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Modelling range dynamics of terricolous lichens of the genus *Peltigera* in the Alps under a climate change scenario

Chiara Vallese [a], Juri Nascimbene [a], Paolo Giordani [b], Renato Benesperi [c, *], Gabriele Casazza [d]

[a] *Department of Biological Geological and Environmental Sciences, University of Bologna, Italy*
[b] *Dipartimento di Farmacia (DIFAR), Università di Genova, Italy*
[c] *Dipartimento di Biologia, Università degli Studi di Firenze, Italy*
[d] *Institut Méditerranéen de Biodiversité et d'Ecologie Marine et Continentale Aix Marseille Univ, Avignon Univ, CNRS, IRD, IMBE Technopôle de L'Arbois-Méditerranée, BP 80, 13 545 Aix-en-Provence Cedex 4, France*

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A B S T R A C T

Climate change is expected to strongly impact biodiversity in Alpine ecosystems and species distribution modelling is increasingly used to provide anticipatory information to guide conservation. In this study, (1) we quantified the range loss, range gain, range change and range turnover caused by climate change in the genus *Peltigera* a group of terricolous lichens widespread across the Alps, and then (2) we evaluated the relationships between the predictors of range dynamics and functional traits. Our results indicate moderate range dynamics for species of the genus *Peltigera* across the Alps under a climate change scenario. This would imply a relative stability and resistance of these lichens to climate change that may reflect the local persistence of the species under sub-optimal conditions. Our results also suggest that range dynamics could be associated with functional traits mainly related to water-use strategies and to a trade-off between dispersal and establishment ability. This finding suggests that functional traits may strongly modulate the lichen response to climate change and that species with similar functional traits are prone to similar selective pressures.

1. Introduction

There is an increasing amount of evidences that climate change will impact ecosystems and society considerably in the next decades (IPCC, 2014). Even if the effects are expected in most terrestrial ecosystems (Schmitz et al., 2003; Rands et al., 2010), most predictive models concur that the rate of temperature change caused by increased levels of greenhouse gases in the atmosphere will be particularly impacting both at high latitudes (Holland and Bitz, 2003) and on high elevation environments (Gobiet et al., 2014; Pepin et al., 2015). In the Alps, an annual average increase of 1.5 °C (0.25 °C per decade) is expected in the first half of the 21st century. This rate is expected to accelerate reaching an increase of 3.3 °C (0.36 °C per decade) within the second half of the 21st century. Precipitation is also expected to change, decreasing in summer, particularly in the south of the Alps, and increasing in winter (Heinrich et al., 2013; Gobiet et al., 2014). In addition, global radiation and relative humidity are expected to change causing cascading impacts such as floods, droughts, decreasing snow cover, and other natural hazards (Gobiet et al., 2014).

Apart from direct consequences on human activities in Alpine areas, climate change is also expected to impact Alpine ecosystems that are an irreplaceable reserve of biodiversity, including recognized endemism hotspots (Nagy et al., 2003). As the geographic and local ranges of most plants and animals living in these ecosystems are influenced by climatic factors, any shift in magnitude or variability of climatic factors can impact the Alpine biota considerably (Bellard et al., 2012). In particular, range size reduction (Loarie et al., 2008; Dirnböck et al., 2011; Casazza et al., 2014; Guerrina et al., 2016) and altitudinal shifts (Lenoir et al., 2008; Chen et al., 2011;

* Corresponding author.
E-mail address: renato.benesperi@unifi.it (R. Benesperi).

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Alexander et al., 2017; Dainese et al., 2017; Rumpf et al., 2018) are the most common responses already observed, posing concern for biodiversity conservation and for ecosystem functioning.

Besides observational and long-term monitoring studies, whose potential for tracking climate change impacts on the Alpine biota is irreplaceable (Lamprecht et al., 2018), predictive modelling (e.g. SDM - species distribution models) is increasingly used to forecast the consequences of climate change (Beaumont et al., 2008) providing anticipatory information to guide conservation efforts. However, while this approach is widely used for animals and plants (Thuiller et al., 2005; Parmesan, 2006; Brambilla and Ficetola, 2012; Alexander et al., 2017), its application to poorly detectable taxa is still in its infancy, as in the case of lichens (Ellis, 2019), a complex symbiotic network mainly composed of a fungus (mycobiont) and a photosynthetic partner (photobiont), and also hosting diverse microbial communities (Grube et al., 2009).

With roughly 3000 species, lichens greatly contribute to biodiversity (Nimis et al., 2018) and ecosystem functioning (Zedda and Rambold, 2015) in the Alps. In particular, terricolous lichens that are among the main components of the biological soil crusts (Türk and Gärtner, 2001) are involved in crucial ecosystem processes, including nutrient cycling, soil stabilization, and water dynamics (Elbert et al., 2012). As an example, cyanolichen-dominated soil crusts (i.e. lichens with cyanobacterial photobiont in contrast to chlorolichens that host green algae) are very effective in nitrogen and carbon fixation (Pietrasiak et al., 2013). This is fundamental for triggering ecosystem succession in oligotrophic environments, as for example in periglacial areas (Nascimbene et al., 2017). Similarly to epiphytes (Bässler et al., 2016; Nascimbene and Spitale, 2017), terricolous lichens may be strongly impacted by climate change that is expected to cause community-level effects, such as species loss and compositional shifts (Escolar et al., 2012). These effects are likely to explain range dynamics (i.e., the inter-relationship between range lost and gained) of single species, thus providing a basis for species distribution modelling of these organisms.

