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Little time left. Microrefuges may fail in mitigating the effects of climate change on epiphytic lichens

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1 **Little time left. Microrefuges may fail in mitigating the effects of climate change on epiphytic**
2 **lichens.**

3
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14
15 **Abstract**

16 Climate change is already causing considerable reductions in biodiversity in all terrestrial ecosystems.
17 These consequences are expected to be exacerbated in biomes that are particularly exposed to change,
18 such as those in the Mediterranean, and in certain groups of more sensitive organisms, such as
19 epiphytic lichens. These poikylhydric organisms find suitable light and water conditions in the
20 microhabitat on trunks under the tree canopy. Despite their small size, epiphytic communities
21 contribute significantly to the functionality of forest ecosystems.

22 In this work, we surveyed epiphytic lichen communities in a Mediterranean area (Sardinia, Italy) and
23 hypothesized that 1) the effect of microclimate on lichens at tree scale is mediated by the functional
24 traits of these organisms and that 2) micro-refuge trees with certain morphological characteristics can
25 mitigate the negative effects of future climate change.

26 Results confirm the first hypothesis, while the second is only partially supported, suggesting that the
27 capability of specific trees to host favourable conditions may not be sufficient to maintain the
28 diversity and ecosystem functionality of lichen communities in the Mediterranean.

29
30 **Running Title:** Microclimate buffering of trees for lichens

31
32 **KEYWORDS**

33 Lichens, Stemflow, throughfall, microclimate, trees, Fourth Corner Analysis

34 **1 INTRODUCTION**

35 Climate change is causing increasing impacts on biodiversity, and future projections agree on
36 predicting [negative impacts a worsening for on](#) a wide range of biota and ecosystems (Thomas et al.,
37 2004; Pacifici et al., 2015). Still, there are some groups of organisms which, due to their biological
38 characteristics, are more prone to change. Several multitaxon studies have led to robust arguments
39 supporting the existence of a response gap between organisms with different sensitiveness to climate
40 change (Maclean & Wilson, 2011; Ovaskainen et al., 2020). For example, non-vascular cryptogams,
41 and in particularly lichens (Ellis, 2019), could be more affected than vascular plants and even
42 bryophytes (Di Nuzzo et al., 2021; Nascimbene & Spitale, 2017). Lichens biological features make
43 them extremely sensitive to climate change. They are poikilohydric symbiotic organisms that
44 maintain a complex internal micro-ecosystem based on the interaction between non-lichenized fungi
45 and bacteria, in addition to the two primary symbionts represented by ascomycetes and green algae
46 or cyanobacteria (Hawksworth & Grube, 2020; Spribille et al., 2016, 2020). Lichens lack protective
47 tissues and therefore depend on the surrounding atmosphere for gas exchange, light and water supply
48 (Kranter et al., 2008).

49 Various studies have shown how climate change can impact lichens at different levels, including
50 decrease in population size (Rubio-Salcedo et al., 2015), loss of alpha diversity, variations in beta
51 diversity (Di Nuzzo et al., 2021), alterations in functional composition (Giordani et al., 2019), shifts
52 or reductions in climatic suitability and ecological niche (Nascimbene et al., 2016, 2020; Hurtado et
53 al., 2020; Rubio-Salcedo et al., 2015; Vallese et al., 2021). Although the small size of these organisms
54 may suggest that they are a secondary element of ecosystems, several studies have demonstrated the
55 importance of their ecological functionality, which could be seriously altered as a result of climate
56 change (Asplund & Wardle, 2017; Porada et al., 2013, 2018; Ellis et al., 2021). Some of these impacts
57 derive from direct effects that hamper lichen dehydration/hydration cycles with negative
58 consequences on their vitality (Phinney et al., 2018; Proctor & Tuba, 2002). In other cases, indirect
59 effects may occur that alter the biotic interactions between lichens and other organisms. For example,
60 [fire regimes alteration, induced by warming temperatures, can negatively affect for long time lichen](#)
61 [communities by altering local microclimatic conditions](#)-(Jesse et al. 2018, Jesse et al. 2020). [At the](#)
62 [same time,](#) Nascimbene et al. (2020) showed the consequences of the increased suitability for invasive
63 tree species that are less suitable to lichen colonization. However, most of these models inform on
64 climate change projections at landscape scales which describe the macroclimatic conditions likely
65 occurring over large areas (Rubio-Salcedo et al., 2015). If, on one hand, it is evident that there is a
66 strict connection between macroclimate and the microclimate occurring at a more detailed scale, on
67 the other hand, it is likely that these relationships are not constant either along spatial gradients or on
68 a temporal scale (Haesen et al., 2021).

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69 In recent years, numerous studies debated the relevance of microclimate in determining the
70 probability of species occurrence in climate change scenarios (De Frenne et al., 2019; Maclean et al.,
71 2015; Zellweger et al., 2019; Schall & Heinrichs, 2020; Miller et al., 2017). Most of these studies
72 indicate that forests, and trees in general, play a fundamental role in shaping the microclimate and in
73 establishing potential climatic microrefugia (De Frenne et al., 2021). Ultimately, microrefugia can
74 serve to buffer climate variability and thus slow down the process of extinction caused by it (Morelli
75 et al., 2020; Keppel & Wardell-Johnson, 2015; Hannah et al., 2014). The interaction between
76 topographic concavity of the terrain and canopy structure delineates the capability of a site to act as
77 a climate microrefuge (Lenoir et al., 2017). This effect is potentially observable at any scale and,
78 indeed, the scale plays a key role. In fact, to better understand what the effects of climate change
79 might be, it is essential to circumscribe the microclimate to which a given target organism is actually
80 subject (De Frenne et al., 2019). For example, in the case of epiphytic lichens, the microrefuge effect
81 could be already observable at the tree scale. In fact, canopy increases shading and distributes
82 precipitations in terms of throughfall, stemflow and water intercepted by the trunk (Porada &
83 Giordani, 2021; Porada et al., 2018; Van Stan, II et al., 2020). Tree crown also causes a considerable
84 decrease in sub-canopy vs free-air temperatures (Lenoir et al., 2017) lowering the maximum
85 temperature down to -3°C and potentially counteracting the expected temperature increase in future
86 scenarios of up to 1°C. As temperature rise, the capacity of a forest to maintain different temperature
87 could a consequence of different dynamics. On the one hand, temperature under the canopy could
88 increase proportionally with the macro scale temperature, and the difference from the macro scale
89 temperature is just in terms of absolute values. This have been described as a “perfect coupling”
90 (sensu De Frenne et al. 2021) and to which hereafter will be referred as “mitigation”. On the other
91 hand, the canopy could influence temperature by maintaining a steadier temperature, i.e., the increase
92 of temperature under the canopy is no perfectly related with the increase in macro scale temperature.
93 Hereafter we will refer to this dynamic as “buffer” (De Frenne et al. 2021).

94 Proportionally, the gap between macro- and microclimate may be less relevant for populations of
95 large species (e.g. tree species), compared to those of small organisms (De Frenne et al., 2019).
96 Microclimate buffering-mitigation is merely decisive for obligate epiphytes whose relationships with
97 tree crown and trunk determine each step of their life cycle (Giordani et al., 2020; Ellis et al., 2014;
98 Ellis & Eaton, 2021). For example, for hygrophilous lichens, microclimatic refugia have a significant
99 effect in maintaining a growth rate on vital levels (Ellis, 2020), or in determining the probability of
100 survival and development of recruits (Benesperi et al., 2018). The relevance of microrefuges is
101 considerably higher the harsher the climatic conditions, for example e.g. in semi-arid Mediterranean
102 environments where models predict the most drastic changes in terms of temperature increase and

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precipitation decrease (Giorgi & Lionello, 2008)(~~Smith et al., 2020~~). In fact, similarly to what has been predicted for semi-arid forest in North America (Smith et al., 2020), in this environments lichen species are more susceptible to climate-induces -changes determining the importance of microclimatic refugia.

