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RESEARCH

Interactions among vascular plants, bryophytes, and lichens in grassland communities along elevational gradients

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Abstract

Grasslands in temperate Europe are key biodiversity hotspots, supporting not only a rich vascular flora but also diverse communities of bryophytes and lichens. However, the processes shaping lichens and bryophytes in these ecosystems, particularly along environmental gradients, remain understudied. We investigated the relative roles of abiotic factors (elevation and rock abundance) and biotic drivers (vascular plant cover and height) in determining both the taxonomic and functional diversity of bryophytes and lichens in two protected grassland sites in central Italy. Across 80 plots spanning wide elevational gradients, we measured species richness and functional diversity for both bryophytes and lichens, and applied piecewise structural equation modeling to test causal relationships. Our results revealed that vascular plant structure (particularly vegetation cover and height) was the main determinant of lichens and bryophytesdiversity. Both facets of diversity in bryophytes and lichens were negatively affected by dense and tall vascular vegetation, likely due to shading and competition for space. Abiotic factors, such as elevation and rock abundance, influenced lichens and bryophytesonly indirectly, by altering vascular plant structure. An exception was bryophyte species richness, which was directly promoted by rock abundance through increased habitat heterogeneity and reduced vascular plant competition. Site-specific effects, likely related to substrate type (calcareous vs. siliceous), also played a significant role, particularly in shaping bryophyte communities. These findings suggest that biotic interactions, especially competition with vascular plants, play a more central role than direct abiotic filtering in determining lichens and bryophytesdiversity in grassland ecosystems. Our study provides a functional, multi-taxa framework for understanding elevational patterns of lichens and bryophytesdiversity and highlights the importance of considering vegetation structure in grassland conservation and management strategies.

Keywords Assembly rules · Biodiversity · Functional diversity · SEM · Vegetation

Introduction

Natural and semi-natural grasslands are habitats characterized by high diversity and are considered as biodiversity hotspots in temperate Europe (Wilson et al. 2012; Biurrun et al. 2021). One of the causes of this high biodiversity is linked to the multitude of microhabitats present in grassland ecosystems, justifying their high conservation value (Habel et al. 2013; Dengler et al. 2014).

Alongside the richness of vascular plant species, grassland habitats are also important reservoirs for the biodiversity of the non-vascular vegetation, in particular lichens and bryophytes (Deane-Coe and Stanton 2017; Martin and Mallik 2017; Löbel et al. 2006; Turtureanu et al. 2014; Biurrun et al. 2021), and invertebrates (Zulka et al. 2014). A multitude of complex processes were depicted between vascular

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plants and other organisms in grasslands, for example, a direct effect of vegetation structure on ant species and trait composition (e.g., Frenette-Dussault et al. 2013; Mugnai et al. 2021). At the same time, competition and facilitation interactions are known to occur among vascular plants, bryophytes, and lichens in grasslands, albeit they are far less studied (Wietrzyk-Pelka et al. 2021). On the one hand, in grasslands, vascular plants could exert a strong competitive pressure on bryophytes and lichens. Vascular plants produce litter that could eventually cover lichens and bryophytess (Ellis et al. 2011), reduce the available space for their occupancy (Ingerpuu et al. 2005; Boch et al. 2018), and create a shading effect that strongly reduces the amount of light reaching the underlying lichens and bryophytes communities (Jägerbrand et al. 2012; Graglia et al. 2001). Such competitive interactions could have a negative effect on both richness and abundance of bryophytes (Löbel et al. 2006; Müller et al. 2012; Klink et al. 2017) and lichens (Bruun et al. 2006, Cornelissen et al. 2001), and could also play an important role in determining the structure of such communities (Fergus et al. 2017). On the other hand, at least at low vascular plant cover, there is also some evidence of facilitation processes occurring between these organisms, especially between vascular plants and bryophytes (Ingerpuu et al. 2005). For example, the cover of vascular plants could reduce the underlying temperature and wind speed that in turn reduce evaporation, allowing lichens and bryophytes to experience longer periods of hydration (Ingerpuu et al. 2005). The relative importance of competition and facilitation could also vary along environmental gradients (Ingerpuu et al. 2005) or vegetation succession (Hagenberg et al. 2022; García de León et al. 2016; Dettweiler-Robinson et al. 2013).

