

RESEARCH ARTICLE

Divergent responses of alpine bryophytes and lichens to climate change in the Swiss Alps

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Abstract

Questions: The alpine vegetation of the Alps is particularly vulnerable to climate change, as the temperature increase in this region is twice the global average and the available area for new colonisations decreases with increasing elevation. While numerous studies have investigated the response of vascular plants to a warming climate in the alpine belt, only a handful have investigated that of cryptogams in the European Alps. Based on a 21-year monitoring project, we assessed the effects of climate change on cryptogams along elevation, from the treeline to the subnival belt.

Location: Four GLORIA summits in Valais (Switzerland).

Methods: Between 2001 and 2022, terricolous lichens and bryophytes (from 2008) were inventoried in 52 1-m² plots distributed across four summits: 2360m a.s.l. (tree-line), 2550m (lower alpine), 2990m (upper alpine) and 3210m (subnival). Changes in species cover and richness were analysed using generalised linear mixed-effects model (GLMMs).

Results: For bryophytes, total cover remained stable overall. However, six species declined significantly between 2008 and 2022, and the species richness decreased after 2015. For terricolous lichens, total cover significantly increased on the lower alpine summit, while species richness increased on the upper alpine and subnival summits.

Conclusions: Bryophytes have probably suffered from the increasingly dry conditions, with a succession of very warm and dry summers over the last decades. Terricolous lichens have taken advantage of the warmer conditions to increase their cover on the lower alpine summit, and new species have colonised the upper summits. However, as they compete with vascular plants for soil and light, they may suffer from shrub and tree encroachment in the future and will be limited upwards by the rarity of developed soils. The large topo-climatic gradient (850m) and the length of the time series suggest that similar trends are likely to be more widespread across the Alps.

KEYWORDS

bryophytes, climate change, drought, European Alps, GLORIA, lichens, monitoring, permanent plots, Switzerland, temperature

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1 | INTRODUCTION

Mountain regions have been clearly identified as biodiversity hotspots (Rahbek et al., 2019), as a consequence of their diverse and constraining topo-climatic conditions and Quaternary climate oscillations (Körner, 2004; Theodoridis et al., 2016). As a result, high-elevation regions typically host a large number and a high proportion of endemic plant species (Cowling & Samways, 1995; Hobohm, 2014). However, these ecosystems are particularly exposed to the detrimental effects of ongoing warming (e.g., Theurillat & Guisan, 2001; Rixen & Wipf, 2017), which could lead to a significant loss of global diversity in the future (Engler et al., 2011).

Since the end of the 19th century, temperatures have already risen by 1.1 K in Europe, and by more than 2 K in Switzerland, and are expected to rise further in the course of the 21st century (Bednar-Friedl et al., 2022; Fischer et al., 2022). In Switzerland, the mean summer temperatures in 1991–2020 were 1.49 K warmer than in 1961–1990. Simultaneously, an increase in extreme weather events has been observed. For example, six major heat waves (in 2003, 2007, 2015, 2018, 2019 and 2022) have affected the European Alps in the last 20 years (Russo et al., 2015; MétéoSuisse, 2023).

This warming affects vascular plants in different ways. With an earlier snowmelt (Vorkauf, Marty, et al., 2021b), alpine plants tend to start their development accordingly, with the exception of those that depend on photoperiodism (e.g. Vitasse et al., 2017; Vorkauf, Kahmen, et al., 2021a). Improved conditions for species that are mainly limited by temperature and snow cover have led to an upward shift in distribution ranges (e.g., Matteodo et al., 2013; Winkler et al., 2016; Steinbauer et al., 2018) and a general greening of the Alps above the treeline (Choler et al., 2021; Rumpf et al., 2022). This redistribution of species, and especially the arrival of tall subalpine plants in the short alpine grasslands (Matteodo et al., 2013), poses a threat to the highly specialised alpine and nival plant species and lichens (Britton et al., 2009; Kulonen et al., 2018). In addition, as a result of the earlier snowmelt (Vorkauf, Marty, et al., 2021b), the water available for plant growth in spring and summer is potentially decreasing (Matteodo et al., 2016).

Cryptogams are involved in a wide range of ecosystem functions and services, such as atmospheric nitrogen and carbon fixation (Deane-Coe & Stanton, 2017) and water retention (Hallingbäck & Hodgetts, 2000). As some of the first organisms to colonise rocky surfaces, bryophytes and lichens initiate soil formation and play a role in its stabilisation (Chen et al., 2000; Hallingbäck & Hodgetts, 2000), contributing strongly to the creation of a substrate on which vascular plants can later colonise. In alpine belt, bryophytes and fruticose lichens are facilitating plant growth by buffering soil temperature extremes and by retaining soil moisture (Jespersen, 2013; Jaroszynska et al., 2023). Both bryophytes and lichens are also an important food source for arthropods, earthworms and gastropods and, at least in boreal regions, for ungulates during winter, in the absence of other fodder (Longton, 1992). In addition, cryptogams are useful bioindicators of air and water quality (Hallingbäck & Hodgetts, 2000), including in alpine environments (Xiao et al., 2021).

Despite their importance and particular abundance in the alpine belt, the response of bryophytes and lichens to climate change has rarely been studied, and mostly in northern Europe and the Arctic. According to Asplund et al. (2022), poikilohydric bryophytes and lichens perceive environmental conditions differently from homeohydric vascular plants because they differ in their water economy and nutrient acquisition strategies. Monitoring and experimental studies have observed a decrease in lichens and/or bryophytes, often associated with an increase in graminoid or shrub cover (Walker et al., 2006; Michelsen et al., 2011; Elmendorf et al., 2012; Hagenberg et al., 2022). Surprisingly, results have varied widely in relation to other ecological factors, especially soil moisture (Cornelissen et al., 2001; Alatalo et al., 2017): in some cases, there was a decrease in lichens but an increase in bryophytes (Vanneste et al., 2017), while in other cases the opposite was true (Molau & Alatalo, 1998). Some experiments have concluded that lichen regression was particularly significant when the temperature increase was combined with elevated nitrogen input (Molau & Alatalo, 1998; Klanderud, 2008). Only few studies on cryptogams and climate change have been published for the Alps: Hohenwallner et al. (2011) listed nine snowbed bryophytes that can be used as indicators of snow cover decrease, and Bergamini et al. (2009) observed a 222 m elevational shift upslope for cryophilous bryophytes.