The sensitiveness of lichens to climatic factors is mainly related to their poikilohydric nature (Oliver et al., 2000). Their metabolic activity (e.g. photosynthesis) depends on the water content of the thallus which tends to reach an equilibrium with that of the surrounding environment (Insarov and Schroeter, 2002; Green et al., 2008). Thus, the physiology of lichens is closely coupled with ambient temperature and moisture conditions, which influence thallus water saturation and desiccation (Gauslaa, 2014; Merinero et al., 2014). This condition is particularly restrictive for cyanolichens whose photosynthetic activity can be triggered exclusively by liquid water instead of air humidity, as in the case of chlorolichens (Lange et al., 1986). From this perspective, there is increasing awareness on the fact that the response of lichens to climatic factors may be mediated by functional traits mainly related to water-use strategies, photosynthetic performance, and nitrogen fixation (Giordani et al., 2012; Matos et al., 2015). For example, thallus thickness influences the water holding capacity of the species. Thick thalli may need more time than thin thalli to saturate but they are able to store higher amounts of water, thus sustaining their metabolic activity for longer. With decreasing precipitation frequency and the negative effect of warming on air humidity, the water-storage strategy associated with thick thalli may be more favourable than the rapid moisture-uptake strategy associated with thin thalli (Hurtado et al., 2020). On the other hand, under changing climate a trade-off between dispersal and establishment ability may determine range dynamics of the species (Löbel and Rydin, 2010). Lichens may produce both sexual and asexual diaspores (Nash, 2008). The former are expected to be more suitable for long-range dispersal (Ronnås et al., 2017) but imply the availability of a new photobiont and successful re-establishment of the lichen symbiosis. The latter are more suitable for local dispersal and establishment due to the simultaneous occurrence of the symbiotic partners (Scheidegger and Werth, 2009; Werth et al., 2014). Depending on the speed and size of environmental change, asexual diaspores would be more effective in resisting non-optimal conditions and reestablishing and developing viable populations in newly available habitats where a species' climatic suitability is met (Ellis, 2019).

In this study, we (1) quantified range dynamics of a selected genus of terricolous lichens widespread across the Alps, and then (2) we evaluated the potential relationships between the descriptors of range dynamics and some selected functional traits that may reflect the response of lichens to climate. We selected terricolous species in the genus *Peltigera* as a suitable model system since (a) they are cyanolichens (including two tripartite species that also contain green algae), thus functionally relevant components of the biological soil crusts of the Alps and potentially very responsive to changing climate; (b) their distribution spans several elevational belts, including both strictly arctic-alpine species of high elevation ranges and temperate-boreal species mainly related to the montane and subalpine belts, making it possible to account for a gradient of inter-specific sensitivity to climate change; (c) they have strong inter-specific variability of functional traits (e.g. thallus thickness), including contrasting dispersal strategies (sexual and asexual); (d) species occurrences data for these large foliose lichens are relatively abundant and more taxonomically reliable compared to small crustose lichens that are scarcely detectable in the field and to several fruticose lichens (e.g. those in the genus *Cladonia*) that require laboratory techniques and equipment for correct identification. This would allows a robust use for species distribution modelling.

2. Materials and methods

2.1. Study area, species selection and occurrence data

The study area includes the whole Alps, as defined according to the International Unified Orographic Subdivision of the Alpine System (Marazzi, 2005). According to the altitudinal distribution of *Peltigera* in this area (Nimis et al., 2018), the 15 species that rise up to the alpine belt were selected for our modelling analysis (Table 1). Species occurrence data were obtained from the GBIF network (https://www.gbif.org/), from the Information system on the Italian lichens — ITALIC 5.0 (Nimis and Martellos, 2017) and from the personal databases of the authors. Finally, to mitigate pseudo-replication, occurrences of each species were spatially filtered by retaining only one occurrence per grid cell of about 1 × 1 km spatial resolution. A final data set of 33,432 occurrences, ranging from 8214 to 26 occurrences per species (Table 1), was used in the analyses.

2.2. Bioclimatic variables

Nineteen bioclimatic variables representative of the period 1979–2013 were downloaded from CHELSA database website (http://chelsa-climate.org/) at a 30-s (i.e., about 1 km × 1 km) spatial resolution (Karger et al., 2017) for the extent of Europe. These variables combine together temperature and precipitation in order to obtain biologically relevant variables that are assumed to be important for limiting the distribution of lichen species (Nascimbene et al., 2016). To reduce collinearity and to minimize model overfitting, we performed a pairwise Pearson correlation between bioclimatic predictors. We retained four predictors that were not highly correlated ($r \leq |0.70|$): BIO1-Annual Mean Temperature, BIO4-Temperature Seasonality, BIO12-Annual Precipitation and BIO15-Precipitation Seasonality.

Table 1
Species of the genus Peltigera that are recorded in the Alps according to Nimis et al., (2018). For each species the total number of records are shown, along with their functional traits and the range of altitudinal belts where they are usually found. We distinguished the species with only cyanobacteria as photobiont (cyano) from the one with both cyanobacteria and green algae (cyano + algae). We reported values referring to the type of reproductive strategy that is mainly adopted from each species by dividing in sexual (sex) and vegetative (veg) strategy. We also showed two different values of thallus thickness by dividing samples in thick (thick) and thin (thin) thalli. Metabolites, Pruina and Tomentum are reported as presence (x) and absence (−) values. Values refer to Altitudinal belts: Mesomediterranean belt (1), Submediterranean/colline belt (2), Montane belt (3), Subalpine belt (4), Alpine (5) and Nival (6).

Species	Record	Photobiont	Repr.	Metab.	Thickn.	Pruina	Toment.	Belt
•*Peltigera aphthosa*	2827	cyano + algae	sex	x	thick	−	x	3–6
•*Peltigera canina*	5466	cyano	sex	−	thin	−	x	1–5
•*Peltigera didactyla*	2679	cyano	veg	−	thin	−	x	2–6
•*Peltigera elisabethae*	357	cyano	veg	x	thin	x	−	3–5
•*Peltigera kristinssonii*	349	cyano	sex	−	thin	−	x	3–5
•*Peltigera lepidophora*	446	cyano	veg	−	thin	−	x	3–6
Peltigera leucophlebia	2747	cyano + algae	sex	x	thin	−	x	2–5
•*Peltigera malacea*	1330	cyano	sex	x	thick	x	x	3–5
•*Peltigera neckeri*	542	cyano	sex	x	thick	x	−	1–5
•*Peltigera polydactylon*	2054	cyano	sex	x	thick	−	−	2–5
•*Peltigera ponojensis*	121	cyano	sex	−	thin	−	x	2–5
•*Peltigera praetextata*	8214	cyano	veg	−	thin	−	x	1–5
•*Peltigera rufescens*	4471	cyano	sex	−	thick	x	x	1–6
•*Peltigera scabrosa.*	681	cyano	sex	x	thick	−	−	3–5
•*Peltigera venosa*	1122	cyano + algae	veg	x	thick	−	−	2–5