Species richness is generally considered one of the main measures of biodiversity (i.e., taxonomic facet of diversity), but it may not always depict changes in biodiversity (e.g., Chase et al. 2019). On the contrary, functional traits (i.e., functional facet of diversity) have a universal approach, as they do not rely on species taxonomic identity. They inform on ecosystem multifunctionality and services, and they more easily and rapidly respond to environmental changes (Violle et al. 2014; Gagic et al. 2015; Mugnai et al. 2022). Moreover, both lichens and bryophytes respond strongly to environmental gradients such as climate (Matos et al. 2017) since they functionally differ from vascular plants in their lack of specialized structures to regulate rates of water loss from their tissues (i.e., poikilohydry) and poor ability to take up nutrients from the soil. Additionally, it has been demonstrated how rocks and stones strongly influence lichens and bryophytes' diversity of grasslands, since they consist of suitable microhabitats for many terricolous and epilithic species (Bergauer et al. 2022; Cole et al. 2008; Hespanhol et al. 2011). Among the functional traits of lichens and bryophytesrelated to environmental changes, bryophytes growth form and shoot length are related to water retention and temperatures (Glime 2017), frequency of sexual reproduction is influenced by humidity and stresses (Austrheim et al. 2005), while leaf length could enhance the functional distinction between species. Regarding lichens, growth form is influenced mainly by water availability and temperatures (Nascimbene and Marini 2015; Di Nuzzo et al. 2021), and type of reproduction is influenced by habitat stability and temperature (Seymour et al. 2005; Hurtado et al. 2019; Di Nuzzo et al. 2021). Despite the demonstrated importance of including functional traits in multi-taxa studies, a limited number of authors have addressed biodiversity following this approach (see Roos et al. 2019; Asplund et al. 2022), and none have focused on grassland ecosystems.

One of the most important natural environmental gradients is the elevational one. Such gradients have proved to be pivotal to exploring the effect of climate-induced changes on biodiversity since they encompass the variation of abiotic factors in a relatively short distance, simulating wider climatic and ecological succession in time (Di Nuzzo et al. 2021). Moreover, the consideration of multiple taxa within the same community may depict more precisely the processes acting on biodiversity and better discern whether some abiotic factors are predictors of diversity (Sundqvist et al. 2013; Peters et al. 2016). Previous studies have measured the response of vascular plant functional diversity to elevational gradients, with contrasting conclusions (see Bello et al. 2013; Pescador et al. 2015) and few studies have considered the functional diversity of lichens and bryophytes (see Asplund et al. 2022), despite their importance as components of many ecosystems, especially at high elevations: for example they have a pivotal role in nutrients cycles and litter decomposition, represent microhabitats or shelters for many microorganism groups, and represent food resources for terrestrial invertebrates (e.g. Asplund and Wardle 2017).

Hence, we aimed at assessing whether elevational patterns of lichens and bryophytes diversity were directly driven by the abiotic factors (e.g., elevation and rock abundance) or mediated by biotic drivers (i.e., characteristics of vascular plant vegetation through competition processes). To disentangle how such processes shape lichens and bryophytes communities, we followed multiple approaches considering both taxonomic (with species diversity limited by the number of available niches due to homogeneous environment or strong biotic interactions) and functional (with trait divergence when competition with vascular plants prevails over environmental filtering) facets of diversity. We hypothesized that in a grassland ecosystem, the predominance of vascular vegetation plays the role of the main predictor of lichens and bryophytes diversity, affecting not only species diversity, as already demonstrated (e.g., Bergauer et al. 2022; Hagenberg et al. 2022), but also their functional traits, thus resulting in a lower importance of abiotic conditions such as elevation compared to competition in shaping these communities.

