Journal of
Plant Ecology

Research Article

Ecological indicators predict functional diversity dynamics following glacier retreat

Gianalberto Losapio[1,2,*], Lucía Mottet[1], Nora Khelidj[1], Bao Ngan Tu[1,2],
Bruno E.L. Cerabolini[3], Stephanie Grand[1], Natasha de Vere[4] and Antoine Guisan[1,5]

[1]Institute of Earth Surface Dynamics, University of Lausanne, 1015 Lausanne, Switzerland, [2]Department of Biosciences, University of Milan, 20133 Milan, Italy, [3]Department of Biotechnologies and Life Sciences, University of Insubria, Varese, Italy, [4]Natural History Museum of Denmark, University of Copenhagen, Copenhagen, Denmark, [5]Department of Ecology and Evolution, University of Lausanne, Lausanne, Switzerland

*Corresponding author. E-mail: Gianalberto.Losapio@unimi.it

Handling Editor: Bernhard Schmid

Received: 28 March 2025, **First Decision:** 9 June 2025, **Accepted:** 5 July 2025, **Online Publication:** 19 July 2025

Citation: Losapio Gianalberto, Mottet Lucía, Khelidj Nora, Tu Bao Ngan, Cerabolini Bruno E.L., Grand Stephanie, de Vere Natasha, Guisan Antoine (2025) Ecological indicators predict functional diversity dynamics following glacier retreat. *J Plant Ecol* **18**:rtaf110. https://doi.org/10.1093/jpe/rtaf110

Abstract

The retreat of glaciers due to climate change is reshaping mountain landscapes and biodiversity. While previous research has documented vegetation succession after glacier retreat, our understanding of functional diversity dynamics is still limited. In this case study, we address the effects of glacier retreat on plant functional diversity by integrating plant traits with ecological indicator values across a 140-year chronosequence in a subalpine glacier landscape. We reveal that functional richness and functional dispersion decrease with glacier retreat, while functional evenness and functional divergence increase, suggesting a shift toward more specialized and competitive communities. Our findings highlight the critical role of ecological factors related to soil moisture, soil nutrients and light availability in shaping plant community dynamics. As years since deglaciation was a key factor in regression and machine learning models, encapsulating time-lagged, spatial and historical processes, we highlight the need of including time into phenomenological or mechanistic models predicting biodiversity change following glacier retreat. The integrative approach of this case study provides novel insights into the potential response of alpine plant communities to climate change, offering a deeper understanding of how to predict and anticipate the effects of glacier extinction on biodiversity in rapidly changing environments.

Keywords: alpine ecosystems, biodiversity change, climate change, community dynamics, glacier retreat, global warming, Landolt values, plant functional traits

生态指标预测植物功能多样性对冰川退缩的响应特征

摘要：气候变化背景下，冰川退缩正在重塑山地景观及其生物多样性。尽管已有研究报道了冰川退缩对植被演替过程的影响，但关于冰川退缩后植物功能多样性动态的认知仍较为有限。本研究基于一条覆盖140年的冰川退缩时间序列，测定植物性状和土壤湿度、养分状况与光照条件等生态指标，探究冰川退缩对植物功能多样性的影响及其调控因素。结果显示，功能丰富度和功能离散度随着冰川退缩而下

降，而功能均匀度和功能分异度则呈现相反趋势，表明植物群落向更加专化且具竞争优势的方向演化。研究进一步揭示了生态指标在群落动态中的关键作用。此外，冰川退缩时间在回归分析和机器学习模型中均表现为核心预测因子，在预测冰川退缩后生物多样性变化的现象学或机制模型中应纳入时间效应。本研究结果为理解高山植物群落对气候变化的响应机制提供了新视角，也为预测快速环境变化背景下冰川消退对生物多样性的影响提供了理论依据。

关键词：高山生态系统，生物多样性变化，气候变化，群落动态，冰川退缩，全球变暖，Landolt指示值，植物功能性状

INTRODUCTION

Increasing global temperatures are causing the current retreat of glaciers worldwide (IPCC 2019, 2022). Glacier retreat has been increasingly documented as a key driver of ecological change in mountain ecosystems (Khelidj *et al.* 2025; Casallas *et al.* 2025), affecting the evolution of populations and the structure of communities and landscapes (Losapio *et al.* 2025; Milner *et al.* 2007, 2017). Glacier retreat also leads to the emergence of new habitats characterized by barren, nutrient-poor terrains that are gradually colonized by diverse plant species that replace one another over space and time (Bosson *et al.* 2023; Cantera *et al.* 2024; Chapin *et al.* 1994; Ficetola *et al.* 2021). This process of primary succession not only alters species composition but also drives changes in plant functional traits (Caccianiga *et al.* 2006; Khelidj *et al.* 2024; Losapio *et al.* 2021), which are critical for both species persistence and ecosystem functioning (Brown *et al.* 2018; Cadotte 2017; Losapio and Schöb 2017). While the general patterns of plant primary succession following glacier retreat are relatively well understood, the mechanisms by which functional traits respond to the newly created environments remain less explored. Understanding how functional diversity (FD) responds to glacier retreat and ecological changes is crucial for predicting the future of biodiversity, especially under scenarios of continued warming and loss of glaciers.

Functional traits are measurable properties of plants that influence their fitness and performance in specific environments (Díaz *et al.* 2016; Garnier Navas and Grigulis 2016; Pérez-Harguindeguy *et al.* 2013). Traits include morphological characteristics, such as leaf area (LA) and canopy height (CH), and reflect physiological conditions like leaf nitrogen content (LNC) and specific leaf area (SLA). Functional traits are increasingly recognized as powerful tools for understanding ecological processes because they directly link species' phenotype to ecological functions, such as nutrient cycling, productivity, and resilience to environmental stressors (Ackerly 2004; Bongers *et al.* 2021; Cadotte 2017; Losapio and Schöb 2017). In the context of glacier retreat, functional traits can provide insights into the response of plants to rapidly changing conditions (Caccianiga *et al.* 2006; Ricotta *et al.* 2016). For example, traits that confer drought tolerance, such as high leaf dry-matter content (LDMC) or enable efficient nutrient uptake like low species LA, are likely to be advantageous in the nutrient-poor and moisture-limited environments of glacier forelands. Additionally, understanding how these traits vary in plant communities along environmental gradients (Guisan *et al.* 2019) and across different successional stages (Khelidj *et al.* 2024) can help anticipate which functional changes will affect communities in these changing environments over time. Despite the growing interest in functional traits, how FD changes with glacier retreat over space time remains poorly quantified, limiting our understanding of the consequences of glacier retreat on ecological processes and ecosystem functions.

FD, which encompasses the community-weighted mean, range and distribution of functional traits, is critical for assessing ecological functions and strategies of multiple traits, species and communities at once (Cadotte-Carscadden and Mirotchnick 2011; Gross *et al.* 2009; Ricotta *et al.* 2016), going beyond traditional taxonomic analyses. High FD often indicates a robust ecosystem with a wide range of functional strategies, potentially leading to greater stability and resilience in the face of environmental disturbances and stressors. Conversely, low FD can suggest a dominance of few functional strategies (Laliberté and Legendre 2010; Mason *et al.* 2005, 2012), potentially making the ecosystem more vulnerable to changes in environmental conditions. When environmental conditions change rapidly and species are colonizing and replacing each other, like in the case of glacier forelands, FD can provide important insights into the processes of community assembly and ecosystem development (Brown *et al.* 2018; Gross *et al.* 2009; Shipley *et al.* 2017).

A multifaceted approach to FD analysis provides specific ecological insights, from the diversity of available functional roles (functional richness) to the uniformity of resource use (functional evenness), degree of niche differentiation (functional divergence) and the distribution of functional strategies (functional dispersion) (Mason *et al.* 2005; Schleuter *et al.* 2010). Such an integrated approach allows to investigate both the extent and distribution of functional trait space occupied by plant communities after glacier retreat (Khelidj *et al.* 2024). However, the dynamics of FD following glacier retreat remain poorly understood and difficult to predict, particularly in relation to changes of specific ecological conditions that follow glacier retreat and ecological succession.

Yet, it is important to recognize that community development and vegetation succession are shaped by other latent environmental factors beyond time alone, including soil and climate conditions (Burga *et al.* 2010; Charles *et al.* 2025; Ficetola *et al.* 2021; Losapio *et al.* 2021; Raffl *et al.* 2006; Tu *et al.* 2024; Walker *et al.* 2010). A possible solution to the challenge of considering changes in soil and climate along with time is inferring latent ecological conditions by means of bioindication principles (Diekmann 2003). Ecological indicator values (EIVs) (Landolt *et al.* 2010; Scherrer and Guisan 2019) reflect the environmental preferences of species and allow to characterize the local ecological context in an indirect way via the composition of the plant community (Fan *et al.* 2025; Scherrer *et al.* 2024). This way, EIVs such as those developed by Landolt and colleagues for the Swiss flora (Landolt *et al.* 2010) provide a standardized method for both assessing how species respond to environmental gradients as well as to inferring latent environmental conditions such as humidity, temperature and soil nutrients (Diekmann 2003; Scherrer and Guisan 2019; Shipley *et al.* 2017). Combining EIVs with FD analysis allows gaining a more comprehensive understanding of the adaptive strategies and ecological functions of plant communities (Wenskus *et al.* 2025).

This case study provides a novel framework for understanding the processes of community assembly and how functional strategies shift in the rapidly changing environmental conditions created by the retreat of glaciers during the last century. We integrate EIV with plant traits across different stages of succession following the retreat of a subalpine glacier. We address the following research questions: (1) How do EIVs and FD change after glacier retreat? (2) How do EIVs predict FD along with time over the succession? Following the successional gradient patterns (Bazzaz 1990; Caccianiga *et al.* 2006; Chapin *et al.* 1994) and the 'peak biodiversity' concept (Losapio *et al.* 2025), we hypothesize that intermediate stages of succession promote species with fast-growth strategies, which are gradually replaced by species with traits enhancing competitive ability and resource conservation toward the end of succession (Khelidj *et al.* 2024; Losapio *et al.* 2021). This case study aims to contribute not only to our understanding of primary succession after glacier retreat but also to provide novel insights into understanding the broader implications of climate change for mountain biodiversity and ecological processes.

