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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 Muggia[3], Paolo Giordani[4**], Luana Francesconi[1],

4   Renato Benesperi[5], Alessandro Chiarucci[1], Valter Di Cecco[6], Luciano Di Martino[6], Luca Di

5   Nuzzo[5], Gabriele Gheza[1], Piero Zannini[1], Juri Nascimbene[1]

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

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16   * These authors contributed equally

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

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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

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 effects of climate change, that is being increasingly explored, is that of genetic diversity influencing the 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 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 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 x 1 m using the software QGis 3.10 (FIGURE 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

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

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

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 km^2 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)42 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

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 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

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

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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). 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 mechanism need further clarification and may even involve complex biotic interaction 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 future warmer and drought conditions, 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 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 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.

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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.

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REFERENCES

Alexander, J.M., Chalmandrier, L., Lenoir, J., Burgess, T.I., Essl, F., Haider, S., Kueffer, C., McDougall, K., Milbau, A., Nuñez, M.A., Pauchard, A., Rabitsch, W., Rew, L.J., Sanders, N.J., Pellissier, L., 2018. Lags in the response of mountain plant communities to climate change. Glob. Change Biol. 24, 563–579. https://doi.org/10.1111/gcb.13976

Allen, J.L., Lendemer, J.C., 2016. Climate change impacts on endemic, high-elevation lichens in a biodiversity hotspot. Biodivers. Conserv. 25, 555–568. https://doi.org/10.1007/s10531-016-1071-4

Barbosa, A.M., Brown, J.A., Jimenez-Valverde, A., Real, R., 2020. modEvA: Model Evaluation and Analysis. Barbosa, A.M., Brown, J.A., Jimenez-Valverde, A., Real, R.

Blasi, C., Di Pietro, R., Pelino, G., 2005. The vegetation of alpine belt karst-tectonic basins in the central Apennines (Italy). Plant Biosyst. - Int. J. Deal. Asp. Plant Biol. 139, 357–385. https://doi.org/10.1080/11263500500350150

Cavender-Bares, J., Kozak, K.H., Fine, P.V.A., Kembel, S.W., 2009. The merging of community ecology and phylogenetic biology. Ecol. Lett. 12, 693–715. https://doi.org/10.1111/j.1461-0248.2009.01314.x

Conti, F., Ciaschetti, G., Di Martino, L., Bartolucci, F., 2019. An annotated checklist of the vascular flora of Majella National Park (Central Italy). Phytotaxa 412, 1–90. https://doi.org/10.11646/phytotaxa.412.1.1

Di Nuzzo, L., Vallese, C., Benesperi, R., Giordani, P., Chiarucci, A., Di Cecco, V., Di Martino, L., Di Musciano, M., Gheza, G., Lelli, C., Spitale, D., Nascimbene, J., 2021. Contrasting multitaxon responses to climate change in Mediterranean mountains. Sci. Rep. 11, 4438. https://doi.org/10.1038/s41598-021-83866-x

Ellis, C.J., Coppins, B.J., Dawson, T.P., Seaward, M.R.D., 2007. Response of British lichens to climate change scenarios: Trends and uncertainties in the projected impact for contrasting biogeographic groups. Biol. Conserv. 19.

Faith, D.P., 1992. Conservation evaluation and phylogenetic diversity. Biol. Conserv. 61, 1–10. https://doi.org/10.1016/0006-3207(92)91201-3

Futschik, A., Winkler, M., Steinbauer, K., Lamprecht, A., Rumpf, S.B., Barančok, P., Palaj, A., Gottfried, M., Pauli, H., 2020. Disentangling observer error and climate change effects in long-term monitoring of alpine plant species composition and cover. J. Veg. Sci. 31, 14–25. https://doi.org/10.1111/jvs.12822

Gheza, G., Di Nuzzo, L., Vallese, C., Benesperi, R., Bianchi, E., Di Cecco, V., Di Martino, L., Giordani, P., Hafellner, J., Mayrhofer, H., Nimis, P.L., Tretiach, M., Nascimbene, J., 2021. The lichens of the Majella National Park (Central Italy): an annotated checklist. MycoKeys 78, 119–168. https://doi.org/10.3897/mycokeys.78.62362

