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Plant microhabitats mediate the effects of glacier retreat on soil microbial diversity and community assembly

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ABSTRACT

Soil microorganisms and plants provide together the vast majority of key ecosystem functions and services, but the effects of climate change such as glacier retreat on soil microorganism–plant interactions remain poorly understood. Here, we investigated how plant microhabitats shape fungal and bacterial diversity, community composition, and functional diversity with glacier retreat over space-time. We analysed 234 microbial communities from bulk soil, rhizosphere soil, and plant root endosphere across four deglaciation stages that span c 160 years of glacier retreat. Our results indicate that fungi and bacteria follow distinct spatio-temporal dynamics: bacterial α-diversity declined within 100 years after glacier retreat, whereas fungal α-diversity gradually increased. On the contrary, β-diversity of both bacteria and fungi decreased with glacier retreat, primarily through reduced turnover, indicating directional disassembly and species exclusion. Community composition changed across scales, that is depending on the interactions between glacier retreat and plant microhabitats. Plant roots harbour the most distinct soil microorganism communities, which were particularly constrained at the latest deglaciation stage. Finally, functional diversity analysis revealed that functional guilds varied with deglaciation depending on plant microhabitats. Arbuscular mycorrhizal fungi, epiphytic fungi, plant pathogens, chemo-heterotrophic bacteria and nitrifying bacteria decrease with glacier retreat, while ectomycorrhizal fungi, endophyte, saprotrophic fungi, and cellulolytic bacteria increase with glacier retreat. Our findings reveal that both broad temporal and local spatial factors drive soil microbial community assembly and functions, with implications for plant-microorganism interactions and nutrient cycling dynamics in post-glacial landscapes.

1. Introduction

The Earth is experiencing numerous fast changes due to global warming. A striking example is the unprecedented rate of glacier retreat worldwide (Bosson et al., 2023; Zemp et al., 2019, 2025). Glaciers cover 706,000 km^2 globally outside of the Greenland and Antarctic ice sheets, equal to c 10 % of the earth surface (Zemp et al., 2019). However, just between the period of 2000–2023, 5 % of the global ice mass has been lost, with a sharp increase after 2012 (Zemp et al., 2025). This number rises to 38 % for the European Alps. The future holds no better news with 22 % to 51 % of glacial areas projected to be lost by the end of this XXI century (Bosson et al., 2023). As glaciers retreat, new ice-free areas (hereafter, glacier forelands) are open for colonisation by specialized plants and soil microorganisms (Cauvy-Frauni'e and Dangles, 2019; Ficetola et al., 2024; Losapio et al., 2021) which could disappear with the extinction of glaciers (Cauvy-Frauni'e and Dangles, 2019; Donhauser and Frey, 2018; Losapio et al., 2025; Wilkes et al., 2023). However, how emerging soil microorganism–plant interactions develop and respond to glacier retreat remains poorly understood.

Microorganisms including fungi and bacteria are among the first colonisers of glacier forelands (Bradley et al., 2014; Donhauser and Frey, 2018; Schulz et al., 2013) where they perform many key ecological functions and ecosystem processes, such as nutrient and carbon cycling (Bradley et al., 2014; Liu et al., 2016), further influencing plant

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colonisation and ecosystem development. Bacterial communities are more important in the first stages of glacier foreland colonisation, with a shift toward fungal dominance in the latter stages (Cutler et al., 2014; Fern'andez-Mart'ınez et al., 2017; Gyeong et al., 2021; Jiang et al., 2018). Organic carbon and nitrogen typically increase due to the presence of autotrophic and nitrogen-fixing bacteria (e.g. cyanobacteria). Saprotrophic fungi are the primary degraders that enhance nutrient cycling by breaking down complex organic molecules (Dighton et al., 1987). In addition to nutrient cycling and fixation, microorganisms are beneficial to plants by providing otherwise inaccessible nutrients via symbiotic interactions, like arbuscular mycorrhizae or ectomycorrhizae. They can also be detrimental, as some microbes exhibit pathogenic or parasitic interactions with plants (Trivedi et al., 2020). However, few studies have assessed the colonisation of plants and microorganisms together on glacier forelands, hindering our understanding of the response of soil microorganism–plant interactions to glacier retreat.

Following the colonisation of pioneer herbaceous plants, glacier forelands undergo important and rapid changes in plant communities, developing into more complex ecosystems such as shrublands and mature forests (Ficetola et al., 2024; Tu et al., 2024). In doing so, plants are the main driver of soil pH acidification and soil organic carbon inputs (Charles et al., 2025). Those soil properties influence microbial communities and diversity (Brown and Jumpponen, 2014; Eslaminejad et al., 2020; Liu et al., 2023; ?). In addition to glacier retreat, each individual plant creates complex microhabitats in the soil across different plant microhabitats, from the bulk soil (general surrounding soil), to the rhizosphere (the narrow zone influenced by root exudates), to finally the root endosphere (the internal root tissues) (Trivedi et al., 2020). Yet, there is controversial evidence on the effects of plant microhabitats on soil microorganisms as some studies found a progressive decline in microbial diversity from the bulk to the rhizosphere to the roots (Trivedi et al., 2020), whereas other studies have highlighted the enriched colonisation of more diverse microbial communities in the rhizosphere (Beckers et al., 2017; Prashar et al., 2014). Furthermore, the influence of plants on bacterial and fungal communities in glacier forelands remains unclear. On one hand, several studies suggest that bacterial communities are more strongly influenced by plant communities while fungal communities appear to be more strongly shaped by stochastic processes (Brown and Jumpponen, 2014; Jiang et al., 2018; Liu et al., 2023). On the other hand, other studies reported the opposite trend where fungi are heavily influenced by plants while no response has been reported for bacteria (Cutler et al., 2014). However, these conclusions have been drawn based on a selected set of few (less than ten) plant species, leaving broad uncertainties on the general roles of plants for the assembly and diversity of soil microorganism communities facing glacier re-treat. Given the central role of soil microorganisms in biogeochemical cycles and ecosystem development, understanding their response to glacier retreat and plant colonisation is critical for predicting the future of soil biodiversity and ecosystem functioning in rapidly changing environments.

Here, we addressed the following questions: (1) How do plants mediate the effects of glacier retreat on bacterial and fungal diversity and community composition? (2) How do these patterns vary with plant microhabitats (i.e. bulk, rhizosphere and roots)? (3) How does functional diversity of fungi and bacteria shift with glacier retreat among plant microhabitats? We hypothesize that both micro spatial scale, i.e., plant microhabitats, and macro temporal scale, i.e., time since glacier retreat, jointly influence microbial com-munity structure, reflecting changes in plant–microbe interactions over space and time. It is also reasonable to hypothesize that the composition of fungal functional groups changes with both glacier retreat and plant microhabitats, indicating shifts in ecological strategies and functions. To the best of our knowledge, this is the first study assessing the interactive effects of macro temporal scale (i.e., hundreds of years) and micro spatial scale (i.e., centimeters) across multiple plant species on the development of soil microbial communities.

2. Methods

2.1. Study site

The study was carried out on the glacier foreland of the Mont Miné glacier (Valais, Switzerland). The glacier has retreated by 2.53 km and lost 130 m of height since *c* 1850 (Lambiel et al., 2016). The valley has a relatively dry climate with a mean annual precipitation of 720 mm; the mean annual temperature is 4.5 °C and the annual mean 0 °C isotherm is situated around 2600 m a.s.l (Lambiel et al., 2016), (Evolène station, mean 1987–2012). Terrain age was reconstructed using existing geochronology of Mont Min'e and Ferpecle glaciers, complemented with our own additional reconstruction based on historical cartography (https://map.geo.admin.ch) and field validation of moraine margins (Tu et al., 2024). We adopted a chronosequence approach and conducted a stratified-random sampling by dividing the glacier foreland into 4 glacier retreat stages (Fig. 1) (Tu et al., 2024).

Stage 1 (S1) is between the 1989 moraine and glacier tongue in 2023, that is $S1 = 17$ years on average; it is a typical alluvial zone composed of patchy vegetation, pioneer plants and bare soil, dominated by *Poa Alpina, Agrostis rupestris* and *Epilobium fleischerii*. Stage 2 (S2) is between the 1925 and 1989 moraines, that is $S2 = 66$ years on average; is a transition from the pioneer community toward more developed and nutrient-rich grasslands. This stage is dominated by *Anthyllis vulneraria* and *Achillea erba-rotta*. Stage (S3) 3 is between the 1900 and 1925 moraines, that is $S3 = 110$ years on average; it is an open shrubland dominated by *Ranunculus montanus*, *Potentilla aurea* and *Vaccinium myrtillus*. Stage 4 (S4) is between the 1900 and c 1865 moraines, that is $S4 = 140$ years on average; it is a stable forest dominated by *Larix decidua*, *Picea abies*, *Rhododendron ferrugineum* and *Vaccinium myrtillus* that represents the "climax" vegetation and also occurs outside the glacier foreland. Notably, pioneer vegetation in S1 and S2 is mainly composed of glacier specialists that hardly grow outside the glacier foreland (Tu et al., 2024; Charles et al., 2025). Along the glacier foreland, soil pH became increasingly acidic with an acidification rate of 0.02 units per year, while plant communities shift from herbaceous to coniferous forest (Charles et al., 2025). Such shifts were accompanied by an increase in soil carbon and nitrogen content, although C/N ratio increases by fivefold and as nutrients become scarcer in the long term (Charles et al., 2025).