METHODS

Study site

The Mont Miné glacier foreland in Val d'Hérens, Switzerland (46°3′33″ N, 7°32′54″ E) was selected for this case study given its well-preserved moraine system (Lambiel *et al.* 2016; Nicolussi *et al.* 2022) and its minimal elevation variation (1961–2000 m a.s.l.). The Mont Miné glacier has retreated by approximately 2.53 km since the end of the Little Ice Age (*c* 1860) as of 2023 (GLAMOS 2023). Given its topography and hence the absence of an elevation gradient that covaries with terrain age, this glacier foreland offers a valuable system for investigating the impacts of climate change on biodiversity and ecological communities (Fig. 1).

Integrating geochronological information on glacier dynamics from the catchment (Lambiel *et al.* 2016; Nicolussi *et al.* 2022) with historical cartographic reconstructions (Federal Office of Topography 2023; GLAMOS 2023) and field validation, we reconstructed a chronosequence to capture different stages of ecosystem development through time and across the glacier foreland by estimating terrain age corresponding to the time that has passed since the glacier retreated (Fig. 1). Four major chronosequence stages were identified along the glacier foreland, which represent terrains exposed since at least the year 1989, 1925, 1900 and 1864. The age of each stage was estimated as the mean between two adjacent moraines, resulting in the following average terrain

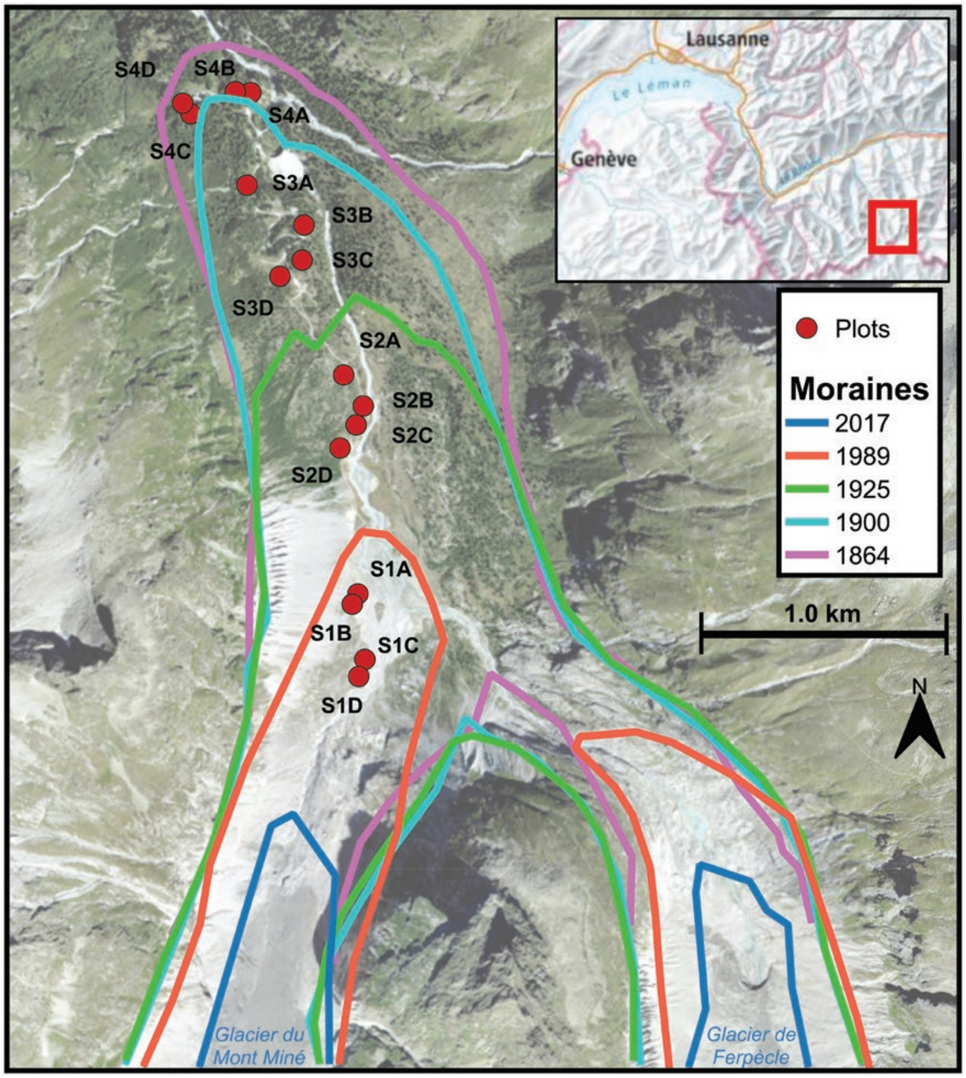


Figure 1: Study area with Mont Miné and Ferpècle glaciers in the Valais Alps and the geolocation of the sixteen surveyed plots across four main stages of glacier retreat (Stage 1, Stage 2, Stage 3 and Stage 4), reconstructed using moraines marking the former glacier positions since the 1860s. Background map: © Federal Office of Topography, Swisstopo.

ages: 17 years for Stage 1, 65 years for Stage 2, 110 years for Stage 3 and 140 years for Stage 4. Sampling was conducted exclusively on the west side of the foreland to avoid disturbances from hydropower activities on the eastern side (Lambiel *et al.* 2016).

Data collection

Within each stage, we randomly selected four sampling sites, totaling 16 sites. At each site, four 5 m × 5 m quadrats were established, covering an area of 100 m^2 per stage. Within each quadrat, plant communities were surveyed by recording species composition and estimating plant cover with a visual accuracy of 10%. Species identification followed *Flora Alpina* (Aeschimann *et al.* 2004). In total, we recorded 127 plant species across 32 families (Supplementary Table S1).

As ecological indicators, Landolt EIVs were considered as they are the most accurate and complete in describing soil factors and climate factors for the examined flora (Landolt *et al.* 2010). The following Landolt EIVs for soil factors were considered: (i) Soil moisture (F, here called H) ranging from very dry (1) to water-saturated soils (5); (ii) Soil reaction (R) ranging from extreme acidity with pH 3–4.5 (1) to basic reaction with pH > 6.5 (5); (iii) Soil nutrient (N) ranging from extremely infertile (1) to over-fertilized soils (5). The following Landolt EIVs for climate factors were considered: (i) Light availability (L) ranging from plants growing in shade with less than 3% relative illumination (1) to full sun (5); Air temperature (T), for plants typical of cold environment (1) to indicators of warmer places (5); Continentality (K, here called C) for plants whose center of distribution ranges from regions with oceanic climate (1) to continental climate (5). Although we do not expect macroscale differences in climate along the examined gradient, we considered climate-related EIVs like T and K to explore potential changes in microclimate conditions that might be reflected by the local plant community. After extracting Landolt EIVs and cross-referencing with the results of the plant community survey, 93 plant species with complete EIVs were retained for the statistical analysis (Supplementary Table S2).

We considered a set of 10 plant functional traits representing key ecological strategies relevant for plant growth, reproduction, and nutrient cycling (Díaz *et al.* 2016; Garnier Navas and Grigulis 2016; Gross *et al.* 2009; Shipley *et al.* 2017; Wright *et al.* 2005). The following traits were considered: lateral spread (LS), CH, LNC, leaf carbon content (LCC), leaf carbon-to-nitrogen ratio (CN), LA, SLA, leaf fresh weight (LFW), leaf dry weight (LDW) and LDMC. These leaf traits were obtained by integrating trait database (Kattge *et al.* 2020) with public, published data (Dalle Fratte *et al.* 2021; Khelidj *et al.* 2024; Losapio *et al.* 2021). After cross-referencing these datasets with the plant community survey, 53 plant species out of 93 with complete trait and EIVs data were finally retained for the statistical analysis (Supplementary Table S3). These species include the 51.42%, 56.7%, 59.3% and 64.7% of total vegetation cover at Stage 1, Stage 2, Stage 3 and Stage 4, respectively; hence, they are a representative subset of local communities. For each trait, we calculated the mean value for each species across all specimens to produce species-level trait means.

Functional diversity

To assess changes in FD across successional stages in the Mont Miné glacier foreland and in relation to EIVs, we selected FD indices that reflect different aspects of community structure: functional richness (FRic), functional evenness (FEve), functional divergence (FDiv), and functional dispersion (FDis). Each index captures a different facet of FD (Mason *et al.* 2005; Schleuter *et al.* 2010), including dimensions of richness (the extent of niche space occupied), evenness (distribution within that space) and divergence (degree of species differentiation). Their combined use provides both diverse insights into and a comprehensive picture of how different functional strategies coexist over time and contribute to ecosystem processes following glacier retreat. These indices were calculated based on species-level trait means using the *FD* R package (Laliberté *et al.* 2014; Laliberté and Legendre 2010).

FRic represents the total volume of functional trait space occupied by the community, and is equivalent to the convex hull volume of the species in trait space (Villéger *et al.* 2008). Ecologically, FRic reflects the range of functional roles within a community and indicates the diversity of strategies available for resource use, competition and adaptation. Higher FRic values suggest a broader niche space, potentially enhancing ecosystem resilience by supporting a variety of ecological functions (Cornwell and Ackerly 2009; Mason *et al.* 2005).

FEve measures the evenness of trait distribution within the functional space, and was calculated using a minimum spanning tree which connects all species based on their trait distances (Villéger *et al.* 2008). The higher the FEve, the more regular the distribution of species along resource gradients, suggesting efficient and balanced resource use across the community. In contrast, low FEve values imply clustering in specific areas of trait space, potentially indicating competitive dominance or environmental filtering (Mason *et al.* 2012).

FDiv quantifies the degree of divergence from the centroid in trait space, focusing on species that deviate most from average community traits. This index highlights niche differentiation, where higher FDiv values indicate greater specialization and ecological complementarity among species (Villéger *et al.* 2008). FDiv is particularly useful for identifying communities where species have distinct functional roles as it underscores the degree to which species occupy different ecological niches to minimize niche overlap (Mason *et al.* 2005).

