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Range Shift and Climatic Refugia for Alpine Lichens Under Climate Change

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ABSTRACT

Aim: The mountain biodiversity is highly threatened by climate change, with many species facing habitat reduction and/or local extinction. Poikilohydric organisms like lichens are extremely sensitive to environmental conditions and changes. A comprehensive overview of the impact of climate change on the future distribution of lichens is still missing. Thus, we quantified the range shift, loss in suitable areas and potential climatic refugia for more than 250 lichens, exploring these trends for each species and grouping them by their ecological needs and functional traits.

Location: Alps chain and surrounding areas (Europe).

Methods: We performed species distribution models to investigate the range shifts of 272 lichens under different climate change scenarios. Range shift was investigated by modelling gain and loss in suitability score along the elevational gradient, for each species separately and grouping them based on growth forms and temperature-affinities. Based on the 'high suitability score stability' index we developed maps of potential refuge areas.

Results: We predicted a huge loss of habitat suitability over time, especially under the SSP5-5.8. Fruticose lichens and cryophilous species will be the most impacted. Moreover, contrary to the assumption of an upward range shift, most species showed no significant relationship between altitude and increase in habitat suitability, suggesting different redistribution patterns for lichens. In the same way, climatic refugia are not only identified at high elevations but also in deep valleys and cold exposure.

Main Conclusions: The response of lichens to climate change is extremely heterogeneous, and an upper-range shift is less common than expected. Spatial redistribution is highly distinct among functional groups. The identified climatic refugia confirm this pattern, underlining the urgent need to improve the conservation effort, especially for fruticose and cryophilic species.

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1 | Introduction

Climate change, one of the leading causes of biodiversity loss, is severely impacting mountain ecosystems worldwide (Egan and Price 2017). In particular, the Alps are experiencing twice the warming rate of the Northern Hemisphere (Auer et al. 2007), a rise that is expected to accelerate further in the 21st century (Gobiet et al. 2014). Warming will also be associated with a decrease in snow cover and a change in the seasonality of precipitation, with increased summer drought, especially in the southeastern Alps (Gobiet et al. 2014; Kotlarski et al. 2023). Under these ongoing rapid changes in climate, habitat loss, species extinctions and shifting distribution rates are expected to increase (Dirnböck et al. 2011; Dullinger et al. 2012; Gheza et al. 2024; Lenoir and Svenning 2015; Steinbauer et al. 2018).

Altitudinal shifts of plant species to cooler, higher altitudes have been observed since the early 20th century (Lenoir and Svenning 2015; Rew et al. 2020), with accelerating warming rates (Chen et al. 2011; Steinbauer et al. 2018). These events have the potential to cause changes in the current communities and increase competition with cold-adapted species (Pauli et al. 2007). High-altitude species are therefore facing strong risk, as in many cases they have no higher areas to exploit (Dullinger et al. 2012; Pauli et al. 2012). However, microclimatic variations with respect to regional climate due to landscape features could allow cold-adapted species to persist in situ (Suggitt et al. 2018). The high topographic and landscape heterogeneity of the Alps, which provided glacial refugia during interglacial stages (Favarger and Robert 1962), could therefore shelter species from local extinction.

Species distribution models (SDMs) are powerful tools for understanding the influence of climate change on biodiversity, allowing for the forecasting of species range dynamics on a large scale (Guisan and Zimmermann 2000; Zurell et al. 2016), thus providing early warning information for optimising species conservation policies. However, while these models are widely used for well-known taxa (Porfirio et al. 2014), as in the case of vascular plants (e.g., Atwater and Barney 2021; Boisvert-Marsh et al. 2014; Gottfried et al. 2012; Rota et al. 2022) or birds (e.g., Huang et al. 2023; Le Louarn et al. 2018; Stralberg et al. 2015; Virkkala et al. 2010), only a few studies on lichens do exist (see the review Ellis 2019).

Lichens are a relevant component of mountain ecosystems, often dominant in high-altitude areas (Asplund and Wardle 2017). They play crucial ecosystem roles, as they are involved in nutrient cycling, soil formation and stabilisation and water dynamics (Elbert et al. 2012; Ellis et al. 2021; Porada et al. 2016), also providing habitat and food for other organisms (Asplund and Wardle 2017). Moreover, lichens are known to be very sensitive to climatic factors, especially moisture and temperature (Di Nuzzo et al. 2021; Nascimbene and Marini 2015). Being poikilohydric organisms, their internal water content tends to reach equilibrium with the surrounding environment (Insarov and Schroeter 2002; Oliver et al. 2000). Therefore, their physiology is closely linked to environmental moisture and temperature, which influence thallus water saturation (Green et al. 2008; Gauslaa 2014). Consequently, the expected future increase in temperature and drought may induce severe and frequent desiccation events, which may hinder photosynthetic activity, reduce growth rate (Hawkins et al. 2003; Insarov and Schroeter 2002) and increase respiratory carbon loss (Meyer et al. 2023; Sundberg et al. 1999). The response of lichens to climatic factors may be mediated by functional traits mainly related to water-use strategies, such as growth form (Ellis et al. 2021; Vallese et al. 2021; Wan and Ellis 2019). Previous studies have shown better resistance to drought for lichens with a crustose growth form due to their tolerance to desiccation (Bässler et al. 2016; Nascimbene and Marini 2015), while fruticose lichens, especially filamentous forms, suffer from excessive rewetting that depresses net assimilation (Coxson and Coyle 2003; Stevenson and Coxson 2007).

Therefore, lichen species distribution is expected to be impacted by climate change in the future (Giordani and Incerti 2008). Previous research forecasted a contraction of many species' ranges under several future scenarios (Devkota et al. 2019; Ellis 2019; Rubio-Salcedo et al. 2017; Vallese et al. 2021), especially for high-altitude (Allen and Lendemer 2016) and arctic/alpine lichens (Ellis et al. 2007). Likewise, some species may expand their range or shift to climatically suitable areas (Devkota et al. 2019; Insarov and Schroeter 2002; Mallen-Cooper et al. 2023; Nelsen and Lumbsch 2020; Zhao et al. 2019), particularly Mediterranean species (Rubio-Salcedo et al. 2017). These patterns are supported by some observational studies (Aptroot and Van Herk 2007; Herk et al. 2002; von Hirschheydt 2023). However, studies incorporating the lichen biota of the Alps are scanty and mostly limited to a few species, functional or taxonomic groups (Nascimbene et al. 2016; Nelsen and Lumbsch 2020; Vallese et al. 2021). In addition, the potential altitudinal shift for lichens based on SDMs was only investigated for the species *Lobaria pindarensis* Räsänen in the Himalayas (Devkota et al. 2019). To our knowledge, only Mayo De La Iglesia et al. (2024) observed an increase in terricolous lichen richness in the last two decades in the highest elevations, thus hypothesising an effective upward shift of lichen species. However, a recent study conducted on different organisms shows that only 42.9% of range shifts are supported by observations (Rubenstein et al. 2023).

