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

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Abstract

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

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

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

Running Title: Microclimate buffering of trees for lichens

KEYWORDS

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

1 INTRODUCTION

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

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

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

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Proportionally, the gap between macro- and microclimate may be less relevant for populations of large species (e.g. tree species), compared to those of small organisms (De Frenne et al., 2019). Microclimate ~~buffering~~ mitigation is merely decisive for obligate epiphytes whose relationships with tree crown and trunk determine each step of their life cycle (Giordani et al., 2020; Ellis et al., 2014; Ellis & Eaton, 2021). For example, for hygrophilous lichens, microclimatic refugia have a significant effect in maintaining a growth rate on vital levels (Ellis, 2020), or in determining the probability of survival and development of recruits (Benesperi et al., 2018). The relevance of microrefuges is considerably higher the harsher the climatic conditions, for example ~~e.g.~~ in semi-arid Mediterranean environments where models predict the most drastic changes in terms of temperature increase and 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-km^2 area of western Sardinia, Italy, where human population density is very low (~40 persons/km^2), 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 (~~Sq,~~ 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*).

2.4 Tree-level measurements of environmental variables

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

2.5 Statistical downscaling of bioclimatic variables

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

2.6 Partitioning precipitations into stemflow and throughfall at tree level

The overall precipitation was partitioned into stemflow and throughfall at tree level. These two facets of precipitation are strictly related to canopy and bark characteristics. Throughfall represents the precipitation that passes through the canopy due to presence of gaps or branch drips. Conversely, stemflow is the water that flows on the bark drained from the canopy (Sadeghi et al., 2020). In general, 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.

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 ~~buffering~~mitigation. 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:

$$Delta\ Tmax\ (BIO5) = 2℃ \times Canopy\ effect + 1℃ \times Concavity\ effect$$
$$Delta\ T\ seasonality\ (BIO4) = 1℃ \times Canopy\ effect + 0.5℃ \times Concavity\ effect$$

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 boostrapped 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.large~~foliose large, ~~Frut~~ fruticose and ~~S~~squamulose species~~q~~. 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.swo~~foliose gelatinous swollen and ~~Cr.co~~crustose conspicuous species.

Considering microclimate descriptors, ~~Fol.n~~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 ~~Fol.gel~~species. The seasonality of precipitations (BIO15) determined contrasting responses between crustose inconspicuous ~~Cr.in~~ and foliose narrow-lobed ~~Fol.n~~ species. Among the components of sub-canopy precipitation, throughfall inhibited the presence of crustose inconspicuous ~~Cr.in~~ and squamulose~~Sq~~, while enhancing fruticose~~Frut~~ species. Water intercepted by the trunk inhibited the presence of broad-lobed foliose species~~Fol.b~~, 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 ~~Frut~~ and foliose gelatinous swollen~~Fol.gel.swo~~, ~~Fol.large~~foliose large, squamulose ~~Sq~~ and crustose inconspicuous ~~Cr.in~~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~~Frut~~, squamulose ~~Sq~~ and foliose gelatinous swollen species ~~Fol.gel.swo~~ are expected to maintain a significant relationship with the microrefuge capacity in all future scenarios, while for foliose large ~~Fol.large~~ and crustose inconspicuous ~~Cr.in~~ 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~~Fol.b~~, foliose narrow-lobed ~~Fol.n~~ and crustose conspicuous species ~~Cr.co~~ 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

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

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

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

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

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

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

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

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

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

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

Limitations and perspectives

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

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

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

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

Table 2. Results of the GLMM models. Confidence intervals an p-values were obtained using bootstrap with 1000 iterations. Abbreviations of lichen growth forms are illustrated in Figure 1.

