



HAL
open science

Dynamics and drivers of mycorrhizal fungi after glacier retreat

Alexis Carteron, Isabel Cantera, Alessia Guerrieri, Silvio Marta, Aurélie Bonin, Roberto Ambrosini, Fabien Anthelme, Roberto Sergio Azzoni, Peter Almond, Pablo Alviz Gazitúa, et al.

► **To cite this version:**

Alexis Carteron, Isabel Cantera, Alessia Guerrieri, Silvio Marta, Aurélie Bonin, et al.. Dynamics and drivers of mycorrhizal fungi after glacier retreat. *Nature*, 2024, 620 (7974), pp.562-569. 10.1111/nph.19682 . hal-04538457

HAL Id: hal-04538457

<https://hal.inrae.fr/hal-04538457v1>

Submitted on 28 Oct 2024

HAL is a multi-disciplinary open access archive for the deposit and dissemination of scientific research documents, whether they are published or not. The documents may come from teaching and research institutions in France or abroad, or from public or private research centers.

L'archive ouverte pluridisciplinaire **HAL**, est destinée au dépôt et à la diffusion de documents scientifiques de niveau recherche, publiés ou non, émanant des établissements d'enseignement et de recherche français ou étrangers, des laboratoires publics ou privés.

1 **TITLE**

2 Dynamics and drivers of mycorrhizal fungi after glacier retreat

3

4 Please cite this paper as:

5

6 Carteron, A. et al. 2024. Dynamics and drivers of mycorrhizal fungi after glacier retreat. *New*
7 *Phytologist*, DOI: 10.1111/nph.19682.

8

9 **AUTHORS**

10 Alexis Carteron^{1,2}, Isabel Cantera¹, Alessia Guerrieri^{1,3}, Silvio Marta^{1,4}, Aurélie Bonin^{1,3},
11 Roberto Ambrosini¹, Fabien Anthelme⁵, Roberto Sergio Azzoni⁶, Peter Almond⁷, Pablo Alviz
12 Gazitúa⁸, Sophie Cauvy-Fraunié⁹, Jorge Luis Ceballos Lievano¹⁰, Pritam Chand¹¹, Milap Chand
13 Sharma¹², John J. Clague¹³, Justiniano Alejo Cochachín Rapre^{14†}, Chiara Compostella⁶, Rolando
14 Cruz Encarnación¹⁴, Olivier Dangles¹⁵, Andre Eger¹⁶, Sergey Erokhin¹⁷, Andrea Franzetti¹⁸,
15 Ludovic Gielly¹⁹, Fabrizio Gili^{1,20}, Mauro Gobbi²¹, Sigmund Hågvar^{22,23}, Norine Khedim²⁴, Rosa
16 Isela Meneses^{25,26}, Gwendolyn Peyre²⁷, Francesca Pittino^{18,28}, Antoine Rabatel²⁹, Nurai
17 Urseitova¹⁷, Yan Yang³⁰, Vitalii Zaginaev³¹, Andrea Zerboni⁶, Anaïs Zimmer³², Pierre
18 Taberlet^{19,23}, Guglielmina Adele Diolaiuti¹, Jerome Poulénard²⁴, Wilfried Thuiller¹⁹, Marco
19 Caccianiga³³, Gentile Francesco Ficetola^{1,19}

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

- 38 12. Centre for the Study of Regional Development - School of Social Sciences, Jawaharlal
39 Nehru University, New Mehrauli Road, 110067 New Delhi, India
40 13. Department of Earth Sciences, Simon Fraser University, 8888 University Drive, Burnaby,
41 V5A 1S6, Canada
42 14. Área de Evaluación de Glaciares y Lagunas, Autoridad Nacional del Agua, Huaraz, Peru
43 15. CEFÉ, Univ Montpellier, CNRS, EPHE, IRD, Univ Paul Valéry Montpellier 3,
44 Montpellier, France
45 16. Mannaki Whenua - Landcare Research, Soils and Landscapes, 54 Gerald St, Lincoln
46 7608, New Zealand
47 17. Institute of Water Problems and Hydro-Energy, Kyrgyz National Academy of Sciences,
48 720033, Frunze, 533, Bishkek, Kyrgyzstan
49 18. Department of Earth and Environmental Sciences (DISAT) - University of Milano-
50 Bicocca, Milano, Italy
51 19. Université Grenoble Alpes, Université Savoie Mont Blanc, CNRS, LECA, F-38000
52 Grenoble, France
53 20. Department of Life Sciences and Systems Biology, University of Turin, Via Accademia
54 Albertina 13, 10123 Turin, Italy
55 21. Research and Museum Collections Office, Climate and Ecology Unit, MUSE-Science
56 Museum, Corso del Lavoro e della Scienza, 3, 38122 Trento, Italy
57 22. Faculty of Environmental Sciences and Natural Resource Management (INA),
58 Norwegian University of Life Sciences, Universitetstunet 3, 1433 Ås, Norway
59 23. UiT - The Arctic University of Norway, Tromsø Museum, Tromsø, Norway
60 24. Université Savoie Mont Blanc, Université Grenoble Alpes, EDYTEM, F-73000
61 Chambéry, France
62 25. Herbario Nacional de Bolivia: La Paz, La Paz, Bolivia
63 26. Universidad Católica del Norte, Antofagasta, Chile
64 27. Department of Civil and Environmental Engineering, University of the Andes, Bogotá,
65 Colombia
66 28. Swiss Federal Institute for Forest, Snow and Landscape Research. Zürcherstrasse 111,
67 8903 Birmensdorf
68 29. Université Grenoble Alpes, CNRS, IRD, INRAE, Grenoble-INP, Institut des Géosciences
69 de l'Environnement (IGE, UMR 5001), F-38000 Grenoble, France
70 30. Institute of Mountain Hazards and Environment, Chinese Academy of Sciences,
71 Chengdu, 610041, China
72 31. Mountain Societies Research Institute, University of Central Asia, Bishkek, Kyrgyzstan,
73 720001, Toktogula 125/1
74 32. Department of Geography and the Environment, University of Texas at Austin, 78712
75 Austin, TX, USA
76 33. Dipartimento di Bioscienze, Università degli Studi di Milano, via Celoria 26, 20133
77 Milano, Italy

78 † This author deceased

79
80 Corresponding author: Alexis Carteron alexis.carteron@unimi.it

81
82 Word counts

83	Introduction: 1425
84	Materials and Methods: 2224
85	Results: 509
86	Discussion: 2267

87 **SUMMARY**

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

109
110 Key words: ecological succession, glacier forelands, soil, metabarcoding, ectomycorrhizal fungi,
111 arbuscular mycorrhizal fungi

112 INTRODUCTION

113 Glaciers have been retreating around the world for the past century, and more than half of the
114 world's glaciers are expected to be lost in this century (Hock *et al.*, 2019; Rounce *et al.*, 2023;
115 Bosson *et al.*, 2023). While glacier retreat poses significant challenges, it is essential to
116 investigate the consequences associated with these changes. Understanding the dynamics of the
117 resulting large ice-free areas is vital for addressing the broader environmental impacts of glacier
118 retreats as they play a crucial role in mountain ecosystems as climate refugia, hosting unique
119 biodiversity and providing essential ecosystem services (Körner, 2004; Palomo, 2017; Cauvy-
120 Fraunié & Dangles, 2019; Brighenti *et al.*, 2021; Zimmer *et al.*, 2022). With the projected
121 increase in deglaciated areas in the future, there is a need to better understand the consequent
122 biotic dynamics and predict the ecosystem development of deglaciated areas (Prach & Walker,
123 2020; Ficetola *et al.*, 2021; Rumpf *et al.*, 2022; Bosson *et al.*, 2023). By understanding changes
124 in diversity and ecological processes, analyses of successional gradients could help define
125 effective strategies for management and adaptation of these newly exposed areas. However, in
126 order to draw general ecological patterns and measure biodiversity changes, it is necessary to
127 apply standardized sampling design on multiple glacier forelands around the globe (Chang &
128 Turner, 2019), but such analyses are lacking (Cauvy-Fraunié & Dangles, 2019).

129
130 Glacier retreat exposes new land for colonization of biota, which then diversifies, leading to
131 further soil development (Wietrzyk-Pełka *et al.*, 2020; Khedim *et al.*, 2021; Pothula & Adams,
132 2022). Colonisation by plants after glacier retreat is a crucial element in the formation of novel
133 ecosystems (Clements, 1916; Tansley, 1935). The soil biological crust as well as nurse plants
134 which facilitate the establishment of other plants, are essential in this process (Zimmer *et al.*,
135 2018; Llambí *et al.*, 2021). Mycorrhizal associations are the most common and important
136 mutualistic symbioses in terrestrial ecosystems (Martin *et al.*, 2018) and play a key role in the
137 development of ecosystems (Chapin *et al.*, 1994; Jumpponen *et al.*, 2012; Benavent-González *et*
138 *al.*, 2019). In nutrient-poor environments, mycorrhizal fungi can be particularly important for
139 enhancing plant growth and survival (Smith & Read, 2008; van der Heijden *et al.*, 2015).
140 Mycorrhizas are known to play a key role in soil development, including biogeochemical
141 processes such as nutrient cycling and carbon sequestration (Read & Perez-Moreno, 2003;
142 Tedersoo & Bahram, 2019; Steidinger *et al.*, 2019). Local-scale analyses from mid-latitude

143 glaciers have shown that non-mycorrhizal and facultative mycotrophic plants tend to
144 predominate immediately after glacier retreat, followed by an increase in mycorrhizal types and
145 in fungal species richness in older communities (Cázares *et al.*, 2005; Oehl *et al.*, 2011; Blaaliid
146 *et al.*, 2012). However, these trends are not always monotonous and may even appear
147 idiosyncratic (Helm *et al.*, 1999; Trowbridge & Jumpponen, 2004). This is illustrated by the fact
148 that some mycorrhizal fungal taxa have been found to be indicators of both early (Rime *et al.*,
149 2015) and late successional stages (Guerrieri *et al.*, 2022b). Understanding the dynamics and
150 drivers of plant-fungal mycorrhizal associations is therefore pivotal for inferring key ecological
151 processes during early ecosystem development (Tedersoo & Bahram, 2019) but, so far, no
152 studies have analyzed variability in mycorrhizas in multiple independent ecological successions
153 following glacier retreat.