For future conditions (i.e., 2061–2080), we chose two representative concentration pathways representing moderate (RCP 4.5) and extreme (RCP 8.5) possible future emission trajectories and coded according to a possible range of radiative forcing values in the year 2100 relative to preindustrial values (IPCC, 2014) adopted by the Intergovernmental Panel on Climate Change for its fifth Assessment Report (AR5). For the purpose of this work, we discarded the representative concentration pathway representing optimistic possible future emission trajectories (i.e., RCP 2.6) because, under this climate, Mediterranean and Alpine ecosystems are predicted to remain within the climatic variability of the Holocene (Guiot and Cramer, 2016; Fauquette et al., 2018). We selected RCPs projections from five different General Circulation Models (GCM), which represent the physical processes that govern the general circulation of planetary atmosphere or oceans, following the recommendations of Sanderson et al. (2015). In particular, two models (CESM1-CAM5 and CESM1-BGC) were provided by the Community Earth System Model CESM, one model (MIROC5) by the International Centre for Earth Simulation ICES, one model (CMCC-CM) by the Centro Euro-Mediterraneo sui Cambiamenti Climatici and the last one (MP-ESM-MR) by the Max Planck Institute for Meteorology.

2.3. Species distribution models

Species occurrence data and the four selected variables were used to construct distribution models using Package *Biomod2* (Thuiller et al., 2016) implemented in (R Development Core Team, 2008). To account for model-based uncertainties in the modelling process we used four SDM techniques belonging to three different categories of models: regression methods, decision trees methods and machine learning algorithms. In particular, multivariate adaptive regression splines (MARS – Friedman, 1991) and Generalized Mixed Models (GLM – McCullagh and Nelder, 1989) are regression methods, random forest (RF – Breiman, 2001) is a decision trees method and Maxent (Phillips et al., 2006) is a machine learning algorithm.

For each taxon we generated a set of pseudo-absences, setting the number and the method of selection of pseudo-absences according to Barbet-Massin et al. (2012). The split-sample cross-validation was repeated 10 times, using a random subset (30%) of the initial data set. Model performance was evaluated using two different evaluation measures: the area under the curve (AUC; Hanley and McNeil, 1982) of a ROC plot and the true skill statistic (TSS; Allouche et al., 2006). Eventually, because the choice of threshold is critical by increasing or decreasing prediction bias, we transformed continuous suitability maps into binary presence-absence projections using three different thresholds implemented in the R package *PresenceAbsence* (Freeman and Moisen, 2008) for those performing equally or better than others (Liu et al., 2005; Cao et al., 2013): the method based on equal sensitivity and specificity, the method based on maximizing sensitivity and specificity, and the method based on maximizing the distance between the observed ROC plot and the top-left corner (0,1) in a ROC plot.

2.4. Spatial index for distribution under different time periods

The percentage of predicted future range change (RC), in relation to the present-day predicted distribution, was estimated using the formula $RC = 100 \times (G - L)/PR$, where G is the number of grid cells projected to be not suitable under present climate but suitable under future climate, L is the number of grid cells projected to be suitable under present climate but not suitable under future climate and PR is the number of grid cells projected suitable under current climatic scenario. A negative RC value indicates a loss in overall range, whereas a positive value indicates an increase in overall range size. The range turnover (RT) per cell of the climate envelope range was estimated using $RT = 100 \times (L + G)/(PR + G)$. A RT value of 0 indicates no shift in range, whereas a value of 100 indicates a complete range shift when compared with the predicted range under current conditions. The percentage of range gain (RG) was calculated using the formula $RG = (G/PR)$ x 100, the percentage of range loss (RL) was calculated by the formula $RL = (L/PR)$ x100. A Kendall tau correlation coefficient was employed to determine the relationships between the percentage of RL, RG, RC and RT. We also performed a Kruskal-Wallis test in order to test any differences between future scenarios.

2.5. Morpho-functional traits

To understand which functional traits may be more useful to explain the degree of range shift, we considered traits that are potentially implicated, directly or indirectly, in the response of the *Peltigera* species to climatic factors, with particular reference to

management of water and light, and to dispersal capability. Traits may shape current and future distribution of species in different ways. Some traits related to physiological performance of species may affect the tolerance of species to climate determining the climatic space potentially available to species and in turn their distribution. However, traits that determine reduced dispersal capability might hinder the species to establish in climatically suitable locations resulting in narrower climatic and geographical space occupied by the species than expected by climatic tolerance only (Soberon, 2010). Moreover, poor dispersal ability may affect future distribution of species not enabling them to keep pace with future climate change. We took into account the following traits related to physiological tolerance:

- Type of photobiont. Lichens in symbiosis with chlorococcoid algae, but which also have cyanobacteria in specialized structures called cephalodia perform better in dry conditions than lichens in symbiosis with cyanobacteria (Carniel et al., 2016).
- Thickness of the thallus. This characteristic is linked to the water retention capacity of the species: with the same environmental conditions, thicker thalli can maintain more water for a longer period of time than thin thalli (Phinney et al., 2018). Based on quantitative data obtained from Martínez (1999), this trait was applied as a categorical variable which can take two values: i) thick thallus (>300 μm) and ii) thin thallus (<300 μm).
- Presence or absence of pruina. The pruina consists of surface deposits of calcium oxalates which in the lichen thallus play both structural roles in the dehydration-rehydration cycles (Modenesi et al., 2000) and provide protection from solar radiation (Giordani et al., 2003).
- Presence or absence of tomentum. The tomentum has been proposed as an additional strategy for modulating water loss and CO_2 diffusion within the thallus (Snelgar and Green, 1981).
- Presence or absence of secondary metabolites. These substances are synthesized in the cortex and/or in the medulla and are usually involved in photoprotective functions and are related to water potential (Gauslaa and Solhaug, 2004).