Methods

Study sites

This study was conducted in two mountains (Fig. 1) included in protected sites situated in central Italy (Tuscany): Pania della Croce (44.035756°N, 10.319390°E) and Monte Prado (44.248877°N, 10.405821°E). These mountains are located within the regional park of Alpi Apuane and within the national park of Appennino Tosco-Emiliano, respectively. Pania della Croce reaches 1858 m a.s.l. with a 5 °C annual mean temperature and 1208 mm of annual precipitation, while Monte Prado's maximum elevation is 2054 m a.s.l. and is characterized by an annual mean temperature of 3 °C and annual precipitation of 1056 mm (Karger et al. 2017). The two sites differ in the type of substrate: Pania della Croce is mainly constituted by calcareous rocks, while Monte Prado by a siliceous substrate.

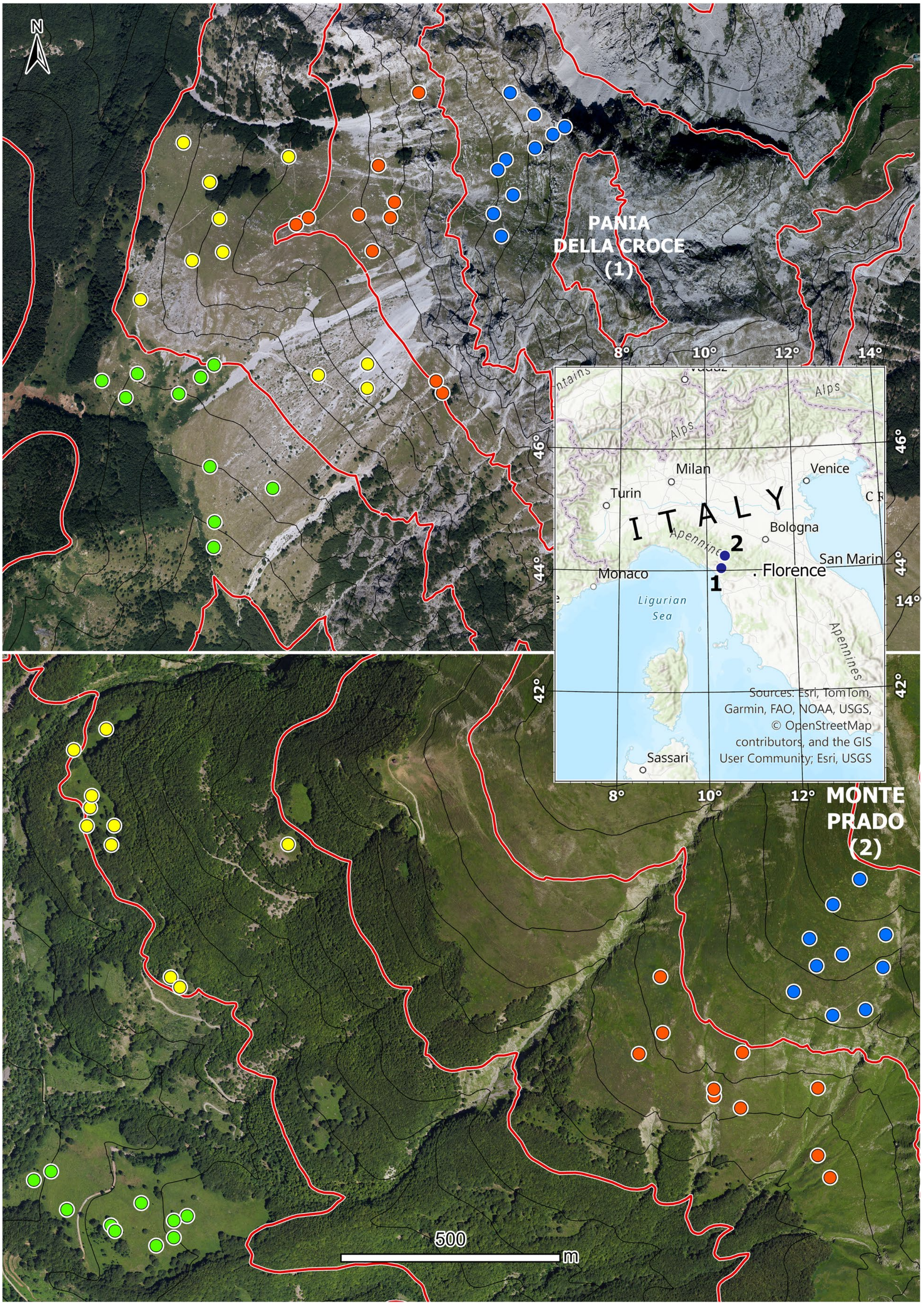
Two areas of about 0.7 km^2 were delimited in both sites, in both cases situated on west-facing slopes of the mountains and covering an elevational gradient of 800 m (from 1000 to 1800 m a.s.l. for Pania della Croce and from 1200 to 2000 m a.s.l. for Monte Prado). Each area included grassland patches classified as semi-natural dry grasslands and scrubland facies on calcareous substrates (Festuco-Brometalia order, important sites for orchids; habitat code 6210*) and siliceous alpine and boreal grasslands (habitat code 6150) according to the HaSCITu (Habitat in the Sites of Conservation Interest in Tuscany) program (http://www.regione.toscana.it/-/la-carta-degli-habitat-nei-siti-natura-2000-toscani). In both areas, grazing and other anthropogenic disturbances (e.g., mowing) are absent, and the treeline reaches around 1120 m a.s.l. for Pania della Croce site and 1690 m a.s.l. for Monte Prado site.