154
155 Many plants rely on mycorrhizal fungi, which are limited in their dispersal potential (Brundrett,
156 2002; van der Heijden *et al.*, 2015; Tedersoo *et al.*, 2020). Mycorrhizal fungi are highly
157 dependent on the presence of host plants to complete their lifecycle (van der Heijden *et al.*,
158 2015). Therefore, in the case of newly exposed terrains, the mycorrhizal fungal community could
159 depend on the presence of host plants (Zobel & Öpik, 2014) and, similarly, the scarcity of
160 mycorrhizal fungal propagules may limit plant colonization (Dickie *et al.*, 2013; Chaudhary *et*
161 *al.*, 2018; Delavaux *et al.*, 2021). Recently, the availability of mycorrhizal fungi has been shown
162 to play an important role in shaping island flora worldwide, the so-called “mycorrhizal filter”
163 (Delavaux *et al.*, 2019). However, arbuscular mycorrhizal (AM) and ectomycorrhizal (EcM)
164 fungi, which are the two major mycorrhizal types (Brundrett & Tedersoo, 2018; Steidinger *et al.*,
165 2019; Soudzilovskaia *et al.*, 2020), differ in their nutrient-acquisition strategies, host specificity
166 and dispersal traits such as spore size (Kivlin, 2020). EcM fungi are expected to disperse better
167 with their tiny spores (generally $< 9,000 \mu\text{m}^3$, on average $> 2,000$ times smaller than AM fungal
168 taxa), potentially enabling them to establish quickly in new habitats. In contrast, the presence and
169 development of AM fungi in plant roots could be favoured in early stages of ecosystem
170 development because of their lower host specificity compared to EcM fungi (Veresoglou &
171 Rillig, 2014; van der Heijden *et al.*, 2015). Additionally, AM fungi associate with more than
172 70% of all plant species (van der Heijden *et al.*, 2015; Soudzilovskaia *et al.*, 2020) and are
173 expected to impose a lower energy cost to plant hosts in stressful habitats than EcM fungi

174 (Tedersoo & Bahram, 2019). Dispersal limitation and habitat tolerance are critical drivers of
175 ecological successions (Makoto & Wilson, 2019), and even though EcM fungi should better
176 disperse than AM ones, AM host plants tend to be favoured and more abundant in stressful and
177 early stages of development (Cázares *et al.*, 2005; Lambers *et al.*, 2008; Tedersoo & Bahram,
178 2019). Examining patterns of mycorrhizal fungi following glacier retreat at the worldwide scale
179 would allow a simultaneous comparison of the early dynamics between mycorrhizal fungal
180 types.

181
182 Spatial and temporal patterns of community dynamics following the glacier retreat include
183 changes in the number of taxa at a local site (alpha-diversity) and modifications of community
184 composition (beta-diversity) over time. However, these patterns are contingent on the identity of
185 the organisms or the target communities (Cauvy-Fraunié & Dangles, 2019; Hanusch *et al.*,
186 2022). For instance, the richness of spiders and vascular plants can increase fourfold over a
187 century, while the increase in richness is much smaller for dipterans (Pothula & Adams, 2022).
188 Also, the diversity of mycorrhizal fungi is expected to change over time, although patterns
189 emerging from both EcM and AM taxa are complex. For example, while Jumpponen *et al.*
190 (2002) observed that the number of EcM fungal sporocarps increases with time since glacier
191 retreat, data based on high-throughput sequencing of root-associated fungi portray a context-
192 dependent picture, with patterns depending on the proglacial area sampled (Blaalid *et al.*, 2012;
193 Davey *et al.*, 2015). Similarly, the number of AM taxa has been observed to increase towards
194 older sites only in part of the analyzed glacier forelands (Trowbridge & Jumpponen, 2004; Oehl
195 *et al.*, 2011), suggesting a strong influence of local conditions. A comprehensive integration of
196 alpha- and beta-diversity analyses is therefore needed to understand soil biodiversity responses to
197 glacier retreat, and such analysis must also consider local conditions like microhabitat that can
198 significantly influence soil communities (Oehl *et al.*, 2011; Blaalid *et al.*, 2012; Jumpponen *et*
199 *al.*, 2012; Rime *et al.*, 2015; Wietrzyk-Pełka *et al.*, 2020). To this aim, fine-scale data integrating
200 information on both biotic and abiotic components of proglacial environments is necessary, but
201 challenging to obtain (Ficetola *et al.*, 2021; Marta *et al.*, 2023).

202
203 The aim of our study was to assess the dynamics and the drivers of mycorrhizal fungi in order to
204 assess how they establish after the retreat of glaciers, and how biotic and abiotic factors locally

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

221

222 **METHODS**

223 *Sample collection*

224 From 2014 to 2020, we collected soil samples from 1251 plots within 265 sites located in the
225 forelands of 46 mountain and high-latitude glaciers (Fig. 1) from five continents, including
226 regions with different climatic conditions and rates of glacier retreat (Zemp *et al.*, 2019).

227 Information on times of deglaciation over the past centuries in these forelands is available from
228 Marta *et al.* (2021).

229

230 In each glacier foreland, we selected three to 17 suitable sites (mean = 5.8 sites per foreland, SD
231 = 2.5) that became ice-free from 1 to 483 years before sampling. For each site, the age since
232 glacier retreat was used as a proxy of the time available for ecosystem development; i.e. we used
233 a chronosequence approach for the study of ecological successions (space-for-time substitution;
234 Walker *et al.*, 2010). At each site, we established 2-10 plots (mean = 4.7 plots, SD = 0.8) of 1
235 m², evenly spaced at a distance of 20 m, where possible. Within each plot, we collected five soil

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

242

243 *Biotic and abiotic conditions*

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

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

275

276 *DNA sequences acquisition*

277 The molecular and bioinformatic workflows are detailed in Guerrieri *et al.* (2022b) for fungi and
278 in Cantera *et al.* (In press) for plants. Briefly, sequences were obtained after the following steps:
279 (i) mixing soil samples collected at each plot with phosphate buffer (Taberlet *et al.*, 2012). (ii)
280 Extraction of eDNA using the NucleoSpin® Soil Mini Kit. (iii) PCR amplification in four
281 replicates with the Fung02 primer pair, targeting the ITS1 region for fungi (forward: 5'-
282 GGAAGTAAAAGTCGTAACAAGG-3', reverse: 5'-CAAGAGATCCGTTGYTGAAAGTK-
283 3') (Epp *et al.*, 2012) and the Sper01 primer targeting the chloroplast trnL-P6 loop for vascular
284 plants (forward: 5'-GGGCAATCCTGAGCCAA-3', reverse: 5'-
285 CCATTGAGTCTCTGCACCTATC-3') (Taberlet *et al.*, 2007). PCR reactions included
286 bioinformatic blanks, extraction and amplification of negative controls, and positive controls (see
287 below). (iv) Library preparation and sequencing of purified samples using the MiSeq (fungi; $2 \times$
288 250 bp) and HiSeq 2500 (plants; $2 \times$ 150 bp) Illumina platforms. Positive controls consisted of
289 16 non-tropical plant species belonging to 15 families (Taxaceae, Lamiaceae, Salicaceae,
290 Polygonaceae, Betulaceae, Oleaceae, Pinaceae, Caprifoliaceae, Pinaceae, Aceraceae, Poaceae,
291 Rosaceae, Brassicaceae, Geraniaceae, Ericaceae) and two fungal strains (*Saccharomyces*
292 *cerevisiae*, *Cryptococcus neoformans*) at known concentrations. The positive controls were used
293 to confirm that PCRs correctly amplified the present taxa.

294

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

298 corresponding PCR replicate before dereplication. Singletons were discarded as well as artefacts
299 that had lower and/or higher length than expected (i.e. sequences <68 bp for fungi and <10 or
300 >220 bp for plants). We also discarded sequences containing ambiguous bases. The remaining
301 high-quality sequences were clustered into molecular operational taxonomic units (MOTUs)
302 considering optimal thresholds of intra- and inter-specific variations at 95% for fungi and at 97%
303 for plants (Bonin *et al.*, 2023). These thresholds identified the distribution of sequence
304 similarities among different individuals belonging to the same species, and among different
305 species belonging to the same genus. This allows to minimize the risk that different sequences of
306 the same species are assigned to different MOTUs (over-splitting) while balancing the risk that
307 different species are grouped in the same MOTU (over-merging). On the basis of the analysis of
308 various clustering thresholds using sequences extracted from the EMBL (version 140) database
309 (Bonin *et al.*, 2023), 95% emerged as the threshold balancing over-splitting and over-merging for
310 Fung02, and 97% for Sper01 (Bonin *et al.*, 2023). For each marker, we built a reference database
311 by running in silico PCRs on the public sequence database EMBL (version 140) using the *ecopcr*
312 program (Ficetola *et al.*, 2010) and allowing a maximum of three mismatches per primer. The
313 obtained databases were curated to keep only sequences assigned at the species, genus and
314 family levels. For each MOTU, we made a taxonomic assignment using the *ecotag* program of
315 the OBITools (Boyer *et al.*, 2016). In order to limit the presence of contaminants (Ficetola *et al.*,
316 2015; Boyer *et al.*, 2016; Zinger *et al.*, 2019), MOTUs were not included in the analyses if they
317 had: i) a best identity score below 80% and total read count in the dataset below five (based on
318 bioinformatic blanks) for fungi; or ii) a best identity score below 90% and total read count below
319 eight for plants. In addition, MOTUs were not included if they were detected in only one PCR
320 replicate of the same sample or in more than one extraction or amplification of negative controls
321 (potential false positives and contaminants; Ficetola *et al.*, 2015; Zinger *et al.*, 2019). Finally, we
322 summed the four PCR replicates to obtain the final MOTU table following the relaxed stringency
323 method (Mächler *et al.*, 2021).