The European project GLORIA (Global Observation Research Initiative in Alpine Environments; Grabherr et al., 2001) aims to monitor plant species composition under climate change by conducting long-term observations on permanent plots in alpine environments. Ideally, each study site includes four summits in the same mountain range that are distributed from the treeline ecocline to the limits of vascular plant life in the nival belt. This project, initiated in 2001 in Europe, was later extended to all the other continents (www.gloria.ac.at). Although cryptogams are not part of the mandatory monitoring programme, they are included in some of the boreal and Arctic sites (e.g., Michelsen et al., 2011; Vanneste et al., 2017; Hagenberg et al., 2022) and in one of the three Swiss sites (Vittoz et al., 2010).

The aim of this study is to determine the response of bryophytes and lichens to climate change in the Swiss Alps over the last two decades. Our hypotheses are: (a) bryophyte and lichen cover will be negatively affected by increasing vascular plant cover; (b) changes in community composition will be more important around the treeline and in the lower alpine belt than in the upper alpine and subnival belts, because of the strong decrease in snow cover and the upward shift of the treeline.

2 | METHODS

2.1 | Study site and plant inventories

The four summits of the GLORIA site in Valais (Switzerland) are (Figure 1): La Ly (LAL, 2360 m a.s.l.; approximately at the treeline in the 1990s), Mont Brûlé (BRU, 2550 m; lower alpine), Pointe du Parc (PAR, 2990 m; upper alpine, approximately at the grassline;

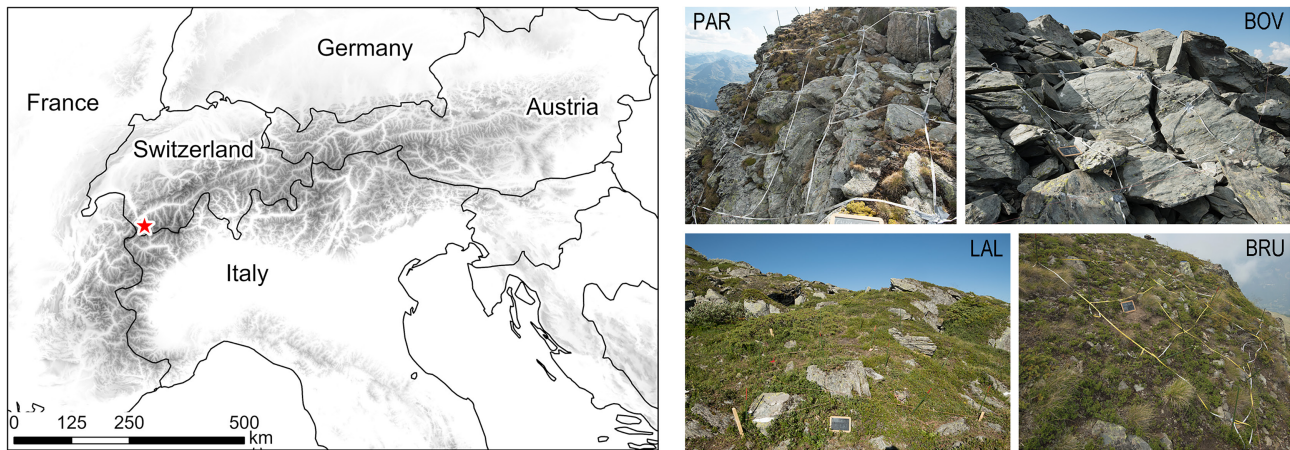


FIGURE 1 Location of the four GLORIA summits (red star) in the Swiss Alps (46.01°N, 7.23°E). On the right, photographs of the four eastern 3 × 3 m quadrats in 2022: LAL, La Ly, 2360m; BRU, Mont Brûlé, 2550m; PAR, Pointe du Parc, 2990m; BOV, Pointe de Boveire, 3210m. In each quadrat, the four 1-m² plots at the corners were inventoried.

Bürli et al., 2021) and Pointe de Boveire (BOV, 3210m; subnival). These summits lie roughly in an equilateral triangle with sides of 4 km, on gneiss (largely dominated by siliceous minerals, with rare calcium-rich veins). LAL and BRU were once extensively grazed by cattle but have been abandoned for many decades. Chamois or ibex tracks (drops or grazing) were very rarely observed during GLORIA surveys.

The sampling methodology followed the GLORIA field manual (Pauli et al., 2015), with surveys conducted every seven years (2001, 2008, 2015 and 2022; bryophytes from 2008). Four 3 × 3 m quadrats were established on each summit, facing each of the four cardinal points and with the lower limit lying 5 m below the summit. Each quadrat was divided into nine 1 × 1 m plots, with the plots at the four corners inventoried (Appendix S1). A total of 52 plots were inventoried: the southern and western quadrats on PAR and the western quadrat on BOV were left out, because the terrain was too steep and unstable. The aspect of each plot was noted in terms of the cardinal direction (N, NNW, NW, WNW, etc.; Appendix S2). The total cover of vascular plants, bryophytes, lichens, rocks, litter and bare ground was visually estimated as a percentage of the plot area (Appendix S3), together with the cover of each individual species. All bryophyte species were included, including those growing on rock, whereas only lichens growing on soil (terricolous lichens) were included. As bryophyte and lichen cover were estimated together in 2001 (cryptogam cover), total lichen cover and total bryophyte cover were calculated by adding the cover of each individual species. The nomenclature follows Swissbryophytes (2023; <https://www.swissbryophytes.ch>) for bryophytes, and Nimis et al. (2018) for lichens.

