Coexistence despite competition: Bryophyte diversity is buffered against vascular plant dominance over succession.

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Contributions

M.H. and R.R.J. designed the study. M.H. conducted field work. M.H. performed the processing and analysis of the data with inputs from R.R.J.. M.H. and R.R.J. drafted the initial version of the manuscript.

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Competing interests

The authors declare no competing interests.

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Abstract

In alpine landscapes, vascular plants and also bryophytes are key biological features shaping the trajectories of primary succession following glacial retreat. Yet research on ecological successions is mainly centered around vascular plants, and potential interactions between both taxonomic groups have been largely disregarded. In this study, we examine successional processes impacting both groups across a 170-year gradient developing into a natural grassland ecosystem in the Austrian Alps. Utilizing multispectral 3D whole community phenotyping and introducing *ecological dispersion* as a metric reflecting a community's ecological, calculated as the dispersion of ecological indicator values, we gain a mechanistic understanding of the interactions between bryophyte and vascular plant diversity along grassland succession. Our findings show an increase in diversity for both groups over time, with vascular plants demonstrating a transitional community composition pattern along the successional gradient. Bryophytes, in contrast, do not show a consistent pattern of community compositional change over succession and are less affected by microclimate and soil nutrients, highlighting opportunistic colonization strategies with bryophyte communities showing increased ecological dispersion over time. Structural equation modeling reveals that vascular plant growth structure, quantified via digital community features from multispectral 3D plant scanning, negatively affects bryophyte diversity and ecological dispersion, suggesting competitive interactions with vascular plants. Our research underlines the complex dynamics between bryophyte and vascular plant communities during alpine grassland succession and stresses the importance of including both groups in succession studies to fully grasp biodiversity development and succession mechanisms.

Introduction

Bryophyte and vascular plant successions have been studied in various environments (Favero-Longo *et al.*, 2012; Arróniz-Crespo *et al.*, 2014; García de León *et al.*, 2016; Wietrzyk, Węgrzyn and Lisowska, 2016; Måren *et al.*, 2018; Prach and Walker, 2020) highlighting distinct responses of both groups to changes in their biotic and abiotic environment over time (Måren *et al.*, 2018; Hanusch *et al.*, 2022). However, major ecological theories on plant succession have been predominantly centered around vascular plants neglecting bryophytes (Clement and Touffet, 1990; Saure *et al.*, 2014; Pulsford, Lindenmayer and Driscoll, 2016; Ficetola *et al.*, 2021). Although local species inventories of both groups are simultaneously shaped by the same processes (i.e., biotic interactions, dispersal, and environmental filtering over succession (Chase, 2003; Chase and Myers, 2011; Chase *et al.*, 2011), these assembly processes are only well documented and understood for vascular plants which differ from bryophytes in multiple aspects. For example, bryophytes are able to colonize various substrate types, including rocks and scree and are generally more limited by environmental filtering rather than dispersal abilities (Patiño and Vanderpoorten, 2018). However, vascular plants are more limited by dispersal abilities and tend to selectively colonize specific substrate types, subsequently establishing and alter site-specific habitat characteristics such as soil pH, microclimate, and soil nutrient content (Odum, 1969; Hanusch *et al.*, 2022). Additionally, vascular plant vegetative structures and roots can restrict the substrate and light availability for bryophyte colonization (During and van Tooren, 1990). These dynamics suggest that vascular plants can directly shape bryophyte community composition by altering the microenvironment shared by vascular plants and bryophytes and influencing resource availability. Assumptions and hypotheses regarding plant succession and community assembly should thus incorporate bryophytes to account for their unique responses to environmental and biotic changes.

The recognition of potential interdependencies between vascular plants and bryophyte communities over succession is largely based on studies from forest ecosystems in which woody plants predominate (Fenton and Bergeron, 2006, 2013; Jean *et al.*, 2017; Fischer *et*

al., 2019). However, in successional seres that (at least temporarily) develop into grassland ecosystems, such as most pro-glacial successions, herbaceous plants and dwarf shrubs form vegetation mats that create environmental conditions notably different from the stratified layers that trees create in forest ecosystems (Prach and Walker, 2020). Yet, successional research within grassland ecosystems insufficiently considered such interdependencies and interactions between bryophytes and vascular plants (Saure *et al.*, 2014; Måren *et al.*, 2018).

In developing grassland ecosystems, a characteristic outcome of ecological succession is the progressive augmentation of vascular plant biomass. Within such dense vegetation mats more homogenous microenvironmental conditions prevail, marked by modified temperature, light, and moisture regimes which can influence the growth and diversity of bryophytes (Bergamini *et al.*, 2001). As a result, only a select array of bryophyte species is expected to persist and thrive under the conditions shaped by increased vascular plant growth. However, extensive studies in non-successional grassland settings have revealed a wide spectrum of mutual relationships between vascular plant biomass and bryophyte diversity spanning from negative and positive correlations, curvilinear effects, or no discernible impact of vascular plant biomass on bryophyte diversity at all (Ingerpuu, Kull and Vellak, 1998; Virtanen *et al.*, 2000; Bergamini *et al.*, 2001; Peintinger and Bergamini, 2006; Virtanen and Crawley, 2010). The dynamics and extent of interactions between vascular plants and bryophytes during succession, particularly the increasing structural dominance of vascular plants, thus remain a critical area of investigation in successional research.

To assess the interactions between vascular plants and bryophytes, field measurements of plant biomass or vegetation structure are required that often use destructive methods that can significantly alter the trajectory of successional seres (Catchpole and Wheeler, 1992). The adoption of 3D multispectral plant scanning technology offers a non-invasive approach to capturing morphological and physiological traits of entire plant communities, potentially serving as a suitable alternative to traditional destructive methods (He, Hanusch, Saueressig, *et al.*, 2023; Zieschank and Junker, 2023). Through digital whole-community phenotyping, parameters can be measured that provide insights into community features, such as biomass

estimates and morphological characteristics indicative of vegetation structure that are typically not accessible through observational field studies. Similar to community-weighted means, these parameters represent the trait frequency distribution across an entire community, circumventing the need for species-specific measurements. This methodology opens novel avenues for researching vegetation growth structure and can accurately mirror the ecological conditions experienced by bryophytes that grow among or within vascular plant mats. Consequently, this technique facilitates deeper insights into the biotic interactions between both groups.