FDis represents the mean distance of each species from the centroid in trait space, weighted by relative abundance (Laliberté and Legendre 2010). Unlike other indices, FDis is independent of species richness, making it an effective metric for comparing communities with varying species numbers. High FDis values suggest a wide distribution of functional strategies, potentially contributing to ecosystem resilience and adaptability. FDis is valuable for capturing the functional breadth of a community and understanding how species abundances relate to trait variability (Laliberté and Legendre 2010).

Data analysis

To investigate the ecological conditions and functional composition of plant communities, we calculated community-weighted means (CWMs) for each EIV and functional trait. CWMs represent the mean value of an EIV or a functional trait within a community, weighted by the relative abundance of each species. This approach provides quantitative insights into community-level conditions and strategies, and their responses to glacier retreat and ecological gradients. CWMs were calculated as:

$$\mathrm{CWM}y = \sum_{i=1}^{S} p_i \times y_i \tag{1}$$

where p_i is the relative abundance of each species i occurring in a community composed of S species, and y_i is the EIV or functional trait value for the species i. This analysis was performed for each response variable y (i.e. a single EIV or functional trait) across all sampling plots and successional stages, allowing us to assess how EIV and FD shift in relation to glacier retreat. CWMs were calculated using the '*FD*' package in R (Laliberté *et al.* 2014; Laliberté and Legendre 2010), ensuring consistency with other FD analyses.

To address the first research question, we used linear regression models to test for differences in each CWM_y and FD index (response variables in separate models) across the succession (predictor, categorical variable with Stage 1 as reference level) (Fox and Weisser 2019). Type-II Analysis of Variance was applied to the fitted model to calculate F-tests for predictor significance using the '*car*' R package (Fox and Weisser 2019). Inference of model parameters was conducted using the Wald method, which computes confidence intervals and associated P-values by dividing the parameter estimate (intercept and slope) by its standard error, then comparing this statistic against a t-distribution with residual degrees of freedom (Lüdecke *et al.* 2020). Cohen's f was calculated as effect size to assess the magnitude of change in each index across stages (Ben-Shachar *et al.* 2020), helping to interpret the ecological relevance of observed trends across indices.

To address the second research question and assess the multivariate relationships among glacier retreat, EIVs, functional traits and FD, we first conducted a Principal Component Analysis (PCA) using the '*FactoMineR*' package in R (Lê *et al.* 2008). PCA was chosen to reduce data dimensionality while preserving the primary variation in the dataset, enabling us to visualize and interpret the key ecological gradients and functional trait variation. After calculating the proportion of variance explained by each PC, we identified the variables that were significantly associated with as well as contributing the most to the first two PC by looking at correlation coefficients between variables and PC using the '*dimdesc*' function of '*FactoMineR*' (Lê *et al.* 2008). In a preliminary, exploratory way, we also considered the strength and direction of univariate relationships between EIVs and FD (Supplementary Fig. S1).

Then, to make inference on the ecological drivers of FD, we used two complementary approaches: a parametric model (linear regression) and a non-parametric, machine learning algorithm (random forest [RF]). In both cases, CWM of functional traits and FD indices were considered as response variables with respect to glacier retreat (years since glacier retreat), while CWMs of EIVs (H, R, N, L, T, C), which were used as predictors.

An initial linear model was fitted for each response variable using all predictor variables. To refine each model and identify the most significant predictors, we performed stepwise model selection based on Akaike Information Criterion (AIC) using the '*stepAIC*' function of '*MASS*' R package (Venables and Ripley 2002). This approach systematically removed nonsignificant predictors, yielding a more parsimonious model. Although this procedure is highly sensitive to the order of the predictors in the model, given the relatively low number of predictors and their non-collinearity, stepwise selection would still provide an efficient approach for this case study. For each final model, we evaluated the effects of the selected predictors using type-II analysis of variance (F-test), inferring model parameters with 95% CIs and P-values, and calculating Cohen's f standardized effect sizes.

Finally, to further examine the relative importance of EIVs for predicting FD, we implemented a RF model with permutation testing to assess the statistical significance of variable importance. The RF model was chosen for its ability to handle complex, nonlinear relationships and for being robust to assumptions on data distribution. As mentioned above, functional traits and FD indices were modeled as a function of years since glacier retreat and EIVs. The '*rfPermute*' R package (Archer 2023) was used to build the model, which included 5000 decision trees on 500 bootstrap samples of the initial data to provide robust significance testing for variable importance, yielding 2 500 000 samples. Following model training, we summarized the results to evaluate model performance (see Appendix R script). For each model, the importance and significance of predictors were assessed based on the percentage of increase in mean square error when their values are randomly permuted (ΔMSE). To summarize predictor importance over all FD indices, we calculated the average predictor importance index ($\overline{\Delta \text{MSE}}$).

RESULTS

Four out of the six EIVs significantly changed with successional stages (Supplementary Table S5). Cohen's effect size of glacier retreat was large for soil moisture ($f = 1.26$), soil reaction ($f = 1.93$), soil nutrient ($f = 1.27$) and light availability ($f = 1.93$); it was medium but insignificant for air temperature ($f = 0.49$) and continentality ($f = 0.81$).

Looking at the direction of changes and trends (Fig. 2; Supplementary Table S6), CWMs of EIVs for soil moisture increase with glacier retreat at the latest, 140-year successional stage ($\beta = 0.38$ [0.17–0.59], $P = 0.002$). On the contrary, CWMs of EIVs for soil reaction decrease with glacier retreat at the 110-year stage ($\beta = -0.70$ [from −1.13 to −0.27], $P = 0.004$) and 140-year stage ($\beta = -1.22$ [from −1.65 to −0.79], $P < 0.001$). CWMs of EIVs for soil nutrient marginally decrease at the 65-year stage ($\beta = -0.25$ [from −0.51 to −0.01], $P = 0.061$) and 110-year stage ($\beta = -0.25$ [from −0.52 to −0.01], $P = 0.060$), while significantly decrease with glacier retreat at the 140-year stage ($\beta = -0.53$ [from −0.80 to −0.27], $P = 0.001$). CWMs of EIVs for light availability marginally decrease at 110-year stage ($\beta = -0.45$ [from −0.90 to −0.01], $P = 0.052$) and significantly decrease with glacier retreat at 140-year stage ($\beta = -1.20$ [from −1.65 to −0.75], $P < 0.001$). CWMs of EIVs for air temperature show no evidence of significant directional change associated to glacier retreat stages. CWMs of EIVs for continentality decrease with glacier retreat at the latest, 140-year successional stage ($\beta = -0.32$ [from −0.59 to −0.59], $P = 0.002$).

Nine out of 10 plant functional traits significantly or marginally (one) changed along the succession (Supplementary Table S7). Cohen's effect size of glacier retreat was large for LS ($f = 1.11$), LNC ($f = 0.93$), LCC ($f = 2.17$), leaf carbon:nitrogen ration (CN, $f = 1.18$), LA ($f = 1.00$), LDW ($f = 1.32$), LFW ($f = 1.27$), LDMC ($f = 1.36$) and CH ($f = 1.74$); it was medium but insignificant for SLA ($f = 0.64$).

Looking at the direction of change and trends of plant functional traits (Fig. 3; Supplementary Table S6), CWMs of LS, CH, LCC, CN, LDW, and LDMC

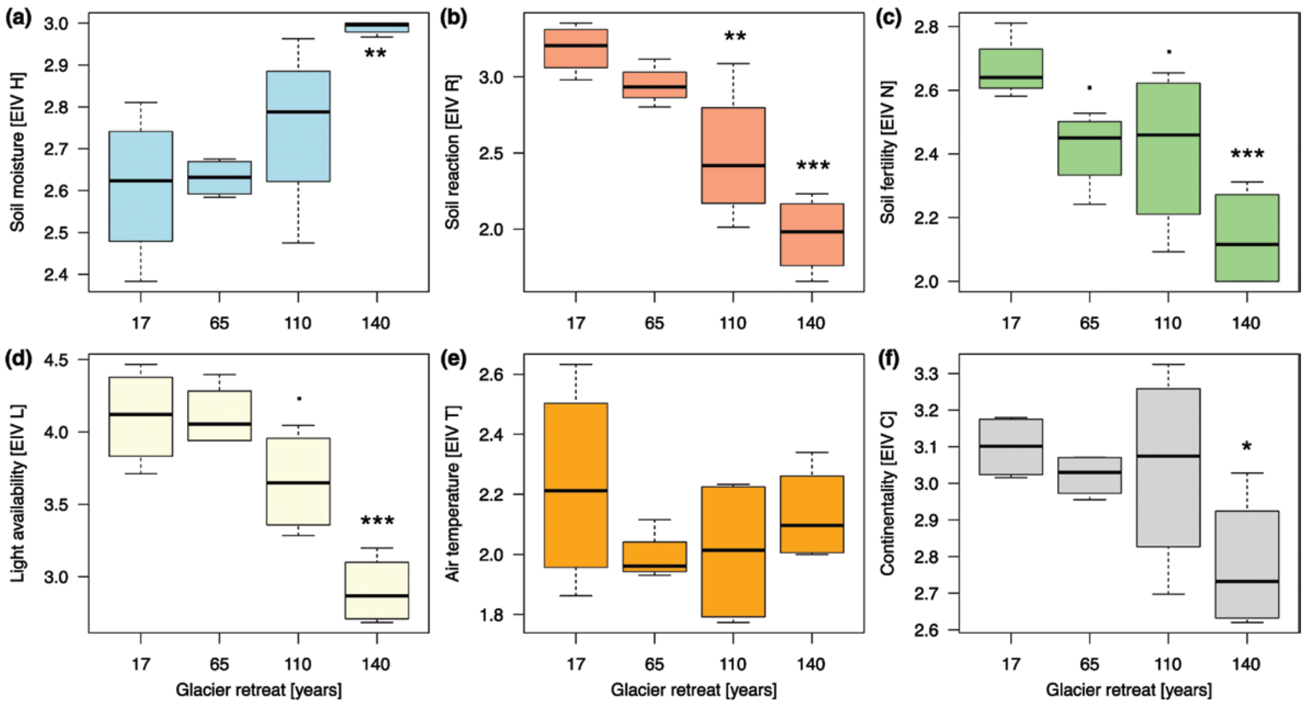


Figure 2: Community-weighted means of landolt ecological indicator values (EIVs) of plant communities along the ecological succession triggered by glacier retreat. Symbols include statistical significance (. = $0.1 < P < 0.05$, * = $0.05 < P < 0.01$, ** = $0.01 < P < 0.001$, *** = $P < 0.001$) of the differences between stages and Stage 1 at 17 years since glacier retreat, which was considered as reference level in the regression model.

