





Glacier extinction homogenizes functional diversity via ecological succession

Nora Khelidj¹  | Marco Caccianiga²  | Bruno E. L. Cerabolini³  | Duccio Tampucci²  | Gianalberto Losapio^{1,2} 

¹Faculty of Geosciences and Environment, Institute of Earth Surface Dynamics, University of Lausanne, UNIL Mouline, Lausanne, Switzerland

²Department of Biosciences, University of Milan, Milan, Italy

³Department of Biotechnologies and Life Sciences, University of Insubria, Varese, Italy

Correspondence

Gianalberto Losapio, Faculty of Geosciences and Environment, Institute of Earth Surface Dynamics, University of Lausanne, UNIL Mouline, Lausanne 1015, Switzerland.
Email: Gianalberto.Losapio@unil.ch

Funding information

Italian Ministry of University and Research, Grant/Award Number: P2022N5KYJ; Schweizerischer Nationalfonds zur Förderung der Wissenschaftlichen Forschung, Grant/Award Number: PZ00P3_202127

Co-ordinating Editor: Peter Christiaan le Roux

Abstract

Questions: The disappearance of glaciers threatens biodiversity and the functioning of ecosystems. Yet, questions remain about the response of functional diversity to glacier retreat. How does glacier retreat influence functional diversity? How does glacier retreat influence the relationship between taxonomic diversity and functional diversity? How does glacier retreat impact community mean and intraspecific trait variability (ITV) of key functional traits?

Location: Four retreating glacier ecosystems in the Italian Alps. Plant communities spanning 0 to ca 5000 years on average after glacier retreat, including a scenario of glacier extinction.

Methods: We quantified functional diversity analyzing twelve plant traits associated to carbon and nitrogen cycling, resource allocation, and reproduction of 117 plant species. We addressed how functional diversity changes with glacier retreat and taxonomic diversity (i.e., plant species richness).

Results: Plant functional diversity decreases with glacier extinction while increasing with species richness. The positive relationship between taxonomic and functional diversity becomes flatter, that is, less important, with glacier retreat. We document sharp changes in functional niche position and breadth with glacier retreat. Key functional traits associated with carbon cycling and resource allocation change substantially with ecological succession triggered by glacier retreat. Traits associated to nitrogen cycling show little change. We also found that flowering start shifted earlier in the season while flowering period increased with glacier retreat.

Conclusion: Our results demonstrate the pervasive impact of glacier extinction on the functioning of plant communities. Changes in functional mean and functional variation indicate shifts in niche position and niche breadth which could have implications for species adaptation to changing environments.

KEYWORDS

Alpine communities, biodiversity change, climate change, evenness, functional redundancy, glacier environments, intraspecific trait variability, novel ecosystems

This article is a part of the Special Issue "Plant community responses to climate change", edited by Richard Michalet, Jiri Dolezal, Jonathan Lenoir, Peter C. le Roux, Sabine Rumpf and Sonia Wipf.

This is an open access article under the terms of the [Creative Commons Attribution-NonCommercial](https://creativecommons.org/licenses/by-nc/4.0/) License, which permits use, distribution and reproduction in any medium, provided the original work is properly cited and is not used for commercial purposes.

© 2024 The Author(s). *Journal of Vegetation Science* published by John Wiley & Sons Ltd on behalf of International Association for Vegetation Science.

1 | INTRODUCTION

An iconic symptom of the current climate crisis is the disappearance of glaciers worldwide (Frédéric et al., 2015; Roe et al., 2017; Zemp et al., 2019). The recent report of the Intergovernmental Panel on Climate Change (IPCC) highlights how glaciers are unique and threatened ecological and human systems whose disappearance is a major reason for concern (IPCC, 2022). Glaciers cover about 10% of terrestrial land and part of the ocean (Hugonnet et al., 2021). They are known to host specialist species adapted to the unique thermal and hydrological condition created by glaciers (Cauvy-Fraunié & Dangles, 2019). Although the consequences of glacier retreat on plant species diversity are increasingly documented (Jacobsen et al., 2012; Cauvy-Fraunié & Dangles, 2019; Stibal et al., 2020; Losapio et al., 2021; Bourquin et al., 2022; Fodelianakis et al., 2022), little attention has been paid to how functional diversity would respond to glacier extinction (Caccianiga et al., 2006; Losapio et al., 2021). It is important and valuable to understand changes in functional diversity of these novel, fast-changing glacier environments in order to develop effective solutions for anticipating the impact of global warming.

With the retreat of glaciers, new ice-free terrains are colonized by living organisms, prompting changes in species richness and composition over time, a process termed ecological succession (Matthews, 1992; Chapin et al., 1994; Walker & del Moral, 2003; Erschbamer et al., 2008; Burga et al., 2010; Erschbamer & Caccianiga, 2016). Previous studies indicate that species richness increases with glacier retreat in the short term by making space for plant colonization and hence initiating primary succession (Matthews, 1992; Chapin et al., 1994; Walker & del Moral, 2003; Raffl et al., 2006; Ficetola et al., 2021). However, this pattern of increasing biodiversity holds true only as long as glaciers are still present in the landscape (Jacobsen et al., 2012; Erschbamer & Caccianiga, 2016; Stibal et al., 2020; Losapio et al., 2021; Anthelme et al., 2022). As glacier foreland ecosystems comprise unique habitats that host distinctive organisms (Erschbamer & Caccianiga, 2016; Bourquin et al., 2022; Fodelianakis et al., 2022), their extinction would reduce biodiversity via both direct changes in environmental conditions and indirect changes in biotic interactions (Losapio et al., 2021). Since many Alpine glaciers will disappear within the next three decades (Zekollari et al., 2019), we may face up to 30% loss in species diversity locally in glacial ecosystem (Jacobsen et al., 2012; Losapio et al., 2021). Estimates of functional diversity response could help us understand the processes behind the changes in plant community composition following glacier retreat. However, to date, no such estimates have been made. Although habitat protection is important to support biodiversity and functioning in glacier ecosystems, we also need to anticipate and predict which species to conserve or which communities to restore on a functional basis. Functional diversity can provide a process-based framework to identify priority species for conservation.

Functional diversity is more informative about ecological processes compared to taxonomy and taxonomic diversity (Díaz &

Cabido, 2001; Caccianiga et al., 2006; Díaz et al., 2016; Losapio et al., 2018; Zanzottera et al., 2020). Functional diversity can be approached by looking at functional traits, which are morphological, chemical or phenological features that affect the fitness of organisms (Violle et al., 2017). The combination of traits within species defines their functional type and adaptations, and reflects the abiotic and biotic environment (Díaz & Cabido, 2001). Furthermore, functional traits are also at the basis of ecosystem functioning in a given environment (Reich et al., 2003; Wright et al., 2004; Funk et al., 2017; Schleuning et al., 2023). One of the main causes of trait differences between species is the surrounding environment that filters and selects for specific traits and trait combinations. Previous studies addressing the effects of glacier retreat on functional diversity reported sharp changes in trait composition related to seed dispersal and Grime (Grime, 2001) strategies (Erschbamer & Caccianiga, 2016). Following the retreat of an Alpine glacier (Rutor glacier), Caccianiga et al. (2006) reported a shift from “ruderal, fast growing” species with high leaf nitrogen content to “stress-tolerant” (*sensu* Grime (2001)) plants with low N content. When considering *leaf economic spectrum* traits (Reich et al., 2003; Wright et al., 2004), Losapio et al. (2021) documented a shift from pioneer species with “acquisitive” strategies (high specific leaf area) to late-successional species with “conservative” strategies (low specific leaf area and high leaf dry-matter content) along four Alpine glacier forelands. Such a trait turnover was accompanied by a shift from facilitative to competitive interactions among plants (Losapio et al., 2021). Similarly, Greinwald et al. (2021) reported changes in dispersal type and plant height that were consistent between two glaciers with contrasting geology. Yet, functional traits can vary substantially within species. However, these few previous studies addressing the effects of glacier retreat on functional diversity have the limitations of addressing a small number of sites or traits while considering trait average only. Given these limitations, it remains unknown how functional diversity changes with glacier retreat, and to what degree changes in functional diversity are mediated by changes in species richness. Looking at functional diversity patterns may help us to understand the broader, functional consequences of glacier retreat, how species assemble after glacier retreat and the underlying processes.

Intraspecific trait variability (ITV) is often overlooked in community ecology, although it may be crucial for understanding key ecological processes (de Bello et al., 2011; Violle et al., 2012; Siefert et al., 2015; Losapio & Schöb, 2017; Kitagawa et al., 2022). The drivers of ITV range from genetic effects to environmental influence on development and phenotypic plasticity (Cornwell & Ackerly, 2009; Kraft et al., 2014). The consequences of ITV concern conservation genetics, biodiversity dynamics, and ecosystem functioning (Cadotte et al., 2011; Volf et al., 2016; Losapio et al., 2018; Bongers et al., 2021; Carmona et al., 2021). Notably, the higher the ITV, the higher the niche breadth (Schöb et al., 2012). Hence, changes in ITV and ITV-based functional diversity can be used to estimate changes in niche breadth at both species and community level, respectively. Nevertheless, the effects of glacier retreat on ITV across plant communities remain unexplored. Furthermore, the higher the ITV, the

higher the potential for local adaptation (Cornwell & Ackerly, 2009; Volf et al., 2016). Species with high ITV have higher chances to adapt to changing environmental conditions. Likewise, communities with high ITV-based functional diversity are expected to display higher resilience and adaptive potential. Species with low ITV have lower chances of local adaptation, and can pose higher potential for diversification. Understanding changes in functional mean (i.e., niche position) and functional dispersion (i.e., niche breadth) is therefore key for encompassing genetic variability, developmental constraints, and phenotypic plasticity in conservation planning (Roches et al., 2021) that aims at adaptation and mitigation of glacier extinction impact on ecosystems.

