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## Bryophyte colonisation on recently deglaciated lands in the European Alps

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### ABSTRACT

**Introduction.** There is an increasingly urgent need for knowledge of primary succession along glacier forelands in order to improve our understanding of biodiversity changes at high elevations. Bryophytes play a key ecological role in primary succession, especially in the early stages, but bryophyte colonisation on alpine glacier forelands is still poorly studied. We investigated the first stages of bryophyte primary succession along a chronosequence on a glacier foreland in the European Alps.

**Methods.** Bryophytes on the Sforzellina glacier (Central Italian Alps) were sampled during the summer of 2022 in areas where the glacial front occurred in 1989, 2003, 2015 and 2019. At each site, six plots of 1 m × 1 m (5 m apart from each other) were sampled. For the most frequent species, plant and shoot size were measured to analyse growth trends throughout the succession.

**Key results and discussion.** In total, 13 moss species and two liverwort species were found. The mean number of species increased with the number of years since deglaciation, following an 'addition and persistence' model. The first pioneer species, *Pohlia filum* (Schimp.) Mårtensson and *Ptychostomum* sp., were present only 3 years after deglaciation; the occurrence of bulbils may help the former colonise bare ground quickly. Sporophytes had appeared 7 years after deglaciation. In *P. filum*, both shoot and plant size increased during the first stages of succession but had decreased on 33-year-old substrates. This pattern could be related to the fact that this species usually occurs on soils with very low organic matter content.

### KEYWORDS

Biodiversity; pioneer; *Pohlia filum*; primary succession; traits

### Introduction

As glacier retreat due to climate change accelerates, there is an increasingly urgent need for knowledge of primary succession along glacier forelands in order to improve our understanding of the dynamics and future development of high-elevation and high-latitude biodiversity (Erschbamer and Caccianiga 2016; Fickert 2017; Cauvy-Fraunié and Dangles 2019; Hågvar et al. 2020). Bryophytes play a key ecological role in glacial primary succession (Hågvar et al. 2020). In northern Europe, Hågvar and Pedersen (2015) and Flø and Hågvar (2013) documented the effectiveness of mosses as early colonisers, due to inblown moss fragments and diaspores. Given their role as early colonisers, bryophytes constitute an important food source for pioneer invertebrates living close to glaciers, where vascular plants are often absent (Hågvar and Pedersen 2015; Hågvar et al. 2020). Moss-associated cyanobacteria (Arróniz-Crespo et al. 2014) and the moss-associated microbiome in the soil (Klarenberg et al. 2023) play a key role in nitrogen fixation, an important process for nutrient accumulation during primary succession. In addition, mosses could facilitate

vascular plant colonisation by hosting plant seedlings (Delach and Kimmerer 2002; Gavini et al. 2019).

Despite their ecological importance in primary succession, particularly during the early stages (Hågvar et al. 2020), bryophyte colonisation on glacier forelands is still poorly studied (Chernova et al. 2021). Only a few reports have described floristic diversity or primary succession of bryophytes on glacier forelands worldwide (e.g. European Alps: Caccianiga et al. 2002; Scandinavia: Stork 1963; High Arctic: Wietrzyk-Pelka et al. 2021; Altai: Chernova et al. 2021; Canada: Birks 1980, Jones and Greg 2003; Andes: Arróniz-Crespo et al. 2014; Antarctica: Favero-Longo et al. 2012). In the European Alps, studies specifically addressing moss primary succession on glacier forelands are scarce, even considering local studies (e.g. Gärtner 2010). In almost every study looking at plant primary succession on glacier forelands, bryophytes are reported only as total cover or occurrence, or else only the most abundant species are reported (e.g. Burga 1999; Raffl and Erschbamer 2003). Bryophytes are not considered even in multitaxa studies obtained

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through DNA metabarcoding (e.g. Rosero et al. 2021; Fice-tola et al. 2024). Interesting data can be retrieved from bryophyte checklists compiled for high-elevation environments that include glacier forelands and moraines (e.g. Pottier 1920; Valle et al. 2024), but they usually do not take into account the successional stage at which the species have been observed. Furthermore, many local studies are not easily available for researchers to access.

In the present study, we aimed to provide a detailed description of the first stages of bryophyte primary succession along a glacier foreland of the European Alps, recording the occurrence and abundance of bryophyte species on sites with a known deglaciation age, and covering a time span of 3–33 years, in order to elucidate the colonisation process of the glacier foreland with high temporal resolution.

## Materials and methods

### Study area

The study was performed on 21 July 2022 on the Sforzellina glacier (Italian Alps, Lombardy; 46°20′55″N, 10°30′50″E), located in the southeastern Alps, in the Ortles-Cevedale group (Figure 1). The glacier covers an elevation range between 2790 m and 3060 m (Smiraglia and Diolaiuti 2015) under the Corno Tre Signori peak (3376 m a.s.l.), within the Stelvio National Park. The substrate of the study site is characterised by micaschists, paragneiss and orthogneiss (Chiesa et al. 2011; Montrasio et al. 2012) with poorly developed soil. The climate in the Stelvio National Park is continental (precipitation at Forni glacier, 812 mm/year at 2100 m a.s.l.).

The Sforzellina glacier is one of the best-known glaciers in Lombardy from a glaciological point of view: information is available about the glacier front