We took into account the following traits related to dispersal capability:

- Sexual or vegetative reproductive strategy. Sexual reproduction by ascospores enables species to dispersal for long distances while vegetative reproduction by isidia, or isidia-like structures (e.g. schizidia) only allows for short distance dispersal (Singh et al., 2015). This trait can affect the occupancy of the species' realised climatic niche limiting the climatic and geographical space occupied by the species.

Data on traits were retrieved from Vitikainen (1994); Goward et al. (1995) and Martínez (1999). Principal Component Analysis (PCA) was used to explore range variations according to the future scenarios with respect to the selected morpho-functional traits of the species. Range descriptors were used as active variables and traits as supplementary variables in the PCA. Spearman's correlations between both active and supplementary variables and the PCA dimensions were tested ($p < 0.05$ as reference threshold). PCA was calculated using *FactoMineR* package (Lê et al., 2008) in R environment.

3. Results

Under current climate conditions, model evaluation indices mainly indicated a good model performance for all modelling techniques in all species (Table 2). The highest AUC values ranged from 0.848 to 0.977 and TSS values ranged from 0.612 to 0.892. No statistically significant differences were detected between the different climate change scenarios affecting the range change parameters.

3.1. Range gain and range loss

In general, under future climatic conditions range loss (RL) varied from 0.00% to 41.02% in RCP4.5 scenario and from 0.00% to 61.96% in the RCP 8.5 scenario, suggesting that *Peltigera* species will maintain the majority of their current range (blue shade in Figs. 1 and 2). The highest RL was detected in *Peltigera didactyla*, *P. elisabethae, P. neckeri, P. polydactylon*, and *P. venosa* showing a RL between 16.38% and 41.02% in RCP 4.5 scenarios and between 25.19% and 61.96% in RCP8.5 (Table 3, grey shade in Fig. 1b–f and Fig. 2b–f). The range loss will mainly occur at low elevation in the peripheral parts of the Alps suggesting that in general species will contract their range toward the higher elevations of the mountain chain. The range gain (RG) is generally low, ranging from 0.01% to 18.64% in RCP 4.5 scenario and from 0.01% to 21.51% in RCP 8.5 scenario. The higher values were detected for *Peltigera* in *Peltigera aphthosa*, *P. elisabethae*, *P. kristinssonii*, *P. polydactylon*, and *P. praetextata*, from 4.17% to 18.64% in RCP 4.5 scenarios and from 4.57% to 21.51% in RCP 8.5 scenarios (Table 3). The newly suitable areas are expected to mainly occur at high elevation, in the central part of the Alps (Fig. 1a, c, 2a, 2c).

3.2. Range change

Range change (RC) values were mainly slightly negative, meaning that species are expected to experience a weak decrease in the overall range under both future climate change scenarios (Table 3). In particular, *P. ponojensis* was the only one species with positive values of RC, while *Peltigera didactyla*, *P. elisabethae*, *P. neckeri*, and *P. venosa* had more negative RC values in both scenarios (Table 3). In line with the low RG values, RC (RCP 4.5 scenario Kendal Tau correlation = −0.83; $p < 0.001$; RCP 8.5 scenario Kendal Tau correlation = −0.9; $p < 0.001$) is negatively correlated with RL values.

3.3. Range turnover

Peltigera didactyla, *P. elisabethae*, *P. neckeri, P. polydactylon*, and *P. venosa* showed the highest values of range turnover (RT) in both RCP 4.5 and RCP 8.5 scenarios (Table 3). The Kendall tau correlation coefficient showed that the percentage of RT (4.5 scenario Kendal Tau correlation = 0.95; $p < 0.001$; 8.5 scenario Kendal Tau correlation = 0.9; $p < 0.001$) is positively correlated with the percentage of RL.

3.4. Relationship between range variations and species morpho-functional traits

The first two factors of the PCA represented respectively 76.79% and 23.17% of the total variance (Fig. 3). The two axes were correlated to all descriptors of range variation for both scenarios, and with selected functional traits. Particularly, the first axis was highly and significantly positively correlated with RT ($r = 0.998$; $p < 0.0001$) and RL ($r = 0.986$; $p < 0.0001$), and significantly negatively correlated with RC ($r = -0.931$ for 8.5 scenario, $r = -0.865$ for 4.5 scenario; $p < 0.00001$ in both cases). Species with tomentum were associated with negative values of first axis ($r = -0.469$; $p < 0.05$), and therefore with slightly positive or weakly negative RC values. In contrast, taxa with pruina on the upper cortex were positively associated with first axis ($r = 0.362$; $p < 0.05$), and therefore with high RT and RL values.

Table 2
Evaluation of modelling techniques used for the analysis: Generalized Linear Models (GLM), Multivariate Adaptive Regression Splines (MARS), Maxent (MAX), Random Forest (RF). Statistics given are the mean values for area under the curve (AUC) and the true skill statistic (TSS). Values given in brackets are the associated standard deviations. Accuracy classification for AUC: 1>excellent>0.9>good>0.8>fair>0.7>poor>0.6>fail; accuracy classification for TSS: 1> excellent>0.8>good>0.6>fair>0.4>poor>0.2>fail.

