Dynamics and drivers of mycorrhizal fungi after glacier retreat

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TITLE

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AUTHORS

Alexis Carteron[1,2], Isabel Cantera[1], Alessia Guerrieri[1,3], Silvio Marta[1,4], Aurélie Bonin[1,3], Roberto Ambrosini[1], Fabien Anthelme[5], Roberto Sergio Azzoni[6], Peter Almond[7], Pablo Alviz Gazitúa[8], Sophie Cauvy-Fraunié[9], Jorge Luis Ceballos Lievano[10], Pritam Chand[11], Milap Chand Sharma[12], John J. Clague[13], Justiniano Alejo Cochachín Rapre[14†], Chiara Compostella[6], Rolando Cruz Encarnación[14], Olivier Dangles[15], Andre Eger[16], Sergey Erokhin[17], Andrea Franzetti[18], Ludovic Gielly[19], Fabrizio Gili[1,20], Mauro Gobbi[21], Sigmund Hågvar[22,23], Norine Khedim[24], Rosa Isela Meneses[25,26], Gwendolyn Peyre[27], Francesca Pittino[18,28], Antoine Rabatel[29], Nurai Urseitova[17], Yan Yang[30], Vitalii Zaginaev[31], Andrea Zerboni[6], Anaïs Zimmer[32], Pierre Taberlet[19,23], Guglielmina Adele Diolaiuti[1], Jerome Poulenard[24], Wilfried Thuiller[19], Marco Caccianiga[33], Gentile Francesco Ficetola[1,19]

1. Dipartimento di Scienze e Politiche Ambientali, Università degli Studi di Milano, via Celoria 10, 20133 Milano, Italy
2. Université de Toulouse, Ecole d'Ingénieurs de PURPAN, UMR INRAE-INPT DYNAFOR, Toulouse, France
3. Argaly, Bâtiment CleanSpace, 354 Voie Magellan, 73800 Sainte-Hélène-du-Lac, France
4. Institute of Geosciences and Earth Resources, CNR, Via Moruzzi 1, 56124, Pisa, Italy
5. AMAP, Univ Montpellier, IRD, CIRAD, CNRS, INRAE, Montpellier, France
6. Dipartimento di Scienze della Terra "Ardito Desio", Università degli Studi di Milano, Via L. Mangiagalli 34, 20133 Milano, Italy
7. Department of Soil and Physical Sciences, Lincoln University, Lincoln 7647, New Zealand
8. Departamento de Ciencias Biológicas y Biodiversidad, Universidad de Los Lagos, Osorno, Chile
9. INRAE, UR RIVERLY, Centre de Lyon-Villeurbanne, Villeurbanne, France
10. Instituto de Hidrología, Meteorología y Estudios Ambientales IDEAM, Bogotá, Colombia
11. Department of Geography, School of Environment and Earth Sciences, Central University of Punjab, VPO- Ghudda, Bathinda -151401, Punjab, India

12. Centre for the Study of Regional Development - School of Social Sciences, Jawaharlal Nehru University, New Mehrauli Road, 110067 New Delhi, India
13. Department of Earth Sciences, Simon Fraser University, 8888 University Drive, Burnaby, V5A 1S6, Canada
14. Área de Evaluación de Glaciares y Lagunas, Autoridad Nacional del Agua, Huaraz, Peru
15. CEFE, Univ Montpellier, CNRS, EPHE, IRD, Univ Paul Valéry Montpellier 3, Montpellier, France
16. Mannaki Whenua - Landcare Research, Soils and Landscapes, 54 Gerald St, Lincoln 7608, New Zealand
17. Institute of Water Problems and Hydro-Energy, Kyrgyz National Academy of Sciences, 720033, Frunze, 533, Bishkek, Kyrgyzstan
18. Department of Earth and Environmental Sciences (DISAT) - University of Milano-Bicocca, Milano, Italy
19. Université Grenoble Alpes, Université Savoie Mont Blanc, CNRS, LECA, F-38000 Grenoble, France
20. Department of Life Sciences and Systems Biology, University of Turin, Via Accademia Albertina 13, 10123 Turin, Italy
21. Research and Museum Collections Office, Climate and Ecology Unit, MUSE-Science Museum, Corso del Lavoro e della Scienza, 3, 38122 Trento, Italy
22. Faculty of Environmental Sciences and Natural Resource Management (INA), Norwegian University of Life Sciences, Universitetstunet 3, 1433 Ås, Norway
23. UiT - The Arctic University of Norway, Tromsø Museum, Tromsø, Norway
24. Université Savoie Mont Blanc, Université Grenoble Alpes, EDYTEM, F-73000 Chambéry, France
25. Herbario Nacional de Bolivia: La Paz, La Paz, Bolivia
26. Universidad Católica del Norte, Antofagasta, Chile
27. Department of Civil and Environmental Engineering, University of the Andes, Bogotá, Colombia
28. Swiss Federal Institute for Forest, Snow and Landscape Research. Zürcherstrasse 111, 8903 Birmensdorf
29. Université Grenoble Alpes, CNRS, IRD, INRAE, Grenoble-INP, Institut des Géosciences de l'Environnement (IGE, UMR 5001), F-38000 Grenoble, France
30. Institute of Mountain Hazards and Environment, Chinese Academy of Sciences, Chengdu, 610041, China
31. Mountain Societies Research Institute, University of Central Asia, Bishkek, Kyrgyzstan, 720001, Toktogula 125/1
32. Department of Geography and the Environment, University of Texas at Austin, 78712 Austin, TX, USA
33. Dipartimento di Bioscienze, Universitá degli Studi di Milano, via Celoria 26, 20133 Milano, Italy

† This author deceased

Corresponding author: Alexis Carteron alexis.carteron@unimi.it

Word counts

SUMMARY

- The development of terrestrial ecosystems depends greatly on plant mutualists such as mycorrhizal fungi. The global retreat of glaciers exposes nutrient-poor substrates in extreme environments and provides a unique opportunity to study early successions of mycorrhizal fungi by assessing their dynamics and drivers.
- We combined environmental DNA metabarcoding and measurements of local conditions to assess the succession of mycorrhizal communities during soil development in 46 glacier forelands around the globe, testing whether dynamics and drivers differ between mycorrhizal types.
- Mycorrhizal fungi colonized deglaciated areas very quickly (< 10 years), with arbuscular mycorrhizal fungi tending to become more diverse through time compared to ectomycorrhizal fungi. Both alpha- and beta-diversity of arbuscular mycorrhizal fungi were significantly related to time since glacier retreat and plant communities, while microclimate and primary productivity were more important for ectomycorrhizal fungi. The richness and composition of mycorrhizal communities were also significantly explained by soil chemistry, highlighting the importance of microhabitat for community dynamics.
- The acceleration of ice melt and the modifications of microclimate forecasted by climate change scenarios are expected to impact the diversity of mycorrhizal partners. These changes could alter the interactions underlying biotic colonization and belowground-aboveground linkages, with multifaceted impacts on soil development and associated ecological processes.

