Coexistence despite competition: Vegetation structural complexity shapes bryophyte diversity over succession.

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Abstract

Vascular plants and bryophytes are key components driving the development of diverse ecosystems following glacial retreat. Unravelling biotic interaction mechanisms between both groups is crucial for understanding the generation of biodiversity under natural conditions. Focusing on a 170-year primary succession gradient in the Austrian Alps, this study examines mechanisms of competitive interaction between vascular plants and bryophytes during the initial phases of ecosystem establishment. Using data on vegetation structural complexity derived from multispectral 3D-scans of vegetation, the local habitat's substrate diversity, and vascular plant and bryophyte taxonomic composition, this study provides a mechanistic understanding of plant-plant interactions within a natural ecosystem. Vascular plants dominate the vertical niche through complex growth structures, which negatively affect bryophyte diversity. A pattern that is uniquely detectable by estimates of vegetation structural complexity. Path analysis confirms that vegetation structural complexity drives competition through a reduction of realized niche sizes of bryophyte communities, a concept introduced here as ecological dispersion. This study demonstrates the advantages of 3D-laser-scanning approaches in capturing the complexity of vegetation structure and its impacts on ecosystem dynamics. The findings underscore the importance of vegetation structural complexity in the establishment and maintenance of natural ecosystems and underscore the potential of 3D-

laser-scanning methods in future studies to inform biodiversity conservation and restoration approaches in similar environments.

Introduction

Although the importance of physical vegetation structure for ecosystem functioning and biodiversity was recognized early in ecological research (MacArthur, MacArthur and Preer, 1962; Odum, 1969), research in this area has only recently gained momentum, driven largely by advances in remote sensing technology (LaRue, Fahey, *et al.*, 2023). Tools such as portable 3D laser scanners now allow to accurately estimate the arrangement of physical vegetation structures at various scales and resolutions, and the modeling of vegetation metrics from data that previously required labor-intensive fieldwork or destructive field-sampling (Catchpole and Wheeler, 1992; Gámez and Harris, 2022; Fei *et al.*, 2023; Zieschank and Junker, 2023).

Metrics of vegetation structural complexity (VSC) are considered valuable surrogates for quantifying the occupancy of plants in 3D-niche space (LaRue, Fahey, *et al.*, 2023), which is closely associated with ecosystem functioning and biotic interactions with other organisms (Srivastava, 2006). As VSC expands the three-dimensional habitat space for other organisms, it increases niche diversity, and promotes resource partitioning, making it widely considered beneficial for biodiversity. Accordingly, positive associations between VSC and species diversity have been demonstrated for plant (Coverdale and Davies, 2023), animal (Tews *et al.*, 2004; Traylor *et al.*, 2022), and belowground diversity (Lang et al., 2023). However, most of these insights are derived from forest ecosystems, where trees create strong vertical stratification with a distinct vertical layering (Davies and Asner, 2014; Gough *et al.*, 2019). Grasslands, in contrast, exhibit limited vertical stratification, as most plants grow within the same horizontal layer where they compete for light and other resources Vascular plants are expected to possess a competitive advantage due to their larger size and greater structural robustness, when competing with smaller-growing plants, such as bryophytes. This enables vascular plants to dominate the vertical axis, thereby restricting bryophytes'

access to essential resources like light and space. Thus, the condensed horizontal structure of grasslands challenges the assumption that VSC may universally promote the diversity of associated organismal groups within a shared habitat.

Successional gradients that develop into grassland, such as those forming after glacial retreat, provide an ideal opportunity to study how changes in VSC impact other organisms and interactions within these systems. Ecological successions are characterized by a gradual increase in vascular plant biomass, and thus VSC, which in turn will affect bryophytes growing within the same habitat. However, estimating biotic interactions from observational field-data is notoriously challenging, and particularly so in the context of ecological succession (Blanchet, Cazelles and Gravel, 2020; Hanusch *et al.*, 2023, 2024). Accordingly, analyses based on field observations should be complemented by clear assumptions on the ecological mechanisms driving these interactions to enhance interpretation and reliability:

As succession progresses, vascular plants increasingly dominate the shared habitat by developing more complex growth structures. These structures form dense mats that occupy much of the available space and significantly alter local habitat conditions (Breen and Lévesque, 2006; Cutler, Belyea and Dugmore, 2008; Gavini *et al.*, 2019). Within these mats more uniform microenvironmental conditions prevail that are marked by altered temperature, light, and moisture levels, ultimately affecting the growth and diversity of bryophytes growing within them (van Tooren *et al.*, 1990; Bergamini *et al.*, 2001; Werger *et al.*, 2002; Fergus, Gerighausen and Roscher, 2017). Bryophyte communities are expected to respond dynamically to these changes in local environmental conditions, reflected in shifts of their realized ecological niches. Ecological Indicator Values (EIVs), ordinal scales representing species' growth optima along environmental gradients, provide a tool for assessing such shifts (Diekmann, 2003). Assessing the dispersion of growth optima across multiple environmental factors at the community scale, provides a measure that approximates the community's multidimensional realized niche. High dispersion indicates a diverse habitat capable of supporting species with a variety of ecological preferences, whereas low dispersion indicates more homogenous habitats favoring species with similar ecological

preferences. Accordingly, the dispersion of growth optima of a community, introduced here as *ecological dispersion*, could serve as a framework for exploring how VSC homogenizes local habitat conditions in grasslands, ultimately impacting bryophyte diversity in the process.

Studying structural properties of vascular plant communities in grassland usually required destructive field measurements that can significantly alter or destroy the plant communities (Catchpole and Wheeler, 1992; Zehm, Nobis and Schwabe, 2003). As an alternative to traditional destructive methods, the use of 3D multispectral plant scanning technology provides a non-invasive way to capture morphological features of entire plant communities. The scans allow to obtain various community features (Zieschank and Junker, 2023), such as digital biomass or estimates of vegetation structure. Similar to community-weighted means, these estimates represent the trait frequency distribution across an entire community. Estimating community features through 3D-laser-scanning thus offers new opportunities to study how VSC affects fine-scale ecological processes, while circumventing labor-intensive species-specific, or individual-based measurements (He, Hanusch, Saueressig, *et al.*, 2023).

Focusing on a 170-year primary succession gradient in the Ödenwinkel glacier forefield, Austrian Alps, this study investigates the role of vascular plant structural complexity in shaping bryophyte diversity during the development of a natural ecosystem. It is shown that vegetation structural complexity has a negative effect on bryophyte diversity which is caused by a reduction of the bryophyte communities' realized niche sizes during succession. Comparing estimates of VSC obtained through whole-community 3D multispectral laser-scanning with traditional vascular plant community metrics, such as species composition, plant cover, and taxonomic or functional diversity, revealed that VSC uniquely revealed competitive interactions. By capturing the spatial and physical arrangement of vegetation, structural complexity offers a clearer understanding of the natural dynamics driving the development of biodiverse ecosystems. It thus holds the potential to inform succession-based restoration approaches in similar environments.