Sampling

We surveyed in 2020 (in May for Pania della Croce and in June for Monte Prado) 40 2 × 2 m quadrat plots for each area (80 in total) distributed along the elevational gradient. To ensure an even spatial distribution of replicates, each area was divided into four elevational belts, each one covering 200 m of elevation. Within each belt, ten plots were randomly placed (with a minimum distance of 20 m and a maximum distance of 350 m between two plots). In each plot, vegetation and environmental variables were surveyed following the EDGG protocol (European Dry Grassland Group, see Dengler et al. 2016), with vascular plants, epigeic bryophytes, and epigeic lichens identified at species level and their abundances estimated as percentage of coverage down to 0.1%. Community of vascular plants was also characterized by the measurement of structural parameters of vegetation, namely plant cover (total coverage in the plot of vascular plant species in %) and plant height (mean vegetation height measured in five random points). As environmental variables (see Dengler et al. 2016 for methodology), we estimated the fraction of soil covered by rocks (percentage cover of rocks with diameter > 63 mm after virtually removing all vegetation and litter), microrelief (perpendicular distance in cm between lowest and highest ground points), and elevation registered at the plot level with a portable GPS with 4 m of horizontal precision.

We selected a set of functional traits of bryophytes (life form, shoot length, frequency of sporophyte, and maximum leaf length), and lichens (growth form, type of reproduction, type of photobiont, and presence or absence of secondary metabolites), responding well to micro-environmental variation (Giordani et al. 2014; Hurtado et al. 2019; Sulavik et al. 2021; Di Nuzzo et al. 2021). The traits were measured at species level (thus not considering intraspecific trait variation) and in case of numerical traits we used the mean value assuming to be representative for mature healthy individuals. For lichens and bryophytes, we considered all the species occurring in the plots and we characterized them by a set of functional traits retrieved from Hill et al. (2007) for bryophytes and Nimis and Martellos (2020) for lichens. Lichen growth forms were modified from Nimis and Martellos (2020). Species belonging to the genus *Cladonia* with a persistent primary thallus were labeled as "mixed".

Bryophyte and lichen diversity patterns were evaluated using species richness for the taxonomic facet, as it has been widely considered an adequate index for lichens and bryophytes in these contexts (e.g., Ingerpuu et al. 2005; Bruun et al. 2006; Boch et al. 2016; Boch et al. 2018), and Mean species Pairwise Dissimilarity (hereafter MPD) for the functional one. MDP measures the expected functional dissimilarity between a pair of species randomly selected from the community (Bello et al. 2016). Moreover, functional MPD is unrelated to species richness, allowing the measurement of the functional diversity with an index which is independent of the taxonomic facet (Clarke and Warwick 1998; Bello et al. 2016). MPD was calculated using functional dissimilarity matrix with Gower distance (Gower 1971) and weighing it for abundances of species (Bello et al. 2016). In order to perform statistical analyses and differentiate the functional space of empty or poor-species communities, a value of 0 has been attributed to plots with no species



