https://doi.org/10.5194/egusphere-2024-991
Preprint. Discussion started: 5 April 2024

Plant–soil interactions underline the development of novel ecosystems after glacier retreat

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Abstract. An emblematic symptom of climate change is the retreat of glaciers worldwide. As glaciers retreat, new terrains are exposed to colonization by a variety of organisms, leading to succession in plant communities and changes in soil properties. However, little is known about how the development of novel ecosystems emerging after glacier retreat depends on plant–soil interactions. Here, we investigated how glacier retreat influences the relationships between plant communities and soil functioning. We examined the diversity and structure of plant communities (functional composition, diversity, ecological indicators) and analyzed soil properties (pH, organic carbon, total nitrogen, C/N ratio, texture, available and total elements) along a glacier foreland comprising four stages of glacier retreat. The dominance of plant functional types shifts from herbaceous to shrubs and ultimately trees. Plant diversity initially increases after glacier retreat, along with an increase in soil organic matter and nutrients. Over 120 years, soils acidify at a rate of 0.02 units per year, the C/N ratio increases while plant diversity decreases. These findings provide novel evidence on the geo-ecological processes driving the development of new ecosystems that emerge from glacier retreat. As climate is warming and glaciers are retreating at increasing rates, pioneer herbaceous communities are quickly replaced by coniferous forests. As a result, biodiversity decreases while organic matter accumulation and soil acidity become more pronounced. We highlight that local plant–soil interactions should be the target of biodiversity conservation efforts and landscape management plans aimed at mitigating the impact of glacier extinction on biodiversity and ecological systems.

1 Introduction

The Holocene geological epoch has been marked by the Little Ice Age at the end of the 13th century, which allowed glaciers to grow and advance (Grove, 2001). Industrialization based on fossil fuels and related greenhouse gas emissions increased

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atmospheric CO_2 concentration marked the end of the LIA in *c* 1850 (IPCC, 2022). Extractions and combustion of fossil fuels have caused an average global warming of about 1 °C as compared to pre-industrial levels (Ripple et al., 2020). The increase in temperature and its effects are much more pronounced in cold regions such as alpine areas (IPCC, 2022). For instance, in Switzerland, average annual temperature has increased by 2.1 °C since 1864 (Changement climatique Suisse - MétéoSuisse, 2020). This trend is expected to continue as global warming is currently increasing by 0.2 °C per decade (IPCC, 2022). Thus by 2030 and 2050, temperatures are expected to increase further by 1.5 °C (IPCC, 2022). Given this global warming trends, glaciers have been retreating since the end of the LIA, with a strong acceleration over the last 30 years (Zemp et al., 2019). The retreat of glaciers is expected to accelerate in the coming years, leading to worldwide glacier extinctions (Bosson et al., 2019; Cook et al., 2023). Even glaciers which will not disappear will see drastic reductions in their the mass, volume, and surface area, leading to changes in biodiversity patterns and biological functions (Cauvy-Fraunié and Dangles, 2019; Lee et al., 2017). By 2100, glaciers in Central Europe will have lost between 60 and 100 % of their mass, depending on projected climate conditions, exposing vast areas to species colonization and turnover (Bosson et al., 2023; Rounce et al., 2023). Understanding these ecosystems in transition is key to anticipate changes and preserve their ecosystem services and functions (Bosson et al., 2023).

The retreat of glaciers exposes new terrains prompting the colonization of living organisms such as pioneer plants (Burga et al., 2010; Kaufmann et al., 2002; Eichel et al., 2013). Within a few years, herbs, mosses, lichens and soil biota create diverse and complex communities (Losapio et al., 2015; Rosero et al., 2021; Tu et al., 2024). Such novel interactions trigger ecological changes in the soil and more widely in the ecosystem (Burga et al., 2010; Cauvy-Fraunié and Dangles, 2019; Ficetola et al., 2021; Losapio et al., 2021). However, glacier retreat can also have negative impacts on the biodiversity of these ecosystems (Bosson et al., 2019; Stibal et al., 2020). Indeed, in the long term (*c* 100 years), glacier retreat and especially glacier loss involve three major ecological changes at the local scale: a loss of glacial habitat, a gain of soil habitat, and a decrease in the influence of glacier microclimate on surrounding habitats (Cauvy-Fraunié and Dangles, 2019). Yet, the consequences of glacier extinction vary between plant species (Losapio et al., 2021; Erschbamer, 2007). On one hand, generalist plant species, with their great capacity for adaptation, can expand their distribution and increase in abundance. On the other hand, specialist plant species, which are adapted to the particular conditions of glacier margins, shrink their distribution until disappearance (Cauvy-Fraunié and Dangles, 2019; Stibal et al., 2020; Losapio et al., 2021). However, little is known about how soil development affects plant biodiversity. Understanding which soil factors drive the structure and diversity of plant communities is key for biodiversity maintenance once glaciers are extinct.

The loss of glaciers implies a change in the development of soils. This is because ice-free soil is exposed to new forms of chemical and biological weathering, from which it was previously shielded (Burga et al., 2010; Dümig et al., 2011; Esperschutz et al., 2011; Khedim et al., 2021). A soil that has been ice-free for a longer period of time typically shows a higher degree of development than a young soil located near the current glacier front that shows almost no signs of chemical alteration (Burga et al., 2010). In brief, the development of vegetation and soil on a large scale is determined by the time since deglaciation. However, granulometry, substrate moisture content, microclimate and other smaller-scale factors are crucial for

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vegetation development too (Burga et al., 2010). Indeed, soil development depends directly on feedbacks between the nature of the parent rock, climate, weather and biological agents (Burga et al., 2010; D'Amico et al., 2014). Thus, the colonization of vegetation modifies soil properties, which in turn have an impact on the development of vegetation (D'Amico et al., 2014). Yet, the majority of research is still conducted with a monodisciplinary approach by looking at glacier retreat impact on separate «compartments» of vegetation or microbial communities or soil properties (Egli et al., 2012; Khedim et al., 2021). There are only a few multidisciplinary studies that combine the pedological and biological approach to understand how soil and vegetation develop jointly in a context of glacial retreat (Bernasconi et al., 2011; Burga et al., 2010; Wietrzyk et al., 2018). The current lack of understanding on the biodiversity responses to glacier extinction (Stibal et al., 2020; Losapio et al., 2021) encourages the study of the responses of glacier retreat on biodiversity, and more specifically on the interactions between glacier loss, soils and vegetation.

In this study, we address the following research questions: How does glacial retreat influence the development of biodiversity and plant communities? How do plant–soil interactions drive ecosystem development after glacier retreat? We hypothesize that an increase in soil carbon and nitrogen content drives plant diversity. We also expect that an increase in plant diversity will lead to an increase in soil organic matter, which will further increase soil nutrient content while decreasing soil pH. We expect that soil acidity will increase whereas plant diversity will decrease in late stages of ecosystem development.

2 Materials and Methods

2.1 Study site

We studied the ecosystems emerging from the former common glacial front of the Mont Miné Glacier and the Ferpècle Glacier, canton of Valais, Swiss Alps (Figure 1). The geology of the region is composed of several successive alpine geological units (Lambiel et al., 2016). The study area is located at a unit composed mainly of orthogneiss, metagabbro and breccia (Lambiel et al., 2016). The climate of the valley (Evolène station, mean 1987–2012) is relatively dry with a mean annual precipitation of 720 mm; the mean annual temperature is 4.5 °C and the 0 °C isotherm is situated around 2600 m a.s.l (Lambiel et al., 2016).