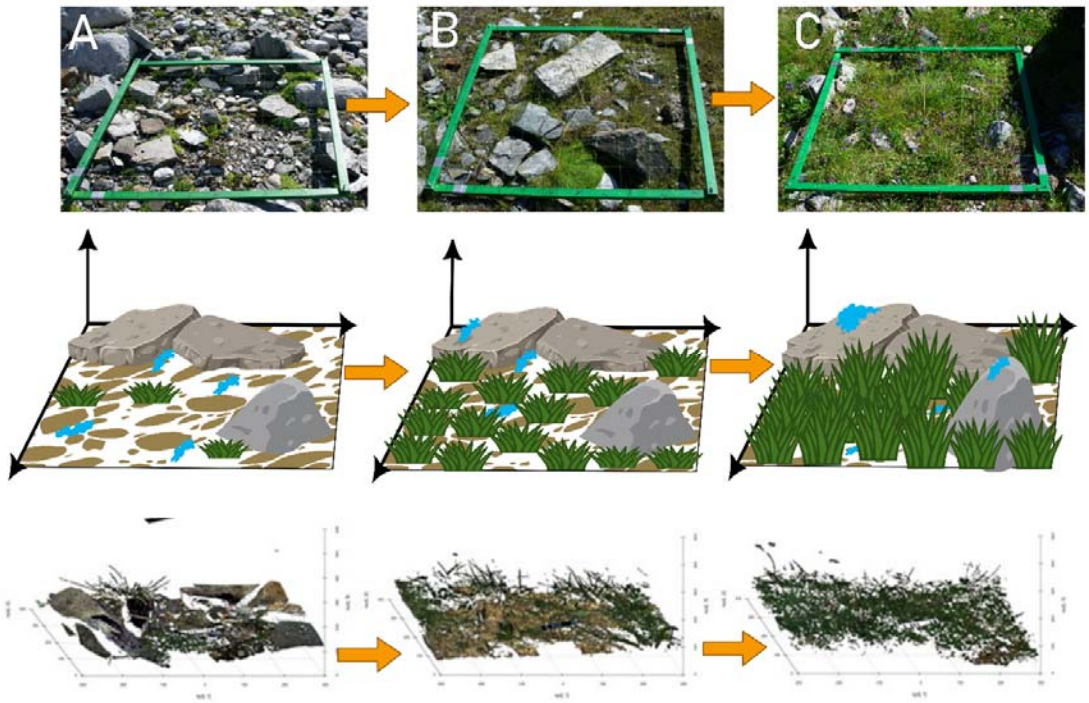

Figure 1: Conceptual overview of the successional increase in vascular plant structural complexity. Each triplet, comprising a photograph, 3D conceptual sketch, and 3D plant scan, represents a plot with increasing successional age and vegetation structural complexity. In the conceptual sketches, bryophyte patches are highlighted in blue to illustrate changes in the habitats exploited by bryophyte species and their realized ecological niches in response to increasing plant structure. As structural complexity increases, it homogenizes local habitat conditions, while substrate weathering facilitates bryophyte colonization of habitats such as bare rock sticking out from the vegetation. This process buffers bryophyte diversity against vascular plant dominance over time. (A) Photograph, sketch and scan of a plot with low vegetation structural complexity and high proportion of open substrate or rocks, approximate time since deglaction: 6 years (B) medium structural complexity, approximate time since deglaction: 35 years (C) high structural complexity, approximate time since deglaction: 100 years. 3D-scans adapted from He *et al.*, (2023) and sketches published by OpenClipArt, permission granted under CC BY 3.0 and CC0 1.0 Universal.

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: November 2024; 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. A full dataset, i.e. no NA value for any variable, was used for this study representing a subset of *n* = 107 out the total *n* = 135 plots. 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).

Biotic and 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 composition of the plots, the percentage cover of bare ground, litter, scree and solid rock were estimated.

During the 2019 field season, all bryophyte and vascular plant species on each plot were identified and recorded (*n* = 42 in 135 plots), noting their coverage at a 0.1% resolution. This was accomplished by using 1m² vegetation relevés subdivided into 100 squares, each measuring 10 × 10 cm. Likewise, all vascular plant species (n = 93 across 135 plots) were recorded (He, Hanusch, Ruiz-Hernández, *et al.*, 2023). Both communities were sampled in the same plots, which allows a direct comparison of potential interactions between both groups (Junker *et al.*, 2021). Furthermore, vascular plant functional traits were measures based on estimates of leaf area and weight, specific leaf area, and growth height as described in Junker *et al.* (2020) and He, Hanusch, Saueressig, *et al.* (2023).

Plant community phenotyping and vegetation structural complexity.

In the vegetation period 2021 (from 16 July to 23 July), an on-site plot scanning in the field was conducted with a multispectral 3D scanner 'PlantEye' (Phenospex, F500, Heerlen, the Netherlands). For a detailed description of the set-up and data obtained, see Zieschank and Junker, (2023) and Supplemental Figure 1. 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. From these clouds, a set of community level morphological features can be estimated that have been shown to correlate well with real world manual measurements (Zieschank and Junker, 2023). In this study digital community measurements of biomass (BM), leaf area index (LAI) and growth height-corrected light penetration depth (LPD). Settings of Software used to calculate community features followed He *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. Thus, a growth height-corrected LPD-index was calculated by subtracting LPD from the on average highest 10 %. 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 vascular plant 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 sparse vegetation with a low number of leaves. The estimates of BM represent a digital approximation of the standing biomass, and is calculated as the product of height and 3D leaf area.