A limiting factor for species distribution models is the requirement of massive quantities of high-quality data on the presence of organisms in space and time. These data are in general scarce, and often absent for most lichen taxa. In this perspective, combining different data sources can overcome this problem and provide an accurate database of georeferenced occurrences about the lichen biota of the Alps, one of the most relevant areas for lichen biodiversity in the Alps (Nimis 1993).

In this study, we developed SDMs to analyse the effects of climate change on the lichen biota of the Dolomites under different climate change scenarios. Given the high sensitivity of lichens to climate factors, such as warming and drought (Ellis 2019), we expected a significant loss of habitat suitability for most of the species within their current distribution ranges. Furthermore, considering that the response of lichen communities to climatic factors is mediated by functional traits (Di Nuzzo et al. 2021; Ellis et al. 2021; Rubio-Salcedo et al. 2017; Vallese et al. 2021; Wan and Ellis 2019), we evaluated differences in the response to climate change of different functional groups. In particular, we

FIGURE 1 | Location of the study area. The black rectangle enclosing the Alps indicates the calibration area of the models. The prediction area is shaded in red, corresponding to the Dolomites area.

expected that crustose species would adapt to climate change better than fruticose and foliose lichens, due to their tolerance to desiccation (Bässler et al. 2016; Nascimbene and Marini 2015) and that cold-adapted species would be more affected (Allen and Lendemer 2016; Ellis et al. 2007; Di Nuzzo et al. 2021).

Due to lichens' vulnerability, proper identification of refugia is necessary as a key process for climate change conservation planning (Baumgartner et al. 2018). Hence, we identified areas that could retain climate suitability in the future and thus provide in situ climate refuges for different functional and temperature-affinities groups, with a focus on sites outside current protected areas. Refugia for *thermophilous* species are expected to be more widespread across the territory, while *cryophilous* species are likely to be confined to higher elevations.

Finally, we investigated the influence of altitude on the changes in habitat suitability for each species. We expected that many species would move upward in response to warming. However, counterintuitive patterns, such as downhill shifts, were already detected for plants, mainly due to changes in water balance across complex topography (Crimmins et al. 2011). Given the strong influence of water availability on lichen physiology (Insarov and Schroeter 2002; Hawkins et al. 2003; Green et al. 2008; Gauslaa 2014), diverse types of re-distribution along the altitudinal gradient could be expected for lichens as well.

2 | Materials and Methods

2.1 | Study Area

We fitted SDMs for a rectangular bounding geometry (xmin: 4.857935 ymin: 43.52642 xmax: 16.59528 ymax: 48.35353) enclosing the Alps (Figure 1), defined by the ISMSA/SOIUSA classification (International Standardised Mountain Subdivision of the Alps/Suddivisione Orografica Internazionale Unificata del Sistema Alpino), the most recent geographic classification system of the Alps (Marazzi 2005).

Model prediction was performed for the Dolomites areas (Figure 1), located in the northeast of Italy. The area embraces all the main Italian massifs formed by dolomitic rock. Spanning an area of 11,735 km^2, it follows northward the Pusteria and Gail valleys, on the west the Adige and Isarco valleys, extending further to include the Brenta Dolomites and the Friulan Alps on the east, while southward it reaches the Venetian and Carnic Prealps, in order to include the 'Little Dolomites' as well (Bosellini 1989).

Widely explored by lichenologists through the centuries, the Dolomites are one of the most relevant areas for lichen biodiversity in the Alps (Nimis 1993). In fact, these mountains currently harbour more than 2000 infrageneric lichen taxa documented by more than 74,000 georeferenced records (Francesconi et al. 2024).

The Dolomites are characterised by an important geodiversity, which distinguishes them from all other mountains in the world (Panizza 2009). The Dolomites landscape consists of suggestive high cliffs of light-coloured dolomite, towering above smooth slopes of dark clayey and volcanoclastic rocks (Soldati 2010). For this uniqueness of their geology and topography (Messner and Tappeiner 2010), they were declared a UNESCO World Heritage Site in 2009.

The climate of this large area differs substantially from one extreme to the other. In general, it belongs to the Alpine biogeographical region (Blasi et al. 2014) and it varies along both an altitudinal and a longitudinal gradient (Pedrotti 2018; Pignatti and Pignatti 2016). Moving northwards from the most southern ranges, the climate changes from oceanic to continental. In fact, the southern mountains are influenced by moist air from the Adriatic Sea, which entails a wetter climate with frequent fog and heavy rainfall, even in summer. On the contrary, in the internal ranges, the winter and summer are generally dry, and rainfall is concentrated in autumn and spring (Gafta and Pedrotti 1998).

2.2 | Lichen Data

In this study, lichen occurrences were obtained from three sources: the Dolichens dataset (Francesconi et al. 2024), herbaria aggregated in ITALIC 7.0 (Conti et al. 2023; Martellos et al. 2023; Nimis 2024), and herbarium specimen data from the GBIF (GBIF.org 2024). We retained only occurrence data collected after 1975 and with a coordinate uncertainty of 500 m or less. To reduce spatial bias due to pseudo-replication of occurrences, we performed spatial thinning using the 'thin' function of the 'spThin' R package (Aiello-Lammens et al. 2015). This function returns a dataset with the maximum number of records for a given thinning distance (250 m in our study, performed without interactions). Then, we retained only the species with at least 25 occurrence records, a limit that has been shown to provide reliable results in modelling studies (Guisan et al. 2017). The resulting dataset includes 25 to 469 occurrence records of 272 infrageneric taxa, for a total of 21,884 occurrences. The data originates mainly from the Dolichens database (15,388; 70%), while ITALIC (5253, 24%) and GBIF (1243, 6%) contribute to smaller portions of the dataset.

Nomenclature and information on species' traits refer to ITALIC 7.0 (Nimis 2024). We classified each species into four growth form functional traits: fruticose, foliose, squamulose and crustose. Moreover, lichen species have been assigned to three groups based on their ecological affinity to temperature, in consideration of the altitudinal distribution reported on ITALIC: (a) *thermophilous*, including temperate species found at low altitudes (e.g., *Anaptychia ciliaris*, *Cladonia foliacea*), (b) *intermediate*, including species found in an intermediate range of temperature conditions (e.g., *Cetraria islandica* subsp. *islandica*, *Pseudevernia furfuracea* var. *furfuracea*), and (c) *cryophilous*, including cold-adapted and strictly arctic-alpine species (e.g., *Solorina crocea*, *Dacampia hookeri*). The list of the species with the categorization into growth form and temperature affinities group is provided in Appendix S1.