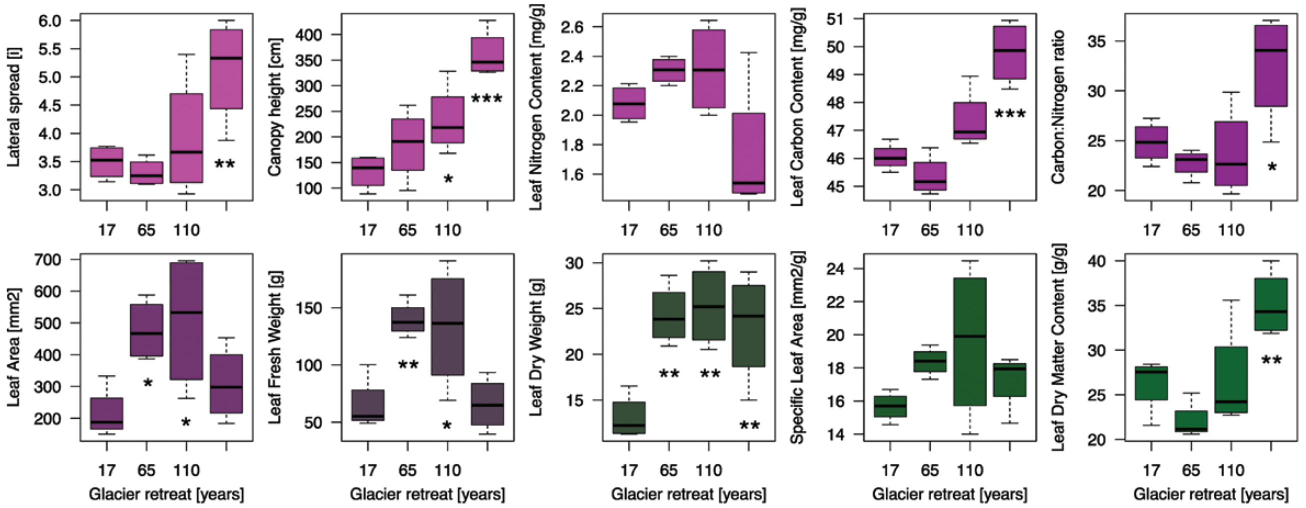


Figure 3: Plant functional traits CWM along the ecological succession triggered by glacier retreat. Symbols include statistical significance (* = 0.05 < P < 0.01, ** = 0.01 < P < 0.001, *** = P < 0.001) of the differences between stages and Stage 1 at 17 years since glacier retreat, which was considered as reference level in the regression model.

significantly increase with glacier retreat, with a minimum detectable change at the latest 140-year stage. On the contrary, LA, LFW and SLA were the highest at the intermediate stages of 65 and 110 years (Supplementary Table S6).

One FD index out of four, namely FDis, was significantly associated to succession overall (Supplementary Table S8). Cohen's effect size of glacier retreat was large for FDis (f = 1.37), and it was medium but unsignificant for FRic (f = 1.83), FEve (f = 0.60) and FDiv (f = 0.57). Yet, both FRic (Fig. 4a) and FDis (Fig. 4d) significantly decrease with glacier retreat at the latest, 140-year successional stage (β = –5.32 [from –10.10 to –0.54], P = 0.032, and β = –0.44 [from –0.67 to –0.21], P = 0.001, respectively). Furthermore, both FEve (Fig. 4b) and FDiv (Fig. 4c) marginally increase at the 140-year successional stage (β = 0.10 [from –0.01 to 0.21], P = 0.062, and β = 0.12 [from –0.02 to 0.26], P = 0.091, respectively).

To address the second question, the PCA (Fig. 5; Supplementary Table S9) identified major patterns in the variation of EIVs and FD as glacier retreats. The first component (PC1) and the second component (PC2) accounted for 50.8% and 20.3% of the variance, respectively, hence explaining together 71.1% of the total variance. Key variables positively contributing to PC1 are functional traits LCC, LS, LDMC, CAN and CN, as well as EIVs of soil moisture and years since glacier retreat; EIVs of soil reaction, soil nutrient, light availability and continentality, as well as LNC, LFW, FDis and FRic are negatively associated with PC1. PC2 is positively associated with traits including LDW, LA, LFW, SLA and LNC, as well as years since glacier retreat and FDiv. These trends reflect a major gradient in soil development which captures differences in resource allocation, carbon economy and plant size, separating pioneer and late plant communities adapted to high versus low soil nutrient and light environments, respectively (Supplementary Fig. S2).

To address the third question, the final model for functional traits (n = 10) included glacier retreat (years) 8 times out of 10, soil nutrient EIVs 7 times, light availability EIVs 6 times, soil moisture EIVs twice, EIVs of soil reaction and continentality once, while air temperature EIVs were never selected as the major predictor in any final model (Fig. 6a; Supplementary Table S4). For FD indices (n = 4), the final model included glacier retreat (years), soil nutrient EIVs, and light availability EIVs two times out of four, soil moisture EIVs, soil reaction EIVs, and continentality once, and air temperature EIVs none (Fig. 6a; Supplementary Table S4). Overall, on average, soil nutrient EIVs had the strongest effects on FD ($\bar{f} = 0.52$), followed by glacier retreat ($\bar{f} = 0.39$), light availability EIVs ($\bar{f} = 0.29$), and soil moisture EIVS ($\bar{f} = 0.14$).

Qualitatively similar results were obtained using the RF algorithm (Fig. 6b; Supplementary Table S10). Glacier retreat (years) was among the most important predictors for eight functional traits and one FD index ($\overline{\Delta \mathrm{MSE}} = 17.2\%$); soil moisture and soil reaction EIVs were among the most important predictors for five functional traits and two FD

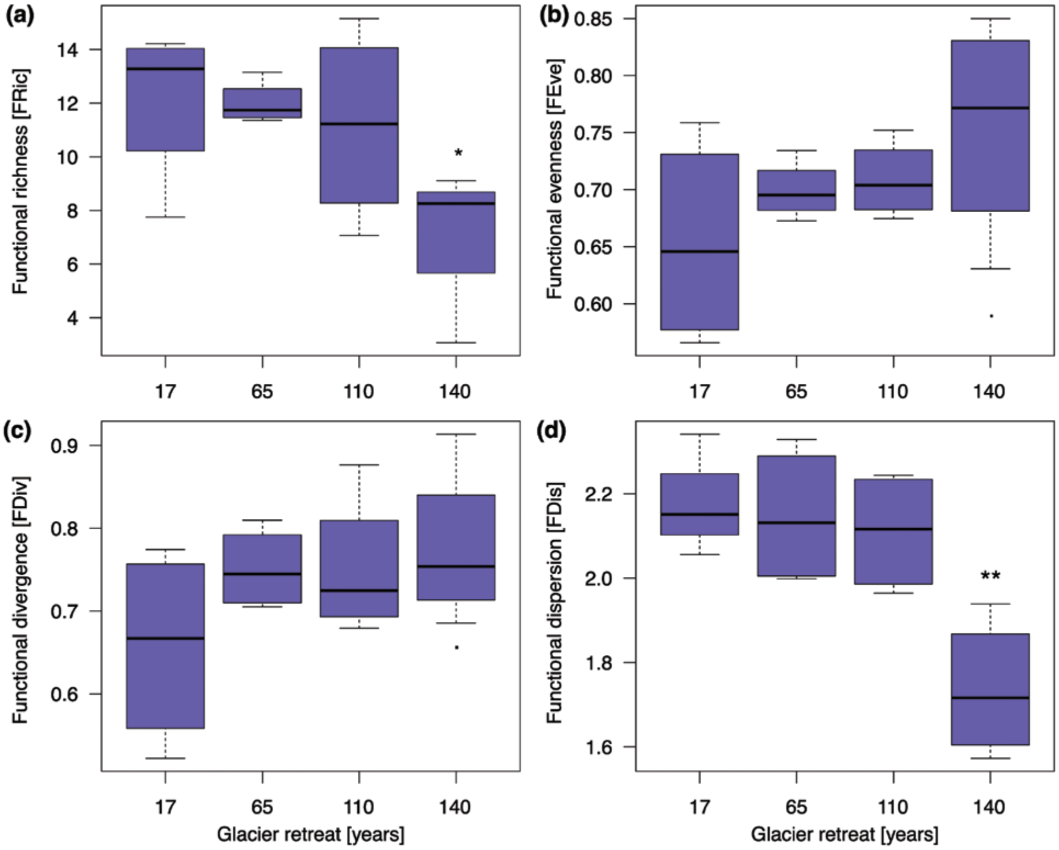


Figure 4: Functional diversity indices along the ecological succession triggered by glacier retreat. Symbols include statistical significance (. = 0.1 < P < 0.05, * = 0.05 < P < 0.01, ** = 0.01 < P < 0.001) of the differences between stages and Stage 1 at 17 years since glacier retreat, which was considered as reference level in the regression model.

indices ($\overline{\Delta \mathrm{MSE}} = 13.2\%$ and $\overline{\Delta \mathrm{MSE}} = 16.5\%$, respectively); light availability EIVs were among the most important predictors for five functional traits, but no FD index ($\overline{\Delta \mathrm{MSE}} = 14.1\%$); soil nutrient EIVs was among the most important predictors for three functional traits and one FD index ($\overline{\Delta \mathrm{MSE}} = 10.6\%$); air temperature and continentality EIVs were among the most important predictors for one FD index and no functional traits ($\overline{\Delta \mathrm{MSE}} = 0.5\%$ and $\overline{\Delta \mathrm{MSE}} = 4.7\%$, respectively).