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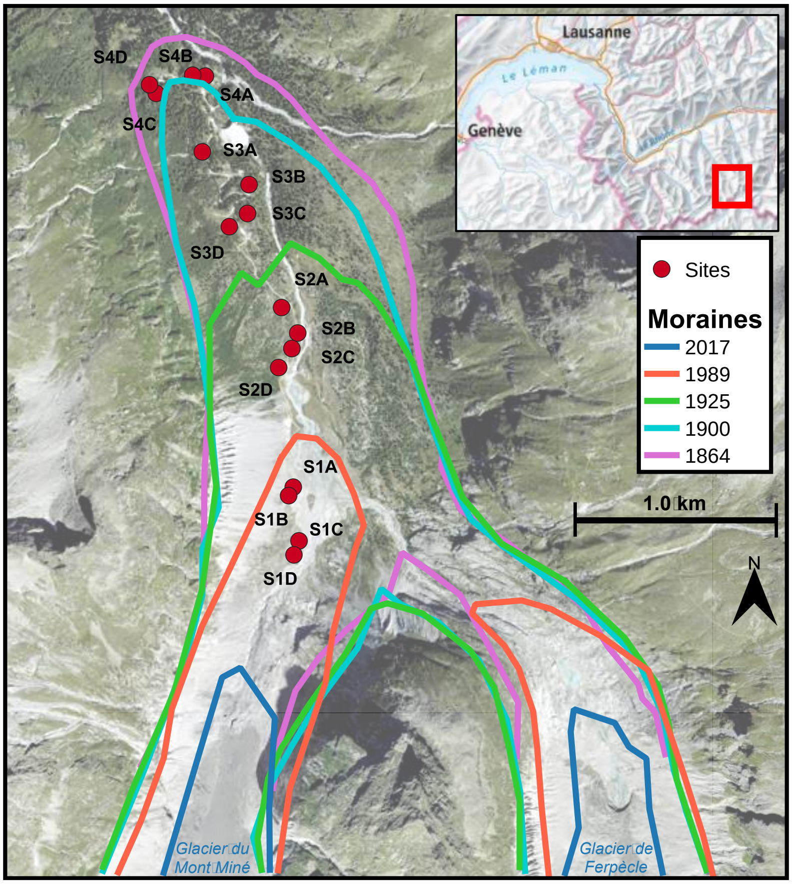

Figure 1: Study area with Mont Miné and Ferpècle glaciers in the Valais Alps and the geo-location of the 16 surveyed plots. The plots are found across four main glacier extent stages, reconstructed using moraines marking the former glacier positions since the 1860s (background map: © Federal Office of Topography swisstopo).

From the glacier front to downstream (LIA moraines), we established a transect of around 2 km. This transect is independent of elevation gradient, which ranges between 1890 and 1990 m a.s.l. Stages of ecosystem development were determined based on the position of frontal and lateral moraines from historical cartography and field observations (Federal Office of Tropography, 2021). We selected four stages:

- Pioneer stage: 1989–2022 AD
- Early stage: 1925–1989 AD
- Intermediate stage: 1900–1925 AD
- Late successional stage: 1864–1900 AD

Stage 1 includes all the terrains in the recently deglaciated sector, and stage 4 includes the terrains furthest downstream from the current glacier margins. The four stages are all about 250 m wide. Then, for each stage, a mean year since deglaciation was calculated considering the ages. This yields 23, 60, 110 and 142 years for stage 1, stage 2, stage 3, and stage 4, respectively.

For each stage, we randomly selected four plots of 3x3 m. Hereafter, these plots are named "a" to "d". In total, we had 16 plots (Fig. 1). In each plot, we conducted vegetation surveys, and collected vegetation data and soil samples as explained below.

2.2 Plant community analysis

Vegetation surveys were carried out during the month of June and July 2022. Plots were resurveyed every two weeks for completeness until the end of August. In each plot, all plants were identified to species level according Swiss Flora (Eggenberg, 2018; Laubert et al., 2018). Then, the surface cover of each plant species was assessed visually. Three botanists estimated independently the area occupied by each species for the stratum to which it belongs with a visual approximation of 10%. The average of the three estimates was taken. Data were pooled at the plot level.

These data were then used to determine the ecological properties of plant communities for each plot: (1) **Shannon diversity index (*H*)**, which corresponds to the sum of relative abundance of each species on the same plot. This was calculated as: $H = -\sum_i p_i \ln p_i$, where p_i is the proportion of species cover of each species i; (2) **Average reaction index**; for each species, the reaction value from Landolt et al. (2010) ecological values was extracted, corresponding to the soil pH conditions required for the species to thrive. This value was then weighted according to the abundance of each species and an averaged over all species (i.e., community weighted mean). Reaction values can range from 1 to 5, with 1 corresponding to very acidic pH values and 5 to basic pH values; and (3) **Plant functional groups** representing the relative dominance of trees, shrubs, dwarf-shrubs, forbs, and graminoids. Plants have been classified according to *infoflora.ch* into one of these five groups. The percentage of each group was calculated by weighting the abundance of each species.

2.3 Soil samples analysis

Soil sampling took place during dry and sunny weather conditions. A soil sample was taken from the top 10 cm of soil after removing stones (> 5 cm) and the organic layer. For two plots in stage 4 (4a, 4b), as the organic layer was very thick, it was not possible to remove it completely to reach an organo-mineral horizon. Litter and the first few centimeters of soil composed of slightly degraded organic debris were discarded, the remaining soil samples represent organic horizons. This approach was motivated to address organic matter accumulation in the soil –as explained below– and to avoid its misrepresentation due to yearly litter deposition. For each plot, at least 200 g of soil were taken back to the lab. Samples were air dried, weighed, and sieved to 2 mm using a square-mesh sieve. The mass fraction of coarse fragments was recorded. A subsample was ground to 20 microns or finer using a planetary mill (Pulverisette 7, Fritsch). Quality control procedures included the use of applicable standards and quality checks, plus between 10 and 20 % of blind duplicate analyses. Removing 4a and 4b datapoints does not qualitatively change the results (Charles and Losapio, 2024).

We conducted soil analyses including measurement of soil texture and acidity. To track organic matter accumulation in the soil, while avoiding litter deposition, we also determined organic carbon and total nitrogen content, and calculated the C/N ratio. Finally, we assessed major elements content and availability by combining total element analysis using X-rays fluorescence and extractable elements analysis by the Mehlich-3 universal soil extractant.

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Soil texture was determined by laser granulometry (Beckmann Coulter particle size analyzer) after digestion of the organic matter with hydrogen peroxide and sample dispersion in sodium hexametaphosphate. The active acidity ($pH_{(water)}$) was assessed potentiometrically on sieved soil in accordance with AFNOR standard NF X-31-103, 1998, using a soil/solution ratio of 1:2.5. Soil organic matter (C) and total nitrogen (N) content were determined with a CHNS Elemental Analyser (Thermo Finnigan Flash EA 1112) on oven-dried, ground samples. As the presence of inorganic carbon cannot be ruled out for samples with $pH_{(water)} > 6.5$ (Walthert et al., 2010), carbonates were removed by acid fumigation (Harris et al. 2001) of these samples. Results were expressed on the basis of the initial, oven-dried soil mass.