324

325 *Mycorrhizal type assignment*

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

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

336

337 *Data analyses*

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

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

363
364 To assess the potential impacts of time, glacier identity, habitat (i.e. productivity, plant diversity,
365 N, P, pH, temperature, TWI) and regional mycorrhizal dominance on patterns of AM and EcM
366 fungal alpha-diversity, we used a random forest algorithm fitting nonlinear multiple regressions
367 with the *randomForest* (Cutler & Wiener, 2022) and *rfPermute* (Archer, 2022) packages. We set
368 the number of bootstrap replicates (*n**tree*) to 600, with convergence verified visually by assessing
369 the cumulative error rate. The optimal *m**try* (number of variables randomly sampled as
370 candidates at each split) was determined using *tuneRF* function and set at two for AM fungi and
371 three for EcM fungi. Variable importance was based on the increase in the mean squared error
372 (%incMSE), and their significance was estimated after 5000 repetitions. Plant alpha-diversity (q
373 = 1) was calculated based on the plant MOTU data. For this analysis, we used data from 793
374 plots in 32 proglacial areas.

375
376 We assessed the potential drivers of AM and EcM fungal beta-diversity (i.e. changes in
377 community composition between plots belonging to the same foreland, $N = 2031$) using the
378 generalized dissimilarity modelling (GDM) approach with the *gdm* package (Fitzpatrick *et al.*,
379 2022). This approach is well suited to identify the drivers of community dissimilarity across
380 plots and to analyse relationships potentially affected by non-linearity. Beta-diversity between
381 the communities inhabiting different plots was related to differences in time and habitat
382 variables, as well as to geographic distances. Furthermore, as a measure of plant community
383 changes, we performed a principal coordinate analysis (PCoA) from the plant dissimilarity
384 matrix using the Jaccard index and used the scores of the first axis for each plot as an
385 explanatory variable. We focused on dissimilarities between pairs of plots located in the same
386 foreland (i.e. pairs of plots located in different forelands were excluded from GDM), as our aim
387 was to assess the factors determining community variation within each landscape. Regional
388 mycorrhizal dominance was not included in this analysis, as all the plots within the same
389 foreland share the same dominance values. Plots with zero MOTU of fungi or vascular plants
390 were excluded. Variable significance was estimated after 1000 permutations.

391
392 The following variables were log-transformed prior to modelling to reduce skewness: time since
393 glacier retreat, vascular plant alpha-diversity N, P, TWI and NDVI. Additional R packages used
394 for data wrangling and visualization included: *dplyr* (Wickham *et al.*, 2017), *ggplot2* (Wickham,
395 2016), *ggspatial* (Dunnington, 2018), *ggrepel* (Slowikowski *et al.*, 2021), *phyloseq* (McMurdie
396 & Holmes, 2013), *rnaturalearth* (South, 2017), *tidyr* (Wickham & Henry, 2019) and *vegan*
397 (Oksanen *et al.*, 2017).

398

399 **RESULTS**

400 *Colonization dynamics*

401 Soil eDNA metabarcoding of the ITS1 region yielded a total of 43,104,065 high-quality filtered
402 fungal sequences that were grouped into 3331 MOTUs (Table S1), 563 of which were classified
403 as putative EcM or AM fungi (303 EcM and 260 AM fungal MOTUs). Overall, mycorrhizal
404 fungi were detected in 58% of the plots. The diversity of the overall fungal community rapidly
405 increases from a few MOTUs immediately after glacier retreat, up to ~200 MOTUs per plot after
406 100 years (Fig. S2). Just one year after glacier retreat, non-mycorrhizal fungi were already
407 present in more than half of the plots (Fig. S2). Mycorrhizal fungi were detected < 10 years after
408 glacier retreat, with a quick increase in the following decades (Fig. S2). In these recently
409 deglaciated plots, the first EcM fungi were detected after four years and the first AM fungi after
410 one year. Glomeraceae is the most common AM fungal family throughout the stages of
411 ecosystem development (Fig. S3). The five most abundant fungal families that include EcM
412 fungi were all present a few years after glacier retreat (Cortinariaceae, Inocybaceae, Russulaceae,
413 Sebacinaceae, Suillaceae; Fig. S3), while the EcM fungal families Clavulinaceae, Gloniaceae
414 and Rhizopogonaceae were only detected at later stages of development (> 36 years, Fig. S3). In
415 the early stages, AM and EcM fungi show similar richness (95% credible interval of their
416 difference in richness overlaps zero from 1 to ~50 years; Fig. 2) but, with time, the AM fungal
417 diversity tended to become higher compared to EcM fungi and the difference increased
418 afterwards (significant relationship; slope = 0.09, standard error = 0.03). The probability for AM
419 and EcM fungi to be present in the overall fungal community greatly increased with time since
420 glacier retreat (especially after 10 to 20 years; Fig. S4).

421

422 *Environmental drivers of alpha-diversity*

423 Random forest models suggested that the alpha-diversity of mycorrhizal fungi is explained by
424 local conditions, in addition to time and glacier identity (variation explained by the model being
425 49% and 51% for AM and EcM fungi, respectively; Fig. 3). All habitat variables showed
426 significant effects, except nitrogen concentration for EcM fungi (Table S3). For both mycorrhizal
427 types, chemical features of soil (N, P, pH) **tend** to have lower importance compared to the other
428 variables. Time since glacier retreat, productivity, soil temperature and regional mycorrhizal
429 dominance **are** the variables with the strongest influence on the diversity of both mycorrhizal
430 types. In addition, the local diversity of vascular plants **is** a particularly strong predictor of AM
431 fungal diversity.

432

433 *Environmental drivers of beta-diversity*

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

441

442 **DISCUSSION**

443 *Early dynamic of mycorrhizal fungi*

444 The dynamics of mycorrhizal fungi during early succession have attracted great interest due to
445 their importance in ecosystem development (Allen *et al.*, 1992; Nara, 2006; Jumpponen *et al.*,
446 2012), along with the role played by nurse plants, the microtopography and the soil biological
447 crust (Zimmer *et al.*, 2018; Llambí *et al.*, 2021; Bayle *et al.*, 2023). Glacier forelands are
448 nutrient-poor (Khedim *et al.*, 2021; Pothula & Adams, 2022), and this poses unique challenges
449 for mycorrhizal establishment. The colonization of mycorrhizal fungi in deglaciated terrains
450 shows a delay compared to that of the overall fungal community. Both AM and EcM fungi,
451 however, manage to colonize quickly following glacier retreat, with the most abundant
452 mycorrhizal fungal families already present at the earliest stages of development (< 17 years).

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

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

470
471 *Plants as drivers of mycorrhizal fungal diversity?*

472 Both AM and EcM fungi have been reported to associate with plant species that are found in
473 barren substrates at the earliest stages of succession following glacier retreat. However,
474 colonization of plant roots by mycorrhizal fungi in such environments is often scarce (< 10%;
475 Cázares *et al.*, 2005; Oehl *et al.*, 2011). Some mycorrhizal plant species have the ability to
476 establish and grow in proglacial areas even without their fungal symbionts (Fujiyoshi *et al.*,
477 2011; Oehl *et al.*, 2011), allowing these facultative nonmycorrhizal plants to bypass the
478 “mycorrhizal filter” (Delavaux *et al.*, 2019). This suggests that the diversity of mycorrhizal fungi
479 might be shaped by plant diversity, as supported by the strong relationship between mycorrhizal
480 diversity and plant richness.

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

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

490 Climate change induces vegetation expansion and increases plant biomass (“greening”) at
491 high elevations and could thus influence mycorrhizal fungal diversity, accelerating their
492 colonization of these environments (Anderson *et al.*, 2020; Rumpf *et al.*, 2022). Mycorrhizal
493 fungal diversity may be promoted by plant biomass, but also by plant richness depending on their
494 host specificity (van der Heijden *et al.*, 2015; Kivlin *et al.*, 2022). In turn, a greater mycorrhizal
495 fungal diversity can determine positive feedbacks on plant diversity and ecosystem functioning
496 (van der Heijden *et al.*, 1998), as mycorrhizal fungi are known to enhance plant survival and
497 growth (Smith & Read, 2008), particularly in nutrient-poor environments (van der Heijden *et al.*,
498 2008). However, climate change can also reduce vegetation in alpine ecosystems (“browning”),
499 due to changes in precipitation patterns and reduced snow cover (Phoenix & Bjerke, 2016; Liu *et al.*
500 *et al.*, 2021; Rumpf *et al.*, 2022; Marta *et al.*, 2023). Such browning could weaken the benefits
501 provided by mycorrhizal associations by impeding mycorrhizal diversity, resulting in lower
502 nutrient availability for the remaining plants, although some ruderal mycorrhizal fungus could
503 persist (Hiiesalu *et al.*, 2023). The overall responses of the ecosystems to climate changes is thus
504 difficult to predict, as it depends on the types of vegetation and mycorrhizas involved (Tedersoo
505 & Bahram, 2019).