Finally, it is worth noticing that both FRic and FDis increase with increasing soil nutrient EIVs ($\beta = 9.58$ [3.28–15.89], $P = 0.006$, and $\beta = 0.80$ [from –0.09 to 1.69], $P = 0.074$). Soil nutrient EIVs is also positively associated with increasing LNC ($\beta = 1.31$ [0.45–2.18], $P = 0.006$) while negatively associated with LS ($\beta = -2.71$ [from –4.37 to –1.05], $P = 0.005$), LCC ($\beta = -3.02$ [from –5.58 to –0.47], $P = 0.024$), CN ($\beta = -16.78$ [from –27.54 to –6.01], $P = 0.005$), and CAN ($\beta = -2.54$ [from –4.08 to –0.99], $P = 0.004$).

DISCUSSION

Our study sheds new light on the relationships between glacier retreat, EIVs and plant FD within a subalpine glacier ecosystem, providing novel insights into the factors driving community assembly in response to rapidly changing environmental conditions. We demonstrate that glacier retreat drives substantial shifts in FD, with EIVs playing a crucial role in predicting these changes. Particularly, soil-related EIVs including soil nutrient availability, moisture, and pH exhibited significant directional shifts over successional stages, reflecting changes in resource availability and habitat conditions. FD metrics responded in distinct ways: functional richness (FRic) and functional dispersion (FDis) declined with succession, suggesting a reduction in the range of available functional strategies over time, while functional evenness (FEve) and functional divergence (FDiv) showed marginal increases, indicating greater niche differentiation in later stages.

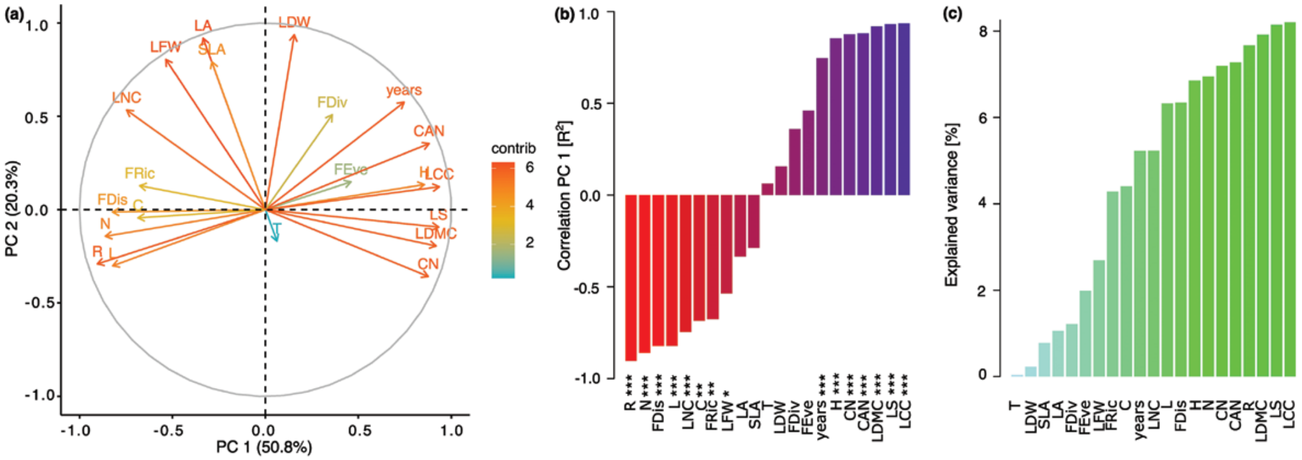
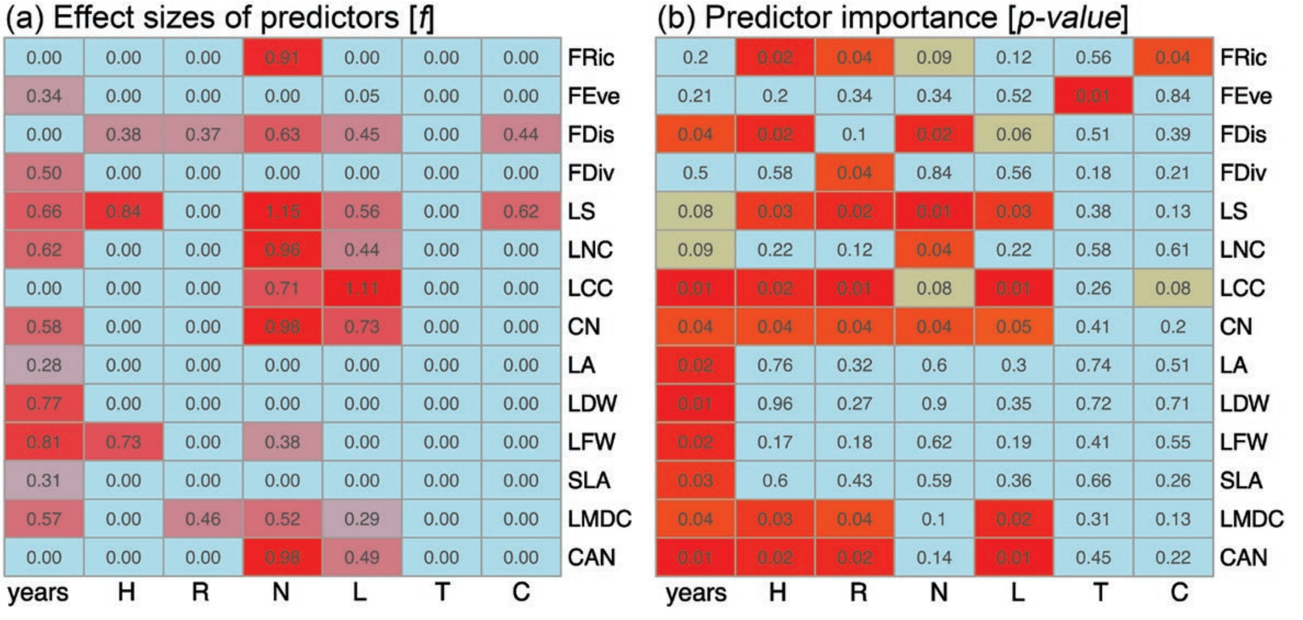


Figure 5: Principal component analysis of the relationships among glacier retreat (years), ecological indicators (soil humidity ‘H’, soil ph ‘R’, soil nutrients ‘N’, light ‘L’, temperature ‘T’, continentality ‘C’), plant traits (Lateral Spread ‘LS’, Leaf Nitrogen Content ‘LNC’, Leaf Carbon Content ‘LCC’, leaf Carbon:Nitrogen ratio ‘CN’, Canopy height ‘CAN’), and FD indices (Functional Dispersion ‘FDis’, Functional Richness ‘FRic’, Function Evenness ‘FEve’, Functional Divergence ‘FDiv’). (a) Factor map of the variables contributing to the first two components. The color gradient represents the contribution of variables. Map of the sites is reported in Supplementary Fig. S1. (b) Correlation of the variables with the first component. Significance of P is reported as following: * = 0.05 < P < 0.01, ** = 0.01 < P < 0.001, *** = P < 0.001. (c) Contributions of variables according to their explained variance.



(a) Effect sizes of predictors [*f*]

years	H	R	N	L	T	C	
0.00	0.00	0.00	0.91	0.00	0.00	0.00	FRic
0.34	0.00	0.00	0.00	0.05	0.00	0.00	FEve
0.00	0.38	0.37	0.63	0.45	0.00	0.44	FDis
0.50	0.00	0.00	0.00	0.00	0.00	0.00	FDiv
0.66	0.84	0.00	1.15	0.56	0.00	0.62	LS
0.62	0.00	0.00	0.96	0.44	0.00	0.00	LNC
0.00	0.00	0.00	0.71	1.11	0.00	0.00	LCC
0.58	0.00	0.00	0.98	0.73	0.00	0.00	CN
0.28	0.00	0.00	0.00	0.00	0.00	0.00	LA
0.77	0.00	0.00	0.00	0.00	0.00	0.00	LDW
0.81	0.73	0.00	0.38	0.00	0.00	0.00	LFW
0.31	0.00	0.00	0.00	0.00	0.00	0.00	SLA
0.57	0.00	0.46	0.52	0.29	0.00	0.00	LMDC
0.00	0.00	0.00	0.98	0.49	0.00	0.00	CAN

(b) Predictor importance [*p-value*]

years	H	R	N	L	T	C	
0.2	0.02	0.04	0.09	0.12	0.56	0.04	FRic
0.21	0.2	0.34	0.34	0.52	0.01	0.84	FEve
0.04	0.02	0.1	0.02	0.06	0.51	0.39	FDis
0.5	0.58	0.04	0.84	0.56	0.18	0.21	FDiv
0.08	0.03	0.02	0.01	0.03	0.38	0.13	LS
0.09	0.22	0.12	0.04	0.22	0.58	0.61	LNC
0.01	0.02	0.01	0.08	0.01	0.26	0.08	LCC
0.04	0.04	0.04	0.04	0.05	0.41	0.2	CN
0.02	0.76	0.32	0.6	0.3	0.74	0.51	LA
0.01	0.96	0.27	0.9	0.35	0.72	0.71	LDW
0.02	0.17	0.18	0.62	0.19	0.41	0.55	LFW
0.03	0.6	0.43	0.59	0.36	0.66	0.26	SLA
0.04	0.03	0.04	0.1	0.02	0.31	0.13	LMDC
0.01	0.02	0.02	0.14	0.01	0.45	0.22	CAN

Figure 6: Ecological indicator values (soil humidity ‘H’, soil ph ‘R’, soil nutrients ‘N’, light ‘L’, temperature ‘T’, continentality ‘C’) and glacier retreat (years) as predictors of plant traits (Lateral Spread ‘LS’, Leaf Nitrogen Content ‘LNC’, Leaf Carbon Content ‘LCC’, leaf Carbon:Nitrogen ratio ‘CN’, Canopy height ‘CAN’), and FD indices (Functional Dispersion ‘FDis’, Functional Richness ‘FRic’, Function Evenness ‘FEve’, Functional Divergence ‘FDiv’). (a) Cohen’s *f* effect size estimating how much variance in FD variables is accounted for by EIVs in the final regression model. This model, built upon stepwise selection according to AIC, includes major predictors as highlighted in reddish colors and excludes less significant predictors, which are highlighted in light blue. (b) Variable importance in the Random Forest model measured via the percentage of increase in mean square errors, proportional to color gradient intensity; scores indicate the associated P-values.