Finally, an estimation of plant-available elements was obtained using a Mehlich III extraction (Mehlich, 1984) following the method of Ziadi and Sen Tran (2007). Element concentrations were determined by inductively coupled plasma optical emission spectrometry (ICP-OES, Agilent 5800). Total concentrations of major and minor elements were determined by X-ray fluorescence (XRF). The XRF analyses were performed on fused-disks prepared from 1.2 g of calcined sample powder mixed with lithium tetraborate (1:5 ratio) and using a wavelength-dispersive PANalytical Axios^{mAX} spectrometer fitted with a 4 kW Rh X-ray tube.

2.4 Data analysis

All data were grouped into a single dataset including dependent variables described in Table 1 and two predictors. The two corresponding predictors are: (1) stage of ecosystem development (categorical variable ranging from 1 to 4), and (2) the years since the stage was ice-free (numerical variable), referred to as «years». Data analysis was performed with R software v 4.3.1 (R Core Team 2023).

Dependent variable	Description
Plant diversity	Shannon diversity index
Plant reaction value	Community weight man of reaction index from Landolt ecological indicator values
Plant functional groups	Proportion of each group including trees, shrubs, dwarf-shrubs, forbs and graminoids
Soil pH	Soil $pH_{(water)}$
SOC	Soil organic carbon content (SOC)
Ntot	Soil total nitrogen content
C/N	Organic carbon / total nitrogen ratio
Granulometry	Particle size distribution including proportion of sand, silt and clay
Available elements	Concentrations of available P, K, Ca, Mg, Na, Mn, Al
Total elements	Proportions of oxides of Si, Al, Fe, K, Mg, Ca, Na, Ti, Mn, P

Table 1: Dependent variables with corresponding description used in the statistical models.

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As exploratory analysis, Pearson correlation values were calculated among all dependent variables, making it possible to obtain a correlation matrix and observe linear relationships between pairs of variables (results reported in SI). First, a Principal Component Analysis (PCA) was performed on the dataset to explore the structure of the data, identify trends, and groupings of soil and vegetation variables using *FactoMineR* package (Le et al., 2008). This approach allowed us to reduce the dimensionality of the data while identifying the principal components that capture most of the variance in the data. Next, histograms were used to visualize the distribution of each dependent variable prior to using parametric tests and linear regression. When the data did not follow a normal distribution, the variables concerned were transformed; this included organic carbon, total nitrogen, and C/N ratio variables, which were log transformed to obtain a normal distribution.

Third, each variable was analyzed separately in response to each predictor (either stage or years, two separate models) through linear regression models (Fox and Weisberg, 2019). The combination of these two predictors enabled us to run two similar but complementary models. The first model, with the categorical predictor of ecosystem development, allows inference on the response variable measured among the stages. The second model, with the linear predictor of glacier retreat, allows inference on the trend of the measured response variables. For each model, we performed an analysis of variance (ANOVA) with an F-test on three nested/hierarchical models to assess which model best explains the variation in the dependent variable. The following regression models were evaluated:

a. a null model with the response variable explained by the intercept only, such as *lm(response variable~1)*
b. a linear model with the response variable explained by a predictor, such as *lm(response variable~predictor)*
c. in the case of years since glacier retreat as predictor, a quadratic model with a polynomial function, such as *lm(response variable~poly(predictor,2))*

The significance of the model was assessed considering the p-value associated with the F-statistic. Significance was considered at the 5% threshold. Next, the model with the lowest Akaike Information Criterion (AIC) was preferred, as it indicates a better compromise between fit to data and model complexity.

Once the best model had been chosen, a type-II anova was performed to test whether the variation in the response variable is statistically explained by the predictor, that is, whether glacier retreat influences the dependent variable. To this end, we use the R *car* package (Fox and Weisberg, 2019). The F-statistic and the associated p-value were employed to test the null hypothesis holding that the independent variable has no significant effect on the dependent variable. Next, model parameters were estimated using least squares and we calculated Cohen's size effect (using R *effectsize* package, Ben-Shachar et al., 2020). To assess model robustness, the distribution of residuals and their homoscedasticity (i.e., the variance of residuals is constant) was assessed using R *parameters* package (Lüdecke et al., 2020). As model output with categorical and numerical predictors are qualitatively similar, we report in the manuscript results of the former, while the latter are available in the R code (Charles and Losapio, 2024).

Finally, a path analysis was carried out using the *lavaan* package (Rosseel, 2012) to examine the complex relationships between soil, vegetation, and glacier retreat, and to test models of causal relationships among them. In line with the hypotheses of this work, the response variables selected are those with high eigenvalues in the PCA descriptive analysis and those with a

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high correlation with the predictor in the linear regressions. The variables finally selected were (1) years since deglaciation, (2) soil organic carbon (SOC), (3) soil pH and (4) plant diversity. Model performance and robustness was assessed by looking at indicators of the model's fit to the observed data according to Rosseel (2012). The following parameters were considered all together: Goodness of Fit Index (GFI), Adjusted Goodness of Fit Index (AGFI), Chi-square (Chisq), Comparative Fit Index (CFI), Root Mean Square Error of Approximation (RMSEA), Relative Fit Index (RFI) and Standardized Root Mean Square Redisual (SRMR). The selected model is represented by the following set of equations:

$$SOC \sim pH\ + Plant\ diversity\ + Years\ since\ deglaciation$$

$$Plant\ diversity \sim Years\ since\ deglaciation$$

$$pH \sim Years\ since\ deglaciation$$

3 Results

3.1 Principal component analysis of vegetation and soil variables

The first dimension of the PCA explains 47.8 % of total variance, and the second dimension explains 17.2 % (Fig. 2). The first dimension mainly explains variables related to ecosystem development, whereas the second dimension explains more variables related to the geomorphological processes (Fig. 2). Indeed, the first dimension includes vegetation variables, such as plant diversity, species richness, proportion of plants in each group including tree, shrubs, dwarf-shrubs, graminoids and forbs, and average reaction index together with soil properties such as soil organic carbon, total nitrogen, carbon/nitrogen ratio and available elements. Soil organic carbon is positively correlated with available elements such as Ca, Mg, Al, K, Na, P and Mn, as well as with total nitrogen and the C/N ratio. Correlation rates are over 0.75 for soil organic carbon and total nitrogen with all the available elements. Organic carbon is highly negatively correlated with soil pH (-0.78) and with average reaction index (-0.79). Also, pH and average reaction index are highly correlated with a positive correlation of 0.91. Correlations were also observed between the proportion of plants in each group: a positive correlation between trees and dwarf-shrubs (0.83), and a negative correlation between the latter variables and forbs (~-0.8).

The second dimension explains the variables linked to the site's mineralogy, with a negative correlation between bulk soil concentration of sodium and silica oxides–and calcium, magnesium, aluminum, and iron oxides. No correlation is observed between these variables and available elements to plants, except for phosphorous oxides which are highly correlated with all available elements (>0.9).