2.2. Specimen collection

Sample collection took place during summer 2022 in dry and sunny weather conditions. We set up four 3 × 3 m (9 m^2) plots in each stage ($N = 16$) (Fig. 1). Plots were randomly chosen within each stage on the right-hand bank of Mont-Min'e glacier foreland. As this glacier foreland provides limited differences in elevation range, ranging from 1961 to 2000 m a.s.l, there are no significant differences in bioclimatic conditions among plots which may covary with terrain age. Areas disturbed by hydropower activities were avoided. In each plot, we surveyed plant communities by recording species composition and estimating plant cover visually (accuracy 10 %). Plant species were identified according to Flora Helvetica (Lauber et al., 2024). We recorded a total of 130 plant species belonging to 32 families (Table S1). We then calculated the *Shannon diversity index* (H) of plant community in each plot (Charles et al., 2025; Dixon, 2003;?). Plants were further classified into functional groups as trees, shrubs, dwarf-shrubs, forbs, and graminoids following the infoflora database (www.infoflora.ch). Then, the relative cover of each group was calculated by summing the weighted cover of plant species belonging to the same functional group.

We collected samples at three different levels of soil: Bulk soil, Rhizosphere, and Root Endosphere. Bulk soil represents the average soil microorganism community of the plot. We collected soil samples from the upper layer (10 cm) after removing organic matter (O horizon) and stones. We collected about 100 g of soil at each corner and in the middle

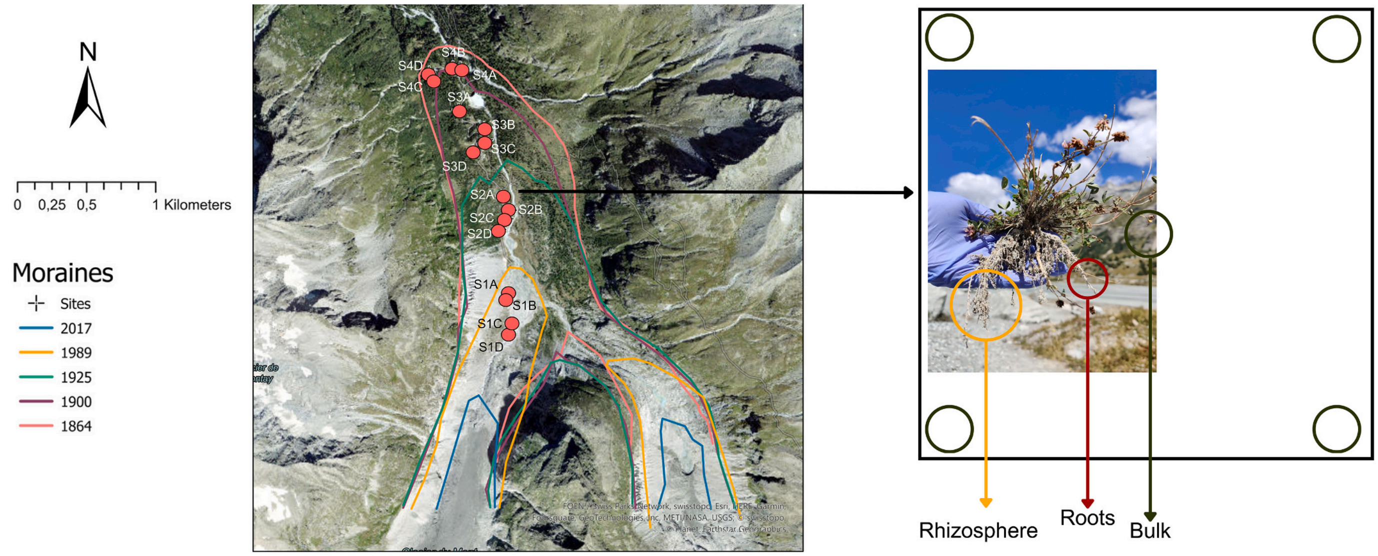

Fig. 1. Fieldwork methodology. Map of the study area (Mont-Min'e fore-land). The plots are shown by the red point. The different moraines are shown by the colored line; Orange = Stage 1, Green = Stage 2, Purple = Stage 3, Red = Stage 4. The image on the right shows the sampling method on a plot. Green circle at the four corner and the middle = Bulk soil, Orange circle = Rhizosphere, Brown circle = Roots.

of the plot. We then homogenized the five sub-samples into one sample per plot ($N = 16$). Coarse materials, such as roots or rocks, were removed. After separating 200 g for further soil chemical analysis, the rest of the soil was stored for microbial community identification.

To better understand soil microorganism–plant interactions, we further sampled and analysed the rhizosphere, i.e. the soil attached to the root sys-tem of plants, and the root endosphere, i.e., the entire root tissue. The rhizosphere includes the microorganisms living at the plant–soil interface. The root endosphere includes the soil microorganisms living inside the roots of plants.

We sampled $N = 40$ individual plants per plot. The number of individual plants per plot was kept constant while plant species richness varies among plots, from 4 to 8, in a way proportional to species richness (Table S1). As a matter of facts, sampling all plant species was not only feasible but would have biased results of soil microorganism diversity associated to plants as plant richness varies itself Charles et al. (2025). Therefore, we selected a representative plant species pool by optimizing a combination of the following criteria: (1) species representative of the vegetation in proglacial habitats (Price et al., 2023); (2) species unique to the plot; (3) species unique to the glacier retreat stage; (4) generalist species occurring over three to four stages; (5) species most visited by insects (Tu et al., 2024). Individual plants species growing within the same plot were pooled together in sterile plastic bags, resulting in one sample per plant species per plot ($N = 110$ samples per type; Table S1). Sampling was conducted at the end of the blooming season in late August 2022. Samples were stored at −20 °C immediately, and moved at −80 °C after a couple of days until further use. Shovel and knife were sterilized using 5 % bleach after sampling each plant species.

2.3. *DNA analysis of soil, rhizosphere and root endosphere*

Bulk soil samples were individually sieved through a sterilized 2 mm mesh; 2 g of soil from each sample were collected for DNA extraction. Rhizosphere samples were carefully separated from roots and sieved through a 2 mm mesh; 2 g of soil from each sample was used for DNA extraction. Roots were disentangled and traced back to each individual to ensure that no roots from other species were collected in the field. When possible, fine roots from each sample were selected and mixed together. The mix was dipped in liquid nitrogen and then put in TissueLyzer II with stainless steel beads (QIAGEN, Hillden Germany) at 30 HZ for 1 min in order to obtain a fine powder of root tissue. 2 g of samples were collected for DNA extraction. Soil and root genomic DNA were extracted from 250 mg of each sample using DNeasy soil pro kit (QIAGEN, Hillden Germany) following manufacturer's instructions. DNA samples were quantified using Quantus Fluorometer (QuantiFluor dsDNA System, Promega) following manufacturer instructions.

We used different primers that target both fungi and bacteria. The ITS2 region of the ribosomal RNA (rRNA) was amplified to identify fungi with the primer pair fiITS7 (GTGARTCATCGAATCTTTG) (Ihrmark et al., 2012) and ITS4 (TCCTCCGCTTATTGATATGC) (White et al., 1990). The identification of bacteria was performed by amplifying the V3–V4 region of 16 s rRNA using the primer pair 341F (CCTAYGGGDBGCWSCAG) and 806R (GGACTACNVGGGTHTCTAAT) (Frey et al., 2016). The PCR reactions (ran three times with triplets pooled per sample), library preparation and sequencing (PE 250 bp) on Illumina NovaSeq 6000 were performed by G'enome Quebec Montreal. The raw sequence data reported in this paper were deposited in NCBI (SAMN52929225-SAMN52929700) that are publicly accessible at ncbi.nlm.nih.gov.