2.2 | Topo-climatic variables

To derive climatic variables, monthly temperature and precipitation records for 1995–2022 from 112 weather stations of the

MeteoSwiss network were normalised to 0 m a.s.l., using the lapse rates of the linear regressions to model the relationships between either temperature or precipitation as a function of elevation in a digital elevation model (DEM) of the Valais (monthly temperature or monthly sum of precipitation vs elevation), with a resolution of 25 m (DHM25; SwissTopo; <https://www.swisstopo.admin.ch/en/height-model-dhm25>). The residuals of the linear models were interpolated to the wider region of Valais to avoid edge effects around the GLORIA summits, by relying on inverse distance-weighted interpolation (IDW; Randin et al., 2009) using the function 'gstat()' of the *gstat* R package (Pebesma, 2004) and the function 'interpolate()' of the *raster* package (Hijmans et al., 2023), and then added to the normalised values of either temperature or precipitation at 0 m a.s.l. (regression intercepts). Finally, the spatially normalised and interpolated values of temperature and precipitation (representing regression intercepts locally adjusted by the interpolated residuals) were re-projected to the actual elevation of the landscape using the 25-m DEM.

Monthly potential evapotranspiration (ETp) was calculated using the formula of Turc (1961), taking into account the daily global solar radiation per month. The water balance during the growing season (June–September) was calculated as the difference between precipitation gains and ETp losses. Finally, the pluri-annual means (seven years) of temperature and water balance, calculated for each 25-m pixel containing a quadrat of four plots, were used in analyses (1995–2001 for the 2001-survey; 2002–2008 for the 2008-survey, 2009–2015 for the 2015-survey, 2016–2022 for the 2022-survey).

2.3 | Effect of topo-climatic, abiotic and biotic factors on cryptogam cover

The influence of topo-climate on total bryophyte and lichen cover was first analysed using generalised linear mixed-effects models

(GLMMs) with a logistic link function and a binomial error distribution. As mean temperature and water balance in the growing season were negatively correlated, they were tested separately as fixed-effect variables, with plot ID number as a random intercept in the GLMMs.

The same GLMMs were used to study separately the effect of plot characteristics on the total bryophyte and lichen cover, respectively. Each characteristic was individually added to the model as a fixed effect, with plant litter, rock and bare ground cover as abiotic factors, and the vascular plant cover and its squared value (to evaluate a potential non-linear response curve) as biotic factors. In addition, the total lichen or bryophyte cover and their squared values were also added as fixed effects in the bryophyte and lichen cover models, respectively.

2.4 | Changes in total cover over time

Generalised linear mixed-effects models were again used to analyse changes in bryophyte, lichen and vascular plant cover over time in individual plots. Plot ID was used as the random intercept, while summit elevation was maintained as a fixed effect. However, elevation was added as an interaction with time (elevation \times year) to highlight the potential differences in cryptogam cover variation between the four summits over the years. All GLMMs testing changes in cryptogam and vascular plant cover were calibrated using the 'glmer()' function of the *lme4* R package (Bates et al., 2015).

Non-metric multidimensional scaling (NMDS) was used to visualise the changes at the community level. The 'metaMDS()' function of the *vegan* R package was used on Bray–Curtis dissimilarity matrices, after logarithmic transformation of species cover. Analyses were performed separately for bryophytes and lichens, firstly on the whole data set and secondly by summit. The coordinates of the plots along the first two axes were correlated with topo-climatic variables using the 'envfit()' function, followed by 999 permutations to calculate *p*-values.

2.5 | Changes in cryptogam cover at the species level

Only species occurring in at least 10% of all inventories (16 out of 156 inventories for bryophytes; 21 out of 208 for lichens) were retained to assess changes at the species level. If a species was absent from a plot in one of the surveys and present in the same plot in another survey, the absence was assigned a cover of 0%. Similar to changes in total cover, changes in species cover were tested using GLMMs with a logistic link function and a quasi-binomial error distribution. Temperature and growing-season water balance were tested separately as fixed-effect variables with plot ID as the random intercept in GLMMs. The function 'glmPQL()' from the R *MASS* package (Venables & Ripley, 2002) was used to calibrate the GLMMs.

2.6 | Changes in species richness over time and effect of topo-climate

We used GLMMs to analyse changes in bryophyte and lichen species richness over time in plots. The variable plot ID was used as a random intercept term while summit elevation and time, including their interaction effect (elevation \times year) were included as fixed effects in the model formula. Species richness was similarly evaluated in relation to mean temperature and water balance during the growing season. GLMMs were calibrated with a log link function and a Poisson error distribution using the 'glmer()' in the *lme4* R package.

2.7 | Ecological indicator values

Ecological indicator values for temperature and moisture were extracted from van Zuijlen et al. (2023) for bryophytes and mostly from Nimis (2023) for lichens, with complements from other sources (see Appendix S13) for missing values. GLMMs, calibrated with a Poisson distribution, were used to analyse the weighted mean indicator values over time in plots, with plot ID as a random intercept and time as a fixed effect.

All statistical analyses were performed using R 4.2.1 (R Development Core Team, 2022).

3 | RESULTS

3.1 | Species identification and selection

A total of 78 bryophyte taxa (Appendix S4) and 93 lichen taxa (Appendix S5) were identified in the 52 plots. More specifically, 62 different bryophyte taxa were found in 2008, 63 in 2015 and only 55 in 2022. For lichens, the number of taxa observed increased from 29 in 2001, to 52 in 2008, 68 in 2015, and 74 in 2022. All species of the genus *Lepraria* were excluded from the analyses, due to the high risk of misidentification (they cannot be identified with a high confidence in the field).

3.2 | Effect of abiotic and biotic factors on total cryptogam cover

Mean growing-season temperature increased significantly after 1990, with a trend between 0.51K/decade on LAL and 0.63K/decade on BOV. Mean growing-season water balance decreased significantly after 1990, with a trend between 60.1mm/decade on LAL and 95.0mm/decade on BOV (Appendix S6). This decrease is particularly evident after 2007. On the lower summits (LAL, BRU) negative values (higher potential evapotranspiration than precipitation) were recorded in the 2003, 2009, 2018, 2019 and 2022 growing seasons.