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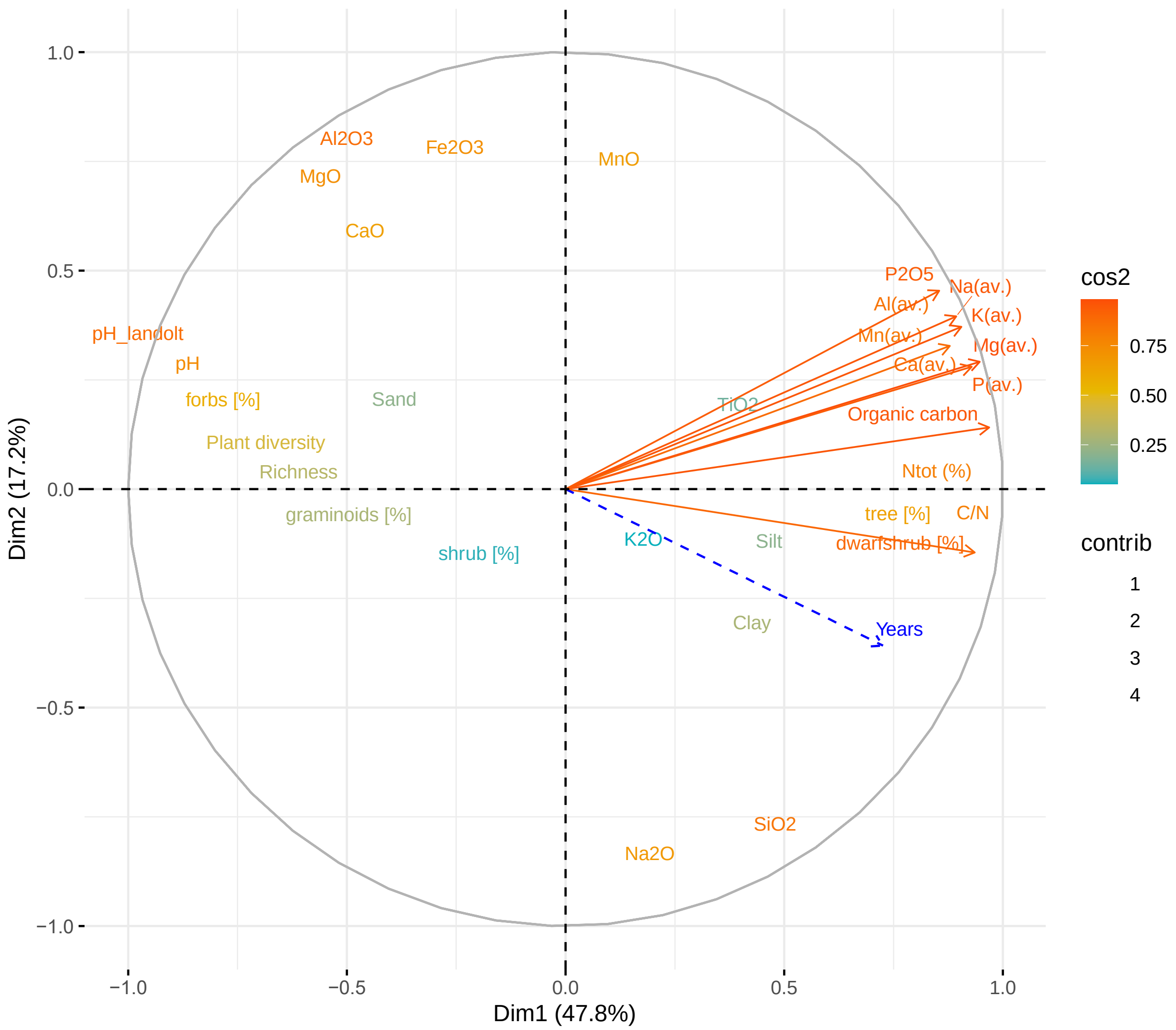

Figure 2: Principal Component Analysis (PCA) biplot of variables. We report squared cosine (cos2) and contribution (contrib) of each variable. Cos2 shows the importance of a component for a given variable. A cos2 value close to 1 shows a better representation of the variable by the PC. Contrib represents the contribution of each variable to a component. The higher the contribution, symbolized by a darker arrow, the more the observation contributes to the component. Years since glacier retreat was included as a passive variable. For variable acronyms, refer to Table 1.

3.2 Vegetation development

Regression analysis shows that glacier retreat influences plant diversity (F=10.68, p<0.05) (Fig. 3). Plant diversity increases following glacier retreat in the first stages, but then diversity decreases in the late stage (Fig. 3a). Stage 1, which corresponds to recently ice-free area, is statistically different from stage 2 (p<0.05) as diversity increases from a median of 2.4 to 3. Then, stages 2 and 3 are statistically no different from each other (p>0.05) and have a similar median value around 3 and 2.9. Diversity then falls from stage 3 to stage 4 (p<0.05) as the diversity index decreases to a median value of 1.7, which corresponds to a 40 % decrease compared to stage 3. Overall, in stage 4, there is a 30 % reduction in diversity compared with stage 1.

The reaction index decreases with glacier retreat (F=12.91, p<0.05) (Fig 3b). For each stage, the median reaction value drops from 3.2 to 2.9, 2.4 and finally 1.9 from stages 1 to 4, respectively. Our stages data therefore goes from lightly acidic to neutral, to acidic and finally to very acidic. Stage 4 is the only stage which is statistically different from all other stages (p<0.05).

The proportion of different plant groups change with glacier retreat (Fig. 3c). Statistics confirm that glacier retreat influences proportion of forbs (F=5.827, p<0.05), shrubs (F=3.583, p<0.05) and dwarf-shrubs (F=5.977, p<0.05). In stages 1 and stage 2, forbs and graminoids are more prevalent than other plant groups. The median values for the proportions of forbs are around 51 % in stage 1 and 76 % in stage 2, while for graminoids they are around 20 % and 13 %, respectively. Forbs also dominate in stage 3 (median value of 55 %), before decreasing in stage 4 (median value of 21 %) (p<0.05). In stage 4, trees and dwarf-shrubs are more prevalent as tree species account for 10 % of vegetation. Dwarf-shrubs show a statistically significant increase from stage 3 to stage 4 (p<0.05) rising from a median of 20 % to 43 %.