2.3 | Climate Data

Climate variables were downloaded from the Climatologies at High Resolution for the Earth's Land Surface Areas (CHELSA) portal (Karger et al. 2021). Using the 'ClimDatDownloadR' R packages (Jentsch et al. 2023), we downloaded the 19 bioclimatic predictors available for baseline (i.e., 1981–2010) and future (i.e., 2071–2100) climate at 30 arc sec (~1 km) spatial resolution, clipped for the Alps bounding box. We selected two future Shared Socio-economic Pathways (SSPs) representing very stringent (SSP1-2.6) and high (SSP5-8.5) greenhouse gas emission scenarios (IPCC 2021). To account for variability in the forecasts (Karger et al. 2017; Stralberg et al. 2015), we used SSP's projections from all the five available non-interdependent General Circulation Models (GCMs), representing physical processes in the atmosphere, ocean, cryosphere and land surface: GFDL-ESM4, IPSL-CM6A-LR, MPI-ESM1-2-HR, MRI-ESM2-0, UKESM1-0-LL.

2.4 | Bioclimatic Predictors Downscaling and Selection

Bioclimatic variables retrieved at 30 arc-second resolution may not adequately characterise the microclimatic conditions that lichens experience. Thus, all the variables for current and future climate were downscaled to a resolution suitable for our study: 250 m.

For temperature variables, we statistically downscaled each variable fitting three models: generalised linear model (GLM), generalised additive model (GAM) and gradient-boosted trees model (GBM), with the temperature variable as covariate and topoclimatic variables (aspect, tri, northness, eastness and solar radiation) as independent variables. Topoclimatic variables were extracted from a high-resolution DEM (90 m/pixel from OpenTopography 2021, aggregated at 30 arc-second resolution), using the 'terra' packages (Hijmans et al. 2024); solar radiation was calculated as described in McCune and Keon (2002). To account for model-based uncertainties, for each model, a split-sample 5-fold cross-validation was carried out, using the 'caret' R packages v. 6.0–92 (Kuhn 2008). The predictions at 250 m were ensembled by weighted averaging the model outputs by means of the 5 root-mean-square errors (RMSE), referring to each fold model.

For precipitation-related variables, since they have no clear relationship with topographic variables, we obtained a 250 m/pixel resolution by means of cubic spline interpolation of CHELSA raster layers, using the 'resample' function of the 'terra' packages (Hijmans et al. 2024).

Possible multicollinearity within the set of 19 candidate predictors was assessed through a correlation matrix within pairs of variables with Pearson correlation >0.75 (see Figure S2-1). The process led to the selection of three uncorrelated variables, which are known to be among the most relevant in influencing lichens distribution (Coyle and Hurlbert 2016; Mallen-Cooper et al. 2023; Rubio-Salcedo et al. 2017): BIO8 (mean daily mean air temperatures of the wettest quarter), BIO15 (precipitation seasonality), BIO17 (mean monthly precipitation amount of the driest quarter).

To account for spatial uncertainty for each occurrence, we averaged the extracted values of the bioclimatic variables within a buffer corresponding to the associated uncertainty value. This allows us to address the spatial mismatch between the resolution of climate predictors (250 m) and the coordinate uncertainty associated with species occurrences (up to 500 m).

2.5 | Species Distribution Models

Model averaging is a popular technique for reducing the uncertainty of model predictions (Dormann et al. 2018). For SDMs, ensembles of well-tuned models can perform stronger than any of the components (Valavi et al. 2022). Therefore, to predict the current potential distribution of lichens in the Dolomites, we averaged a set of two tree-based models 'projections', among the best-performing models according to Valavi et al. (2022): the Boosted regression trees (BRT) and the Random forest (RF). The two models were performed using the 'enmSdmX' R packages (Smith et al. 2023). Details of model parameters and training strategies are provided in Table S2-1. Model performance was assessed through a 5-fold cross-validation procedure, using two commonly adopted evaluation metrics: the Area Under the Receiver Operating Characteristic curve (AUC) and the True Skill Statistic (TSS) (Allouche et al. 2006; Elith et al. 2006). Standard model validation is challenging for species with few occurrences (< 50), as it can lead to inadequately sized test sets, compromising metric reliability and potentially inflating accuracy (Jiménez-Valverde 2020; Collart and Guisan 2023). Therefore, for these species, we employed the 'pooling evaluation' method proposed by Collart et al. (2021) to ensure robust model assessment. The ensemble was performed by weighing the predictions of the BRT and RF models based on their AUC scores on the training data.

For each species, we generated 10 replicate sets of pseudo-absences, in a 10:1 ratio with the number of presence points. A small number of pseudo-absences proved to be efficient for the selected models (Barbet-Massin et al. 2012). For the generation, we use the function 'pseudoAbsences' of the 'mopa' R packages (Iturbide et al. 2015), with an exclusion buffer of 500 m from the presence point, over the calibration area. We set the prevalence to 0.5 because the equally weighted presences and pseudo-absences produced the most accurately predicted distribution pattern (Barbet-Massin et al. 2012).

Considering the irregular distribution of occurrences in the study area, predictor space where there is no training data support should be considered problematic (Meyer et al. 2023). Therefore, to retain only the area where the prediction models can be reliably applied, the models' predictions were masked by the 'Area of Applicability' (AOA), derived from the 'aoa' function of the 'CAST' R packages (Meyer et al. 2023). AOA calculation was performed for the current bioclimatic variables, and each of the 10 sets of future conditions (two scenarios and five GCMs), using bioclimatic variables as predictors and species occurrence dataset as training data.

Therefore, the final likelihood under current conditions was the result of averaging the projected maps obtained from the two algorithms and the 10 sets of pseudo-absences, whereas the likelihood under future conditions was the average of 100 combinations (two algorithms, 10 sets of pseudo-absences, and five GCMs). This allowed us to assess projected uncertainty due to the variability attributable to statistical methods and the modelled climate. Variable importance was averaged both across the 10 generated pseudo-absence sets and across the results of the two statistical models employed, using relative contributions in BRT and permutation importance in RF.