Key words: ecological succession, glacier forelands, soil, metabarcoding, ectomycorrhizal fungi, arbuscular mycorrhizal fungi

INTRODUCTION

Glaciers have been retreating around the world for the past century, and more than half of the world's glaciers are expected to be lost in this century (Hock *et al.*, 2019; Rounce *et al.*, 2023; Bosson *et al.*, 2023). While glacier retreat poses significant challenges, it is essential to investigate the consequences associated with these changes. Understanding the dynamics of the resulting large ice-free areas is vital for addressing the broader environmental impacts of glacier retreats as they play a crucial role in mountain ecosystems as climate refugia, hosting unique biodiversity and providing essential ecosystem services (Körner, 2004; Palomo, 2017; Cauvy-Fraunié & Dangles, 2019; Brighenti *et al.*, 2021; Zimmer *et al.*, 2022). With the projected increase in deglaciated areas in the future, there is a need to better understand the consequent biotic dynamics and predict the ecosystem development of deglaciated areas (Prach & Walker, 2020; Ficetola *et al.*, 2021; Rumpf *et al.*, 2022; Bosson *et al.*, 2023). By understanding changes in diversity and ecological processes, analyses of successional gradients could help define effective strategies for management and adaptation of these newly exposed areas. However, in order to draw general ecological patterns and measure biodiversity changes, it is necessary to apply standardized sampling design on multiple glacier forelands around the globe (Chang & Turner, 2019), but such analyses are lacking (Cauvy-Fraunié & Dangles, 2019).

Glacier retreat exposes new land for colonization of biota, which then diversifies, leading to further soil development (Wietrzyk-Pełka *et al.*, 2020; Khedim *et al.*, 2021; Pothula & Adams, 2022). Colonisation by plants after glacier retreat is a crucial element in the formation of novel ecosystems (Clements, 1916; Tansley, 1935). The soil biological crust as well as nurse plants which facilitate the establishment of other plants, are essential in this process (Zimmer *et al.*, 2018; Llambí *et al.*, 2021). Mycorrhizal associations are the most common and important mutualistic symbioses in terrestrial ecosystems (Martin *et al.*, 2018) and play a key role in the development of ecosystems (Chapin *et al.*, 1994; Jumpponen *et al.*, 2012; Benavent-González *et al.*, 2019). In nutrient-poor environments, mycorrhizal fungi can be particularly important for enhancing plant growth and survival (Smith & Read, 2008; van der Heijden *et al.*, 2015). Mycorrhizas are known to play a key role in soil development, including biogeochemical processes such as nutrient cycling and carbon sequestration (Read & Perez-Moreno, 2003; Tedersoo & Bahram, 2019; Steidinger *et al.*, 2019). Local-scale analyses from mid-latitude

glaciers have shown that non-mycorrhizal and facultative mycotrophic plants tend to predominate immediately after glacier retreat, followed by an increase in mycorrhizal types and in fungal species richness in older communities (Cázares *et al.*, 2005; Oehl *et al.*, 2011; Blaalid *et al.*, 2012). However, these trends are not always monotonous and may even appear idiosyncratic (Helm *et al.*, 1999; Trowbridge & Jumpponen, 2004). This is illustrated by the fact that some mycorrhizal fungal taxa have been found to be indicators of both early (Rime *et al.*, 2015) and late successional stages (Guerrieri *et al.*, 2022b). Understanding the dynamics and drivers of plant-fungal mycorrhizal associations is therefore pivotal for inferring key ecological processes during early ecosystem development (Tedersoo & Bahram, 2019) but, so far, no studies have analyzed variability in mycorrhizas in multiple independent ecological successions following glacier retreat.

Many plants rely on mycorrhizal fungi, which are limited in their dispersal potential (Brundrett, 2002; van der Heijden *et al.*, 2015; Tedersoo *et al.*, 2020). Mycorrhizal fungi are highly dependent on the presence of host plants to complete their lifecycle (van der Heijden *et al.*, 2015). Therefore, in the case of newly exposed terrains, the mycorrhizal fungal community could depend on the presence of host plants (Zobel & Öpik, 2014) and, similarly, the scarcity of mycorrhizal fungal propagules may limit plant colonization (Dickie *et al.*, 2013; Chaudhary *et al.*, 2018; Delavaux *et al.*, 2021). Recently, the availability of mycorrhizal fungi has been shown to play an important role in shaping island flora worldwide, the so-called "mycorrhizal filter" (Delavaux *et al.*, 2019). However, arbuscular mycorrhizal (AM) and ectomycorrhizal (EcM) fungi, which are the two major mycorrhizal types (Brundrett & Tedersoo, 2018; Steidinger *et al.*, 2019; Soudzilovskaia *et al.*, 2020), differ in their nutrient-acquisition strategies, host specificity and dispersal traits such as spore size (Kivlin, 2020). EcM fungi are expected to disperse better with their tiny spores (generally < 9,000 μm^3, on average > 2,000 times smaller than AM fungal taxa), potentially enabling them to establish quickly in new habitats. In contrast, the presence and development of AM fungi in plant roots could be favoured in early stages of ecosystem development because of their lower host specificity compared to EcM fungi (Veresoglou & Rillig, 2014; van der Heijden *et al.*, 2015). Additionally, AM fungi associate with more than 70% of all plant species (van der Heijden *et al.*, 2015; Soudzilovskaia *et al.*, 2020) and are expected to impose a lower energy cost to plant hosts in stressful habitats than EcM fungi

(Tedersoo & Bahram, 2019). Dispersal limitation and habitat tolerance are critical drivers of ecological successions (Makoto & Wilson, 2019), and even though EcM fungi should better disperse than AM ones, AM host plants tend to be favoured and more abundant in stressful and early stages of development (Cázares *et al.*, 2005; Lambers *et al.*, 2008; Tedersoo & Bahram, 2019). Examining patterns of mycorrhizal fungi following glacier retreat at the worldwide scale would allow a simultaneous comparison of the early dynamics between mycorrhizal fungal types.

Spatial and temporal patterns of community dynamics following the glacier retreat include changes in the number of taxa at a local site (alpha-diversity) and modifications of community composition (beta-diversity) over time. However, these patterns are contingent on the identity of the organisms or the target communities (Cauvy-Fraunié & Dangles, 2019; Hanusch *et al.*, 2022). For instance, the richness of spiders and vascular plants can increase fourfold over a century, while the increase in richness is much smaller for dipterans (Pothula & Adams, 2022). Also, the diversity of mycorrhizal fungi is expected to change over time, although patterns emerging from both EcM and AM taxa are complex. For example, while Jumpponen *et al.* (2002) observed that the number of EcM fungal sporocarps increases with time since glacier retreat, data based on high-throughput sequencing of root-associated fungi portray a context-dependent picture, with patterns depending on the proglacial area sampled (Blaalid *et al.*, 2012; Davey *et al.*, 2015). Similarly, the number of AM taxa has been observed to increase towards older sites only in part of the analyzed glacier forelands (Trowbridge & Jumpponen, 2004; Oehl *et al.*, 2011), suggesting a strong influence of local conditions. A comprehensive integration of alpha- and beta-diversity analyses is therefore needed to understand soil biodiversity responses to glacier retreat, and such analysis must also consider local conditions like microhabitat that can significantly influence soil communities (Oehl *et al.*, 2011; Blaalid *et al.*, 2012; Jumpponen *et al.*, 2012; Rime *et al.*, 2015; Wietrzyk-Pełka *et al.*, 2020). To this aim, fine-scale data integrating information on both biotic and abiotic components of proglacial environments is necessary, but challenging to obtain (Ficetola *et al.*, 2021; Marta *et al.*, 2023).