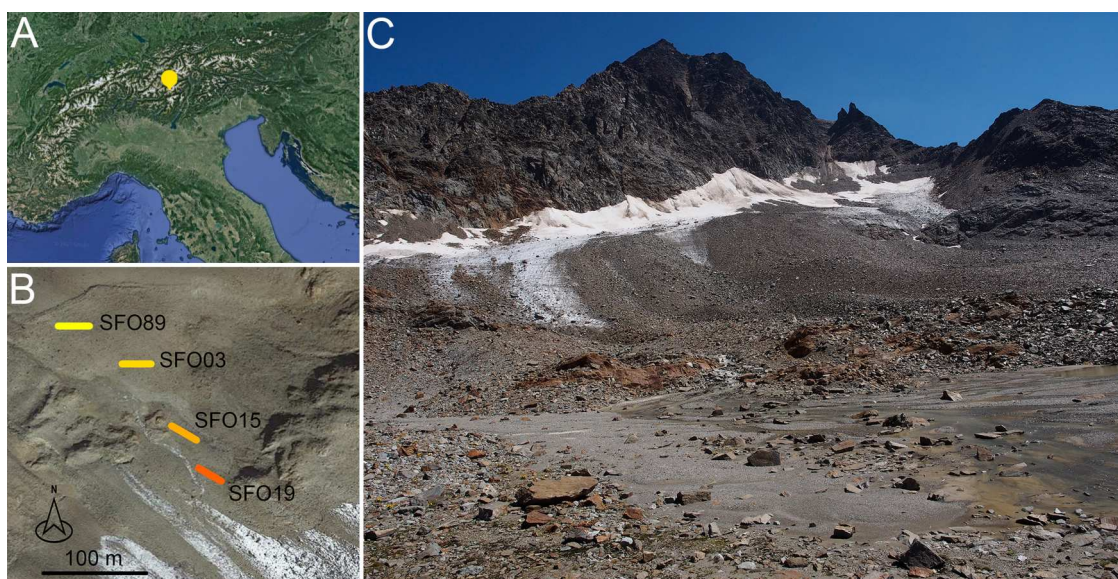
dynamics from 1925 to the present day (Marta et al. 2021). Marta et al. (2021) identified the positions of the glacial front at different phases after the Little Ice Age (in 1850, 1920, 1954, 1989, 2003, 2006, 2012 and 2015). The study area considered in the current research consists of the most recent portion of the chronosequence, represented by the areas vacated by the glacier after the end of the latest advance phase, from 1989 to 2019, i.e. areas deglaciated 3–33 years before the sampling year.

### Sampling design

Bryophytes were sampled on a transect running linearly through the areas where the glacial front occurred in 1989 (SFO89), 2003 (SFO03), 2015 (SFO15) and 2019 (SFO19); the historical position of the glacier was obtained from high-resolution data in Marta et al. (2021) (see Figure 1). At each site, bryophytes were sampled at six plots of 1 m × 1 m approximately 5 m apart from each other. The plots were aligned with the historical glacier position to place them on terrains that had been deglaciated the same number of years previously.

In the study area as a whole, the substrate consists of glacial till with heterogeneous grain-size distribution, ranging from chaotically arranged metric blocks to glacial silt (Figures 1 and 2). The area is level (slope < 10°) but surrounded by steep slopes and occasionally affected by meltwater from the nearby glacier and the long-lasting snow cover (see Figure 2).

At each plot, all bryophytes were collected that were distinguishable macroscopically or with the aid of a hand lens, and all vascular plant species present were recorded as presence/absence data. The overall cover



**Figure 1.** (A) Geographical position of the Sforzellina glacier in the Central Italian Alps. (B) Sampling sites (represented as a transect) along the glacier foreland (for site codes, see *Sampling plan*). (C) A general view of Sforzellina young glacier foreland; the photograph was taken at the approximate location of site SFO03. Credits: A and C, M. Caccianiga; B, Google Earth orthophoto.



**Figure 2.** Examples of plots from each of the four different sites corresponding to the different deglaciation stages surveyed. (A) SFO2019 (3 years since deglaciation). (B) SFO2015 (7 years since deglaciation). (C) SFO2003 (19 years since deglaciation). (D) SFO1989 (33 years since deglaciation). E, F, G and H represent, respectively, *Pohlia filum*, *Ptychostomum* sp., *Polytrichum piliferum* and *Polytrichum juniperinum* found on Sforzellina glacier foreland. Photographs: B. Valle.

value of bryophytes was visually evaluated with a resolution of 5%; for cover values < 5%, additional values of 1% and < 1% were recorded. The collected samples were stored in paper bags to allow them to be dehydrated and preserved until identification. Samples are stored in the Herbarium Universitatis Mediolanensis (HbMI Università Degli Studi di Milano).

### Species identification and data analysis

Species identification was carried out using a stereomicroscope and a transmission light microscope (Leitz DM RD; Leica, Wetzlar, Germany), following the dichotomous keys of Smith (1978), Cortini Pedrotti (2001, 2005), Holyoak (2021) and Hugonnot and Chavoutier (2021). For further verification, the identified moss

species were compared with entries in the illustrated atlas by Lüth (2019). Nomenclature follows Hodgetts et al. (2020). Some taxa (i.e. *Cephaloziella* sp., cf. *Gymnomitrium adustum*, cf. *Sanionia uncinata*, *Sciurohypnum* cf. *glaciale*) were present only as single, small specimens lacking sporophytes and could not be identified with certainty or to species level. For the genus *Ptychostomum*, we based identification mainly on spore diameter and papillosity (Smith 1973; Cortini Pedrotti 2001, 2005; Holyoak 2021); identification at species level was thus possible only when sporophytes were present, specimens lacking ripe capsules being recorded as *Ptychostomum* sp.

For every site, the presence of vegetative diaspores (e.g. bulbils) or sporophytes of each species was reported. Species attributes (life form, sexual and

vegetative reproduction) were obtained from Hill et al. (2007). For sexual reproduction of *Tortula* spp. information was obtained from Cortini Pedrotti (2001), as it is not present in Hill et al. (2007).

### Species trait measurement

Graph paper and a stereomicroscope were used to measure the plant diameter and shoot size of the most frequent species. These measurements were then used to analyse growth trends throughout the succession. Measurements were performed on *Oncophorus integerrimus*, *Pohlia filum*, *Ptychostomum* spp. (including all three congeneric species found) and *Racomitrium canescens*. Plant diameter was measured by considering the diameter of the largest tuft for each species in each plot. Shoot length was determined as the mean value of five shoots randomly sampled without sporophytes (if possible) for each plot, and measured with graph paper.

### Data analysis

Differences in number of species, plant diameter and shoot length among the different age classes were tested using analysis of variance (ANOVA) and Tukey's post hoc test, using the PAST software version 4.03 (Hammer et al. 2001).