However, the effect of optimal microclimatic conditions on lichen communities is not apparent, nor unique, since functional traits mediate the response of each species to environmental variations (Violle et al., 2007). Traits come into play individually or interactively, in a more or less marked way and determine the possibility of species occurrence and survival (Ellis et al., 2021). As for lichens, several works have highlighted how some functional traits are decisive in response to climatic factors (Giordani et al., 2012, 2019; Matos et al., 2015; Hurtado et al., 2020, 2019; Ellis et al., 2021). For example, the photobiont type determine the type of water source preferred, as cyanolichens require liquid water to activate photosynthesis (Lange et al. 1986, Gauslaa 2014). Among others, thallus growth form seems to be one of the most responsive traits, being relevant in establishing a trade-off between photosynthetic capacity and photorespiration (Gauslaa, 2014; Merinero et al., 2014).

For the first time, in this work we explicitly take into consideration the relevance of growth form in the response of epiphytic lichen communities to microclimatic factors, highlighting the differences, that exist and that we could expect in the future, in sites with greater or lesser capacity to act as climatic microrefuges.

We formulated two consequential hypotheses:

~~a)-a)~~ functional traits mediated the response of lichen communities to microclimate in the Mediterranean environment, and this response is detectable against the confounding effect of other microenvironmental variables. Moreover, different functional groups show contrasting responses to microclimatic drivers, and

~~b)-b)~~ based on the relationships between functional traits and microclimate, microrefuges at the tree scale, characterized by particularly favorable conditions of light, water and temperature, can mitigate the predicted effects of climate change on lichen communities on growth form already linked with these conditions. By contrast, the mitigation on other growth forms could be hindered by the absence of other environmental conditions, e.g. light.

2 METHODS

2.1 Study area

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We carried out the study in a 1260-km² area of western Sardinia, Italy, where human population density is very low (~40 persons/km²), and local sources of air pollution are negligible. Along an altitudinal gradient that ranged from sea level to 1200 m, the main vegetation types were Mediterranean maquis, Mediterranean garigue, and evergreen holm oak forest. This latter was mixed with deciduous oaks, which demonstrated a progressive compositional shift from xero-thermophilic to mesophilic communities up to the highest altitude. Stone pine plantations, cork oak stands, arable fields, and pastures for sheep breeding locally replaced natural plant communities along the same altitudinal gradient. Mean annual rainfall and temperature ranged from 600 mm and 15 °C, respectively, along the coast to 1100 mm and 13 °C, respectively, at the highest elevations.

2.2 Sampling

Based on a stratified random sampling design, we selected coordinates pairs to obtain 70 sampling points, which were allocated into nine strata obtained by aggregation of CORINE land cover classes, proportionally to the surface occupied by each stratum within the survey area. In the field, each sampling point was positioned using a GPS and used as the SW corner of an N-oriented 20 × 20-m plot. Within each plot, proportionally to the tree cover, we randomly selected and sampled 1 to 6 trees. Following Asta et al. (2002), we recorded the occurrence of corticolous lichen species in each 10 × 10-cm squares of a sampling grid, which consisted of a 10 × 50 cm ladder that was divided into five quadrants and systematically placed on the N, E, S, and W sides of each tree bole, with the top edge 1.5m above ground level.

2.3 Growth form

All lichen species were categorized by their growth form. We used a modified version of the categorization proposed by Aragon et al. (2016, 2019) (Figure 1, Table S7). To better differentiate crustose lichens, species were split into conspicuous (~~Cr-co~~, e.g. *Pertusaria*) and inconspicuous (~~Cr-in~~, e.g. *Catillaria*, *Arthonia*) on the basis of the capability of the species to develop a well-defined thallus or not, respectively. Squamulose species were considered all those species with squamulose thallus (~~Seq~~, e.g. *Fuscopannaria*, *Normandina*), without considering further sub-divisions of this category. Regarding foliose species, we differentiated between foliose narrowed-lobed (lobes narrower than 0.5 mm: ~~Fol-n~~, e.g. *Physcia*) and foliose broad-lobed (lobes wider >0.5mm: ~~Fol-b~~). In addition, we used a foliose large category which comprehended larger foliose species (~~Fol-large~~, e.g. *Lobaria*, *Peltigera*). Moreover, we also categorized those species with foliose gelatinous swollen thallus (~~Fol-gel.swo~~, e.g. *Collema*). For fruticose species (~~Frut~~) we did not consider sub-categories (e.g. filamentous as in *Usnea* or composite thallus as in *Cladonia*).

171

172 **2.4 Tree-level measurements of environmental variables**

173 A set of environmental variables were also recorded on each tree. Some of these variables have been
174 used to quantify the sub-canopy microclimate (see paragraphs 2.6 and 2.7). In contrast, others have
175 been directly used as predictors in the fourth corner analysis (see paragraph 2.8) to estimate the effect
176 of non-climatic confounding factors on the composition of lichen communities. Variables included
177 chemical-physical characteristics of the bark and some aspects related to the habitat in which the trees
178 were located. We report brief descriptions of the variables along with recording procedures,
179 calculations and range values in Table 1. More details on the protocols are given in Supplementary
180 materials.

181

182 **2.5 Statistical downscaling of bioclimatic variables**

183 Bioclimatic variables with 1km resolution were obtained from CHELSA database (Karger et al.,
184 2017). To minimize model overfitting, we performed a pairwise Pearson correlation between
185 bioclimatic predictors. We retained four predictors that were not highly correlated ($r < |0.70|$). We
186 selected temperature seasonality (BIO4), maximum temperature of the warmest month (BIO5),
187 annual precipitation (BIO12) and seasonality of precipitation (BIO15). Moreover, we downloaded
188 the same variables also for four climate change scenarios: RCP 2.6 and RCP 8.5 for two time periods
189 2041-2060 and 2061-2080. RCPs were selected from the CESM1-CAM5 model. We downscaled
190 each bioclimatic variable, both current and future, following the procedure used by Lenoir et al.
191 (2017). In particular, we used a Geographic Weighted Regression (GWR) model (Fotheringham et
192 al., 2002). As predictor variables we used Northness, Eastness, altitude, slope, land use, insolation,
193 and distance from the sea. These variables are frequently used in similar studies to model the
194 topoclimate and, as in our case, microclimate (Lenoir et al., 2017). Topographic predictors were
195 calculated using the open source software QGIS 3.10.12 using a 10m DTM. Finally, the GWR was
196 run using R 3.6 (R Core Team) through the *gwr* function in the *spgwr* package (Bivand et al., 2020).
197 Bandwidth was calculated through the *gwr.sel* function.