The aim of our study was to assess the dynamics and the drivers of mycorrhizal fungi in order to assess how they establish after the retreat of glaciers, and how biotic and abiotic factors locally

drive their alpha- and beta-diversity. We analyzed a large number of post-glacial chronosequences from different regions of the world in order to find common patterns characterizing ecosystem development (Jumpponen *et al.*, 2012; Ficetola *et al.*, 2021; Marta *et al.*, 2023) as well as to facilitate predictions of global shifts in mycorrhizal types and associated ecological processes (Tedersoo & Bahram, 2019).To this aim, we implemented a global-scale standardized dataset based on environmental DNA (eDNA) metabarcoding, by conducting a comprehensive inventory of 1251 plots in 46 independent chronosequences on forelands of mountain and high-latitude glaciers (Fig. 1), spanning from 1 to ~500 years since the time of glacier retreat. Even though EcM fungal species are able to disperse better, we hypothesized that AM fungi would dominate immediately after glacier retreat because AM host plants tend to predominate early in succession (Lambers *et al.*, 2008; Tedersoo & Bahram, 2019). We further hypothesized that time since glacier retreat and vegetation features would be major drivers of mycorrhizal fungal diversity. Local abiotic characteristics, such as soil physico-chemical properties, may further shape the microhabitats these fungi experience, thus we expect that abiotic factors are additional drivers of mycorrhizal diversity, jointly with spatial factors (Bahram *et al.*, 2015; Davison *et al.*, 2015).

METHODS

Sample collection

From 2014 to 2020, we collected soil samples from 1251 plots within 265 sites located in the forelands of 46 mountain and high-latitude glaciers (Fig. 1) from five continents, including regions with different climatic conditions and rates of glacier retreat (Zemp *et al.*, 2019). Information on times of deglaciation over the past centuries in these forelands is available from Marta *et al.* (2021).

In each glacier foreland, we selected three to 17 suitable sites (mean = 5.8 sites per foreland, SD = 2.5) that became ice-free from 1 to 483 years before sampling. For each site, the age since glacier retreat was used as a proxy of the time available for ecosystem development; i.e. we used a chronosequence approach for the study of ecological successions (space-for-time substitution; Walker *et al.*, 2010). At each site, we established 2-10 plots (mean = 4.7 plots, SD = 0.8) of 1 m^2, evenly spaced at a distance of 20 m, where possible. Within each plot, we collected five soil

subsamples at a distance of 1 m (Fig. S1). The soil was sampled to a depth of 0-20 cm, and litter was excluded, as well as other plant materials. The subsamples from the same plot were pooled, resulting in a composite soil sample of ~200 g per plot. After homogenization of the composite sample, 15 g of soil were taken and placed within 6 hours in a sterile box to be dried with 40 g of silica gel. This method allowed reliable preservation of eDNA (Guerrieri *et al.*, 2021). An additional soil sample at each plot was also taken for soil chemistry analyses.

Biotic and abiotic conditions

Habitat characteristics were determined at the plot level by estimating primary productivity, plant diversity, soil temperature, topographic wetness index and, for a subset of 32 glacier forelands (out of a total of 46), soil chemistry. Total nitrogen (N) concentration was measured for each plot by elemental analysis (Flash2000 OEA analyzer, ThermoFisher). Soil pH was measured using a pH-meter from a suspension composed by 4 g of soil and 10 ml of bi-distilled water. Depending on pH values, two different methods were used to measure assimilable phosphorus (P) through inductively coupled plasma mass spectrometry (iCAP RQ ICP-MS, ThermoFisher): the Bray and Kurtz method (Bray & Kurtz, 1945) for samples with $pH < 6.5$ and the Olsen method (Olsen, 1954) for samples with $pH \geq 6.5$. As an indicator of primary productivity, we used the normalized difference vegetation index (NDVI), which is known to be positively related to annual aboveground net primary production (Paruelo *et al.*, 1997). Yearly maximum productivity was retrieved from the optical satellite data acquired by Sentinel-2 (ESA, COPERNICUS, S2) at 10 m resolution and averaged over the 2016-2019 period using Google Earth Engine and the *rgee* R package (Aybar *et al.*, 2022). Because proglacial areas tend to have complex topography and lengthy snow cover, yearly maxima were preferred over standard masking algorithms in order to remove the noise caused by cloudiness (Lillesand *et al.*, 2015). Plant diversity was estimated based on the plant MOTU data (see next section for details). Fine-scale subsurface soil temperature (5 cm below surface) was estimated using a global microclimatic model approach, calibrated using data-loggers placed in 175 stations from polar, equatorial and alpine glacier forelands, as described in Marta *et al.* (2023). As a proxy of potential soil moisture, we used the topographic wetness index (TWI) calculated with the *dynatop* R package (Smith & Metcalfe, 2022), based on the ASTER Global Digital Elevation Model (version 3, Abrams *et al.*, 2020) with 1 arc-second resolution (~30 m at the equator). The

TWI is based on the slope and the upstream contributing area. It has been found to correlate also with factors other than soil moisture such as plant species composition or soil pH, and its ability to predict soil moisture varies as a function of the focus environment and the algorithm used (Kopecký *et al.*, 2021), hence analysis using the TWI should be interpreted with care. To account for the potential impact of regional tree mycorrhizal type dominance (regional mycorrhizal dominance, hereafter) on alpha-diversity dynamics, we obtained the percentage of EcM and AM tree types (calculated as the percentage of tree basal area) for each foreland, based on model projections at 1° × 1° resolution (Steidinger *et al.*, 2019).

DNA sequences acquisition

The molecular and bioinformatic workflows are detailed in Guerrieri *et al.* (2022b) for fungi and in Cantera et al. (In press) for plants. Briefly, sequences were obtained after the following steps: (i) mixing soil samples collected at each plot with phosphate buffer (Taberlet *et al.*, 2012). (ii) Extraction of eDNA using the NucleoSpin® Soil Mini Kit. (iii) PCR amplification in four replicates with the Fung02 primer pair, targeting the ITS1 region for fungi (forward: 5'-GGAAGTAAAAGTCGTAACAAGG-3', reverse: 5'-CAAGAGATCCGTTGYTGAAAGTK-3') (Epp *et al.*, 2012) and the Sper01 primer targeting the chloroplast trnL-P6 loop for vascular plants (forward: 5'- GGGCAATCCTGAGCCAA-3', reverse: 5'-CCATTGAGTCTCTGCACCTATC-3') (Taberlet *et al.*, 2007). PCR reactions included bioinformatic blanks, extraction and amplification of negative controls, and positive controls (see below). (iv) Library preparation and sequencing of purified samples using the MiSeq (fungi; 2 × 250 bp) and HiSeq 2500 (plants; 2 × 150 bp) Illumina platforms. Positive controls consisted of 16 non-tropical plant species belonging to 15 families (Taxaceae, Lamiaceae, Salicaceae, Polygonaceae, Betulaceae, Oleaceae, Pinaceae, Caprifoliaceae, Pinaceae, Aceraceae, Poaceae, Rosaceae, Brassicaceae, Geraniaceae, Ericaceae) and two fungal strains (*Saccharomyces cerevisiae, Cryptococcus neoformans*) at known concentrations. The positive controls were used to confirm that PCRs correctly amplified the present taxa.