2.6 | Re-Distribution Under Climate Change Analysis

For each occurrence, we extracted the value of predicted habitat suitability at current conditions and for the two future scenarios. Differences in habitat suitability between present and the two different future scenarios for the lichen biota were assessed by implementing linear mixed models (LMMs), with a Gaussian family error distribution ($SS \sim SSP$), and a random effect (slope) for each taxon (Breslow and Clayton 1993). Further, we tested the effects of growth forms and temperature affinities by adding an interaction term ($SS \sim SSP * trait$). All LMMs were built with the R package *glmmTMB* (Brooks et al. 2017).

For each species, we tested the effect of altitude on differences in habitat suitability (ΔSS) for each emission pathway by fitting linear models ($\Delta SS \sim altitude$). For those species with a positive relation with altitude, we also calculated the minimum value in the altitude range in which we predicted a gain in habitat suitability (positive value of ΔSS).

Moreover, we developed maps of predicted climatic refugia for each species by calculating a 'high suitability score stability' (HHSS) index by multiplying the predicted habitat suitability at the current conditions with those in future scenarios. This index, calculated for each species, was then summed up by aggregating species based on their growth form as well as their temperature affinities (cryophilous, intermediate and thermophilous species), and then scaled on a scale of 0 to 1. The index was then spatialized to highlight the potential climatic refugia for distinct groups. To assess conservation gaps in protecting future climatic refugia, we considered their overlap with Strictly Protected Areas (StPAs) present, (as IUCN categories Ia—Strict Nature Reserve, and II—National Park, whereas Ib—Wilderness Reserve not being present in Italy; EC 2022). In Italy, the Official List of Protected Natural Areas (EUAP), established according to law 394/91, includes all the national and regional Pas, together with State Nature Reserves and Integral Nature Reserves, corresponding to the StPAs category II and Ia, respectively. The spatial layers of StPAs were downloaded from the National Geoportal site (Geoportale MASE 2024).

3 | Results

The relative importance of the selected climatic variables in the species distribution models differed among species but was rather consistent among growth form groups (Figure 2, Table S2-2). Mean temperatures of the wettest quarter (BIO8) and precipitation seasonality (BIO15) on average contributed the most to explain the distribution of lichens in the study area, with an average of 43.9% and 42.9% relative contribution, respectively.

The models generally performed well, as indicated by TSS and AUC values exceeding 0.75 (Figure S2-2). The general results indicated a huge projected loss of habitat suitability for the lichen biota of the Dolomites by 2070 to 2100, across both emission pathways (Figure 3, Table S2-3). Currently, the mean habitat suitability score (SS) of the lichens is 0.815 (±0.003), a value expected to decrease by 0.159 (±0.002) under the mitigation scenario (SSP1-2.6) and more than double (0.319 ± 0.002) in the worst-case scenario (SSP5-8.5). In the worst-case scenario, fruticose lichens will undergo higher SS losses than the average, in contrast to crustose lichens, which exhibit lower-than-average SS drops (Figure 3, Appendix S2). Under the mitigation

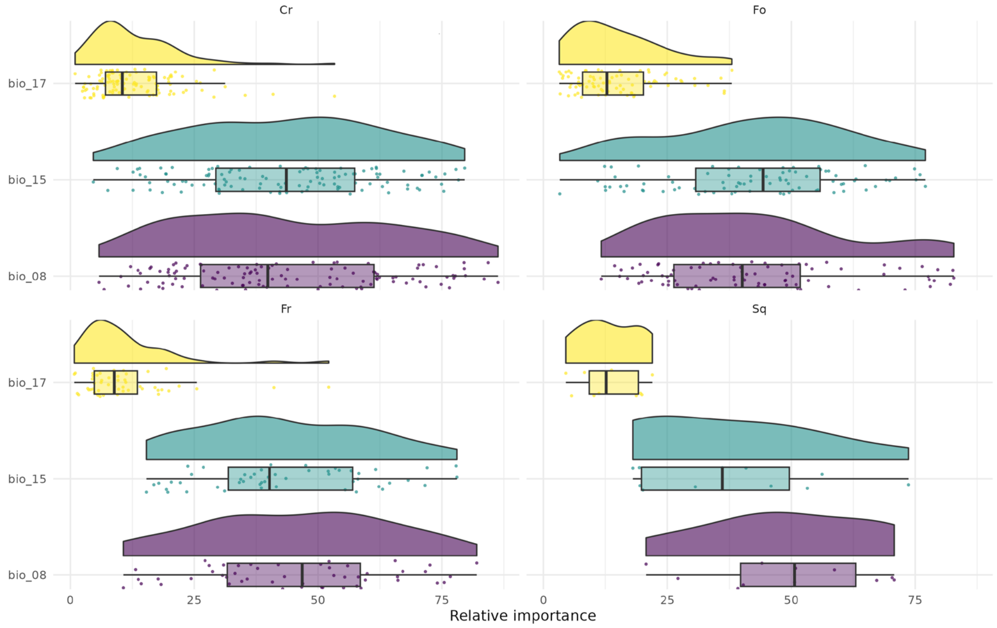

FIGURE 2 | Relative variable importance of Boosted Regression Trees (BRT) models explaining habitat suitability for different growth forms. Cr, Crustose; Fo, Foliose; Fr, Fruticose; Sq, Squamulose.

scenarios, cryophilous species will be subjected to minor loss than average. In contrast, thermophilous species will face SS losses higher than average. Under the high-emission scenario, this pattern is reversed (Appendix S2).

Spatial visualisation of the HHSS index showed that the climatic refugia with high values are more pronounced in the mitigation scenario (Figure S3-1–3), while they shrink in the high-emissions scenario (Figure S3-2,4). In general, these refugia are located in the Brenta Dolomites and the northwesternmost part of the study area. It is evident that a large portion of refugia is located outside the StPAs, as exemplified by the entirety of the Fiemme Dolomites (Figure 4 and Figure S3-5–7). Hotspots of HHSS index are quite comparable among growth forms (Appendix S3) but differ considerably between cryophilous species and other temperature-affinity groups. Intermediate and thermophilous species show climatic refugia not only at high elevations but also in the valleys and on the southeastern slopes of some massifs (Figure 4 and Figure S3-3).

All 272 species show a mean negative difference between current and future scores in their occurrences, under both scenarios. In the mitigation scenario, 18.8% of taxa (51) will be subject on average to a slight loss of SS (up to 0.1), the majority (78.4%) to a mean loss between 0.1 and 0.3. Only 8 taxa (2.9%) will face a drop above 0.3 in SS: *Pyrenula nitida*, *Lecanora cenisia*, *Lecidea confluens*, *Ochrolechia androgyna*, *Rhizoplaca chrysoleuca*, *Usnea subfloridana*, *Pertusaria coccodes* and *Polyozosia hagenii*. In the worst-case SSP5-8.5 scenario, no species will experience an average loss lower than 0.1 of SS. In contrast, 38.6% (105) will incur mean losses between 0.1 and 0.3, 44.5% (121) between 0.3 and 0.4, and 16.9% >0.4, among which 6 species will suffer heavy losses, over 0.5 of SS: *Baeomyces placophyllus*, *Usnea barbata*, and again *P. coccodes*, *O. androgyna, L. confluens* and *R. chrysoleuca*.