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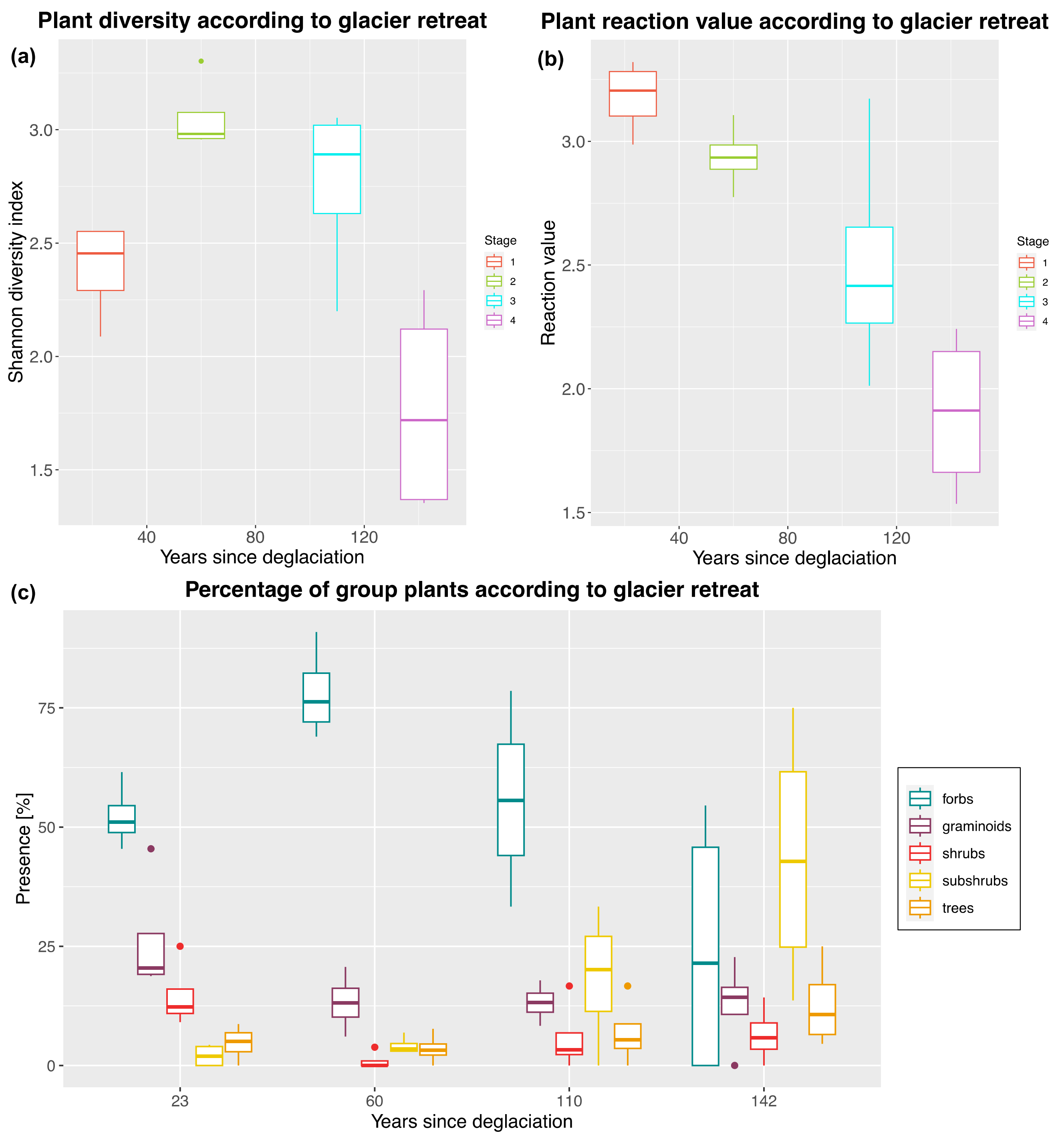

245 **Figure 3:** Vegetation development following glacier retreat, including **(a)** plant diversity, calculated using the Shannon diversity index; **(b)** plant reaction value which corresponds to the community-weighted average reaction index from Landolt et al. (2010); **(c)** plant functional groups which corresponds to the relative abundance of each plant group, including forbs, graminoids, shrubs, dwarf-shrubs, and trees; boxplots have been jittered for facilitating data visualization; the actual years since deglaciation is the written one.

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3.3 Soil development

Soil organic carbon, total nitrogen and C/N ratio are influenced by glacier retreat (Fig. 4), as evidenced by the statistics (Corg: *F*=36.75, *p*<0.05; Ntot: *F*=10.81, *p*<0.05; C/N: *F*=23.47, *p*<0.05).

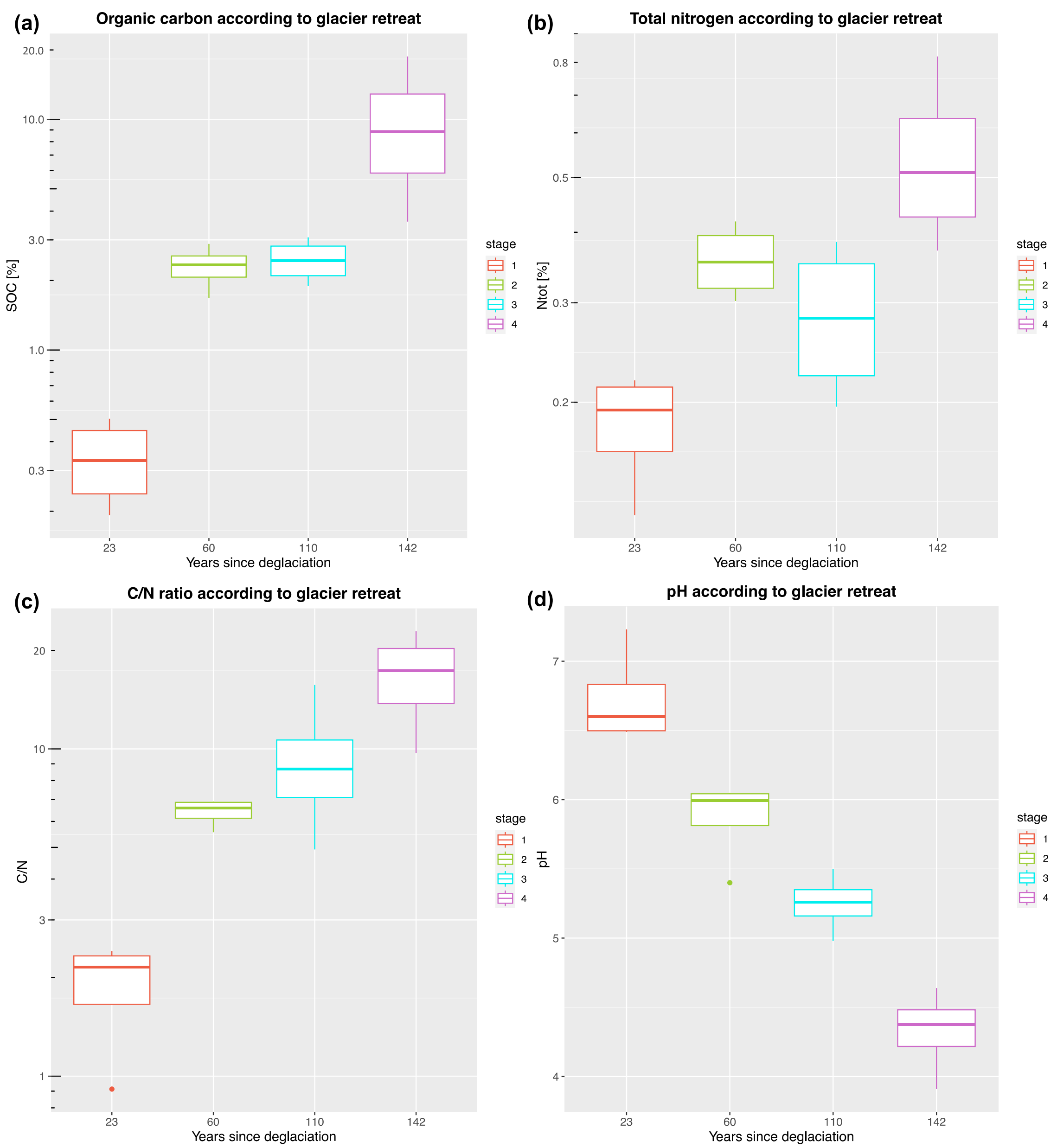

Figure 4: Soil development following glacier retreat (years since deglaciation across stages 1 to 4) including **(a)** organic carbon (SOC), **(b)** total nitrogen (Ntot), **(c)** C/N ratio , and **(d)** pH. Y scale is log distributed in plot a to c with untransformed values of SOC, Ntot, and C/N.

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Overall, we can see an increase of SOC with glacier retreat. Carbon content increases by 26 times between stage 1 and stage 4. SOC content is very low in stage 1, on average 0.3 %, and increases (p<0.05) in stage 2 (Fig. 4a). Values then stagnate between stages 2 and 3, before increasing further to 9.1 % in stage 4. Statistically, all stages are different from each another (p<0.05), except for stages 2 and 3 which are rather similar, around *c* 2.4 % of SOC content. Stages 2 and 3 also show the most homogeneous values, while stages 1 and 4 have more scattered values. In fact, stage 4 has values ranging from 3.6 % to 19 %.