The bioinformatic workflow was conducted using OBITools software (Boyer *et al.*, 2016). As in Guerrieri *et al.* (2022), paired-end reads were first assembled with the *illuminapairedended* program and only sequences with an alignment score > 40 were kept and then assigned to the

corresponding PCR replicate before dereplication. Singletons were discarded as well as artefacts that had lower and/or higher length than expected (i.e. sequences <68 bp for fungi and <10 or >220 bp for plants). We also discarded sequences containing ambiguous bases. The remaining high-quality sequences were clustered into molecular operational taxonomic units (MOTUs) considering optimal thresholds of intra- and inter-specific variations at 95% for fungi and at 97% for plants (Bonin *et al.*, 2023). These thresholds identified the distribution of sequence similarities among different individuals belonging to the same species, and among different species belonging to the same genus. This allows to minimize the risk that different sequences of the same species are assigned to different MOTUs (over-splitting) while balancing the risk that different species are grouped in the same MOTU (over-merging). On the basis of the analysis of various clustering thresholds using sequences extracted from the EMBL (version 140) database (Bonin *et al.*, 2023), 95% emerged as the threshold balancing over-splitting and over-merging for Fung02, and 97% for Sper01 (Bonin *et al.*, 2023). For each marker, we built a reference database by running in silico PCRs on the public sequence database EMBL (version 140) using the *ecopcr* program (Ficetola *et al.*, 2010) and allowing a maximum of three mismatches per primer. The obtained databases were curated to keep only sequences assigned at the species, genus and family levels. For each MOTU, we made a taxonomic assignment using the *ecotag* program of the OBITools (Boyer *et al.*, 2016). In order to limit the presence of contaminants (Ficetola *et al.*, 2015; Boyer *et al.*, 2016; Zinger *et al.*, 2019), MOTUs were not included in the analyses if they had: i) a best identity score below 80% and total read count in the dataset below five (based on bioinformatic blanks) for fungi; or ii) a best identity score below 90% and total read count below eight for plants. In addition, MOTUs were not included if they were detected in only one PCR replicate of the same sample or in more than one extraction or amplification of negative controls (potential false positives and contaminants; Ficetola *et al.*, 2015; Zinger *et al.*, 2019). Finally, we summed the four PCR replicates to obtain the final MOTU table following the relaxed stringency method (Mächler *et al.*, 2021).

Mycorrhizal type assignation

We assigned mycorrhizal types using the FUNGuild database (Nguyen *et al.*, 2016). From the identified genera and families, the following ones were considered as EcM (ectomycorrhizal) fungi: *Austropaxillus, Cantharellus, Cenococcum, Clavulina*, Cortinariaceae, Gomphidiaceae,

Helvella, *Inocybe*, *Lactarius*, *Leucophleps*, *Rhizopogon*, *Russula*, Sebacinaceae, *Suillus* and Tuberaceae (Nguyen *et al.*, 2016). For AM (arbuscular mycorrhizal) fungi, the following families and orders were considered: Acaulosporaceae, Archaeosporaceae, Archaeosporales, Diversisporaceae, Diversisporales, Glomeraceae, Glomerales and Paraglomeraceae (Nguyen *et al.*, 2016). We note that dark septate endophytes are an additional group of potential symbiotic fungi, but their identification based on a functional database is too limited to include them in the present study.

Data analyses

At the plot level, we assessed alpha-diversity by calculating the number of MOTUs, representing taxonomic richness, and the Shannon diversity index, which corresponds to diversity estimated using Hill's number with q = 1. Diversity estimates using q = 1 are appropriate for eDNA metabarcoding data, as they are robust to differences in bioinformatic treatments (Calderón-Sanou *et al.*, 2020; Mächler *et al.*, 2021). Analyses were performed on non-rarefied data (McMurdie & Holmes, 2014), but we note that the diversity (q=1) values calculated on non-rarefied data are highly correlated with estimates obtained using rarefaction (Table S2). We used linear mixed models to test the hypothesis that AM fungi colonize first. First, we quantified the difference in diversity (estimated with q = 1) between AM and EcM fungi for each plot. Positive values indicated greater diversity of AM communities, whereas negative values indicated greater diversity of EcM communities. The mixed model included the difference in diversity as the independent variable, time was the independent variable, glacier and site nested within glacier were random factors and with a Gaussian error distribution. We also used linear mixed models to test the probability that AM and EcM fungi are present in the overall fungal community after glacier retreat. In this case, presence/absence of at least one MOTU of either AM or EcM fungi in each community was the dependent variable, time was the independent variable, glacier and site nested within each glacier were the random factors, modeled assuming a Bernoulli distribution. Models were implemented in the *brms* package (Bürkner, 2017). The models ran on four parallel chains, each with a length of 10,000 iterations. A burn-in of 1,000 iterations, thinning rate of 10, and uninformative priors provided by the *brms* package were used. Convergence was assessed by visually inspecting the Markov chains, considering it satisfactory when $\hat{R} < 1.01$. The absence of spatial autocorrelation was evaluated by examining spline

correlograms using the *ncf* package (Bjornstad & Cai, 2022). In principle, AM and EcM might show non-identical levels of variability or amplification rates with the tested primer, thus this analysis should be viewed as a comparison of their relative trends.

To assess the potential impacts of time, glacier identity, habitat (i.e. productivity, plant diversity, N, P, pH, temperature, TWI) and regional mycorrhizal dominance on patterns of AM and EcM fungal alpha-diversity, we used a random forest algorithm fitting nonlinear multiple regressions with the *randomForest* (Cutler & Wiener, 2022) and *rfPermute* (Archer, 2022) packages. We set the number of bootstrap replicates (*ntree*) to 600, with convergence verified visually by assessing the cumulative error rate. The optimal *mtry* (number of variables randomly sampled as candidates at each split) was determined using *tuneRF* function and set at two for AM fungi and three for EcM fungi. Variable importance was based on the increase in the mean squared error (%incMSE), and their significance was estimated after 5000 repetitions. Plant alpha-diversity (q = 1) was calculated based on the plant MOTU data. For this analysis, we used data from 793 plots in 32 proglacial areas.

We assessed the potential drivers of AM and EcM fungal beta-diversity (i.e. changes in community composition between plots belonging to the same foreland, N = 2031) using the generalized dissimilarity modelling (GDM) approach with the *gdm* package (Fitzpatrick *et al.*, 2022). This approach is well suited to identify the drivers of community dissimilarity across plots and to analyse relationships potentially affected by non-linearity. Beta-diversity between the communities inhabiting different plots was related to differences in time and habitat variables, as well as to geographic distances. Furthermore, as a measure of plant community changes, we performed a principal coordinate analysis (PCoA) from the plant dissimilarity matrix using the Jaccard index and used the scores of the first axis for each plot as an explanatory variable. We focused on dissimilarities between pairs of plots located in the same foreland (i.e. pairs of plots located in different forelands were excluded from GDM), as our aim was to assess the factors determining community variation within each landscape. Regional mycorrhizal dominance was not included in this analysis, as all the plots within the same foreland share the same dominance values. Plots with zero MOTU of fungi or vascular plants were excluded. Variable significance was estimated after 1000 permutations.

The following variables were log-transformed prior to modelling to reduce skewness: time since glacier retreat, vascular plant alpha-diversity N, P, TWI and NDVI. Additional R packages used for data wrangling and visualization included: *dplyr* (Wickham *et al.*, 2017), *ggplot2* (Wickham, 2016), *ggspatial* (Dunnington, 2018), *ggrepel* (Slowikowski *et al.*, 2021), *phyloseq* (McMurdie & Holmes, 2013), *rnaturalearth (South, 2017)*, *tidyr* (Wickham & Henry, 2019) and *vegan* (Oksanen *et al.*, 2017).

RESULTS

Colonization dynamics

Soil eDNA metabarcoding of the ITS1 region yielded a total of 43,104,065 high-quality filtered fungal sequences that were grouped into 3331 MOTUs (Table S1), 563 of which were classified as putative EcM or AM fungi (303 EcM and 260 AM fungal MOTUs). Overall, mycorrhizal fungi were detected in 58% of the plots. The diversity of the overall fungal community rapidly increases from a few MOTUs immediately after glacier retreat, up to ~200 MOTUs per plot after 100 years (Fig. S2). Just one year after glacier retreat, non-mycorrhizal fungi were already present in more than half of the plots (Fig. S2). Mycorrhizal fungi were detected < 10 years after glacier retreat, with a quick increase in the following decades (Fig. S2). In these recently deglaciated plots, the first EcM fungi were detected after four years and the first AM fungi after one year. Glomeraceae is the most common AM fungal family throughout the stages of ecosystem development (Fig. S3). The five most abundant fungal families that include EcM fungi were all present a few years after glacier retreat (Cortinariaceae, Inocybaceae, Russulaceae, Sebacinaceae, Suillaceae; Fig. S3), while the EcM fungal families Clavulinaceae, Gloniaceae and Rhizopogonaceae were only detected at later stages of development (> 36 years, Fig. S3). In the early stages, AM and EcM fungi show similar richness (95% credible interval of their difference in richness overlaps zero from 1 to ~50 years; Fig. 2) but, with time, the AM fungal diversity tended to become higher compared to EcM fungi and the difference increased afterwards (significant relationship; slope = 0.09, standard error = 0.03). The probability for AM and EcM fungi to be present in the overall fungal community greatly increased with time since glacier retreat (especially after 10 to 20 years; Fig. S4).