Here, we addressed the following questions: (1) how does glacier retreat influence functional diversity? (2) How does glacier retreat influence the relationship between taxonomic diversity and functional diversity? (3) How does glacier retreat impact community mean and ITV of key functional traits? We hypothesize that ecological succession triggered by glacier retreat will drive a decrease of functional diversity. We expect a generally positive taxonomic-functional diversity relationship (Schöb et al., 2012, 2017). Given the known shift in plant species composition with succession, we hypothesize that ITV increases for “acquisitive” traits (e.g. leaf carbon and nitrogen content) while decreasing for “conservative” traits (e.g. leaf dry-matter content).

2 | METHODS

2.1 | Study system

The study was conducted on the foreland of four glacier ecosystem sites: Vedretta d'Amola glacier, Western Trobio glacier, Rutor glacier, and Vedretta di Cedec glacier (Losapio et al., 2021). In each foreland, we established a transect of ca 2 km from the glacier terminus (or glacier surface in the case of Vedretta d'Amola debris-covered glacier) to the grasslands adjacent to Little Ice Age (LIA) b moraines. Such transect spans terrains from recently ice-free to thousands of years old, such that plant communities range from 0 (surface of debris-covered glacier) to ca 10,000 years after glacier retreat. Terrain age was estimated as the mean between two moraines (Losapio et al., 2021); this way, terrains outside the LIA moraines were approximated to an average of 5000 years old. Along each transect, three to seven plots of 25–100 m² were randomly placed in each stage of glacier retreat (Losapio et al., 2021). In particular, we placed 34 plots at Vedretta d'Amola glacier, 30 plots at Western Trobio glacier, 59 plots at Rutor glacier, and 27 plots at Vedretta di Cedec glacier; the differences were driven by the heterogeneity and extension of the examined glacier ecosystems. In each plot, we surveyed plant communities by recording the presence/absence of plant species. Overall, $n=117$ plant species were recorded and further analyzed across $n=170$ plots in the four sites.

This system represents a gradient of plant community development over space and time, that is, primary succession

(Matthews, 1992; Chapin et al., 1994; Walker & del Moral, 2003). Terrains outside the LIA moraines can represent a scenario of glacier extinction as they are not influenced anymore by the previous occurrence of the glacier (Erschbamer & Caccianiga, 2016). We refer to this scenario as glacier extinction. On the contrary, terrains inside the LIA moraines are still influenced by adjacent glacier masses. We refer to this gradient as glacier retreat. As the retreat of glaciers triggers plant colonization and primary succession, the effects of glacier retreat on functional diversity are meant to be mainly understood as indirect, that is mediated by successional changes in vegetation. Yet, it is important to clarify and highlight the role glaciers play in shaping biodiversity (Erschbamer, 2007). First, ecological succession occurs only after glacier retreat, that is, in the presence of retreating glaciers. Second, once glaciers are extinct, that is in the absence of glaciers, ecological succession will no longer be triggered but will terminate and vegetation will tend toward final stages (Chapin et al., 1994; Erschbamer & Caccianiga, 2016).

2.2 | Functional diversity analysis

We considered plant traits relevant for plant growth, reproduction, and biogeochemical functions (Hodgson et al., 1999; Díaz et al., 2016), namely: leaf carbon content (LCC), leaf nitrogen content (LNC), carbon-to-nitrogen ratio (CN), leaf area (LA), specific leaf area (SLA), leaf fresh weight (LFW), leaf dry weight (LDW), leaf dry-matter content (LDMC), canopy height (CAN), lateral spread (LS), flowering start (FS), and flowering period (FP).

Traits were measured following standard protocols (Pérez-Harguindeguy et al., 2013). We sampled fully expanded leaves from the outer canopy of 5–15 individuals (adult healthy plants) randomly selected for each species. Each species was sampled once per site. Leaf material was stored at 4°C overnight to obtain full turgidity for determination of LFW and LA (Pérez-Harguindeguy et al., 2013). LA was determined using a digital scanner and the software Leaf Area Measurement (LAM ver.1.3; University of Sheffield, UK) (Dalle Fratte et al., 2021). LDW was then determined following drying for 24 h at 105°C. SLA was calculated as the ratio between LA and LDW. LDMC was calculated as the ratio between LDW and LFW. LNC and LCC were quantified from dried leaf material using three randomly selected replicates per species and site that were processed with a CHNS-analyzer (FlashEA 1112 series Thermo-Scientific) following the method outlined by Dalle Fratte et al. (2021). Canopy height and lateral spread were measured directly in the field. Lateral spread values were then categorized according to Hodgson et al. (1999) assigning them to one of the six categories (i.e., 1=short-lived and non-spreading species, to 6=widely creeping perennial species with more than 79 mm between ramets). FS is defined as the month in which flowers were first produced. FP is the number of months from the appearance of the first to the last flowers. We complemented our own original trait measurements with publicly available trait data (Kattge et al., 2020). Both FS and FP were collected from Aeschmann et al. (2004).

To investigate changes in functional diversity with glacier retreat, we first considered functional dispersion (FDis) and functional evenness (FEve) (Mason et al., 2012). For this analysis, we considered the following traits: LNC, LCC, CN, LA, LDW, LFW, SLA, LDMC, and CAN. FDis estimates the average differences among species in the multidimensional trait space, calculated as the weighted mean distance from each and all individual species in the trait space to the centroid (i.e., grand mean) (Laliberté & Legendre, 2010). This index is important for understanding the multidimensional variance of functional traits within plant communities. FEve estimates the regularity of functional trait distribution by measuring the degree to which plant species differ from each other in the multidimensional space in terms of regularity and uniformity of trait values (Carmona et al., 2021). It indicates the variety of distinct ecological niches in the community and is important for understanding how plant species may interact and share resources (Schleuter et al., 2010) as plant communities develop. These two functional diversity indices are also potential indicators of community assembly processes and plant species coexistence (Mason et al., 2013). In our study context, they can shed new light on whether plant species are complementary or redundant in their functions and the degree to which their niches overlap or diverge as plant communities develop after glacier retreat. Functional diversity indices were measured with the “dbFD” function in the *FD* R package (Laliberté & Legendre, 2010). For each trait, we considered both trait average and ITV. Traits were then averaged for each species over sites. To measure ITV, for each species, we calculated the coefficient of variation ($CV_{k,i}$) of each trait as following: $CV_{k,i} = \frac{SE_{k,i} \times \sqrt{n_{k,i}}}{\bar{k}_i}$, where the standard error SE and mean \bar{k}_i were taken for each trait k and for each species i . This CV measures ITV, an often overlooked component of functional diversity analysis. These patterns in ITV indicate changes in niche breadth with glacier retreat at the species level.

Finally, we calculated FDis and FEve considering both species trait average (\bar{k}_i) and ITV ($CV_{k,i}$). That is, ITV was used as a “trait value” itself to compute FDis and FEve. Changes in ITV-based functional diversity provides a clue on the homogeneity in ITV among species within communities, indicating the degree to which species with similar ITV co-occur in the same community. Low ITV-based FDis and FEve indicate high homogeneity in ITV, suggesting low differentiation in the way species are plastic and can potentially adapt to environmental changes. Conversely, high ITV-based FDis and FEve indicate a high degree of heterogeneity in the way species display plasticity. This can indicate a community composed by species with different niche breadths and adaptive potential. The rationale for looking at ITV is that average trait values describe just one dimension of functional diversity, that is, the first moment, whereas CV encompasses also the deviation of traits from the average, that is, the second central moment. This allowed us to look at the degree to which species with similar trait means exhibit similar, higher or lower degree of phenotypic plasticity. Likewise, one can look at how species with similar intraspecific trait variations display different trait means. High values of FDis for ITV indicates high degree of dispersion between species with similar trait variation, whereas

low values indicates high degree of overlap in trait range. Low values of FEve for ITV indicate regular spacing of ITV while high values indicate high skewness and overlap within and among species. This allowed us to address the differences between communities in terms of dispersion (i.e., niche breadth) around the same mean (i.e., niche position) or whether communities with similar dispersion exhibit different means. Biologically, ITV can reflect key ecological processes such as range shift or range expansion and evolutionary processes such as the potential of species to adapt to new environments (Schöb et al., 2012; Kraft et al., 2014). Ultimately, comparing ITV-based FDis and FEve among communities provides a clue on the degree to which communities differ in their potential for local adaptation and diversification with glacier retreat. Measuring FDis and FEve for ITV ($CV_{k,i}$) allowed us to address differences and regularities in ITV, as opposed to average of traits only, expressed by plant species within and among communities (Schöb et al., 2017).