198

199 **2.6 Partitioning precipitations into stemflow and throughfall at tree level**

200 The overall precipitation was partitioned into stemflow and throughfall at tree level. These two facets
201 of precipitation are strictly related to canopy and bark characteristics. Throughfall represents the
202 precipitation that passes through the canopy due to presence of gaps or branch drips. Conversely,
203 stemflow is the water that flows on the bark drained from the canopy (Sadeghi et al., 2020). In general,
204 comparing the same amount of rainfall, bark thickness and branch angles are important factors in

determining the amount of stemflow and throughfall. Though, for stemflow, the ratio between canopy height and width seems to play a more important role (Sadeghi et al., 2020). To model stemflow and throughfall for each tree we used the Gash Analytical Model as reported in Valente et al. (1997). Tree features were measured both in the field and in laboratory, while species-specific traits were retrieved from the available literature. A detailed description of the whole process is presented in the Supplementary materials (paragraph S1). Stemflow and throughfall are two important facets of the overall precipitation in forests as they are an important source of water, nutrients and other chemical compounds for lichens attached to the trunk. Stemflow is could be an importance source of liquid water. This is especially important for cyanolichens, which require liquid water to reactivate photosynthesis (Lange et al. 1986). Nevertheless, high amount of stemflow could led to suprasaturation in certain species, hindering photosynthesis (Lakatos et al. 2006). At the same time, the throughfall could act as a source or of vapor water, as the evaporation following a rain event enhance the air relative humidity or, more rarely, of liquid water, when rain falls directly on the thallus. Thus, different regimes of stemflow and throughfall could select different species based on their functional traits, e.g. growth forms, photobionts.

220

2.7 Modelling sub-canopy temperature

Following Lenoir et al. (2017), we assessed the impact of the climatic buffering-mitigation effect on sub-canopy temperature by setting a maximum of 3°C reduction in T max of the warmest month (BIO5) due to the combined effect of topographic concavity (−1°C) and canopy structure (−2°C). With a similar procedure, we have described the potential buffering-mitigation of T seasonality (BIO4) by setting a maximum of -1.5°C of reduction (-1°C due to the effect canopy, -0.5°C to the concavity effect). These values were supported by periodic direct measurements at sites within the study area where above- and below-canopy temperature data were available.

To quantify the canopy effect, we used a PCA to explore the patterns of variables related to the structure of the sampled trees. In particular, we included tree height, canopy height, canopy area, Leaf Area Index (LAI), and tree cover of the plot. Then, we used the loadings of each tree on the dimensions associated with increasing canopy size and coverage to calculate a canopy effect for each tree. Similarly, the percentage value of topographic concavity in the area surrounding each tree was used to estimate the contribution of the concavity effect to temperature bufferingmitigation. The concavity was obtained from the digital terrain model (DTM) of the study area at 10m resolution, using the SAGA processing module 'terrain surface texture', integrated into QGIS 3.10. Finally, the sub-canopy temperature buffering-mitigation of each tree to above-canopy conditions was calculated as follows:

$$\begin{aligned}\Delta T_{max} (B105) &= 2^{\circ}\text{C} \times \text{Canopy effect} + 1^{\circ}\text{C} \times \text{Concavity effect} \\ \Delta T_{seasonality} (B104) &= 1^{\circ}\text{C} \times \text{Canopy effect} + 0.5^{\circ}\text{C} \times \text{Concavity effect}\end{aligned}$$

2.8 Fourth Corner Analysis

To explore the presence and strength of possible associations between functional traits and environmental variables we performed a fourth corner analysis. This method combines three matrices: (i) a sample units x species abundance, (ii) sample units x environmental variables and (iii) a species x traits matrix. Different type of solution of the ‘fourth corner problem’ have been proposed (Dray & Legendre, 2008; Dray et al., 2014; Brown et al., 2014). We used the model-based approach proposed by Brown et al. (2014) as it allows to test the strength of the interaction between environmental variables and functional traits. The method proceeds by fitting a model with all species abundances at the same time as a function of environmental variables, species traits and their interaction. We used a binomial error distribution in the generalized linear model using the *traitglm* function in the *mvabund* R package (Wang et al., 2020). For model selection, a least absolute shrinkage and selection operator (LASSO penalty) was used, which is used to simplify interpretation as it switches any terms that do not explain any variation to zero. The model was used to predict abundances in the four different climate change scenarios (RPC 2.6 and 8.5, 2040-2061 and 2061 - 2080). All predictors based on tree measurements were kept the same for prediction, while those which comprehend also temperature or precipitation (e.g. *throughfall*) were parameterized based on the ratios between current and future conditions. Predicted abundances were relativized to the maximum frequency in each square to be more comparable. These ratios were modeled using habitat, type of future climatic model (PC2.5, etc.), and microrefuge capacity. Models were performed through *glmmTMB* function from *glmmTMB* package (Brooks et al., 2017), using *beta_family* as family error distribution. To obtain more robust confidence intervals and p-values all models were bootstrapped with 1000 iterations using the *parameters* package (Lüdecke et al., 2020).

2.9 Identification of climatic microrefuge capacity of trees

We assessed the climatic microrefuge capacity of each sampled trees using a species-neutral approach. This method does not take into consideration the different microclimatic [requests](#) [requirements](#) of individual species or functional groups but assesses the microrefuge capacity based solely on the relationship between the morphological characteristics of the site and the buffering effect that it can exert on macroclimate.

In particular, we used the [buffering-mitigation](#) effects calculated as described in paragraph 2.7 to define the ability of each tree to act as a climatic microrefuge for epiphytic lichens. We quantified the microrefuge capacity in terms of percentile distribution of the [buffering-mitigation](#) effect of the temperature on the trees.

3 RESULTS

3.1 Quantifying the microrefuge capacity of trees

Based on the combination of the canopy and the concavity effects, we have defined the ability of each tree to act as a climatic microrefuge for epiphytic lichens.

The first 3 components of the PCA on the structural characteristics of trees accounted for 92.9% of the overall variance (Figure 2a). The first component (Dim1=49.6%) was associated with increasing tree height, canopy height and canopy area. Consistently with a distinction between trees located in open vs forested areas, the second component (Dim2=25.3%) described contrasting gradients of LAI vs tree cover. However, both latter variables were positively associated with the third dimension (Dim3=16.6%). As positive values of Dim1 and Dim3 were associated with increasing canopy coverage, we used the loadings of trees on Dim1 and Dim3 to calculate the canopy effect on the microclimatic [buffering-mitigation](#) of each tree. When taking into account also the effect of topographic concavity, we estimated that on average the sampled trees would be able to lower BIO5 by -1.3 °C (min = -0.3 °C, max = -2.7 °C) and BIO4 by -0.4 °C (min = -0.1 °C, max = -1 °C) (Figure 2b).

3.2 Hypothesis a) The response of the lichen communities to microclimate is mediated by functional traits. Different functional groups show contrasting responses to the microclimate

The Fourth Corner analysis returns interactions between microenvironmental variables and the abundance of epiphytic lichens that are mediated by their growth form (Figure 3).

The growth form was involved in mediating the response to both microclimatic variables, and other microenvironmental factors related to other characteristics of the tree bark. For example, among others, bryophyte coverage had strong positive effects on the abundance of [Fol-largefoliose large](#), [Frut-fruticose](#) and [Squamulose species](#). This latter group was also positively influenced by bark pH and buffer. The capability of the bark of buffering pH was also relevant for [Fol-gel-swefoliose gelatinous swollen](#) and [Cr-ecocrustose conspicuous species](#).