Environmental drivers of alpha-diversity

Random forest models suggested that the alpha-diversity of mycorrhizal fungi is explained by local conditions, in addition to time and glacier identity (variation explained by the model being 49% and 51% for AM and EcM fungi, respectively; Fig. 3). All habitat variables showed significant effects, except nitrogen concentration for EcM fungi (Table S3). For both mycorrhizal types, chemical features of soil (N, P, pH) tend to have lower importance compared to the other variables. Time since glacier retreat, productivity, soil temperature and regional mycorrhizal dominance are the variables with the strongest influence on the diversity of both mycorrhizal types. In addition, the local diversity of vascular plants is a particularly strong predictor of AM fungal diversity.

Environmental drivers of beta-diversity

The beta-diversity of mycorrhizal fungi is related to the variation of multiple predictors (Fig. 4, Table S4). The considered factors explain a substantial amount of beta-diversity of both AM and EcM fungi (40-44%). Differences in time since glacier retreat are, by far, the main factor influencing AM fungal community changes. Changes in pH, vascular plant community, productivity and geographic proximity are also important for the beta-diversity of AM fungal communities. In contrast, EcM fungal community variation is mostly explained by changes in TWI, followed by geographic proximity and productivity.

DISCUSSION

Early dynamic of mycorrhizal fungi

The dynamics of mycorrhizal fungi during early succession have attracted great interest due to their importance in ecosystem development (Allen *et al.*, 1992; Nara, 2006; Jumpponen *et al.*, 2012), along with the role played by nurse plants, the microtopography and the soil biological crust (Zimmer *et al.*, 2018; Llambí *et al.*, 2021; Bayle *et al.*, 2023). Glacier forelands are nutrient-poor (Khedim *et al.*, 2021; Pothula & Adams, 2022), and this poses unique challenges for mycorrhizal establishment. The colonization of mycorrhizal fungi in deglaciated terrains shows a delay compared to that of the overall fungal community. Both AM and EcM fungi, however, manage to colonize quickly following glacier retreat, with the most abundant mycorrhizal fungal families already present at the earliest stages of development (< 17 years).

These results highlight the remarkable speed at which mycorrhizal fungi can colonize these environments, even considering the limited amount of fungal propagules typically found in young glacier forelands (Oehl *et al.*, 2011; Jumpponen *et al.*, 2012). As for plant pollen, fungal spores might be transported by wind to glacier surfaces and released during glacier retreat (Surova *et al.*, 1992). The quick establishment of EcM fungi might be facilitated by their tiny spores, and this might also be true for some AM fungi showing specific traits, such as *Diversispora* and *Acaulospora* (Oehl *et al.*, 2011; Chaudhary *et al.*, 2020).

Contrary to our expectations, AM fungi did not exhibit a higher diversity during the early stages of succession (<50 years) compared to EcM fungi. Specific dispersal attributes, as well as low host specificity and low energetic cost paid by host plants (Tedersoo & Bahram, 2019), may be key features favouring establishment of mycorrhizal fungi in such resource-poor and extreme environments. The tight relationships between AM fungi and pioneer plants could be counterbalanced by their limited dispersion capacity compared to that of EcM fungi. Even though some mycorrhizal fungi are able to colonize quickly, our results stress the importance of time and habitat formation on the development of mycorrhizal fungal communities (Cázares & Trappe, 1994; Oehl *et al.*, 2011; Chaudhary *et al.*, 2018), as also found in glacier forelands for other organisms such as ground beetles and nematodes (Brambilla & Gobbi, 2014).

Plants as drivers of mycorrhizal fungal diversity?

Both AM and EcM fungi have been reported to associate with plant species that are found in barren substrates at the earliest stages of succession following glacier retreat. However, colonization of plant roots by mycorrhizal fungi in such environments is often scarce (< 10%; Cázares *et al.*, 2005; Oehl *et al.*, 2011). Some mycorrhizal plant species have the ability to establish and grow in proglacial areas even without their fungal symbionts (Fujiyoshi *et al.*, 2011; Oehl *et al.*, 2011), allowing these facultative nonmycorrhizal plants to bypass the "mycorrhizal filter" (Delavaux *et al.*, 2019). This suggests that the diversity of mycorrhizal fungi might be shaped by plant diversity, as supported by the strong relationship between mycorrhizal diversity and plant richness.

If plant hosts are capable of colonizing the barren substrates of forelands before mycorrhizal fungi, they may drive the subsequent establishment of early fungal mycorrhizal communities, rather than the other way around (Oehl *et al.*, 2011; Jumpponen *et al.*, 2012).

Indeed, the dynamics of mycorrhizal communities have been found to somewhat parallel that of local plant communities (Davey *et al.*, 2015). As expected, both alpha- and beta-diversity of mycorrhizal fungi showed a strong relationship with the diversity, composition and regional mycorrhizal dominance of plant communities (Figs. 3 and 4). The significant link between mycorrhizal fungal diversity and primary productivity further supports the role of plants in shaping the mycorrhizal fungal community, usually in primary succession (Zobel & Öpik, 2014).

Climate change induces vegetation expansion and increases plant biomass ("greening") at high elevations and could thus influence mycorrhizal fungal diversity, accelerating their colonization of these environments (Anderson *et al.*, 2020; Rumpf *et al.*, 2022). Mycorrhizal fungal diversity may be promoted by plant biomass, but also by plant richness depending on their host specificity (van der Heijden *et al.*, 2015; Kivlin *et al.*, 2022). In turn, a greater mycorrhizal fungal diversity can determine positive feedbacks on plant diversity and ecosystem functioning (van der Heijden *et al.*, 1998), as mycorrhizal fungi are known to enhance plant survival and growth (Smith & Read, 2008), particularly in nutrient-poor environments (van der Heijden *et al.*, 2008). However, climate change can also reduce vegetation in alpine ecosystems ("browning"), due to changes in precipitation patterns and reduced snow cover (Phoenix & Bjerke, 2016; Liu *et al.*, 2021; Rumpf *et al.*, 2022; Marta *et al.*, 2023). Such browning could weaken the benefits provided by mycorrhizal associations by impeding mycorrhizal diversity, resulting in lower nutrient availability for the remaining plants, although some ruderal mycorrhizal fungy could persist (Hiiesalu *et al.*, 2023). The overall responses of the ecosystems to climate changes ist thus difficult to predict, as it depends on the types of vegetation and mycorrhizas involved (Tedersoo & Bahram, 2019).