Species	Evaluation	GLM	MARS	MAX	RF
P. aphthosa	AUC	0.896(0.013)	0.872(0.045)	0.913(0.003)	0.970(0.003)
	TSS	0.701(0.024)	0.699(0.104)	0.693(0.015)	0.840(0.009)
P. canina	AUC	0.893(0.011)	0.852(0.048)	0.912(0.005)	0.962(0.004)
	TSS	0.681(0.029)	0.664(0.044)	0.674(0.01)	0.805(0.013)
P. didactyla	AUC	0.864(0.014)	0.867(0.023)	0.892(0.004)	0.963(0.002)
	TSS	0.624(0.025)	0.652(0.045)	0.635(0.014)	0.803(0.012)
P. elisabethae	AUC	0.889(0.011)	0.900(0.035)	0.921(0.012)	0.948(0.011)
	TSS	0.692(0.012)	0.694(0.052)	0.708(0.042)	0.766(0.038)
P. kristinssonii	AUC	0.954(0.025)	0.934(0.078)	0.956(0.023)	0.943(0.034)
	TSS	0.892(0.07)	0.855(0.156)	0.872(0.044)	0.879(0.043)
P. lepidophora	AUC	0.907(0.01)	0.872(0.04)	0.907(0.011)	0.950(0.01)
	TSS	0.728(0.021)	0.692(0.078)	0.700(0.03)	0.798(0.019)
P. leucophlebia	AUC	0.916(0.006)	0.897(0.03)	0.938(0.004)	0.973(0.004)
	TSS	0.752(0.02)	0.740(0.059)	0.765(0.01)	0.852(0.014)
P. malacea	AUC	0.909(0.008)	0.883(0.055)	0.927(0.006)	0.973(0.004)
	TSS	0.729(0.024)	0.701(0.056)	0.734(0.017)	0.848(0.015)
P. neckeri	AUC	0.874(0.011)	0.860(0.05)	0.894(0.009)	0.946(0.014)
	TSS	0.612(0.025)	0.643(0.081)	0.629(0.023)	0.749(0.04)
P. polydactylon	AUC	0.869(0.011)	0.885(0.026)	0.907(0.004)	0.956(0.006)
	TSS	0.642(0.017)	0.676(0.049)	0.684(0.013)	0.791(0.015)
P. ponojensis	AUC	0.848(0.019)	0.853(0.031)	0.856(0.025)	0.907(0.026)
	TSS	0.619(0.04)	0.628(0.08)	0.621(0.07)	0.701(0.047)
P. praetextata	AUC	0.919(0.011)	0.896(0.028)	0.935(0.002)	0.977(0.002)
	TSS	0.747(0.023)	0.724(0.046)	0.731(0.006)	0.85(0.007)
P. rufescens	AUC	0.881(0.011)	0.862(0.028)	0.902(0.005)	0.962(0.003)
	TSS	0.649(0.023)	0.621(0.059)	0.64(0.017)	0.803(0.009)
P. scabrosa	AUC	0.893(0.008)	0.878(0.037)	0.913(0.01)	0.966(0.006)
	TSS	0.737(0.016)	0.719(0.071)	0.711(0.023)	0.839(0.018)
P. venosa	AUC	0.914(0.009)	0.936(0.043)	0.924(0.005)	0.962(0.006)
	TSS	0.722(0.018)	0.797(0.084)	0.726(0.013)	0.807(0.017)

The second axis was positively correlated with RG in both scenarios ($r = 0.808$, $p < 0.001$). Species with vegetative reproduction were associated with positive values of second axis ($r = 0.522$; $p < 0.0001$), and species with thin thalli ($r = -0.553$; $p < 0.0001$) were associated with negative values of second axis, and therefore with low RG.

4. Discussion

Our results indicate moderate range dynamics for the terricolous species of the genus *Peltigera* in the Alps under a climate change scenario. This would imply a relative stability and resistance of these terricolous lichen communities to climate change that may reflect the local persistence (i.e. resistance to extirpation) of the species under sub-optimal conditions (Alexander et al., 2017). However, range loss is expected to occur mainly at low elevation and in peripheral areas of the Alps and to be only partially buffered by range gain at higher elevation, in the inner core of the Alps. This pattern is corroborated by the correlation between RL and both RC and RT, indicating that variations in distribution are expected to be mainly related to species range reduction rather than to the colonization of newly suitable areas. Results also support the view that species behavior, in terms of range dynamics, could be associated with functional traits mainly related to water-use strategies and to a trade-off between dispersal and establishment ability. These groups of traits are respectively directly and indirectly correlated to climatic factors. In climate change scenarios, these features may circumscribe the ability of the species to acclimatize and migrate under altered environmental conditions (Ellis, 2019).

Species with very low range dynamic values are mainly generalists that are currently distributed along a wide elevational gradient, as in the case of *P. praetextata*, *P. canina*, and *P. rufescens*. In contrast, species with more sensitive range dynamics are mainly those with their optimum in the montane belt, as in the case of *P. elisabethae*, *P. neckeri*, and *P. polydactylon*. However, while the former species are expected to buffer range losses in the lower part of the elevational gradient and in the peripheral areas of the Alps with range gain at higher elevations in the inner part of the mountain chain, the two latter species are expected to be poorly compensated in their range losses. Species mainly related to subalpine-alpine belts (e.g. *P. malacea*, *P. aphthosa*, *P. leucophlebia*) have moderate range dynamics and are expected to track their climatic suitability shifting to higher elevations, in the inner part of the Alps. However, among them, two species seem to be prone to high range loss: *P. didactyla* and *P. venosa*. The former is an ephemeral lichen of disturbed mineral soil (Nimis, 2016). It, thus, behaves as a stress-tolerant species that could be overwhelmed by more competitive species that are expanding their range upwards. The latter is mainly restricted to peculiar microhabitat conditions in cold humid sites (Nimis, 2016). It usually forms patchy populations on vertical, humus-rich soil in north exposed niches where it often occurs together with some already rare arctic-alpine lichens such as *Nephroma expallidum*, and *Lobaria linita* (Nascimbene and Caniglia, 2003). Our results are in line with general expectation on plants and animals that there will be a decrease of cryophilic species and an increase of thermophilic species at high altitude (Gottfried et al., 2012; Lamprecht et al., 2018; Rumpf et al., 2018). These processes may be the starting point of a structural modification of high elevation lichen communities.