Considering microclimate descriptors, foliose narrow-lobed species were positively influenced by long dehydration times of the bark (T50) and by high Tmax of the warmest quarter (BIO5), and by temperature seasonality (BIO4). The same variables strongly limited the occurrence of foliose gelatinous swollen species. The seasonality of precipitations (BIO15) determined contrasting responses between crustose inconspicuous species and foliose narrow-lobed species. Among the components of sub-canopy precipitation, throughfall inhibited the presence of crustose inconspicuous species and squamulose species, while enhancing fruticose species. Water intercepted by the trunk inhibited the presence of broad-lobed foliose species, which, in turn, were enhanced by a high amount of stemflow. Fol.la were enhanced by long dehydration time of the bark and partially by a high throughfall.

3.3 Hypothesis b) Microrefuges at the tree scale can mitigate the predicted effects on hosted lichen communities in scenarios of climate change.

Using GLMM models, we analyzed the relationship between the abundance of each growth form as a function of the microrefuge capacity of trees in the different climate change scenarios (Table 2, Figure 4). Under the current conditions, a strong microrefuge effect has been observed for fruticose species and foliose gelatinous swollen species, foliose large species, squamulose species and crustose inconspicuous species—whose abundance increases linearly or even exponentially with microrefuge capacity of the trees. Although in a context of progressive reduction of abundance, among these growth forms, fruticose species, squamulose species and foliose gelatinous swollen species are expected to maintain a significant relationship with the microrefuge capacity in all future scenarios, while for foliose large species and crustose inconspicuous species—in 2040 and 2060, both in the optimistic scenario RCP 2.6 and in the pessimistic scenario RCP 8.5, the models predicted a drastic reduction in abundance, regardless of the microrefuge capacity of the host trees.

On the other hand, broad-lobed foliose species, foliose narrow-lobed species and crustose conspicuous species—under the current conditions were more abundant on trees with lower microrefuge capacity, showing a negative trend according to this variable. According to the model, these growth forms are expected to undergo a progressive decrease in abundance which may be more marked on trees with less microrefuge capacity.

4 DISCUSSION

340

341 Exploring the relationships between microclimate and biodiversity is a key issue to better understand
342 the direct and indirect impacts of global change on the biota (De Frenne et al., 2021). In particular,
343 unraveling species-climate relationships at the local scale will likely provide a more comprehensive,
344 precise, and detailed picture of the interactions between abiotic factors and organisms and,
345 consequently, enable more accurate predictions on potential community changes (Bramer et al., 2018;
346 De Frenne et al., 2019; Zellweger et al., 2019). Following this research line, as an innovative
347 contribution of this work, we have been able to delineate the interactions between microclimatic
348 variables in Mediterranean epiphytic lichen communities, providing a detailed picture of the expected
349 changes in the near future. Our results partially support our two consequential hypotheses about the
350 response of epiphytic lichen communities to microclimate and to global changes, which are hereafter
351 discussed.

352

353 ***Hypothesis a) Growth form mediates the response of epiphytic lichen communities to***
354 ***microclimate***

355 Our results reveal significant relationships between lichen functional traits and different
356 environmental variables related to microclimate. Thallus growth form primarily characterizes the
357 response to microclimatic variables, with contrasting responses between different growth form-based
358 functional groups (Figure 5). In particular, community compositional shifts correspond to different
359 growth forms prevailing under different conditions of sub-canopy temperatures and precipitation
360 components, consistent with the effects of the amount, duration, and physical state of water
361 availability for epiphytic communities (Gauslaa, 2014; Giordani & Incerti, 2008; Ås Hovind et al.,
362 2020; Phinney et al., 2019; Gauslaa & Solhaug, 1998). Along the microclimatic variation, we found
363 a gradient of growth form turnover connected with specific water requirements. In conditions of
364 throughfall precipitation prevalence, high light availability and low temperature seasonality, fruticose
365 lichens are favored. Under larger canopies with reduced maximum temperatures and high rainfall
366 interception and stemflow along the trunk, broad-lobed foliose lichens thrive as their thalline structure
367 is more suitable for intercepting running water. Interestingly, when stemflow decreases, as in both
368 cases of lower annual rainfall and higher bark water retention capacity, community composition shifts
369 from broad-lobed foliose lichens to crustose growth forms. As such, the water retention capacity of
370 the bark seems to play a fundamental role in defining the duration of the activity periods of lichen
371 communities. In sub-arid Mediterranean environment where water is a limiting factor, the uptake of
372 bark water extends the period of activity with positive net photosynthesis by up to 21% (Porada &
373 Giordani, 2021). Irrespectively of the total precipitation amount, narrow-lobed foliose lichens

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374 respond to temperature conditions, being fostered by high maximum values and large seasonal
375 differences. Their prevalence under the harshest temperature conditions could be simply related to
376 the minimal competitive pressure by species with different growth form in such conditions, more than
377 to specific advantage provided by lobe narrowness *per se*.

378

379 ***Hypothesis b) Micro-refuge trees locally ~~buffer-mitigate~~ climate change effects on epiphytic***
380 ***lichen community***

381 Our models provide a complex picture that is only partially consistent with the hypothesis of a
382 positive effect of micro-refuge trees on the abundance of epiphytic lichen functional groups. In fact,
383 the current distribution pattern of many lichen growth forms is strongly associated to the
384 microclimatic ~~buffer-mitigation~~ capacity exerted by the host trees by means of specific morpho-
385 physical-chemical canopy and bark traits. However, these combinations of host and epiphyte traits
386 may not still hold with the same balance in the future. In particular, we have outlined three distinct
387 situations which are summarized schematically in Figure 6:

388

389 *Micro-refuge trees will continue to preserve some lichen functional groups in the future*

390 We estimate that the climatic microrefuge capacity of some trees could prove decisive in enabling
391 the survival of certain functional groups that are already ~~linked to these microhabitats~~ present in these
392 ~~environmental conditions~~. These groups are rather morphologically heterogeneous, including
393 fruticose, squamulose and foliose gelatinous growth forms. Fruticose survival could be due to the
394 ~~buffering-mitigation~~ potential of the trees on which they live combined with their intrinsic resilience.
395 On the other hand, the trees colonized by squamulose and foliose gelatinous lichens are located in
396 areas less impacted by macroclimatic scenarios, so their mitigation potential seems sufficient to
397 neutralise macro-scale exacerbation.

398

399 *Micro-refuge trees will not be enough to save species that have already paid their ~~part of~~ extinction*
400 *debt*

401 A second situation can be depicted for the growth forms preferentially found under mild
402 conditions, on trees with high ~~buffering-mitigation~~ potential. According to our results, two of these
403 groups, large foliose and crustose inconspicuous lichens, shall not resist to the future water shortage
404 and warming, with even the trees with highest ~~buffering-mitigation~~ potential apparently unable to
405 ensure micro-refuge conditions for these lichens, hence destined to an irreparable decline. Most
406 likely, these groups in the Mediterranean have already paid a large part of their extinction debt (Ellis
407 et al., 2017; Ellis & Coppins, 2017). Presumably, these lichens have already been relegated for a long

time to climatic refugia, where they are maintaining residual populations. On the other hand, for large foliose lichens, which include well-known species of the genus *Lobaria*, several works have already predicted a drastic decrease in the climatic suitability for these species and their host trees (Nascimbene et al., 2020).

Xerophilous species will decline and will not be able to exploit the micro-refuges.