Although total bryophyte cover was higher on LAL than on the other summits (Figure 2a), it was globally not related to mean

growing-season temperature but positively to growing-season water balance (Figure 3a; Appendix S7). This means that the total bryophyte cover decreases towards drier conditions. Furthermore, total bryophyte cover was related to the quadratic term of vascular plant cover and negatively related to lichen and litter cover (Figure 3a; Appendix S7).

Lichens showed large differences in total cover between summits, with a maximum cover on the lower alpine summit (BRU) and a significant decrease towards the upper summits (Figure 2b). This corresponds to a significant relationship with mean growing-season temperature (Figure 3b; Appendix S7). Litter, rocks and bare soil had a significant and negative effect on lichen cover. Both vascular plant and bryophyte covers had a significant effect on lichen cover, with a negative quadratic coefficient for vascular plant cover and a negative linear coefficient for bryophyte cover.

3.3 | Changes in total cover over time

Total bryophyte cover did not change significantly between the three inventories ($p=0.064$; Figure 2a; Appendix S8), and the differences between summits remained stable. Conversely, the total lichen cover increased significantly over time ($p<0.0001$), but differently between summits ($p<0.0001$ for interaction; Figure 2b; Appendix S8): their cover increased on BRU while remaining stable on the other three summits.

Vascular plant cover decreased with elevation ($p<0.0001$) and time ($p=0.044$), without interaction effect (same decrease in time on each summit; Figure 2c; Appendix S8).

The NMDS with the complete bryophyte data set showed a stable composition over time. Similarly, the communities of the two lower summits (LAL, BRU) showed no trend. Conversely, the bryophyte communities of the upper summits (PAR, BOV) showed a directional shift corresponding to increasing mean temperature and decreasing water balance, although not significant (Appendix S9).

According to NMDS, the lichen communities shifted slightly towards the upper summits, especially between 2001 and 2008 (Appendix S10). Separated by summit, the communities on LAL were

stable over time but the 2022 inventory on BRU was clearly different from that in the previous years, with a shift corresponding to increasing mean temperatures and decreasing water balance values. Similarly, lichen communities on PAR and BOV showed an important directional shift, both in parallel with increasing mean temperatures (Appendix S10).

3.4 | Changes at the species level

Of the 18 retained bryophyte species, six species showed a significant decrease in cover over time: *Barbilophozia hatcheri*, *B. lycopodioides*, *Dicranum scoparium*, *Hymenoloma compactum*, *Polytrichum alpinum* and *P. juniperinum* (Figure 4). All of them, except *B. lycopodioides*, had a cover negatively related to the growing-season mean temperature and all, except *P. alpinum*, had a positive relationship to growing-season water balance. However, three of them (*B. lycopodioides*, *H. compactum*, *P. juniperinum*) had higher covers in 2015 than in 2008, possibly reflecting natural fluctuations. Conversely, *Pohlia nutans* had a small increase in cover between 2008 and 2022, and its cover was negatively related to growing-season water balance (Figure 4; Appendix S11).

Six out of the 21 lichen species showed significant changes in cover over time (Figure 5): *Cladonia ecmocyna*, *Cladonia macroceras* and *Cladonia macrophyllodes* decreased, whereas *Candelariella aggregata*, *Cladonia coccifera s.l.* and *Cladonia pyxidata* increased. The decreasing *Cl. macrophyllodes* had a cover negatively related to mean temperature and *Cl. macrophyllodes* and *Cl. ecmocyna* were positively related to growing-season water balance. Conversely, the cover of the three increasing species was positively related to mean temperature (only without Bonferroni correction for *Cl. pyxidata*) and negatively related to water balance (Appendix S12).

3.5 | Species richness

Bryophyte species richness decreased with elevation ($p=0.033$), although not regularly, with PAR being the richest summit and BOV

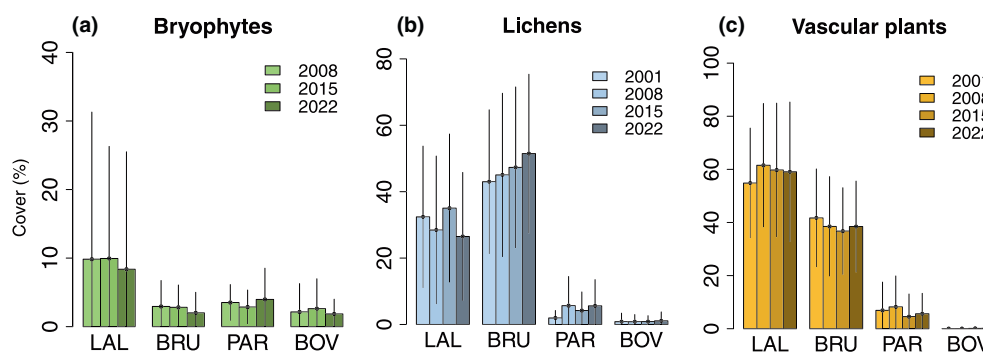


FIGURE 2 Bar plots of the mean total cryptogam and vascular plant cover for each year and summit, with error bars: (a) bryophytes, (b) lichens and (c) vascular plants. According to GLMMs, bryophyte cover was stable ($p=0.064$), lichen cover increased ($p<0.0001$) and vascular plant cover decreased ($p=0.044$) with time. See Figure 1 for summit abbreviations.