2.4. *Bioinformatics*

Sequencing reads quality control was performed with BBDuk from the BBmap software (v.39.01), with the following parameters: Adapter trim-ming (ktrim = r, k = 23, mink = 11, hdit = 1, tpe, tbo); Quality trimming with 90 % accuracy (qtrim = r, trimq = 10); quality filtering (maq = 10); phix removal (k = 31, hdist = 1) (Bushnell et al., 2014). Sequencing reads that passed the quality filter were imported into QIIME2 v2022.11.1 (Bolyen et al., 2019), with default parameters used if not specified for further bioinformatic analyses. Primer sequences of the target amplicon regions were trimmed using qiime cutadapt trim-paired tool to remove 16 s primer sequences and ITSxpress v1.8.1 (Rivers et al., 2018) to remove 5.8S and LSU adjacent regions of the ITS2 amplicon. Trimmed amplicon sequences were denoised following DADA2 v1.26.0 (Callahan et al., 2016) implementation of qiime2 with qiime dada2 denoise-paired tool with both –p-trunc-len-f and –p-trunc-len-r set to 0. Denoised amplicon sequence variants (ASVs) for the ITS2 region obtained from DADA2 were further clustered at 97 % similarity threshold using Vsearch v2.21.1 (Rognes et al., 2016) implemented in qiime vsearch cluster-features-de-novo tool (hereafter referred as fungal OTUs). No clustering step was applied to ASVs from the 16 s region (hereafter referred as bacterial ASVs). The taxonomic assignment of both fungal OTUs and bacterial ASVs reference sequences was performed with qiime feature-classifier classified-sklearn tool (Pedregosa et al., 2011) using the UNITE v9.0 (Kõljalg et al., 2005) and SILVA v138 (Glöckner, 2019) reference database respectively.

2.5. Statistical analyses

Statistical analyses were conducted using R v 4.3.2 (R Development Core Team, 2023). We normalised the number of fungal OTUs and bacterial ASVs via proportion using Total Sum Normalization (TSS) and rescaled to pseudocounts by multiplying by 100′000 (McKnight et al., 2019). Singletons were removed prior to scaling, but low number of sequences have been kept for the analyses. Inference analysis was performed using Generalized Linear Mixed Models (GLMM) with the glmmTMB function (R package glmmTMB v1.1.8). Each GLMM model was followed by pairwise comparisons using emmeans() (R package emmeans v1.8.9). Significant differences were considered when p-value < 0.05. The normality of the residuals was assessed using simulated residuals() from the DHARMa package (v.0.4.7). Unless other-wise specified, models were fitted with a normal distribution with no data transformation.

2.5.1. Alpha diversity

To understand the interactive effects of plant microhabitat and glacier retreat on soil microbial communities, we computed the two alpha (α) diversity indices of Chao 1 richness and Shannon-Wiener diversity. The function estimate_richness() of R package phyloseq (v1.46.0) was used to this end (McMurdie and Holmes, 2013). We tested the effects of glacier retreat (deglaciation stage; categorical variable with four levels and S1 as reference level), plant microhabitats (categorical variable with three levels and rhizosphere as reference one) and their interaction as fixed effects; α-diversity indices of Chao and Shannon where the response variables (two separate models); plot was considered as a random effect.

2.5.2. Beta diversity

To further investigate the role of plant microhabitat and glacier retreat on soil microbial communities, we then computed beta (β) diversity to investigate the community variation between each plant microhabitat and glacier retreat. We calculated the total dissimilarity by computing distances be-tween samples using the Jaccard distances, based on presence and absence for both fungal OTUs and bacterial ASVs separately. This β-diversity distance was calculated for each stage by comparing different plots within the same stage and only between each sample origin. Then, we tested the effects of glacier retreat, plant microhabitats, and their interaction (fixed effects) on β-diversity (response with beta-family distribution), while plots were a random effect, using the glmmTMB package (Brooks et al., 2017) for both the fungi and bacteria (two separate models).

To investigate the processes driving community variation across different plant microhabitats, we further partitioned β-diversity into Turnover and Nestedness components. Turnover quantifies the degree of replacement be-tween species, while nestedness quantifies the degree of new species addition to the community without replacement (Fontana et al., 2020). We compared Turnover and Nestedness between Bulk and Rhizosphere (Comparison 1) and between Rhizosphere and Roots (Comparison 2) across the four stages. To this end, we used the beta.pair() function from the betapart R package (v.1.6) (Baselga and Orme, 2012).

We assessed betadiversity component with GLMM. To test the effects of stages, and the comparison (1 or 2) and their interaction (fixed effects) on both turnover and nestedness (response), we set pairwise plot comparison as a random effect, and used the beta-family distribution from the glmmTMB package for both fungi and bacteria models. To ensure model assumptions, we squared the bacterial community dissimilarity matrix on the turnover model and used an exponential transformation for both bacterial and fungal dissimilarity matrices for the nestedness model.

To visualise dissimilarities in community composition and its relation-ship with environmental predictors, we used a Non-metric multidimensional scaling (NMDS) ordination using the metamds() function of the vegan pack-age (v 2.6-4) and tested the correlation be-tween the ordination configuration (i.e. the community dissimilarities) and the environmental predictors using the envfit() function also from the vegan package. To assess the differences in both bacterial and fungal community composition between the different plant microhabitats and across the different stages of glacier retreat, we used a Permutational Multivariate Analysis of Variance (PERMANOVA) as implemented in adonis() function of the vegan package with 999 permutations.

2.5.3. Functional diversity

Finally, we investigated the changes in functional diversity following glacier retreat. Functional diversity, more specifically the primary lifestyle of fungi has been assigned to fungal OTUs taxonomically classified at the genus or higher level using the FungalTrait database (Põlme et al., 2020). We grouped the different primary life forms as the following: "*Plant pathogen*", (dung-, litter-, nectar/tap-, pollen-, soil-, unspecified-, wood-) "*Saprotroph*", (algal-, animal-, lichen-, myco-, protistan-) "*Parasite*", (foliar-, root-) "*Endophyte*", "*Lichenized*", "*Epiphyte*", "*Arbuscular mycorrhizal*", "Ectomycorrhizal". For the analyses, we removed the "Unspecified" and "other" functional groups. To look at bacterial function (i.e., metabolic or other eco-logically relevant functions such as nitrification, denitrification, or fermentation), we associated our OTU table with the FAPROTAX dataset (script 1.2.1) (Louca et al., 2016). For the analyses, we removed the "Unspecified" and "other" functional groups.

To look at bacterial functions (i.e. metabolic or other ecologically relevant functions such as nitrification, denitrification or fermentation), we used the FAPROTAX dataset (script 1.2.1) (Louca et al., 2016). To reduce the number of functional groups, we removed groups with similar function and glmm parameters. For both bacteria and fungi, we tested the presence of the different functional group across the stages of glacier retreat and the different plant microhabitats with GLMM using a Poisson distribution with Stage, plant microhabitats and their interaction as fixed effects and plot as a random effect.

3. Results

3.1. How do plants mediate the effects of glacier retreat on bacterial and fungal diversity and community composition?

We obtained in total, after singletons removal and quality filtering, 14′335 fungal OTUs and 239′456 bacterial ASVs, which represent on average 284.18 (+−106.06) OTUs and 3368.32 (+−1403.79) ASVs per sample. In fungi, Ascomycota and Basidiomycota were highly dominant and made up the majority of fungi found at the phylum level. In bacteria, the majority of ASVs belong to the phylum Proteobacteria, Actinobacteria, and Acidobacteria (Figs. S2–S5).

The alpha diversity pattern changed when looking at taxa Chao1 richness estimator or Shannon- Wiener diversity index. We found that the Chao richness estimator of both Fungi and bacteria was influenced by both glacier retreat ($p < 0.001, p < 0.001$), plant microhabitats ($p < 0.001$, $p < 0.001$), and their interaction ($p = 0.011$, $p < 0.001$), while Shannon-Wiener diversity index was only influenced by plant microhabitats for both fungi and bacteria ($p < 0.001, p < 0.001$). In fungi, the community richness increased after stage 1 as stage 3 and 4 had the highest richness estimates and stage 1 the lowest ($p = 0.004, p < 0.001$). No differences were observed across the other stages (Fig. 2a). The richness estimates and diversity index were the lowest in the roots compared to Bulk and Rhizosphere ($p < 0.001, p < 0.001$) and that no differences were observed between the latter neither in richness or diversity (Fig. 2b). The trend in bacteria was different as we observed a significant increase in community richness, from stage 1 to stage 2 ($p =$

