dataset was selected by comparing the tree topologies obtained from the 3-gene (3G) and the 6-gene (6G) datasets. Both datasets were analysed with the Maximum Likelihood (ML) and the Bayesian approaches. The ML approach was run in the program RAxML v8.2. (Stamatakis, 2014), applying the GTRGAMMA model and running 1000 bootstrap replicates. Two runs of four simultaneous Markov chains were run for 2,000,000 generations and trees were sampled every 100th generation. A MCMC heated chain was set with a "temperature" value of 0.15. The distribution of log-likelihood scores was examined using the program Tracer v1.5 (Rambaut et al., 2018) to determine that the stationary phase for each search was reached and chains had achieved convergence. The first 25% of the sampled topologies were discarded as part of a burn-in procedure, while the remaining trees were used for calculating the posterior probabilities in the majority rule consensus tree. The convergence of the chains was also confirmed by the convergent diagnostic of the Potential Scale Reduction Factor (PSRF), which approached 1 (Ronquist et al., 2011). The phylogenetic trees were visualized in TreeView v1.6.6 (Page, 1996). In either analysis, the outgroup taxa were represented by the species in our dataset belonging to the order *Verrucariales*, i.e. *Agonimia tristicula, Catapyrenium cinereum, C. daedaleum, Placidium lachneum* and *P. squamulosum*.

2.3. Diversity and structure indices

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

The phylogenetic structure was evaluated using the Net Relatedness Index (NRI), and the Nearest Taxon Index (NTI) (Webb, 2000; Webb et al., 2002) that represent respectively the standardised effect size of Mean Phylogenetic Distance of taxa (MPD) and Mean distance to the nearest taxon (MNTD) (Webb, 2000; Webb et al., 2002). NRI and NTI reflect phylogenetic structures in different parts of the phylogeny. NRI is based on the mean phylogenetic distance (MPD) of an assemblage. In contrast, NTI is based on the mean nearest neighbour distance (MNND), within the assemblage and its nearest neighbour in the assemblage phylogeny. NTI is therefore most sensitive to clustering or overdispersion near the tips of the pool phylogeny. Negative values indicate phylogenetic overdispersion (i.e., species are more distantly related than expected by chance), positive values indicate phylogenetic clustering (i.e., species are more closely related than expected by chance). NRI and NTI were calculated using the 'ses.mpd' and the 'ses.mntd' functions in the 'picante' R package (Kembel et al., 2010) and multiplying by −1 the resulting values. We used a null model with 999 randomizations that shuffles the species occurrences randomly within plots, thereby maintaining species richness.

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

2.4. Climatic variables

We downloaded 19 bioclimatic variables representative of the period 1979–2010 from CHELSA database website (http://chelsa-climate.org/). The variables have a 1 km^2 spatial resolution and were consequently downscaled to a 20 m resolution. Thus, all the variables were downscaled to a resolution suitable for our study. We downscaled the temperature-related variables by fitting a generalized linear model (GLM) (Jaberalansar et al., 2018) as covariate, and altitude and northness as independent variables, this latter were extracted from 20 m resolution Digital Elevation Model (DEM). In this way, we re-projected each temperature variable to 20 m/pixel resolution. In the case of precipitation-related variables, since they did not have a clear relationship with topographic variables, we used linear interpolation of CHELSA rasters to obtain a 20 m/pixel resolution. To reduce the collinearity, we performed a pairwise Pearson correlation between bioclimatic predictors. We retained those variables that were not highly correlated (pairwise Pearson correlation $<|0.75|$), always considering the ecology of the taxa considered. Therefore, we selected four variables: BIO1-Annual Mean Temperature, BIO7-Temperature Annual Range (BIO5-Max Temperature – BIO6-Min Temperature), BIO12-Annual Precipitation, and BIO17-Precipitation of the Driest Quarter.

2.5. Data analysis

The effects of bioclimatic variables on phylogenetic diversity were investigated using generalized additive models (GAMs). All possible combinations of linear and smoothed terms were evaluated. For each phylogenetic index, we selected the formula that maximized the amount of deviance accounted (D-squared) and minimized the Akaike Information Criterion (AIC). In addition, the interactions between BIO1 with BIO12, and between BIO1 with BIO17 were included in the model.

The importance of each variable was estimated using the 'varImp' function in 'caret' package (Kuhn, 2008). Response curves of the single climatic variables were performed with 'inflated response curves'(Zurell et al., 2012), modified for quantitative response variables. The response curves for interaction variables were calculated without using the inflate approach, and the fixed variables have been set to their mean value.