Ecological factors and time passing

Regression and machine learning models converged in highlighting the dominant role of soil nutrient and light availability EIVs in shaping FD, while climatic indicators such as air temperature and continentality were weak predictors of functional trait variation. These findings suggest that microhabitat conditions and soil development exert a stronger influence on community assembly and dynamics than bioclimatic/macroclimatic factors, emphasizing the importance of integrating EIVs with FD to better understand vegetation responses to glacier retreat and climate change. These findings also reveal that FD evolves predictably after glacier retreat, highlighting the critical role of ecological factors, particularly soil nutrient and light availability, in shaping functional trait distribution over space and time. These results contribute to a deeper understanding of the functional strategies of plant communities in response to climate change and glacier retreat (Khelidj *et al.* 2024).

Indicators such as soil moisture, soil reaction, soil nutrient and light availability were highly responsive to glacier retreat, as evidenced by large effect sizes, indicating significant shifts in ecological conditions over time. Soil moisture indicators increased at later successional stages, suggesting that progressive soil development enhances water retention capacities via pioneer herbaceous species modification of bedrock. Pioneer herbaceous species play a key role in enhancing water retention during the initial stages of soil development in glacier forelands (Charles *et al.* 2025; Eichel 2019; Losapio *et al.* 2025). Through root growth, pioneer plants contribute to the physical stabilization of the substrate via aggregate formation, initiating the accumulation of organic matter and ultimately improving the soil's ability to retain water (An *et al.* 2025; Charles *et al.* 2025; Li *et al.* 2021; Wang *et al.* 2024). Root exudates and litter inputs promote microbial colonization and organic matter transformation, further increasing soil porosity and moisture-holding capacity (Almela *et al.* 2022; Bhattacharya *et al.* 2022; Rao *et al.* 2023; Wang *et al.* 2024). These biological processes are particularly important in nutrient-poor, recently deglaciated soils where abiotic water retention is initially low.

In contrast, indicators of soil nutrient, reaction and light availability decreased, likely due to the accumulation of organic matter, the litter deposition and canopy shading by late-successional shrubs and coniferous trees, which host few plant species adapted to acidic, low-light environments. These shifts in EIVs align with previous studies documenting successional changes in soil properties and vegetation in glacier forelands (Bernasconi *et al.* 2011; Burga *et al.* 2010; Charles *et al.* 2024, 2025), where initial colonizers gradually create conditions favorable for more competitive species (Caccianiga *et al.* 2006; Ficetola *et al.* 2021; Khelidj *et al.* 2024; Losapio *et al.* 2021). Yet, we report a clear decrease in soil nutrient EIVs despite the potential increase in soil nutrient content (Charles *et al.* 2024), a pattern that may be due to rapid nutrient uptake and nitrogen sequestration by competitive species (Caccianiga *et al.* 2006). This process is further evidenced below by shifts in functional traits related to carbon and nitrogen economy in late stages. The distinct trajectories of EIVs provide a nuanced perspective on how soil development and resource availability act as selective pressures for community assembly and dynamics throughout succession in this study.

Time, measured as years since deglaciation, plays a central yet integrative role. While EIVs provide proxies for specific ecological factors such as soil fertility, light availability, and moisture, the time factor captures additional dimensions of biodiversity change that are not fully explained by abiotic factors alone. These include, most notably, (i) the decreasing influence of glacial conditions on biodiversity, and (ii) the cumulative effects of the time passing on species dispersal, colonization probability and species-specific demographic processes.

With increasing time since deglaciation, the direct influence of glaciers on geophysical conditions of glacier foreland habitats, such as physical disturbance and microclimate cooling, gradually diminishes. In the early stages of succession, biodiversity is strongly shaped by abiotic filters created by glaciers (Erschbamer and Caccianiga 2016; Losapio *et al.* 2021), which limit colonization to a small set of stress-tolerant pioneer species. With increasing glacier retreat, and hence distance from glaciers, biotic processes such as plant–soil feedbacks, facilitation, organic matter accumulation and microbial activity modify these initial conditions (Eichel 2019; Charles *et al.* 2025; Losapio *et al.* 2025; Mason *et al.* 2012), loosening abiotic filters. As a result, community assembly becomes increasingly driven by biotic interactions and ecological filtering rather than by glacial legacies. This temporal transition reflects a shift from physical to biological control over ecosystem development.

Time passing also influences the probability of species dispersal and colonization, and constrains species-specific demographic processes. Longer time allows for a broader, richer pool of species to reach and establish in newly exposed habitats, constrained by factors such as dispersal distance, germination, survival and reproductive timing (Erschbamer and Caccianiga 2016), while also allows for stochastic processes such as priority effects and local extinctions (Walker *et al.* 2010). Furthermore, time constraints demographic processes, influencing differential establishment and growth of species and communities. For example, a forest cannot occur on 30-year terrains as trees need more time to germinate, growth and reproduce. This dual role of time reinforces the importance of using both temporal and ecological variables in models of succession and biodiversity change (Losapio *et al.* 2025). While EIVs could help us mechanistically understand community assembly, years since deglaciation encapsulates time-lagged, spatial and historical processes needed to phenomenological predict biodiversity change following glacier retreat.

Functional traits and biodiversity change

Nine out of 10 plant functional traits showed significant or marginal changes following glacier retreat, reflecting changes in species composition and inherent ecological responses to the changing environmental conditions (Losapio *et al.* 2025). Traits such as LS, CH, LCC, leaf carbon:nitrogen content and LDMC increased with succession, suggesting a shift toward species with larger size and greater carbon allocation and nutrient sequestration, which are advantageous in more stable, resource-enriched environments. In contrast, traits associated with rapid resource acquisition, such as LA, SLA and LNC, were highest at intermediate successional stages. These findings align with the hypothesis that intermediate stages of succession promote species with fast-growth strategies, which are gradually replaced by species with traits enhancing competitive ability and resource conservation towards the end of succession (Bazzaz 1990; Caccianiga *et al.* 2006; Chapin *et al.* 1994; Khelidj *et al.* 2024; Losapio *et al.* 2021). Indeed, these trait dynamics highlight a functional shift from resource-acquisitive to resource-conservative strategies, a trend documented in successional studies within glacier forelands and other primary successions (Burga *et al.* 2010; Cutler *et al.* 2008; Fastie 2013; Ficetola *et al.* 2021).

Our findings indicate that FDis was the strongest index associated to succession, as evidenced by a large effect size and a marked decrease at the latest stage of 140 years. The decline in FDis suggests that the range of trait combinations within the community narrows with glacier retreat, which could reflect a shift toward a more specialized set of functional strategies (Laliberté and Legendre 2010; Mason *et al.* 2012). This trend suggests increased niche partitioning and competitive exclusion as the habitat stabilizes (e.g. lower physical/topographic disturbance) and becomes more productive (e.g. higher soil fertility). While FRic also decreased significantly at the 140-year stage, its overall association with succession was weaker, with a medium but nonsignificant effect size. This pattern suggests that, although the total volume of functional space occupied by species initially expands as communities diversify, it ultimately contracts in later stages as fewer species dominate. Interestingly, FEve and FDiv showed marginal increases in the later successional stages, suggesting a shift toward greater resource use complementarity and niche differentiation (Mason *et al.* 2005; Villéger *et al.* 2008). This pattern is consistent with previous studies suggesting that FD declines as competitive exclusion intensifies in more stable stages (Cadotte 2017; Garnier *et al.* 2016; Khelidj *et al.* 2024).

The decrease in functional richness and dispersion, coupled with an increase in evenness and divergence, underscores the potential dual role of FD in early successional stages: promoting resilience by accommodating a range of functional strategies while also enabling long-term stability through niche partitioning (Khelidj *et al.* 2024). These trends support the hypothesis that FD mediates ecosystem resilience by fostering a balance between redundancy and specialization within plant communities (Bongers *et al.* 2021; Díaz *et al.* 2016).

Notably, EIVs could predict functional traits and FD, indicating that variation in FD was strongly influenced by shifting ecological conditions, particularly soil nutrient, soil moisture, soil reaction and light availability. These indicators thus suggest that ecological factors associated to soil and canopy development act as critical ecological mechanisms shaping and selecting both the composition and functionality of plant communities over space and time. These results reinforce the notion that FD is closely tied to environmental gradients (Diekmann 2003; Guisan *et al.* 2019; Losapio and Schöb 2017; Scherrer and Guisan 2019), suggesting that the development of ecosystems is driven by trait selection to the specific ecological conditions created by glacier retreat. The stronger predictive power of EIVs for soil conditions and light along with the weak association of air temperature and continentality EIVs with FD might reflect the buffering effect of microhabitats, and the importance of local biotic factors in shaping community assembly and dynamics.

Interestingly enough, EIVs of large-scale climate factors such as those associated to air temperature and continentality fall short in predicting FD. This result is not surprising given the absence of covariation between terrain age and elevation, which may potentially confound the effects of glacier retreat by climate on its own, and given the low climatic variability over the Mont Minè glacier foreland. The results of this case study suggest that while these climatic variables undoubtedly influence broader ecological patterns (Losapio *et al.* 2025), their direct impact on the specific functional strategies of plant communities in the examined glacier foreland may be overshadowed by more local environmental factors such as soil pH, light conditions, and nutrient availability.