Giménez-Benavides, L., Escudero, A., García-Camacho, R., García-Fernández, A., Iriondo, J.M., Lara-Romero, C., Morente-López, J., 2018. How does climate change affect regeneration of Mediterranean high-mountain plants? An integration and synthesis of current knowledge. Plant

349   Biol. 20, 50–62. https://doi.org/10.1111/plb.12643

350   Giordani, P., Malaspina, P., Benesperi, R., Incerti, G., Nascimbene, J., 2019. Functional over-
351   redundancy and vulnerability of lichen communities decouple across spatial scales and
352   environmental   severity.   Sci.   Total   Environ.   666,   22–30.
353   https://doi.org/10.1016/j.scitotenv.2019.02.187

354   Giorgi, F., Lionello, P., 2008. Climate change projections for the Mediterranean region. Glob.
355   Planet. Change 63, 90–104. https://doi.org/10.1016/j.gloplacha.2007.09.005

356   Gottfried, M., Pauli, H., Futschik, A., Akhalkatsi, M., Barančok, P., Benito Alonso, J.L., Coldea,
357   G., Dick, J., Erschbamer, B., Fernández Calzado, M.R., Kazakis, G., Krajči, J., Larsson, P.,
358   Mallaun, M., Michelsen, O., Moiseev, D., Moiseev, P., Molau, U., Merzouki, A., Nagy, L.,
359   Nakhutsrishvili, G., Pedersen, B., Pelino, G., Puscas, M., Rossi, G., Stanisci, A., Theurillat, J.-P.,
360   Tomaselli, M., Villar, L., Vittoz, P., Vogiatzakis, I., Grabherr, G., 2012. Continent-wide
361   response of mountain vegetation to climate change. Nat. Clim. Change 2, 111–115.
362   https://doi.org/10.1038/nclimate1329

363   Green, T.G.A., Sancho, L.G., Pintado, A., 2011. Ecophysiology of desiccation/rehydration cycles in
364   mosses and lichens., 1st ed, Plant Desiccation Tolerance. Springer: Berlin, Germany,.

365   Hall, T., 1999. BioEdit: a user-friendly biological sequence alignment editor and analysis program
366   for Windows 95/98/NT. Nucleic Acids Symp Ser 41.

367   Harrell, F.E., 2019. "Package 'hmisc'." CRAN2018 2019 (2019): 235-6.

368   Hastie, T.J., Tibshirani, R.J., 2017. Generalized additive models, Routledge. ed.

369   Hurtado, P., Matos, P., Aragón, G., Branquinho, C., Prieto, M., Martínez, I., 2020a. How much
370   matching there is in functional, phylogenetic and taxonomic optima of epiphytic macrolichen
371   communities along a European climatic gradient? Sci. Total Environ. 712, 136533.
372   https://doi.org/10.1016/j.scitotenv.2020.136533

373   Hurtado, P., Prieto, M., Aragón, G., Escudero, A., Martínez, I., 2019. Critical predictors of
374   functional, phylogenetic and taxonomic diversity are geographically structured in lichen
375   epiphytic communities. J. Ecol. 107, 2303–2316. https://doi.org/10.1111/1365-2745.13189

376   Hurtado, P., Prieto, M., de Bello, F., Aragón, G., López-Angulo, J., Giordani, P., Díaz-Peña, E.M.,
377   Vicente, R., Merinero, S., Košuthová, A., Benesperi, R., Bianchi, E., Mayrhofer, H.,
378   Nascimbene, J., Grube, M., Wedin, M., Westberg, M., Martínez, I., 2020b. Contrasting
379   Environmental Drivers Determine Biodiversity Patterns in Epiphytic Lichen Communities along
380   a European Gradient. Microorganisms 8, 1913. https://doi.org/10.3390/microorganisms8121913

381   Kassambara, A., 2020. Package 'ggpubr.'

382   Kembel, S.W., Cowan, P.D., Helmus, M.R., Cornwell, W.K., Morlon, H., Ackerly, D.D.,
383   Blomberg, S.P., Webb, C.O., 2010. Picante: R tools for integrating phylogenies and ecology.
384   Bioinformatics 26, 1463–1464. https://doi.org/10.1093/bioinformatics/btq166

385   Kluge, J., Kessler, M., 2011. Phylogenetic diversity, trait diversity and niches: species assembly of
386   ferns along a tropical elevational gradient: Phylogenetic and trait diversity of ferns. J. Biogeogr.
387   38, 394–405. https://doi.org/10.1111/j.1365-2699.2010.02433.x