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

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

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

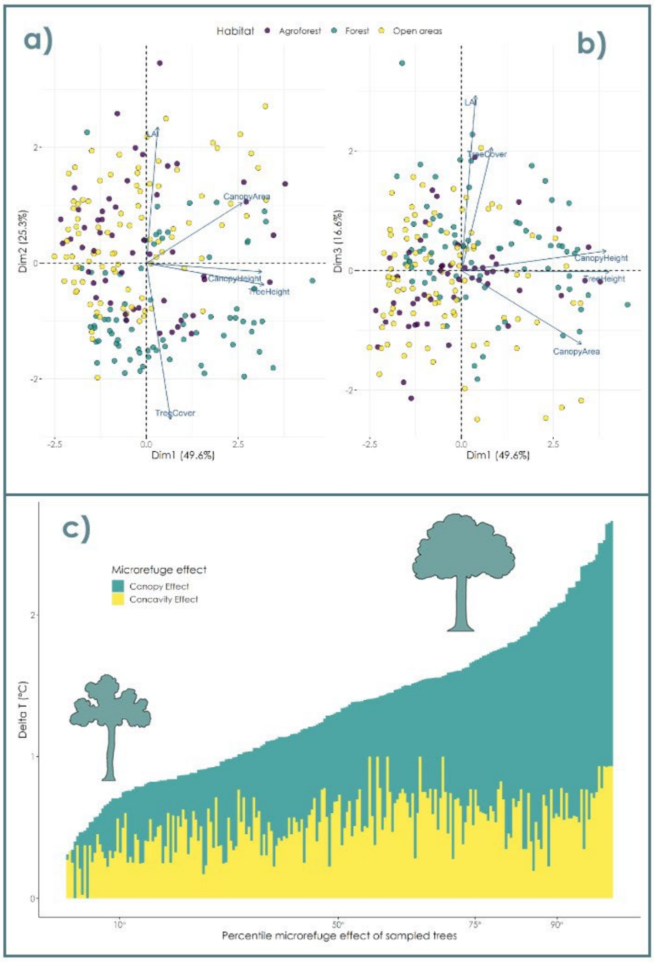


Figure 3. Results of the fourth corner analysis relating the functional trait "growth form" of lichen species to the related microenvironmental variables found on trees colonised by epiphytic communities. The micro-environmental variables are distinguished between a set of descriptors of the physical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

~~The abbreviations of the lichen growth forms are as in Figure 1.~~

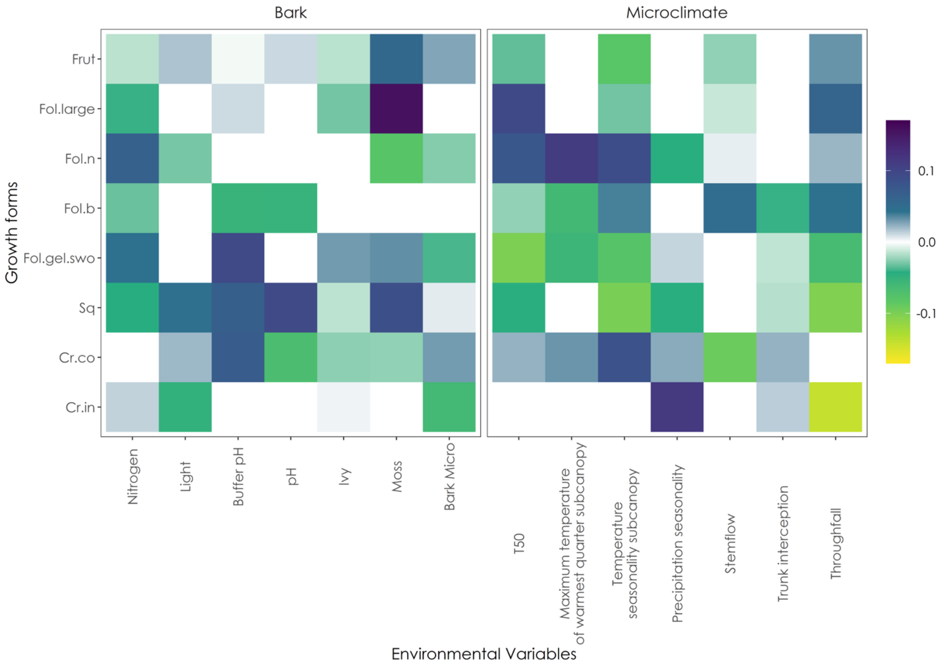


Figure 4. Expected differences in terms of relative abundance for different microrefugia capacity comparing current conditions with different climate change scenarios (RCP2.6 and RCP8.5), different years (2040 and 2060) and different habitat (Forest, Agroforest and Open areas) for each growth form. Abbreviations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