Sources: Esri, TomTom, Garmin, FAO, NOAA, USGS, © OpenStreetMap contributors, and the GIS User Community; Esri, USGS

◀ **Fig. 1** Map of the study sites (1 for Pania della Croce and 2 for Monte Prado) and spatial distribution of sampling points. Elevational belts are delimited by red contour lines and sampling points are color-coded depending on the belt (in order green, yellow, red and blue from the lower to the upper elevational belts)

(empty functional space) and a value of 0.0001 to plots with one species (point-like functional space).

Statistical analyses

For all analyses, we used the statistical software R (version 4.1.2, R Development Core Team, http://www.R-project.org*)*.

Since abiotic (i.e., elevation and rocky fraction of soil) and biotic (i.e., vascular plant, bryophyte, and lichen communities) predictor variables were expected to show complex interrelationships, confirmatory path analyses (piecewise structural equation modelling, SEM) were applied in separate models to explore their causal relationships with bryophyte and lichen diversity. An initial model containing the possible causal drivers of lichens and bryophytes communities and their interrelationships was set up based on the current knowledge (Fig. 2). We hypothesized that the abiotic variables (elevation, rock abundance and site) influenced primarily the structure of vascular plant community (vegetation height and cover), which in turn influenced the taxonomic and functional diversity of bryophytes and lichens. Model fit was assessed using Fisher's C statistic, where $p > 0.05$ indicates that the data are well represented by the model. Piecewise SEMs were based on generalized linear models (GLM) using the R package 'piecewiseSEM' (Lefcheck 2016). We fitted linear models for vegetation cover and vegetation height, while for species richness and functional diversity of lichen and bryophytes, we performed a series of generalized linear models with different error family distributions. In particular, we used the Poisson family for lichen richness through the 'glm' function of the ***stats*** package and a Negative Binomial ('nbinom1') family for bryophyte richness using the 'glmmTMB' function from ***glmmTMB*** package (Brooks et al. 2017). Regarding the functional traits of both bryophytes and lichens, we used a Beta family ('ordbeta') through the 'glmmTMB' function. When using 'glmmTMB' models, we set microrelief as random effect to take into account the preference of microhabitats by lichens and bryophytes (Hespanhol et al. 2011; Sulavik et al. 2021). Model residuals were inspected using the ***DHARMa*** package (Hartig 2022). As the 'site' had only two levels, it was treated as a fixed effect, since the low number of levels may lead to unreliable estimates of random variance components (Harrison et al. 2018).

Results

A total of 45 bryophyte species and 7 lichen species were recorded in total. In the sampled plots, we recorded a maximum of 13 bryophytes species and a maximum of 6 lichen species, and a minimum of 0 species for both taxa. Bryophyte FD ranged from 0 to 0.60 (mean values of 0.33 for Pania della Croce and 0.10 for Monte Prado), while lichen FD ranged from 0 to 0.67 (mean values of 0.02 for Pania della Croce and 0.11 for Monte Prado).

The piecewise structural equations models performed were statistically significant for both lichens and bryophytes communities and for both facets of diversity (Fig. 3). Moreover, SEMs explained 40% of the variation in vascular plant cover, due to the negative effect of rock abundance, and 58% of the variation in vascular plant height, attributable to the negative effect of elevation and a significant difference between sites.

Piecewise SEM explained 59% of the variation in bryophyte taxonomic diversity, which was attributable to positive effects of rocks and negative effects of plant height (Fig. 3a). By contrast, piecewise SEM explained the 26% of variation in bryophyte functional diversity and significantly affected by vegetation cover and height (Fig. 3b). Regarding lichens, SEM explained 69% of the variation in taxonomic diversity, attributable to negative effects of vascular plant coverage and height, and 49% of the variation in functional diversity (Fig. 3c), also attributable to negative effects of vascular plant coverage and height (Fig. 3d). The effect of different sites (and hence substrates) resulted significant for both facets of bryophyte diversity (Fig. 3a and b) and lichen taxonomic diversity (Fig. 3c).