Vegetation structural complexity is not directly observable and there is still no consensus over the definition of structural complexity or how to measure it (Atkins *et al.*, 2018; Loke and Chisholm, 2022). In this study vegetation structural complexity is quantified as a univariate variable generated through a principal component analysis (PCA; R package 'vegan' v2.6-4; Oksanen et al., 2019) conducted on estimates of BM, LAI, and growth height-corrected LPD derived from 3D laser scanning. The first principal component (PC1), which explained 84.0% of the variance, was used as the structural complexity metric.

Traditional metrics of vascular plant communities

To examine whether vegetation structural complexity adds additional information or is redundant to traditional vascular plant community metrics in explaining bryophyte diversity, multiple metrics were assessed: vascular plant species cover, species richness, taxonomic composition, functional diversity. Species richness was calculated as the number of vascular plant species per plot, taxonomic composition was summarized using the first principal component (15% explained variance) from a PCA of vascular plant species composition. Functional diversity was quantified as functional divergence using the fd_fdiv command in the fundiversity-package (v1.1.1, R) based on trait measurements of leaf area and weight, specific leaf area, and height. High values of functional divergence suggest functional niche differentiation, which may capture similar aspects of spatial niche occupancy as structural complexity. Species cover was measured as the total horizontal extent of vascular plants on each plot. Pearson correlations were conducted to evaluate the relationships among these metrics and structural complexity, as well as with bryophyte diversity.

Calculation of ecological dispersion

Ecological dispersion provides a novel framework for examining biotic interactions by highlighting shifts in community tolerances driven by changing habitat conditions. Vascular plant structural complexity acts as an important ecological feature that alters local habitat conditions, which can be analyzed through the niche optima of bryophyte species growing among the vascular plant layer on a plot. High ecological dispersion values indicate diverse environmental conditions that support species with varying ecological preferences, whereas low values reflect more homogenous habitats favoring species with similar ecological preferences. To calculate ecological dispersion of bryophyte communities, EIV data for bryophytes were obtained from the 2017 updated version of BryoATT (Preston and Bosanquet, 2007). 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.

To evaluate whether the selected Ecological Indicator Values (EIVs) represent ecologically meaningful variables, the relationship between each EIV and the structural complexity

variable was assessed individually using Spearman's rank correlation. Spearman correlation was chosen because a linear relationship was not expected between the community-weighted means and structural complexity. This is due to the community-weighted means being largely influenced by the occurrence of specific species with associated EIV values, which can cause abrupt shifts in the community means. Community-weighted means of F and N showed a significant positive relationship with structural complexity (rho_F = 0.19, p_F = 0.05; rho_N = 0.23, p_N = 0.01), while community-weighted means of L showed a significant negative relationship (rho_L = -0.23, p_L = 0.01), and no significant relationship with R (rho_R = -0.13, p_R = 0.17).

In a next step, ecological dispersion was calculated as follows: First the ordinal EIV for each species were transformed into a continuous form. A multidimensional functional space was built using principal coordinate analysis (ape v5.7-1 package, R) based on Euclidean-distances of the four EIV-values (Maire *et al.*, 2015; De Bello *et al.*, 2021). Second, ecological dispersion was calculated based on the axes coordinate of each species in each of the four dimensions by using fd_fdis command in the fundiversity-package (v1.1.1, R).

Path analysis

To infer the effects of vascular plant structural complexity on bryophyte diversity, a path analysis was conducted using the R package lavaan (v0.6-1.7; Rosseel, 2012; Tsukahara, 2023). Path analysis was selected for its ability to disentangle direct and indirect effects among multiple interacting variables and obtain estimates of the explained variance (R^2) by predictors. The model included key variables hypothesized to influence bryophyte diversity: Time since deglaciation was included as a proxy for plot age, representing the increasing likelihood of heterogeneous dispersal events over time (Hanusch *et al.*, 2022; Ficetola *et al.*, 2024). Vegetation structural complexity served as a proxy for competitive interactions, capturing how the physical structure of vascular plant communities may restrict bryophytes growing within the plant layer. To account for potential shared extrinsic factors affecting both vascular plants and bryophytes, substrate diversity, calculated as the Shannon diversity of relative cover of substrate types (bare ground, litter, scree, and solid rock), was included as a