CONCLUSIONS

By linking FD with EIVs, we provide a novel perspective on how plant communities assemble, adapt, and function under rapidly changing environmental conditions. Yet, future research should incorporate wider, long-term monitoring and additional environmental variables, such as soil microbiota and microclimate variation. It should also extend to other altitudinal and biogeographical ranges to fully understand the adaptive potential of mountain ecosystems facing glacier extinction.

In summary, the integration of EIVs with FD offers a comprehensive approach to understanding ecological factors underlying community assembly and development while forecasting broader ecological changes. The results of this case study have broader implications for the future of biodiversity in mountain ecosystems, considering increasing rates of glacier retreat. The ecological dynamics we observed here could extend to other mountain landscapes, highlighting the importance of monitoring FD together with ecological indicators while offering valuable insights into understanding how plant communities respond and potentially adapt to ongoing climate change.

Supplementary Material

Supplementary material is available at *Journal of Plant Ecology* online.

Table S1: Survey of plant communities in Mont Minè glacier foreland in summer 2022.
Table S2: Landolt's Ecological Indicator Values (EIVs) for each plant species.
Table S3: Functional traits of each plant species.
Table S4: Summary table of model coefficient estimates for functional diversity and functional traits.
Table S5: Summary table of EIV response to glacier retreat.
Table S6: Summary table of model coefficient estimates for EIV response to glacier retreat (stages).
Table S7: Summary table of functional traits response to glacier retreat.
Table S8: Summary table of functional diversity response to glacier retreat.
Table S9: Summary table of Principal Component Analysis (PCA).
Table S10: Importance of predictors (columns) for functional diversity and functional traits (Response) in random forest models as measured by percentage increase in mean square error.
Table S11: Summary table of model coefficient estimates for functional traits response to glacier retreat (stages).
Table S12: Summary table of model coefficient estimates for functional diversity response to glacier retreat (stages).
Figure S1: Univariate relationships between glacier retreat and EIVs (*x*-axis) and functional trait diversity (*y*-axis).
Figure S2: Map of the Principal Component Analysis (PCA) examining the relationships among glacier retreat, ecological indicators, and functional trait diversity.

Authors' Contributions

Gianalberto Losapio (Conceptualization, Data curation, Formal analysis, Funding acquisition, Investigation, Methodology, Project administration, Supervision, Writing—original draft), Lucía Mottet (Data curation, Formal analysis, Investigation, Validation, Writing—review & editing), Nora Khelidj (Data curation, Formal analysis, Investigation, Writing—review & editing), Bao Ngan Tu (Formal analysis, Investigation, Methodology, Writing—review & editing), Bruno Enrico Leone Cerabolini (Data curation, Resources, Writing—review & editing), Stephanie Grand (Data curation, Resources, Supervision, Writing—review & editing), Natasha de Vere (Investigation, Resources, Writing—review & editing), and Antoine Guisan (Conceptualization, Supervision, Writing—review & editing)

Funding

This work was supported by the Swiss National Science Foundation [Grant number PZ00P3_202127], the Italian Ministry of Education and Research [PRIN 2022 PNRR MITEX P2022N5KYJ], and Biodiversa + [grant agreement number 101052342].

Acknowledgements

We thank the Service des forêts, de la nature et du paysage of Canton du Valais for providing sampling permission. We thank the Biodiversity Change group for providing feedbacks. We thank the Associate Editor and the reviewer for commenting on the submitted version of this manuscript.

Conflict of interest statement. The authors declare that they have no conflict of interest.

Data Availability

Data and R script are publicly and freely available on GitHub at the following link https://github.com/losapio/JPE2025EIV.

REFERENCES

Ackerly D (2004) Functional strategies of chaparral shrubs in relation to seasonal water deficit and disturbance. *Ecol Monogr* **74**:25–44. https://doi.org/10.1890/03-4022

Aeschimann D, Lauber K, Moser DM, *et al.* (2004) *Flora Alpina*. Haupt, Bern.

Almela P, Casero C, Justel A, *et al.* (2022) Ubiquity of dominant cyanobacterial taxa along glacier retreat in the Antarctic peninsula. *FEMS Microbiol Ecol* **98**:fiac029. https://doi.org/10.1093/femsec/fiac029

An Y, Wang Le, Zhang M, *et al.* (2025) Plant functional traits and community characteristics jointly shape soil carbon, nitrogen, and phosphorus storage in passively restored wetlands following agricultural abandonment. *J Plant Ecol* **18**:rtaf084. https://doi.org/10.1093/jpe/rtaf084

Archer E (2023) *rfPermute: Estimate Permutation p-Values for Random Forest Importance Metrics*. https://CRAN.R-project.org/package=rfPermute

Bazzaz FA (1990) Plant–plant interactions in successional environments. In Grace JB, Tilman D (eds). *Perspectives on Plant Competition*. Academic Press, 239–263. https://doi.org/10.1016/B978-0-12-294452-9.50016-3

Ben-Shachar MS, Lüdecke D, Makowski D (2020) Effectsize: estimation of effect size indices and standardized parameters. *J Open Source Softw* **5**:2815. https://doi.org/10.21105/joss.02815

Bernasconi SM, Bauder A, Bourdon B, *et al.* (2011) Chemical and biological gradients along the damma glacier soil chronosequence, Switzerland. *Vadose Zone J* **10**:867–883. https://doi.org/10.2136/vzj2010.0129

Bhattacharya P, Tiwari P, Talukdar G, *et al.* (2022) Shifts in bacterial community composition and functional traits at different time periods post-deglaciation of Gangotri Glacier, Himalaya. *Curr Microbiol* **79**:91. https://doi.org/10.1007/s00284-022-02779-8

Bongers FJ, Schmid B, Bruelheide H, *et al.* (2021) Functional diversity effects on productivity increase with age in a forest biodiversity experiment. *Nat Ecol Evolution* **5**:1594–1603. https://doi.org/10.1038/s41559-021-01564-3

Bosson JB, Huss M, Cauvy-Fraunié S, *et al.* (2023) Future emergence of new ecosystems caused by glacial retreat. *Nature* **620**:562–569. https://doi.org/10.1038/s41586-023-06302-2

Brown LE, Khamis K, Wilkes M, *et al.* (2018) Functional diversity and community assembly of river invertebrates show globally consistent responses to decreasing glacier cover. *Nat Ecol Evol* **2**:325–333. https://doi.org/10.1038/s41559-017-0426-x

Burga CA, Krüsi B, Egli M, *et al.* (2010) Plant succession and soil development on the foreland of the morteratsch glacier (pontresina, switzerland): straight forward or chaotic? *Flora* **205**:561–576. https://doi.org/10.1016/j.flora.2009.10.001

Caccianiga M, Luzzaro A, Pierce S, *et al* (2006) The functional basis of a primary succession resolved by CSR classification. *Oikos* **112**:10–20. https://doi.org/10.1111/j.0030-1299.2006.14107.x

Cadotte MW (2017) Functional traits explain ecosystem function through opposing mechanisms. *Ecol Lett* **20**:989–996. https://doi.org/10.1111/ele.12796

Cadotte MW, Carscadden K, Mirotchnick N (2011) Beyond species: functional diversity and the maintenance of ecological processes and services. *J Appl Ecol* **48**:1079–1087. https://doi.org/10.1111/j.1365-2664.2011.02048.x

Cantera I, Carteron A, Guerrieri A, *et al.* (2024) The importance of species addition 'versus' replacement varies over succession in plant communities after glacier retreat. *Nat Plants* **10**:256–267. https://doi.org/10.1038/s41477-023-01609-4

Casallas LMV, Khelidj N, Morán-Ordóñez A, *et al.* (2025) Global impacts of glacier retreat on ecosystem services provided by soil and vegetation in mountain regions: a literature review. *Ecosyst Serv* **73**:101730. https://doi.org/10.1016/j.ecoser.2025.101730

Chapin FS, Walker LR, Fastie CL, *et al.* (1994) Mechanisms of primary succession following deglaciation at Glacier Bay, Alaska. *Ecol Monogr* **64**:149–175. https://doi.org/10.2307/2937039

Charles C, Khelidj N, Mottet L, *et al.* (2024) Plant–soil interactions drive development of novel ecosystems after glacier retreat. *Res Square* https://doi.org/10.21203/rs.3.rs-4647918/v1

Charles C, Khelidj N, Mottet L, *et al.* (2025) The effects of glacier retreat on plant diversity and soil development. *Arct Antarct Alp Res* **57**:2483455. https://doi.org/10.1080/15230430.2025.2483455

Cornwell WK, Ackerly DD (2009) Community assembly and shifts in plant trait distributions across an environmental gradient in Coastal California. *Ecol Monogr* **79**:109–126. https://doi.org/10.1890/07-1134.1

Cutler NA, Belyea LR, Dugmore AJ (2008) The spatiotemporal dynamics of a primary succession. *J Ecol* **96**:231–246. https://doi.org/10.1111/j.1365-2745.2007.01344.x

Dalle Fratte M, Pierce S, Zanzottera M, *et al.* (2021) The association of leaf sulfur content with the leaf economics spectrum and plant adaptive strategies. *Funct Plant Biol* **48**:924–935. https://doi.org/10.1071/FP20396

Díaz S, Kattge J, Cornelissen JHC, *et al.* (2016) The global spectrum of plant form and function. *Nature* **529**:167–171. https://doi.org/10.1038/nature16489

Diekmann M (2003) Species indicator values as an important tool in applied plant ecology – a review. *Basic Appl Ecol* **4**:493–506. https://doi.org/10.1078/1439-1791-00185

Eichel J (2019) Vegetation succession and biogeomorphic interactions in glacier forelands. In Heckmann T, Morche D (eds). *Geomorphology of Proglacial Systems*. Cham: Springer, 327–349. https://link.springer.com/chapter/10.1007/978-3-319-94184-4_19

Erschbamer B, Caccianiga MS (2016) Glacier forelands: lessons of plant population and community development. In Cánovas F, Lüttge U, Matyssek R (eds). *Progress in Botany*, Vol. **78**. Cham: Springer International Publishing, 259–284. https://doi.org/10.1007/124_2016_4

Fan Y, Zhang C, Hu W, *et al.* (2025) Development of soil quality assessment framework: a comprehensive review of indicators, functions, and approaches . *Ecol Indic* **172**:113272. https://doi.org/10.1016/j.ecolind.2025.113272

Fastie CL (2013) Causes and ecosystem consequences of multiple pathways of primary succession at Glacier Bay, Alaska. *Ecology* **76**:1899–1916. https://doi.org/10.2307/1940722

Federal Office of Topography (2023) *Swisstopo*. https://map.geo.admin.ch/

Ficetola GF, Marta S, Guerrieri A, *et al.* (2021) Dynamics of ecological communities following current retreat of glaciers. *Annu Rev Ecol Evol Syst* **52**:405–426. https://doi.org/10.1146/annurev-ecolsys-010521-040017

Fox J, Weisser S (2019) *An R Companion to Applied Regression*, 3rd edn. Thousand Oaks, CA: Sage.