### Results

In total, 13 species of mosses and two species of liverworts were found (Table 1, Appendix 1). Six species had sporophytes (see Table 1). *Pohlia filum* (see Figure 2E) developed sporophytes at sites that had been deglaciated 7 (1 of 6 plots), 19 (3 of 6 plots) and 33 (2 of 6 plots) years previously. *Ptychostomum* spp. (see Figure 2F) had sporophytes only 7 and 19 years after deglaciation, and *Tortula* spp. had sporophytes in the single plot where they were present. Based on spore traits, we assessed the occurrence of three species of *Ptychostomum* (spore diameter in parentheses): *P. creberrimum* (14–16  $\mu\text{m}$ ), *P. pallescens* (18–22  $\mu\text{m}$ ) and *P. inclinatum* (25–30  $\mu\text{m}$ ). The spore surface was smooth in *P. creberrimum* and papillose in *P. pallescens* and *P. inclinatum*.

The mean number of species increased with the number of years since deglaciation for both bryophytes and vascular plants. For both groups, the increase was significant from 3 to 7 years, and from 7 to 19 years, after deglaciation (Figure 3). The first pioneer species were observed 3 years after deglaciation (see Table 1, Figure 3) for bryophytes represented by the mosses *Pohlia filum* and *Ptychostomum* sp. Three years after deglaciation, the mean number of bryophyte species per plot was 0.5. The steepest increase in the mean number of species along the

chronosequence occurred, for both bryophytes and vascular plants, from 3 to 7 years after deglaciation (from 0.5 to 2.8 and from 0.6 to 3.3 species per plot for bryophytes and vascular plants, respectively). In the following successional stages, the number of species increased at a slower pace, particularly for bryophytes, with no significant increase from 19 to 33 years after deglaciation (see Figure 3). Bryophytes and vascular plants reached a mean of 5.1 and 7.6 species per plot, respectively (33 years after deglaciation in both cases) and a maximum of 6 and 10 species per plot, respectively.

Cover values were low, reaching a maximum of 5% at two plots 33 years after deglaciation, and remaining < 1% at all the plots 3 years after deglaciation and at all but one plot 7 years after deglaciation (see Appendix 1).

Most of the observed bryophytes share a 'turf' life form, consisting of loosely or closely packed vertical shoots with limited branching. The only exceptions were *Sciuro-hypnum* cf. *glaciale*, with a 'mat' life form, and cf. *Sanionia uncinata*, showing a 'weft' life form with intertwining, branched layers. *Ptychostomum pallescens* form tufts as a primary life form, but the turf life form also occurs (Hill et al. 2007).

Relations between shoot length or plant diameter and the number of years since deglaciation are shown in Figure 4. Trends for shoot length differed among the analysed species (see Figure 4A): although in *Oncophorus integerrimus* shoot length did not vary significantly, for *Pohlia filum* it increased until 19 years after deglaciation, after which it decreased, and the same pattern was observed for plant diameter in *P. filum* (see Figure 4B). All differences in both shoot length and plant diameter in *P. filum* between one stage and the next were significant. The results for *Ptychostomum* sp. and *Racomitrium canescens* showed a general decrease in shoot length; the decrease was significant from 7 to 19 years after deglaciation for *Ptychostomum*, and from 19 to 33 years after deglaciation for *Racomitrium* (see Figure 4A). *Oncophorus integerrimus* and *P. filum* showed a positive trend regarding plant diameter in relation to number of years since deglaciation, although in the oldest terrains *P. filum* tufts were of decreased size (differences among sites were not significant; see Figure 4B). *Ptychostomum* sp. showed only isolated shoots in the first 3 years after deglaciation; its peak plant diameter was reached on terrains that had been deglaciated 7 years previously, and a significant decrease was observed from 7 to 19 years after deglaciation. The plant diameter results for *R. canescens* showed no significant trends.

### Discussion

On the Sforzellina glacier, bryophytes are able to colonise deglaciated terrains at least 3 years after deglaciation. A visual inspection of the immediate proximity of

**Table 1.** Species frequency at each sampling site (calculated as a percentage of plots in which the species was present for a total of six at each site). Frequency value classes indicated by different colours and degrees of shading.

Species (mode of reproduction, where known)	Deglaciation year (no. of years since deglaciation)			
	2019 (3)	2015 (7)	2003 (19)	1989 (33)
<b>Mosses</b>				
<i>Pohlia filum</i> (Schimp.) <sup>a</sup> Mårtensson (D)	33%	100% <sup>b</sup>	100% <sup>b</sup>	100% <sup>b</sup>
<i>Ptychostomum</i> sp. (M)	17%	100%	83%	83%
<i>Ptychostomum creberrimum</i> (Taylor) J.R.Spence & H.P.Ramsay		83% <sup>b</sup>	17% <sup>b</sup>	
<i>Ptychostomum inclinatum</i> (Sw. ex Brid.) J.R.Spence		33% <sup>b</sup>		
<i>Ptychostomum pallescens</i> (Schleich. ex Schwaegr.) J.R.Spence		33% <sup>b</sup>	17% <sup>b</sup>	
<i>Oncophorus integerrimus</i> Hedenäs (M)		17%	33%	67%
<i>Racomitrium canescens</i> (Hedw.) Brid. (D)		50%	50%	83%
<i>Tortula mucronifolia</i> Schwägr. (A)		17% <sup>b</sup>		
<i>Tortula hoppeana</i> (Schultz) Ochyra (A)			17% <sup>b</sup>	
<i>Bryum</i> sp.			33%	
<i>Polytrichum piliferum</i> Hedw. (D)			83%	100%
<i>Polytrichum juniperinum</i> Hedw. (D)				33%
cf. <i>Sanionia uncinata</i> (Hedw.) Loeske (M)				17%
<i>Sciuro-hypnum</i> cf. <i>glaciale</i> (Schimp.) Ignatov & Huttunen (M)				17%
<b>Liverworts</b>				
<i>Cephaloziella</i> sp.				17%
cf. <i>Gymnomitrium adustum</i> Nees (M)				17%

A, autoicous; D, dioecious; M, monoecious.