Assembly processes impact species differently, depending on common life strategies or a species' functional and metabolic traits. Approaches that investigate community assembly through a trait-based lens, linking ecomorphological features to assembly processes have significantly advanced our comprehension of community assembly (McGill *et al.*, 2006; Götzenberger *et al.*, 2012). However, for certain groups with a reduced morphology such as bryophytes, the measurement of functional and especially morphological traits on an individual level poses a challenge, hindering the direct linkage of trait expression to assembly processes (Holyoak and Pedersen, 2007; Hanusch *et al.*, 2020). In such instances, utilizing ecological indicator values (EIVs) that are based on the optima of a species' realized ecological niche, such as Ellenberg's indicator values, can offer valuable insights into understanding community dynamics and underlying processes without explicit measurements of functional traits. While it is widely acknowledged that functional trait measurements provide detailed information about plant functional strategies, EIVs provide a convenient way to summarize and compare species' ecological preferences without directly measuring individual-based functional traits (De Bello *et al.*, 2021).

Like functional traits, EIVs can be used to calculate diversity indices such as functional dispersion providing a measure for a community's range of reactions to environmental change. While this is a departure from the traditional use of functional dispersion as a measure of a community's functional composition, the use of EIVs instead of functional traits shifts the focus of the analysis on the conditions of the habitat (i.e. *ecological dispersion* reflecting the

heterogeneity of ecological conditions each community tolerates) rather than the functional roles of species within the ecosystem. High ecological dispersion implies that the environment surrounding a community satisfies a variety of habitat requirements (i.e. less specialized communities with a broad range of ecological preferences), conversely low ecological dispersion points to an environment that purges a community to comprise species with more similar niche optima. In the context of successional research, ecological dispersion provides a new window through which community assembly processes can be examined, as it acknowledges shifts in community tolerances that are driven by environmental changes occurring over succession. While taxonomic diversity metrics are also commonly used for assessing the impact of assembly processes on community composition, their ease of evaluation comes at the expense of potentially overlooking ecological mechanisms that could be identified from approaches based on species-specific niche optima. In the context of succession, an integrative approach combining the taxonomic composition of communities with their associated ecological dispersion thus holds the potential to provide novel insights into the drivers of community assembly acknowledging shifting conditions along a successional gradient.

In this study, we integrate taxonomic composition and estimates of vegetation structural complexity obtained through whole-community phenotyping of vascular plant communities, along with environmental variables, to examine the effects of specific factors impacting community assembly of vascular plants and bryophyte communities and their EIV-based ecological dispersion over a 170-year successional gradient following glacial retreat in the Austrian Alps. We compare the effects of various biotic and abiotic factors on vascular plant and bryophyte communities to highlight distinct responses to environmental changes of both groups. Additionally, we specifically address the simultaneous impacts of time-related processes, abiotic factors, and interactions with vascular plants through increasing vegetation structural complexity on the diversity and associated ecological dispersion of bryophyte communities evaluating the following hypotheses and expectations:

1. Theories on the development and assembly of plant communities over succession mostly focus on factors that shape vascular plant communities. Given their physiological differences, we anticipate that bryophyte community assembly will be influenced by distinct factors and with varying intensities compared to vascular plants. We thus evaluate the correlation between the observed taxonomic compositions of bryophyte and vascular plant communities and several variables that are considered representative of different assembly mechanisms: substrate composition, soil nutrient content, and soil temperature as proxies for environmental filtering, composition of vascular plant and bryophyte communities as a proxy for biotic dependencies and time since deglaciation a proxy for the increasing chance of successful colonization events over time. By contrasting these correlations with data derived from randomly generated null-model communities, we aim to illuminate distinct assembly patterns distinguishing the two groups.
2. Due to their narrow environmental tolerances, bryophytes likely exhibit significant changes in community composition along successional gradients, dependent on shifts in microhabitat and associated ecological niche availability. As succession progresses, we anticipate a homogenization of microhabitats available to bryophytes due to the formation of dense vegetation mats by vascular plants. We expect that this habitat homogenization leads to a decrease in diversity and associated ecological dispersion of the bryophyte community, as only bryophyte species that are suitably adapted are able to grow under these conditions.
3. Assembly processes do not operate in isolation but jointly affect the diversity of local communities. We hypothesize that bryophyte diversity and ecological dispersion along the successional gradient are jointly influenced by time since deglaciation, the abiotic environment, and increasing vascular plant dominance. Using a structural equation modeling approach, we aim to disentangle and quantify the relative contributions of each factor, expecting that these variables collectively shape bryophyte diversity and community structure over time.

Our study will contribute to our knowledge of ecosystem development under natural conditions, particularly highlighting how bryophyte and plant communities change and interact in newly exposed habitats following glacial retreat. Our study not only sheds light on the patterns of biodiversity establishment in grasslands but also provides valuable insights into the mechanisms driving these processes, thereby informing ecological succession-based restoration efforts in similar environments.

Methods

Study design The study was conducted in the long-term ecological research platform Ödenwinkel which was established in 2019 in the Hohe Tauern National Park, Austria (Dynamic Ecological Information Management System – site and dataset registry: https://deims.org/activity/fefd07db-2f16-46eb-8883-f10fbc9d13a3, last access: December 2023;(Junker *et al.*, 2020). A total of *n* = 135 permanent plots were established within the glacier forefield of the Ödenwinkelkees, which was covered by ice at the latest glacial maximum in the Little Ice Age around 1850. The plots represent a successional gradient spanning over 1.7km in length at an altitude ranging from 2070 to 2170 m a.s.l. with a minimum distance of 5 m between plots. Plots were defined as squares with an area of 1x1 m and were all oriented in the same cardinal direction. More detailed descriptions of the research platform, exact plot positions and details on the surrounding environment can be found in Junker et al. (2020) and Hanusch et. al (2022).

Abiotic sampling.