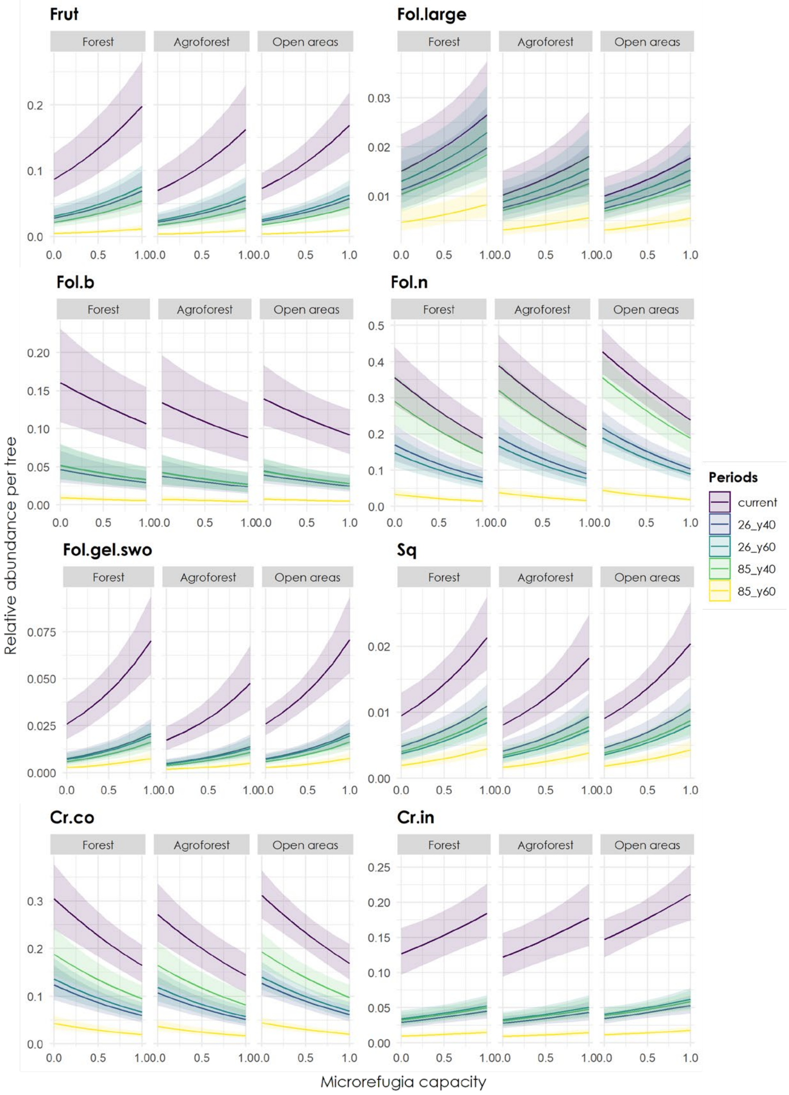


Figure 5. Summary diagram of the main responses of epiphytic lichens to the microclimate mediated by the growth form tested with hypothesis a) and according to the results obtained from the fourth corner analysis shown in Figure 3. Abbreviations of lichen growth forms are illustrated in Figure 1.