Discussion

The results obtained allowed us to disentangle the complex relationships between abiotic and biotic processes acting on the lichens and bryophytes components of the grassland communities investigated. Vegetation cover and height were the most important direct factor determining both facets of lichens and bryophytes diversity. In contrast, elevation had only an indirect effect, reducing vascular plant cover along the gradient and thus reducing competition.

The direct relationship between rock abundance and vascular plant cover confirms the negative effect of shallow soils and outcrops on vascular plant biomass production (e.g., Auestad et al. 2008; Bernard-Verdier et al. 2012; Yang et al. 2017; Mugnai et al. 2023). Moreover, a negative direct relationship between elevation and vegetation height was also found, suggesting that the environmental pressure, such

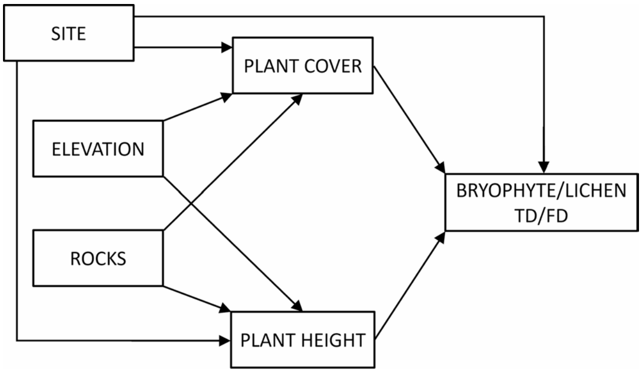


Fig. 2 Structure of the a priori model for piecewise structural equation modelling (SEM) exploring the effects of site, elevation, rock abundance, and plant community characteristics on bryophyte and lichen facets. Arrows show hypothesized causal relationships

as lower temperatures, may select for shorter vascular plant species (Molina-Venegas et al. 2016; Mota et al. 2018).

Regarding lichens and bryophytes diversity, we found that bryophyte taxonomic diversity was the only facet that is directly affected by abiotic parameters. In fact, the presence of rock outcrops (harsh patches for colonization of vascular plants) represents spaces with low competition from vascular plants (i.e., available niches which enhance a higher number of bryophyte species; see Bergauer et al. 2022), that create points of discontinuity in the homogeneous herb layer, creating microhabitats which promote richness and more variation in the composition of bryophyte communities (Hespanhol et al. 2011; Peñaloza-Bojacá et al. 2018; Ren et al. 2021). The negative effect of vascular plant competition was confirmed by the significant effect operated