Plot age was estimated according to plots' relative position compared with historical records of eight deglaciation periods (year 1850, 1890, 1929, 1969, 1977, 1985, 1998, 2013) (Junker et al. 2020). To assess the substrate compositions of the plots, we estimated the percentage cover of bare ground, litter, scree and solid rock. We analysed soil samples to measure soil nutrient content (N, P, K, Mg) as well as soil pH (AGROLAB Agrar und Umwelt GmbH Sarstedt, Germany). Additionally, we recorded the mean seasonal soil temperature of the plots using temperature loggers with a resolution of 0.5°C (MF1921G iButton, Fuchs Elektronik,

Weinheim, Germany) buried 10 cm north of each plot center, at a depth of 3 cm below ground during field work in 2019 (Junker *et al.*, 2020; Ohler, Lechleitner and Junker, 2020). The thermo-loggers were set to start on 13 August 2019 and were stopped on 9 August 2020 with a total of 2048 measurements recorded on 362 days. Seasonal mean temperature was calculated based on the recordings between 13 August–16 September 2019 and 26 June–9 August 2020 representing the period in which the plots were free of snow cover before and after the winter 2019/2020.

Vascular plant and bryophyte community composition.

In the 2019 field-period, we recorded all vascular plant species (n = 93 in 135 plots), documenting their occurrence and quantifying plant coverage with a resolution of 0.1%. Likewise, we identified and recorded bryophyte species on each plot (n = 42 in 135 plots), noting their coverage at a 0.1% resolution. Both communities were sampled in the same plots, which allows a direct comparison of how different assembly processes affect their communities and potential mutual effects between these two groups.

Plant community phenotyping.

In the vegetation period 2021 (from 16 July to 23 July), we conducted an on-site plot scanning in the field with a multispectral 3D scanner 'PlantEye' (Phenospex, F500, Heerlen, the Netherlands, (He, Hanusch, Saueressig, *et al.*, 2023; Zieschank and Junker, 2023). The plant eye is equipped with an active sensor that projects a near-infrared (940 nm) laser line vertically onto the plant canopy (Kjaer and Ottosen, 2015; Maphosa *et al.*, 2017). Each scan has a resolution of < 1 pixel*mm $^{-1}$ and the data points of each scan are merged to generate a 3D point cloud out of which a set of parameters that provide community level measurements of morphological features can be generated that have been shown to correlate well with real world manual measurements (Zieschank and Junker, 2023). In this study we used digital community measurements of biomass (BM), leaf area index (LAI) and growth height-corrected light penetration depth (LPD) as proxies for vegetation structure. Settings of Software used to calculate community features followed (He, Hanusch, Saueressig, *et al.*, 2023). LPD is a

measure for the depth to which light can penetrate through the vegetation layer. The plant eye calculates this value as the distance between the on average highest 10 % and on average lowest 20 % parts of the vegetation layer that the light can penetrate through. As a result, the uncorrected, raw measurements of LPD are not independent of the vegetation's growth height. We thus calculated a growth height-corrected LPD-index by subtracting LPD from the average growth height. This index is an estimate of the height of the lowest and most dense 20 % of the vegetation in which most bryophyte species grow within the vegetation mats. Low growth height-corrected LPD values indicate a shorter, scattered vegetation; high values indicate a higher, more dense vegetation. The LAI measures the density of leaves in a given area, representing the ratio of one-sided leaf area to ground area (Coverdale and Davies, 2023); i.e. high values indicate a denser vegetation with a high number of leaves, low numbers indicate a scattered vegetation with a low number of leaves.

Comparison of vascular plant and bryophyte community composition along the successional gradient. To test our two first conjectures, we calculated Shannon-diversities of bryophyte and vascular plant communities using the R package 'vegan' v2.6-4 (Oksanen *et al.*, 2019) and correlated them with time since deglaciation as independent variable to assess successional changes in alpha-diversities of both groups using Pearson's correlation. We then correlated these diversity estimates with median percentage cover of bryophytes and vascular plants per plot using Spearman's rank correlation coefficient. This step aims to answer the question whether more diverse communities comprise smaller growth patches per species, hinting at small-scale environmental heterogeneity as a driver of diversity. We further conducted a Non-metric Multidimensional Scaling (NMDS) analysis on the community composition data of bryophytes and vascular plants to visualize changes in the species inventories along the successional gradient. Subsequently, an 'envfit' analysis was employed to determine how the communities of both focal groups change along the successional gradient using time since deglaciation as independent variable.

Comparison of biotic and environmental features, and space on community composition. We conducted a Mantel correlation using Bray-Curtis dissimilarities on vascular

plant and bryophyte species abundances with soil nutrient contents, substrate composition, temperature, and spatial distances to assess the relative importance of various biotic and abiotic filters on community composition of both groups. For all environmental features and spatial data used in Mantel correlations, we calculated Euclidean distances: The dataset on soil nutrient properties included soil pH and logarithmized soil nutrient contents (N, P, K, Mg); the dataset on substrate composition comprised the percentage cover of bare ground, litter, scree and solid rock; the temperature data resembled the mean growing season temperatures; spatial data comprised the spatial distances between plots. We repeated the Mantel correlation for n = 1000 null models generated from the bryophyte and vascular plant community data using the function nullmodel, method = 'r2d' implemented in the R package bipartite v2.19 (Dormann, Gruber and Fründ, 2008). This method generates random community tables with fixed row and column sums using the Patefield's algorithm (Patefield, 1981). To quantify the deviation of observed Mantel statistic from null model expectations (i.e. standardized effect size, SES), we calculated Z-scores as $Z = (X - Mu)/SD$. Mu and SD represent the mean r-value and standard deviation of null models, and X is the observed r-value using the bryophyte or vascular plant community data respectively. With respect to Mantel correlations of various factors with community compositions, SES provide a quantitative measure of the strength of a specific factor influencing community assembly. Observed values that lie within or below the range of the null-model expectations indicate that the specific feature does not exert a stronger or weaker effect on community assembly than random chance. Observed values that lie above null-model expectations indicate that the effect of a specific environmental feature on community assembly is stronger than expected by chance.