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

3. Results

Species richness of local communities included in our plots ranged from 0 to 18 species per plot, with a mean value of 3.3. We included in

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.

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

the analyses 60 lichen species both according to the sequences retrieved from GenBank and 101 plots in which more than two species were recorded (Appendix 1). The final sequences dataset contained a large amount of missing data (44%). The best supported phylogenetic tree was obtained from the 3-gene (3G) datasets. A comparison with literature (Nimis and Martellos, 2021) then revealed that the 3G-tree topology that fits better with our dataset was obtained by the Bayesian approaches and consisted of 60 ingroups and 54 internal nodes, with no polytomies (Appendix 3).

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

3.1. Climatic drivers of phylogenetic indices

Phylogenetic diversity (PD) was positively related with annual precipitation (BIO12) while the phylogenetic structure indices (NRI and NTI) were negatively affected by increasing values of BIO12. Low values of BIO12 led to positive values only for NRI (Fig. 2). In the case of PD, we also found a slightly positively correlation with the Precipitation of the Driest Quarter (BIO17) (Appendix 5). In contrast, NRI and NTI were negatively correlated with BIO17 (Appendix 5).

Variation in annual temperature (BIO1) did not affect PD except for a negative effect at very low temperature (Appendix 5).

Annual temperature and precipitation had an interactive effect. At low temperatures, PD increased with annual precipitation. Conversely, at higher temperatures, PD slightly decreased with increasing precipitation. PD reached the highest values at medium-low temperature and high precipitation values (Fig. 3).

Variation in BIO1 also affected the phylogenetic structure indices that showed quite similar patterns. In general, both NRI and NTI had negative values at medium-low temperature, the fitted response curve assumed a hump shape in the case of NRI. Higher temperature led to positive values for both NRI and NTI (Fig. 4). The difference between the Maximum and Minimum Temperature (BIO7) also appeared to be an important variable influencing phylogenetic structure indices with positive values for both NRI and NTI at higher values of BIO7 and negative at very low values for NTI (Fig. 4).

4. Discussion

Climate Change will affect the high elevation lichen communities of Mediterranean mountains both in terms of taxonomic and functional diversity (Di Nuzzo et al., 2021) and in their phylogenetic diversity. Our results reveal a non-random pattern of phylogenetic diversity correlated to climate along elevation gradients, showing a higher diversity in high moisture and mid-to low-temperature environments, and a lower phylogenetic diversity under dry-arid conditions. The progressive dryness promotes an increasing change in climate, points to a general threat to phylogenetic diversity and the associated pattern in community structure. Communities adapted to high elevation and mostly those living in the southern mountains of our hemisphere will be most affected as the conditions in which they specialize alter (Rehm et al., 2015).