Conspicuous crustose, narrow- and broad-lobed lichens, which include some of the most common taxa, are currently more abundant on trees with low micro-refuge capacity. As shown by the fourth corner analysis results, this situation can certainly be traced back to their ecological demands already outlined in the previous section. In fact, these growth forms are favored by harsh microclimatic environment that can hardly be found on the trunk of trees with high capacity of climate buffering mitigation. Consistent with this preference for more extreme context, even in future climate change scenarios, these growth forms shall not increase their abundance in micro-refuge trees. However, contrary to what might be expected, our results for both the optimistic and pessimistic scenarios indicate that these lichens shall undergo a drastic abundance decrease on trees more suited to their ecological requirements. Therefore, even for more xerophilous and thermophilic species, the future water shortage and temperature regimes shall exceed the limit of their potential ecological niche under the canopy of trees.

Consequences for Mediterranean forest ecosystem

What would happen if micro-refuge trees were no longer able to provide a suitable microclimate for epiphytic lichens? In addition to conservation issues related to the reduction and/or loss of lichen diversity, the scenarios outlined by our models also raise some considerations at the scale of forest ecosystems in Mediterranean regions. It is clear that in these environments lichens are a minor component in terms of biomass, but, especially with reference to epiphytic communities, they constitute, together with bryophytes, a unique microhabitat for several groups of organisms (Asplund et al., 2018; Asplund & Wardle, 2017). Small arthropods and terrestrial mollusks are primarily or even exclusively linked to lichens (Asplund & Wardle, 2017). For these organisms, epiphytic communities represent sources of water and food, refuge, hunting and nesting areas. The effects of a local decrease in epiphytic communities can also translate into considerable consequences at regional or continental scales on basic ecosystem functions such as those related to the water cycle. For example, Porada et al. (2018) have shown that in terrestrial ecosystems the total evaporation of free water from the forest canopy and soil surface increases by 61% when non-vascular vegetation is included.

442

443

444 ***Limitations and perspectives***

445 Although our work has provided a detailed picture of the environmental relationships controlling the
 446 composition of epiphytic lichen communities, there are certainly some limitations that need to be
 447 considered and which could be the starting point for further studies.

448 First, it is well established that obligate epiphytes have a close relationship with their tree
 449 substrate. Recent studies have shown that the decoupling of these relationships could be an additional
 450 indirect effect of climate change (Nascimbene et al., 2020). Our models did not take into account the
 451 potential changes of host tree species. In other words, in our model, results of the future scenarios
 452 refer to trees in the study area that have equivalent micro-refuge capacity to those actually observed.
 453 This may be as an oversimplification, especially when considering our results for predictive purposes.
 454 However, under a pure research perspective, it allows us to focus on the microclimatic effect net of
 455 other confounding factors, including, as non-exhaustive examples, effects of warming and water
 456 shortage on morpho-physical-chemical tree properties. Ideally, integrating the study of the functional
 457 ecology of epiphytic communities with the development of models capable of simulating the growth
 458 of their tree substrates (Trotsiuk et al., 2020) under different environmental conditions could lead to
 459 a more refined prediction of epiphyte dynamics. [Similarly, another possible limitation of this work is](#)
 460 [that we take into account mitigation and not buffering. Maintaining a more stable temperature could](#)
 461 [lead to less dramatic changes in terms of temperature in respect to those predicted considering](#)
 462 [mitigation, leading to less pronounced impact on lichen species.](#)

463 Moreover, we have modelled the lichen abundances by taking a static approach that is unable
 464 to weigh any differences that the various species may show throughout their life cycle (Benesperi et
 465 al., 2018), including the establishment and development phases of new thalli that can be very critical
 466 for determining the continuity of the colonization.

467 A further limitation is that our models consider functional groups separately and exclude
 468 community interactions, which obviously occur in the real system and can shape community
 469 composition. These interactions include both competitive and facilitative processes that may
 470 contribute to slowing, accelerating or modifying the effects of abiotic factors on communities (Saiz
 471 et al., 2021). The relationships between community interactions and the severity of environmental
 472 conditions is a hot topic of interest in plant ecology research (Brooker et al., 2008; Le Bagousse-
 473 Pinguet et al., 2014; Bonanomi et al., 2016). In the case of epiphytes, and lichens in particular, much
 474 less is known and it is certainly a field of research worthy of investigation in the near future.

Codice campo modificato

Our models predict drastic changes and reduction of epiphytic lichen communities in the worst climate change scenarios. Nevertheless, lichens are able to colonize much more extreme habitats, such as deserts, where they face high temperatures and low water availability. Lichens, as many other organisms, are predicted to migrate to their track suitable climate space (Ellis 2019). Consequently, it could be hypothesized that, in the future, species adapted to dry and warm condition could find here their suitable conditions, replacing the native flora. For example, increasing of warm-temperate or subtropical species have already been observed in Europe for epiphytic lichens (Aproot et al. 2007). Distributional shifts induced by climate change are mainly based on species' climatic space. However, other factors such as climate change rate, dispersal capacity and habitat connectivity are fundamental in determining the capacity of species to migrate and track their suitable climatic conditions (Ellis 2019).

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DATA AVAILABILITY STATEMENT

Data used in this study are available in Figshare at <https://doi.org/10.6084/m9.figshare.17022026>.

CONFLICT OF INTEREST

The authors declare no conflict of interest.

AUTHORS' CONTRIBUTIONS

P.G. designed the study; P.G., G.I., and P.M collected the data; L.D.N. and P.G analysed the data; P.G., L.D.N., R.B., J.N., and G.I., interpreted the results. L.D.N. and P.G. wrote the first draft of the manuscript; L.D.N, P.G., G.I., R.B., J.N., A.P., and P.M. edited and reviewed the manuscript.

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Table 1. Descriptive statistics of the predictors used to determine the relationships between epiphytic lichen communities and tree microenvironment in the study area.

Predictor	Description	Units	Source	Mean	Std. dev.	Min	Max
Nitrogen	Potential NH ₃ emission	Kg ha ⁻¹	Calculated	2602.376	4165.895	0.000	18668.660
Light	Direct solar radiation	MJm ⁻² d ⁻¹	Measured	0.506	0.653	0.035	4.670
Buffer pH	Bark buffer pH	pH unit	Measured	3.96E-05	5.62E-06	0.000	0.000
pH	Bark pH	pH unit	Measured	6.411	0.513	4.070	7.220
Ivy	Ivy cover	Proportion	Estimated	0.019	0.089	0.000	0.613
Moss	Bryophyte cover	Proportion	Estimated	0.059	0.168	0.000	0.925
Bark Micro	Bark microstructure	No unit	PCA on collected data	0.426	0.188	0.000	1.000
T50	Bark loss water halftime	min	Measured	114.190	76.265	13.000	341.000
Maximum temperature of wettest quarter subcanopy	Maximum temperature of wettest quarter	°C*10	Modelled on CHELSA BIO5	246.242	17.671	211.300	280.500
Temperature Seasonality subcanopy	Temperature variation over the year (Standard deviation of monthly mean temperature)	NA	Modelled on CHELSA BIO4	4741.476	225.095	4116.649	5191.110
Precipitation Seasonality subcanopy	Variation in monthly precipitation over the year (Coefficient of variation of monthly precipitation)	NA	Modelled on CHELSA BIO15	54.318	1.708	51.227	57.869
Stemflow	Stemflow	mm y ⁻¹	Modelled on CHELSA BIO12	59.815	59.540	0	448.2
Trunk interception	Water intercepted and retained by the tree bark	mm y ⁻¹	Modelled on CHELSA BIO12	40.239	29.432	1.300	231.055
Throughfall	Throughfall precipitation	mm y ⁻¹	Modelled on CHELSA BIO12	434.064	101.657	80.000	706.700