Calculation of ecological dispersion

To calculate ecological dispersion of bryophyte and vascular plant communities, we obtained EIV data for bryophytes from the 2017 updated version of BryoATT (Preston and Bosanquet, 2007), and plant EIV data were sourced from the official list of Ellenberg's indicator values for vascular plants (Ellenberg *et al.*, 1991). In total, EIV assignments for L (light), R (pH), F (humidity), and N (nutrients) were successfully made for n = 32 bryophyte species (i.e. 76% of

all recorded bryophyte taxa) and *n* = 87 vascular plant species (i.e. 94% of all recorded vascular plant taxa). Ecological dispersion was calculated as follows: First we calculated Euclidean distances between species based on the ordinal EIV values (De Bello *et al.*, 2021). Second, we calculated ecological dispersion based on the distances by using fd_fdis command in the fundiversity-package (v1.1.1, R). To assess the extent to which ecological dispersion (i.e. the range of ecological strategies within a community) deviates from a baseline or expected pattern along a gradient of ecological succession, we again calculated the standardized effect size (SES) of ecological dispersion using Z-scores as $Z = (X - Mu)/SD$ generated from n = 1000 null models using the bryophyte and vascular plant community data as mentioned before. Mu and SD represent the mean r-value and standard deviation of ecological dispersion from null models, and X is the observed ecological dispersion using the bryophyte or vascular plant community data respectively. With respect to ecological dispersion, SES can be seen as a metric that quantifies how much the observed dispersion differs from what would be anticipated under a null-model predicting based on random chance. SES-values of ecological dispersion equaling zero resemble that a community is as dispersed, as expected by random chance. Positive values resemble a community that is more dispersed as expected by random chance indicating that the local environment offers a habitat that allows species to colonize that have diverse ecological preferences. Negative values resemble a community that is less dispersed as expected by random chance indicating that the local environment constraints the community to include species with more similar ecological preferences than would be expected by random chance.

Structural equation analysis.

To infer the joint effects of various factors acting simultaneously on bryophyte diversity, we ran a structural equation model using the R-package lavaan v0.6-1.7 (Rosseel, 2012; Tsukahara, 2023). According to our third conjecture, we included vascular plant structural properties, substrate composition and time since deglaciation as a proxy for successful colonization events happening over time in our model in the model. As our study is set within a linear successional gradient along the glacier forefield, spatial distance is nested within time since

deglaciation (Mantel-test: $r^2 = 0.88$, $p < 0.001$) and is thus not taken into account in our model. To address potential biotic interactions with vascular plants, we used plant growth structure as a proxy for competitive effects with bryophytes growing within the vascular plant layer and calculated the diversity of substrate composition using the Shannon diversity index (from here on referred to as substrate diversity). Plant growth structure is not directly observable but can be modeled as a latent variable derived from three observable variables obtained through digital whole-community phenotyping: digital biomass estimates, leaf area index and growth-height corrected light penetration depth. Accordingly, the model was set to distinguish effects of vascular plant growth structure, the diversity of substrate composition and time-related processes on bryophyte diversity and associated ecological dispersion. All variables were standardized by z-transformation by subtracting the mean and dividing through the standard deviation. In our model, time since deglaciation acts as an exogenous variable, exerting direct influence on three components: plant growth structure, substrate diversity, and bryophyte diversity. Plant growth structure and substrate diversity again exert direct impacts on bryophyte diversity. Furthermore, the influences of time since deglaciation, plant growth structure, and substrate diversity on bryophyte diversity are mediated to have indirect effects on the ecological dispersion of bryophyte communities. As we assume that several simultaneous processes may act over time, we calculated total indirect effects of time since deglaciation on ecological dispersion (i.e. temporal processes including effects of changing substrate diversity and plant growth structure over time) and additionally calculated separate indirect effects of time since deglaciation on ecological dispersion for the effects mediated through substrate diversity, plant growth structure, and time since deglaciation in isolation (i.e. temporal processes without effects of changing substrate diversity and plant growth structure). This model enables us to evaluate how changes in the ecosystem directly or indirectly influence diversity and associated ecological dispersion among bryophytes while also accounting for simultaneous processes acting jointly on bryophyte diversity. To test whether the impact of plant growth structure on bryophytes is not due to covariance through shared extrinsic factors affecting both vascular plants and bryophytes, we developed two alternative model structures.

In these models, we replaced the latent variable representing plant growth structure with either vascular plant diversity or the first principal component axis derived from a PCA of vascular plant species compositional data.

Results

Comparison between effects of assembly processes on vascular plant bryophyte communities. Bryophyte diversity and vascular plant diversity showed a significant positive correlation with time since deglaciation ($t_{bryophtes} = 2.36$, $df_{bryophtes} = 132$, $r^2_{bryophtes} = 0.10$, $p_{bryophtes} = 0.02$; $t_{plants} = 3.39$, $df_{plants} = 131$, $r^2_{plants} = 0.10$, $p_{plants} < 0.001$; Supplementary figure 1). While bryophyte diversity showed a significant negative correlation with median patch size of bryophytes, vascular plant diversity showed a significant positive correlation ($df_{bryophtes} = 132$, $rho_{bryophtes} = -0.22$, $p_{bryophtes} = 0.01$; $df_{plants} = 131$, $rho_{plants} = 0.28$, $p_{plants} = 0.001$; Supplementary figure 2). Bryophyte succession patterns do not follow a predictable transition from early to late successional communities ($r^2 = 0.20$, $p = 0.27$; Fig. 1A) . In contrast, the composition of vascular plant species exhibited a significant change with time since deglaciation indicating a gradual transitioning from early to late vascular plant communities ($r^2 = 0.40$, $p < 0.001$; Fig. 1B).

Mantel correlations indicate distinct influences of assembly factors for bryophyte and vascular plant communities (Fig. 1C). For vascular plant composition soil nutrients emerged as the most important feature, followed by spatial distance, bryophyte composition and temperature. Vascular plant composition showed a weaker correlation with substrate composition than expected by random chance. Conversely, bryophyte communities were predominantly affected by substrate composition, let aside vascular plant composition. Temperature and soil nutrients exhibited weaker correlations with bryophyte composition than expected by random chance.