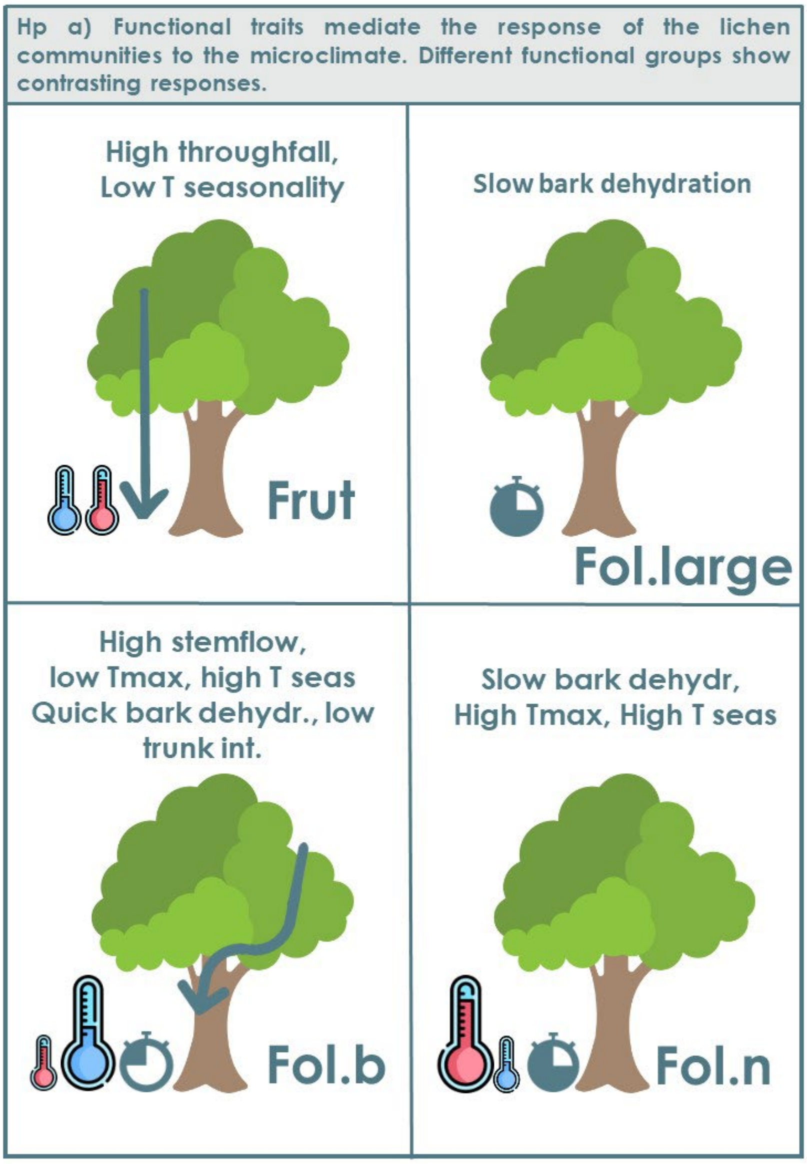
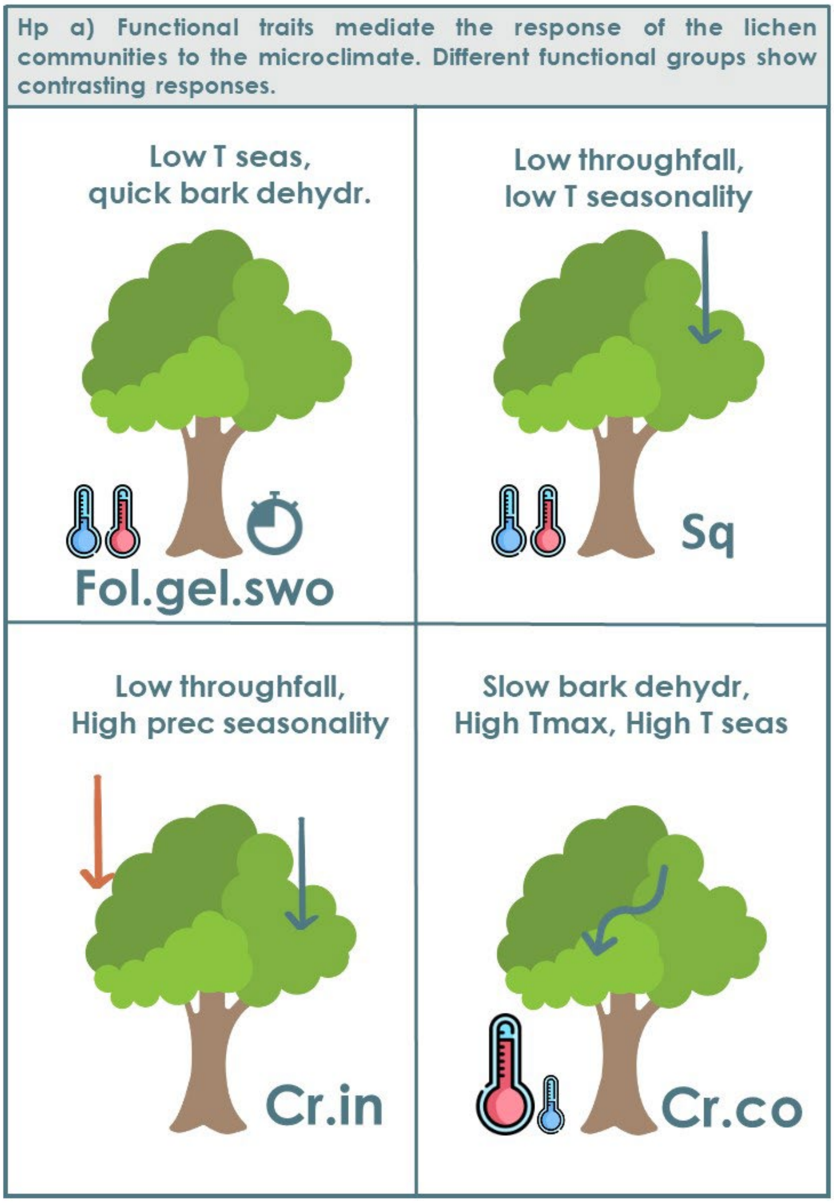


Figure 5. Continuing.



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

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