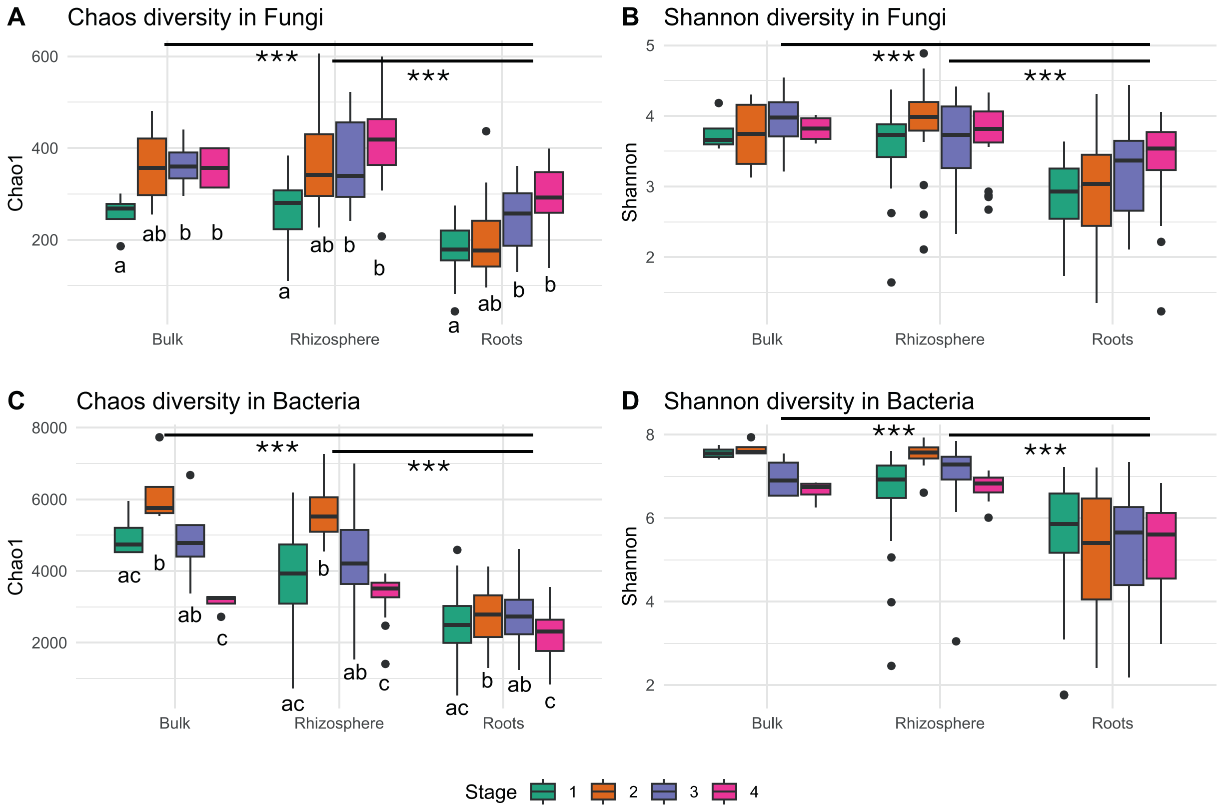

Fig. 2. Alpha diversity of microbes across stages and plant microhabitats. The horizontal line indicates the significance across plant microhabitats and the letter indicate the significance across stages.

0.029) that remained unchanged (i.e. no significant difference) from stage 2 to 3 and finally a significant decrease from stage 3 to stage 4 (p = 0.034) (Fig. 2c). Bacterial richness gradually decreased from the bulk to the rhizosphere (p = 0.046) and from the rhizosphere to the roots ($p <$ 0.001), the difference between the Bulk and the roots is also significant ($p <$ 0.001). The Diversity was the lowest in the Roots compared to both Rhizosphere ($p <$ 0.001) and Bulk ($p <$ 0.001)and that no differences were observed between the latter (Fig. 2d), similarly to fungi.

The total betadiversity in bacteria and fungi was influenced by glacier retreat ($p <$ 0.001, $p <$ 0.001), plant microhabitat ($p <$ 0.001,$p <$ 0.001) and their interactions ($p <$ 0.001, $p <$ 0.001). For fungi, betadiversity decreased at the latest stage, with stage 4 having significantly less dissimilarity than in stage 2 ($p <$ 0.001)and 3 (p = 0.004) . In plant microhabitats, the beta diversity was higher in roots compared to Bulk ($p <$ 0.001) and Rhizosphere ($p <$ 0.001) and no differences were observed between Bulk and Rhizosphere (Fig. 3a). In bacteria we observed a drop in betadiversity in stage 4 that significantly lowered betadiversity compared to stages 1 to 3 ($p <$ 0.001). The three different plant microhabitats had different values of betadiversity, Roots had the highest value ($p <$ 0.001), followed by Rhizosphere ($p <$ 0.001) and finally Bulk ($p <$ 0.001) (Fig. 3b). Tables with detailed results are available in Supplementary files S6–S7.

3.2. How do these patterns vary with plant microhabitats?

We further decomposed the betadiversity into turnover (species replacement) and nestedness (species addition) to highlight the processes behind the dissimilarity between the different plant microhabitats. Turnover and Nestedness were both influenced by glacier retreat (fungi: $p <$ 0.001, p = 0.001; bacteria: $p <$ 0.001, p = 0.003), plant

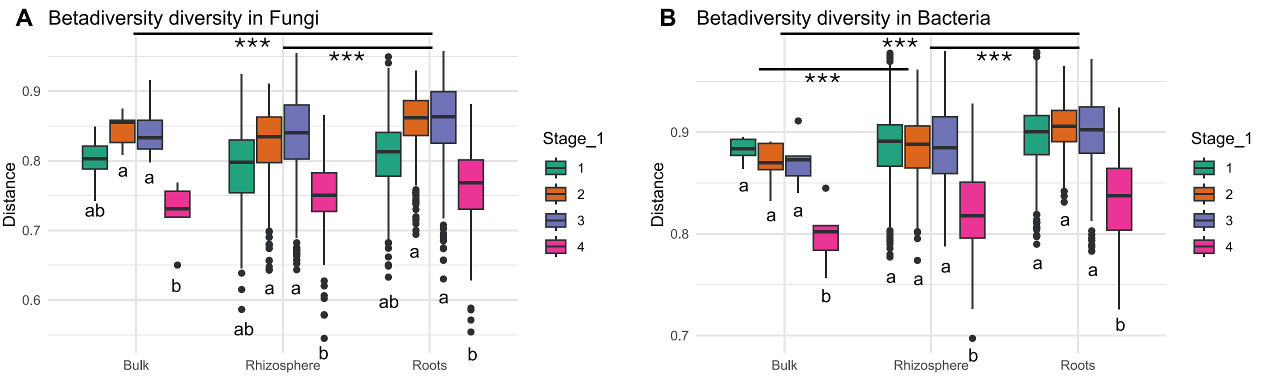

Fig. 3. Beta diversity of soil microorganisms across stages and plant microhabitats. Bray-Curtis distance is calculated between communities within each stage. The horizontal line indicates the significance among plant micro-habitats and letters indicate the significance among stages.

microhabitats (fungi: $p < 0.001$, $p < 0.001$; bacteria: $p < 0.001$, $p < 0.001$) and their interactions (fungi: $p = 0.015$, $p = 0.001$, bacteria: $p < 0.001$, $p < 0.001$). Turnover was much higher than nestedness with values around 0.8 against while nested-ness was 0.05 in both fungi and bacteria (Fig. 4b and d). Fungal turnover decreased in the last stage as stage 4 has significantly lower turnover values compared to both stage 2 ($p = 0.007$) and stage 3 ($p = 0.001$). The turnover between Rhizosphere-Roots is significantly higher than the one between Bulk- Rhizosphere ($p < 0.001$) (Fig. 4b). In bacteria we also observed a drop of the turnover value in the latest stage, with stage 4 having the lowest value compared to stage 1-2-3 ($p < 0.001$). Contrarily, to fungi, bacterial turnover was the highest between the Bulk and the Rhizosphere ($p < 0.001$) (Fig. 4d). Nestedness was significantly higher in both fungi and bacteria between Rhizosphere–Roots than between Bulk–Rhizosphere ($p < 0.001$, $p < 0.001$). No difference was observed across stages in bacterial nestedness (Fig. 4 c), while nestedness in fungi was significantly lower in stage 3 than stage 2 ($p = 0.030$).

NMDS (Fig. 5) results show different fungi and bacteria communities in terms of taxonomic composition between the different stages ($R = 0.61$, $p < 0.001$; $R = 0.523$, $p < 0.001$) as well as between the different plant microhabitats ($R = 0.21$, $p < 0.001$; $R = 0.092$, $p < 0.001$). Fitted environmental variables were significantly correlated with the NMDS and species composition. Fungi community composition was best explained by pH ($R = 0.85$, $p < 0.001$), the proportion of subshrubs (dwarf shrubs) in the plot ($R = 0.57$, $p < 0.001$), the carbon to nitrogen ratio ($R = 0.56$, $p < 0.001$), the carbon concentration ($R = 0.49$, $p < 0.001$) and nitrogen concentration ($R = 0.49$, $p < 0.001$). Bacteria community composition is best explained by pH ($R = 0.85$, $p < 0.001$), the carbon to nitrogen ratio ($R = 0.57$, $p < 0.001$), the proportion of subshrubs ($R = 0.51$, $p < 0.001$), and the nitrogen ($R = 0.46$, $p < 0.001$) and carbon concentration ($R = 0.45$, $p < 0.001$). Tables with detailed results are available in Supplementary files S6–S7.

3.3. How do functional groups shift with successional stage and plant micro-habitats?

We could assign 48 % of the fungal community to different functional groups. Saprophytic fungi were the most frequent group (59 %), followed by plant pathogens (11 %) and ectomycorrhizal fungi (10 %).