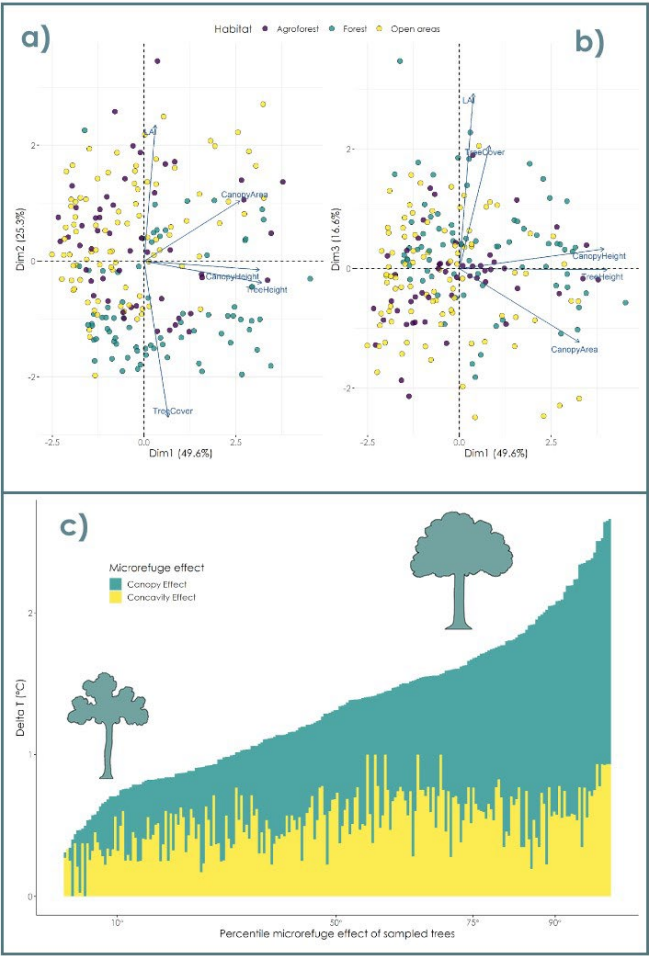
755 Table 2. Results of the GLMM models. Confidence intervals and p-values were obtained using
756 bootstrap with 1000 iterations. [Abbreviations of lichen growth forms are illustrated in Figure 1.](#)
757

Term	Estimate	Bootstrap 2.5%	Bootstrap 97.5%	p value
Frut				
Intercept	-2.352	-2.750	-1.937	<.001
Microrefuge capacity	0.948	0.668	1.247	<.001
RCP 2.6 year 2040 vs. current	-1.204	-1.305	-1.095	<.001
RCP 2.6 year 2060 vs. current	-1.101	-1.212	-0.999	<.001
RCP 8.5 year 2040 vs. current	-1.462	-1.576	-1.354	<.001
RCP 8.5 year 2060 vs. current	-3.048	-3.188	-2.902	<.001
Habitat Agroforest vs. Forest	-0.236	-0.794	0.307	0.428
Habitat Open areas vs. Forest	-0.203	-0.589	0.263	0.398
Fol.large				
Intercept	-4.180	-4.603	-3.741	<.001
Microrefuge capacity	0.580	0.159	1.005	0.006
RCP 2.6 year 2040 vs. current	-0.300	-0.471	-0.130	<.001
RCP 2.6 year 2060 vs. current	-0.157	-0.329	0.027	0.104
RCP 8.5 year 2040 vs. current	-0.375	-0.549	-0.202	<.001
RCP 8.5 year 2060 vs. current	-1.190	-1.368	-1.010	<.001
Habitat Agroforest vs. Forest	-0.394	-0.849	0.046	0.072
Habitat Open areas vs. Forest	-0.413	-0.782	-0.006	0.05
Fol.b				
Intercept	-1.660	-2.100	-1.207	<.001
Microrefuge capacity	-0.465	-0.777	-0.186	0.002
RCP 2.6 year 2040 vs. current	-1.376	-1.479	-1.274	<.001
RCP 2.6 year 2060 vs. current	-1.251	-1.351	-1.147	<.001
RCP 8.5 year 2040 vs. current	-1.258	-1.373	-1.159	<.001
RCP 8.5 year 2060 vs. current	-3.015	-3.161	-2.860	<.001
Habitat Agroforest vs. Forest	-0.207	-0.788	0.367	0.508
Habitat Open areas vs. Forest	-0.181	-0.658	0.323	0.5
Fol.n				
Intercept	-0.595	-0.949	-0.263	<.001
Microrefuge capacity	-0.868	-1.131	-0.603	<.001
RCP 2.6 year 2040 vs. current	-0.988	-1.088	-0.889	<.001
RCP 2.6 year 2060 vs. current	-1.160	-1.260	-1.055	<.001
RCP 8.5 year 2040 vs. current	-0.299	-0.392	-0.210	<.001
RCP 8.5 year 2060 vs. current	-2.771	-2.919	-2.628	<.001
Habitat Agroforest vs. Forest	0.139	-0.270	0.580	0.578
Habitat Open areas vs. Forest	0.306	-0.083	0.690	0.112
Fol.gel.swo				
Intercept	-3.633	-4.033	-3.265	<.001
Microrefuge capacity	1.046	0.733	1.385	<.001
RCP 2.6 year 2040 vs. current	-1.271	-1.439	-1.109	<.001
RCP 2.6 year 2060 vs. current	-1.336	-1.493	-1.177	<.001
RCP 8.5 year 2040 vs. current	-1.527	-1.682	-1.350	<.001
RCP 8.5 year 2060 vs. current	-2.298	-2.480	-2.127	<.001
Habitat Agroforest vs. Forest	-0.415	-0.817	0.006	0.054
Habitat Open areas vs. Forest	0.017	-0.348	0.384	0.926
Sq				
Intercept	-4.650	-4.976	-4.338	<.001
Microrefuge capacity	0.829	0.507	1.153	<.001
RCP 2.6 year 2040 vs. current	-0.679	-0.861	-0.501	<.001
RCP 2.6 year 2060 vs. current	-0.937	-1.121	-0.747	<.001
RCP 8.5 year 2040 vs. current	-0.857	-1.058	-0.674	<.001
RCP 8.5 year 2060 vs. current	-1.573	-1.757	-1.379	<.001
Habitat Agroforest vs. Forest	-0.167	-0.442	0.142	0.286
Habitat Open areas vs. Forest	-0.052	-0.287	0.208	0.692
Cr.co				
Intercept	-0.827	-1.156	-0.496	<.001
Microrefuge capacity	-0.803	-1.095	-0.504	<.001
RCP 2.6 year 2040 vs. current	-1.130	-1.256	-1.005	<.001
RCP 2.6 year 2060 vs. current	-1.019	-1.143	-0.902	<.001
RCP 8.5 year 2040 vs. current	-0.635	-0.754	-0.526	<.001
RCP 8.5 year 2060 vs. current	-2.285	-2.433	-2.139	<.001
Habitat Agroforest vs. Forest	-0.154	-0.517	0.229	0.472
Habitat Open areas vs. Forest	0.029	-0.318	0.372	0.862
Cr.in				
Intercept	-1.933	-2.230	-1.644	<.001
Microrefuge capacity	0.445	0.186	0.708	<.001
RCP 2.6 year 2040 vs. current	-1.559	-1.665	-1.456	<.001
RCP 2.6 year 2060 vs. current	-1.400	-1.515	-1.295	<.001
RCP 8.5 year 2040 vs. current	-1.453	-1.563	-1.347	<.001
RCP 8.5 year 2060 vs. current	-2.686	-2.824	-2.550	<.001
Habitat Agroforest vs. Forest	-0.043	-0.425	0.351	0.808
Habitat Open areas vs. Forest	0.173	-0.128	0.462	0.252