388   Kuhn, M., 2008. Building Predictive Models in *R* Using the **caret** Package. J. Stat. Softw. 28.
389   https://doi.org/10.18637/jss.v028.i05

390   Li, R., Kraft, N.J.B., Yu, H., Li, H., 2015. Seed plant phylogenetic diversity and species richness in
391   conservation planning within a global biodiversity hotspot in eastern Asia: Phylogeny and
392   Biodiversity Conservation. Conserv. Biol. 29, 1552–1562. https://doi.org/10.1111/cobi.12586

393   Lüdecke, D., 2017. Package 'ggeffects.

394   Marini, L., Nascimbene, J., Nimis, P.L., 2011. Large-scale patterns of epiphytic lichen species
395   richness: Photobiont-dependent response to climate and forest structure. Sci. Total Environ. 409,
396   4381–4386. https://doi.org/10.1016/j.scitotenv.2011.07.010

397   Mazel, F., Davies, T.J., Gallien, L., Renaud, J., Groussin, M., Münkemüller, T., Thuiller, W., 2016.
398   Influence of tree shape and evolutionary time-scale on phylogenetic diversity metrics. Ecography
399   39, 913–920. https://doi.org/10.1111/ecog.01694

400   McCain, C.M., Grytnes, J.-A., 2010. Elevational Gradients in Species Richness, in: John Wiley &
401   Sons, Ltd (Ed.), Encyclopedia of Life Sciences. John Wiley & Sons, Ltd, Chichester, UK, p.
402   a0022548. https://doi.org/10.1002/9780470015902.a0022548

403   Mountain Research Initiative EDW Working Group, 2015. Elevation-dependent warming in
404   mountain   regions   of   the   world.   Nat.   Clim.   Change   5,   424–430.
405   https://doi.org/10.1038/nclimate2563

406   Nascimbene, J., Marini, L., 2015. Epiphytic lichen diversity along elevational gradients: biological
407   traits reveal a complex response to water and energy. J. Biogeogr. 42, 1222–1232.
408   https://doi.org/10.1111/jbi.12493

409   Nascimbene, J., Mayrhofer, H., Dainese, M., Bilovitz, P.O., 2017. Assembly patterns of soil-
410   dwelling lichens after glacier retreat in the European Alps. J. Biogeogr. 44, 1393–1404.
411   https://doi.org/10.1111/jbi.12970

412   Nascimbene, J., Spitale, D., 2017. Patterns of beta-diversity along elevational gradients inform
413   epiphyte conservation in alpine forests under a climate change scenario. Biol. Conserv. 216, 26–
414   32. https://doi.org/10.1016/j.biocon.2017.09.021

415   Nimis, P., Martellos, S., 2004. Keys to the lichens of Italy I. Terricolous species. Edizioni
416   Goliardiche, Trieste.

417   Nimis, P.L., Martellos, S., 2021. ITALIC 6.0 - the information system on Italian lichens. Version
418   6.0. . Univ. Trieste Dept Biol. URL http://dryades.units.it/italic.

419   Nimis, P.L., Martellos, S., 2020. Towards a digital key to the lichens of Italy. Symbiosis 82, 149–
420   155. https://doi.org/10.1007/s13199-020-00714-8

421   O'Brien, E.M., 2006. Biological relativity to water?energy dynamics. J. Biogeogr. 33, 1868–1888.
422   https://doi.org/10.1111/j.1365-2699.2006.01534.x

423   Orange, A., James, P.W., White, F.J., 2001. Microchemical methods for the identification of
424   lichens. Twayne Publishers, Woodbridge.

425   Page, R.D.M., 1996. Tree View: An application to display phylogenetic trees on personal
426   computers. Bioinformatics 12, 357–358. https://doi.org/10.1093/bioinformatics/12.4.357

427 Palombo, C., Chirici, G., Marchetti, M., Tognetti, R., 2013. Is land abandonment affecting forest
428   dynamics at high elevation in Mediterranean mountains more than climate change? Plant
429   Biosyst. - Int. J. Deal. Asp. Plant Biol. 147, 1–11.
430   https://doi.org/10.1080/11263504.2013.772081

431 Parmesan, C., 2006. Ecological and Evolutionary Responses to Recent Climate Change. Annu. Rev.
432   Ecol. Evol. Syst. 37, 637–669. https://doi.org/10.1146/annurev.ecolsys.37.091305.110100

433 Prieto, M., Martínez, I., Aragón, G., Verdú, M., 2017. Phylogenetic and functional structure of
434   lichen communities under contrasting environmental conditions. J. Veg. Sci. 28, 871–881.
435   https://doi.org/10.1111/jvs.12544

436 QGIS.org, 2021. QGIS Geographic Information System.

437 R Core Team, 2021. R: A language and environment for statistical computing. R   Foundation for
438   Statistical Computing, Vienna, Austria.