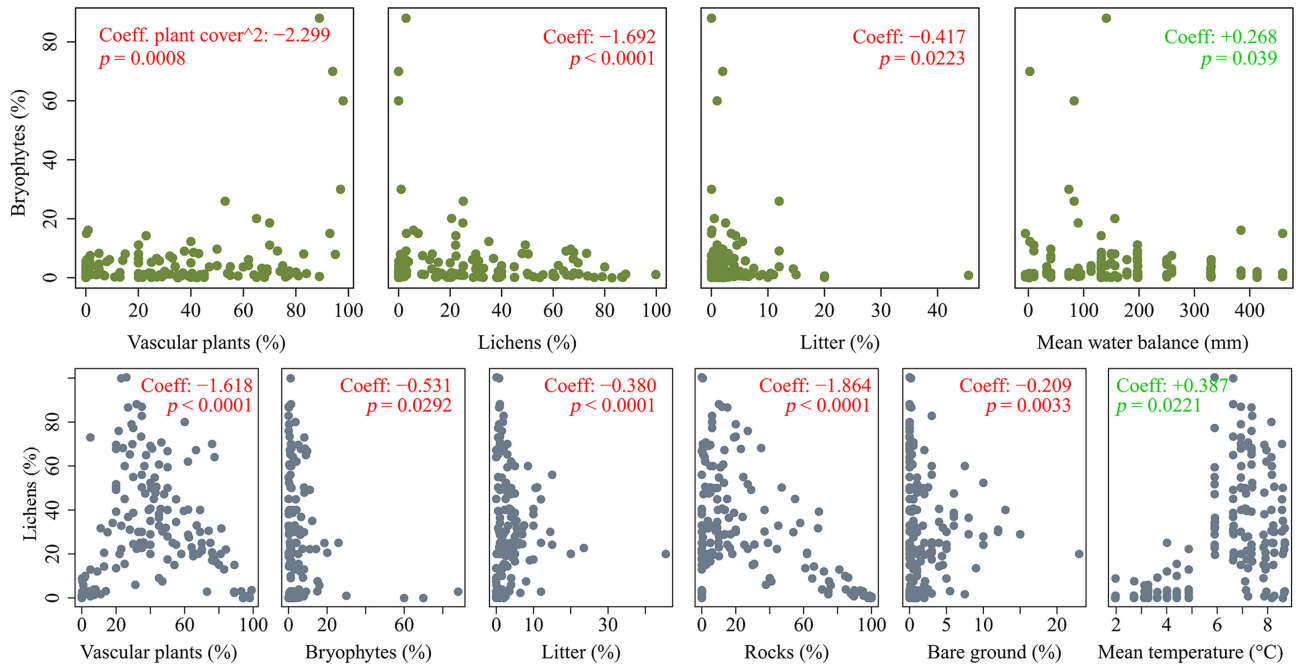


FIGURE 3 Significant relationships between bryophyte cover (upper row) and lichen cover (lower row) with environmental predictors (see Appendix S7 for supplementary graphs). Coefficients and p -values from GLMMs are shown in the graphs: negative relationships are in red and positive ones in green.

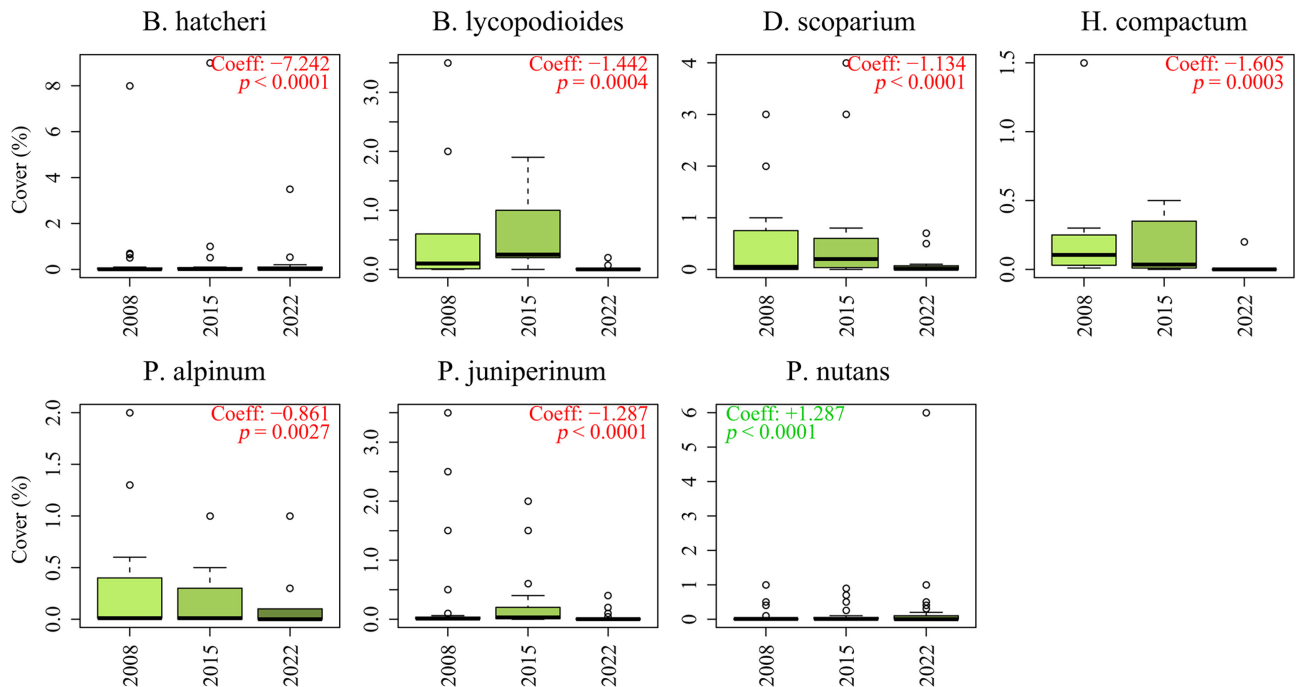


FIGURE 4 Distribution of cover of *Barbilophozia hatcheri*, *Barbilophozia lycopodioides*, *Dicranum scoparium*, *Himenoloma compactum*, *Polytrichum alpinum*, *Polytrichum juniperinum* and *Pohlia nutans* in the plots for the three surveys. The box plots are bounded by the first and third quartiles, the black line is the median and the dots correspond to outliers. Coefficients and p -values from GLMMs are shown in the graphs: negative relations are in red and positive relations in green.

the poorest. Species richness decreased over time ($p=0.0016$), especially between 2015 and 2022, but without differences between summits (Figure 6a; Appendix S13), and was not related to the topoclimatic variables. The mean decrease by plot was $18.2 \pm 37.7\%$.