Arbuscular mycorrhiza (AM), Ectomycorrhizal (EM), Endophyte, Epiphyte, and Saprotroph taxa were affected by both glacier retreat (AM: $p < 0.001$, EM: $p = 0.006$; Endo: $p < 0.001$; Epi: $p < 0.001$; Sap: $p < 0.001$) and plant microhabitats (AM: $p < 0.001$; EM: $p < 0.001$; Endo: $p < 0.001$; Epi: $p < 0.001$; Sap: $p < 0.001$), while Lichenized Fungi, Parasites, and Plant pathogens were only affected by plant microhabitats (LF: $p < 0.001$; Para: $p < 0.001$; PP: $p < 0.001$). Statistical interactions were not significant in any of the groups (Fig. 6). The richness of AM fungi decreased in the latest stage 4 ($p < 0.001$), and both Rhizosphere and Roots had less AM taxa compared to Bulk soil ($p < 0.001$, $p = 0.006$) . Ectomycorrhizal com-munity richness gradually increased following glacier retreat, and the stage 4 has more observed EM fungi compared to stage 1 ($p = 0.037$) and decreased from Bulk to Rhizosphere ($p < 0.001$) to roots ($p < 0.001$).

Endophyte gradually increased following glacier retreat with both stage 3 and 4 having the highest number of endophytic fungal richness compared to stage 1 ($p = 0.027$, $p = 0.004$). Roots had a lower number of endophytic taxa compared to Bulk ($p < 0.001$) and Rhizosphere ($p < 0.001$). Epiphytic taxa gradually decreased following glacier retreat with stage 1 having the highest value compared to stage 2 ($p = 0.015$) and stage 3 and stage 4 ($p < 0.001$), with Roots showing a lower number of epiphytic taxa richness compared to the Rhizosphere ($p < 0.001$). Saprotrophic fungi gradually increased following glacier retreat with stage 1 having less saprotrophic fungi compared to stage 3 and 4 ($p < 0.001$) and stage 2 was lower than stage 4 ($p = 0.008$).

Roots showed a lower number of saprotrophic taxa compared to bulk ($p < 0.001$) and rhizosphere ($p < 0.001$). Lichenized taxa were less abundant in the Roots compared to the Rhizosphere ($p < 0.001$) and the

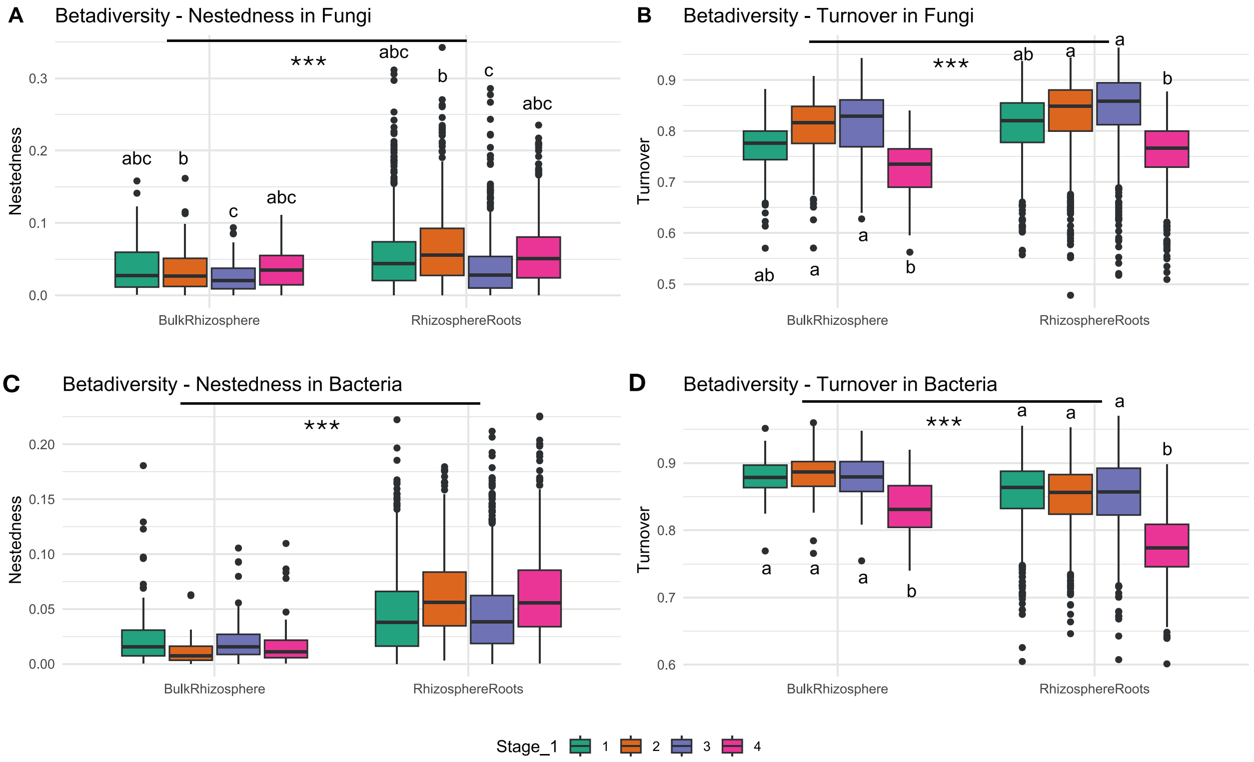

Fig. 4. Beta diversity partitioning of microbe across stages and plant microhabitats. Nestedness and turnover are calculated between samples within each stage. The horizontal line indicates the significance across plant micro-habitats and the letter indicate the significance across stages.

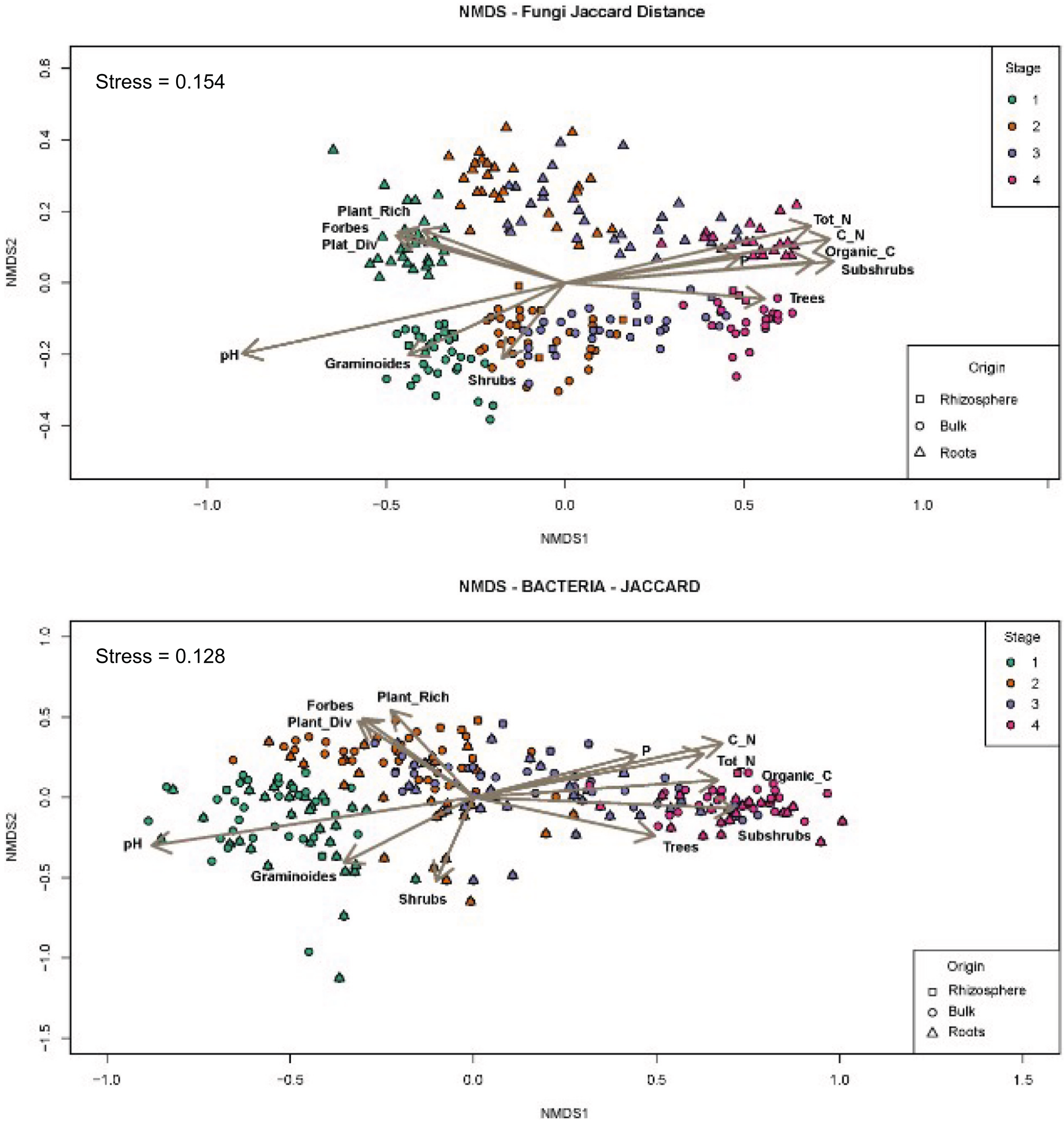

Fig. 5. Non-metric multidimensional scaling ordination (NMDS) of (A) fungi and (B) bacteria, along deglaciation stages (colours) and across plant microhabitats (shapes). Vectors of all tested environmental variables were overlaid onto the ordination space. The arrow indicates the direction of most rapid change in the variable, and its length is proportional to the correlation between ordination and the variable.