Furthermore, we assessed the impact of glacier retreat on functional uniqueness of plant species, which assess how unique is a trait in a given community. Functional uniqueness was calculated starting from functional redundancy (Violle et al., 2007; Ricotta et al., 2016). Functional redundancy indicates the degree to which functional traits are expressed by different species, or in other words whether species express similar or overlapping traits. The higher the redundancy the more stable is an ecosystem and the less vulnerable it to species loss (Ricotta et al., 2016). Yet, the higher the functional uniqueness the higher its conservation value. We adopted a framework based on functional dissimilarities among species for summarizing different facets of functional redundancy (Ricotta et al., 2016). This index was computed for trait average \bar{k}_i only. We first calculated the pairwise trait distance for all traits k between each pair of species i and j at each site. We used the Gower dissimilarity function “gowdis” in the *FD* R package (Laliberté & Legendre, 2010) which first converts the trait matrix composed of i species in rows and k traits in columns into a square distance matrix with plant species i , j in rows and columns. Then, it calculates dissimilarity coefficients s_{kji} between each species pair i – j as $s_{kji} = 1 - \frac{|x_{ki} - x_{kj}|}{x_{k,max} - x_{k,min}}$, where x_{ki} and x_{kj} are the trait values for each pair of species i and j , respectively, and $x_{k,max}$ and $x_{k,min}$ are the maximum and minimum values of each trait k , respectively. A distance matrix was created for each site separately. Then, we quantified the uniqueness of species mean traits by addressing the degree to which a community is unique as compared to a scenario where all species would be maximally dissimilar (Ricotta et al., 2016). This was accomplished by crossing the species-by-species distance matrix with the species-by-plot occurrence matrix, that is subsetting s_{kji} for species i , j occurring in each plot. We then calculate functional uniqueness for each plot at each site as $U^* = \frac{1-D}{1-Q}$, where D and Q are the Gini-Simpson diversity index and Rao quadratic diversity index, respectively (Ricotta et al., 2016; Pavoine, 2020). For computing functional uniqueness we used the “uniqueness” function of the *adiv* R package (Pavoine, 2020).

Finally, we investigated trait average and ITV for each individual trait separately at the community level. For each plot, we computed the observed trends in trait average (i.e., community mean) and ITV



for the following traits: LNC, LCC, CN, CAN, SLA, LDMC, LA, LDW, LFW, FS, FP, and LS. We did so by means of the “functcomp” function of the *FD* R package (Laliberté & Legendre, 2010).

We used linear mixed-effects models to analyze the relationship between functional diversity and glacier retreat. The model was implemented using the “lmer” function in the *lme4* R package (Bates et al., 2015). The response variables were FDis and FEve of trait average and trait variation (four separate models) as well as functional uniqueness (U^*); the predictors included the quadratic effect of years since glacier retreat (log-transformed), taxonomic diversity (plant species richness), and the interaction between years and richness; sites were considered as a random intercept. To evaluate the model output, we used the “anova” function of the *car* R package to perform an analysis of variance (ANOVA) on the fitted model (Fox & Weisser, 2019). We provided estimates of the model parameters and their corresponding confidence intervals using the Satterthwaite method (Kuznetsova et al., 2017). We also calculated and reported effect size as Cohen's f statistic considering partial effects using the “t_to_r” function of the *effectsize* R package (Ben-Shachar et al., 2020). For single traits, we performed a mixed-effects model where community mean \bar{k} and intraspecific variation CV_k of each trait were regressed against “years since glacier retreat” using a second-degree polynomial and a random intercept for “site” (two separate models per each trait). We reported the parameter estimates, standard errors, confidence intervals, degrees of freedom, t -values, p -values, Cohen's f effect size, and corresponding confidence intervals.

With glacier retreat and primary succession, many geoecological factors other than time (i.e., years since glacier retreat) play a role in driving both plant colonization and community development, including microclimate, soil conditions, topography, disturbance, and species interactions (Erschbamer and Caccianiga, 2016; Losapio et al., 2021; Ficetola et al., 2021). Here, glacier retreat can be considered as (i) a direct, proximate cause by making new space and creating new niches, or (ii) a distal cause of functional diversity change which influences taxonomic diversity by changing a suite of underlying environmental conditions. For the sake of synthesis, hereafter we consider glacier retreat as (i) a proximate cause when referring to the creation of niche space, and (ii) a distal cause when referring to turnover and taxonomic–functional diversity relationships.

3 | RESULTS

3.1 | Functional diversity indices

First, we addressed the impact of glacier retreat on functional dispersion (FDis) and functional evenness (FEve), analyzing both plant trait average and plant ITV. We found that years since glacier retreat had large effects (Cohen's $f=0.65$, $p < 0.001$) on trait average FDis (Figure 1a). These effects were negative and nonlinear as FDis decreased exponentially with increasing years since glacier retreat ($r_l = 0.22$ [0.06, 0.37], $r_q = -0.35$ [-0.47, -0.19]). Similarly, glacier

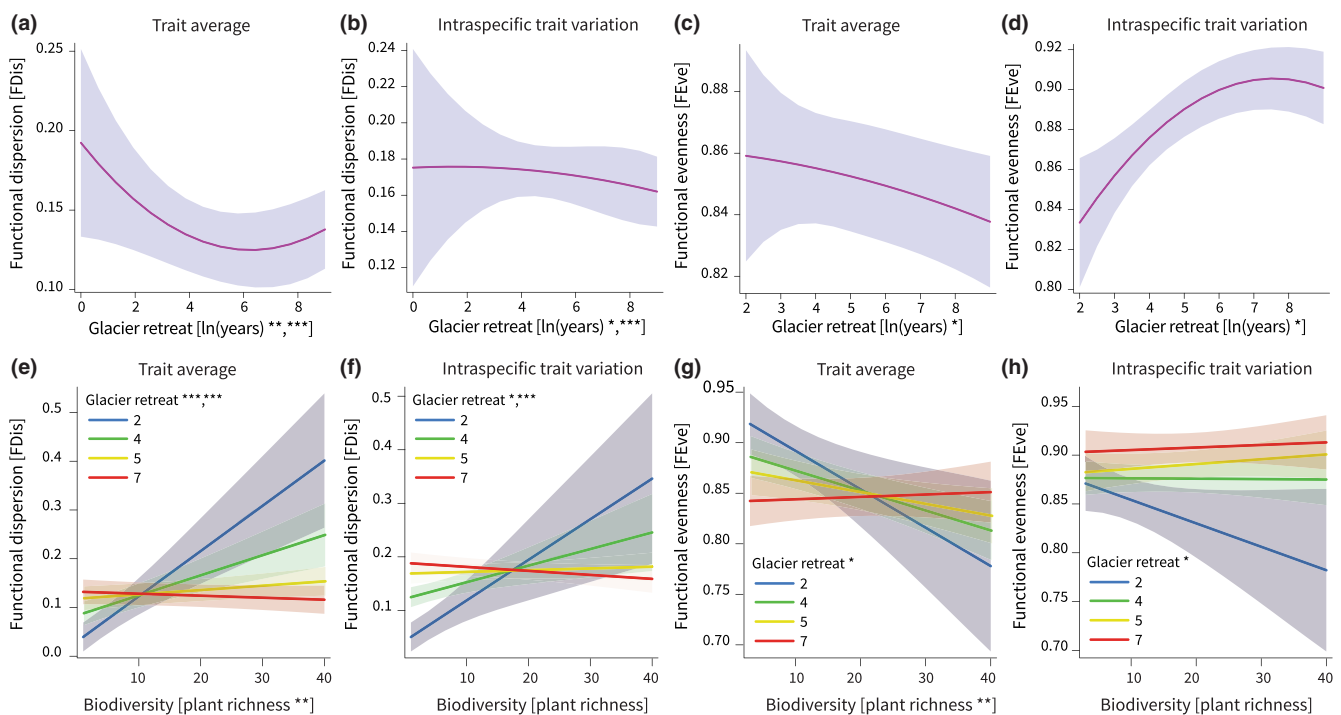


FIGURE 1 Relationship between functional diversity (y-axis), glacier retreat (a–d; log-transformed years after glacier retreat on x-axis), and biodiversity (e–h; plant species richness on x-axis). We report overall trends with 95% CI along with significance of model parameters (*, $0.05 < p < 0.1$; **, $0.01 < p < 0.001$; ***, $p < 0.001$; asterisks on the x-axis indicate significance of linear and quadratic terms of single predictor, while asterisks inside the figure indicate significance of statistical interaction between predictors).

retreat had large, negative effects ($f=0.77$, $p < 0.001$) on the FDis of ITV (Figure 1b), which also decreased exponentially with years since glacier retreat ($r_l=0.19$ [0.02, 0.34], $r_q=-0.45$ [-0.56, -0.31]). Considering the FEve, glacier retreat had large effects ($f=0.47$, $p < 0.001$, Figure 1c) that decreased FEve of trait average ($r_l=-0.42$ [-0.54, -0.27], $r_q=0.03$ [-0.14, 0.19]). Instead, glacier retreat had medium effects ($f=0.24$, $p < 0.025$) on FEve of ITV (Figure 1d), with negative effects as ITV became more homogeneous with increasing years since glacier retreat ($r_l=0.18$ [0.01, 0.34], $r_q=0.10$ [-0.07, 0.26]).