Contrasting responses between mycorrhizal types

The divergent responses of different mycorrhizal types to environmental stressors can be related to their contrasting roles in plant nutrition and protection (Mohan *et al.*, 2014; Tedersoo & Bahram, 2019; Bennett & Classen, 2020). These differences likely contribute to the varying importance of drivers shaping mycorrhizal fungal diversity following glacier retreat (Figures 3 and 4). Multiple factors affected the dynamics of mycorrhizal communities, including time, regional mycorrhizal dominance and local conditions such as productivity. In addition, the diversity of AM fungi was significantly influenced by plant diversity, while microclimate was

particularly important for EcM fungi. These findings highlight the interplay between mycorrhizal types, abiotic factors and plant-microbe interactions in shaping mycorrhizal community dynamics along environmental changes (Davey *et al.*, 2015; Rasmussen *et al.*, 2022; Kivlin *et al.*, 2022). Geographical distribution also plays a role, for instance with potential differences between forelands located in tropical *vs* temperate regions, or located in regions with climatic conditions supporting different mycorrhizal types (Steidinger *et al.*, 2019; Guerrieri *et al.*, In press).

Differences between mycorrhizal types are also clear for beta-diversity (i.e. changes in community composition). That of AM fungi is mostly explained by time, whereas a microhabitat parameter (potential soil moisture) is the key factor for EcM fungi (Abrego *et al.*, 2020). These results are congruent with AM fungi being more affected by dispersal limitations. In fact, a strong relationship between beta-diversity and time, after taking into account differences for key biotic and abiotic parameters, is often taken as evidence of a major role of dispersal limitation (Makoto & Wilson, 2019; Ficetola *et al.*, 2021), which may determine time lags between glacier retreat, habitat development and the formation of AM communities. Conversely, for EcM fungi, habitat filtering could play a more important role (Davey *et al.*, 2015; Castilho *et al.*, 2020; Delavaux *et al.*, 2021), even though both processes seem important. Consequently, AM and EcM richness and composition could respond differently to global changes. Given the close links between plant diversity and mycorrhizal diversity, these contrasting responses of AM and EcM fungi could be exacerbated if different plant species also show distinct responses to global changes (Fei *et al.*, 2022). Nevertheless, the strong impact of plant communities on AM fungi, which are obligate biotrophs, could be counterbalanced by their lower host specificity (van der Heijden *et al.*, 2015). Soil chemistry, temperature and moisture are additional drivers of alpha- and beta-diversity of mycorrhizal fungi. As climate affects the rate of rock weathering (Walker *et al.*, 2010) and, more generally, soil development, composition and biodiversity (Khedim *et al.*, 2021; Guerrieri *et al.*, In press), climatic modifications probably impact the dynamics and communities of mycorrhizal associations both directly and indirectly. AM fungi could be influenced indirectly by climate change through plant diversity changes, whereas the impact might be more direct for the EcM fungi because of their sensitivity to temperature and moisture (Tedersoo & Bahram, 2019).

Limitations of observational and eDNA approaches

The use of a chronosequence approach (space-for-time substitution) to draw inferences on the evolution of ecosystems requires caution (Johnson & Miyanishi, 2008). Unmeasured factors such as disturbances (e.g. landslides), which often occur in glacial and periglacial environments, can also influence ecosystem development and might have affected our observations (Fickert & Grüninger, 2018; Wietrzyk-Pełka *et al.*, 2020). In our sampling design, these impacts were minimized by avoiding locations known to have been affected by past disturbances (Marta *et al.*, 2021). Furthermore, shifting climate conditions reduce our power and confidence in replicating past patterns of succession (Prach & Walker, 2020), as well as in predicting mycorrhizal dynamics and subsequent impacts on ecological processes that go beyond the coupling between plant and fungal partners (Fei *et al.*, 2022). Nonetheless, chronosequence analysis remains the most appropriate approach for the study of ecosystem development over centuries (Walker *et al.*, 2010; Poorter *et al.*, 2021). Studies have suggested that the analyses of chronosequences provide results that are consistent with replicated community analyses of permanent plots (Foster & Tilman, 2000; Sytsma *et al.*, 2023; Cantera *et al.*, In press). Further research aiming at disentangling the effects of microbes on plants and vice-versa in proglacial environments could benefit from manipulative experiments on permanent plots to explicitly test causal relationships (Yang *et al.*, 2021).

Caution should also be taken when interpreting ecological data derived from eDNA metabarcoding (Zinger *et al.*, 2019). Although eDNA offers valuable information, it has some limitations, particularly in the estimation of microbial function and biomass. Encouragingly, previous investigations conducted in proglacial environments have demonstrated high concordance between eDNA-based analyses and traditional surveys, resulting in consistent biodiversity estimates (Cantera *et al.*, In press). In principle, our results may be influenced by the amplification of inactive or dead organisms retained in the soil. Nevertheless, studies on environments that experienced known changes of communities suggest that eDNA mostly represent the organisms living during the last few years (Foucher *et al.*, 2020; Ariza *et al.*, 2023), and the amplification of dead organisms probably has a limited effect in our study system, which spans multiple centuries of ecosystem evolution from barren substrates. Furthermore, the primers and the mycorrhizal database used are not free of biases toward specific taxa. For example, the ITS1 primers underamplify some groups of fungi (Nilsson et al., 2019). To limit this issue, we

used a modified version of ITS primers (Epp *et al.*, 2012), adapted to reduce bias on Glomeromycota (Taberlet *et al.*, 2018). Despite some limitations, general fungal ITS primers tend to offer good estimates of both EcM and AM fungal communities, and their relative responses to environmental variables (Berruti *et al.*, 2017; Lekberg *et al.*, 2018). Finally, the functional assignment of fungal sequences is an area of considerable promise within mycorrhizal research (Fei *et al.*, 2022; Tedersoo *et al.*, 2022; Baldrian *et al.*, 2022), still the interpretation of results should be taken with care, given that information on several taxa is still incomplete.

Conclusion

Local biotic and abiotic factors deeply impact the successional dynamic of mycorrhizal fungi following glacier retreat at high elevations and latitudes. Time is not always the most important factor, highlighting the key roles of additional factors that contribute to the patterns observed within and across forelands, such as vegetation and microclimate. However, as many biological and chemical features of proglacial environments change through time, a key challenge is to assess the intricate co-variation among ecosystem attributes. Our study also stresses the importance of initial site conditions, glacier location (through the effect of local factors, such as regional climate or species pool) and surrounding environments in the formation of mycorrhizal symbiosis (Fig. 3; Cázares *et al.*, 2005; Fujiyoshi *et al.*, 2011; Jumpponen *et al.*, 2012; Steidinger *et al.*, 2019; Wojcik *et al.*, 2021). A substantial part of mycorrhizal diversity patterns remained unexplained (models explained ~50% of variation), suggesting a role of stochastic processes (Wojcik *et al.*, 2021) and/or unmeasured factors such as disturbances and biogeographical factors that require further study (Cázares & Trappe, 1994; Ficetola *et al.*, 2021). The major role of plants in the dynamics of mycorrhizal communities highlights the need for research integrating data on plants and fungi to elucidate the mechanisms underlying ecosystem development. AM fungi exhibit a broad host range and associate with both trees and herbaceous plants (van der Heijden *et al.*, 2015). This broad host spectrum can facilitate their establishment in proglacial areas even in the absence of trees, for instance above the tree line, compared to EcM fungi, which associate primarily with trees. On the other hand, some EcM trees, such as Salix *spp.*, can colonize ice-free surface in less than 10 years (Fickert & Grüninger, 2018), and some herbaceous colonizers of glacier forelands are also known to associate with EcM fungi such as *Bistorta vivipara* (Davey *et al.*, 2015). The complexity of interactions between early-colonizing plants

and mycorrhizal fungi highlights the importance of fine-scale sampling and detailed analyses focusing on symbiotic interactions. A further step to improve our understanding of mycorrhizal dynamics during ecosystem development would include the integration of multitrophic interactions with herbivores, fungal feeders and other root symbionts such as nitrogen-fixing bacteria and dark septate endophytes fungi.