Bulk soil ($p < 0.001$). Parasitic fungi reached their maximum in the Rhizosphere, then Bulk ($p < 0.001$), and were the least abundant in the roots ($p = 0.01$). Plant pathogen taxa were the most abundant in the Rhizosphere compared to the bulk ($p < 0.001$) and roots ($p < 0.001$). Tables with detailed results are available in Supplementary file S8.

Leveraging the FAPROTAX database, we assigned a function to 57′303. Bacterial OTUs which corresponded to 24 % of the total OTUs present in our dataset. We removed the function with less than 1 % of the taxa (574) assigned. We initially obtained 53 groups and retained 25 after filtering. Both glacier retreat and microhabitats and their interactions affected Aerobic Ammonia Oxidation ($p < 0.001, p < 0.001, p = 0.014$); Chemoheterotrophy ($p < 0.001$, $p < 0.001$, $p = 0.013$); Chloroplasts ($p < 0.001, p < 0.001, p = 0.039$); Intracellular Parasites ($p < 0.001, p < 0.001, p < 0.001$); Nitrification ($p < 0.001, p < 0.001, p = 0.015$); Non-photosynthetic Cyanobacteria ($p < 0.001, p < 0.001, p = 0.045$); Predatory or Exoparasitic ($p < 0.001, p < 0.001, p = 0.004$).

Both glacier retreat and microhabitats and their interactions affected, but not their interactions affected Aerobic Chemoheterotrophy ($p < 0.001$, $p < 0.001$); Animal Parasites/Symbionts ($p < 0.001$, $p = 0.015$); Anoxygenic Photoautotrophy ($p < 0.001, p < 0.001$); Aromatic Compound Degradation ($p < 0.001, p < 0.001$); Aromatic Hydrocarbon Degradation ($p < 0.001$, $p < 0.001$); Cellulolysis ($p < 0.001$, $p < 0.001$); Denitrification ($p < 0.001$, $p < 0.001$), Fermentation ($p < 0.001$, p¡0.001), Human Associated (p¡0.001, p¡0.001); Hydrocarbon Degradation ($p < 0.001, p < 0.001$); Nitrate Reduction ($p < 0.001, p < 0.001$); Nitrogen Respiration ($p < 0.001$, $p < 0.001$); Oxygenic

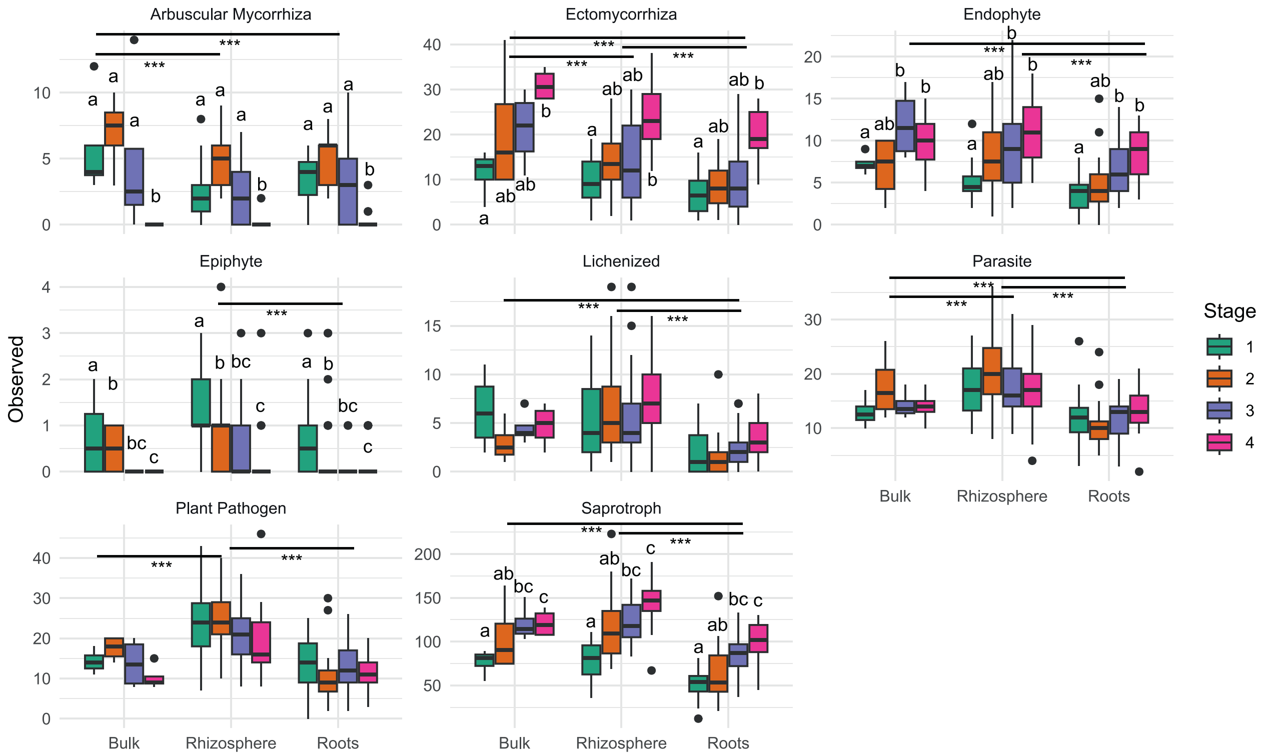

Fig. 6. Functional richness of the main fungal groups. The horizontal line indicates the significance among plant microhabitats and the letter indicate the significance among stages.

Photoautotrophy ($p < 0.001$, $p < 0.001$) Photoautotrophy and Photoheterotrophy ($p < 0.001$ and $p < 0.001$); Ureolysis ($p < 0.001$, $p < 0.001$). Nitrogen Fixation was only affected by stages ($p < 0.001$) and not by plant microhabitats (Fig. 7).

Chemoheterotrophic bacteria (both aerobic and not defined) were the most abundant across the samples. They decreased in the last stage as they were less abundant in stage 4 compared to stage 1 ($p = 0.008$), stage 2 ($p < 0.001$) and stage 3 ($p = 0.024$) and were less frequent in the roots compared to Bulk and Rhizosphere ($p < 0.001$). Bacteria associated with Aromatic Compound Degradation were the highest in the early

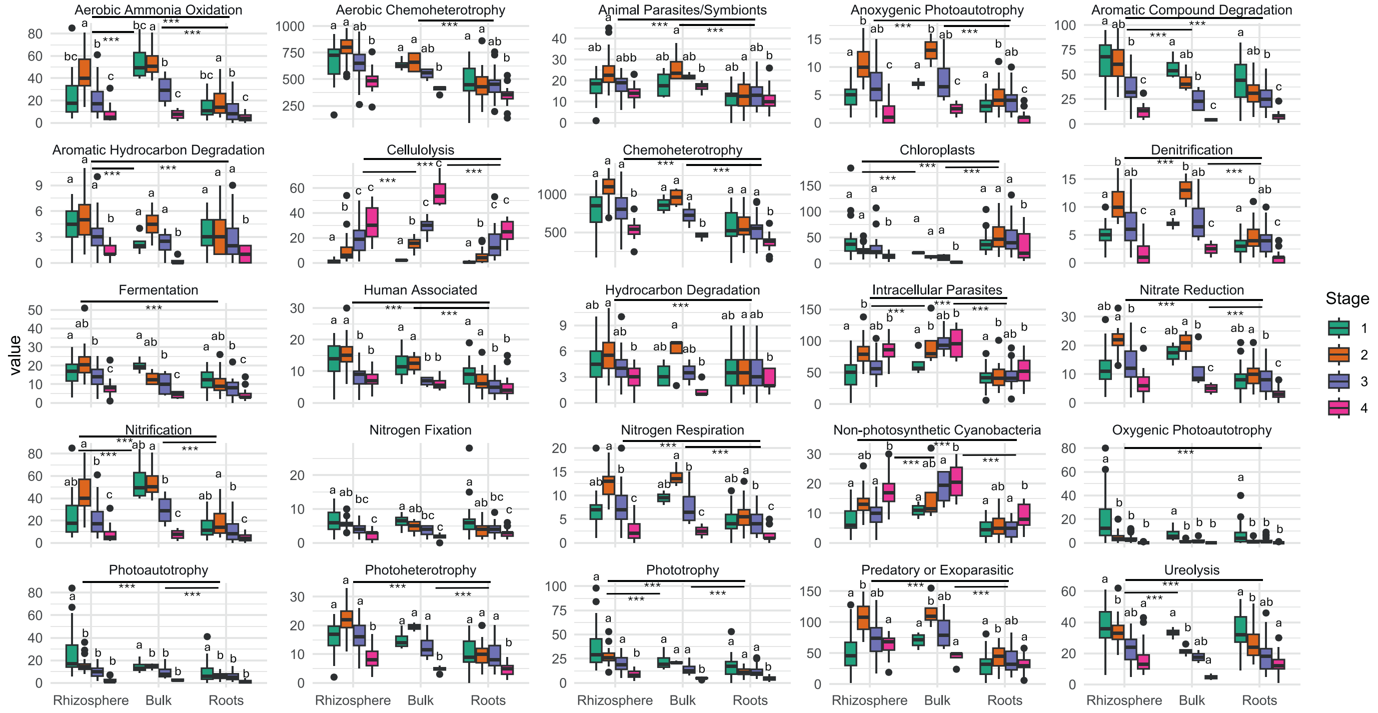

Fig. 7. Functional richness of the main Bacterial groups. The horizontal line indicates the significance among plant microhabitats and the letter indicate the significance among stages.