Total nitrogen content in the soil increases from stage 1 to stage 2 (p<0.05), with low total nitrogen levels in stage 1 around 0.2 % increasing to 0.36 % at stage 2 (Fig. 4b). Nitrogen is higher in stage 2, which differs from stage 1 (p<0.05) but not from stages 3 and 4 (p>0.05). The median value in stage 3 is around 0.29 % while it is 0.5 % in stage 4. Stage 3 shows greater heterogeneity of values than stage 2.

The C/N ratio shows an overall increase with glacier retreat (Fig. 4c). First, stage 1 shows very low ratios, with a median of 2 %, then, although increasing with stages, C/N ratios remain low for stages 2 and 3 with median values of 6.6 % and 8.7 %, respectively. As with organic carbon and total nitrogen, stages 2 and 3 are not statistically different from each other (p>0.05), whereas all the other stages differ between each other (p<0.05). The C/N ratio then increases for stage 4, with higher values and a median of 17.4 %. Finally, stages 1 and 2 show more homogeneous values and are more aggregated than stages 3 and 4, with more scattered values.

Soil pH decreases after glacier retreat (F=123, p<0.05; Fig. 4d). Stage 1, corresponding to 23 years since the glacier retreated, has the highest values, with a median of 6.6. It is followed by stage 2 with a median of 6, stage 3 with 5.3 and stage 4 with 4.4, showing a steady decrease in pH. Stage 4 shows minimum values down to 3.9. The y-intercept is 7.1 and the estimated decrease in pH is 0.02 pH units per year of glacial retreat. All stages are statistically different from each other (p<0.05), and we can document a trend of linear pH decrease with glacier retreat.

3.4 Plant–Soil interactions

A path analysis model provides a simplified overview of the complex relationships between glacier retreat, vegetation development and soil properties (Fig. 5). Glacier retreat influences directly and indirectly soil organic carbon; glacier retreat also negatively influences plant diversity and pH; finally, both pH and plant diversity contributed to soil organic carbon.

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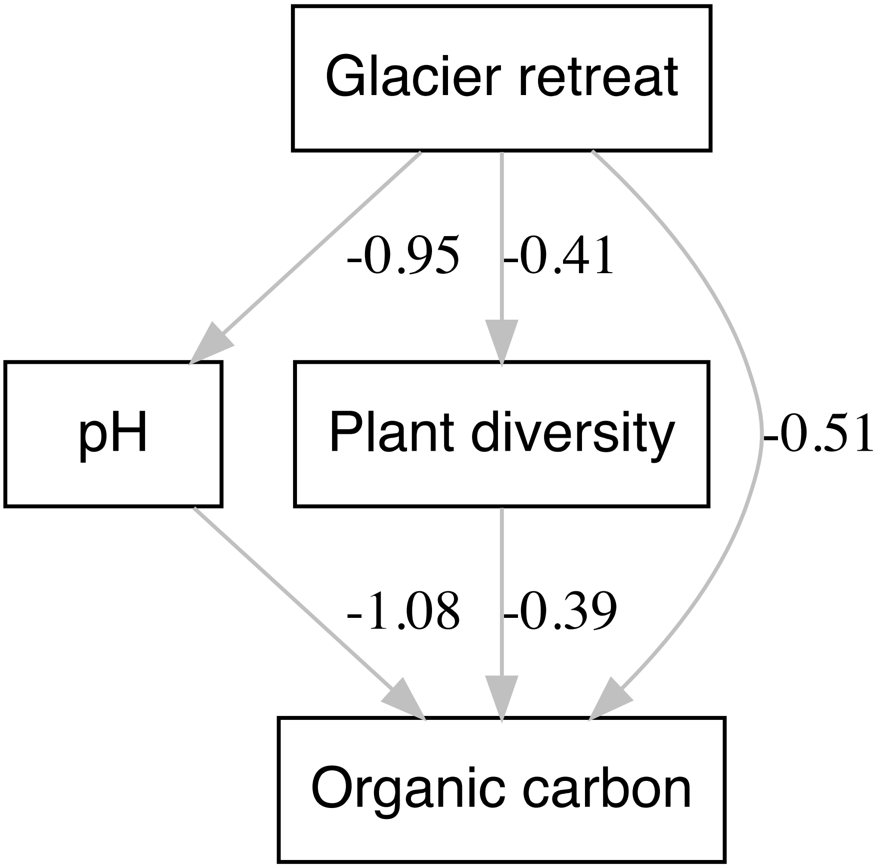

Figure 5: Path analysis reporting multiple causal pathways among glacier retreat, vegetation and soil development. Soil development is characterized by changes in pH and soil organic carbon, vegetation by plant diversity, and glacier retreat by years since deglaciation.

4 Discussion

4.1 Vegetation development

By taking a stage-by-stage look at how vegetation develops, we can see the development of vegetation in this new ecosystem from a pioneer stage (stage 1) to a late successional stage (stage 4). In the first stage of ecosystem development, the presence of species such as *Epilobium fleischeri*, *Saxifraga aizoides*, *Oxyria dygnia*, *Trifolium pallescens*, *Hieracium staticifolium*, and *Lotus corniculatus* corresponds to pioneer vegetation that establishes on shallow, nutrient-poor soil composed of rocky debris. These species possess adaptation strategies to the disturbances they face due to surrounding gravitational processes (Eichel et al., 2013) and to specific climatic conditions (Eichel, 2019). In this way, these herbaceous plants, specifically forbs, become established and have a strong presence in this new ecosystem. Shrubs are also present but less abundantly and at an early growth stage. Indeed, some young woody plants like *Larix decidua*, *Salix spp.*, and *Betula pendula* are found in stage 1, but in juvenile forms. Here, the Shannon diversity index is already relatively high. This trend is also observed by Bernasconi et al.

(2011) and Losapio et al. (2021), who note that plant diversity initially increases with glacier retreat before decreasing in the late stage.

Intermediate stages undergo rapid primary vegetation succession, characterized by an increasing prevalence of dwarf-shrubs and trees, while forbs still remain abundant. Here, new woody plant species such as *Rhododendron ferrugineum* appear. This emergence is also facilitated by the pioneers of first stage who have modified the environment and act as facilitators (Losapio et al., 2021). Indeed, plant colonization of pioneer stages modifies soil conditions and facilitates further colonization (Ficetola et al., 2021; Losapio et al., 2021). This is the case for certain *Fabaceae* plants, such as *Trifolium pallescens* and *T. badium*, which, through mutualistic interactions with bacteria, play a key role in nitrogen fixation. This, in turn, facilitates the establishment of other plant species as is the case for some new forb species that appear, such as *Ranunculus montanus*, *Achillea erba-rotta*, and *Cerastium arvense*. The coexistence of pioneer species and new species results in maximum species diversity index in intermediate stages, in line with Matthews (1992). In our study, it is possible to consider these two stages (i.e., stages 2 of 60 years and stage 3 of 110 years) as a single mid-successional stage as no notable difference emerged in terms of plant diversity. Yet, changes in environmental conditions changed and increase in competition for space and nutrient (Losapio et al., 2021) lead to a decrease of pioneer plants, such as *Epilobium fleischeri* and *Campanula scheuchzeri* (Paternoster, 1983). These specialist species, adapted to proglacial environmental conditions, give way to more generalist species (Cauvy-Fraunié and Dangles, 2019).