Garnier E, Navas ML, Grigulis K (2016) *Plant Functional Diversity*. Oxford University Press.

GLAMOS (2023) *Swiss Glacier Volume Change*. Glacier Monitoring Switzerland. https://doi.org/10.18750/volumechange.2023.r2023

Gross N, Kunstler G, Liancourt P, *et al.* (2009) Linking individual response to biotic interactions with community structure: a trait-based framework. *Funct Ecol* **23**:1167–1178. https://doi.org/10.1111/j.1365-2435.2009.01591.x

Guisan A, Mod HK, Scherrer D, *et al.* (2019) Scaling the linkage between environmental niches and functional traits for improved spatial predictions of biological communities. *Glob Ecol Biogeogr* **28**:1384–1392. https://doi.org/10.1111/geb.12967

IPCC (2019) *IPCC Special Report on the Ocean and Cryosphere in a Changing Climate*. Cambridge and New York: Cambridge University Press. https://doi.org/10.1017/9781009157964

IPCC (2022) Climate change 2022: impacts, adaptation, and vulnerability. In Pörtner HO, Roberts DC, Tignor M, *et al.* *Contribution of Working Group II to the Sixth Assessment Report of the Intergovernmental Panel on Climate Change*. Cambridge University Press. https://doi.org/10.1017/9781009325844

Kattge J, Bönisch G, Díaz S, *et al.* (2020) TRY plant trait database—enhanced coverage and open access. *Glob Change Biol* **26**:119–188. https://doi.org/10.1111/gcb.14904

Khelidj N, Balestra S, Caccianiga MS, *et al.* (2025) Plants' contributions to people shift with glacier extinction. *Plant Environ Interact* **6**:e70041. https://doi.org/10.1002/pei3.70041

Khelidj N, Caccianiga M, Cerabolini BEL, *et al.* (2024) Glacier extinction homogenizes functional diversity via ecological succession. *J Veg Sci* **35**:e13312. https://doi.org/10.1111/jvs.13312

Laliberté E, Legendre P, Shipley B (2014) *FD: Measuring Functional Diversity from Multiple Traits, and Other Tools for Functional Ecology*. R Package Version 1.0-12. https://cran.r-project.org/web/packages/FD/index.html

Laliberté E, Legendre P (2010) A distance-based framework for measuring functional diversity from multiple traits. *Ecology* **91**:299–305. https://doi.org/10.1890/08-2244.1

Lambiel C, Maillard B, Kummert M, *et al.* (2016) Geomorphology of the Hérens valley (Swiss Alps). *J Maps* **12**:160–172. https://doi.org/10.1080/17445647.2014.999135

Landolt, E, Bäumler B, Erhardt A, *et al.* (2010) *Flora Indicativa. Ökologische Zeigerwerte Und Biologische Kennzeichen Zur Flora Der Schweiz Und Der Alpen. Ecological Indicators Values and Biological Attributes of the Flora of Switzerland and the Alps*, 2nd ed. Bern: Haupt.

Lê S, Josse J, Husson F (2008) FactoMineR: an R package for multivariate analysis. *J Stat Softw* **25**:1–18. https://doi.org/10.18637/jss.v025.i01

Li J, Chen H, Guo K, *et al.* (2021) Changes in soil properties induced by pioneer vegetation patches in coastal ecosystem. *Catena* **204**:105393. https://doi.org/10.1016/j.catena.2021.105393

Losapio G, Cerabolini BEL, Maffioletti C, *et al.* (2021) The consequences of glacier retreat are uneven between plant species. *Front Ecol Evol* **8**:520. https://doi.org/10.3389/fevo.2020.616562

Losapio G, Lee JR, Fraser CI, *et al.* (2025) Impacts of deglaciation on biodiversity and ecosystem function. *Nat Rev Biodiversity* **1**:371–385. https://doi.org/10.1038/s44358-025-00049-6

Losapio G, Schöb C (2017) Resistance of plant–plant networks to biodiversity loss and secondary extinctions following simulated environmental changes. *Funct Ecol* **31**:1145–1152. https://doi.org/10.1111/1365-2435.12839

Lüdecke D, Ben-Shachar MS, Patil I, *et al.* (2020) Extracting, computing and exploring the parameters of statistical models using R. *J Open Source Softw* **5**:2445. https://doi.org/10.21105/joss.02445

Mason NWH, Mouillot D, Lee WG, *et al.* (2005) Functional richness, functional evenness and functional divergence: the primary components of functional diversity. *Oikos* **111**:112–118. https://doi.org/10.1111/j.0030-1299.2005.13886.x

Mason NWH, Richardson SJ, Peltzer DA, *et al.* (2012) Changes in coexistence mechanisms along a long-term soil chronosequence revealed by functional trait diversity. *J Ecol* **100**:678–689. https://doi.org/10.1111/j.1365-2745.2012.01965.x

Milner AM, Fastie CL, Chapin FS, *et al.* (2007) Interactions and linkages among ecosystems during landscape evolution. *BioScience* **57**:237–247. https://doi.org/10.1641/B570307

Milner AM, Khamis K, Battin TJ, *et al.* (2017) Glacier shrinkage driving global changes in downstream systems. *Proc Nat Acad Sci USA* **114**:9770–9778. https://doi.org/10.1073/pnas.1619807114

Nicolussi K, Roy ML, Schlüchter C, *et al.* (2022) The glacier advance at the onset of the little ice age in the Alps: new evidence from Mont Miné and Morteratsch glaciers. *Holocene* **32**:624–638. https://doi.org/10.1177/09596836221088247

Pérez-Harguindeguy N, Díaz S, Garnier E, *et al.* (2013) New handbook for standardised measurement of plant functional traits worldwide. *Aust J Bot* **61**:167–234. doi:http://dx.doi.org/10.1071/BT12225

Raffl C, Mallaun M, Mayer R, *et al.* (2006) Vegetation succession pattern and diversity changes in a glacier valley, Central Alps, Austria. *Arct Antarct Alp Res* **38**:421–428. https://doi.org/10.1657/1523-0430(2006)38[421:vspadc]2.0.co;2

Rao S, Miao X-Y, Fan S-Y, *et al.* (2023) Seven-decade forest succession reveals how species colonization and extinction drive long-term community structure dynamics. *J Plant Ecol* **16**:rtad008. https://doi.org/10.1093/jpe/rtad008

Ricotta C, de Bello F, Moretti M, *et al.* (2016) Measuring the functional redundancy of biological communities: a quantitative guide. *Methods Ecol Evol* **7**:1386–1395. https://doi.org/10.1111/2041-210X.12604

Scherrer D, Guisan A (2019) Ecological indicator values reveal missing predictors of species distributions. *Sci Rep* **9**:3061. https://doi.org/10.1038/s41598-019-39133-1

Scherrer D, Lüthi R, Bugmann H, *et al.* (2024) Impacts of climate warming, pollution, and management on the vegetation composition of Central European Beech Forests. *Ecol Indic* **160**:111888. https://doi.org/10.1016/j.ecolind.2024.111888

Schleuter D, Daufresne M, Massol F, *et al.* (2010) A user's guide to functional diversity indices. *Ecol Monogr* **80**:469–484. https://doi.org/10.1890/08-2225.1

Shipley B, Belluau M, Kühn I, *et al.* (2017) Predicting habitat affinities of plant species using commonly measured functional traits. *J Veg Sci* **28**:1082–1095. https://doi.org/10.1111/jvs.12554

Tu BN, Khelidj N, Cerretti P, *et al.* (2024) Glacier retreat triggers changes in biodiversity and plant–pollinator interaction diversity. *Alp Bot* **134**:171–182. https://doi.org/10.1007/s00035-024-00309-9

Venables WN, Ripley BD (2002) Modern applied statistics with S. *Technometrics* **45**:111. https://doi.org/10.1198/tech.2003.s33

Villéger S, Mason NWH, Mouillot D (2008) New multidimensionale functional diversity indices for a multifaceted framework in functional ecology. *Ecology* **89**:2290–2301. https://doi.org/10.1890/07-1206.1

Walker LR, Wardle D, Bardgett RD, *et al.* (2010) The use of chronosequences in studies of ecological succession and soil development. *J Ecol* **98**:725–736. https://doi.org/10.1111/j.1365-2745.2010.01664.x

Wang X, Huang P, Ma M, *et al.* (2024) Effects of riparian pioneer plants on soil aggregate stability: roles of root traits and rhizosphere microorganisms. *Sci Total Environ* **940**:173584. https://doi.org/10.1016/j.scitotenv.2024.173584

Wenskus F, Hecht C, Hering D, *et al.* (2025) Effects of floodplain decoupling on taxonomic and functional diversity of terrestrial floodplain organisms. *Ecol Indic* **170**:113106. https://doi.org/10.1016/j.ecolind.2025.113106

Wright IJ, Reich PB, Cornelissen JHC, *et al.* (2005) Modulation of leaf economic traits and trait relationships by climate. *Glob Ecol Biogeogr* **14**:411–421. https://doi.org/10.1111/j.1466-822x.2005.00172.x