506

507 *Contrasting responses between mycorrhizal types*

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

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

522 Differences between mycorrhizal types are also clear for beta-diversity (i.e. changes in
523 community composition). That of AM fungi is mostly explained by time, whereas a microhabitat
524 parameter (potential soil moisture) is the key factor for EcM fungi (Abrego *et al.*, 2020). These
525 results are congruent with AM fungi being more affected by dispersal limitations. In fact, a
526 strong relationship between beta-diversity and time, after taking into account differences for key
527 biotic and abiotic parameters, is often taken as evidence of a major role of dispersal limitation
528 (Makoto & Wilson, 2019; Ficetola *et al.*, 2021), which may determine time lags between glacier
529 retreat, habitat development and the formation of AM communities. Conversely, for EcM fungi,
530 habitat filtering could play a more important role (Davey *et al.*, 2015; Castilho *et al.*, 2020;
531 Delavaux *et al.*, 2021), even though both processes seem important. Consequently, AM and EcM
532 richness and composition could respond differently to global changes. Given the close links
533 between plant diversity and mycorrhizal diversity, these contrasting responses of AM and EcM
534 fungi could be exacerbated if different plant species also show distinct responses to global
535 changes (Fei *et al.*, 2022). Nevertheless, the strong impact of plant communities on AM fungi,
536 which are obligate biotrophs, could be counterbalanced by their lower host specificity (van der
537 Heijden *et al.*, 2015). Soil chemistry, temperature and moisture are additional drivers of alpha-
538 and beta-diversity of mycorrhizal fungi. As climate affects the rate of rock weathering (Walker *et*
539 *al.*, 2010) and, more generally, soil development, composition and biodiversity (Khedim *et al.*,
540 2021; Guerrieri *et al.*, In press), climatic modifications probably impact the dynamics and
541 communities of mycorrhizal associations both directly and indirectly. AM fungi could be
542 influenced indirectly by climate change through plant diversity changes, whereas the impact
543 might be more direct for the EcM fungi because of their sensitivity to temperature and moisture
544 (Tedersoo & Bahram, 2019).

545

546 *Limitations of observational and eDNA approaches*

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

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

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

584

585 **Conclusion**

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

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

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

620

621 DATA AND CODE AVAILABILITY

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

626

627 FUNDING

628 This study was funded by the European Research Council under the European Community's
629 Horizon 2020 Programme, Grant Agreement no. 772284 (IceCommunities), and by Biodiversa+,
630 the European Biodiversity Partnership under the 2021-2022 BiodivProtect joint call for research
631 proposals, co-funded by the European Commission (GA N°101052342) and with the funding
632 organisations MUR and ANR.

633

634 AUTHOR CONTRIBUTIONS

635 AG, SM, AB, RA, FA, RSA, PA, PAG, SCF, JLCL, PC, MCS, JC, JACR, CC, RCE, OD, AE,
636 SE, AF, LG, FG, MG, SH, NK, RIM, GP, FP, AR, NU, YY, VZ, AZ, AZ, PT, GAD, JP, WT,
637 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

644 The authors declare no competing interests

645

646 REFERENCES

647 **Abrams M, Crippen R, Fujisada H. 2020.** ASTER Global Digital Elevation Model (GDEM) and
648 ASTER Global Water Body Dataset (ASTWBD). *Remote Sensing* **12**: 1156.

649 **Abrego N, Huotari T, Tack AJM, Lindahl BD, Tikhonov G, Somervuo P, Martin Schmidt N,**
650 **Ovaskainen O, Roslin T. 2020.** Higher host plant specialization of root-associated endophytes
651 than mycorrhizal fungi along an arctic elevational gradient. *Ecology and Evolution* **10**: 8989–
652 9002.

653 **Allen MF, Crisafulli C, Friese CF, Jeakins SL. 1992.** Re-formation of mycorrhizal symbioses on
654 Mount St Helens, 1980–1990: interactions of rodents and mycorrhizal fungi. *Mycological*
655 *Research* **96**: 447–453.

656 **Anderson K, Fawcett D, Cugulliere A, Benford S, Jones D, Leng R. 2020.** Vegetation expansion
657 in the subnival Hindu Kush Himalaya. *Global Change Biology* **26**: 1608–1625.

658 **Archer E. 2022.** rfPermute: Estimate Permutation p-Values for Random Forest Importance
659 Metrics.

660 **Ariza M, Fouks B, Mauvisseau Q, Halvorsen R, Alsos IG, de Boer HJ. 2023.** Plant biodiversity
661 assessment through soil eDNA reflects temporal and local diversity. *Methods in Ecology and*
662 *Evolution* **14**: 415–430.

663 **Aybar C, Qiusheng W, Bautista L, Yali R, Barja A, Ushey K, Ooms J, Appelhans T, Allaire JJ,**
664 **Tang Y, et al. 2022.** rgee: R Bindings for Calling the ‘Earth Engine’ API.

665 **Bahram M, Peay KG, Tedersoo L. 2015.** Local-scale biogeography and spatiotemporal variability
666 in communities of mycorrhizal fungi. *New Phytologist* **205**: 1454–1463.

667 **Baldrian P, Bell-Dereske L, Lepinay C, Větrovský T, Kohout P. 2022.** Fungal communities in soils
668 under global change. *Studies in Mycology*.

669 **Bayle A, Carlson BZ, Zimmer A, Vallée S, Rabatel A, Cremonese E, Filippa G, Dentant C, Randin**
670 **C, Mainetti A, et al. 2023.** Local environmental context drives heterogeneity of early succession
671 dynamics in alpine glacier forefields. *Biogeosciences* **20**: 1649–1669.

672 **Benavent-González A, Raggio J, Villagra J, Blanquer Lorite J, Pintado A, Rozzi R, Green TG,**
673 **Sancho L. 2019.** High nitrogen contribution by *Gunnera magellanica* and nitrogen transfer by
674 mycorrhizas drive an extraordinarily fast primary succession in Sub-Antarctic Chile. *New*
675 *Phytologist* **223**.

676 **Bennett AE, Classen AT. 2020.** Climate change influences mycorrhizal fungal–plant interactions,
677 but conclusions are limited by geographical study bias. *Ecology* **101**: e02978.

678 **Berruti A, Desirò A, Visentin S, Zecca O, Bonfante P. 2017.** ITS fungal barcoding primers versus
679 18S AMF-specific primers reveal similar AMF-based diversity patterns in roots and soils of three
680 mountain vineyards. *Environmental Microbiology Reports* **9**: 658–667.

681 **Bjornstad ON, Cai J. 2022.** ncf: Spatial Covariance Functions.

682 **Blaalid R, Carlsen T, Kumar S, Halvorsen R, Ugland KI, Fontana G, Kauserud H. 2012.** Changes
683 in the root-associated fungal communities along a primary succession gradient analysed by 454
684 pyrosequencing. *Molecular Ecology* **21**: 1897–1908.

685 **Bonin A, Guerrieri A, Ficetola GF. 2023.** Optimal sequence similarity thresholds for clustering of
686 molecular operational taxonomic units in DNA metabarcoding studies. *Molecular Ecology*
687 *Resources* **23**: 368–381.

688 **Bosson JB, Huss M, Cauvy-Fraunié S, Clément JC, Costes G, Fischer M, Poulenard J, Arthaud F.**
689 **2023.** Future emergence of new ecosystems caused by glacial retreat. *Nature* **620**: 562–569.

690 **Boyer F, Mercier C, Bonin A, Le Bras Y, Taberlet P, Coissac E. 2016.** obitools: a unix-inspired
691 software package for DNA metabarcoding. *Molecular Ecology Resources* **16**: 176–182.

692 **Brambilla M, Gobbi M. 2014.** A century of chasing the ice: Delayed colonisation of ice-free sites
693 by ground beetles along glacier forelands in the Alps. *Ecography* **37**: 33–42.

694 **Bray RH, Kurtz LT. 1945.** Determination of Total Organic and Available Forms of Phosphorus in
695 Soils. *Soil Science* **59**: 39–46.

696 **Brighenti S, Hotaling S, Finn DS, Fountain AG, Hayashi M, Herbst D, Saros JE, Tronstad LM,**
697 **Millar CI. 2021.** Rock glaciers and related cold rocky landforms: Overlooked climate refugia for
698 mountain biodiversity. *Global Change Biology* **27**: 1504–1517.

699 **Brundrett MC. 2002.** Coevolution of roots and mycorrhizas of land plants. *New Phytologist* **154**:
700 275–304.