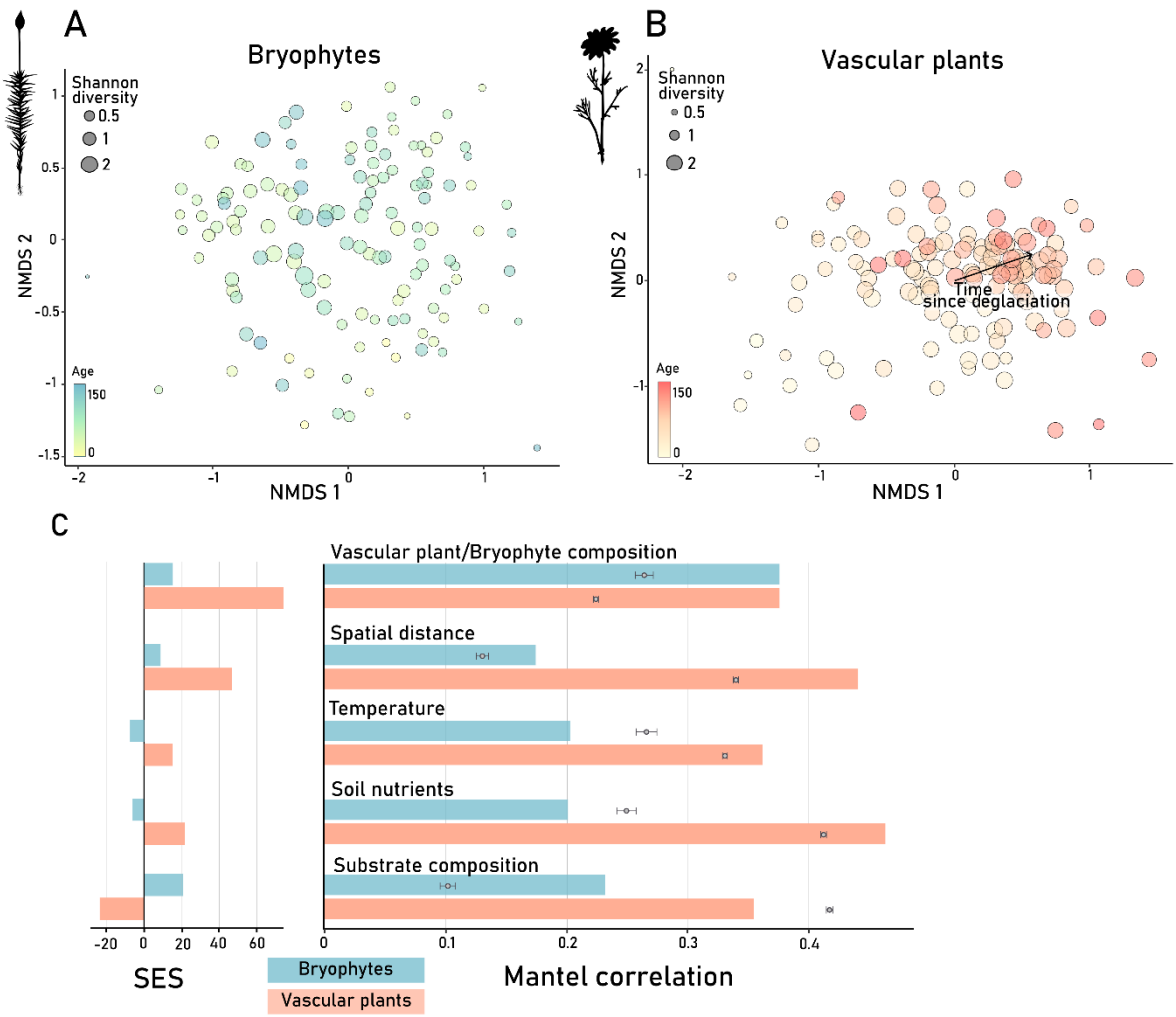

Figure 1: Nonmetric Multidimensional Scaling representation of plot similarity based on Bray-Curtis dissimilarities calculated using quantitative species composition for A) bryophyte and B) vascular plant communities with closer proximity indicating higher similarity. Circle color intensity increases with higher age and increasing circle sizes display higher Shannon diversity of communities. Arrows indicate trends of increasing plot age. C) Mantel correlation analysis of community similarity of vascular plants (red bars) and bryophytes (blue bars) with vascular plant/bryophyte composition, spatial distance, temperature, soil nutrients, and substrate composition. Barplots on the right side of the figure display observed Mantel r-values, with corresponding null model expectation. Mean Mantel r-values of null models denoted by circles and their standard deviation represented as whiskers. The left side shows standardized effect sizes for each correlation highlighting the differential affection of vascular plants and bryophytes to assembly processes. Silhouette images were obtained from PhyloPic (http://phylopic.org) under a public domain license (CC0 1.0 license).

Ecological dispersion. Ecological dispersion exhibited a significant linear increase for bryophyte communities along the successional gradient (t = 2.97, df = 126, r = 0.26, p < 0.01, Fig. 2A), in contrast to vascular plant communities, which showed no such trend (t = -0.58, df = 128, r = -0.05, p = 0.56, Fig. 2B). Bryophytes and vascular plants demonstrated primarily negative SES-values, with median values of -3.5 (SD = ±5.4) for bryophytes and -2.95 (SD =

±6.73) for vascular plants suggesting significant constraints on their ecological dispersion across the successional gradient. Bryophytes demonstrated a significant linear increase in the standardized effect sizes of ecological dispersion indicating a diminishing constraint on ecological dispersion (t = 2.01, df = 126, r = 0.18, p = 0.04), while vascular plants did not show a significant pattern in SES (t = -1.14, df = 128, r = -0.10, p = 0.25).