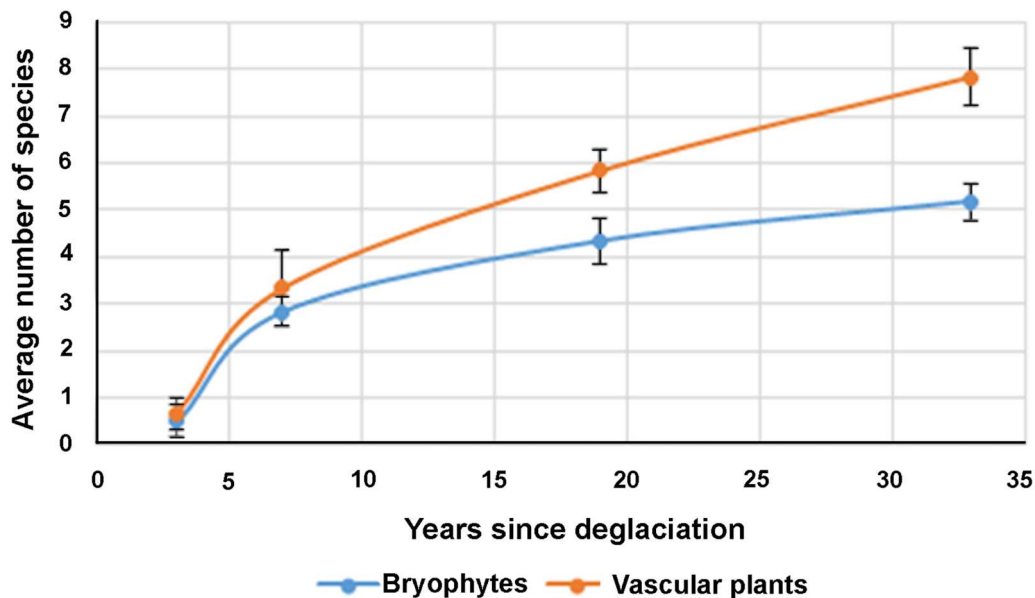
<sup>a</sup>Bulbils present.

<sup>b</sup>Sample with sporophytes.

the glacier and of supraglacial debris did not reveal any individuals, but tiny diaspores and propagules could have been overlooked. Our finding is similar to the findings of studies of Scandinavian glacier foreland, where tiny pioneer mosses were observed 3–4 years after deglaciation (Stork 1963; Hågvar et al. 2020). The observed importance of vascular plants with respect to bryophytes could represent a typical trait of alpine early-successional stages; Caccianiga and Andreis (2004) showed bulk cover values for bryophytes that were systematically lower than those of vascular plants, and always < 5%, on terrains younger than 30 years, which was consistent with our findings. This pattern has also been reported by Matthews (1992 and references therein) for the European Alps and for some sites in Scandinavia and Greenland. Alpine glacier forelands are often characterised by a coarse grain size of glacial deposits, due to the

overall steep topography. This pattern could represent a limit to bryophyte establishment on flatter terrains with fine grain size and higher humidity; indeed, phanerogams are reported to occur as the main pioneer on gravelly and stony till (Matthews 1992).

The first bryophytes found along Sforzellina glacier foreland were *Pohlia filum* and *Ptychostomum* sp. *Pohlia filum* was noteworthy for the occurrence of bulbils, found on every collected sample, that could help in quickly colonising bare ground through vegetative reproduction (Elven 1980; Hågvar and Pedersen 2015), while sporophytes were absent 3 years after deglaciation and appear afterwards. The patterns of both shoot length and plant diameter in *P. filum* show a decrease after 30 years, probably because this species is usually linked to soils with very low organic matter content (Shaw 1981). In general, *Pohlia* and *Bryum* genera seem to include important

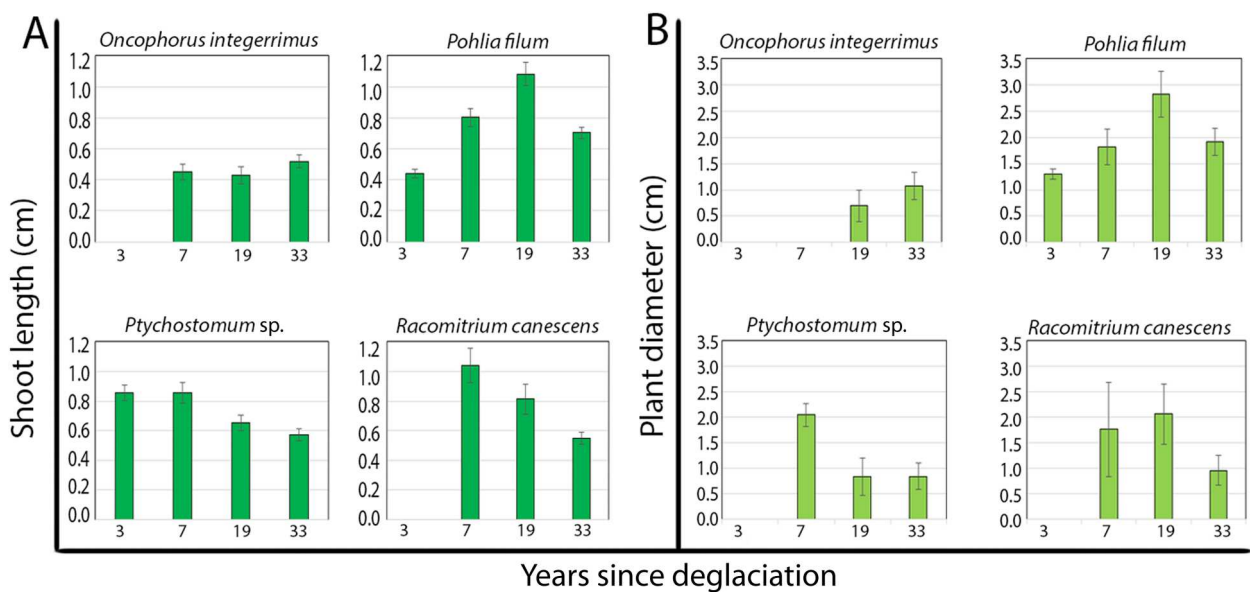


**Figure 3.** Mean number of bryophyte and vascular plant species in relation to number of years since deglaciation. Error bars indicate standard error. For both bryophytes and vascular plants, the increase was significant from 3 to 7 years, and from 7 to 19 years, after deglaciation (ANOVA and Tukey's post hoc test, respectively,  $p < 0.005$  and  $< 0.005$  for bryophytes and  $p = 0.019$  and  $0.029$  for vascular plants).

pioneer mosses in glacial areas (Stork 1963; Burga 1999; Hågvar and Pedersen 2015). However, to our knowledge, the three species of *Ptychostomum* found on the Sforzellina glacier, namely *P. creberrimum*, *P. inclinatum* and *P. pallescens*, have not been reported in previous work as pioneer species along glacier forelands.