The last successional stage consists of a conifer forest that occupies the majority of the surface. This stage is characterized by the dominance of trees and dwarf-shrubs, made also possible by the absence of grazing. Between stage 1 and stage 4, i.e. in almost 120 years, the presence of dwarf-shrubs increases by a factor of around 20. *Larix decidua*, a typical pioneer tree, is already well established, while the presence of forbs decreases where dwarf-shrubs are abundant. Most forbs species have disappeared due to increasing competition with other species (Losapio et al., 2021) as between stage 1 and stage 4 the presence forbs was halved. Furthermore, the colonization of Ericaceous shrubs like *Rhododendron ferrugineum* in stage 4 limits the establishment of forbs, as they provide shade and create a thick litter layer (D'Amico et al., 2014). This leads to decreased diversity and species richness considering the dominance of certain species such as *Rhododendron ferrugineum*, *Vaccinium myrtillus*, *Vaccinium vitis-ideae*, and *Larix decidua*.

In summary, over the course of the successional stages, this ecosystem is characterized by an increase in species richness and plant diversity, which ultimately diminishes in the late stage with the establishment of a coniferous forest. This transition from specialist vegetation in stage 1 to generalist vegetation in stage 4 results in a decrease in richness of almost 50 %, and a decrease in diversity of 30 % between stages 1 and 4.

4.2 Soil development

The results obtained in our study confirm that glacier retreat decreases pH, and that the older the ecosystem, the more acidic the pH becomes. The geology of the study site, almost devoid of carbonate rocks (Lambiel et al., 2016), confirms that the surrounding rocks do not contribute much to a change in pH, as observed in other studies where pH is basic close to the glacier

https://doi.org/10.5194/egusphere-2024-991
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front (Crocker and Major, 1955; Dong et al., 2016; Wietrzyk et al., 2018). Between the two extremes of our study, i.e. 120 years interval since glacier retreat, pH falls from a median value of 6.6 to 4.4, shifting from neutral to acidic. The estimated decrease in pH is around 2,81% per year, corresponding to a decrease of 0.02 pH units. This linear decrease in pH is explained by the establishment of vegetation, since the organic acids released by decomposing organic matter contribute to a decrease in pH (Wietrzyk et al., 2018). Late development stage shows particularly low pH values in the organic horizon created by accumulation of decomposing organic matter and acidifying litter. In addition, the presence of ectomycorrhizal and ericoid fungi that release acidic compounds is assumed to be high in this stage (D'Amico et al., 2014).

The decrease in pH can also be explained by glacier retreat on its own, since with increasing time the soil undergoes preferential leaching of base cations (Na^+, K^+, Ca^{2+} and Mg^{2+}) which are replaced in soil colloids or dissolved by percolating acids (Bernasconi et al., 2011; Weil and Brady, 2017). However, it can be assumed that the leaching effect is offset by the high organic matter content in late stages and therefore the greater capacity to retain base cations. In fact, an overall increase in the concentration of cations and available elements can be observed in lower pH soils and in plots where the glacier has retreated the longest. This positive correlation between time since glacier retreat and the available elements observed in our study can be explained by the increased weathering associated with the glacier retreat –time on its own– plus the key role of vegetation development and accumulation of organic matter (D'Amico et al., 2014; Darmody et al., 2005). Indeed, the available fraction of elements gradually increases as vegetation develops because plants absorb these elements and recycle them in the surface horizons of the soil (Bormann and Sidle, 1990). Furthermore, the accumulation of decomposed organic matter releases ions, such as calcium, magnesium, and phosphorus into the soil. The concentration of these elements in the soil increases over time, according to previous results (Bernasconi et al., 2011). The dominance of *Larix decidua* and *Ericacea* produces an acidifying litter, increasing acid production in the soil and leading to mineral weathering (D'Amico et al., 2014; Mavris et al., 2010). Moreover, this vegetation is associated with ectomycorrhizal fungi that enhance the rate of weathering in the surface mineral horizons. Indeed, these ectomycorrhizal and ericoid fungi can alter minerals by releasing compounds with acidifying capacity, such as phenolic substances and organic acids (D'Amico et al., 2014). The higher nutrient concentration can thus be explained by slower litter decomposition and a lack of decomposers, resulting in acidic nutrient accumulation in the soil (Bormann and Sidle, 1990).

Glacier retreat influences SOC concentration and total nitrogen concentration too. Changes in soil carbon and nitrogen are qualitatively similar in trend shape, with an overall increase with years since deglaciation. However, in 120 years between pioneer and late stages, carbon increases by 25 times whereas nitrogen increase "only" by *c* 3 times. The increase in plant cover and diversity characterizing by the development of vegetation results in transfer of organic matter to the soil (Burga et al., 2010; Kabala and Zapart, 2012; Wietrzyk et al., 2018). Indeed, SOC corresponds to the carbon contained in the molecules of organic matter while nitrogen comes from the degradation of organic matter and symbiotic fixation by soil microorganisms (Baize, 2018). Low SOC concentrations are explained by the pioneer vegetation that colonizes the soil with limited plant cover. Furthermore, changes in SOC are also due to changes in soil texture as sandy soils have little organic matter retention ability (Weil and Brady, 2017).

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While SOC concentrations are low in pioneer stages, nitrogen concentrations are particularly high in comparison. In fact, total nitrogen are often below 0.1 % in recently ice-free areas which is not the case in our study (Brankatschk, Töwe, Kleineidam, Schloter, & Zeyer, 2011 in Ollivier et al., 2011). The presence of microorganisms involved in the nitrogen cycle including microorganisms associated to nitrogen-fixing plants can explain the high nitrogen values measured in our study (Ollivier et al., 2011). Early and intermediate development stages are characterized by nitrogen fixing plants (i.e., Fabaceae) which soils otherwise poor in N. The C/N ratios of these stages are particularly low, reflecting a high nitrogen input in relation to organic carbon. In the stages 2, 3 and 4, the establishment of growing vegetation and the increasing associated cover mean that more organic carbon is stored in the soil. In stages 2 and 3, SOC and total nitrogen content are similar corresponding to similar vegetation indices in these stages. On the contrary, plants in Ericaceaea family (*Rhododendron ferrugineum*, *Vaccinium myrtillus*, *Calluna vulgaris*) dominate late development stages. This stage shows higher carbon than nitrogen values, an accumulation of organic matter that can seen in the increasing C/N ratio compared with earlier stages, where the accumulation of organic carbon suggests reduced decomposition rates. Nitrogen therefore continued to increase with soil development, but at a lower rate than carbon.

4.3 Plant–soil interactions

Our results show that changes in physico-chemical properties of soils are coupled with vegetation succession and ecosystem development. While low concentrations of available elements in the early stages limit plant growth and establishment (Chapin et al., 1994), the increase of organic carbon, nitrogen, and available elements positively influences the development of certain plant functional groups such as dwarf-shrubs and trees. For example, magnesium and potassium are elements that play crucial roles in certain plant life processes (Wietrzyk-Pełka et al., 2021) and phosphorus is an essential nutrient for plant growth and primary production (Egli et al., 2012; Wietrzyk-Pełka et al., 2021). The presence of these essential elements enables the development of vegetation from a scattered grassland to a closed forest. Furthermore, the presence of bacteria and fungi associated to pioneer plants is decisive for the availability of certain elements, such as phosphorus and nitrogen, for shrubs and trees (Egli et al., 2012).