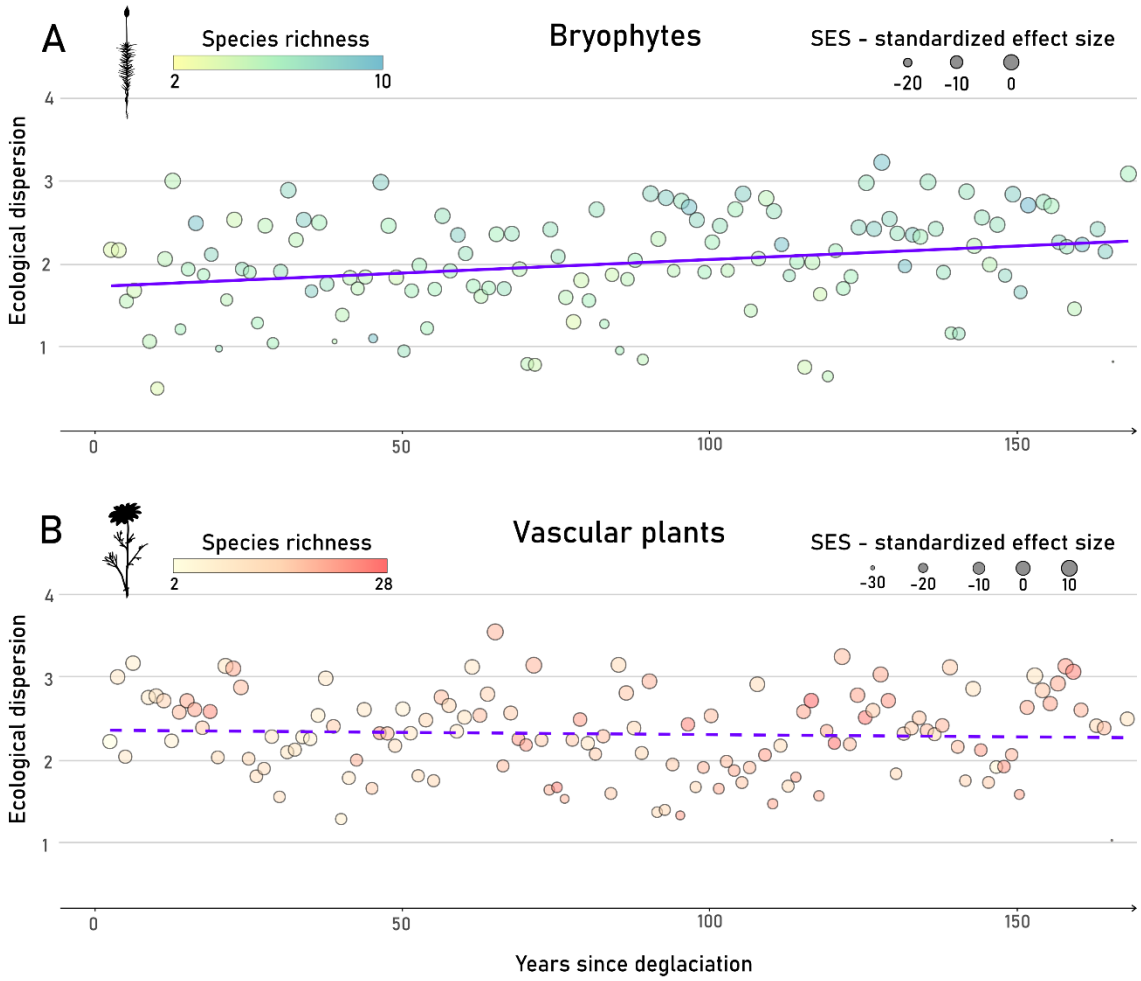

Figure 2: Ecological dispersion along the successional gradient of the Ödenwinkel glacier forefield in A) vascular plant and B) bryophyte communities. The deviation of observed ecological dispersion from null model expectations is illustrated by circle sizes. Circle color depicts species richness. Vascular plant communities exhibit non-monotonic variations in ecological dispersion over time. In contrast, bryophyte communities demonstrate a significant increase in ecological dispersion, suggesting a trend towards a community with less homogenous environmental conditions as their ecological preferences. Silhouette images were obtained from PhyloPic (http://phylopic.org) under a public domain license (CC0 1.0 license).

Structural equation model. The structural equation model provided good model fit (Model fit: $p_{chi\text{-}square} > 0.05$; CFI > 0.95; TLI ≥ 0.9; SRMR = 0.05; RMSEA = 0.05) and revealed significant influences of all exogenous variables on bryophyte diversity (Fig. 3). Time since deglaciation ($\beta = 0.47$, $p < 0.01$) and substrate diversity ($\beta = 0.22$, $p = 0.02$) positively affected bryophyte diversity. Conversely, plant growth structure showed a significant negative correlation with bryophyte diversity ($\beta = -0.56$, $p < 0.01$) indicating that denser vegetation structure had a negative effect on bryophyte diversity. Time since deglaciation had a negative effect on substrate diversity ($\beta = -0.23$, $p = 0.13$) but a positive effect on plant growth structure ($\beta = 0.51$, $p < 0.01$). Bryophyte ecological dispersion was positively affected by bryophyte diversity ($\beta = 0.82$, $p < 0.01$) and experienced positive indirect effects mediated through bryophyte diversity by substrate diversity ($\beta = 0.18$, $p = 0.02$) while plant growth structure had a negative indirect effect on ecological dispersion. The total indirect effects of time since deglaciation on ecological dispersion (i.e. temporal processes including effects of substrate diversity and plant growth structure) were non-significant ($\beta = 0.05$, $p > 0.05$) indicating that several simultaneous processes may act over time that offset each other. Thus, the indirect effects of time since deglaciation on ecological dispersion were separately calculated for the effects mediated through substrate diversity ($\beta = -0.05$, $p > 0.05$), plant growth structure ($\beta = -0.23$, $p = 0.03$), and time since deglaciation in isolation (i.e. temporal processes without effects of substrate diversity and plant growth structure; $\beta = 0.33$, $p < 0.01$). The two alternative models in which we replaced the latent variable representing plant growth structure with either vascular plant diversity or the first PC-axis of vascular plant composition did not show significant effects of vascular plants on bryophyte diversity and associated ecological dispersion (Supplementary tables 1-3).