Bryophyte succession along the Sforzellina glacier foreland follows an 'addition and persistence' model

(Vater and Matthews 2015; Ficetola et al. 2021), probably because in such an extreme habitat, facilitation prevails over competition (Callaway and Lawrence 1997). However, it is important to remember that the present study focused on the first 30 years of succession, and pioneer species may disappear on older terrains. The negative trends for shoot length and plant diameter in pioneer species such as *Pohlia filum* on 33-year-old terrain could represent a trend in this



**Figure 4.** (A) Shoot length of the four most frequent species in relation to number of years since deglaciation. For *Onchophorus integerrimus*, *Pohlia filum* and *Racomitrium canescens* the trends are not significant (ANOVA test and Tukey's post hoc test). *Ptychostomum* spp. trends are significant from 7 to 19 years after deglaciation (ANOVA test and Tukey's post hoc test,  $p = 0.03$ ). (B) Plant diameter of the four most frequent species in relation to number of years since deglaciation. For *P. filum* all differences between one stage and the next are significant (ANOVA and Tukey's post hoc test  $p < 0.005$ ). *Ptychostomum* sp. and *R. canescens* trends are significant from 7 to 19 years after deglaciation (ANOVA and Tukey's post hoc test,  $p = 0.0038$ ) and from 19 to 33 years after deglaciation (ANOVA and Tukey's post hoc test,  $p < 0.005$ ), respectively.

direction, consistent with the disappearance of *P. filum* 47 years after deglaciation on the Morteratsch glacier (Burga 1999).

The observed mosses are acrocarpous, with the exception of cf. *Sanionia uncinata* and *Sciuro-hypnum* cf. *glaciale*, which were recorded only in the older successional stages; this confirms on a small scale what has been observed by Birks (1980) along a Canadian glacier foreland. *Sanionia uncinata* could represent a dominant species in High-Arctic glacier foreland (Uchida et al. 2002), while on the European Alps it seems less abundant and linked to waterlogged sites (Raffl and Erschbamer 2003).

The two liverworts, cf. *Gymnomitrium adustum* and *Cephaloziella* sp., were found in the older stages. The later occurrence of liverworts with respect to mosses and vascular plants confirms the observations summarised by Matthews (1992). *Gymnomitrium adustum* is categorised in the Red List of endangered species in European countries as of Least Concern (LC), where it is present (Górski and Váňa 2011; Hodgetts et al. 2019). Its presence was recorded in Italy only for Piedmont (Aleffi and Schumacker 1995; Aleffi et al. 2023). The moss *Tortula mucronifolia* is reported in the Italian IUCN Red List as Vulnerable (VU; Puglisi et al. 2024), and in the European Red List as Near Threatened (NT) (Hodgetts et al. 2019), and its presence in Lombardy was documented only by historical records (Aleffi et al. 2023). The occurrence of the moss *Oncophorus integerrimus*, recently separated from *O. virens* (Hedenäs 2017), is to our knowledge the first record from Italy, although the species has been recorded for the French Alps and reported as certainly occurring also on the Italian slope (Hodgson 2022). The increase in competition and the final disappearance of the glacier could constitute a severe threat of local extinction for pioneer species such as *Pohlia filum* and rare species such as *Gymnomitrium adustum* and *Tortula mucronifolia*, as hypothesised for pioneer vascular plants by Losapio et al. (2021).

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## Disclosure statement

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**Olga Ligi** recently graduated in biogeosciences (2023) with a thesis on the bryoflora of alpine glacial and periglacial environments. She has skills in sampling, preparation and identification of moss specimens.

**Alessandra Moscatelli** obtained her doctoral degree in 1984 at the University of Siena (Italy). Since 1986, she has worked on sexual reproduction in vascular plants. She has studied mechanisms involved in pollen tube tip growth, the function of the cytoskeletal apparatus and membrane trafficking. She has experience in biochemical and electron/confocal microscopy techniques, and genetic approaches and transient transformation assays allowed her to perform studies on living plant cells. She has worked in international research centres including EMBL (Heidelberg), Biozentrum of Basel University, and Mount Sinai School of Medicine (New York). She is currently an associate professor at the University of Milan.

**Elisabetta Onelli** has worked on taxonomic analyses of C4 plants since her doctoral degree in Biological Sciences at the University of Milan (1992). She has had a permanent position as an assistant professor at the University of Milan in the Plant Cell Biology and Ultramicroscopy Laboratory since 2003. Her studies have characterised factors involved in clathrin-dependent and clathrin-independent endocytic processes in plants and the role played by cytoskeleton and lipid rafts in polarised growth of pollen tubes. Other studies have addressed the effects of heavy metals on plants, phytoremediation for water reuse and reproduction in endangered species. She uses biochemical, cell biology, immunocytochemical and ultramicroscopy techniques.

**Marco Caccianiga** obtained his Ph.D. at the University of Milan, Italy, working on primary succession on alpine glacier forelands. He worked as a postdoctoral fellow at Université Laval, Québec, Canada. At present he is an associate professor at the University of Milan. His research interest focuses on plant life and vegetation dynamics with particular reference to alpine pioneer vegetation, plant–arthropod communities in glacial and periglacial landforms and alpine biogeography.

