



OPEN Spatial and temporal variability of supraglacial algae on an Alpine glacier (Forni Glacier, Italy)

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The assessment of algal biodiversity in mountain glaciers is timely and critical. In this study, we evaluated the biodiversity of algae on an alpine glacier and their spatio-temporal variability in seven supraglacial habitats (snow, bare ice, bédrières, water of cryoconite holes, dirt cones, sparse sediment, and cryoconite) over two years. Biovolume, diversity, and community structure were investigated using microscopy observations, providing a comprehensive quantitative and qualitative assessment of the algae dynamics. Algal communities were highly spatially and temporally variable. The community dynamics at the glacier scale were complex and structured by diverse ecological processes. The difference in species richness explained the major part (82.5%) of the variation in algal community composition among habitats. The snow was characterized by the higher local contribution to beta diversity (LCBD) values and by high replacement values. This habitat typically supported unique combinations of species and contributed greatly to glacier biodiversity (with 6 associated indicator taxa). Dirt cones, sparse sediment, and cryoconite communities showed high rates of species replacement, while the communities of bare ice, bédrières, and water of cryoconite holes showed lower species richness. Bare ice was characterized by the lowest richness, due to the large dominance of *Mesotaenium berggrenii*, which bloomed at the end of the ablation period (biovolume 6 to 14-fold higher at late summer 2023 than in the other dates). Under warmer conditions, the forecasted decrease of snow and ice mass may remove the habitats that contribute most to the total biodiversity of the glacier, affecting the overall community dynamics and impacting the surrounding environments that benefit from the glacier's resources.

Keywords Algae biodiversity, Biovolume, Community composition, Glacier, Italian Alps

Glaciers have been recognized as one of the terrestrial biomes on Earth¹, whose functioning provides a multitude of ecosystem services². Their physical and biological processes generate water, nutrients, and organic matter that are essential not only within the glacier habitat itself but also for the ecosystems that lie downstream³. To strengthen awareness of their functional importance on a global scale and to advance research on these rapidly changing systems, several initiatives have been launched, including the United Nations' designation of 2025 as the International Year of Glaciers' Preservation⁴. This focus is particularly timely, as ongoing and projected climate change is profoundly altering glacier dynamics^{5,6}. Rising air temperatures over the past century have driven

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substantial reductions in glacier area and volume, with melting rates in high-mountain regions accelerating in recent decades in some regions of the world⁷. These changes are, in turn, reshaping the physical and biological processes that sustain glacier ecosystem functioning⁸. The functioning of glaciers is closely related to their biodiversity, the loss of which can have large-scale consequences that are still difficult to predict⁹.

Supraglacial environments are characterized by short food webs¹⁰ but their biodiversity includes a wide array of organisms, including microbes (bacteria, algae, archaea, ciliates, and protozoans), invertebrates (tardigrades, rotifers, nematodes, platyhelminthes, annelids, arthropods such as copepods, springtails, spiders, chironomids, plecoptera, beetles)^{11–13}, bryophytes, and vascular plants^{10,14,15}. A large part of these taxa includes specialist species highly adapted to the glacial environment¹ and endemic or steno-endemic ones (i.e. species with narrow distribution range)^{10,16,17}, which are the most endangered by climate change^{9,18}. The metabolism of these cold-adapted organisms affects the global rate of biogeochemical processes such as iron cycling, methanogenesis, carbon respiration, and fixation^{19–23} (for example, cryoconite holes have the potential to fix as much as 64 Gg of carbon per year through biological activity)¹⁹.