However, investigating changes in SS in every occurrence, we found that for some points the habitat suitability will increase in the future. In the mitigation scenario, 116 taxa show a gain of SS in at least one of their occurrences. Most of them (79) display a SS gain in $<10\%$ of the occurrences, 33 taxa between 10% and 50% of the occurrences, and only a few taxa show positive differences in more than half of the occurrences, such as *Variospora flavescens* in 9 on 15, *Baeomyces rufus* in 6 on 10, *Umbilicaria crustulosa* subsp. *crustulosa* in 7 on 12.

In the worst-case scenario, only 81 taxa will gain SS in some occurrences and the majority (74) display a gain in $<10\%$ of their occurrences. Only 7 species will gain SS between 10% and 26% of their occurrences: *Lathagrium auriforme*, *Parmotrema perlatum*, *Pseudoschismatomma rufescens*, *Pannaria conoplea*, *Peltigera horizontalis*, *Lepra albescens*, *Lecanora intumescens*. Anyway, the predicted SS gain is minimal, although significantly different from 0, with average values of 0.025 ($p<2e^{-16}$, with a maximum value of 0.170) in the SSP1-2.6 scenario and 0.045 ($p<2e^{-16}$, maximum 0.279) in the SSP5-8.5 scenario.

3.1 | Loss and Gain of Habitat Suitability Along the Altitudinal Gradient

The accuracy of the model that tested the effect of altitude on differences in habitat suitability scores (ΔSS) varied depending on the taxon (see Appendix S1). The models explained 0% to 74% of the variance in ΔSS in the SSP1-2.6 scenario and 0% to 84% in the SSP5-8.5 scenario.

In fact, for more than half of the lichens, 162 species (59.5%) and 155 species (57.0%), under the mitigation and the worst-case scenarios, respectively, we detected no linear relationship between differences in habitat suitability and the species' altitudinal range.

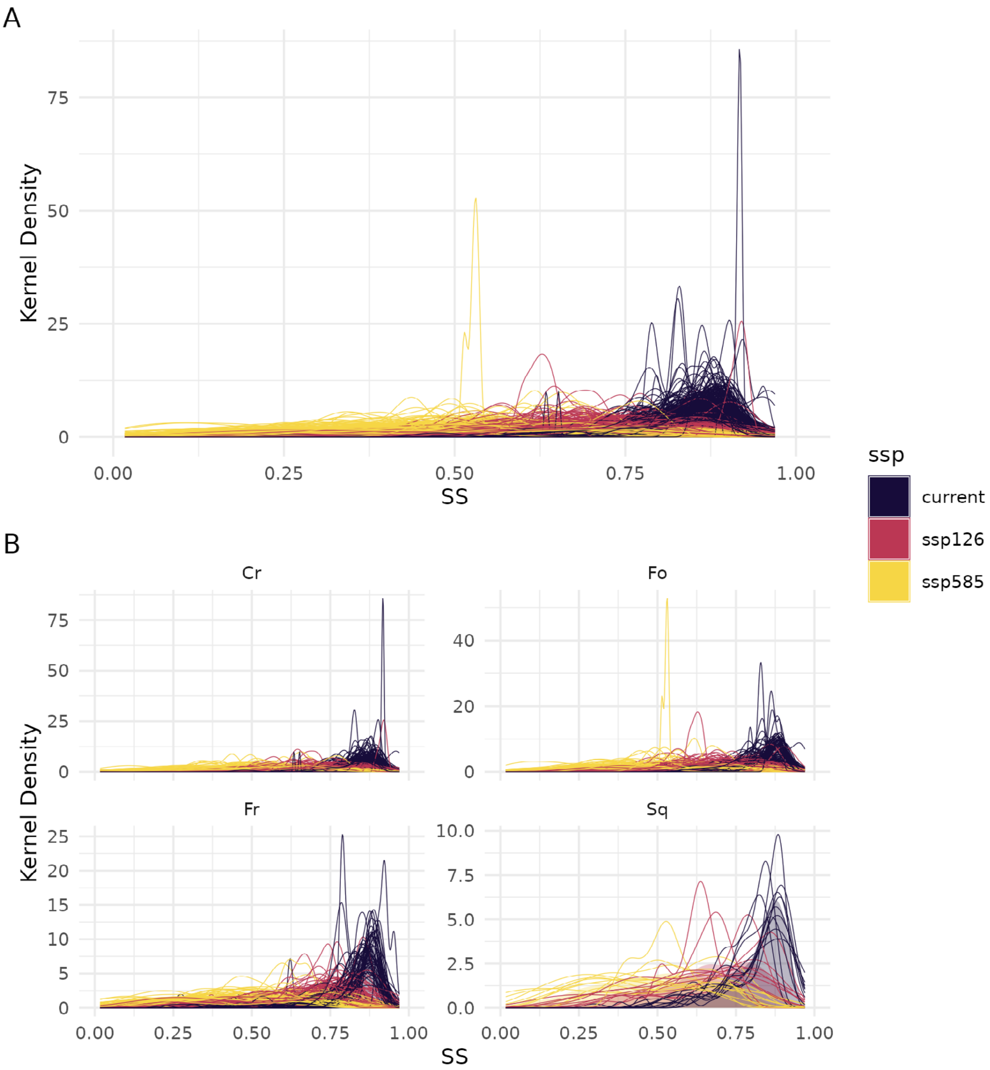

FIGURE 3 | Density distributions of habitat suitability (SS) of each species under current conditions (Panel A), mitigation scenario (SSP1-2.6) and high-emission scenario (SSP5-8.5); the fourth panel below (Panel B) show the pattern divided for different growth forms. Cr, Crustose; Fo, Foliose; Fr, Fruticose; Sq, Squamulose.

Instead, for 103 species (37.9% under SSP1-2.6) and 110 species (40.4% under SSP5-8.5), the altitude had a significant positive effect on ΔSS. Thus, considering that all the 272 species have negative intercepts and on average will lose SS in the future, SS losses will be smaller in the upper part of the altitudinal gradient of these taxa. Only 14 species in the mitigation scenario and 2 species in the high emissions scenario exhibit positive ΔSS above a specific altitude in their relative gradient (Table 1), so in the future, they may gain habitat suitability in occurrences over these altitudes.