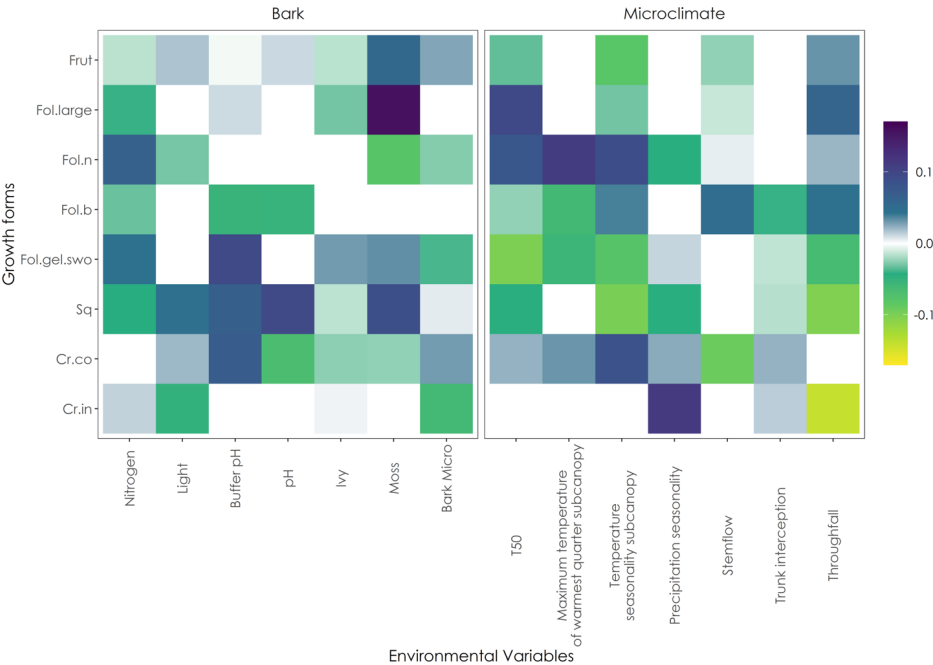
758
 759 Figure 1. Examples of lichen species and growth forms considered in this study: a) fruticose (Frut),
 760 *Ramalina farinacea*; b) Large foliose (Fol.large), *Lobaria pulmonaria*; c) broad-lobed *Parmelia*-like
 761 foliose (Fol.b), *Parmotrema perlatum*; d) narrow-lobed *Physcia*-like foliose (Fol.n), *Physconia*
 762 *distorta*; e) gelatinous foliose (Fol.gel.swo), *Collema furfuraceum*; f) squamulose (Sq), *Normandina*
 763 *pulchella*; g) conspicuous crustose (Cr.co), *Lepra albescens*; h) inconspicuous crustose (Cr.in),
 764 *Chrysothryx candelaris*. A detailed list of all detected species and their corresponding growth forms
 765 can be found in the Supplementary Materials.



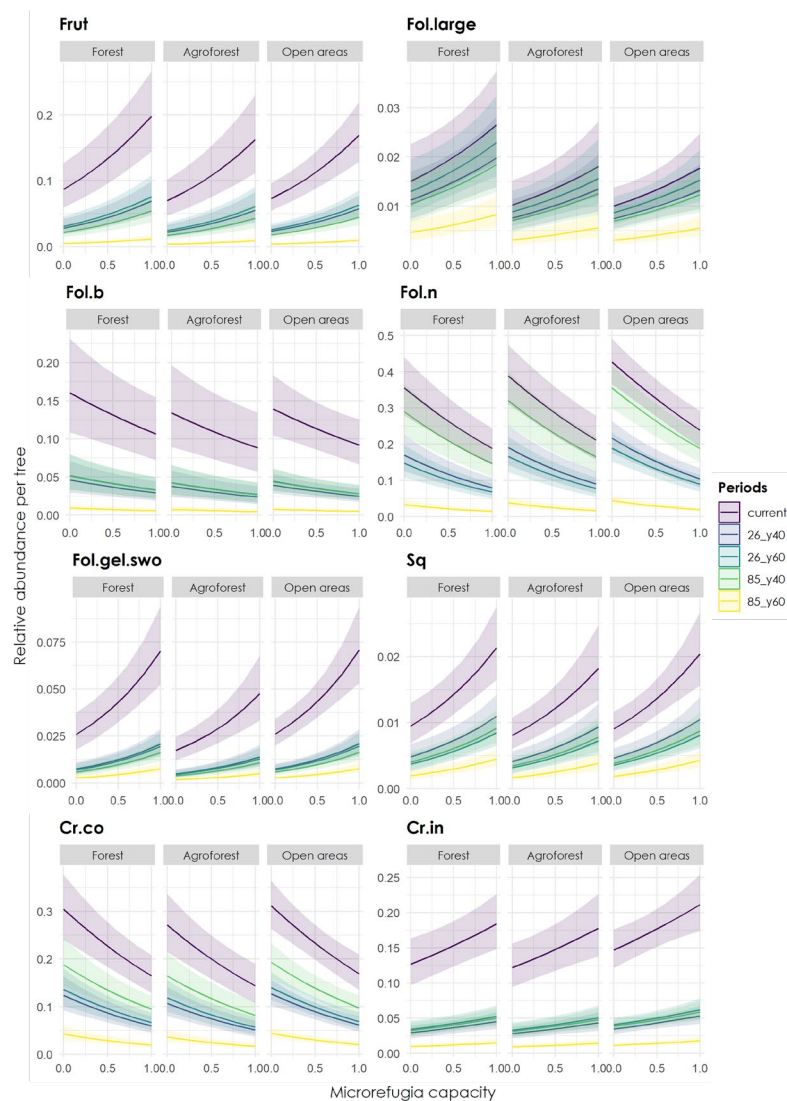
767 Figure 2. Determination of the micro-reproductive capacity of the trees surveyed in the study area.
 768 Figures (a) and (b) show Principal Component Analysis (PCA) of tree morphological characteristics
 769 used to calculate weights to be assigned to the maximum canopy capacity for temperature buffering
 770 suggested by Lenoir et al. (2017) as 2°C: PC1 vs PC2 (a) and PC1 vs PC3 (b). Figure (c) shows the
 771 percentile distribution of the overall micro-refuge capacity of the trees, determined by the sum of
 772 the canopy effect and the concavity effect and expressed as the difference between the temperature
 773 outside the canopy and the temperature below the canopy.