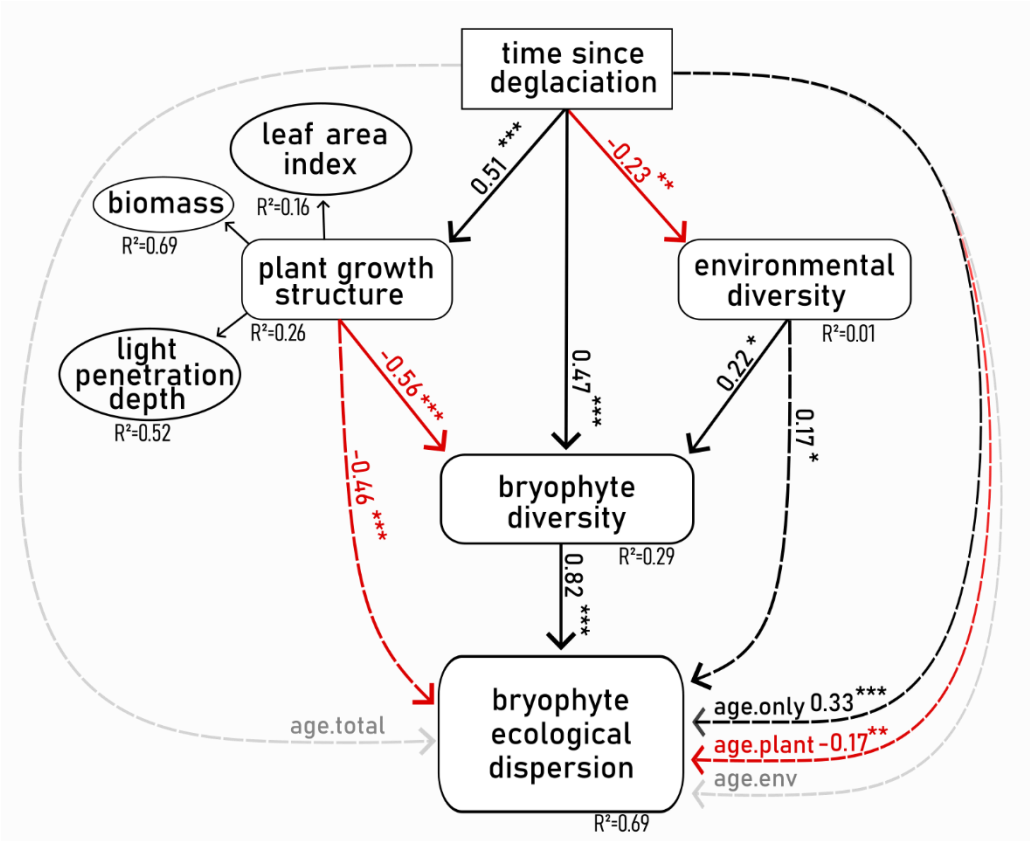

Figure 3: Structural equation analysis of environmental drivers and plant growth structure on bryophyte diversity and Standardized Effect Sizes (SES) of bryophyte ecological dispersion. The path diagram presents direct effects as solid lines. Time since deglaciation influences bryophyte diversity (through species addition over time), abiotic environmental factors, and plant growth structure (modeled as a latent variable comprising digital biomass and light penetration depth), while the latter two have a direct effect on bryophyte diversity, and abiotic environmental factors influence plant growth structure. Indirect effects on the SES of bryophyte ecological dispersion are represented as dotted lines and were calculated through mediation analysis of these variables' direct impacts on bryophyte diversity. Standardized path coefficients are shown for significant relationships, with red coloration indication a negative and black coloration indicating a positive effect.

Discussion

Our study revealed that although bryophyte and vascular plant diversity significantly increase with time since deglaciation, both groups underlie distinct assembly patterns. In contrast to bryophyte composition, vascular plant communities transition predictably along the successional gradient. While vascular plant composition is mostly (i.e. stronger than expected by random chance) affected by spatial distance, soil nutrients and temperature but not by substrate composition, bryophytes were mostly affected by spatial distance and the substrate composition but not by soil nutrients and temperature. We further emphasized mutual

interactions, namely competitive exclusion through the development of denser vascular plant mats as an important driver of diversity and ecological dispersion of bryophyte communities over grassland succession. However, while increasing vascular plant growth leads to a decrease in bryophyte diversity and ecological dispersion, bryophyte diversity is buffered against vascular plant dominance over succession through time-related processes and environmental heterogeneity, most likely opportunistic colonization events on weathered substrate.

Diverging importance of assembly processes for bryophytes and vascular plants Our findings show that bryophyte composition is generally less impacted by spatial distance than vascular plant communities, confirming that dispersal limitation plays a minor role in shaping bryophyte distribution within successional seres (Cichini *et al.*, 2011). Despite other studies showing significant interdependencies of bryophytes with soil microclimate in alpine grasslands (Jaroszynska *et al.*, 2023), soil temperature did not show a stronger correlation with bryophyte community composition than expected by random chance in our study. A previous study examining the microclimatic variability in alpine meadows showed that terrain exposure best explains local soil temperature (Ohler, Lechleitner and Junker, 2020). This suggests that in ecosystems undergoing primary succession, bryophyte communities may be effectively insulated from the soil's microclimatic conditions as they grow on a wide range of terrain features, such as rocks or boulders that stick out of the vegetative layer and are exposed in varying angles to the sun thus experiencing different temperature regimes that may not be fully captured through measurements of the soil temperature. Substrate composition had the strongest impact on the community composition of bryophytes while soil nutrient content did affect bryophyte composition less than expected by random chance. Bryophytes directly take up water and nutrients through their leaf surfaces, bypassing the need for a root system (Bates, 1992). This capability enables them to flourish in nutrient-poor environments and colonize diverse, non-soil-bound substrates, making them less dependent on soil nutrients than vascular plants (Smith, 1982). Recent research revealed a surprisingly high degree of environmental heterogeneity even at fine spatial scales within grassland ecosystems (Conti *et*

al., 2017; Price *et al.*, 2017) and especially glacier forefields are highly dynamic ecosystems that foster a variety of substrates facilitating the establishment of various bryophyte species. Our results thus confirm previous findings that substrate composition is a main driver of bryophyte community composition (e.g. Hylander *et al.*, 2005; Caruso and Rudolphi, 2009; Chen *et al.*, 2017; Spitale, 2017)