439 Rambaut, A., Drummond, A.J., Xie, D., Baele, G., Suchard, M.A., 2018. Posterior Summarization
440   in Bayesian Phylogenetics Using Tracer 1.7. Syst. Biol. 67, 901–904.
441   https://doi.org/10.1093/sysbio/syy032

442 Rehm, E.M., Olivas, P., Stroud, J. & Feeley, K.J., 2015. Losing your edge: climate change and the
443   conservation value of range-edge populations. *Ecol. Evol.* 5, 4315–4326. https://doi-
444   org.ezproxy.unibo.it/10.1002/ece3.1645

445 Ronquist, F., Huelsenbeck, J.P., Teslenko, M., Zhang, C., Nylander, J.A.A., 2011. MrBayes version
446   3.2 Manual: Tutorials and Model Summaries 160.

447 Sancho, L., Pintado, A., Green, T., 2019. Antarctic Studies Show Lichens to be Excellent
448   Biomonitors of Climate Change. Diversity 11, 42. https://doi.org/10.3390/d11030042

449 Singh, G., Dal Grande, F., Divakar, P. K., Otte, J., Crespo, A., Schmitt, I., 2017. Fungal-Algal
450   association patterns in lichen symbiosis linked to macroclimate. New Phytologist, 214(1), 317-
451   329. doi: 10.1111/nph.14366

452 Stamatakis, A., 2014. RAxML version 8: a tool for phylogenetic analysis and post-analysis of large
453   phylogenies. Bioinformatics 30, 1312–1313. https://doi.org/10.1093/bioinformatics/btu033

454 Stanisci, A., Carranza, M.L., Pelino, G., Chiarucci, A., 2011. Assessing the diversity pattern of
455   cryophilous plant species in high elevation habitats. Plant Ecol. 212, 595–600.
456   https://doi.org/10.1007/s11258-010-9849-z

457 Vaidya, G., Lohman, D.J., Meier, R., 2011. SequenceMatrix: concatenation software for the fast
458   assembly of multi-gene datasets with character set and codon information. Cladistics 27, 171–
459   180. https://doi.org/10.1111/j.1096-0031.2010.00329.x

460 Vallese, C., Nascimbene, J., Giordani, P., Benesperi, R., Casazza, G., 2021. Modelling range
461   dynamics of terricolous lichens of the genus Peltigera in the Alps under a climate change
462   scenario. Fungal Ecol. 49, 101014. https://doi.org/10.1016/j.funeco.2020.101014

463 van Gils, H., Conti, F., Ciaschetti, G., Westinga, E., 2012. Fine resolution distribution modelling of
464   endemics in Majella National Park, Central Italy. Plant Biosyst. - Int. J. Deal. Asp. Plant Biol.
465   146, 276–287. https://doi.org/10.1080/11263504.2012.685194

466 Vetaas, O.R., Paudel, K.P., Christensen, M., 2019. Principal factors controlling biodiversity along
467   an elevation gradient: Water, energy and their interaction. J. Biogeogr. 46, 1652–1663.
468   https://doi.org/10.1111/jbi.13564

469 Webb, C.O., 2000. Exploring the Phylogenetic Structure of Ecological Communities: An Example
470   for Rain Forest Trees. 11.