Similarly, lichen richness decreased with elevation ($p < 0.0001$), with BRU being the richest summit and BOV being particularly poor compared to the other summits (Figure 6b). Lichen richness increased over time ($p < 0.0001$), particularly on the two upper

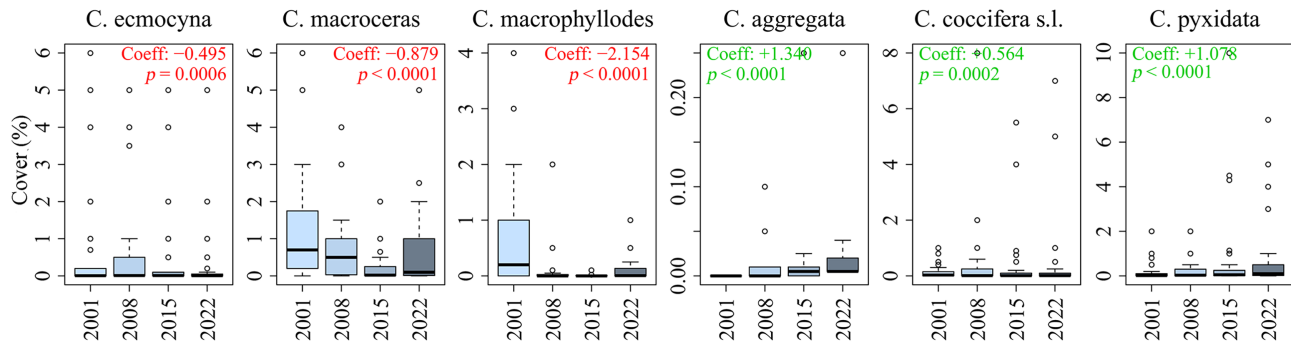


FIGURE 5 Distribution of cover of *Cladonia ecmocyna*, *Cladonia macroceras*, *Cladonia macrophyllodes*, *Candelariella aggregata*, *Cladonia coccifera s.l.* and *Cladonia pyxidata* in the plots for the four surveys. Box plots as in Figure 4.

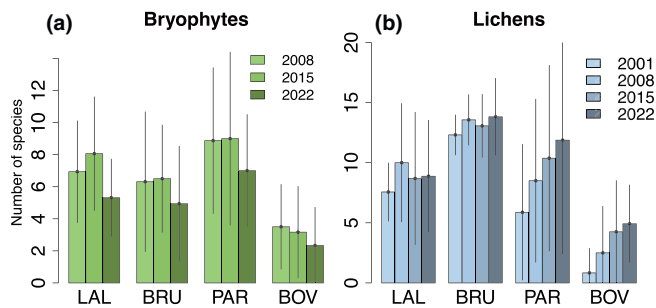


FIGURE 6 Distribution of the species richness on the four summits between the first and last surveys for bryophytes (a; 2008–2022) and lichens (b; 2001–2022). According to GLMMs, bryophyte species richness decreased ($p=0.0016$) and lichen species richness increased ($p<0.0001$) over time. Summit abbreviations as in Figure 2.

summits, with the richness of PAR exceeding that of LAL starting from 2015 onwards and approaching that of BRU, the richest summit (Appendix S13). Species richness per plots increased on average, by $13.3 \pm 42.8\%$ on the two lower summits and by $168 \pm 165\%$ on the two upper summits. On these last summits, 10 empty plots in 2001 counted 2–6 species in 2022. Lichen richness was positively related to mean temperature and negatively related to growing-season water balance ($p<0.0001$).

3.6 | Ecological indicator values

The mean ecological indicator values for temperature for bryophytes were stable over time, whereas the moisture values decreased significantly ($p\text{-value}<0.0001$). The temperature values for lichens increased ($p\text{-value}=0.0087$) but the moisture values were stable (Appendix S14).

4 | DISCUSSION

In line with the observed ongoing warming trends in Europe and in the Alps (OFEV, 2020; IPCC, 2023), the mean temperature at the

summits has risen sharply in recent decades, by 1–1.3K since the start of the GLORIA monitoring in 2001. These warmer temperatures lead to a higher potential evapotranspiration. This has been accompanied by increasingly long, dry summer periods (Ionita & Nagavciuc, 2021) resulting in negative values of the growing-season water balance up to 2550 m. In addition, warmer winters and springs are causing earlier snowmelt (Vorkauf, Marty, et al., 2021b), which is likely to reduce the amount of water available in soils during the summer.

4.1 | Cryptogam cover and vascular plant cover

We hypothesised that the cryptogam cover would be negatively affected by the increasing vascular plant cover. However, at the spatial scale of our study, vascular plant cover decreased slightly between 2001 and 2022 on the summits considered. This may appear to contrast with the general greening observed in the Alps (Rumpf et al., 2022). However, greening in the Alps observed at the landscape scale was far from uniform, occurring mainly in rocky, north-facing habitats (Carlson et al., 2017; Choler et al., 2021). Therefore, a decrease in vegetation cover at 1-m resolution is not inconsistent with the observed greening at a coarser resolution. Furthermore, our area is located in a dry inner valley of the Alps, where vascular plants may have suffered more from the dry conditions during the heat spells (Pauli et al., 2012) than they benefited from the warmer conditions.

Bryophyte cover on these summits depends on several factors: it is positively related to water balance, but not to mean temperature, resulting in weak differences in cover between summits; it is related to the quadratic term of vascular plant cover; and it is negatively influenced by lichen and litter cover. This low contrasting distribution and stability of bryophyte cover is probably due to the fact that they are poikylhydic plants, so their cover is related to water balance, not to temperature. Moreover, there is a high diversity of ecological preferences between species relative to moisture and light (Glime, 2017). Some are heliophilous species on rocks, tolerating desiccation, others are forest species, growing in the shade of chamaephytes (e.g., *Juniperus communis* subsp. *alpina* Čelak.,

Vaccinium spp.), where they can reach cover above 30%. Some occupy the narrow cracks or small holes under rocks, so that they occur in microhabitats unaffected by the measured plot characteristics. Consequently, such ecological diversity and small-scale variation may be difficult to capture in models.