Vascular plants shape bryophyte succession through biotic interactions Contrary to our initial conjecture, we found that ecological dispersion for bryophyte communities increases along the successional gradient. To better understand this pattern, we expanded our analysis to include potential biological interactions between vascular plants and bryophytes via plant growth structure, and time since deglaciation as a proxy for successful colonization events that occur over time (Legendre *et al.*, 2005; Lowe and McPeek, 2014; Hanusch *et al.*, 2022). The structural equation model highlights a negative influence of plant growth structure on bryophyte diversity and associated ecological dispersion, leading these communities towards species inventories that share more homogeneous ecological preferences within more dense and complex vascular plant communities potentially through competitive effects for light and other resources. Despite the ongoing competition with vascular plants, bryophyte communities exhibit greater ecological dispersion with increasing successional age and more diverse substrate compositions. Given that bryophytes in glacier forefields are not considered dispersal limited (Cichini *et al.*, 2011), the observed increase in diversity cannot be solely attributed to slow dispersal events stretching over longer time periods as observed in vascular plant communities (Ulrich *et al.*, 2016; Hanusch *et al.*, 2022; Cantera *et al.*, 2024). For bryophytes, site-specific processes (e.g. substrate weathering), that allow different species of bryophytes to opportunistically and quickly colonize niches as they become available (Prach and Walker, 2020) appear to be more important for successful colonization events. This assumption is underscored by a significant decrease of bryophyte diversity with median percentage cover per bryophyte species showing that a wide range of bryophytes are able exploit even small-scale niche opportunities within a finely varied environmental mosaic. We thus conclude that the mechanisms shaping bryophyte succession in grassland ecosystems encompass a range

of interrelated processes: Successful opportunistic colonization events of available (microhabitat-)niches within a heterogenous environment increase and buffer bryophyte diversity over time against biotic interactions, particularly competition with vascular plants. These processes do not act in isolation but are tightly interwoven, jointly determining the trajectory of bryophyte succession in alpine grassland. Our study especially highlights the influence of biotic interactions with vascular plants in shaping the patterns of bryophyte diversity throughout primary succession. These insights not only provide a mechanistic understanding of the initial development of natural ecosystems but also pave the way for more nuanced future research on the dynamics of plant community development.

Adapting a community feature perspective for ecological research Our study aligns with existing research indicating a negative correlation between the biomass of vascular plants and bryophytes (Ingerpuu, Kull and Vellak, 1998; Virtanen *et al.*, 2000; Bergamini *et al.*, 2001). Yet, biomass only represents a basic approximation of the vascular plant layer's structure and the environmental conditions encountered by bryophytes, particularly in terms of light availability (Spehn *et al.*, 2000; Bergamini *et al.*, 2001). By complementing the plant eye's non-destructive digital measurements of biomass with the leaf area index and growth height-corrected light penetration depth, our approach provides a more accurate representation of the three-dimensional distribution of plants within an ecosystem and the conditions experienced by bryophytes growing within the vegetative layer than traditional measurements of plant biomass and structure (Coverdale and Davies, 2023). An additional benefit of 3D-laser scanning techniques is provision of phenotypic properties of whole plant communities (i.e. *community features* sensu He, Hanusch, Saueressig, *et al.*, (2023)) rather than integrating species-specific traits to community-wide indices. Using community features focuses the analysis on broader effects within ecological communities by acknowledging effects, that cumulate as the sum and mixture of impacts arising from several plant individuals and species. Adopting such a "community feature perspective" could thus provide ecologists with fresh insights into competition effects and other ecological processes that go beyond individual or species-level analyses (He, Hanusch, Saueressig, *et al.*, 2023; Zieschank and Junker, 2023).

Ecological dispersion as a measure for a community's ecological tolerance

In our study, we applied Ellenberg Indicator Values to assess the ecological conditions of the plants' surrounding environment and interpreted their dispersion as a measure of the diversity of ecological strategies within a community. A community with high ecological dispersion indicates a broad range of ecological preferences, suggesting that species within the community can thrive in a variety of habitats and environmental gradients. Conversely, low ecological dispersion may indicate that species are more specialized and adapted to specific conditions, implying a narrower range of ecological tolerance. Understanding ecological dispersion can thus provide insights into the resilience and adaptability of a community to environmental changes and disturbances. In our study, the calculation of ecological dispersion is based on Ellenberg values that were initially developed for vascular plants in Central Europe and have later been adapted to incorporate bryophytes (Düll, 1992; Simmel, Ahrens and Poschlod, 2021). While Hedwall et al. (2019) affirmed the utility of EIVs beyond their original geographic confines, they also highlighted a diminishing applicability for vascular plants in the extreme north. This raises questions about the EIVs' adaptability to alpine settings, which, despite their Central European geography, may mirror environmental characteristics of northern latitudes. This gap presents an avenue for further exploration, particularly regarding the applicability of EIVs for bryophytes in high-altitude ecosystems. However, our preliminary view suggests that the stenotopic nature (i.e., narrowly adapted to specific environmental conditions) of bryophytes when compared to vascular plants, may not significantly hinder the application of EIVs for bryophytes in these environments. While EIV-based ecological dispersion does not capture the full range of functional traits that can influence ecological interactions, such as reproductive strategies, growth forms, or dispersal mechanisms, it proofed to be a valuable tool for assessing a mechanistic understanding for certain vegetation responses to changing biotic and abiotic conditions in our study.

Conclusion

Our research contributes significantly to the discourse on community assembly and successional research (e.g. Drake, 1990; Chang and HilleRisLambers, 2016; Junker *et al.*, 2021; Hanusch *et al.*, 2022; He, Hanusch, Ruiz-Hernández, *et al.*, 2023; Cantera *et al.*, 2024), focusing on the interdependencies between bryophyte and vascular plant communities within alpine successional gradients following glacial retreat. Our findings underscore the complex dynamics of ecological succession, highlighting that bryophyte diversity is buffered against the dominance of vascular plants. This buffering occurs as bryophytes surpass the constraints typically associated with vascular plant growth by opportunistically colonizing diverse microhabitat niches that form as succession progresses.

Incorporating advanced phenotyping methods, such as community features of vegetation structural complexity, and estimates of ecological dispersal could offer deeper insights into the ecological strategies employed by plants in adapting to changing environments. We thus encourage researchers to further employ whole-community phenotyping along with measures of vegetation structure and indices of a community's ecological tolerances. Adapting these methods with traditional individual-based ecological research approaches not only enhances our understanding of primary succession but will also provide valuable insights for the conservation and management of alpine grassland ecosystems in the face of global environmental changes.

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