471 Webb, C.O., Ackerly, D.D., McPeek, M.A., Donoghue, M.J., 2002. Phylogenies and Community
472   Ecology.   Annu.   Rev.   Ecol.   Syst.   33,   475–505.
473   https://doi.org/10.1146/annurev.ecolsys.33.010802.150448

474 Wickham, H., Averick, M., Bryan, J., Chang, W., McGowan, L., François, R., Grolemund, G.,
475   Hayes, A., Henry, L., Hester, J., Kuhn, M., Pedersen, T., Miller, E., Bache, S., Müller, K., Ooms,
476   J., Robinson, D., Seidel, D., Spinu, V., Takahashi, K., Vaughan, D., Wilke, C., Woo, K., Yutani,
477   H.,   2019.   Welcome   to   the   Tidyverse.   J.   Open   Source   Softw.   4,   1686.
478   https://doi.org/10.21105/joss.01686

479 Wirth, V., Hauck, M., Schultz, M., 2013. Die Flechten Deutschlands, 2 Volumes. Eugen Ulmer,
480   Stuttgart.

481 Zhou, Y., Chen, S., Hu, G., Mwachala, G., Yan, X., Wang, Q., 2018. Species richness and
482   phylogenetic diversity of seed plants across vegetation zones of Mount Kenya, East Africa. Ecol.
483   Evol. 8, 8930–8939. https://doi.org/10.1002/ece3.4428

484 Zurell, D., Elith, J., Schröder, B., 2012. Predicting to new environments: tools for visualizing model
485   behaviour and impacts on mapped distributions: Predicting to new environments. Divers. Distrib.
486   18, 628–634. https://doi.org/10.1111/j.1472-4642.2012.00887.x

487

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://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.

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 (°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

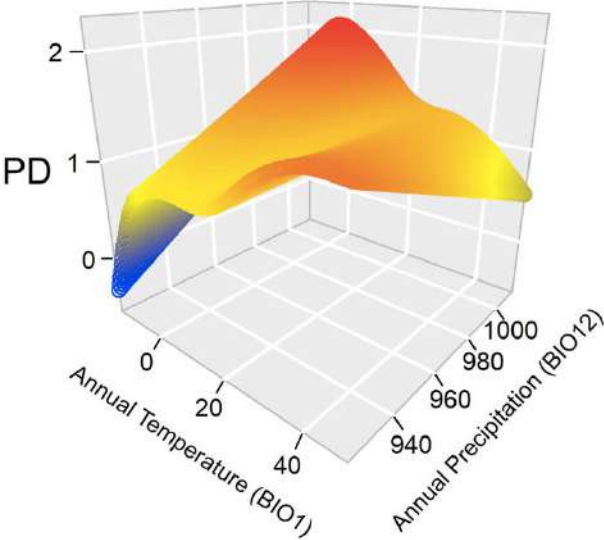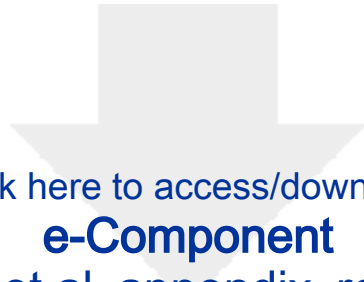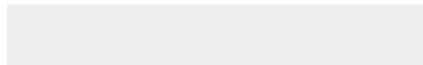| Index	Formula	D-squared	AIC
PD	s(BIO1) +s(BIO7) + s(BIO12) + s(BIO17) + BIO1:BIO12 + BIO1:BIO17	0.42	64
NRI	s(BIO1) + s(BIO7) + s(BIO12) + BIO17 + BIO1:BIO12 + BIO1:BIO17	0.27	316
NTI	s(BIO1) + s(BIO7) + s(BIO12) + s(BIO17) + BIO1:BIO12 + BIO1:BIO17	0.36	-513