univariate variable to represent environmental heterogeneity. Substrate diversity showed a significant correlation with bryophyte and vascular plant species composition (Mantel-test: Mantel $r_{bryophytes} = 0.26$, $p_{bryophytes} < 0.001$; Mantel $r_{vascular\ plants} = 0.36$, $p_{vascular\ plants} < 0.001$), highlighting its relevance to both groups. As the study was conducted along a linear successional gradient in a glacier forefield, spatial distance was highly correlated with time since deglaciation (Mantel-test: Mantel $r = 0.88$, $p < 0.001$) and was therefore excluded from the model to avoid multicollinearity. By incorporating these variables, the analysis aimed to disentangle the mechanisms driving bryophyte diversity over succession. Specifically, it sought to determine whether changes in bryophyte diversity are primarily shaped by environmental heterogeneity, dispersal processes, or interactions with vascular plants. All variables were standardized by z-transformation by subtracting the mean and dividing through the standard deviation.

In the model, time since deglaciation is included as an exogenous variable, exerting direct effects on vegetation structural complexity, substrate diversity, and bryophyte ecological dispersion. Vegetation structural complexity and substrate diversity, in turn, have direct impacts on bryophyte ecological dispersion, representing the influence of vascular plant competition and environmental heterogeneity, respectively. Additionally, the model examines indirect effects of time since deglaciation, vegetation structural complexity, and substrate diversity on bryophyte diversity, mediated through ecological dispersion. Ecological dispersion, representing the variation in the bryophyte communities' ecological niches, is included to provide a mechanistic understanding of how structural and environmental factors influence bryophyte diversity by restricting the number of species that are able to grow under certain habitat conditions.

To evaluate whether vegetation structural complexity provides additional information compared to traditional plant community metrics, four alternative model structures were developed. In each model vegetation structural complexity was replaced with one of the traditional plant community metrics: vascular plant cover, vascular plant species richness, vascular plant species composition (first axis from PCA), or vascular plant functional

divergence. The comparison of these models aimed to determine whether structural complexity captures unique aspects of plant-plant interactions that other metrics fail to address.

Results

Comparison between vascular plant community metrics and their relationship with bryophyte diversity.

Structural complexity showed a significant negative relationship with bryophyte diversity (t = -2.00, df = 104, r^2 = 0.04, p = 0.04), which was not observed with other vascular plant community metrics (Figure 2). Plant cover exhibited a non-linear relationship with bryophyte diversity (t = -2.68, df = 103, r^2 = 0.07, p < 0.01), while plant species richness showed a marginally significant positive linear relationship (t = 1.80, df = 104, r^2 = 0.03, p = 0.06). Neither species composition (p = 0.64) nor functional divergence (p = 0.50) demonstrated a significant linear relationship with bryophyte diversity. Among the vascular plant community metrics, structural complexity showed the highest correlation with plant cover (r = 0.78, p < 0.01), followed by species composition (r = 0.58, p < 0.01), species richness (r = 0.38, p < 0.01), and the lowest correlation with functional divergence (r = 0.23, p = 0.02).