776 Figure 3. Results of the fourth corner analysis relating the functional trait "growth form" of lichen
 777 species to the related microenvironmental variables found on trees colonised by epiphytic
 778 communities. The micro-environmental variables are distinguished between a set of descriptors of
 779 the physical and chemical characteristics of the bark of the trees and a set of descriptors of the
 780 microclimatic characteristics found at the trunk under the canopy. Boxes are coloured according to
 781 traits fourth-corner coefficients: blue and green indicate positive and negative significant trait-
 782 variable association respectively. Details on the measurements and/or calculation of the predictors
 783 are given in Table 1. [Abbreviations of lichen growth forms are illustrated in Figure 1.](#)
 784 [The abbreviations of the lichen growth forms are as in Figure 1.](#)

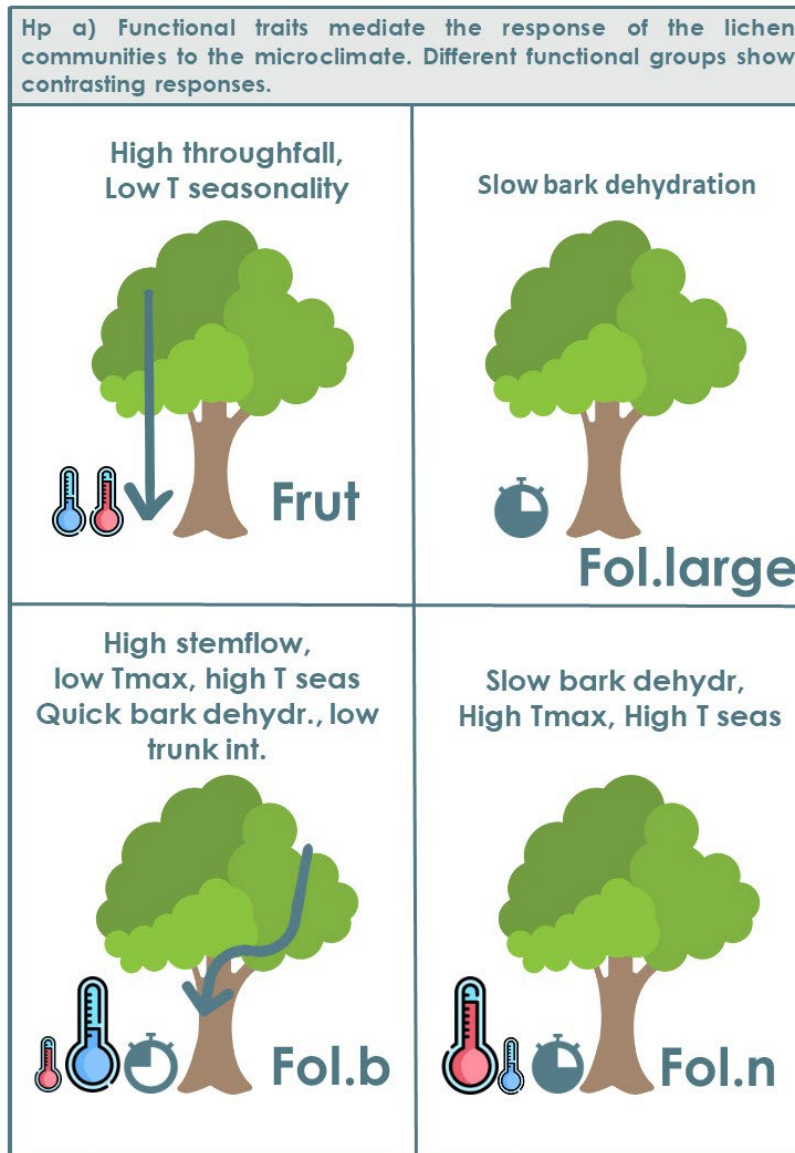


795
 796 Figure 4. Expected differences in terms of relative abundance for different microrefugia capacity
 797 comparing current conditions with different climate change scenarios (RCP2.6 and RCP8.5),
 798 different years (2040 and 2060) and different habitat (Forest, Agroforest and Open areas) for each
 799 growth form. [Abbreviations of lichen growth forms are illustrated in Figure 1.](#)
 800 [Abbreviations: Frut \(Fruticose\), Fol.large \(Foliose large\), Fol.b \(Foliose broad lobed\), Fol.gel.swo](#)
 801 [\(Foliose gelatinous\), Sq \(squamulose\), Cr.co \(Crustose conspicuous\), Cr.in \(Crustose inconspicuous\).](#)



803 Figure 5. Summary diagram of the main responses of epiphytic lichens to the microclimate
804 mediated by the growth form tested with hypothesis a) and according to the results obtained from
805 the fourth corner analysis shown in Figure 3. [Abbreviations of lichen growth forms are illustrated in](#)
806 [Figure 1.](#)

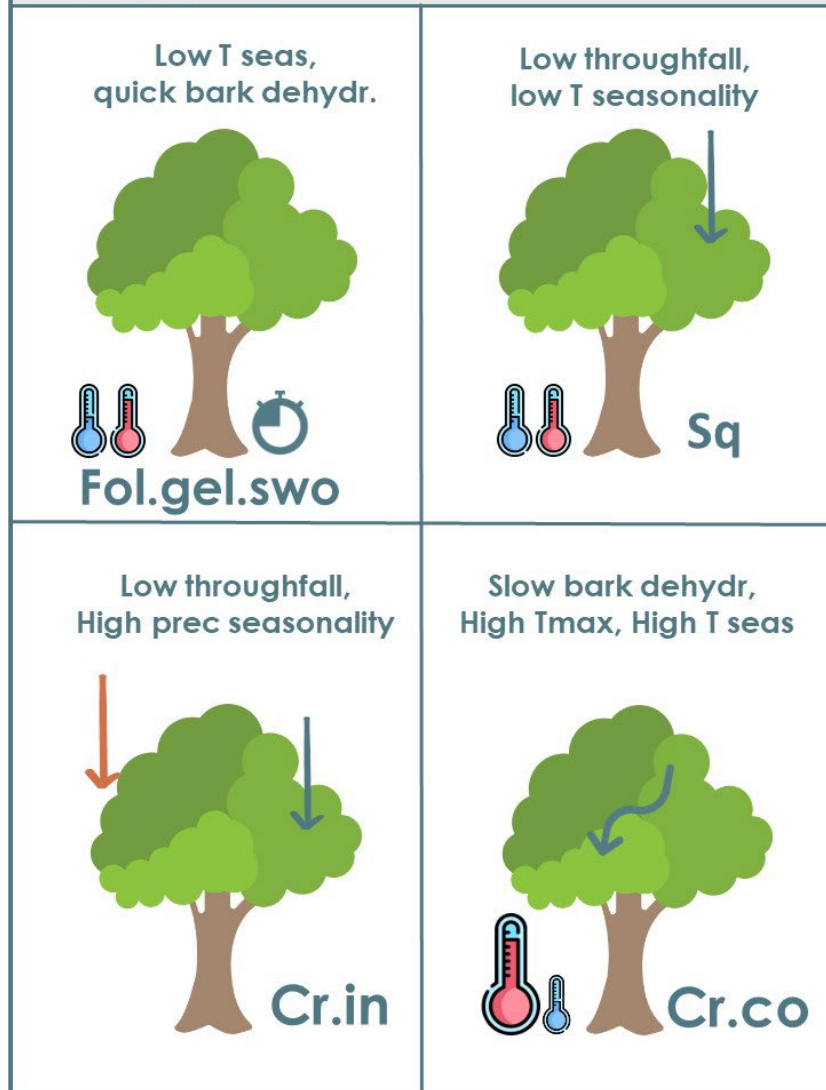
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809

810 Figure 5. Continuing.

Hp a) Functional traits mediate the response of the lichen communities to the microclimate. Different functional groups show contrasting responses.



811
812

813 Figure 6. Traits-mediated future variations of lichen communities on trees with high vs low
814 microrefuge capacity according to hypothesis b).
815