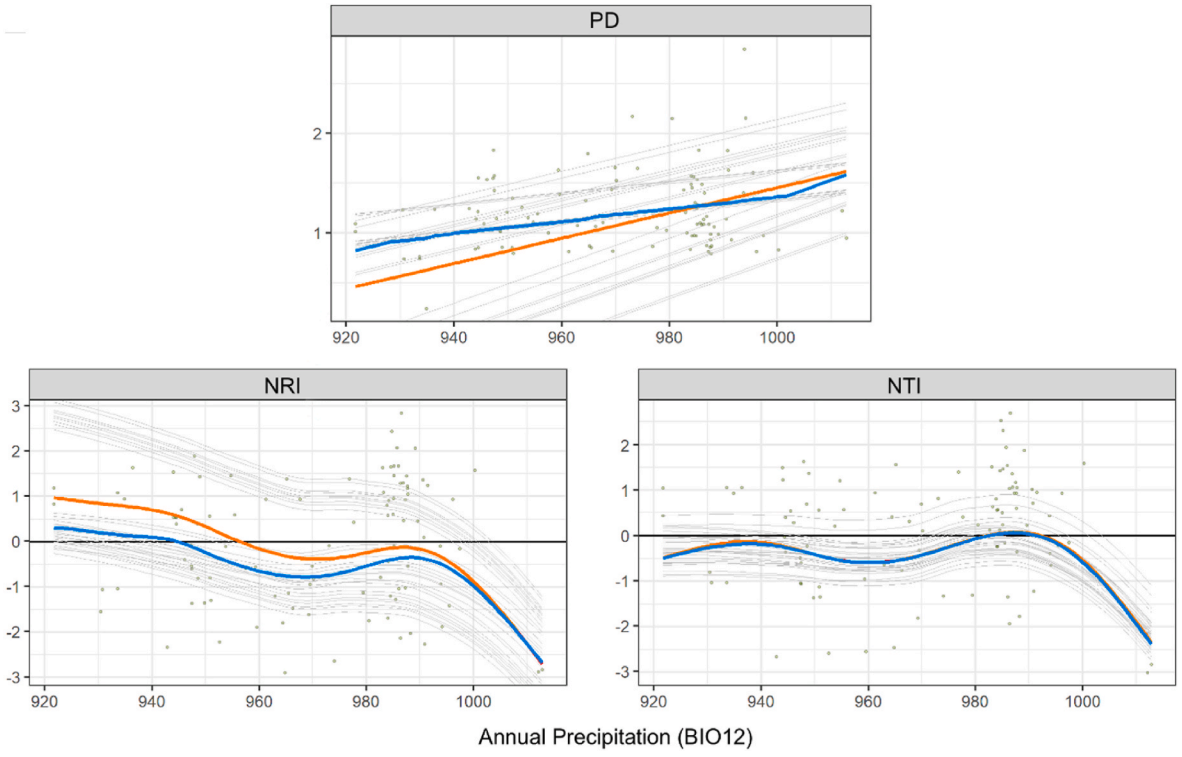

Fig. 2. Pattern in Faith's Phylogenetic Diversity (PD), Net Relatedness Index (NRI), and the Nearest Taxon Index (NTI) in response to Annual Precipitation (BIO12). Grey lines are the 100 inflated response curves, while the mean and the median value of the inflated curves are indicated with orange and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

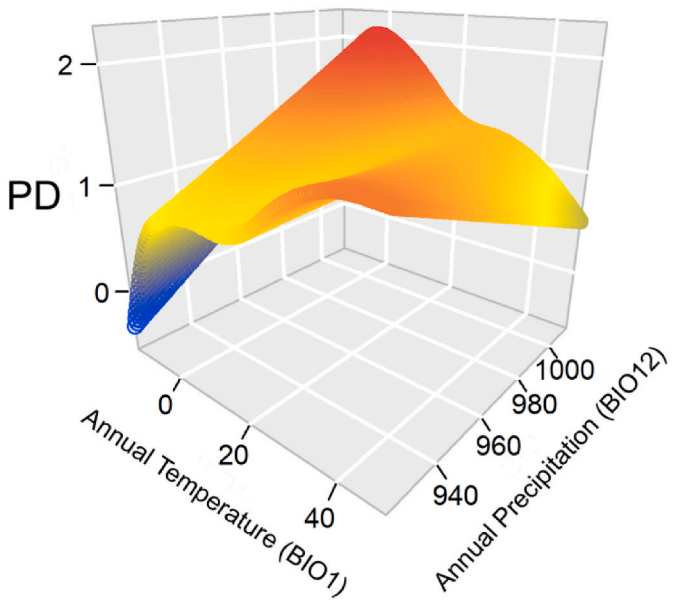

Fig. 3. Interaction's response curve between mean annual temperature (BIO1) and annual precipitation (BIO12) on phylogenetic diversity (PD). Temperature is expressed in degrees Celsius (°C) x 10. Precipitation in millimetres.

Water availability is expected to be the main driver of phylogenetic diversity and structure. In this perspective, the forecasted reduction of precipitation in the Mediterranean basin (Giorgi and Lionello, 2008) may negatively affect lichen phylogenetic diversity. The interaction between precipitation and temperature, reflecting water-energy effects on community diversity patterns, suggests that acclimation to novel climatic conditions may depend on the capability of the species to track changing conditions and combinations of both these factors. In particular, our results indicate that phylogenetic diversity is maximized under intermediate-low temperature and high precipitation, that implies harsher conditions of a warming-drought scenario. While several studies have already revealed the key role of water availability in controlling both taxonomic and functional diversity of lichen communities (Giordani et al., 2019; Hurtado et al., 2020b; Marini et al., 2011), reflecting the poikilohydric nature of the lichen symbiosis, our findings provide support for a negative impact of drought that may modify the genetic structure of the lichen community. This warns about the impact of climate change on the variability of high elevation lichen communities leading to an increase of more closely related taxa in sites where water availability is low, thus resulting in phylogenetic clustering of lichen communities.