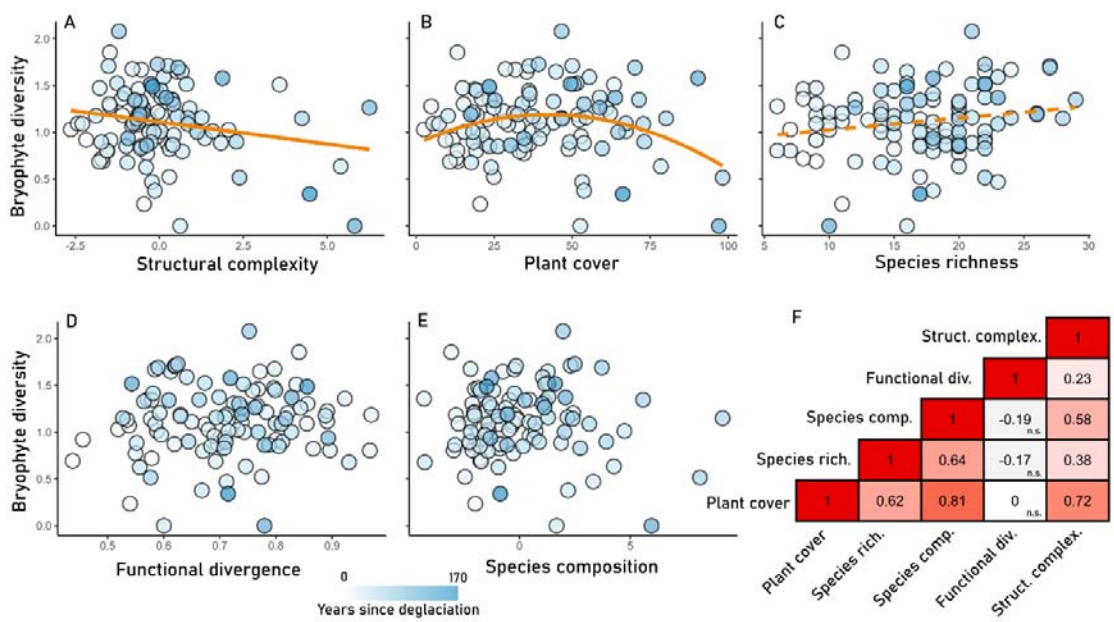

Figure 2: Relationship between bryophyte diversity (BD) and five metrics of the vascular plant community growing in the same habitat across n = 107 plots along a primary succession gradient spanning 170 years. Darker points indicate older plots. Metrics of vegetation structural complexity derived from three-dimensional laser scanning provide distinct information compared to traditional two-dimensional estimates based on relative percentage cover per species (used for vascular plant cover, community composition, and functional divergence) or vascular plant species richness counts. (A) significant negative linear relationship between vascular plant structural composition, estimated as the first axis of a PCA on digital biomass, leaf area index, and height-corrected light penetration depth, and BD. (B) significant non-linear relationship (quadratic fit) between vascular plant cover and BD. (C) marginally significant positive linear relationship between vascular plant richness and BD (D) non-significant relationship between vascular plant community composition and BD. (E) non-significant relationship between vascular plant functional diversity and BD. (F) Pearson correlation heatmap showing relationships among the five plant community metrics. The heatmap highlights the degree of association between these metrics, providing insights into potential overlaps or unique contributions of each measure.

Path analysis

The path analysis provided good model fit (Model fit: $p_{chi\text{-}square}$ > 0.05; CFI > 0.95; TLI > 0.9; SRMR < 0.05; RMSEA = 0.08 with lower bound of confidence interval = 0) and revealed significant influences of all exogenous variables on bryophyte diversity (Figure 3). Time since deglaciation (β = 0.25, p = 0.01) and substrate diversity (β = 0.20, p = 0.03) positively affected bryophyte ecological dispersion. Conversely, plant growth structure showed a significant negative correlation with ecological dispersion (β = -0.29, p < 0.01) indicating that denser vegetation structure had a negative effect on the realized niche size of the bryophyte community. Time since deglaciation had a negative effect on substrate diversity (β = -0.26, p < 0.01) but a positive effect on plant growth structure (β = 0.42, p < 0.01). Bryophyte diversity was positively affected by bryophyte ecological dispersion (β = 0.83, p < 0.01) and experienced positive indirect effects by substrate diversity (β = 0.17, p = 0.03) while plant growth structure had a negative indirect effect (β = -0.24, p < 0.01). 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 (β = 0.07, p = 0.40) indicating that several simultaneous processes may act over time that offset each other. Thus, the indirect effects of time since deglaciation on bryophyte diversity were separately calculated for the effects mediated through substrate diversity (β = -0.04, p = 0.09), plant growth structure (β = -0.10, p = 0.02), and time since deglaciation in isolation (i.e. temporal processes without

effects of substrate diversity and plant growth structure; β = 0.21, p = 0.02). The four alternative models, in which vegetation structural complexity was replaced with one of the four other vascular plant community metrics (vascular plant species richness, functional diversity, cover, and composition) showed no significant effects of these variables on bryophyte diversity or associated ecological dispersion, which highlights vegetation structural complexity as the primary factor influencing bryophyte diversity (Supplementary tables 1-5).