In the alpine belt of the Alps, rainfall is common and years with negative water balance during the growing season were probably exceptional in the past centuries. Therefore, the communities are mainly composed by hygrophilous species and species with limited tolerance to desiccation (e.g., liverworts) that can be critically affected by the speed and intensity of the recent drying events (Vitt et al., 2014; Glime, 2017). The negative relationship with lichen cover may be due to direct competition between the two cryptogram groups for soil (many *Cladonia* species are taller than bryophytes, *Peltigera* spp. partially colonise bryophyte cushions). A non-causal relationship may also partly explain this trend, as the highest bryophyte cover occurs under dense vascular plants, which are inappropriate sites for lichens.

Overall, lichen cover was positively related to temperature, but negatively related to rock, litter, bare ground and bryophyte cover, and followed a unimodal response to vascular plant cover. As only the terricolous lichens were inventoried, a relationship with rock cover would be expected, as their presence is soil-dependent. The availability of soil, or other fine substrate, is severely limited above the upper limit of alpine grasslands (Bürli et al., 2021). In fact, vascular plants, especially graminoids, are essential in high mountains for soil formation because they trap fine aeolian sediments (Küfmann, 2003), retain fine particles released by rock alteration and contribute to soil formation through their litter (Schröter, 1926). Therefore, the low cover of vascular plants in the nival belt results in the absence or scarcity of soils and, consequently, of terricolous lichens. However, the two groups compete for soil and light (Cornelissen et al., 2001; Bruun et al., 2006). Thus, lichens occupy the soil surface when vascular plants are limited by another environmental factor, such as the harsh conditions of high mountains. Conversely, when conditions are optimal for plants, their larger size and density limit lichen growth (Cornelissen et al., 2001; Bruun et al., 2006).

Lichens had their highest cover on the lower alpine summit (BRU). At 2550m, the conditions are not as harsh as on higher summits, where both vascular plants and lichens have drastically lower cover. However, in addition to a shorter growing season and colder temperatures than at the treeline (LAL, 2360m), the conditions on BRU are very windy, due to its position in the landscape. Such conditions reduce competition from vascular plants, especially chamaephytes (Cornelissen et al., 2001), and may explain the significantly higher lichen cover. In fact, due to poikylhydroly, lichens can desiccate and have a lower threshold for photosynthesis (Kappen et al., 1996; Körner, 2021). They are therefore more tolerant of the harsh, alpine-nival conditions than vascular plants. Over the last two decades, lichens may have taken advantage of the warmer temperatures, whereas drought may have inhibited vascular plant growth

(small, significant decrease in cover) and limit bryophytes (no change in cover).

Taking these factors into account, the decrease in lichen cover towards the higher summits was probably due to the cold conditions in the nival belt (Scheidegger, 2021) and to the scarcity of developed soil. The negative relationships with bare ground and litter cover were certainly an artefact of the survey method because these elements are only recorded when visible, that is, not covered by something taller. Therefore, bare ground or litter cover obviously increase when plants and cryptogams decrease, and vice versa.

4.2 | Community composition and elevation

We hypothesised that changes in community composition were more important around the treeline and in the lower alpine belt than in the upper alpine and subnival belts. However, bryophyte and lichen communities evolved differently along the elevation gradient.

The observed stability of the total bryophyte cover since 2008 and the simultaneous decrease in species richness differed from previous observations. For example, Hagenberg et al. (2022) observed a simultaneous decrease in cover and richness, and Vanneste et al. (2017) a stable cover with either increasing or stable richness. In most studies, the decrease in cover was associated with an increase in vascular plant cover, especially shrubs (Walker et al., 2006; Michelsen et al., 2011; Elmendorf et al., 2012). However, vascular plant cover on our summits has decreased only slightly and this cannot explain the observed trends. Although interannual fluctuations in cover cannot be excluded at present for some species with decreasing cover, as their cover increased between 2008 and 2015 before decreasing, heatwaves and dry summers in 2015, 2018, 2019 and 2022 (MétéoSuisse, 2023), associated with reduced snow cover (Vorkauf, Marty, et al., 2021b), could explain the decrease of some species (Glime, 2017). In fact, the water balance has decreased dramatically at all elevations since the start of monitoring, and drought effects were observed on plants in 2022 even in shaded microhabitats, such as holes and narrow cracks under rocks. This is consistent with the decreasing mean ecological indicator values for moisture, and most of the declining species were found on the lower summits (LAL, BRU), which were most affected by the negative water balance. Furthermore, these species had a distribution positively related to high water balance and/or negatively related to high temperatures. Other possible causes can be excluded as we did not observe any signs of disturbance in the plots by comparing the photographs taken at each survey, and we did not record any differences in frequency of visits by wildlife or hikers.

So far, an increase in lichen cover in the context of climate change, as recorded on our lower alpine summit, has only been observed by monitoring on Norwegian summits (Michelsen et al., 2011) and in open-top chambers in Sweden (Molau & Alatalo, 1998). However, such a situation may be temporary if taller vascular plants, especially shrubs and young trees, colonise the summit, as has been observed



in many studies (e.g., Elmendorf et al., 2012; Vanneste et al., 2017; Hagenberg et al., 2022). In BRU, young larches and green alders are already growing 20m below the summit, indicating that the summit is now potentially close to the treeline, as confirmed by other unpublished regional observations and predictive modelling studies (Bütikofer et al., 2024).