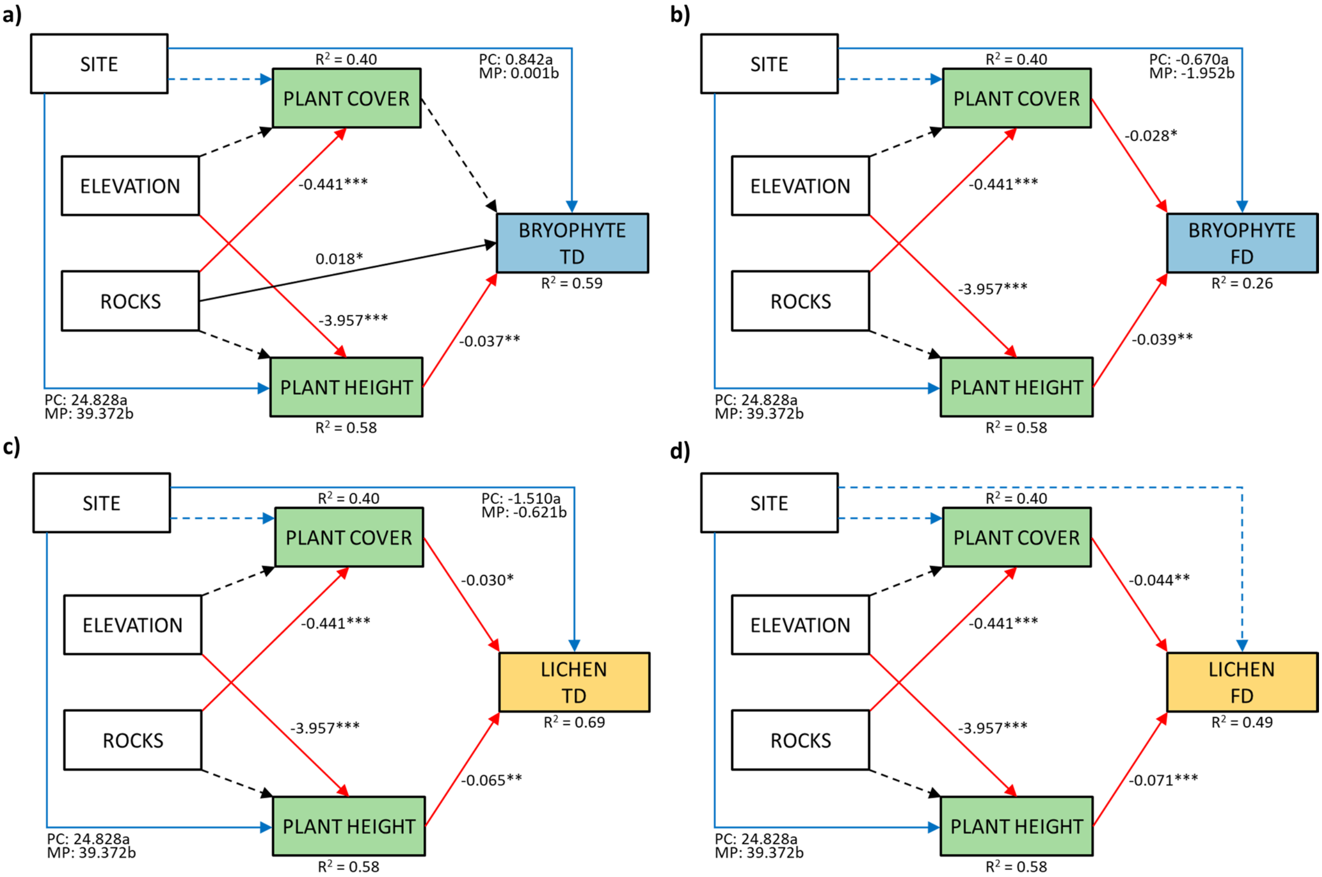


Fig. 3 Structural equation models (piecewise SEMs) exploring the effects of environmental parameters and plant community characteristics on bryophyte (a and b) and lichen (c and d) diversity, for both taxonomic (a and c) and functional (b and d) facets. Solid arrows represent unidirectional significant relationships among variables ($p<0.05$), black arrows denote positive relationships and red ones show negative relationships. Blue arrows indicate relationships between the site (categorical variable) and other variables. Dashed arrows show not significant relationships ($p>0.05$). Standardized parameter estimates are given next to the arrows, where * $p<0.05$, ** $p<0.01$, and *** $p<0.001$. Marginal R^2 (based on fixed effects only) for component models are given above or below the box of respective response variable. The statistics of the models are: (a) Fisher's C = 8.124, $p=0.087$; (b) Fisher's C = 8.523, $p=0.202$; (c) Fisher's C = 11.708, $p=0.069$; (d) Fisher's C = 6.217, $p=0.399$

by vegetation height and cover, which was found to be a stronger factor in shaping bryophyte and lichen taxonomic diversity. In fact, being taller, vascular vegetation creates a shading effect on lichens and bryophytes, thus outcompeting them for light interception, and reducing their richness (Jägerbrand et al. 2012; Leppik et al. 2013; Fergus et al. 2017; Boch et al. 2018; Bergauer et al. 2022; Hagenberg et al. 2022). Hence, our results suggest that the elevational patterns showing an increase of grassland lichens and bryophytes diversity with elevation found by many authors (e.g., Baumann et al. 2016; Fontana et al. 2020) might be due to the progressive decrease of vascular plant biomass caused by environmental stresses like lower temperatures and shallower soils linked to elevation. Thus, our results suggest that competition is likely the main driver that directly assembles lichens and bryophytes taxonomic diversity, with the abiotic parameters (e.g., elevation and temperature) having only indirect effects through the shaping of vascular vegetation (Boch et al. 2018).