In general, under the mitigation scenario, half of the 103 taxa present regression coefficients ≤ 0.00012, that is, a decrease in losses of 0.12 SS per 1000 m, very small values indicating a low influence of altitude on changes in SS (Appendix S1). In the worst-case scenario, the fraction of taxa with such slope values decreases to 27%. By contrast, in the mitigation scenario, only 9 taxa (8.7%) show regression coefficients >0.00025, with an increase in SS of more than 0.25 per 1000 m: *Parmotrema crinitum* ($r=0.00083$, p-value <0.0001, $R^2=0.63$), *Usnea subfloridana* ($r=0.00040$, p-value <0.0001, $R^2=0.62$), *Menegazzia terebrata* ($r=0.000332$, p-value <0.0001, $R^2=0.18$), *Nephromopsis cucullata* ($r=0.00031$, p-value <0.01, $R^2=0.28$), *Staurothele areolata* ($r=0.00030$, p-value <0.01, $R^2=0.31$), *Varicellaria hemisphaerica* ($r=0.00030$, p-value <0.0001, $R^2=0.29$), *Cetraria muricata* ($r=0.00028$, p-value <0.05, $R^2=0.34$), *Nephromopsis nivalis* ($r=0.00027$, p-value <0.05, $R^2=0.16$), *Ramalina thrausta* ($r=0.00027$, p-value <0.0001, $R^2=0.47$), *Blastenia ammiospila* ($r=0.00025$, p-value <0.05, $R^2=0.21$).

Among these, only *R. thrausta* will gain habitat suitability above 1915 m. *P. crinitum* shows the strongest positive relationship with altitude, but despite a decrease in losses of 0.83 of SS per 1000 m, the model does not predict positive ΔSSs in the sampled altitude range, which spans from 995 to 1364 m.

Under the high emissions scenario, taxa with regression coefficients >0.00025 increase to 30 (Appendix S1). Among these, *Punctelia subrudecta* ($r=0.00036$, p-value <0.0001, $R^2=0.84$) and *Xanthoparmelia conspersa* ($r=0.00027$, p-value <0.0001, $R^2=0.50$) will be subject to a gain in habitat suitability over 1160 and 2264 m, respectively. *P. crinitum* remains the species

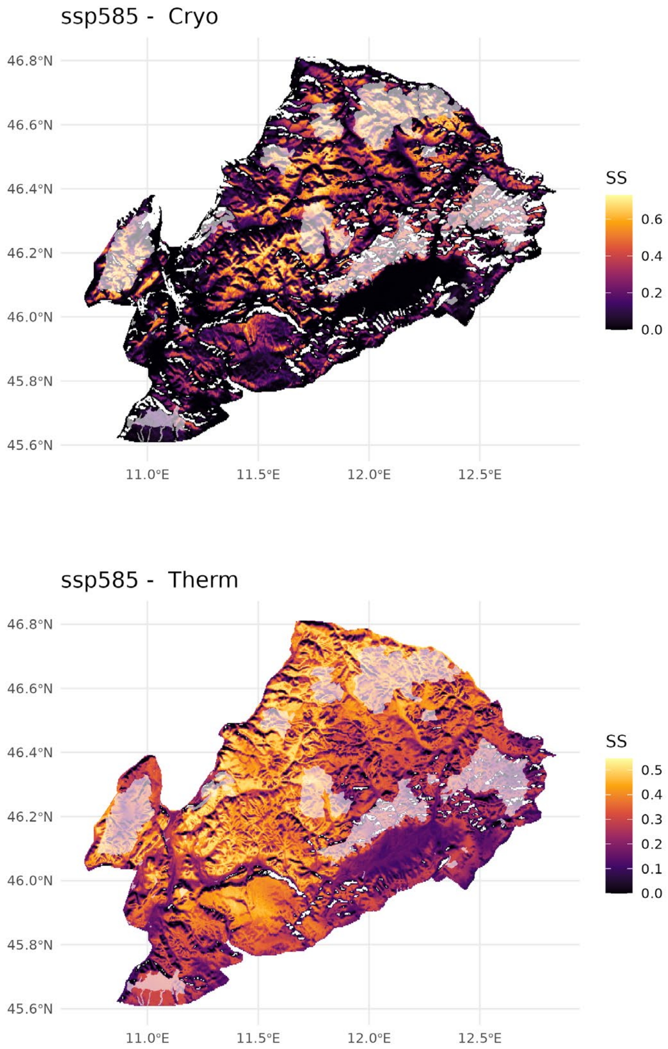

FIGURE 4 | Maps of predicted climatic refugia for the AOA in the high-emission scenario, illustrate as the areas where greatest sum of 'high suitability score stability' index (scaled 0 to 1) for the species aggregated by temperature affinity. Areas outside the AOA are shown in white. Semi-transparent polygons represent protected areas in the study area.

that exhibits the strongest positive relationship even in this scenario ($r = 0.00141$, p-value < 0.0001, $R^2 = 0.68$), with a decrease in losses of 0.14 SS per 100 m altitude. Even in this scenario, no suitability gains are predicted for its occurrence.

In both scenarios, altitude had a significantly negative effect on differences in SS in the future only for 7 taxa (Appendix S1). In the mitigation scenarios, *Chaenotheca chrysocephala*, *Candelariella reflexa*, *Chrysothrix candelaris* and *Lecanora allophana* f. *allophana* are all temperate-montane xerophytic-mesophytic taxa, most of them crustose, epiphytic lichens with green algae as photobiont. Only *Acarospora fuscata* prefers rocks as substratum, *Graphis scripta* has *Trentepohlia* as photobiont, and *Parmeliopsis ambigua* is a narrow-lobed foliose lichen. All the slopes are very close to zero (> -0.00013), denoting a very weak influence of altitude on these species' habitat suitability differences. Only 3 of 7 taxa show slopes < -0.00010, that is, an increase of losses over 0.1 SS per 1000 m. For the other 4 taxa, the rate of increase in SS rising in altitude is between 0.07 and 0.05 per 1000 m. Under the worst-case scenario, 4 taxa show the same relationship with altitude (*C. reflexa*, *C. candelaris*, *Graphis scripta*, *L. allophana* f. *allophana*). The other 3 species are replaced by the narrow-lobed foliose *Physciella chloantha*, the terricolous *Lepraria lobificans* and the saxicolous *Variospora flavescens*. In this scenario, the mean growth rate of SS increases slightly with maximum values of 0.19 per 1000 m.