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## References

- Aleffi M, Cogoni A, Poponessi S. 2023. An updated checklist of the bryophytes of Italy, including the Republic of San Marino and Vatican City State. *Plant Biosystems – An International Journal Dealing with All Aspects of Plant Biology*. 157(6):1259–1307. <https://doi.org/10.1080/11263504.2023.2284136>.
- Aleffi M, Schumacker R. 1995. Check-list and red-list of the liverworts (Marchantiophyta) and hornworts (Anthocerotophyta) of Italy. *Flora Mediterranea*. 5:73–161.
- Arróniz-Crespo M, Pérez-Ortega S, De los Ríos A, Green TGA, Ochoa-Hueso R, Casermeiro MÁ, de la Cruz MT, Pintado A, Palacios D, Rozzi R, et al. 2014. Bryophyte–cyanobacteria associations during primary succession in recently deglaciated areas of Tierra del Fuego (Chile). *PLOS One*. 9(5):e96081. <https://doi.org/10.1371/journal.pone.0096081>.
- Birks HJB. 1980. The present flora and vegetation of the Moraines of the Klutlan Glacier, Yukon Territory, Canada: a study in plant succession. *Quaternary Research*. 14:60–86.
- Burga CA. 1999. Vegetation development on the glacier forefield Morteratsch (Switzerland). *Applied Vegetation Science*. 2(1):17–24. <https://doi.org/10.2307/1478877>.
- Caccianiga M, Andreis C. 2004. Pioneer herbaceous vegetation on glacier forelands in the Italian Alps. *Phytocoenologia*. 34(1):55–89. <https://doi.org/10.1127/0340-269X/2004/0034-0055>.
- Caccianiga M, Luzzaro A, Turri D, Viapiana G, Andreis C. 2002. Indagini sulla flora del ghiacciaio del Rutor (La Thuile-AO). *Revue Valdôtaine d'Histoire Naturelle*. 56:15–35. Italian.
- Callaway RM, Lawrence WR. 1997. Competition and facilitation: a synthetic approach to interactions in plant communities. *Ecology*. 78(7):1958–1965. [https://doi.org/10.1890/0012-9658\(1997\)078\[1958:CAFASA\]2.0.CO;2](https://doi.org/10.1890/0012-9658(1997)078[1958:CAFASA]2.0.CO;2).
- Cauvy-Fraunié S, Dangles O. 2019. A global synthesis of biodiversity responses to glacier retreat. *Nature Ecology and Evolution*. 3(12):1675–1685. <https://doi.org/10.1038/s41559-019-1042-8>.
- Chernova NA, Belova MN, Timoshok EE, Timoshok EN, Skorokhodov SN. 2021. Check-list of mosses on the Maly Aktru glacier foreland (Russian Altai Mountains). *International Journal of Environmental Studies*. 78(6):1037–1043. <https://doi.org/10.1080/00207233.2020.1866346>.
- Chiesa S, Micheli P, Cariboni M, Tognini P, Motta D, Longhin M, Zambotti G, Marcato E, Ferrario A, Ferliga C. 2011. Note illustrative della Carta Geologica d'Italia alla scala 1:50000 – foglio 041 [Explanatory notes for the Geological Map of Italy at a scale of 1:50000 – sheet 041]. Rome: ISPRA – Servizio Geologico d'Italia. Italian.
- Cortini Pedrotti C. 2001. Flora dei muschi d'Italia. 1a parte. Rome: Antonio Delfino Editore. Italian.
- Cortini Pedrotti C. 2005. Flora dei muschi d'Italia. 2a parte. Rome: Antonio Delfino Editore. Italian.
- Delach A, Kimmerer RW. 2002. The effect of *Polytrichum piliferum* on seed germination and establishment on iron mine tailings in New York. *Bryologist*. 105(2):249–255. [https://doi.org/10.1639/0007-2745\(2002\)105\[0249:TEOPPO\]2.0.CO;2](https://doi.org/10.1639/0007-2745(2002)105[0249:TEOPPO]2.0.CO;2).
- Elven R. 1980. The Omnsbreen glacier nunataks – a case study of plant immigration. *Norwegian Journal of Botany*. 27:1–16.
- Erschbamer B, Caccianiga MS. 2016. Glacier forelands: lessons of plant population and community development. In: Cánovas F, Lüttge U, Matyssek R, editors. *Progress in Botany*. Vol. 78. Cham: Springer. [https://doi.org/10.1007/124\\_2016\\_4](https://doi.org/10.1007/124_2016_4).
- Favero-Longo SE, Worland MR, Convey P, Lewis Smith RI, Piervittori R, Guglielmin M, Cannone N. 2012. Primary succession of lichen and bryophyte communities following glacial recession on Signy Island, South Orkney Islands, Maritime Antarctic. *Antarctic Science*. 24(4):323–336. <https://doi.org/10.1017/S0954102012000120>.
- Ficetola GF, Marta S, Guerrieri A, Cantera I, Bonin A, Cauvy-Fraunié S, Ambrosini R, Caccianiga M, Anthelme F, Azzoni RS, et al. 2024. The development of terrestrial ecosystems emerging after glacier retreat. *Nature*. 632:336–342. <https://doi.org/10.1038/s41586-024-07778-2>.
- Ficetola GF, Marta S, Guerrieri A, Gobbi M, Ambrosini R, Fontaneto D, Zerboni A, Poulenard J, Caccianiga M, Thuiller W. 2021. Dynamics of ecological communities following current retreat of glaciers. *Annual Review of Ecology, Evolution, and Systematics*. 52:405–426. <https://doi.org/10.1146/annurev-ecolsys-010521-040017>.
- Fickert T. 2017. Glacier forelands – unique field laboratories for the study of primary succession of plants. In: Godone D, editor. *Glacier evolution in a changing world*. London: InTechOpen; p. 125–146.
- Flø D, Hågvar S. 2013. Aerial dispersal of invertebrates and mosses close to a receding alpine glacier in southern Norway. *Arctic, Antarctic, and Alpine Research*. 45(4):481–490. <https://www.jstor.org/stable/24551604>.
- Gärtner G. 2010. Zur Kryptogamenflora im Rotmoostal [The cryptogamic flora in the Rotmoos Valley]. *Glaziale und periglaziale Lebensräume im Raum Obergurgl, Alpine Forschungsstelle Obergurgl*. 1:145–154. German.
- Gavini SS, Suárez GM, Ezcurra C, d Aizen, MA. 2019. Facilitation of vascular plants by cushion mosses in high-Andean communities. *Alpine Botany*. 129:137–148. <https://doi.org/10.1007/s00035-019-00222-6>.
- Górski P, Váňa. 2011. *Gymnomitrium adustum* – a liverwort new to Slovakia and Poland found in the Tatra Mts (Western Carpathians). *Cryptogamie, Bryologie*. 32(3):275–284. <https://sciencepress.mnhn.fr/sites/default/files/articles/pdf/cryptogamie-bryologie2011v32f3a6.pdf>.
- Hågvar S, Gobbi M, Kaufmann R, Ingimarsdóttir M, Caccianiga M, Valle B, Pantini P, Fanciulli PP, Vater A. 2020. Ecosystem birth near melting glacier: a review on the pioneer role of ground-dwelling arthropods. *Insects*. 11(9):644. <https://doi.org/10.3390/insects11090644>.
- Hågvar S, Pedersen A. 2015. Food choice of invertebrates during early glacier foreland succession. *Arctic, Antarctic, and Alpine Research*. 47(3):561–572. <https://www.jstor.org/stable/24551784>.
- Hammer Ø, Harper DAT, Ryan PD. 2001. PAST: Paleontological statistics software package for education and data analysis. *Palaeontologia Electronica*. 4(1):1–9. [https://palaeo-electronica.org/2001\\_1/past/past.pdf](https://palaeo-electronica.org/2001_1/past/past.pdf).
- Hedenäs L. 2017. Scandinavian *Oncophorus* (Bryopsida, Oncophoraceae): species, cryptic species, and intraspecific variation. *European Journal of Taxonomy*. 315:1–34. <https://doi.org/10.5852/ejt.2017.315>.
- Hill MO, Preston CD, Bosanquet SDS, Roy DB. 2007. BRYOATT. Attributes of British and Irish mosses, liverworts and hornworts. Bangor: NERC Centre for Ecology and Hydrology; Cardiff: Countryside Council for Wales.
- Hodgetts N, Cáliz M, Englefield E, Fettes N, García Criado M, Patin L, Nieto A, Bergamini A, Bisang I, Baisheva E, et al. 2019. A miniature world in decline: European Red List of mosses, liverworts and hornworts. Brussels: IUCN. <https://doi.org/10.2305/IUCN.CH.2019.ERL.2.en>.