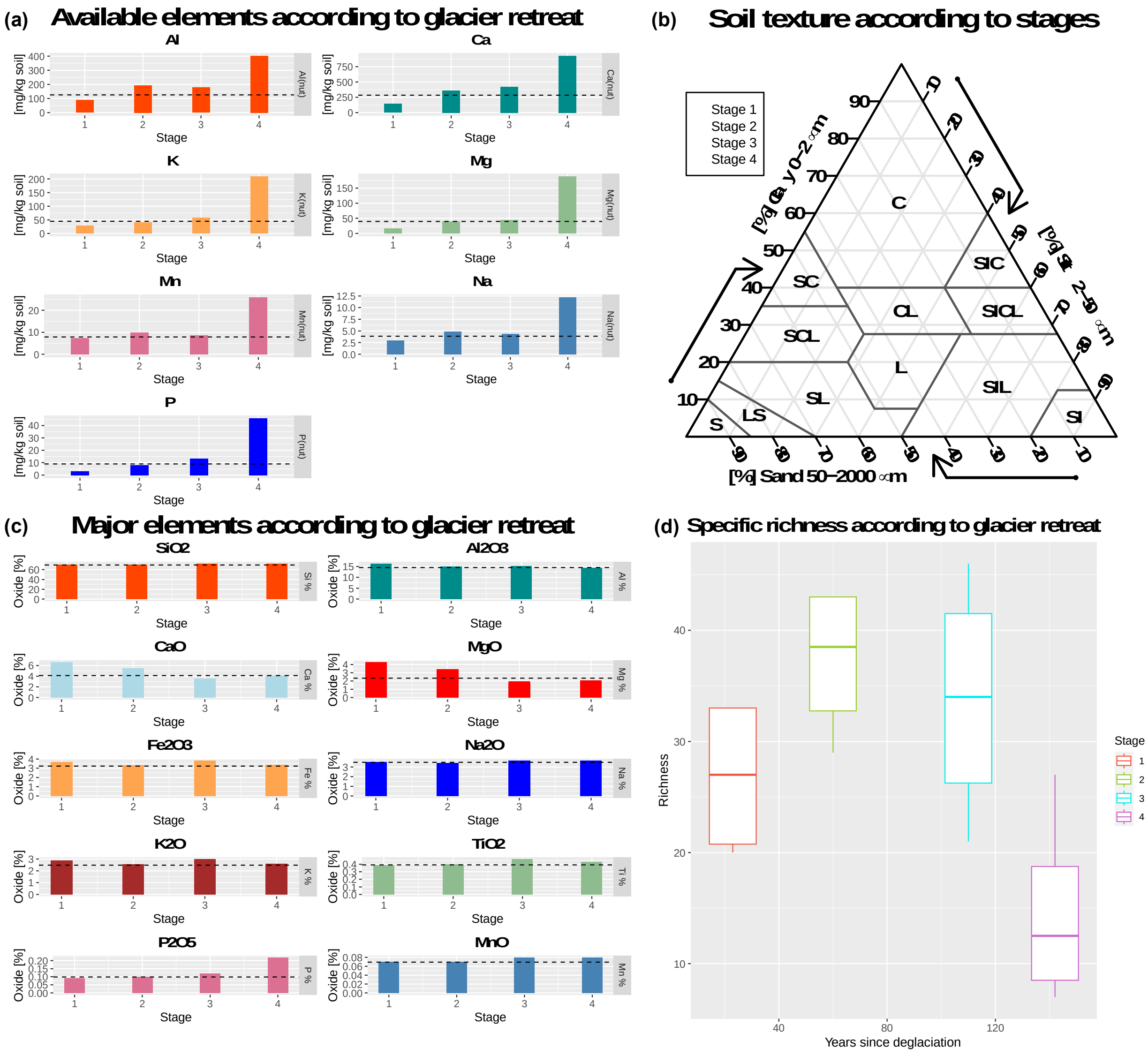
The path analysis model provides an overview of the impact of glacier retreat on soil development and vegetation. This simplified model shows that glacier retreat is a good predictor of soil and vegetation development. Glacier retreat decreases soil pH, which in turn increases soil organic carbon. This model shows that when plant diversity increases, soil organic carbon tends to decrease and that high levels of soil carbon are associated with low plant diversity. This can be explained by the fact that, with increasing glacier retreat in stage 4, there is an accumulation of organic matter and plant diversity is the lowest. Yet, pH has a greater effect on soil organic carbon than plant diversity. Furthermore, according to this model, glacier retreat is not strong enough to explain the effects of plant diversity on organic carbon. This means that glacier retreat has indirect effects on these variables and the relationship between glacier retreat, plant diversity and organic carbon is shaped by other factors. Other variables such as available soil elements, pH and soil microorganisms can play a role in plant diversity, as can microclimatic conditions (Eichel, 2019).

https://doi.org/10.5194/egusphere-2024-991
Preprint. Discussion started: 5 April 2024

5 Conclusion

Glacier retreat influences the development of soil and vegetation in complex ways. Our study highlights the complex, linear and non-linear as well as direct and indirect relationships between plant biodiversity and soil carbon and nutrients in new, emerging ecosystems. As the glacier retreats, new land becomes available, providing an opportunity for a diversity of organisms to colonize these areas. Pioneer plant species enables diversity to increase initially, but with increasing competition and acidifying soil conditions, species become increasingly dominant, and biodiversity decreases ultimately. Soil pH decreases with glacier retreat due to the accumulation of organic acids resulting from the accumulation and decomposition of organic matter. In fact, the development of vegetation over the course of stages enables the soil to grow, enriching it with organic matter and altering the rock. The soil is thus enriched with organic carbon, nitrogen, and plant-available elements. The establishment of mycorrhizal bacteria and fungi, although not examined here, can also contribute to the increase in chemical elements in the soil, as they fix nitrogen and retain nutrients in the soil. Notably, although both soil carbon and nutrient increase, the accumulation of carbon is much faster than nitrogen. These results suggest that novel glacier ecosystems may function as carbon sink by storing carbon in the soil. They also show that nitrogen is a limiting factor and hence small changes in nitrogen levels can have big consequences on biodiversity and ecosystem functioning. As global warming is leading to glacier extinction, mitigation actions shall consider the crucial role plant–soil interactions play in the development and stability of ecosystems.

Supplementary Material: Element content, soil texture and plant richness after glacier retreat



415 **Figure A1:** Additional soil and plants variables according to glacier retreat including plants available elements concentrations (a), soil texture (b), total elements proportions (c) and plant specific richness (d).

Code and data availability

Data are publicly accessible on Zenodo at https://doi.org/10.5281/zenodo.10730935

The R code to analyse data and to reproduce the results and figures reported in this manuscript is publicly accessible on GitHub at https://doi.org/10.5281/zenodo.10731098

Author contribution

GL secured funding for the research. SG and GL led this project development. CC, NK, LMot, NB, NDV, and GL performed field work and collected data. CC performed laboratory analyses with the help of LMon, MF, TA, BB, and OR. CC processed data, conducted statistical analyses, and interpreted results with the help of SG and GL. CC and GL wrote the first draft of the manuscript with contributions from SG and all co-authors.

Competing interests

The authors declare that they have no conflict of interest.

Disclaimer

Acknowledgements

This work was financially supported by the Swiss National Science Foundation (Ambizione grant n. PZ00P3_202127 awarded to GL). GL also acknowledges support from the European Union – NextGenerationEU, Italian Ministry of University and Research (P2022N5KYJ). We are grateful to *Service des forêts, de la nature et du paysage*, *Canton du Valais* for granting research permits and facilitating our research.

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