4 | Discussion

A dramatic reduction in habitat suitability of lichen biota is expected, with double amounts of loss under the high emissions than the mitigation scenario. For the first time, SDMs utilising a finer spatial resolution than the conventional 1 km grid were applied to a multiple-species lichen dataset highlighting that all the species will experience a decrease in suitability in their current occurrence ranges. Hence, future increasing temperatures, especially in the wettest season, and changes in the rainfall regime will likely lead to narrower spatial distribution or even to local or regional extinction for some lichens in the study area. These results are consistent with other studies predicting a huge loss of suitable area for many lichens in the Iberian Peninsula (Rubio-Salcedo et al. 2017), for artic/alpine lichens of Britain (Ellis et al. 2007), and for

TABLE 1 | Species that gain habitat suitability in some part of the species sampled altitude gradient. All the coefficients are significant ($p < 0.05$).

Taxon	Altitude gain (m)	Altitude range	Slope	Min ΔSS	Max ΔSS
SSP1-2.6					
Brodoa intestiniformis	2642	1262–2766	0.00020	−0.3889	0.0213
Cetraria islandica subsp. *islandica*	2767	467–2887	0.00009	−0.4222	0.1059
Cladonia sulphurina	2005	1075–2245	0.00011	−0.1881	0.0257
Farnoldia jurana subsp. *jurana*	2633	1003–2723	0.00010	−0.2638	0.0244
Lathagrium undulatum	2611	1001–2766	0.00008	−0.2874	0.0394
Megaspora verrucosa	2699	1479–2766	0.00024	−0.4493	0.0433
Peltigera leucophlebia	2383	1023–2611	0.00013	−0.3204	0.0359
Polyozosia semipallida	2720	1350–2723	0.00018	−0.3206	−0.0254
Ramalina thrausta	1915	995–2115	0.00027	−0.4496	0.0124
Umbilicaria crustulosa subsp. *crustulosa*	2099	1439–2392	0.00019	−0.2357	0.0426
Umbilicaria cylindrica var. cylindrica	2614	1074–2669	0.00016	−0.3169	−0.0059
Usnea ceratina	1916	1176–2107	0.00012	−0.2251	0.0906
Verrucaria elaeomelaena	1522	222–2404	0.00006	−0.1284	0.0793
Xanthoparmelia conspersa	2134	294–2304	0.00014	−0.4601	−0.0411
SSP5-8.5					
Punctelia subrudecta	1160	270–1213	0.00036	−0.2558	−0.0697
Xanthoparmelia conspersa	2264	294–2304	0.00027	−0.4601	−0.0411

high-elevation lichens endemic to the Appalachians (Allen and Lendemer 2016). Indeed, an increase in temperatures and a decrease in precipitation may limit the distribution of these poikilohydric organisms, negatively affecting key ecophysiological processes (Insarov and Schroeter 2002; Meyer et al. 2023; Sundberg et al. 1999).

However, contrasting patterns may be expected among different species groups. In particular, the response of lichens to climatic factors is mediated by functional traits (e.g., photobiont type and growth form) that determine their performance under specific environmental conditions (Bässler et al. 2016; Nascimbene and Marini 2015; Rubio-Salcedo et al. 2017). Our results indicate a significant difference related to thallus growth forms. Lichens with a crustose growth form will be relatively less impacted by future climatic conditions, whereas fruticose species will be much more susceptible. Indeed, crustose lichens are expected to better resist drought events (Bässler et al. 2016; Nascimbene and Marini 2015) probably due to less surface area exposed to the atmosphere (Büdel and Scheidegger 2008). In contrast, fruticose lichens have a larger exposed surface area, making them more prone to drying and re-wetting cycles (Nascimbene and Marini 2015). In particular, climate change is exacerbating the decline of beard-forming lichens (genera *Usnea* and *Bryoria*), already highly threatened by industrial forestry (Stevenson and Coxson 2007) and nitrogen deposition (Geiser et al. 2021). Indeed, warming could alter their hydration regime and increase respiration during the months of low-light conditions, negatively impacting their occurrence (Esseen et al. 2022). Moreover, climate change will have different effects on species depending on their temperature affinities and the emission scenario considered. Under the mitigation scenario, the limited temperature increase will impact the thermophilous species more than the cryophilous ones, since the effect on the latter will be probably buffered by the limited extent of temperature increase, which will leave sites still suitable for them at high altitudes. On the other hand, under the high-emission scenario, cryophilous species will undergo greater losses of suitability compared to the thermophilous species, as the extreme warming predicted is likely to exceed the temperature conditions suitable for the survival of the species (Finger-Higgens et al. 2022; Sancho et al. 2017). In addition, these differences could also be caused by the change in precipitation regimes expected in the future.

Lichen propagation relies on two main strategies: large asexual diaspores (e.g., isidia, soredia) more effective for local dispersal (Scheidegger and Werth 2009), and small, sexually generated meiospores more useful for long-distance dispersal (Ronnås et al. 2017). This ability to colonise new, suitable habitats through differentiated strategies is relevant because, although lichens are sessile organisms, in an area with great variations in altitude over short distances, such as the Dolomites, a shift along the altitudinal gradient is therefore likely to occur in the future. Our results show that for almost half of the species, a decline in population at the lower limit of their current distributional range is expected, resulting in a contraction of their range towards the upper areas. Nevertheless, only a few of these species exhibit a possible lean upslope: their distribution is likely to shift upwards within their existing range and possibly extend above it. However, many species show a positive, but very weak relationship between altitude and loss of suitability. This corroborates the hypothesis that the lichens of the Dolomites will suffer a general decline throughout their altitudinal range.

In contrast to the general expectation of an upward range shift (Lenoir and Svenning 2015), we observed that, for most of the species, there is no significant linear relationship between altitude and loss of environmental suitability, indicating that lichens will mostly be subject to different redistribution patterns. Moreover, a few species experience higher losses in the higher part of their elevational ranges, even with very low differences. These are xerophilous lichens, mostly epiphytic and crustose with green algae, that is, the most adapted to conditions of warm temperatures and drought, and mostly distributed at low altitudes. In the future, they will therefore be restricted to the bottom of the valleys. These redistribution patterns can be related to two main factors. (1) Local changes in precipitation can lead to counterintuitive altitudinal range shifts, as rainfall does not follow a simple linear relationship with altitude (Barry 2008; Roe 2005). Therefore, as precipitation is a key factor affecting the distribution of lichens (Ellis 2019; Gauslaa 2014), it is possible that in the future species may redistribute along the altitudinal gradient to track suitable precipitation conditions (Crimmins et al. 2011). (2) The high geomorphological heterogeneity of the Dolomites may increase the availability of microclimatic refugia that can influence range-shifting directions, which may not necessarily be upwardly oriented. Dobrowski (2011) suggested that concave environments, such as valleys and depressions, are more likely to have features that make local climates distinct from regional ones. Moreover, topographical and microclimatic conditions of the Dolomites have been shown to provide extensive refuge areas for endemic plants (Rota et al. 2022), and lichens could also benefit as well (Lõhmus et al. 2023). In fact, our results forecast that, for 30% to 40% of lichen species, climate suitability will grow or persist in some localities. This emphasises that, even though these species will experience a reduction in their range, they may persist in some sites, which will provide in situ refuges for residual populations.