Similarly, the more pronounced effect of competition by vascular plants compared to environmental filtering operating along the elevational gradients was confirmed by the functional facets of lichens and bryophytes diversity. In fact, for both bryophytes and lichens, the vascular vegetation characteristics (vascular plant cover and height) were the only environmental parameters that shaped their functional diversity. These results suggest that, similar to taxonomic diversity, the patterns of functional diversity along the elevational gradients found by other authors for bryophytes (Henriques et al. 2017; Ah-Peng et al. 2014) and lichens (Bässler et al. 2016), might not be directly due to the environmental filtering of abiotic parameters but are subordinated by the competition of vascular plants. This is in accordance with previous studies, which found that lichens and bryophytes' functional diversity is inversely related to the abundance of vascular plants, with the latter being the primary driver of biodiversity and having a significantly stronger influence than elevation, which only has indirect effects (Asplund et al. 2022). Nonetheless, it must be noted that as the trait values used here were collated from literature and not obtained via direct measurements of our sampled specimens. Hence, intraspecific trait variability along the gradient was not considered but future studies could explore the role of trait plasticity in lichens and bryophytes as a strategy to cope with competition.

Finally, all facets of biodiversity, except for lichen functional diversity, were significantly influenced by the site. This result might be related to the difference in bedrock type, as Monte Prado is characterized by siliceous bedrock, while Pania della Croce is calcareous. Different bedrock types are related to differences in the physical properties of the soil, such as percolation and water retention, and it is known to influence both plants (Nemer et al. 2021) and lichen diversity (Vallese et al. 2024). Such effects trigger positive feedback related to vegetation structures, which may affect habitat suitability for bryophytes and lichens. For example, in our study, calcareous substrates are characterized by the strong dominance of grass species (e.g., *Brachypodium* sp.), which forms tussocks that strongly outcompete lichens and bryophytes. Siliceous bedrock, on the other hand, presents a weaker dominance of such species, leaving more free microhabitats for lichens and bryophytes. Moreover, in our study, it has been possible to evaluate the role of factors and competition by vascular plants on lichens and bryophytes diversity without the effect of disturbance by grazing and trampling, which have been demonstrated to be a key process in the assemblage of bryophytes and lichens in grassland communities (Rai et al. 2012; Tripp et al. 2019).

Conclusions

We demonstrated that lichens and bryophytes diversity in grassland habitats is directly shaped by the competition of vascular vegetation. In particular, the increasing taxonomic and functional diversity of lichen and bryophytes along the elevational gradient is due to the decrease in height and cover of vascular plants. Thus, abiotic factors such as elevation and availability of suitable microhabitats (i.e., abundance of rocks) affected lichens and bryophytes diversity only indirectly, mediated by their direct effects on vascular vegetation. This case study provides an important framework for understanding the lichens and bryophytes diversity along elevational gradients in grasslands. If further confirmed, our results may substantially advance our knowledge on the assembly rules of lichens and bryophytes communities, and the primary role of biotic factors in respect to abiotic ones. Nevertheless, further studies are needed to widen the findings at larger scales and depict general patterns underpinning the biodiversity of such organisms in grassland ecosystems.

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Author contributions Conceptualization: Michele Mugnai, Lorenzo Lazzaro, Luca Di Nuzzo, Paride Balzani, Clara Frasconi Wendt; Methodology: Michele Mugnai, Lorenzo Lazzaro; Formal analysis and investigation: Michele Mugnai, Lorenzo Lazzaro, Luca Di Nuzzo, Paride Balzani, Clara Frasconi Wendt, Andrea Beltramini, Giulio Ferretti, Alice Misuri; Writing - original draft preparation: Michele Mugnai; Writing - review and editing: Michele Mugnai, Lorenzo Lazzaro, Luca Di Nuzzo, Paride Balzani, Clara Frasconi Wendt, Renato Benesperi, Daniele Viciani.

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Data availability The data used in this paper is accessible in the supplementary material.

Declarations

Competing interests The authors declare no competing interests.

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