- 701 **Brundrett MC, Tedersoo L. 2018.** Evolutionary history of mycorrhizal symbioses and global host
702 plant diversity. *New Phytologist* **220**: 1108–1115.
- 703 **Bürkner P-C. 2017.** brms: An R package for bayesian multilevel models using Stan. *Journal of*
704 *Statistical Software* **80**: 1–28.
- 705 **Calderón-Sanou I, Münkemüller T, Boyer F, Zinger L, Thuiller W. 2020.** From environmental
706 DNA sequences to ecological conclusions: How strong is the influence of methodological
707 choices? *Journal of Biogeography* **47**: 193–206.
- 708 **Cantera I, Carteron A, Guerrieri A, Marta S, Bonin A, Ambrosini R, Anthelme F, Azzoni R,**
709 **Almond P, Gazitúa P, et al. In press.** The importance of species addition versus replacement
710 varies over succession in plant communities after glacial retreat. *Nature Plants*.
- 711 **Castilho R, Bidartondo M, Niskanen T, Clarkson J, Brunner I, Zimmermann S, Senn-Irlet B, Frey**
712 **B, Peintner U, Mrak T, et al. 2020.** Habitat specialization controls ectomycorrhizal fungi above
713 the treeline in the European Alps. *New Phytologist* **229**.
- 714 **Cauvy-Fraunié S, Dangles O. 2019.** A global synthesis of biodiversity responses to glacier
715 retreat. *Nature Ecology & Evolution* **3**: 1675–1685.
- 716 **Cázares E, Trappe JM. 1994.** Spore dispersal of ectomycorrhizal fungi on a glacier forefront by
717 mammal mycophagy. *Mycologia* **86**: 507–510.
- 718 **Cázares E, Trappe JM, Jumpponen A. 2005.** Mycorrhiza-plant colonization patterns on a
719 subalpine glacier forefront as a model system of primary succession. *Mycorrhiza* **15**: 405–416.
- 720 **Chang CC, Turner BL. 2019.** Ecological succession in a changing world. *Journal of Ecology* **107**:
721 503–509.
- 722 **Chapin FS, Walker LR, Fastie CL, Sharman LC. 1994.** Mechanisms of primary succession
723 following deglaciation at Glacier bay, Alaska. *Ecological Monographs* **64**: 149–175.
- 724 **Chaudhary VB, Noliml S, Sosa-Hernández MA, Egan C, Kastens J. 2020.** Trait-based aerial
725 dispersal of arbuscular mycorrhizal fungi. *New Phytologist* **n/a**.
- 726 **Chaudhary B, Sandall E, Lazarski M. 2018.** Urban mycorrhizas: predicting arbuscular
727 mycorrhizal abundance in green roofs. *Fungal Ecology* **40**.
- 728 **Clements FE. 1916.** *Plant succession; an analysis of the development of vegetation*. Washington:
729 Carnegie Institution of Washington.
- 730 **Cutler F original by LB and A, Wiener R port by AL and M. 2022.** randomForest: Breiman and
731 Cutler’s Random Forests for Classification and Regression.

732 **Davey M, Blaaid R, Vik U, Carlsen T, Kauserud H, Eidesen PB. 2015.** Primary succession of
733 *Bistorta vivipara* (L.) Delabre (Polygonaceae) root-associated fungi mirrors plant succession in
734 two glacial chronosequences. *Environmental Microbiology* **17**: 2777–2790.

735 **Davison J, Moora M, Öpik M, Adholeya A, Ainsaar L, Bâ A, Burla S, Diedhiou AG, Hiiesalu I,**
736 **Jairus T, et al. 2015.** Global assessment of arbuscular mycorrhizal fungus diversity reveals very
737 low endemism. *Science* **349**: 970–973.

738 **Delavaux CS, Weigelt P, Dawson W, Duchicela J, Essl F, van Kleunen M, König C, Pergl J, Pyšek**
739 **P, Stein A, et al. 2019.** Mycorrhizal fungi influence global plant biogeography. *Nature Ecology &*
740 *Evolution* **3**: 424–429.

741 **Delavaux CS, Weigelt P, Dawson W, Essl F, van Kleunen M, König C, Pergl J, Pyšek P, Stein A,**
742 **Winter M, et al. 2021.** Mycorrhizal types influence island biogeography of plants.
743 *Communications Biology* **4**: 1–8.

744 **Dickie IA, Martínez-García LB, Koele N, Grelet G-A, Tylianakis JM, Peltzer DA, Richardson SJ.**
745 **2013.** Mycorrhizas and mycorrhizal fungal communities throughout ecosystem development.
746 *Plant and Soil* **367**: 11–39.

747 **Dunnington D. 2018.** *ggspatial: Spatial Data Framework for ggplot2*. [https://CRAN.R-](https://CRAN.R-project.org/package=ggspatial)
748 [project.org/package=ggspatial](https://CRAN.R-project.org/package=ggspatial).

749 **Epp LS, Boessenkool S, Bellemain EP, Haile J, Esposito A, Riaz T, Erséus C, Gusarov VI, Edwards**
750 **ME, Johnsen A, et al. 2012.** New environmental metabarcodes for analysing soil DNA: potential
751 for studying past and present ecosystems. *Molecular Ecology* **21**: 1821–1833.

752 **Fei S, Kivlin SN, Domke GM, Jo I, LaRue EA, Phillips RP. 2022.** Coupling of plant and mycorrhizal
753 fungal diversity: its occurrence, relevance, and possible implications under global change. *New*
754 *Phytologist* **234**: 1960–1966.

755 **Ficetola GF, Coissac E, Zundel S, Riaz T, Shehzad W, Bessièrè J, Taberlet P, Pompanon F. 2010.**
756 An In silico approach for the evaluation of DNA barcodes. *BMC Genomics* **11**: 434.

757 **Ficetola GF, Marta S, Guerrieri A, Gobbi M, Ambrosini R, Fontaneto D, Zerboni A, Poulénard J,**
758 **Caccianiga M, Thuiller W. 2021.** Dynamics of ecological communities following current retreat
759 of glaciers. *Annual Review of Ecology, Evolution, and Systematics* **52**: 405–426.

760 **Ficetola GF, Pansu J, Bonin A, Coissac E, Giguet-Covex C, De Barba M, Gielly L, Lopes CM,**
761 **Boyer F, Pompanon F, et al. 2015.** Replication levels, false presences and the estimation of the
762 presence/absence from eDNA metabarcoding data. *Molecular Ecology Resources* **15**: 543–556.

763 **Fickert T, Grüninger F. 2018.** High-speed colonization of bare ground—Permanent plot studies
764 on primary succession of plants in recently deglaciated glacier forelands. *Land Degradation &*
765 *Development* **29**: 2668–2680.

766 **Fitzpatrick M, Mokany K, Manion G, Nieto-Lugilde D, Ferrier S, Lisk M, Ware C, Woolley S,**
767 **Harwood T. 2022.** gdm: Generalized Dissimilarity Modeling.

768 **Foster BL, Tilman D. 2000.** Dynamic and static views of succession: Testing the descriptive
769 power of the chronosequence approach. *Plant Ecology* **146**: 1–10.

770 **Foucher A, Evrard O, Ficetola GF, Gielly L, Poulain J, Giguet-Covex C, Lacey JP, Salvador-**
771 **Blanes S, Cerdan O, Poulenard J. 2020.** Persistence of environmental DNA in cultivated soils:
772 implication of this memory effect for reconstructing the dynamics of land use and cover
773 changes. *Scientific Reports* **10**: 10502.

774 **Fujiyoshi M, Yoshitake S, Watanabe K, Murota K, Tsuchiya Y, Uchida M, Nakatsubo T. 2011.**
775 Successional changes in ectomycorrhizal fungi associated with the polar willow *Salix polaris* in a
776 deglaciaded area in the High Arctic, Svalbard. *Polar Biology* **34**: 667–673.

777 **Guerrieri A, Bonin A, Gielly L, Ficetola GF. 2022a.** Raw sequencing data for studying the
778 colonization of soil communities after glacier retreat.

779 **Guerrieri A, Bonin A, Münkemüller T, Gielly L, Thuiller W, Ficetola GF. 2021.** Effects of soil
780 preservation for biodiversity monitoring using environmental DNA. *Molecular Ecology* **30**:
781 3313–3325.

782 **Guerrieri A, Cantera I, Marta S, Bonin A, Carteron A, Ambrosini R, Anthelme F, Azzoni R,**
783 **Almond P, Gazitúa P, et al. In press.** Local climate modulates the development of soil
784 nematode communities after glacier retreat. *Global Change Biology*.

785 **Guerrieri A, Carteron A, Bonin A, Marta S, Ambrosini R, Caccianiga M, Cantera I, Compostella**
786 **C, Diolaiuti G, Fontaneto D, et al. 2022b.** Metabarcoding data reveal vertical multitaxa
787 variation in topsoil communities during the colonization of deglaciaded forelands. *Molecular*
788 *Ecology*.

789 **Hanusch M, He X, Ruiz-Hernández V, Junker RR. 2022.** Succession comprises a sequence of
790 threshold-induced community assembly processes towards multidiversity. *Communications*
791 *Biology* **5**: 1–9.

792 **van der Heijden MGA, Bardgett RD, van Straalen NM. 2008.** The unseen majority: soil
793 microbes as drivers of plant diversity and productivity in terrestrial ecosystems. *Ecology Letters*
794 **11**: 296–310.

795 **van der Heijden MGA, Klironomos JN, Ursic M, Moutoglis P, Streitwolf-Engel R, Boller T,**
796 **Wiemken A, Sanders IR. 1998.** Mycorrhizal fungal diversity determines plant biodiversity,
797 ecosystem variability and productivity. *Nature* **396**: 69–72.

798 **van der Heijden MGA, Martin FM, Selosse M-A, Sanders IR. 2015.** Mycorrhizal ecology and
799 evolution: the past, the present, and the future. *New Phytologist* **205**: 1406–1423.