The spatial representation of possible future climate refugia showed a clear northwest-southeast pattern, where refuge areas cluster most in the inner part of the Dolomites, characterised by a continental climate. In fact, the South Alps, especially the eastern part of the ridge, have been subject to significant drying over the past century compared to the northern regions, a pattern that is expected to worsen further by the end of the 21st century (Gobiet et al. 2014). The more conservative climate over time in inland areas affords that the climatic suitability of lichen species will remain high, and populations may persist here. However, a portion of the refuge lands falls outside the present protected areas. This will hamper the effectiveness of these regions in providing refuge for lichens because other factors such as forest management, habitat loss and pollution can impact their survival (Ellis and Yahr 2011; Giordani 2007; Nascimbene, Thor, and Nimis 2013).

Despite our study being based on the largest inventory of lichen occurrences ever compiled for the Alps, some constraints need to be considered for proper result interpretation. First, a potential limitation of our study lies in the risk of niche truncation due to the restricted geographic extent considered. The distribution of lichens remains incompletely known, with many regions still underexplored and new occurrence records continually emerging. These gaps in knowledge may lead to partial representations of species' realised niches. However, expanding the study area beyond our current extent would have introduced additional uncertainty, as it would have required including regions that are substantially under-sampled and could bias niche estimates due to low data density. In this context, we opted for a pragmatic trade-off between minimising niche truncation and ensuring data reliability. It is important to note that for neglected and data-poor taxa such as lichens, niche truncation, if present, tends to lead to conservative estimates of future suitability, highlighting fewer areas as suitable than might actually be the case. From a conservation planning perspective, this implies that any identified climatic refugia are more likely to be robust, albeit potentially under-representative of the full set of suitable conditions. To further mitigate this issue, we defined a study area encompassing a wide climatic gradient, from the Alps to the Mediterranean regions, thus including a broad spectrum of environmental conditions and minimising the likelihood of systematic omission of key portions of the species' realised niche.

Furthermore, improving taxonomic knowledge is required to better interpret the different species-specific responses to climate change. Another possible limitation involves using only climate variables for SDMs, as lichen distributions are frequently explained also by additional predictors, such as habitat structure and air pollution (Ellis 2019; Nascimbene et al. 2020; Stofer et al. 2006; Van Dobben and Ter Braak 1999). However, including additional variables in models for species with few known locations often leads to overfitting models (Radosavljevic and Anderson 2014). Furthermore, their inclusion would hamper the transferability of the results to the future since accurate future projections for these variables are currently lacking. In addition, although our spatial resolution following the downscaling (250 m) takes into account microclimatic variability, smaller topographic structures may be difficult to capture (Randin et al. 2009). The future availability of climate data at a higher resolution could significantly improve the ability of lichen SDMs to determine the distributions of lichens, which are strongly influenced by microclimatic conditions (Rodriguez et al. 2017). Finally, although we accounted for spatial uncertainty by averaging climatic predictors within buffers reflecting each record's reported coordinate uncertainty, a residual mismatch between the resolution of environmental layers (250 m) and the precision of some occurrences (up to 500 m) may persist. This limitation, inherent to most biodiversity datasets, is particularly relevant for cryptic or neglected taxa such as lichens, for which high-resolution and spatially precise data remain scarce. Nevertheless, our approach provides a transparent and conservative solution that mitigates potential biases and supports the reliability of our results. Future improvements in data availability, including finer-scale environmental predictors and more precise georeferencing of occurrences, will undoubtedly allow for even more accurate and spatially resolved modelling. At present, however, the dataset used here represents the best available foundation for large-scale ecological inference on these poorly known organisms.

5 | Conclusion

Climate change will have a significant influence on the lichen biota, resulting in widespread losses for many species across their range, particularly under the high-emission scenario. Similar to other cryptogams, lichens are often overlooked or neglected in conservation plans (Scheidegger and Goward 2002; Nascimbene, Nimis, and Ravera 2013; Gheza et al. 2022). The future projections under different climate change scenarios show very heterogeneous responses of lichens. Indeed, less than half of the species will meet more suitable conditions at high altitudes, and different growth forms and temperature-affinities groups exhibit unique patterns over time. Specifically, fruticose and cryophilic lichens have shown the highest loss in suitability score. Moreover, species upper-range shifts are not as common as theoretically expected. Spatial redistribution is much more complex and the impact of climate change on biodiversity remains largely misunderstood for many neglected taxa. The refugia maps meet the urgent need for appropriate conservation measures for these taxa, providing a step forward to have a better overview of the impact of climate change, and identify the potential areas to focus future protection efforts.

Author Contributions

J.N., L.F. and M.D.M. conceived the basic idea of the manuscript. L.F. and M.C. curated the climate data and compiled the occurrence records. L.F., M.D.M. and L.D.N. performed the analyses. L.F. ran and drafted the initial manuscript. All authors contributed substantially to manuscript drafts and approved the final version.

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Conflicts of Interest

The authors declare no conflicts of interest.

Data Availability Statement

The data that support this study were derived from the following sources: Chelsa (https://chelsa-climate.org/), Copernicus (https://spacedata.copernicus.eu/), GBIF (https://www.gbif.org/), Dolichens (https://italic.units.it/dolichens/), ITALIC 7.0 (https://italic.units.it/). For the proper reproducibility of the analyses, the presence and pseudo-absences table with predictors' values used to perform SDMs is available on this Dryad repository: https://doi.org/10.5061/dryad.ns1rn8q2s.

Peer Review

The peer review history for this article is available at https://www.webofscience.com/api/gateway/wos/peer-review/10.1111/ddi.70079.

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Supporting Information

Additional supporting information can be found online in the Supporting Information section. **Appendix S1:** ddi70079-sup-0001-AppendixS1.xlsx. **Appendix S2:** ddi70079-sup-0002-AppendixS2.docx. **Appendix S3:** ddi70079-sup-0003-AppendixS3.docx.