Next, we explored how taxonomic diversity (i.e., plant species richness) influenced functional diversity and how glacier retreat affected such relationship. We found that species richness had large positive effects on FDis ($f=0.27$, $p < 0.002$, Extended Data Table 1 in Appendix S1) as trait average dispersion increased with increasing species richness overall ($r_s=0.26$ [0.10, 0.40]). Nevertheless, the positive effects of plant species richness on trait average dispersion were decreased by years since glacier retreat ($r_{ls}=-0.28$ [-0.42, -0.13], $r_{qs}=0.37$ [0.22, 0.49]; Figure 1e). Plant species richness on its own had a small effect on the FDis of trait variation ($f=0.14$, $p > 0.01$, Extended Data Table 2 in Appendix S1). Yet, there was a significant interaction between glacier retreat and species richness ($f=0.31$, $p=0.002$). The overall positive relationship between plant species richness and FDis of ITV ($r_s=0.14$ [-0.04, 0.30]) was decreased by years since glacier retreat ($r_{ls}=-0.20$ [-0.35, -0.04], $r_{qs}=0.29$ [0.13, 0.42]; Figure 1f).

Furthermore, plant species richness predicted FEve of trait average on its own ($f=0.26$, $p=0.004$) and depending on glacier retreat ($f=0.37$, $p < 0.001$, Extended Data Table 3 in Appendix S1). In particular, trait average FEve decreased with increasing species richness ($r_s=-0.25$ [-0.40, -0.08]), indicating an increase in heterogeneity with increasing taxonomic diversity. Years since glacier retreat ultimately flattened this relationship ($r_{ls}=-0.29$ [0.12, 0.43], $r_{qs}=-0.03$ [-0.20, 0.14]; Figure 1g) suppressing the positive role of plant

species richness in functional heterogeneity. Species richness had negligible effects on FEve of ITV ($r=-0.13$ [-0.31, 0.07], $p=0.214$; Figure 1h).

Finally, we considered how functional uniqueness changed with years since glacier retreat (Extended Data Table 5 in Appendix S1). We found that years since glacier retreat had strong statistical effects on functional uniqueness ($f=1.132$, $p < 0.001$) as the functional uniqueness of plant species decreased with increasing years since glacier retreat ($r_l=-0.46$ [-0.57, -0.32], $r_q=0.57$ [0.46, 0.66]; Figure 2). Furthermore, functional uniqueness decreased with increasing species richness ($r_s=-0.50$ [-0.61, -0.36]), an effect also mediated by years since glacier retreat ($r_{ls}=0.43$ [0.29, 0.5], $r_{qs}=-0.45$ [-0.56, -0.31]; Figure 2).

3.2 | Single traits

We proceeded with examining how single plant traits changed with years since glacier retreat (Figures 3 and 4; Extended Data Table 6 and Extended Data Table 7 in Appendix S1). Leaf carbon content, on average, increased with years since glacier retreat ($r_l=0.726$ [0.649, 0.783], $r_q=0.334$ [0.183, 0.462]). On the contrary, ITV of leaf carbon content tended to decrease with years since glacier retreat ($r_l=0.111$ [-0.052, 0.266], $r_q=-0.418$ [-0.533, -0.276]). Leaf nitrogen content, on average, increased initially but ultimately decreased with years since glacier retreat ($r_l=0.047$ [-0.115, 0.206], $r_q=0.338$ [-0.465, -0.188]), whereas ITV of leaf nitrogen content increased with years since glacier retreat ($r_l=0.177$ [0.017, 0.324]). The average carbon-to-nitrogen content ratio showed a positive hump-shaped change with years since glacier retreat ($r_l=0.221$ [0.060, 0.364], $r_q=0.372$ [0.226, 0.494]), while the ITV of carbon-to-nitrogen content ratio showed a negative hump-shaped change with years since glacier retreat ($r_l=0.290$ [0.134, 0.424], $r_q=-0.391$ [-0.512, -0.246]).

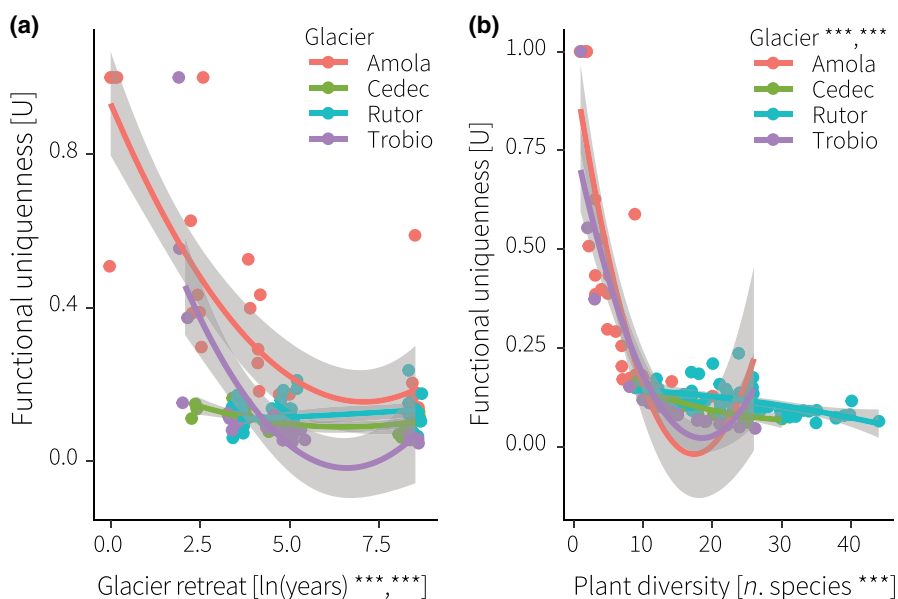


FIGURE 2 Relationship between functional uniqueness (y-axis), glacier retreat (a; log-transformed years after glacier retreat on x-axis), and biodiversity (b; plant species richness on x-axis). We report trends with 95% CI along with significance of model parameters (*, $0.05 < p < 0.1$; **, $0.01 < p < 0.001$; ***, $p < 0.001$; asterisks on the x-axis indicate significance of linear and quadratic terms of single predictor, while asterisks inside the figure indicate significance of statistical interaction between predictors) among sites.

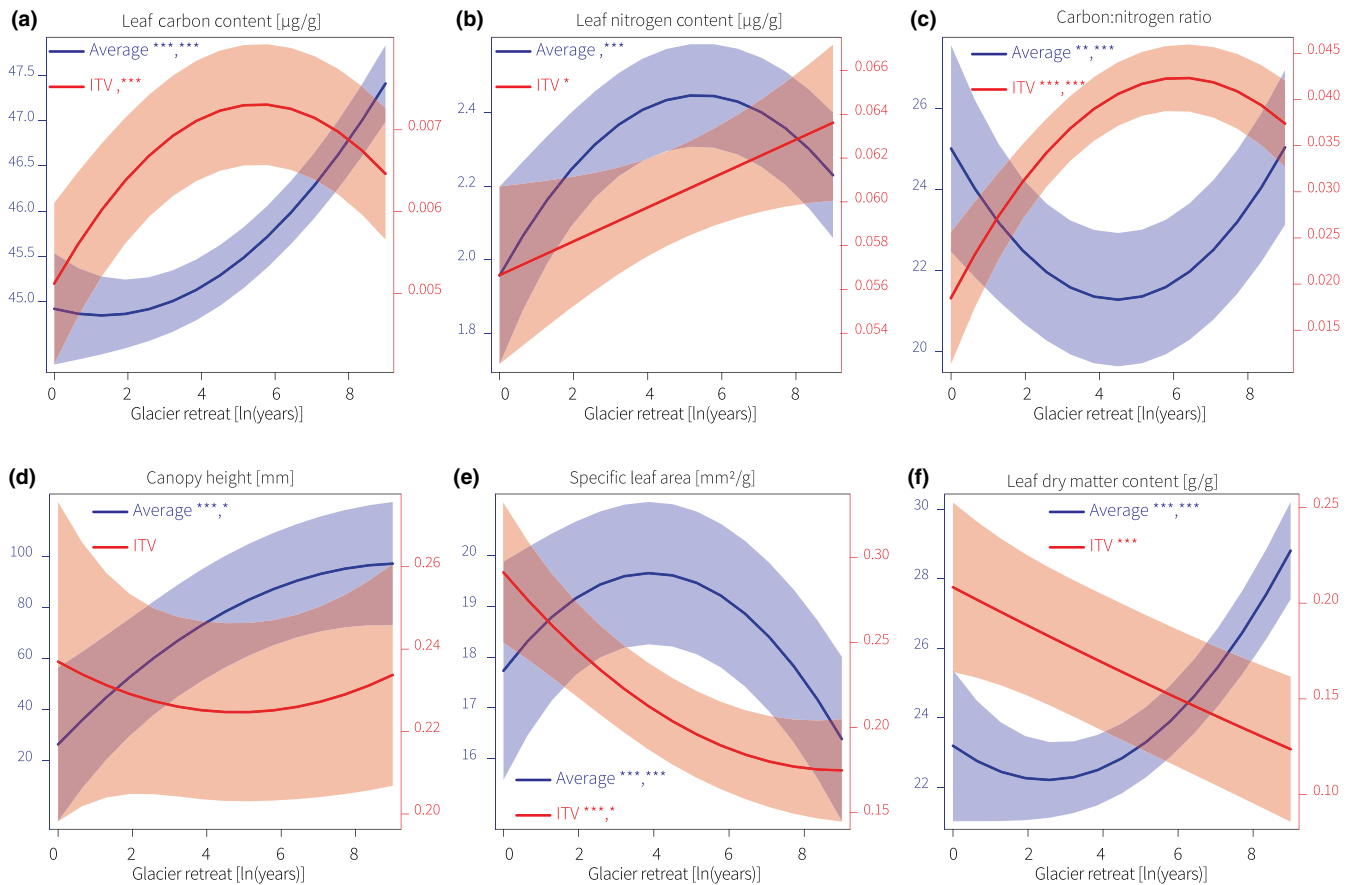


FIGURE 3 Relationship between plant traits (trait average in blue; ITV, intraspecific trait variability in orange; y-axis) and glacier retreat (log-transformed years after glacier retreat, x-axis). (a) Leaf carbon content; (b) leaf nitrogen content; (c) carbon/nitrogen ratio; (d) canopy height; (e) specific leaf area; (f) leaf dry matter content. We report overall trends with 95% CI along with significance of model parameters (*, $0.05 < p < 0.1$; **, $0.01 < p < 0.001$; ***, $p < 0.001$; asterisks inside the figure indicate significance of linear and quadratic terms of glacier retreat variable).