- 800 **Helm DJ, Allen EB, Trappe JM. 1999.** Plant growth and ectomycorrhiza formation by transplants
801 on deglaciated land near Exit Glacier, Alaska. *Mycorrhiza* **8**: 297–304.
- 802 **Hiiesalu I, Schweichhart J, Angel R, Davison J, Doležal J, Kopecký M, Macek M, Řehakova K.**
803 **2023.** Plant-symbiotic fungal diversity tracks variation in vegetation and the abiotic
804 environment along an extended elevational gradient in the Himalayas. *FEMS microbiology*
805 *ecology* **99**: fiad092.
- 806 **Hock R, Bliss A, Marzeion B, Giesen RH, Hirabayashi Y, Huss M, Radić V, Slangen ABA. 2019.**
807 GlacierMIP – A model intercomparison of global-scale glacier mass-balance models and
808 projections. *Journal of Glaciology* **65**: 453–467.
- 809 **Johnson EA, Miyanishi K. 2008.** Testing the assumptions of chronosequences in succession.
810 *Ecology Letters* **11**: 419–431.
- 811 **Jumpponen A, Brown SP, Trappe JM, Cázares E, Strömmer R. 2012.** Twenty years of research
812 on fungal–plant interactions on Lyman Glacier forefront – lessons learned and questions yet
813 unanswered. *Fungal Ecology* **5**: 430–442.
- 814 **Khedim N, Cécillon L, Poulénard J, Barré P, Baudin F, Marta S, Rabatel A, Dentant C, Cauvy-**
815 **Fraunié S, Anthelme F, et al. 2021.** Topsoil organic matter build-up in glacier forelands around
816 the world. *Global Change Biology* **27**: 1662–1677.
- 817 **Kivlin SN. 2020.** Global mycorrhizal fungal range sizes vary within and among mycorrhizal guilds
818 but are not correlated with dispersal traits. *Journal of Biogeography* **n/a**.
- 819 **Kivlin SN, Mann MA, Lynn JS, Kazenel MR, Taylor DL, Rudgers JA. 2022.** Grass species identity
820 shapes communities of root and leaf fungi more than elevation. *ISME Communications* **2**: 1–11.
- 821 **Kopecký M, Macek M, Wild J. 2021.** Topographic Wetness Index calculation guidelines based
822 on measured soil moisture and plant species composition. *Science of The Total Environment*
823 **757**: 143785.
- 824 **Körner C. 2004.** Mountain Biodiversity, Its Causes and Function. *AMBIO: A Journal of the Human*
825 *Environment* **33**: 11–17.
- 826 **Lambers H, Raven JA, Shaver GR, Smith SE. 2008.** Plant nutrient-acquisition strategies change
827 with soil age. *Trends in Ecology & Evolution* **23**: 95–103.
- 828 **Lekberg Y, Vasar M, Bullington LS, Sepp S-K, Antunes PM, Bunn R, Larkin BG, Öpik M. 2018.**
829 More bang for the buck? Can arbuscular mycorrhizal fungal communities be characterized
830 adequately alongside other fungi using general fungal primers? *New Phytologist* **220**: 971–976.
- 831 **Lillesand T, Kiefer RW, Chipman J. 2015.** *Remote Sensing and Image Interpretation, 7th Edition.*
832 Wiley.

- 833 **Liu Y, Li Z, Chen Y. 2021.** Continuous warming shift greening towards browning in the Southeast
834 and Northwest High Mountain Asia. *Scientific Reports* **11**: 17920.
- 835 **Llambí LD, Melfo A, Gámez LE, Pelayo RC, Cárdenas M, Rojas C, Torres JE, Ramírez N, Huber B,**
836 **Hernández J. 2021.** Vegetation Assembly, Adaptive Strategies and Positive Interactions During
837 Primary Succession in the Forefield of the Last Venezuelan Glacier. *Frontiers in Ecology and*
838 *Evolution* **9**.
- 839 **Mächler E, Walser J-C, Altermatt F. 2021.** Decision-making and best practices for taxonomy-
840 free environmental DNA metabarcoding in biomonitoring using Hill numbers. *Molecular Ecology*
841 **30**: 3326–3339.
- 842 **Makoto K, Wilson SD. 2019.** When and where does dispersal limitation matter in primary
843 succession? *Journal of Ecology* **107**: 559–565.
- 844 **Marta S, Azzoni RS, Fugazza D, Tielidze L, Chand P, Sieron K, Almond P, Ambrosini R,**
845 **Anthelme F, Alviz Gazitúa P, et al. 2021.** The Retreat of Mountain Glaciers since the Little Ice
846 Age: A Spatially Explicit Database. *Data* **6**: 107.
- 847 **Marta S, Zimmer A, Caccianiga M, Gobbi M, Ambrosini R, Azzoni RS, Gili F, Pittino F, Thuiller**
848 **W, Provenzale A, et al. 2023.** Heterogeneous changes of soil microclimate in high mountains
849 and glacier forelands. *Nature Communications*.
- 850 **Martin FM, Harrison MJ, Lennon S, Lindahl B, Öpik M, Polle A, Requena N, Selosse M-A. 2018.**
851 Cross-scale integration of mycorrhizal function. *New Phytologist* **220**: 941–946.
- 852 **McMurdie PJ, Holmes S. 2013.** phyloseq: An R package for reproducible interactive analysis and
853 graphics of microbiome census data. *PLOS ONE* **8**: e61217.
- 854 **McMurdie PJ, Holmes S. 2014.** Waste not, want not: Why rarefying microbiome data is
855 inadmissible. *PLOS Computational Biology* **10**: e1003531.
- 856 **Mohan JE, Cowden CC, Baas P, Dawadi A, Frankson PT, Helmick K, Hughes E, Khan S, Lang A,**
857 **Machmuller M, et al. 2014.** Mycorrhizal fungi mediation of terrestrial ecosystem responses to
858 global change: mini-review. *Fungal Ecology* **10**: 3–19.
- 859 **Nara K. 2006.** Ectomycorrhizal networks and seedling establishment during early primary
860 succession. *New Phytologist* **169**: 169–178.
- 861 **Nguyen NH, Song Z, Bates ST, Branco S, Tedersoo L, Menke J, Schilling JS, Kennedy PG. 2016.**
862 FUNGuild: An open annotation tool for parsing fungal community datasets by ecological guild.
863 *Fungal Ecology* **20**: 241–248.
- 864 **Nilsson RH, Anslan S, Bahram M, Wurzbacher C, Baldrian P, Tedersoo L. 2019.** Mycobiome
865 diversity: high-throughput sequencing and identification of fungi. *Nature Reviews Microbiology*
866 **17**: 95.

867 **Oehl F, Schneider D, Sieverding E, Burga CA. 2011.** Succession of arbuscular mycorrhizal
868 communities in the foreland of the retreating Morteratsch glacier in the Central Alps.
869 *Pedobiologia* **54**: 321–331.

870 **Oksanen J, Blanchet FG, Friendly M, Kindt R, Legendre P, McGlenn D, Minchin PR, O’Hara RB,**
871 **Simpson GL, Solymos P, et al. 2017.** vegan: Community Ecology Package.

872 **Olsen SR. 1954.** *Estimation of available phosphorus in soils by extraction with sodium*
873 *bicarbonate*. Washington, D.C. : U.S. Dept. of Agriculture.

874 **Palomo I. 2017.** Climate Change Impacts on Ecosystem Services in High Mountain Areas: A
875 Literature Review. *Mountain Research and Development* **37**: 179–187.

876 **Paruelo JM, Epstein HE, Lauenroth WK, Burke IC. 1997.** ANPP Estimates from NDVI for the
877 Central Grassland Region of the United States. *Ecology* **78**: 953–958.

878 **Phoenix GK, Bjerke JW. 2016.** Arctic browning: extreme events and trends reversing arctic
879 greening. *Global Change Biology* **22**: 2960–2962.

880 **Poorter L, Craven D, Jakovac CC, van der Sande MT, Amissah L, Bongers F, Chazdon RL, Farrior**
881 **CE, Kambach S, Meave JA, et al. 2021.** Multidimensional tropical forest recovery. *Science* **374**:
882 1370–1376.

883 **Pothula SK, Adams BJ. 2022.** Community assembly in the wake of glacial retreat: A meta-
884 analysis. *Global Change Biology* **28**: 6973–6991.

885 **Prach K, Walker LR. 2020.** *Comparative Plant Succession among Terrestrial Biomes of the*
886 *World*. Cambridge: Cambridge University Press.

887 **Rasmussen PU, Abrego N, Roslin T, Öpik M, Sepp S-K, Blanchet FG, Huotari T, Hugerth LW,**
888 **Tack AJM. 2022.** Elevation and plant species identity jointly shape a diverse arbuscular
889 mycorrhizal fungal community in the High Arctic. *New Phytologist* **236**: 671–683.

890 **Read DJ, Perez-Moreno J. 2003.** Mycorrhizas and nutrient cycling in ecosystems – a journey
891 towards relevance? *New Phytologist* **157**: 475–492.

892 **Rime T, Hartmann M, Brunner I, Widmer F, Zeyer J, Frey B. 2015.** Vertical distribution of the
893 soil microbiota along a successional gradient in a glacier forefield. *Molecular Ecology* **24**: 1091–
894 1108.

895 **Rounce DR, Hock R, Maussion F, Hugonnet R, Kochtitzky W, Huss M, Berthier E, Brinkerhoff D,**
896 **Compagno L, Copland L, et al. 2023.** Global glacier change in the 21st century: Every increase in
897 temperature matters. *Science* **379**: 78–83.

898 **Rumpf SB, Gravey M, Brönnimann O, Luoto M, Cianfrani C, Mariethoz G, Guisan A. 2022.** From
899 white to green: Snow cover loss and increased vegetation productivity in the European Alps.
900 *Science* **376**: 1119–1122.

901 **Slowikowski K, Schep A, Hughes S, Dang TK, Lukauskas S, Irisson J-O, Kamvar ZN, Ryan T,**
902 **Christophe D, Hiroaki Y, et al. 2021.** ggrepel: Automatically Position Non-Overlapping Text
903 Labels with ‘ggplot2’.