The observed increase in lichen species richness on the two upper summits may be related to a longer growing season. Improved temperature conditions may have opened up new suitable growing areas for many species, especially in the subnival belt. This is consistent with the observed positive relationships between lichen cover and richness and mean growing-season temperature and with the increasing mean indicator values for temperature. Such an increase in species richness on upper alpine and subnival summits has been extensively documented for vascular plants (e.g., Matteodo et al., 2013; Steinbauer et al., 2018), but never, to our knowledge, for lichens. This confirms the high dispersal potential of lichens, which are able to quickly colonise newly available areas.

The contrasting trends of significantly increasing and decreasing cover in lichen species were probably also related to warming conditions. Indeed, their distribution was related to topo-climatic variables (warm and dry conditions for the increasing species; cold and wet conditions for the decreasing species), in accordance with their respective ecological indicator values for temperature: 1 to 1.5 for the decreasing *Cl. ecmocyna*, *Cl. macroceras* and *Cl. macrophyllodes*; 2.5–3 for the increasing *C. aggregata* and *Cl. pyxidata*.

5 | CONCLUSION

We hypothesised a decrease in bryophyte and lichen cover with increasing vascular plant cover. This was not verified, simply because vascular plant cover decreased on our summits. Terricolous lichens probably took advantage of the reduced competition and warmer conditions to increase their cover, especially on the lower alpine summit. However, shrubs and trees are shifting rapidly, and lichens are likely to lose their important co-dominance in the near future, once shrubs and trees will have colonised the summits. The total cover of bryophytes depends on many factors and seems to be mainly limited by water availability and humidity. Bryophytes will certainly be less sensitive to the changes in vascular plant cover but will suffer from increasing drought conditions. Differences are more species-specific, with some species declining and others benefiting from the forest development. However, these declining species may lead to local extinctions. These should be considered problematic even for widespread species, such as *Dicranum scoparium*, due to the loss of northern and mountain genetic variants (Hedenäs, 2019), which are ecotypes adapted to a cold climate.

The second hypothesis, that the community change would be more pronounced on the lower summits than on the upper ones, was only partially supported. Most of the bryophyte species, whose cover decreased, were present on the two lower summits, where

they probably suffered from repeated heatwaves and droughts, together with an earlier snowmelt. Similarly, the increase in lichen cover was mostly pronounced on the lower alpine summit. However, lichen species richness increased more on the upper alpine and nival summits, and for both groups, the community changes were more important on these summits, according to the NMDS analyses.

These results are valid at the scale of 1-m² plots and could be different on larger areas. Indeed, the analysis of the GLORIA sections (60–500m²) could potentially yield different results, as these sections contain a more diverse range of microhabitats (Vittoz et al., 2010). However, most of the trends observed on 1-m² plots were strong enough to rule out the possibility of bias due to misidentifications, overlooked species and differences in cover estimates, which are always possible in resurveys. Indeed, a strength of our study is that the same lichenologist and bryologist carried out all the surveys, thus limiting observational bias in cover estimates and misidentifications (Futschik et al., 2020). Moreover, the plots are permanently marked, ensuring a precise relocation at each inventory, confirmed by photographs.

Bryophytes and lichens have a very slow growth rate and are likely to have a delayed response to changes in climatic conditions. For this reason, Asplund et al. (2022) highlighted “the importance of including lichens and bryophytes when aiming to understand how photoautotroph communities respond to variation in environmental conditions in space or time”. Therefore, such long-term monitoring of cryptogams is very important and, unfortunately, too rare, compared to vascular plants. It is essential to maintain the existing ones, and similar analyses in other regions and using other scales are most welcome to improve our understanding of the impact of climate change on cryptogams. In addition, it would be important to measure microclimatic conditions at the plant scale. Soil temperature is a better variable than atmospheric temperature to explain plant distribution in the alpine belt (Körner, 2021), but available long-term data were missing for our analyses. Hence, future studies should improve the availability of climatic data at the metre resolution for a better understanding of species distribution and shifts.

AUTHOR CONTRIBUTIONS

Jean-Paul Theurillat and Pascal Vittoz initiated the GLORIA monitoring on these Swiss summits; Mathias Vust inventoried the lichens; Luca Miserere inventoried the bryophytes; Jean-Paul Theurillat, Pascal Vittoz and Christophe Randin inventoried the vascular plants; Rut Mayo de la Iglesia, Christophe Randin and Pascal Vittoz designed the statistical analyses; Rut Mayo de la Iglesia and Christophe Randin analysed the data; Rut Mayo de la Iglesia and Pascal Vittoz wrote the first draft; all authors commented on and completed the manuscript.

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CONFLICT OF INTEREST STATEMENT

None of the authors have any conflict of interest to declare.

DATA AVAILABILITY STATEMENT

In addition to appendices, data are available from the Swisslichen (<https://swisslichens.wsl.ch/en>) and Swissbryophyte (<https://www.swissbryophytes.ch>) databases.

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

Appendix S1. The GLORIA sampling design.

Appendix S2. Locations of the plots on the summits and their topographical characteristics.

Appendix S3. Table of vascular plant, lichen, bryophyte, rock, bare ground and litter covers (in %) for each plot in each survey.

Appendix S4. Table of the bryophyte species, with their frequencies per mountain summit and per year.

Appendix S5. Table of the lichen species, with their frequencies per mountain summit and per year.

Appendix S6. Evolution of the topo-climatic variables on the four summits.

Appendix S7. Influence of abiotic and biotic factors on bryophyte and lichen covers.

Appendix S8. Evolution of bryophyte, lichen and vascular plant cover across time.

Appendix S9. Non-metric multidimensional scaling of bryophyte communities, in the total data set and by summit.

Appendix S10. Non-metric multidimensional scaling of lichen communities, in the total data set and by summit.

Appendix S11. Results of generalised linear mixed-effects model for the influence of time, mean temperature and water balance in the growing season on the cover of 18 retained bryophyte species.

Appendix S12. Results of generalised linear mixed-effects model for the influence of time, mean temperature and water balance in the growing season on the cover of 21 retained lichen species.

Appendix S13. Evolution of bryophyte and lichen species richness over time.

Appendix S14. Evolution of ecological indicator values for temperature and moisture over time.

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