stages and decreased after stage 2, being less abundant in stage 1 compared 3 ($p = 0.003$) and the less abundant in stage 4 compared to 1-2-3 ($p < 0.001$). They were more frequent in the Rhizosphere compared to the Bulk ($p = 0.005$) and Roots ($p < 0.001$). In contrary, Cellulosic bacteria were the lowest in the early stage and increase in the last stage. They were less abundant compared to stage 2–3-4 ($p < 0.001$), then in stage 2 compared to stage 3 ($p = 0.010$) and stage 4 ($p < 0.001$). No change was observed between the stages 3 and 4. They were more abundant in the Bulk compared to Roots ($p < 0.001$) and the Rhizosphere ($p = 0.004$), They were also more abundant in the Rhizosphere compared to the Roots ($p < 0.001$). Bacteria associated with nitrogen fixation, such as Aerobic Ammonia Oxidation or Nitrifying bacteria, showed a decline in stage 4 compared to stage 1-2-3 ($p < 0.001$, $p < 0.001$), and in stage 3 compared to stage 2 ($p < 0.001$, $p < 0.001$). Plant microhabitats also affected the presence of these bacteria. They were the most frequent in the Bulk compared to the Rhizosphere ($p = 0.001$, $p = 0.001$) and the Roots ($p < 0.001$, $p < 0.001$) followed by the Rhizosphere compared to the Roots ($p < 0.001$, $p < 0.001$). Tables with detailed results are available in Supplementary files S9–S10.

4. Discussion

Our study provides novel insights into the assembly patterns of soil microorganism community across temporal macro-scale (hundreds of years of glacier retreat) and spatial micro-scale (centimetres of plant microhabitats). By adding the role of plant microhabitat into the picture, we captured with more precision the processes behind microorganism colonisation following glacier retreat.

4.1. Influence of plants and deglaciation stage on fungal and bacterial com-munities

Our results emphasize the crucial relation between plants and microbes in shaping communities over space-time. Furthermore, the impact of plant microhabitats varies depending on the stage of glacier retreat. This is particularly evident in the alpha diversity models. We observed that plant micro-habitats played a key role in both richness and in Root-associated samples in both bacterial and fungal communities. This aligns with the findings of Trivedi et al. (2020) as root microbiomes generally have lower diversity than rhizosphere and bulk soil. However, our results slightly di-verge from this point, as we did not observe significant differences in alpha diversity between bulk soil and the rhizosphere, the rhizosphere being as rich as the bulk soil. In that context, it is important to highlight that bulk and rhizosphere microbiomes are composed of a mixture of potentially active, dormant, or dead microbes. In contrast, the microbes detected in the root endosphere are mostly active microbes, which contribute to explain the lower richness and diversity in roots Joergensen and Wichern (2018); Li et al. (2019).

Additionally, our findings suggest that alpha diversity does not respond uniformly to different developmental stages across plant microhabitats. For instance, bacterial (Chao) richness estimator exhibited sharp differences across stages in bulk soil and the rhizosphere, whereas the effect of deglaciation stages seems to be weaker in the roots. Previous research on plant micro-habitats along elevation gradients has shown that the effect of elevation was already weakened in the rhizosphere compared to bulk (Praeg et al., 2019). Our results are also divergent from Zhao et al. (2023) who found that the rhizosphere stabilises the alpha diversity and that no changes are observed in forest succession.

The relative importance of plants is also reflected in the total beta diversity. Unlike alpha diversity, beta diversity increases in root-associated communities compared to bulk soil and rhizosphere. In bacterial communities, beta diversity progressively increases from bulk soil to the rhizosphere and then to the roots. This result highlights the strong relationship between plants and microbes and the importance of individual plant species. Indeed, dissimilarity between samples increases when focusing on the rhizosphere or roots, suggesting that different plant species host specific microbes. This suggests that bulk soil would harbour a more general microbial pool from where plants recruit microbes (Zhong Chen et al., 2023). Nevertheless, the overall dissimilarity values remain high, even in bulk soils. Higher differences were observed among the stages, suggesting that succession is the main process influencing the beta diversity of both fungal and bacterial communities as also found by Praeg et al. (2019). The decrease in beta diversity in the last stage implies that with ongoing glacier retreat and probable future glacial extinction, there will be a biotic homogenisation with microbial communities becoming more and more similar to each other, ultimately decreasing global (gamma) diversity.

We also found evidence that plant microhabitats influence both fungal and bacterial species composition on their own as biotic ecological drivers. Variables directly associated with plants (plant richness, plant diversity, and the proportion of different plant groups) significantly impact the microbial communities of both fungi and bacteria, indicating the key role of plant–microorganism interactions in driving community structure and functions. Furthermore, as widely reported (Jiang et al., 2018; Liu et al., 2023; Tripathi et al., 2018; Zhalnina et al., 2015), pH remains the primary driver of both fungal and bacterial communities, a finding already shown that relates to plant colonisation (Liu et al., 2023). However, fungi were more dissimilar among plant microhabitats than bacteria, suggesting different responses to biotic filters of plant microhabitats. Similar results on community clustering were found in the soil of tree species mixtures experiment (Bai et al., 2023). We further demonstrated that species replacement is the dominant process during the transition from bulk soil to the rhizosphere and from the rhizosphere to the root, as indicated by high turnover values compared to relatively low nestedness. Additionally, both nestedness and turnover are influenced by glacier retreat, with their contributions varying at different deglaciation stages.

Notably, turnover followed distinct patterns between fungi and bacteria. In fungal communities, turnover increased during the transition from the rhizosphere to the root, whereas in bacteria, it decreased. This pattern suggests that bacteria are less specialized and less dependent on roots compared to fungi. The higher fungal turnover in roots likely reflects a stronger filter for specific symbiotic partners (e.g., mycorrhizal fungi, endophytes), whereas bacterial communities in the rhizosphere might be more generally selected by root exudates Ulbrich et al. (2022). A similar trend is also evident in species composition as bacteria showed higher community similarity between plant microhabitats than fungi. Indeed, in fungal communities, we observed a clear difference in species composition in roots compared to bulk and rhizosphere, which was less pronounced in bacterial communities. Furthermore, bacterial and fungal communities also show different alpha diversity pat-terns: Fungal diversity increased following glacier retreat, whereas bacterial diversity increased only from stage 1 to stage 2 before sharply decreasing in the final stage 4. Interestingly, bacterial richness followed a pattern similar to plant richness (Brown and Jumpponen, 2014; Charles et al., 2025; Liu et al., 2023). Previous studies on succession showed similar patterns for vegetation and bacteria. Fungal diversity aligned more closely with the trend observed in dwarf shrubs and trees, which increase in our study site after glacier retreat (Charles et al., 2025). Shrubs and trees were also an important driver of fungal community composition. A possible explanation to this divergence could be found in soil acidification as the sharp decrease of pH following glacier retreat (Charles et al., 2025) could inhibit bacterial activity (Delgado-Baquerizo and Eldridge, 2019) but not fungi. Moreover, the C:N ratio increases with glacier retreat, which favors fungal taxa—particularly ectomycorrhizal fungi—over bacteria. Bacterial diversity decreases as the C:N ratio increases, with the lowest diversity observed at the highest ratios. Conversely, low C:N ratios are known to promote bacterial diversity as these nutrient-limited conditions favour fast-growing organisms. Under these conditions, competition with fungi is reduced, as low C:N ratios also limit fungal diversity and abundance (Delgado-Baquerizo et al., 2017; Zechmeister-Boltenstern et al., 2015).