- Hodgetts NG, Söderström L, Blockeel TL, Caspari S, Ignatov MS, Konstantinova NA, Lockhart N, Papp B, Schröck C, Sim-Sim C, et al. 2020. An annotated checklist of bryophytes of Europe, Macaronesia and Cyprus. *Journal of Bryology*. 42(1):1–116. <https://doi.org/10.1080/03736687.2019.1694329>.
- Hodgson A. 2022. Bryophytes of France: the alpine flora of the eastern Queyras. *Field Bryology*. 127:8–23. <https://www.britishbryologicalsociety.org.uk/wp-content/uploads/2022/05/FB127-The-alpine-flora-of-the-eastern-Queyras.pdf>.
- Holyoak DT. 2021. *European Bryaceae*. Newbury: Pisces Publications.
- Hugonnot V, Chavoutier JL. 2021. *Les bryophytes de France*. Vol. 1, Anthocérotes et Hépatiques. Paris: Muséum national d'Histoire naturelle; Mèze: Biotope.
- Jones GA, Greg HRH. 2003. Primary plant succession on recently deglaciated terrain in the Canadian High Arctic. *Journal of Biogeography*. 30(2):277–296. <https://www.jstor.org/stable/3554519>.
- Klarenberg IJ, Keuschnig C, Salazar A, Benning LG, Vilhelmsson O. 2023. Moss and underlying soil bacterial community structures are linked to moss functional traits. *Ecosphere*. 14(3):e4447. <https://doi.org/10.1002/ecs2.4447>.
- Losapio G, Cerabolini B, Maffioletti C, Tampucci D, Gobbi M, Caccianiga M. 2021. The consequences of glacier retreat are uneven among plant species. *Frontiers in Plant Science*. 8:616562. <https://doi.org/10.3389/fevo.2020.616562>.
- Lüth M. 2019. *Mosses of Europe: a photographic flora*. Vols 1–3. Freiburg: Poppen & Ortman.
- Marta S, Azzoni RS, Fugazza D, Tielidze L, Chand P, Sieron K, Almond P, Ambrosini R, Anthelme F, Alviz Gazitúa P, et al. 2021. The retreat of mountain glaciers since the Little Ice Age: a spatially explicit database. *Data*. 6:107.
- Matthews JA. 1992. *The ecology of recently-deglaciated terrain. A geocological approach to glacier forelands and primary succession*. Cambridge (UK): Cambridge University Press.
- Montrasio A, Berra F, Cariboni M, Ceriani M, Deichmann N, Ferliga C, Gregnanin A, Guerra S, Guglielmin M, Jadoul F, et al. 2012. Note illustrative della Carta Geologica d'Italia alla scala 1:50000 – foglio 024 [Explanatory notes for the Geological Map of Italy at a scale of 1:50000 – sheet 024]. Rome: ISPRA – Servizio Geologico d'Italia.
- Pottier MJ. 1920. Liste des Mousses récoltées en Maurienne, en Tarentaise et aux environs du col du Mont-Cenis (côté italien) pendant et après la Session, en juillet–août 1920 [List of mosses collected in Maurienne, Tarentaise and around the Mont-Cenis pass (Italian side) during and after the session, in July–August 1920]. *Bulletin de la Société Botanique de France*. 67(4):LV–LXV. <https://doi.org/10.1080/00378941.1920.10836199>. French.
- Puglisi M, Campisi P, Aleffi M, Bacilliere G, Bonini I, Cogoni A, Dia MG, Miserere L, Privitera M, Tiburtini M, et al. 2024. Red-list of Italian bryophytes. 2. Mosses. *Plant Biosystems – An International Journal Dealing with All Aspects of Plant Biology*. 158(5):1031–1056. <https://doi.org/10.1080/11263504.2024.2386330>.
- Raffl C, Erschbamer B. 2003. Comparative vegetation analyses of two transects crossing a characteristic glacier valley in the Central Alps. *Phytocoenologia*. 34(2):225–240. <https://doi.org/10.1127/0340-269X/2004/0034-0225>.
- Rosero P, Crespo-Pérez V, Espinosa R, Andino P, Barragán Á, Moret P, Gobbi M, Ficetola GF, Jaramillo R, Muriel P, et al. 2021. Multi-taxa colonisation along the foreland of a vanishing equatorial glacier. *Ecography*. 44(7):1010–1021. <https://doi.org/10.1111/ecog.05478>.
- Shaw AJ. 1981. A taxonomic revision of the propaguliferous species of *Pohlia* (Musci) in North America. *The Journal of the Hattori Botanical Laboratory*. 50:1–81. [https://doi.org/10.18968/jhbl.50.0\\_1](https://doi.org/10.18968/jhbl.50.0_1).
- Smiraglia C, Diolaiuti G. 2015. Nuovo catasto dei ghiacciai italiani [New Italian glacier inventory]. Bergamo: Ev-K2-CNR. Italian.
- Smith AJE. 1973. On the differences between *Bryum creberrium* Tayl. and *Bryum pallescens* Schleich ex Schwaegr. *Journal of Bryology*. 7(3):333–337. <https://doi.org/10.1179/jbr.1973.7.3.333>.
- Smith AJE. 1978. *The moss flora of Britain and Ireland*. Cambridge (UK): Cambridge University Press.
- Stork A. 1963. Plant immigration in front of retreating glaciers, with examples from Kebnekajse area, Northern Sweden. *Geografiska Annaler*. 45(1):1–22. <https://doi.org/10.1080/20014422.1963.11881012>.
- Uchida M, Muraoka H, Nakatsubo T, Bekku Y, Ueno T, Kanda H, Koizumi H. 2002. Net photosynthesis, respiration, and production of the moss *Sanionia uncinata* on a glacier foreland in the High Arctic, Ny-Ålesund, Svalbard. *Arctic, Antarctic, and Alpine Research*. 34(3):287–292. <https://doi.org/10.1080/15230430.2002.12003496>.
- Valle B, Ligi O, Invernizzi A, Fiaschi T, Gobbi M, Caccianiga M. 2024. Moss flora of two Alpine glacial and periglacial sites on crystalline and limestone bedrock. *Natural History Sciences*. <https://doi.org/10.4081/nhs.2024.809>.
- Vater AE, Matthews JA. 2015. Succession of pitfall-trapped insects and arachnids on eight Norwegian glacier forelands along an altitudinal gradient: patterns and models. *The Holocene*. 25(1):108–129. <https://doi.org/10.1177/09596836145563>.
- Wietrzyk-Pełka P, Rola K, Patchett A, Szymański W, Węgrzyn MH, Björk RG. 2021. Patterns and drivers of cryptogam and vascular plant diversity in glacier forelands. *Science of the Total Environment*. 770:144793. <https://doi.org/10.1016/j.scitotenv.2020.144793>.