904 **Smith P, Metcalfe P. 2022.** dynatop: An Implementation of Dynamic TOPMODEL Hydrological
905 Model in R.

906 **Smith SE, Read DJ. 2008.** *Mycorrhizal Symbiosis*. Academic Press.

907 **Soudzilovskaia NA, Vaessen S, Barcelo M, He J, Rahimlou S, Abarenkov K, Brundrett MC,**
908 **Gomes SIF, Merckx V, Tedersoo L. 2020.** FungalRoot: global online database of plant
909 mycorrhizal associations. *New Phytologist* **227**: 955–966.

910 **South A. 2017.** rnaturalearth: World Map Data from Natural Earth.

911 **Steidinger BS, Crowther TW, Liang J, Nuland MEV, Werner GDA, Reich PB, Nabuurs G, de-**
912 **Miguel S, Zhou M, Picard N, et al. 2019.** Climatic controls of decomposition drive the global
913 biogeography of forest-tree symbioses. *Nature* **569**: 404.

914 **Surova TG, Vtyurin BI, Troitskiy LS. 1992.** Pollen and spores from glaciers and from the
915 proglacial zone in the arctic and Antarctica. *Polar Geography and Geology* **16**: 167–173.

916 **Sytsma MLT, Lewis T, Bakker JD, Prugh LR. 2023.** Successional patterns of terrestrial wildlife
917 following deglaciation. *Journal of Animal Ecology* **92**: 723–737.

918 **Taberlet P, Bonin A, Zinger L, Coissac E. 2018.** *Environmental DNA: For Biodiversity Research*
919 *and Monitoring*. Oxford: Oxford University Press.

920 **Taberlet P, Coissac E, Pompanon F, Brochmann C, Willerslev E. 2012.** Towards next-generation
921 biodiversity assessment using DNA metabarcoding. *Molecular Ecology* **21**: 2045–2050.

922 **Taberlet P, Coissac E, Pompanon F, Gielly L, Miquel C, Valentini A, Vermet T, Corthier G,**
923 **Brochmann C, Willerslev E. 2007.** Power and limitations of the chloroplast trnL (UAA) intron for
924 plant DNA barcoding. *Nucleic Acids Research* **35**: e14–e14.

925 **Tansley AG. 1935.** The Use and Abuse of Vegetational Concepts and Terms. *Ecology* **16**: 284–
926 307.

927 **Tedersoo L, Bahram M. 2019.** Mycorrhizal types differ in ecophysiology and alter plant
928 nutrition and soil processes. *Biological Reviews* **94**: 1857–1880.

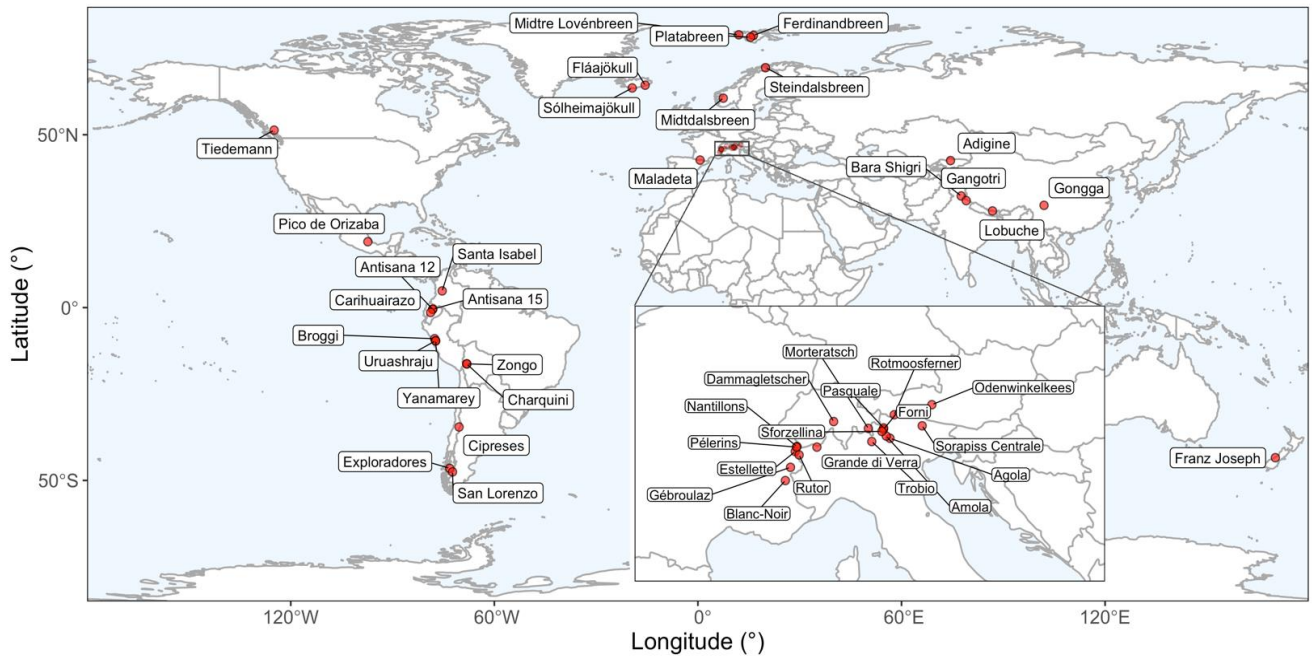
- 929 **Tedersoo L, Bahram M, Zinger L, Nilsson RH, Kennedy PG, Yang T, Anslan S, Mikryukov V.**
 930 **2022.** Best practices in metabarcoding of fungi: From experimental design to results. *Molecular*
 931 *Ecology* **31**: 2769–2795.
- 932 **Tedersoo L, Bahram M, Zobel M.** **2020.** How mycorrhizal associations drive plant population
 933 and community biology. *Science* **367**.
- 934 **Trowbridge J, Jumpponen A.** **2004.** Fungal colonization of shrub willow roots at the forefront of
 935 a receding glacier. *Mycorrhiza* **14**: 283–93.
- 936 **Veresoglou SD, Rillig MC.** **2014.** Do closely related plants host similar arbuscular mycorrhizal
 937 fungal communities? A meta-analysis. *Plant and Soil* **377**: 395–406.
- 938 **Walker LR, Wardle DA, Bardgett RD, Clarkson BD.** **2010.** The use of chronosequences in studies
 939 of ecological succession and soil development. *Journal of Ecology* **98**: 725–736.
- 940 **Wickham H.** **2016.** *ggplot2: Elegant graphics for data analysis*. Springer-Verlag New York.
- 941 **Wickham H, Francois R, Henry L, Müller K.** **2017.** *dplyr: A grammar of data manipulation*.
 942 <https://CRAN.R-project.org/package=dplyr>.
- 943 **Wickham H, Henry L.** **2019.** *tidyr: Tidy messy data*. <https://CRAN.R-project.org/package=tidyr>.
- 944 **Wietrzyk-Pełka P, Rola K, Szymański W, Węgrzyn MH.** **2020.** Organic carbon accumulation in
 945 the glacier forelands with regard to variability of environmental conditions in different
 946 ecogenesis stages of High Arctic ecosystems. *Science of The Total Environment* **717**: 135151.
- 947 **Wojcik R, Eichel J, Bradley JA, Benning LG.** **2021.** How allogenic factors affect succession in
 948 glacier forefields. *Earth-Science Reviews* **218**: 103642.
- 949 **Yang G, Ryo M, Roy J, Hempel S, Rillig MC.** **2021.** Plant and soil biodiversity have non-
 950 substitutable stabilising effects on biomass production. *Ecology Letters* **24**: 1582–1593.
- 951 **Zemp M, Huss M, Thibert E, Eckert N, McNabb R, Huber J, Barandun M, Machguth H,**
 952 **Nussbaumer SU, Gärtner-Roer I, et al.** **2019.** Global glacier mass changes and their
 953 contributions to sea-level rise from 1961 to 2016. *Nature* **568**: 382–386.
- 954 **Zimmer A, Beach T, Klein JA, Recharte Bullard J.** **2022.** The need for stewardship of lands
 955 exposed by deglaciation from climate change. *Wiley Interdisciplinary Reviews: Climate Change*
 956 **13**: e753.
- 957 **Zimmer A, Meneses RI, Rabatel A, Soruco A, Dangles O, Anthelme F.** **2018.** Time lag between
 958 glacial retreat and upward migration alters tropical alpine communities. *Perspectives in Plant*
 959 *Ecology, Evolution and Systematics* **30**: 89–102.

960 **Zinger L, Bonin A, Alsos IG, Bálint M, Bik H, Boyer F, Chariton AA, Creer S, Coissac E, Deagle**
961 **BE, et al. 2019.** DNA metabarcoding—Need for robust experimental designs to draw sound
962 ecological conclusions. *Molecular Ecology* **28**: 1857–1862.