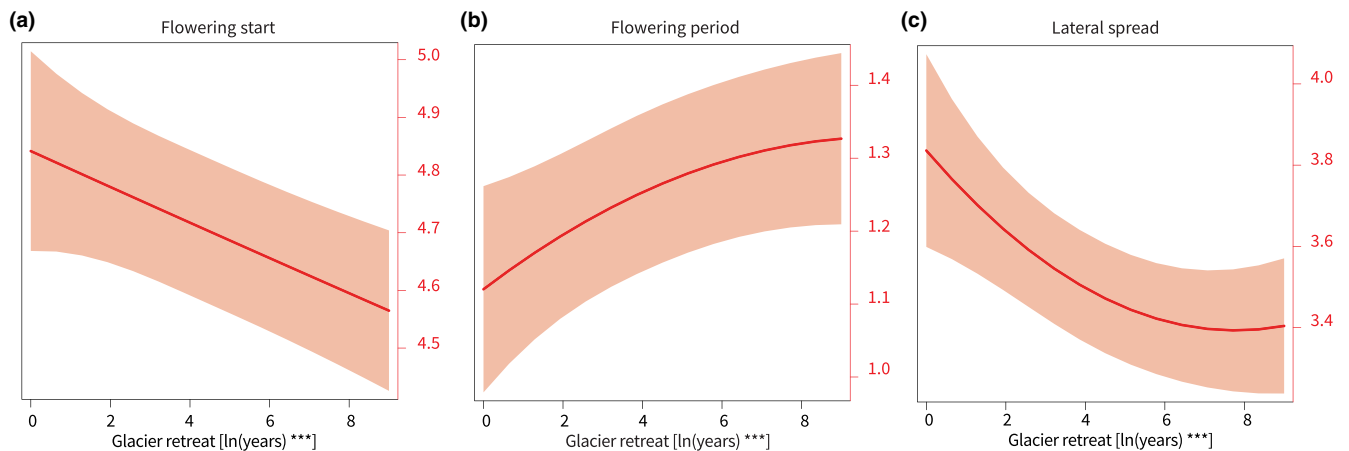


FIGURE 4 Relationship between flowering strategy (a; y-axis), flowering period (b; y-axis), lateral growth (c; y-axis), and glacier retreat (log-transformed years after glacier retreat; x-axis). We report overall trends with 95% CI along with significance of model parameters (*, $0.05 < p < 0.1$; **, $0.01 < p < 0.001$; ***, $p < 0.001$; asterisks on the x-axis indicate significance of linear and quadratic terms of glacier retreat variable).

Considering “leaf economic spectrum” traits, SLA average showed a negative hump-shaped change with glacier retreat ($r_l = 0.314 [-0.446, -0.160]$, $r_q = -0.310 [-0.442, -0.157]$), while SLA

intraspecific variation decreased exponentially with years since glacier retreat ($r_l = -0.474 [-0.580, -0.341]$, $r_q = 0.186 [0.025, 0.332]$). On the contrary, LDMC average increased with years since glacier

retreat ($r_l = -0.577$ [0.463, 0.663], $r_q = 0.329$ [0.176, 0.459]), whereas LDMC intraspecific variation sharply decreased ($r_l = -0.497$ [-0.599, -0.367]).

Notably, average canopy height tended to increase with years since glacier retreat ($r_l = -0.464$ [0.329, 0.572], $r_q = -0.166$ [-0.315, -0.004]). On the contrary, lateral spread decreased with years since glacier retreat ($r_l = -0.294$ [-0.429, -0.139], $r_q = -0.157$ [-0.005, 0.306]; Figure 4). Finally, we also found that flowering start sharply shifted to earlier in the season with years since glacier retreat ($r_l = -0.386$ [-0.507, -0.241]; Figure 4a), while flowering period increased with glacier retreat ($r_l = -0.336$ [0.185, 0.465]; Figure 4b; Appendix S1).

4 | DISCUSSION

Our results indicate that functional diversity of plant communities decreases with glacier retreat. The processes of plant colonization and ecological succession that follow the retreat of glaciers shape the functional structure of vegetation. By triggering ecological succession and ultimately decreasing species richness, glacier retreat creates more functionally homogeneous communities and decreases traits uniqueness (Cauvy-Fraunié & Dangles, 2019; Losapio et al., 2021). Here, for the sake of simplicity and clarity, we considered glacier retreat as a distal cause of functional diversity change. This causality encapsulates a suite of factors and underlying changing environmental conditions, such as soil formation, water content, microclimate change, or degree of perturbation. As the presence of glaciers provides early-successional stages, unique microclimate and ecological conditions, glacier extinction could act as a further driver of functional diversity change. Furthermore, glacier extinction would end the further onset of ecological successions and make early and intermediate successional stages disappearing.

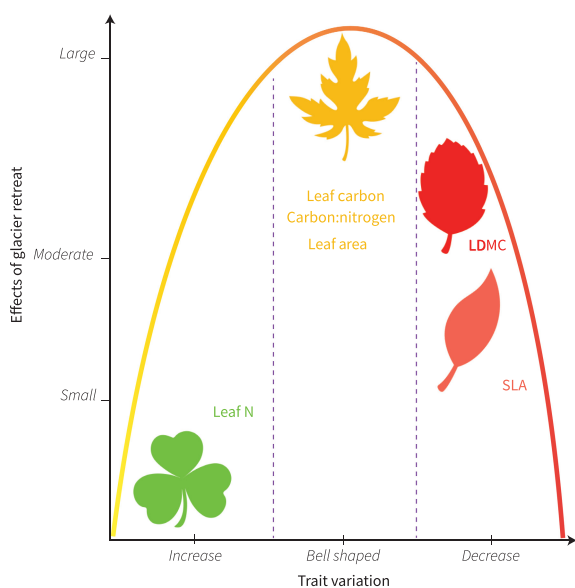


FIGURE 5 Summary of effects of glacier retreat (direction and strength) on the variation of plant functional traits.

4.1 | Functional diversity response

The decrease in functional diversity with glacier retreat could reflect a decrease in both niche differentiation and in the variation of ecological functions performed by diverse, species-rich communities (Schöb et al., 2012; Kraft et al., 2014; Le Bagousse-Pinguet et al., 2015). The ecological succession triggered by glacier retreat had two types of impacts on functional diversity: first, it decreases and homogenizes functional diversity; second, it suppresses the positive effects of species richness on functional diversity. Consistent with modeling results and recent empirical work (Cadotte et al., 2011; Song et al., 2014; Griffin-Nolan et al., 2019; Biggs et al., 2020), the observed decrease in functional diversity can have both positive and negative effects on ecological systems. On one hand, ecosystem functions and opportunities for local adaptation may be accordingly reduced. On the other, the redundancy of function can increase ecosystem stability. When focusing on single traits, our results further demonstrate that glacier retreat and associated changes in species richness strongly impact both trait average and ITV.

To understand the influence of glacier retreat on community structure and functions, we used different trait-based metrics, namely functional dispersion and functional evenness, while considering both trait average and ITV. Our results indicate that functional dispersion and evenness of trait average are the highest in early stages and decrease with glacier retreat. While functional dispersion of ITV remains constant with glacier retreat, ITV-based functional evenness increases with glacier retreat. These results indicate that young environments host more functionally diverse communities which are becoming more functionally uniform toward late developmental stages. There, with glacier extinction, few dominant species exhibit a higher degree of heterogeneity in ITV as compared to pioneer and early communities.

We have not specifically assessed biotic interactions in our study, but one could make inference on biotic processes from functional diversity patterns. The decrease in functional dispersion suggests that traits converge in the long term following glacier retreat. Trait convergence could suggest either strong habitat filtering or strong exclusion of low-competitive traits (Mayfield & Levine, 2010). In our case, the second hypothesis is more plausible as older deglaciated terrains are known to have less harsh environments, hence posing loosened habitat filters, and to host competitive species. Lower values of functional evenness are explained by traits being not evenly distributed among the species and reflecting that some trait values are more dominant than others (Mouchet et al., 2010). Accordingly, the dominance of some traits can also be explained by the exclusion of low-competitive traits.