Our results also align with previous findings (Delgado-Baquerizo and Eldridge, 2019) comparing forests with grassland ecosystems where bacterial richness was lowest in forests and decreased with decreasing pH and increasing soil carbon content. A similar pattern is observed in our study case: bacterial richness is highest in Stage 2 and decreased by two folds in Stage 4. Stage 2 corresponded to a grassland ecosystem with relatively high pH (around 6–6.5), while Stage 4 represented a closed forest dominated by *Larix* species, characterized by acidic soil (pH around 4–4.5). Although ecological patterns can often be transposed across regions, as demonstrated by multiple studies of glacier retreat worldwide Carteron et al. (2024); Cauvy-Frauni'e and Dangles (2019); Ficetola et al. (2024).It remains important to test these patterns across different glaciers worldwide to validate broader generalisations. In particular, our study site is located within the treeline, which raises additional questions about colonisation dynamics. Investigating glacier forelands above the treeline that do not terminate in forests could provide further valuable insights into how plant and microbial communities establish and interact.

4.2. *Microbial functional diversity along the glacier foreland*

Although functional diversity patterns were inferred from only a subset of our samples—since functional assignments relied on general databases (FungalTraits and FAPROTAX). and tools like FAPROTAX predict potential function, not necessarily in situ activity, which can be influenced by environmental conditions. Our results nonetheless indicate that glacier retreat strongly influences functional diversity. These shifts are likely to have important consequences for ecosystem functioning, particularly in relation to carbon and nutrient cycling.

Specifically, we observed an increase in both ectomycorrhizal (EM) and saprotrophic fungi with glacier retreat. EM fungi follow the same trend as shrubs and trees (Charles et al., 2025), which is unsurprising given their well-known symbiotic relationships with those plant groups. For example, EM extensively colonise *Larix decidua* trees, one of the dominant species in the latest stages of our study area (Leski and Rudawska, 2012; Mandolini et al., 2024). EM presence is also known to increase the C:N ratio, as they can utilize soil nitrogen (Jiang et al., 2021), leading to a relative increase in C content with respect to N. The decline in AMF in the later stages aligns with our expectation as AMF are more dominant in grasslands being associated to herbaceous plants (Nguyen et al., 2016; Perotto et al., 2018) and being specialized in utilizing mineral resources, which explains their higher abundance during the early stages (Ferlian et al., 2021). Additionally, the dominance of coniferous trees in latest stages further impacts AMF communities via alteration of soil properties (Ferlian et al., 2021).

Saprotrophic fungi are decomposers capable of breaking down litter (Boddy and Hiscox, 2016), which is highly abundant on the forest floor in the late stages of the study area. Saprotrophic fungi are also largely ubiquitous, which explains their high prevalence, while they enhance nutrient availability. We observed an increase in saprotrophic fungi, conversely to previous observations of a decrease in later stages of vegetation succession with the growth of coniferous trees (Zhao et al., 2023). Moreover, Wang et al. (2023) found that EM and saprotrophic fungi are negatively correlated, as they compete with each other in environments with high litter accumulation (Wang et al., 2023). Nonetheless, the presence of both saprotrophic fungi and EcM may have driven the overall increase in fungal abundance, as they are among the main functional groups, together they represent about 70 % of the assigned functional groups. The presence of these decomposer groups, along with the observed increase in soil carbon, suggests that both saprotrophic and EM fungi are competing for resources, which may limit the decomposition rate—a phenomenon known as the “Gadgil effect.” The main underlying processes is nitrogen limitation driven by the presence of EM fungi, which slows down the activity of saprotrophic fungi, and thus decreases the respiration**?**. The observed increase in EM fungi following glacier retreat is potentially changing the soil carbon storage and nutrient cycling. Understanding this mechanism of carbon sequestration is central to our comprehension of carbon cycling, particularly in the context of rising atmospheric CO_2 levels (Fernandez and Kennedy, 2016). Especially as we anticipate that the glacier foreland will tend to be similar to stage 4.

Chemoheterotrophic bacteria were the most abundant group across our samples, which is not surprising given their global dominance (Labouyrie et al., 2023). However, their abundance declined in the latest successional stage, corresponding to the forest ecosystem. Similar trends were reported by Labouyrie et al. (2023) who further demonstrated that chemoheterotrophs are associated with high soil pH and low C:N ratio values. The low soil pH and a high C:N ratio at late stages would explain the observed decrease in chemoheterotrophic bacteria (Charles et al., 2025). Nitrogen-fixing bacteria increased with glacier retreat up to the third successional stage. However, in the latest stage, characterized by a forest ecosystem, their abundance declined. Similar patterns were observed by Labouyrie et al. (2023)who further demonstrated that nitrogen-fixing bacteria are typically more abundant in environments with a low carbon-to-nitrogen (C:N) ratio. In contrast, our study site exhibits a high C:N ratio in the latest successional stage, which may be caused by the decline in nitrogen-fixer abundance (Charles et al., 2025). In addition, high nitrogen input has been identified as a factor that reduces the presence of nitrogen-fixing bacteria. Similarly, our study site shows the highest nitrogen availability in the latest successional stage, which may further contribute to the decline in nitrogen-fixer abundance observed in the forest ecosystem (Berthrong et al., 2014; Charles et al., 2025; Sepp et al., 2023).

Cellulolytic bacteria followed a similar trend to that of organic carbon, with both increasing along the glacier retreat gradient. This trend likely reflects the progressive accumulation of plant-derived organic matter during the succession of ecosystems (Charles et al., 2025; Schmidt et al., 2008). As vegetation cover increases in later successional stages, more litter and root biomass are introduced into the soil, providing substrates such as cellulose—a major component of plant cell walls—for microbial degradation (Bao et al., 2019). Cellulolytic bacteria play a key role in breaking down these polysaccharides, thereby contributing to carbon cycling and soil development (Schmidt et al., 2008). Their increase with plant abundance has also been observed in other primary successions. In contrast, bacteria involved in the degradation of aromatic compounds showed a decreasing trend. This pattern could be due to a reduction in microbial communities adapted to degrade recalcitrant, low-bioavailability compounds that may dominate in early-stage soils derived from glacial deposits. Early-stage soils, derived from freshly exposed glacial deposits, often contain complex organic compounds (Müller-Tautges et al., 2016).

Taken together, this divergence in microbial functional groups suggests that glacier retreat not only alters microbial abundance but also shifts the dominant metabolic processes in soil. Further steps need to be taken to explore the interactions between different functional groups. Such as looking at co-occurrence networks to understand the assembly processes of microbial communities and functions. In addition, to gain a more detailed understanding of the processes at play, it will be important to improve functional an-notations and/or integrate complementary approaches, such as environmental RNA (metatranscriptomics), which can directly capture active microbial functions (Yates et al., 2021).

5. Conclusion

In summary, our findings reveal that glacier retreat at large scale and plant microhabitats at local scale play an important interactive role in shaping soil microorganism communities. We also reported that the response to these ecological factors is different between taxa and functional groups. Bacterial richness peaked at intermediate stages and drastically decreased in the last stage, following the same pattern as plant richness, whereas fungi rich-ness increased following glacier retreat and peaked at the last stage, following a similar pattern as woody species abundance. We also highlighted that differences in species composition among plant microhabitats were more marked in fungal communities, whereas the bacterial community of rhizosphere and roots was composed of more similar taxa. Although soil microorganisms play a foundational role in ecological processes and ecosystem functions, they are often overlooked in conservation measures. It is therefore important to understand their fate in fast changing environments, especially before the extinction of glaciers will lead to their disappearance from Earth.

CRediT authorship contribution statement

Nora Khelidj: Writing – original draft, Visualization, Methodology, Investigation, Formal analysis, Data curation, Conceptualization. **Ricardo Arraiano Castilho:** Writing – review & editing, Supervision, Methodology, Data curation, Conceptualization. **Bao Ngan Tù:** Writing – review & editing, Methodology, Investigation. **Cecile Charles:** Writing – review & editing, Writing – original draft, Methodology, Formal analysis, Data curation, Conceptualization. **Natasha de Vere:** Writing – review & editing, Writing – original draft, Supervision, Methodology, Conceptualization. **Stephanie Grand:** Writing – review & editing, Writing – original draft, Methodology, Conceptualization. **Antoine Guisan:** Writing – review & editing, Writing – original draft, Supervision, Methodology. **Ian R. Sanders:** Writing – review & editing, Writing – original draft, Supervision, Methodology, Investigation, Conceptualization. **Gianalberto Losapio:** Writing – review & editing, Validation, Supervision, Resources, Project administration, Methodology, Funding acquisition, Data curation, Conceptualization.

Declaration of Generative AI and AI-assisted technologies in the writing process

During the preparation of this work, the authors used OpenAI's ChatGPT in order to assist in reviewing and refining the language and clarity of the manuscript. The AI model provided support in grammar checking, rephrasing complex sentences, and enhancing overall readability, without contributing to the scientific content or interpretation of results. After using OpenAI's ChatGPT, the authors reviewed and edited the content as needed and take full responsibility for the content of the published article.

Declaration of competing interest

The authors declare no competing interests.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.apsoil.2025.106651.

Data availability

Data will be made publicly and freely available on Zenodo upon manuscript acceptance.

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