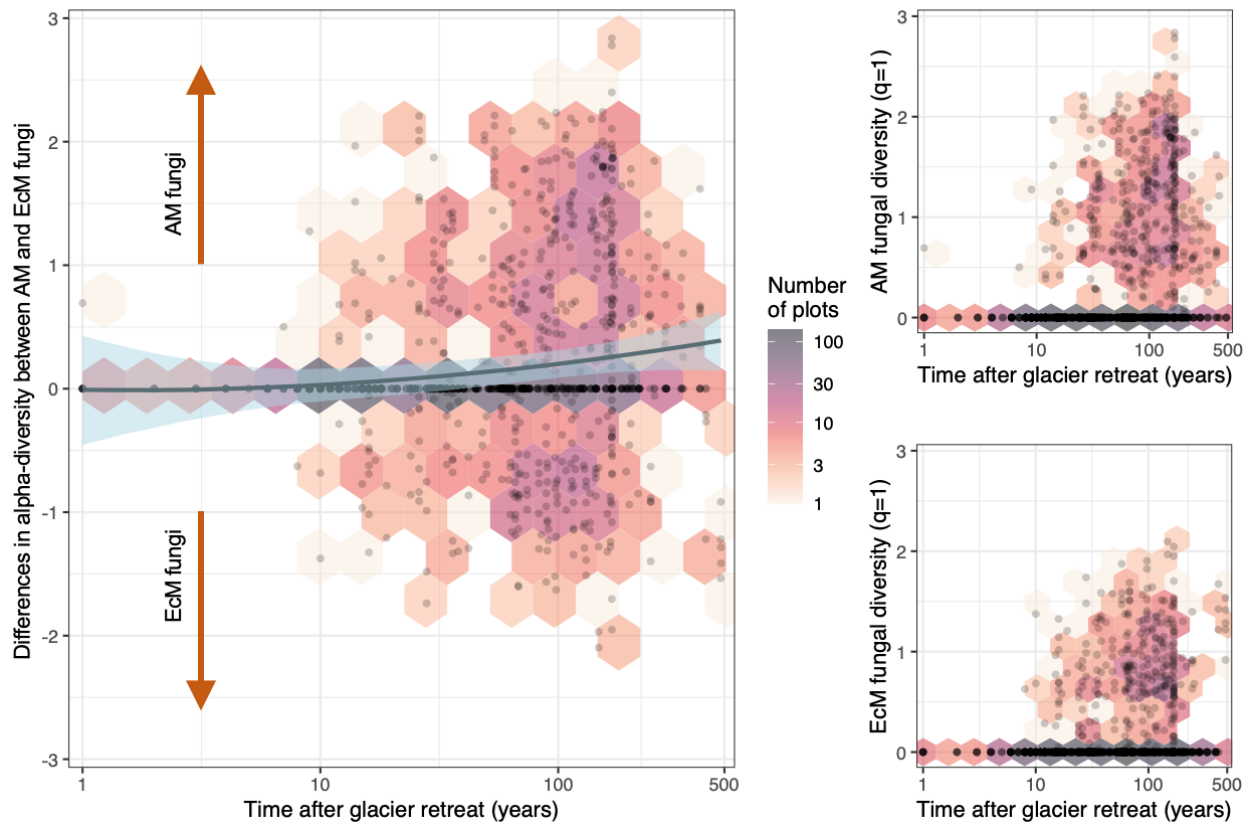
963 **Zobel M, Öpik M. 2014.** Plant and arbuscular mycorrhizal fungal (AMF) communities – which
964 drives which? *Journal of Vegetation Science* **25**: 1133–1140.

965

966 **FIGURES**
967



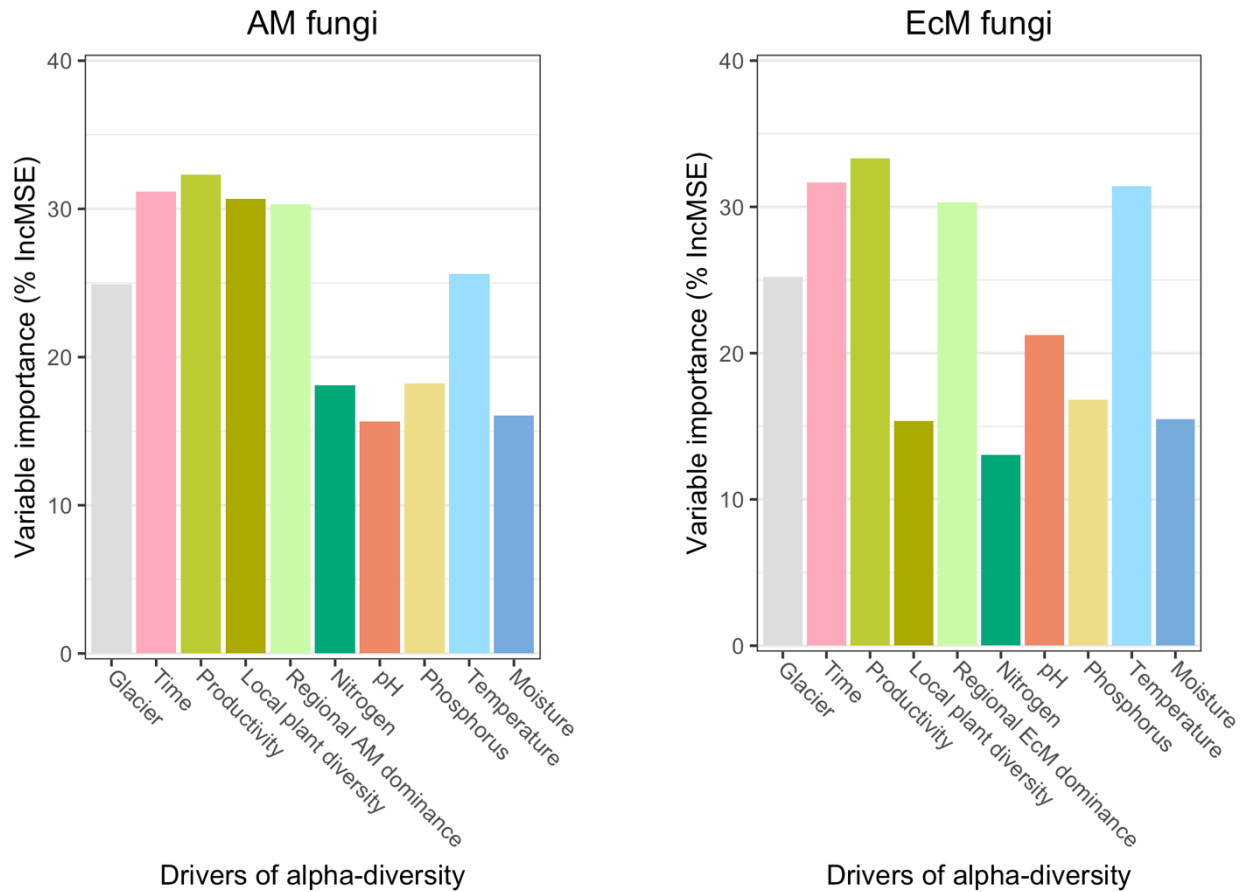
968
969 **Figure 1.** Location of the 46 glaciers whose proglacial areas were sampled for this study. The
970 inset map shows a zoom into the European Alps range.



971

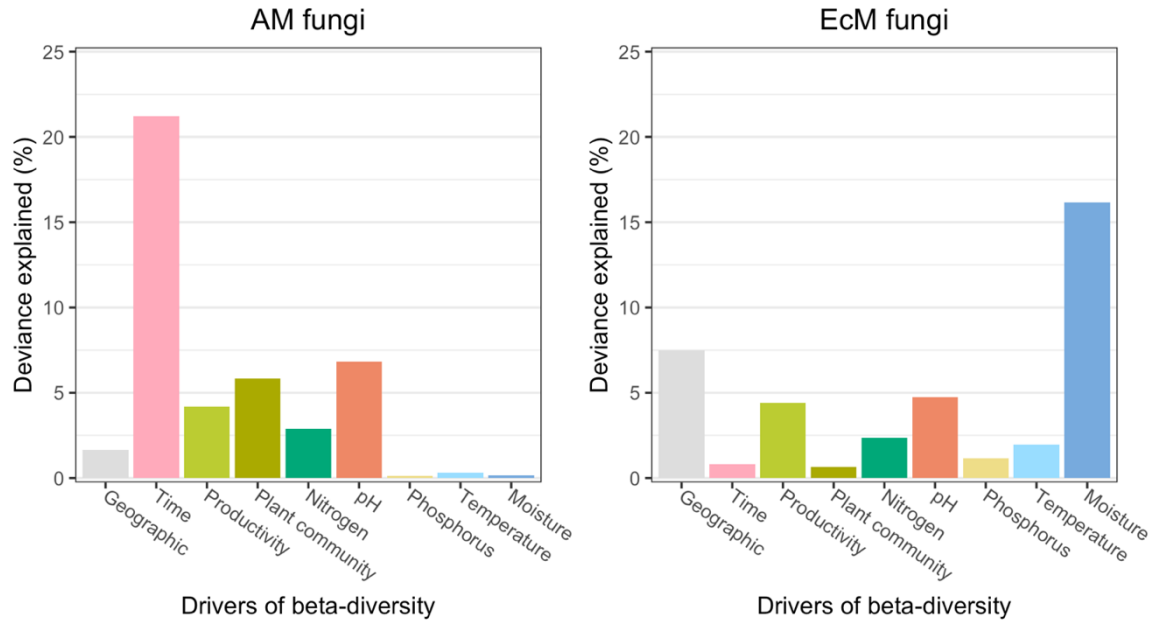
972

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.



979

980 **Figure 3.** Role of glacier identity, time after glacier retreat, soil chemistry (nitrogen, pH,
 981 phosphorus), regional tree mycorrhizal type dominance (regional AM or EcM dominance) and
 982 microclimate (temperature, moisture) on the alpha-diversity ($q = 1$) of AM and EcM fungi.
 983 Variable importance was determined by the increase in mean squared error (IncMSE) using
 984 random forest models. $N = 793$ plots in 32 proglacial areas. Variance explained was 49% and
 985 51% for AM and EcM fungi, respectively. Mean of squared residuals was 0.22 and 0.11 for AM
 986 and EcM fungi, respectively. See Table S3 for more details.



987

988

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