TABLE 1
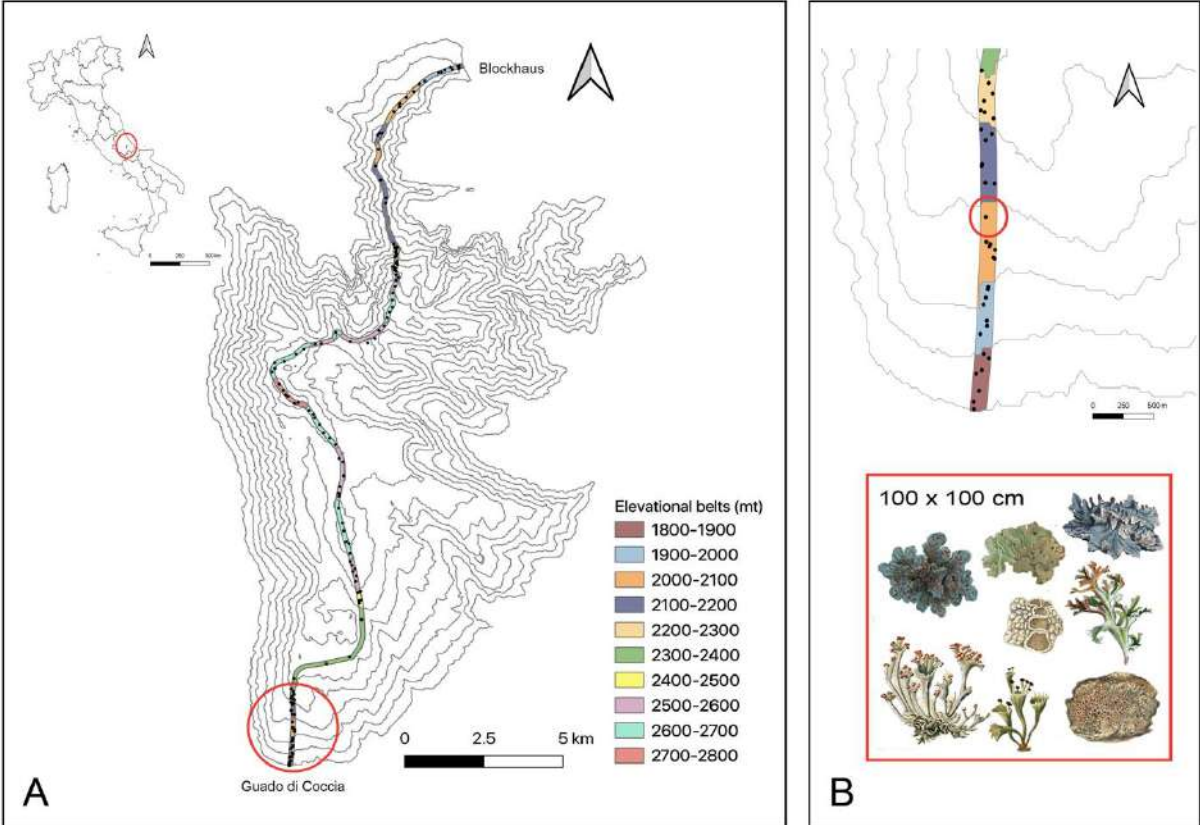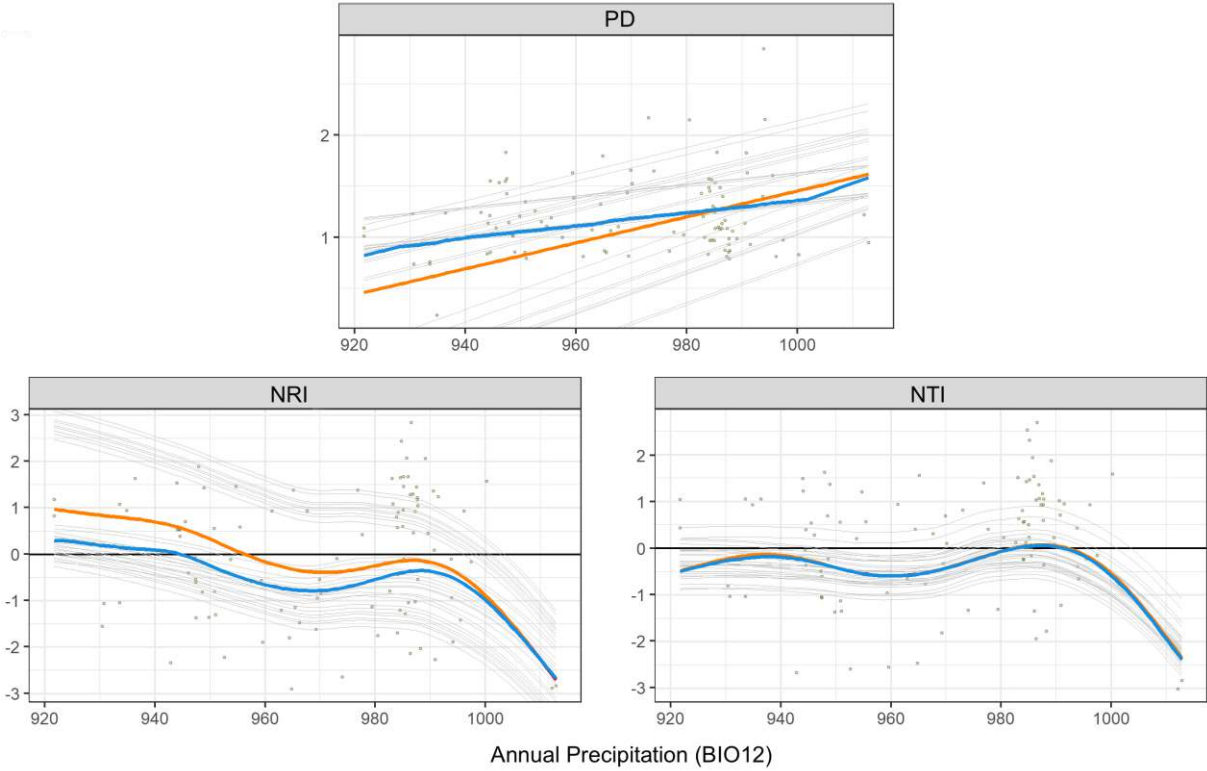
FIGURE 1