The current and expected changes in the rate of glacier ice melt (Rounce *et al.*, 2023; Bosson *et al.*, 2023) and in local climatic conditions (Marta *et al.*, 2023) could affect mycorrhizal partners and types differently, with the potential for causing a mismatch between aboveground and belowground linkages and possibly disrupting the biotic interactions underlying biotic colonization. Future studies integrating data from multiple taxonomic groups would be needed to predict ecosystem-level impacts of these fast-changing habitats, considering the multifaceted consequences on trophic networks and associated ecological processes.

DATA AND CODE AVAILABILITY

The custom code and the data to replicate the results are available at: https://github.com/alexiscarter/mycorrhizal_succession_iceCommunities.
Raw sequencing data from ITS and trnL amplification are deposited at https://doi.org/10.5281/zenodo.6620359 (Guerrieri *et al.*, 2022a).

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AUTHOR CONTRIBUTIONS

AG, SM, AB, RA, FA, RSA, PA, PAG, SCF, JLCL, PC, MCS, JC, JACR, CC, RCE, OD, AE, SE, AF, LG, FG, MG, SH, NK, RIM, GP, FP, AR, NU, YY, VZ, AZ, AZ, PT, GAD, JP, WT, MC and GFF acquired the data. AC and GFF analyzed the data and interpreted the results. AC

638 led the writing of the manuscript. All authors reviewed the drafts and gave final approval for
639 publication.

640 Correspondence and requests for materials should be addressed to AC
641 alexis.carteron@gmail.com

642

643 COMPETING INTERESTS

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646 REFERENCES

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966 **FIGURES**

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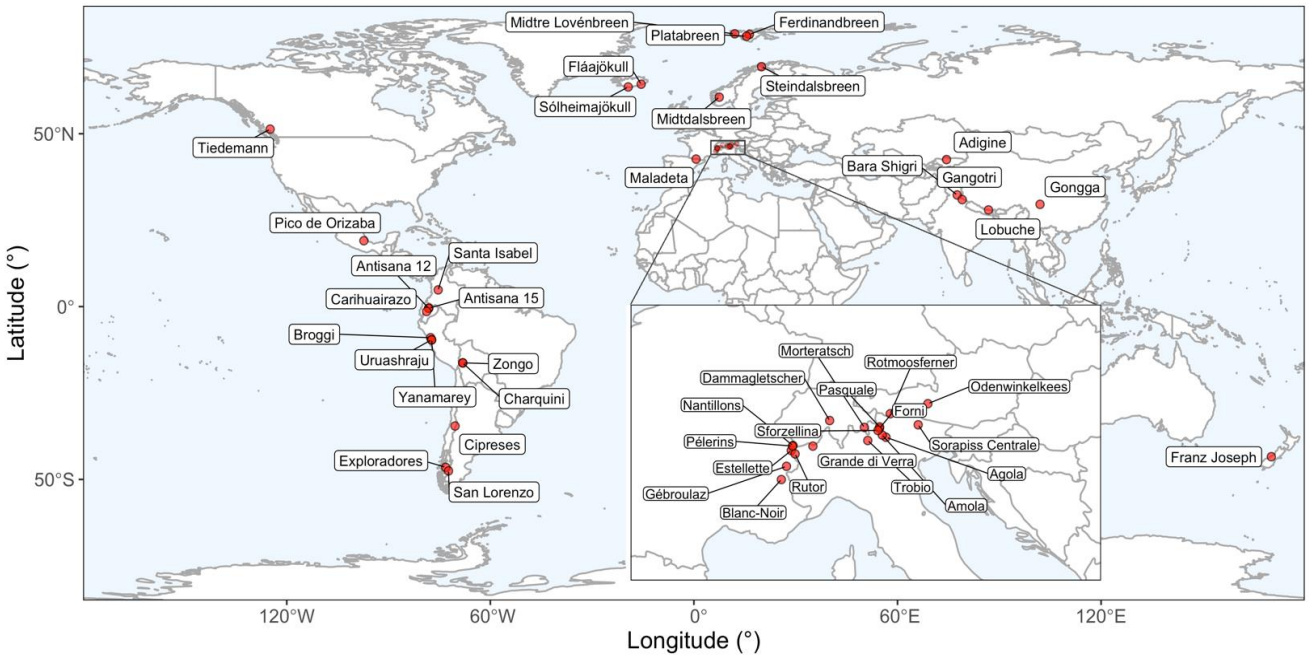

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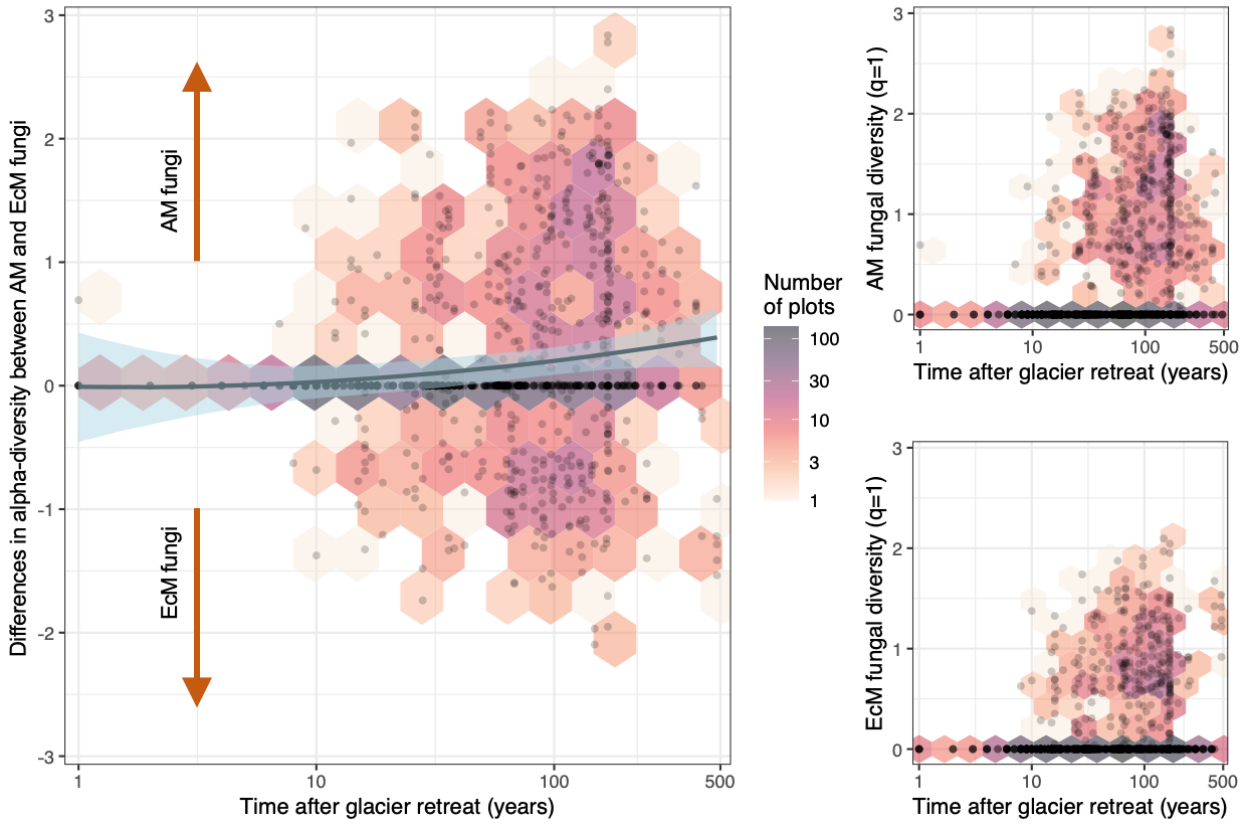
969 **Figure 1.** Location of the 46 glaciers whose proglacial areas were sampled for this study. The

970 inset map shows a zoom into the European Alps range.