## Appendix 1. Raw data for the plot surveys in the present study (species listed in alphabetical order within the liverwort, moss and vascular plant groups).

Variable	CODE (original)																								
	SFO 89M 1	SFO 89M 2	SFO 89M 3	SFO 89M 4	SFO 89M 5	SFO 89M 6	SFO 03M 1	SFO 03M 2	SFO 03M 3	SFO 03M 4	SFO 03M 5	SFO 03M 6	SFO 15M 1	SFO 15M 2	SFO 15M 3	SFO 15M 4	SFO 15M 5	SFO 15M 6	SFO 19M 1	SFO 19M 2	SFO 19M 3	SFO 19M 4	SFO 19M 5	SFO 19M 6	
Year of deglaciation	1989	1989	1989	1989	1989	1989	2003	2003	2003	2003	2003	2003	2003	2003	2003	2003	2003	2003	2003	2003	2003	2003	2003	2003	2003
Latitude	46,35141	46,35140	46,35139	46,35138	46,35139	46,35138	46,35105	46,35104	46,35104	46,35104	46,35103	46,35101	46,35051	46,35049	46,35046	46,35043	46,35040	46,35037	46,35016	46,35013	46,35011	46,35007	46,35007	46,35007	46,35004
Longitude	10,51085	10,51091	10,51096	10,51102	10,51111	10,51116	10,51153	10,51161	10,51167	10,51167	10,51171	10,51177	10,51186	10,51196	10,51203	10,51210	10,51216	10,51222	10,51218	10,51224	10,51231	10,51235	10,51239	10,51244	10,51244
Elevation (m a.s.l.)	2807	2803	2804	2806	2806	2804	2804	2804	2804	2804	2805	2803	2803	2806	2806	2805	2807	2809	2811	2812	2812	2810	2813	2815	2815
Moss cover (%)	1	1	5	5	1	1	1	<1	1	1	1	<1	<1	<1	<1	<1	<1	<1	<1	<1	<1	<1	<1	<1	<1
<b>Mosses</b>																									
<i>Bryum</i> sp.									X																
<i>Oncophorus integerrimus</i>				X	X	X	X	X																	
<i>Pohlia filum</i>	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X
<i>Polytrichum juniperinum</i>	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X
<i>Polytrichum piliferum</i>	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X
<i>Psychostomum</i> sp.	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X
<i>Psychostomum creberrimum</i>																									
<i>Psychostomum inclinatum</i>																									
<i>Psychostomum pallescens</i>																									
<i>Racomitrium canescens</i>	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X
cf. <i>Sanionia uncinata</i>																									
<i>Sciuro-hypnum</i> cf. <i>glaciale</i>	X																								
<i>Tortula hoppeana</i>																									
<i>Tortula mucronifolia</i>																									
<b>Liverworts</b>																									
<i>Cephalozia</i> sp.																									
cf. <i>Gymnomitron adustum</i>																									
<b>Vascular plants</b>																									
<i>Agrostis rupestris</i>	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X
<i>Androsace alpina</i>	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X
<i>Arabis alpina</i>	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X
<i>Arabis caerulea</i>	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X
<i>Cardamine residifolia</i>	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X

(Continued)