Previous studies on ecosystem functioning and multifunctionality showed that higher functional dispersion increases multifunctionality by favoring a more efficient resource use (García-Palacios et al., 2018; Bagousse-Pinguet et al., 2021, 2019). Functional evenness is also found to be key to promote multifunctionality (Bagousse-Pinguet et al., 2021). Although we



did not measure ecosystem functioning directly, our results are consistent with recent literature suggesting that multifunctionality and ecosystem functions related to carbon and nutrient cycling are more diverse in early successional stages than late ones. In addition, we also observed a high proportion of functionally unique traits in early stages. Unique traits have also been shown to be important for promoting new functions in novel ecosystems and to be key attributes to be included in conservation planning. Yet, it is important to highlight that too high levels of functional uniqueness imply low redundancy, which can have negative effects on biodiversity and ecosystem functions by decreasing resilience and stability (Bagousse-Pinguet et al., 2021). Indeed, having multiple copies of a trait allows the ecosystem to be more resilient in case of the loss of species and environmental perturbations (Biggs et al., 2020). Our results suggest that later-developmental communities could be more resilient and stable in the presence of perturbations.

Furthermore, we decomposed the effects of species richness and glacier retreat on functional diversity. It is generally assumed that the higher the taxonomic diversity, the higher the functional diversity, and thus the dispersion between traits (Cadotte et al., 2011). Here, the hypothesis holds true in the early stages of community assembly and ecosystem development. We found that with increasing time, the positive influence of species diversity on functional diversity is suppressed by glacier retreat. This positive relationship between taxonomic and functional diversity became more flat, that is, less important, with time since glacier retreat. This indicates that functional diversity and trait evenness change no matter species richness in late-successional communities. On the contrary, as expected, functional diversity increases with species richness in early-successional communities. Furthermore, we also observed a reduction of trait uniqueness with glacier retreat. A possible explanation is that the rate of decrease in functional diversity is much stronger than that of taxonomic diversity.

4.2 | Single traits and the importance of trait variation

We further assessed changes in single traits considering both niche position (i.e., trait mean) and niche breadth (i.e., ITV) (Figure 5). Both leaf carbon content and leaf nitrogen content show sharp changes with glacier retreat. After their initial increase, nitrogen content decreases in the oldest communities while carbon does not. This yields an initial decrease of C:N ratio after deglaciation but an ultimate increase in oldest communities. These results are similar to trends observed in soil nutrients too (Khedim et al., 2021). Leaf nutrient concentration reflects nutrient availability in the surrounding environment (Zhang et al., 2020). Early stages of deglaciation are characterized by parent material and nutrient-poor soil (Khedim et al., 2021). Accordingly, our results show that plants in pioneer communities have high C:N ratio, indicating the prevalence of autotrophic processes. This process is comparable to the early stages of

terrestrial plant evolution when soil presents poor nutrient content. Plants evolve a high C:N ratio to be able to survive in nutrient-poor environments and resist environmental stress such as cold environments (Zhang et al., 2020). With time, soil becomes richer due to weathering from minerals, the decomposition of plants, and the increase of organisms able to fix atmospheric N (Zhang et al., 2020; Khedim et al., 2021). We captured C:N ratio decreasing with time, a process occurring after the retreat of glaciers and other ecological successions such as volcanic soils.

This trend is further corroborated by the analyses of the leaf economic spectrum, primarily SLA and LDMC (Wright et al., 2004). We found that plants with high SLA and low LDMC increase during early community assembly stages, indicating that plants with fast growth strategy are associated with early colonization. Colonizers are replaced toward later stages by species with low SLA and high LDMC (denser leaves and slow growers), typically more stress-tolerant species (Erschbamer & Caccianiga, 2016; Losapio et al., 2021). Stress-tolerant species can persist in time by outcompeting pioneer species (Losapio et al., 2021). We also observed a sharp increase in plant height. Tussock-dominated patches and shrublands can act as environmental filters, by altering environmental conditions, mainly by modifying light availability. With the increase in plant height, only a limited number of plants have access to maximum sunlight. Light thus becomes a limiting factor for the growth and survival of plant species (Depauw et al., 2020; Happonen et al., 2021). These results suggest that light limitation exerted by shrubs (e.g., *Rhododendron ferrugineum*) and tussock grasses/sedges (e.g., *Carex curvula*) may be a potential mechanism underlying the exclusion of herbaceous, pioneer species and driving biodiversity decline with glacier extinction. Taken together, these results suggest that different forces are driving the community structure of plants and trait distribution of plant communities. Considering trait average and ITV together provides a broader and deeper spectrum of functional diversity response to glacier retreat. Shortly after glacier retreat, plant communities exhibit small and narrow niches for carbon- and nutrient-related traits as well as canopy height. With increasing time since glacier retreat, both mean and variation increase, suggesting niche shift and particularly niche expansion (Schöb et al., 2012; Kraft et al., 2014) in relation to those traits. On the contrary, LDMC mean and variation patterns suggest potential for niche shift toward higher values with narrower niches (Schöb et al., 2017), which suggest potential higher drought resistance but also lower adaptive ability.

Notably, our results indicate that the start of flowering shifted to earlier in the season, while the flowering period lengthened with glacier retreat. These findings suggest that as glacier forelands undergo ecological succession, plant communities shift their phenology to maximize reproductive success in response to changing environmental conditions (Siefert et al., 2015). Earlier flowering could be a response to the extended growing season in late stages as soil temperature and light availability increase earlier in the year (Depauw et al., 2020). This shift may allow plants to exploit favorable conditions sooner, giving them a competitive

advantage in late-successional environments where competition for pollinators is greater (Tu et al., 2024). A prolonged flowering period may enhance the likelihood of successful pollination by spreading the risk of reproductive failure across a longer time frame (Larcher et al., 2010). Overall, these phenological changes indicate the adaptive potential of plant reproductive strategies in response to the shifting environmental pressures associated with glacier retreat. However, with the recent retreat of glaciers at unprecedented rates (Zemp et al., 2015), biotic and abiotic conditions are changing rapidly in glacier ecosystems, posing serious challenges to evolution by constraining the window for adaptation. There is no guarantee that plants will be able to adapt fast enough to the new, fast-changing environmental and climatic conditions. Not only plants may not adapt quickly enough to those new environments, but the decrease in trait dispersion and ITV further leads to a decrease in their ability to adapt to future climates and environments (Rodman et al., 2021). Yet, there is consensus on the importance of maintaining a high level of functional dispersion and redundancy to promote ecosystem processes and support resilience (Tilman, 1997; Díaz & Cabido, 2001; Ricotta et al., 2016). Our results highlight the importance of accounting for functional dispersion and functional variation in multiple traits for designing conservation strategies (Carmona et al., 2021) aimed at anticipating the impact of glacier extinction on biodiversity.

In conclusion, different forces drive plant community assembly and functional development after glacier retreat. The majority of plant functional traits are altered by the rapid retreat of glaciers more than by changes in species richness. We stress that it is key to consider not only habitat protection but also to conserve and restore functional diversity.

AUTHOR CONTRIBUTIONS

Gianalberto Losapio designed the research. Gianalberto Losapio, Marco Caccianiga, Bruno E. L. Cerabolini, and Duccio Tampucci collected data. Nora Khelidj and Gianalberto Losapio analyzed the data. Nora Khelidj and Gianalberto Losapio wrote the manuscript. All authors contributed to editing and reviewing the manuscript.

ACKNOWLEDGMENTS

We thank Chiara Maffioletti for her help during fieldwork, Michele Dalle Fratte and the Cerabolini lab for helping with traits, and the Biodiversity Change group for fruitful discussions. We thank the co-ordinating editor Peter le Roux and three anonymous reviewers for reviewing and commenting on our manuscript. Open access publishing facilitated by Università degli Studi di Milano, as part of the Wiley - CRUI-CARE agreement.

FUNDING INFORMATION

Nora Khelidj and Gianalberto Losapio are financially supported by the Swiss National Science Foundation (Grant no. PZ00P3_202127). This research also benefited from the support of the Italian Ministry

of Education and Research (Grant no. P2022N5KYJ), CLIMACT Starting Grant, and the CROSS Programme Grant awarded to Gianalberto Losapio.

CONFLICT OF INTEREST STATEMENT

The authors declare no competing interests.

DATA AVAILABILITY STATEMENT

The data collected for this study are deposited on GitHub <https://github.com/losapio/JVS-Glacier-extinction-homogenizes-plant-functional-diversity.git>. The R script (no novel code) to reproduce the analyses and figures is also provided on GitHub.