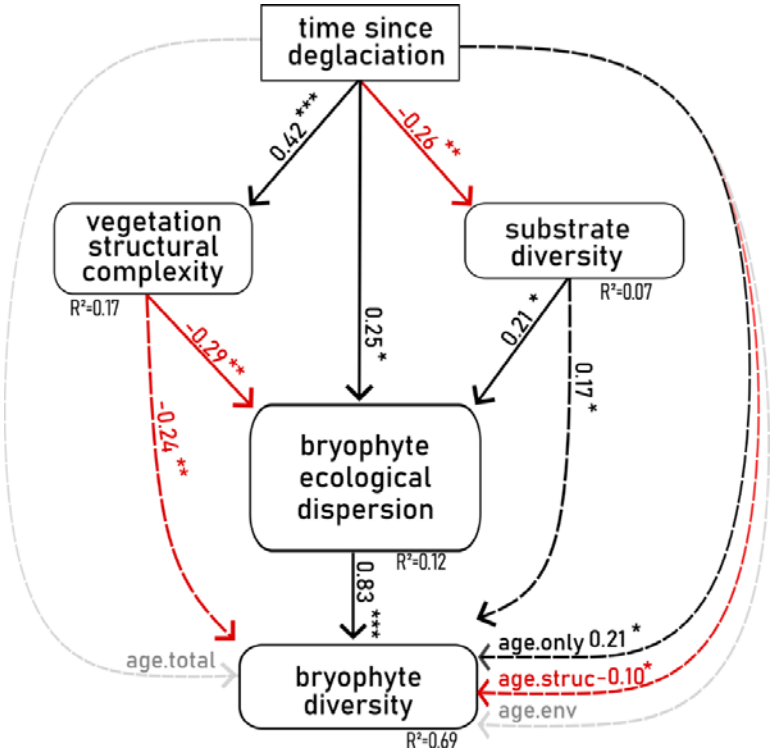

Figure 3: Path analysis of environmental drivers and vegetation structural complexity on bryophyte ecological dispersion and bryophyte diversity. The path diagram presents direct effects as solid lines. Indirect effects are represented as dotted lines and were calculated through mediation analysis. Standardized path coefficients are shown for significant relationships, with red coloration indication a negative and black coloration indicating a positive effect.

Discussion

Biotic interactions, particularly competition driven by the development of dense vascular plant structures, emerge as a key driver of bryophyte diversity over succession.

This observation is explained by a mechanism where vascular plant physical structures homogenize local habitat conditions, thereby reducing the multidimensional realized niche

size — or ecological dispersion — of bryophytes in shared habitats. Furthermore, traditional metrics such as vascular plant cover, species composition, species richness, and functional divergence failed to capture these plant-plant interactions. These finding underscore the importance of vegetation structural complexity as a key determinant of biodiversity.

Vascular plants shape bryophyte succession through biotic interactions

Competition with vascular plants significantly reduces bryophyte diversity in grasslands. These interactions arise through increasingly complex and dense physical structures of vascular plants. (Legendre *et al.*, 2005; Lowe and McPeek, 2014; Hanusch *et al.*, 2022; He *et al.*, 2024). Path analysis revealed that VSC negatively impacts bryophyte diversity and ecological dispersion, resulting in bryophyte communities with more homogeneous ecological preferences in habitats dominated by more complex vascular plant structures. These changes are probably driven by shifts in moisture, as well as intensified competition for light and space along the vertical axis of the three-dimensional niche space. Vascular plants overgrow and overshadow bryophytes, limiting the diversity of bryophyte species able to persist by favoring a select set adapted to these constraints.

However, bryophyte diversity is partially buffered against vascular plant dominance over succession by the availability of diverse growth substrates and time-driven dispersal processes. Despite ongoing competition, bryophyte diversity remains higher on plots with more diverse substrate compositions and on older plots. Bryophytes in glacier forefields are generally not considered dispersal-limited (Cichini *et al.*, 2011), suggesting that of effect of time since deglaciation cannot be solely attributed to slow dispersal processes, which are more typical of vascular plant communities (Ulrich *et al.*, 2016; Hanusch *et al.*, 2022; Cantera *et al.*, 2024). Instead, site-specific processes, such as substrate weathering, likely play a key role by facilitating opportunistic and rapid colonization of newly available niches (Prach and Walker, 2020). Bryophytes grow on a wide range of terrain features, such as rocks or boulders that stick out of the vegetative layer. 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). Glacier forefields, in particular, are highly

dynamic ecosystems that offer a variety of substrates, fostering the establishment of diverse sets of bryophyte species. The positive effect of substrate diversity on bryophyte diversity aligns with previous studies, confirming that substrate availability is a key driver of bryophyte community composition and diversity during succession (e.g. Hylander *et al.*, 2005; Caruso and Rudolphi, 2009; Chen *et al.*, 2017; Spitale, 2017). Accordingly, bryophyte succession in alpine grasslands is driven by a combination of interrelated processes. The successful colonization of microhabitats within a heterogeneous environment helps buffer bryophyte diversity against competition with vascular plants over time.