While the pattern is relatively clear, the exact mechanisms need further clarification and may even involve complex biotic interactions between the multiple components of the lichen symbiosis (Singh et al., 2017). Terricolous lichen communities at the wettest-cold part of the gradient have the highest values in terms of phylogenetic diversity including more distantly related taxa (overdispersed phylogenetic structure). This may reflect the fact that community assembly was related to evolutionary filtering of phylogenetically diverse species that have their main radiation center in boreal to arctic-alpine regions, as in the case of *Nephromopsis nivalis* or *Lecanora epibryon* (Nimis and Martellos, 2021). However, the relatively low diversity of these communities when compared to their counterparts in the Alps and boreal-arctic regions (Nascimbene et al., 2017; Nimis and Martellos, 2021) suggests that Mediterranean mountains may host already phylogenetically depleted assemblages reflecting a baseline of less suitable climatic conditions for this pool of cold-adapted species. Many species of these communities have a relictual distribution pattern, being disjunct from their closest core populations in the Alps. This is for example the case of *Cetraria madreporiformis* whose populations in the Maiella massif are the southernmost of the boreal region in the northern hemisphere (Nimis and Martellos, 2021). This intrinsically extreme situation may be exacerbated by changes in the water-energy dynamics, warning about the loss of the genetically diverse pool of arctic-alpine species.

In the warmer-arid part of the gradient, phylogenetic diversity of terricolous lichen communities is likely maintained by a diverse pool of drought-adapted species (Prieto et al., 2017), as in the case of several crustose lichens (Nascimbene and Marini, 2015). With warmer and drier conditions in the future, ecological processes are likely expected to generate further genetic diversity in these communities triggering a thermophilization process even in high elevation ranges. However, in a previous study (Di Nuzzo et al., 2021) we found support for a lack of species replacement in high elevation ranges probably due to a simultaneous increase of competition with taller vascular plants that may

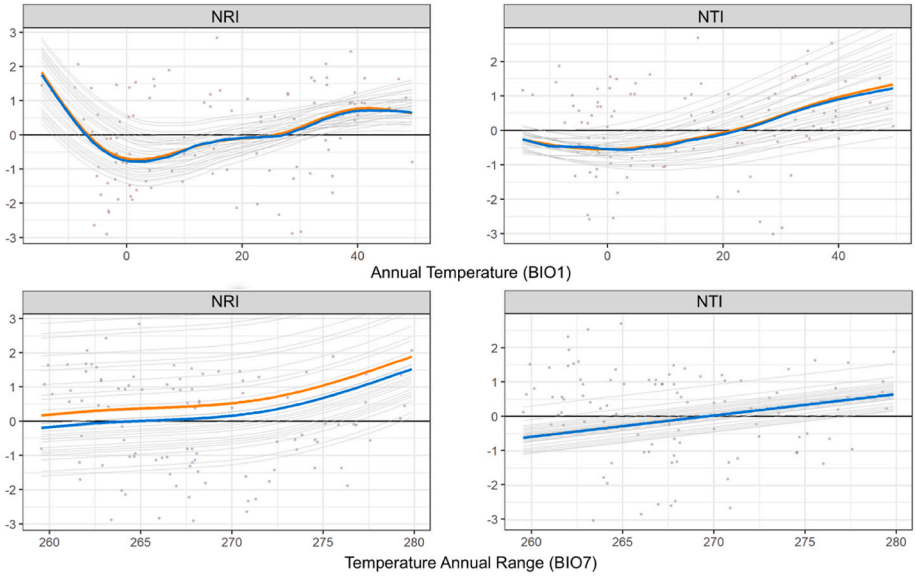

Fig. 4. Pattern in Relatedness Index (NRI), and the Nearest Taxon Index (NTI) in response to Annual Mean Temperature (BIO1) and Temperature Annual Range (BIO7). Grey lines are the 100 inflated response curves, while the mean and the median value of the inflated curves are indicated with orange and blue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

hinder lichen establishment and development. This would hamper the compensation of the loss of phylogenetic diversity in the wettest and coldest part of the gradient, thus resulting in net-loss of phylogenetic diversity of terricolous lichen communities in Mediterranean mountains.

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

Author contributions

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. 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. 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., L.M., R.B. and J.N. contributed to write the draft; C.V., P.G. and J.N. lead the writing.

Declaration of competing interest

The authors have no conflict of interest to declare.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.funeco.2022.101189.

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