ORCID

Nora Khelidj  <https://orcid.org/0009-0007-3232-8923>

Marco Caccianiga  <https://orcid.org/0000-0001-9715-1830>

Bruno E. L. Cerabolini  <https://orcid.org/0000-0002-3793-0733>

Duccio Tampucci  <https://orcid.org/0000-0002-4804-1456>

Gianalberto Losapio  <https://orcid.org/0000-0001-7589-8706>

REFERENCES

- Aeschmann, D., Lauber, K., Moser, D. & Theurillat, J.P. (2004) *Flora alpina*. Bern: Haupt.
- Anthelme, F., Carrasquer, I., Ceballos, J.L. & Peyre, G. (2022) Novel plant communities after glacial retreat in Colombia: (many) losses and (few) gains. *Alpine Botany*, 132, 211–222.
- Bagousse-Pinguet, Y.L., Gross, N., Saiz, H., Maestre, F.T., Ruiz, S., Dacal, M. et al. (2021) Functional rarity and evenness are key facets of biodiversity to boost multifunctionality. *Proceedings of the National Academy of Sciences*, 118, 12128.
- Bagousse-Pinguet, Y.L., Soliveres, S., Gross, N., Torices, R., Berdugo, M. & Maestre, F.T. (2019) Phylogenetic, functional, and taxonomic richness have both positive and negative effects on ecosystem multifunctionality. *Proceedings of the National Academy of Sciences*, 116, 8419–8424.
- Bates, D., Mächler, M., Bolker, B. & Steve, W. (2015) Fitting linear mixed-effects models using lme4. *Journal of Statistical Software*, 67, 1–48.
- Ben-Shachar, M., Lüdtke, D. & Makowski, D. (2020) Effectsize: estimation of effect size indices and standardized parameter. *Journal of Open Source Software*, 5, 2815.
- Biggs, C.R., Yeager, L.A., Bolser, D.G., Bonsell, C., Dichiera, A.M., Hou, Z. et al. (2020) Does functional redundancy affect ecological stability and resilience? A review and meta-analysis. *Ecosphere*, 11, e03184.
- Bongers, F.J., Schmid, B., Bruehlheide, H., Bongers, F., Li, S., von Oheimb, G. et al. (2021) Functional diversity effects on productivity increase with age in a forest biodiversity experiment. *Nature Ecology & Evolution*, 5, 1594–1603.
- Bourquin, M., Busi, S.B., Fodelianakis, S., Peter, H., Washburne, A., Kohler, T.J. et al. (2022) The microbiome of cryospheric ecosystems. *Nature Communications*, 13, 3087.
- Burga, C.A., Krüsi, B., Egli, M., Wernli, M., Elsener, S., Ziefle, M. et al. (2010) Plant succession and soil development on the foreland of the morateratsch glacier (pontresina, Switzerland): straight forward or chaotic? *Flora - Morphology, Distribution, Functional Ecology of Plants*, 205, 561–576.
- Caccianiga, M., Luzzaro, A., Pierce, S., Ceriani, R.M. & Cerabolini, B. (2006) The functional basis of a primary succession resolved by CSR classification. *Oikos*, 112, 10–20.

- Cadotte, M.W., Carscadden, K. & Mirotchnick, N. (2011) Beyond species: functional diversity and the maintenance of ecological processes and services. *Journal of Applied Ecology*, 48, 1079–1087.
- Carmona, C.P., Tammé, R., Pärtel, M., de Bello, F., Brosse, S., Capdevila, P. et al. (2021) Erosion of global functional diversity across the tree of life. *Science Advances*, 7, eabf2675.
- Cauvy-Fraunié, S. & Dangles, O. (2019) A global synthesis of biodiversity responses to glacier retreat. *Nature Ecology & Evolution*, 3, 1675–1685.
- Chapin, F.S., Walker, L.R., Fastie, C.L. & Sharman, L.C. (1994) Mechanisms of primary succession following deglaciation at Glacier Bay, Alaska. *Ecological Monographs*, 64, 149–175.
- Cornwell, W.K. & Ackerly, D.D. (2009) Community assembly and shifts in plant trait distributions across an environmental gradient in coastal California. *Ecological Monographs*, 79, 109–126.
- Dalle Fratte, M., Pierce, S., Zanzottera, M. & Cerabolini, B.E.L. (2021) The association of leaf sulfur content with the leaf economics spectrum and plant adaptive strategies. *Functional Plant Biology*, 48, 924–935.
- de Bello, F., Lavorel, S., Albert, C.H., Thuiller, W., Grigulis, K., Dolezal, J. et al. (2011) Quantifying the relevance of intraspecific trait variability for functional diversity. *Methods in Ecology and Evolution*, 2, 163–174.
- Depauw, L., Perring, M.P., Landuyt, D., Maes, S.L., Blondeel, H., Lombaerde, E.D. et al. (2020) Light availability and land-use history drive biodiversity and functional changes in forest herb layer communities. *Journal of Ecology*, 108, 1411–1425.
- Díaz, S. & Cabido, M. (2001) Vive la différence: plant functional diversity matters to ecosystem processes. *Trends in Ecology & Evolution*, 16, 646–655.
- Díaz, S., Kattge, J., Cornelissen, J.H.C., Wright, I.J., Lavorel, S., Dray, S. et al. (2016) The global spectrum of plant form and function. *Nature*, 529, 167–171.
- Erschbamer, B. (2007) Winners and losers of climate change in a central alpine glacier foreland. *Arctic, Antarctic, and Alpine Research*, 39, 237–244.
- Erschbamer, B. & Caccianiga, M.S. (2016) *Glacier forelands: lessons of plant population and community development*. Cham: Springer International Publishing, pp. 259–284.
- Erschbamer, B., Niederfringer Schlag, R. & Winkler, E. (2008) Colonization processes on a central alpine glacier foreland. *Journal of Vegetation Science*, 19, 855–862.
- Ficetola, G.F., Marta, S., Guerrieri, A., Gobbi, M., Ambrosini, R., Fontaneto, D. et al. (2021) Dynamics of ecological communities following current retreat of glaciers. *Annual Review of Ecology, Evolution, and Systematics*, 52, 405–426.
- Fodelianakis, S., Washburne, A.D., Bourquin, M., Pramateftaki, P., Kohler, T.J., Styllas, M. et al. (2022) Microdiversity characterizes prevalent phylogenetic clades in the glacier-fed stream microbiome. *The ISME Journal*, 16, 666–675.
- Fox, J. & Weisser, S. (2019) *An R companion to applied regression*, 3rd edition. Thousand Oaks, CA: Sage.
- Frédéric, H., Olivier, B., Mattia, B., Lane, S.N., Sébastien, L., Thierry, A. et al. (2015) Erosion by an alpine glacier. *Science*, 350, 193–195.
- Funk, J.L., Larson, J.E., Ames, G.M., Butterfield, B.J., Cavender-Bares, J., Firn, J. et al. (2017) Revisiting the holy grail: using plant functional traits to understand ecological processes. *Biological Reviews*, 92, 1156–1173.
- García-Palacios, P., Gross, N., Gaitán, J. & Maestre, F.T. (2018) Climate mediates the biodiversity–ecosystem stability relationship globally. *Proceedings of the National Academy of Sciences*, 115, 8400–8405.
- Greinwald, K., Gebauer, T., Musso, A. & Scherer-Lorenzen, M. (2021) Similar successional development of functional community structure in glacier forelands despite contrasting bedrocks. *Journal of Vegetation Science*, 32, e12993.
- Griffin-Nolan, R.J., Blumenthal, D.M., Collins, S.L., Farkas, T.E., Hoffman, A.M., Mueller, K.E. et al. (2019) Shifts in plant functional composition following long-term drought in grasslands. *Journal of Ecology*, 107, 2133–2148.
- Grime, J.P. (2001) *Plant strategies, vegetation processes, and ecosystem properties*, 2nd edition. Hoboken, NJ: Wiley.
- Happonen, K., Muurinen, L., Virtanen, R., Kaakinen, E., Grytnes, J., Kaarlejärvi, E. et al. (2021) Trait-based responses to land use and canopy dynamics modify long-term diversity changes in forest understories. *Global Ecology and Biogeography*, 30, 1863–1875.
- Hodgson, J., Wilson, P., Hunt, R., Grime, J. & Thompson, K. (1999) Allocating C-S-R plant functional types: a soft approach to a hard problem. *Oikos*, 85, 282–294.
- Hugonnet, R., McNabb, R., Berthier, E., Menounos, B., Nuth, C., Girod, L. et al. (2021) Accelerated global glacier mass loss in the early twenty-first century. *Nature*, 592, 726–731.
- IPCC. (2022) Climate change 2022: impacts, adaptation, and vulnerability. In: *Contribution of working group II to the sixth assessment report of the intergovernmental panel on climate change*. Cambridge: Cambridge University Press.
- Jacobsen, D., Milner, A.M., Brown, L.E. & Dangles, O. (2012) Biodiversity under threat in glacier-fed river systems. *Nature Climate Change*, 2, 361–364.
- Kattge, J., Bönsch, G., Díaz, S., Lavorel, S., Prentice, I.C., Leadley, P. et al. (2020) Try plant trait database –enhanced coverage and open access. *Global Change Biology*, 26, 119–188.
- Khedim, N., Cécillon, L., Poulenard, J., Barré, P., Baudin, F., Marta, S. et al. (2021) Topsoil organic matter build-up in glacier forelands around the world. *Global Change Biology*, 27, 1662–1677.
- Kitagawa, R., Masumoto, S., Kaneko, R., Uchida, M. & Mori, A.S. (2022) The contribution of intraspecific trait variation to changes in functional community structure along a stress gradient. *Journal of Vegetation Science*, 33, e13112.
- Kraft, N.J.B., Adler, P.B., Godoy, O., James, E.C., Fuller, S. & Levine, J.M. (2014) Community assembly, coexistence and the environmental filtering metaphor. *Functional Ecology*, 20, 1–8.
- Kuznetsova, A., Brockhoff, P.B. & Christensen, R.H.B. (2017) LmerTest package: tests in linear mixed effects models. *Journal of Statistical Software*, 82, 1–26.
- Laliberté, E. & Legendre, P. (2010) A distance-based framework for measuring functional diversity from multiple traits. *Ecology*, 91, 299–305.
- Larcher, W., Kainmüller, C. & Wagner, J. (2010) Survival types of high mountain plants under extreme temperatures. *Flora: Morphology, Distribution, Functional Ecology of Plants*, 205, 3–18.
- Le Bagousse-Pinguet, Y., Börger, L., Quero, J.L., García-Gómez, M., Soriano, S., Maestre, F.T. et al. (2015) Traits of neighbouring plants and space limitation determine intraspecific trait variability in semi-arid shrublands. *Journal of Ecology*, 103, 1657.
- Losapio, G., Cerabolini, B.E.L., Maffioletti, C., Tampucci, D., Gobbi, M. & Caccianiga, M. (2021) The consequences of glacier retreat are uneven between plant species. *Frontiers in Ecology and Evolution*, 8, 1–11.
- Losapio, G., de la Cruz, M., Escudero, A., Schmid, B. & Schöb, C. (2018) The assembly of a plant network in alpine vegetation. *Journal of Vegetation Science*, 29, 999–1006.
- Losapio, G. & Schöb, C. (2017) Resistance of plant–plant networks to biodiversity loss and secondary extinctions following simulated environmental changes. *Functional Ecology*, 31, 1145–1152.
- Mason, N.W., de Bello, F., Mouillot, D., Pavoine, S. & Dray, S. (2013) A guide for using functional diversity indices to reveal changes in assembly processes along ecological gradients. *Journal of Vegetation Science*, 24, 794–806.
- Mason, N.W.H., Richardson, S.J., Peltzer, D.A., de Bello, F., Wardle, D.A. & Allen, R.B. (2012) Changes in coexistence mechanisms along a long-term soil chronosequence revealed by functional trait diversity. *Journal of Ecology*, 100, 678–689.