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973 **Figure 2.** Differences in diversity (q = 1) between AM and EcM fungal communities (left panel)
974 and observed diversity (right panels) after glacier retreat, calculated at the plot-level. In the left
975 panel, points above zero represent a fungal community richer in AM fungi compared to EcM
976 fungi, and the opposite for points below zero. In all panels, the x-axis is on a log scale. N = 1251
977 plots in 46 proglacial areas. The regression curve was obtained through a linear mixed model;
978 shaded areas represent the 95% credible intervals of the regression.

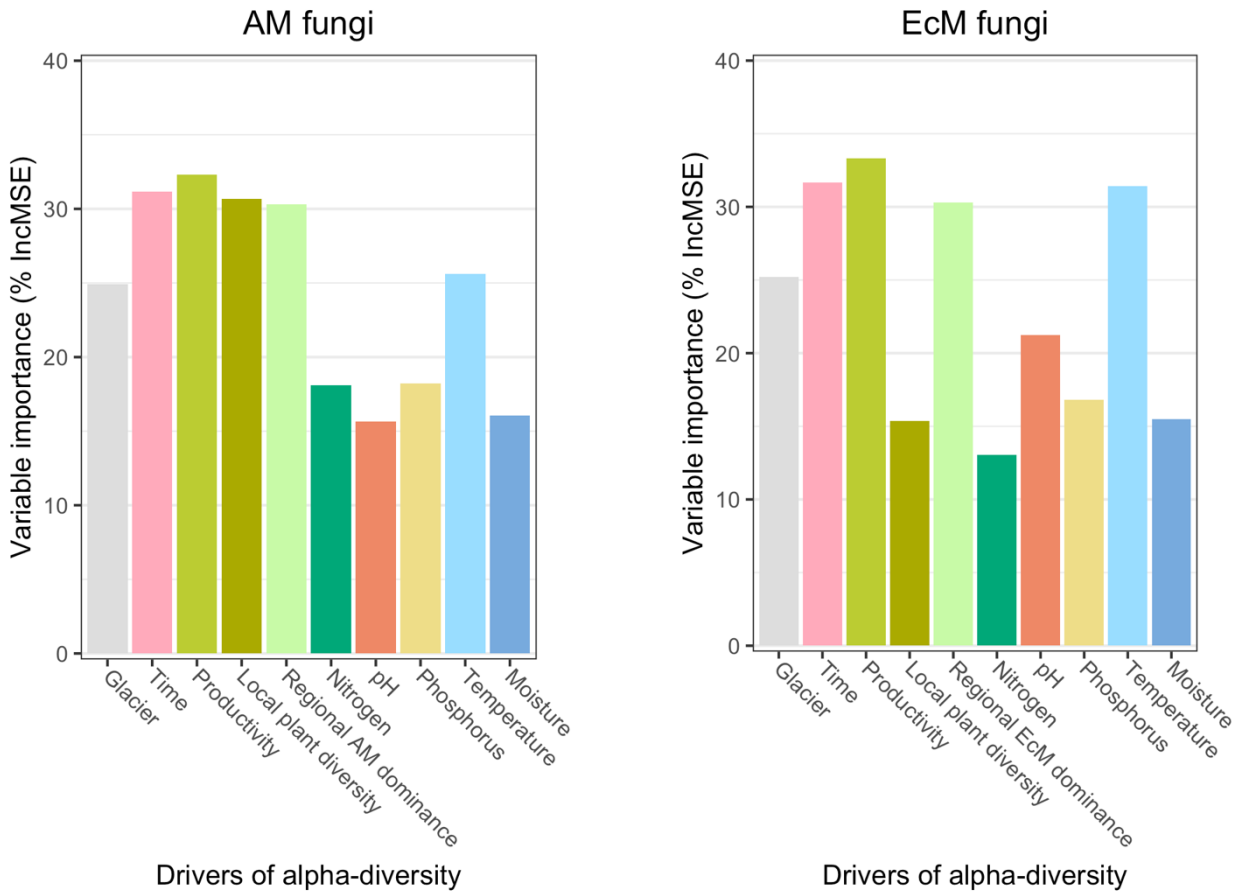

Figure 3. Role of glacier identity, time after glacier retreat, soil chemistry (nitrogen, pH, phosphorus), regional tree mycorrhizal type dominance (regional AM or EcM dominance) and microclimate (temperature, moisture) on the alpha-diversity (q = 1) of AM and EcM fungi. Variable importance was determined by the increase in mean squared error (IncMSE) using random forest models. N = 793 plots in 32 proglacial areas. Variance explained was 49% and 51% for AM and EcM fungi, respectively. Mean of squared residuals was 0.22 and 0.11 for AM and EcM fungi, respectively. See Table S3 for more details.

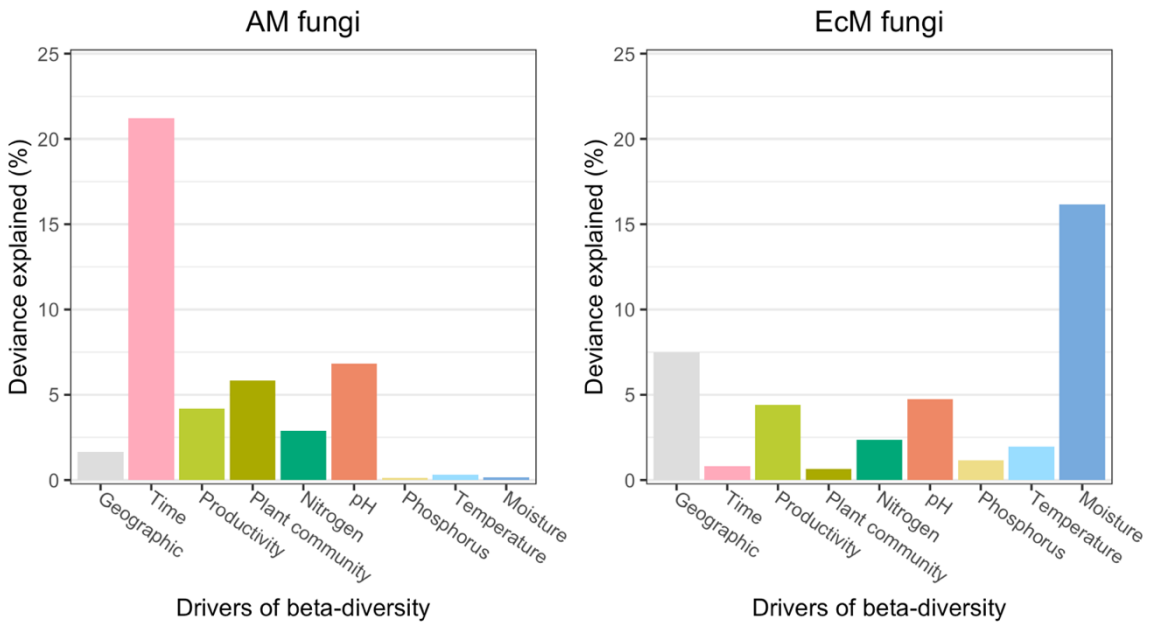

Figure 4. Effects of geographical proximity, differences in time after glacier retreat, soil chemistry (nitrogen, pH, phosphorus) and microclimate (temperature, moisture) on the beta-diversity of AM and EcM fungi using global dissimilarity models (GDMs). The higher the deviance explained, the more important the variable is in explaining beta-diversity patterns. Only changes between plots in the same proglacial area were considered (N = 2031 in 32 proglacial areas). See Table S4 for more details.