We found that water use strategies, as well as trade-offs between dispersal and establishment ability were related to range dynamics under both future scenarios, probably because they enable terricolous lichens to resist to extirpation and to buffer range loss with potential range gain. This finding provides a mechanistic backbone to the expected patterns of range dynamics of terricolous lichens in the Alps. The high RL detected in species

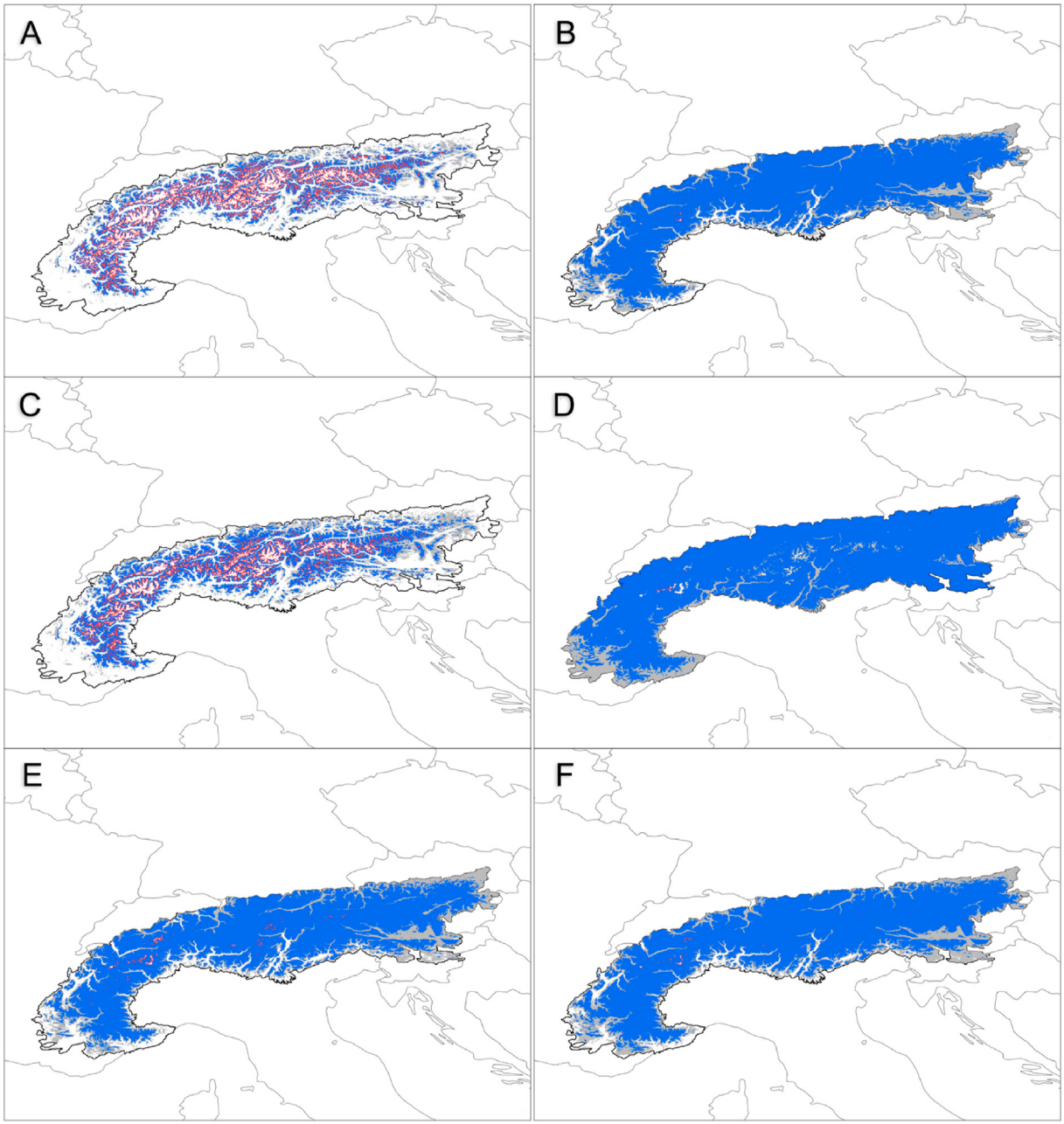


Fig. 1. Range dynamics in 6 different species of *Peltigera* in 4.5 RCP scenario: *P. aphthos*a (A), *P. didactyla* (B), *P. elisabethae* (C), *P. neckeri* (D), *P. polydactylon* (E) and *P. venosa* (F). The grey distribution corresponds to the grinds occupied by the species in present range, the blue represents the overlap between present and future range, the red represents to the grinds that will be occupied by the species in future 4.5 RCP scenario.

producing pruina may be related to the fact that this character may be situation specific, favouring tolerance to provisional oxidative stress induced by light but not favouring species under future climate change. In contrast, the low RL detected in species having a tomentum on the upper cortex may be related to the capacity of tomentum to permanently protect species from dehydration making them more tolerant to the future climate. Moreover, species reproducing vegetatively and with thicker thalli show high RG gain values. On the one hand, thallus thickness may enhance the tolerance of the species to sub-optimal (i.e. warming and drying) conditions. In fact, a thicker thallus makes it possible to retain more water per unit of area, and to better cope with daily and seasonal variations in water availability (Gauslaa, 2014; Hurtado et al., 2020). On the other hand, species that are mainly dispersed by asexual diaspores seem to meet a win-win trade-off in filling their climatic niche, implying that they could simultaneously track their suitable climates through effective local establishment. Despite the fact that asexual propagules are less suitable than sexual ascospores for long-range dispersal (Singh et al., 2015) they are more effective in local recruitment (Scheidegger and Werth, 2009; Nascimbene et al., 2017), enhancing the likelihood of establishment and persistence of new populations. In mountain regions, topographic complexity may result in spatial closeness between optimal and marginal environmental conditions (Soulé, 1973), so that effectiveness in local establishment may be more important than long dispersal capability in filling the potential climatic space. From perspective,