- Matthews, J. (1992) *The ecology of recently-deglaciated terrain: a geo-ecological approach to glacier forelands and primary succession*. Cambridge: Cambridge University Press.
- Mayfield, M.M. & Levine, J.M. (2010) Opposing effects of competitive exclusion on the phylogenetic structure of communities. *Ecology Letters*, 13, 1085–1093.
- Mouchet, M.A., Villéger, S., Mason, N.W.H. & Mouillot, D. (2010) Functional diversity measures: an overview of their redundancy and their ability to discriminate community assembly rules. *Functional Ecology*, 24, 867–876.
- Pavoine, S. (2020) Adiv: an R package to analyse biodiversity in ecology. *Methods in Ecology and Evolution*, 11, 1106–1112.
- Pérez-Harguindeguy, N., Diaz, S., Garnier, E., Lavorel, S., Poorter, H., Jaureguiberry, P. et al. (2013) New handbook for standardized measurement of plant functional traits worldwide. *Australian Journal of Botany*, 61, 167–234.
- Raffl, C., Mallaun, M., Mayer, R. & Erschbamer, B. (2006) Vegetation succession pattern and diversity changes in a Glacier Valley, Central Alps, Austria. *Arctic, Antarctic, and Alpine Research*, 38, 421–428.
- Reich, P.B., Wright, I.J., Cavender-Bares, J., Craine, J.M., Oleksyn, J., Westoby, M. et al. (2003) The evolution of plant functional variation: traits, spectra, and strategies. *International Journal of Plant Sciences*, 164, S143–S164.
- Ricotta, C., de Bello, F., Moretti, M., Caccianiga, M., Cerabolini, B.E. & Pavoine, S. (2016) Measuring the functional redundancy of biological communities: a quantitative guide. *Methods in Ecology and Evolution*, 7, 1386–1395.
- Roches, S.D., Pendleton, L.H., Shapiro, B. & Palkovacs, E.P. (2021) Conserving intraspecific variation for nature's contributions to people. *Nature Ecology & Evolution*, 5, 574–582.
- Rodman, K.C., Veblen, T.T., Andrus, R.A., Enright, N.J., Fontaine, J.B., Gonzalez, A.D. et al. (2021) A trait-based approach to assessing resistance and resilience to wildfire in two iconic north american conifers. *Journal of Ecology*, 109, 313–326.
- Roe, G.H., Baker, M.B. & Herla, F. (2017) Centennial glacier retreat as categorical evidence of regional climate change. *Nature Geoscience*, 10, 95–99.
- Schleuning, M., García, D. & Tobias, J.A. (2023) Animal functional traits: towards a trait-based ecology for whole ecosystems. *Functional Ecology*, 37, 4–12.
- Schleuter, D., Daufresne, M., Massol, F. & Argillier, C. (2010) A user's guide to functional diversity indices. *Ecological Monographs*, 80, 469–484.
- Schöb, C., Butterfield, B.J. & Pugnaire, F.I. (2012) Foundation species influence trait-based community assembly. *New Phytologist*, 196, 824–834.
- Schöb, C., Macek, P., Pistón, N., Kikvidze, Z. & Pugnaire, F.I. (2017) A trait-based approach to understand the consequences of specific plant interactions for community structure. *Journal of Vegetation Science*, 28, 704.
- Siefert, A., Violle, C., Chalmandrier, L., Albert, C.H., Taudiere, A., Fajardo, A. et al. (2015) A global meta-analysis of the relative extent of intraspecific trait variation in plant communities. *Ecology Letters*, 18, 1406–1419.
- Song, Y., Wang, P., Li, G. & Zhou, D. (2014) Relationships between functional diversity and ecosystem functioning: a review. *Acta Ecologica Sinica*, 34, 85–91.
- Stibal, M., Bradley, J.A., Edwards, A., Hotaling, S., Zawierucha, K., Rosvold, J. et al. (2020) Glacial ecosystems are essential to understanding biodiversity responses to glacier retreat. *Nature Ecology & Evolution*, 4, 686–687.
- Tilman, D. (1997) Mechanisms of plant competition. In: Crawley, M.J. (Ed.) *Plant ecology*. Hoboken, NJ: Blackwell Publishing Ltd, pp. 239–261.
- Tu, B.N., Khelidj, N., Cerretti, P., de Vere, N., Ferrari, A., Paone, F. et al. (2024) Glacier retreat triggers changes in biodiversity and plant-pollinator interaction diversity. *Alpine Botany*. Available from: <https://doi.org/10.1007/s00035-024-00309-9>
- Violle, C., Enquist, B.J., McGill, B.J., Jiang, L., Albert, C.H., Hulshof, C. et al. (2012) The return of the variance: intraspecific variability in community ecology. *Trends in Ecology & Evolution*, 27, 244–252.
- Violle, C., Navas, M.L., Vile, D., Kazakou, E., Fortunel, C., Hummel, I. et al. (2007) Let the concept of trait be functional! *Oikos*, 116, 882–892.
- Violle, C., Thuiller, W., Mouquet, N., Munoz, F., Kraft, N.J., Cadotte, M.W. et al. (2017) Functional rarity: the ecology of outliers. *Trends in Ecology & Evolution*, 32, 356–367.
- Volf, M., Redmond, C., Albert, Á.J., Le Bagousse-Pinguet, Y., Biella, P., Götzenberger, L. et al. (2016) Effects of long- and short-term management on the functional structure of meadows through species turnover and intraspecific trait variability. *Oecologia*, 180, 941–950.
- Walker, L.R. & del Moral, R. (2003) *Primary succession and ecosystem rehabilitation*. Cambridge: Cambridge University Press.
- Wright, I.J., Reich, P.B., Westoby, M., Ackerly, D.D., Baruch, Z., Bongers, F. et al. (2004) The worldwide leaf economics spectrum. *Nature*, 428, 821–827.
- Zanzottera, M., Fratte, M.D., Caccianiga, M., Pierce, S. & Cerabolini, B.E.L. (2020) Community-level variation in plant functional traits and ecological strategies shapes habitat structure along succession gradients in alpine environment. *Community Ecology*, 21, 55–65.
- Zekollari, H., Huss, M. & Farinotti, D. (2019) Modelling the future evolution of glaciers in the European Alps under the Euro-Cordex RCM ensemble. *The Cryosphere*, 13, 1125–1146.
- Zemp, M., Frey, H., Gärtner-Roer, I., Nussbaumer, S.U., Hoelzle, M., Paul, F. et al. (2015) Historically unprecedented global glacier decline in the early 21st century. *Journal of Glaciology*, 61, 745–762.
- Zemp, M., Huss, M., Thibert, E., Eckert, N., McNabb, R., Huber, J. et al. (2019) Global glacier mass changes and their contributions to sea-level rise from 1961 to 2016. *Nature*, 568, 382–386.
- Zhang, J., He, N., Liu, C., Xu, L., Chen, Z., Li, Y. et al. (2020) Variation and evolution of C:N ratio among different organs enable plants to adapt to N-limited environments. *Global Change Biology*, 26, 2534–2543.

SUPPORTING INFORMATION

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

Supporting Information. Tables with model parameters.

How to cite this article: Khelidj, N., Caccianiga, M., Cerabolini, B.E.L., Tampucci, D. & Losapio, G. (2024) Glacier extinction homogenizes functional diversity via ecological succession. *Journal of Vegetation Science*, 35, e13312. Available from: <https://doi.org/10.1111/jvs.13312>