FIGURE 2

FIGURE 3

FIGURE 4
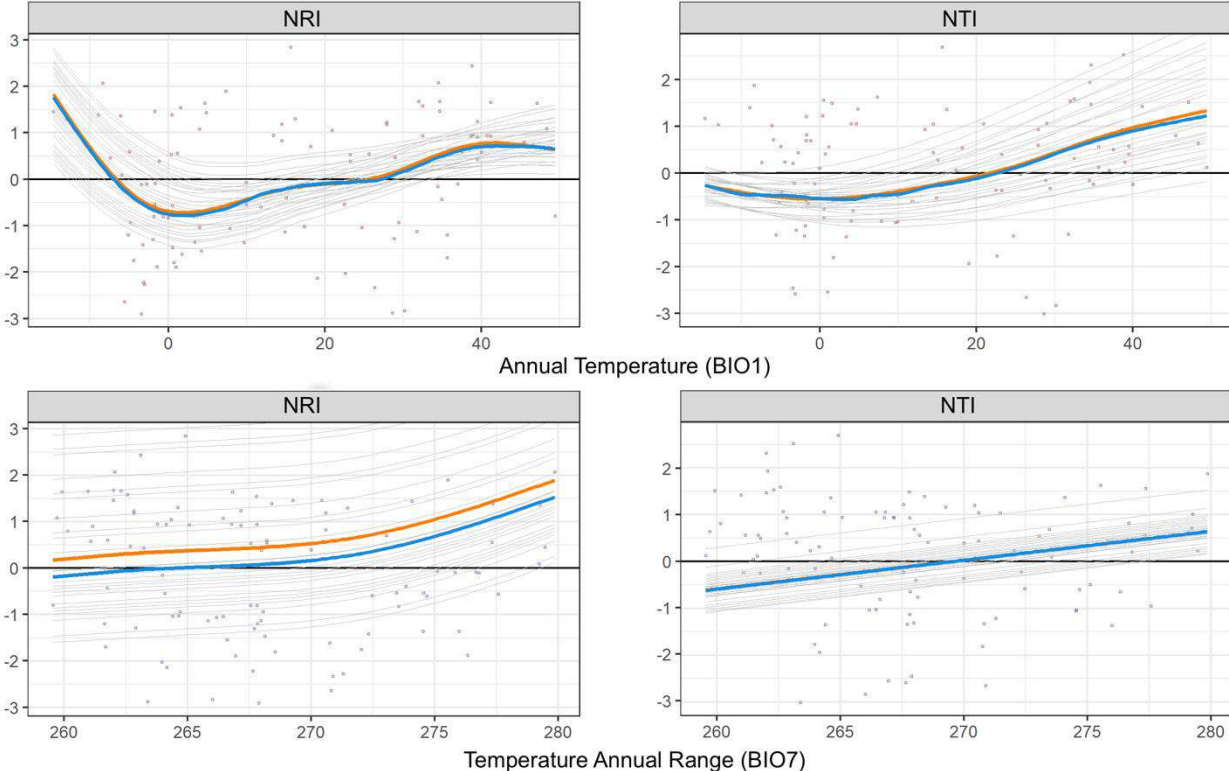
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Conflict of interest statement

The authors have no conflict of interest to declare.