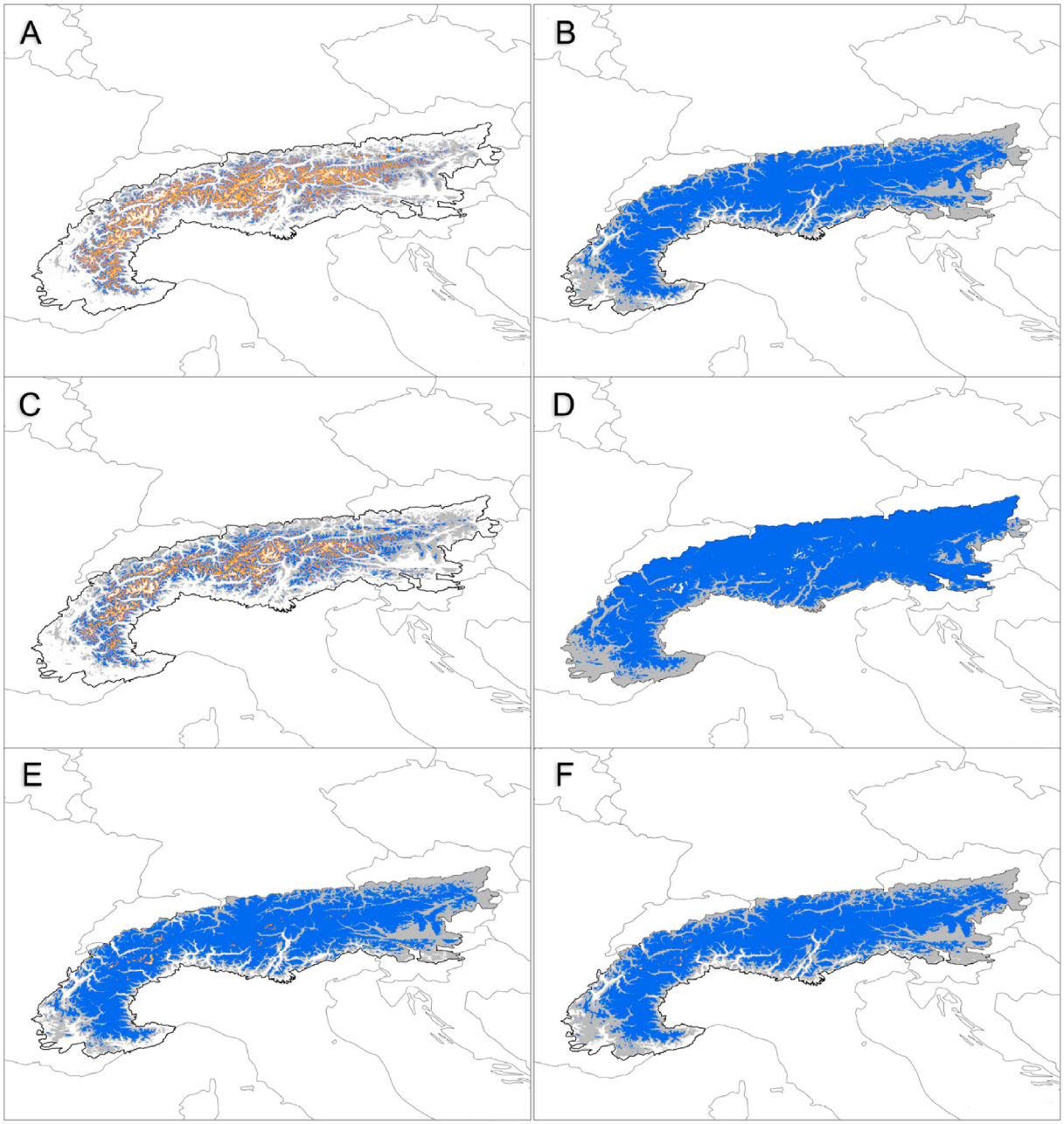


Fig. 2. Range dynamics in 6 species of Peltigera in 8.5 RCP scenario: *P. aphthosa* (A), *P. didactyla* (B), *P. elisabethae* (C), *P. neckeri* (D), *P. polydactylon* (E) and *P. venosa* (F). The grey distribution corresponds to the grinds occupied by the species in present range, the blue represents the overlap between present and future range, the orange represents to the grinds that will be occupied by the species in future 8.5 RCP scenario.

species dispersing by asexual propagules may use a larger portion of their climatic space than species dispersing by ascospores, despite the fact that they are poorer dispersers. Moreover, the high establishment and persistence capacity may allow abundant and viable populations to cope with climate change, both enhancing their local resistance and ensuring moderate spatial shifts that avoid the risk of a mismatch between the mycobiont and the photobiont which would hamper the establishment of the lichen symbiosis. In contrast, sexual reproduction may enhance the capability of lichens to reach distant locations, but may weaken the likelihood of population establishment and persistence due to an inability to persist below a threshold density (Keitt et al., 2001). Even ascospore producing species may fail to disperse over long distances (Morando et al., 2019) and this would represent a further disadvantage for these lichens. The moderate range dynamics that are forecasted by our models may reflect the capability of many species to resist to extirpation in the long term thanks to both effective water storage management and dispersal/establishment strategies. All these findings suggest that the lichen functional traits may strongly modulate the response to climate change, probably because species with similar functional traits are prone to similar selective pressures. These findings suggest that it may be possible to summarize species information into general groups showing recurring patterns of responses to climate change.

Table 3
Percentage of the impacts of climate change on the distribution of 15 species of the genus *Peltigera* for the years 2061–2080 under 4.5 and 8.5 future scenarios. **RC** Percentage of Range change (100 × (meanRG − meanRL)/meanPR), **RG** Percentage of Range gain ((meanRG/meanPR)x100); **RL** Percentage of Range loss ((meanRL/meanPR)x100); **RT** Percentage of Range turnover (100 × (meanRL + meanRG)/(meanPR + meanRG)). Range dynamics were calculated using 5 General Circulation Models (CESM1-CAM5, CESM1-BGC, MIROC5, CMCC-CM and MP-ESM-MR) and two representative concentration pathways (RCP 4.5 and 8.5).