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

Originally developed for vascular plants in Central Europe, EIVs have since been adapted for bryophytesIn this study (Düll, 1992; Simmel, Ahrens and Poschlod, 2021). In this study, they were applied to approximate the bryophyhte community's multidimensional realized niche. Although EIV-based ecological dispersion does not capture the full range of functional traits that influence ecological interactions, it proved to be a valuable tool for gaining mechanistic insights into bryophyte community responses to changing biotic and abiotic conditions along the successional gradient.

Adapting a "three-dimensional perspective" for ecological research

A key advantage of laser scanning techniques is their ability to estimate phenotypic properties of entire plant communities in three dimensions, explicitly accounting for the spatial arrangement of physical plant structures across both horizontal and vertical dimensions. This capability represents a significant improvement over traditional vascular plant community metrics, which are typically derived from two-dimensional assessments based on plant cover or individual-based estimates of abundance (LaRue, Knott, *et al.*, 2023). Such two-dimensional approaches often fail to capture the inherently three-dimensional aspects of structural complexity, and as such overlook critical vertical features that strongly influence ecological dynamics within an ecosystem (Gámez and Harris, 2022). For instance, size-asymmetric competition for light and space is a well-documented driver of

grassland biodiversity (Newman, 1973; Weiner, 1990; Eskelinen *et al.*, 2022). Here, larger plants gain disproportionate access to light, by overshadowing smaller plants and limiting their growth. This form of competition primarily operates along the vertical axis of the three-dimensional habitat space, as it is fueled by the directional supply of light. In this study, structural complexity included measurements of light penetration depth, which refers to the extent light can pass through the upper vegetation layers to reach the lower layers or ground. This metric serves as an important indicator of how the vertical structure of the plant community influences light availability for understory species (Grace, 1999; Zieschank and Junker, 2023). Accordingly, VSC provides a more realistic representation of light availability and spatial constraints that bryophytes experience within the vegetation layer. As a result, VSC proved to be the only metric that captured a significant negative correlation with bryophyte diversity in this study. This finding highlights the importance of assessing structural properties to understand the full spectrum of mechanisms through which vascular plants impact biotic interactions and thus biodiversity.

Although traditional vegetation metrics may not capture the specific dynamics revealed by structural complexity, they offer complementary rather than redundant information. The correlations between structural complexity and other traditional metrics demonstrate that some metrics are more strongly related, while others capture distinct aspects of vascular plant communities. Adopting a “three-dimensional perspective” certainly enables the exploration of ecosystem dynamics at scales beyond individual or species-level analyses. At the same time, metrics such as species richness and functional diversity capture other critical aspects of vascular plant communities, highlighting different aspects of their ecological roles and functions. Ecologists are thus encouraged to select metrics thoughtfully, as each will provide distinct and complementary insights into ecosystem dynamics.

Conclusion

This research contributes to the ongoing integration of structural complexity as a key component of biodiversity (Coverdale and Davies, 2023; LaRue, Knott, *et al.*, 2023). The

findings provide a mechanistic understanding of the interactions between vascular plants and bryophyte communities, highlighting the complex dynamics of ecological succession. They reveal that bryophyte diversity is buffered against vascular plant dominance by exploiting diverse microhabitats that develop over time.

Advanced laser-scanning methods, and the modelling of vegetation structural complexity metrics, offer valuable insights into understanding plant-plant interactions, coexistence and ecosystem dynamics. Integrating structural metrics with traditional vascular plant community metric offers a more comprehensive understanding of ecosystem dynamics, extending beyond successional research. Such integrated approaches will deepen insights into ecosystem processes and support the development of effective conservation and succession-based restoration strategies.

Supplementary Information

Supplementary Figure 1: Digital whole community phenotyping (DWCP) using a customized PlantEye setup (Phenospex, F500, Heerlen, the Netherlands) in the field Figure adapted from He *et al.*, (2023), permission granted under CC BY 3.0.

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