	4.5 future scenario				8.5 future scenario			
Species	%RG	%RL	%RC	%RT	%RG	%RL	%RC	%RT
P. aphthosa	7.45	13.47	−6.02	19.47	10.07	20.21	−10.13	27.51
P. canina	0.03	1.72	−1.68	1.75	0.04	2.38	−2.34	2.41
P. didactyla	0.03	36.23	−36.20	36.25	0.04	46.15	−46.11	46.17
P. elisabethae	18.64	41.02	−22.38	50.29	21.51	61.96	−40.46	68.70
P. kristinssonii	5.33	8.31	−2.98	12.95	4.78	12.41	−7.63	16.40
P. lepidophora	4.19	11.93	−7.74	15.47	4.01	16.24	−12.22	19.47
P. leucophlebia	2.49	14.50	−12.00	16.58	2.61	23.39	−20.78	25.34
P. malacea	0.06	11.63	−11.57	11.68	0.06	19.03	−18.97	19.08
P. neckeri	0.59	25.93	−25.34	26.37	0.58	34.51	−33.93	34.88
P. polydactylon	4.69	16.38	−11.70	20.13	5.47	25.19	−19.71	29.07
P. ponojensis	2.61	1.02	1.59	3.54	2.61	2.21	0.40	4.70
P. praetextata	4.17	6.49	−2.32	10.23	4.57	8.64	−4.07	12.64
P. rufescens	3.67	6.66	−3.00	9.97	4.20	11.58	−7.38	15.14
P. scabrosa	0.06	0.09	−0.03	0.14	0.06	0.14	−0.08	0.19
P. venosa	1.64	30.69	−29.06	31.81	2.11	42.25	−40.13	43.44

5. Conclusions

The application of predictive modelling to forecast the consequences of climate change on terricolous lichens of the Alps proved to be a useful initial approach to create anticipatory information in support of conservation activities devoted to this usually neglected organism group, which nevertheless greatly contributed to biodiversity and ecosystem functioning (Zedda and Rambold, 2015). In particular, coupling species distribution modelling with trait-based analysis provided a promising suggestion to better understand the underlying mechanisms that determine the response of these organisms to climate change.

However, we are aware that our results may fail to exhaustively unravel complex dynamics. We need more significant efforts to develop models that take formally into account various factors. Among others, some gaps to fill are:

- To explore the effect of the microclimate on the suitability of the species, to identify any microrefugia where the species have a higher probability of survival (Lenoir et al., 2017).
- To investigate the effects of climate change on biotic communities as a whole, to inform the species response when biotic interactions within lichen communities, and between terricolous lichens, mosses, and vascular plants, are taken into account (Giordani et al., 2019).

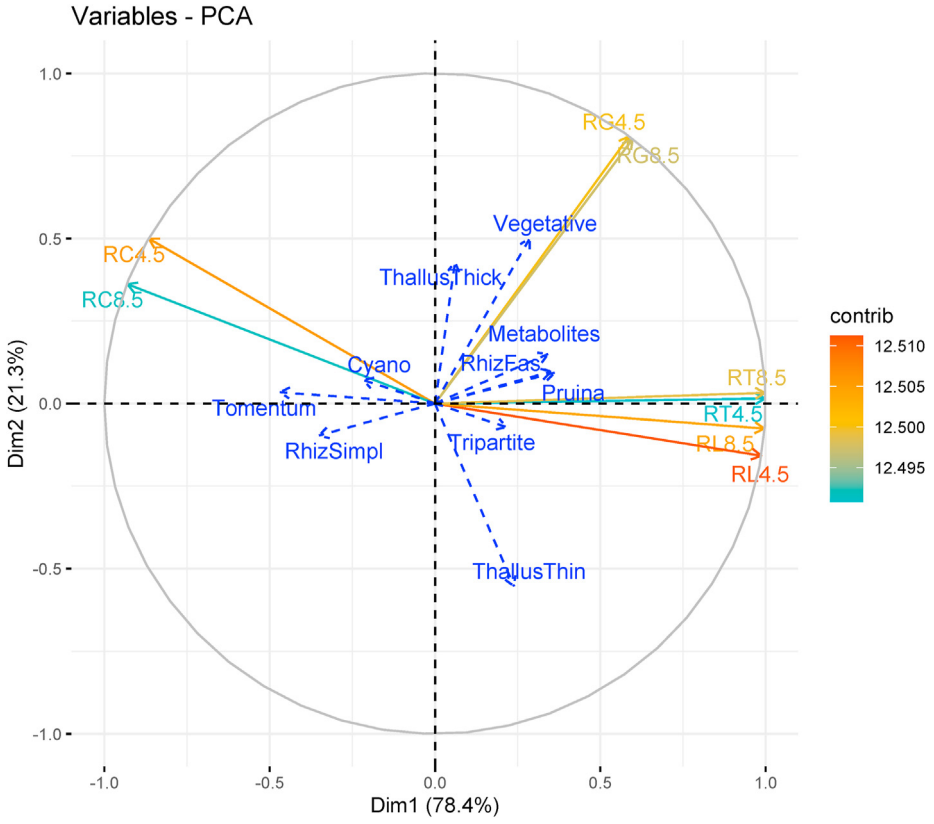


Fig. 3. Representation of the first two factors of a Principal Components Analysis of range variation parameters in relation to morpho-functional traits in *Peltigera* species. Codes refer to range change (RC4.5, RC8.5), range gain (RG4.5, RG8.5), range loss (RL4.5, RL8.5) and range turnover (RT4.5, RT8.5) in future scenarios (RCP4.5 and RCP8.5). The following morpho-functional traits are projected in the dimensional space as supplementary variables: presence of cyanobacteria as photobiont (Cyano), presence of both cyanobacteria and chlorococcoid algae as photobiont (Tripartite), occurrence of structure for vegetative reproduction (Vegetative), occurrence of tomentum (Tomentum) and pruina (Pruina) on the upper surface, species with rhizines with fasciculate (RhizFas) or simple (RhizSimpl) shape, production of secondary metabolites (Metabolites), occurrence of thin (ThallusThin) or thick (ThallusThick) thallus. Contrib represents the percentage contribution of each variable to a given principal component.

- To analyze the intraspecific response of functional traits to environmental drivers to determine the adaptation capacity of species to climate change (Hurtado et al., 2020).

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