However, much of this biodiversity remains insufficiently characterized and poorly quantified, raising the possibility that losses may occur before they are even documented. Substantial knowledge gaps persist, particularly concerning the composition and extent of glacier biodiversity, the ecological interactions that shape these communities, and the organisms inhabiting the distinct microhabitats within glacier ecosystems¹⁰. In addition, published information is not equally available for all glacier taxa and biogeographic areas, with less attention paid to mid-latitude and tropical mountain glaciers compared to polar ones^{3,10}. Glaciers are extremely dynamic ecosystems, especially in alpine regions during the melting season, and such shifts can affect the composition of their ecological communities^{10,24}. However, to date, very little attention has been paid to the temporal and spatial dynamics of glacial biodiversity. In addition, contrasting results have been reported regarding the spatio-temporal dynamics of communities, spanning from no temporal change (observed for bacteria²⁵, to seasonal and annual succession (observed for eukaryotes and algae²⁶, and bacteria²⁷, to spatial variability among different habitats on the same glacier^{28,29}.

The algal component plays a crucial role in the functioning of glacier ecosystems through its role in the production of autochthonous organic matter that sustains a range of heterotrophic glacial microorganisms^{3,10,30,31}, as well as larger organisms such as arthropods³². On mountain glaciers, most studies focus on the characterization of algal communities living in cryoconite holes, ice, and snow, while algal biodiversity of other glacial habitats is still largely unquantified and likely underestimated^{31,33–35}. To date, we still lack a precise understanding of algal biodiversity in all habitats on a glacier surface and its temporal variability.

Here, we present the first thorough spatial description of the algal biodiversity of an Alpine glacier in the Italian Alps, exploring how the biovolume and composition of the algal community vary among the different supraglacial habitats and months. We hypothesize that the total biovolume of algae is dynamic both temporally and spatially, following the variation of parameters that are limiting for their growth (such as solar radiation, air temperature, and water). We also hypothesize differences in diversity and taxonomic composition among the supraglacial habitats, with more taxa adapted to warmer (due to their lower albedo) and more stable (less affected by glacier melt) environments (such as sediment and dust).

Methods

Study site and algae sampling

The sampling campaigns were conducted on the Forni Glacier (46° 23' 32" N, 10° 35' 28" E), the largest Italian valley glacier (10.50 km² in 2016³⁶). The glacier is north-facing and rises between approximately 2,600 and 3,672 m above sea level. On the glacier surface, different supraglacial habitats have been identified for the study of algae, which can be divided into aquatic and terrestrial habitats (Table 1).

On the glacier tongue, we identified 10 sampling areas about 10 × 10 m wide, so that each supraglacial habitat except for SNOW was represented in at least five areas (Fig. 1). This number was chosen to be sure that all supraglacial habitats have a sufficient number of replicates to be representative of the glacier's variability. As the snow and firn were present only in the upper part of the glacier, we defined a sampling area as "upper" area, where 6 replicates were sampled for SNOW (Fig. 1). The sampling campaigns occurred in July 2023, September 2023, July 2024, and September 2024, during the ablation season³⁷. The sampling was thus carried out in different months across two years, allowing us to assess interannual variability. The characteristics of the areas are presented in Table S1.

For terrestrial habitats, 50 mL of substrate was sampled in Falcon tubes. For aquatic habitats, 250 mL of water from bédrières and cryoconite holes were collected in HDPE bottles. For the bare ice and snow, the first 2–3 cm of surface ice and snow was collected in sterile plastic bags for a total volume of ~0.5 L. All these samples were kept cool while in the field and stored at -20 °C within 5 h after collection until further analyses. In addition, meteorological data were acquired from the Automatic Weather Station (AWS) located on the Forni Glacier tongue (AWS1 Forni) to describe air temperature, incoming solar radiation, and precipitation patterns over the sampling periods.

Analysis of the algal community

Algae separation from terrestrial substrates

Algae were separated from terrestrial substrates using the method of purification through high-speed density gradient centrifugation, already adapted for these types of habitats and organisms³⁸. The density gradient medium (Nycodenz, density of 1.31 g mL⁻¹) was carefully placed at the bottom of the Falcon tube beneath the homogenized substrate. Tubes were then centrifuged (10,000 rpm) for 60 min at 4 °C, and the layer containing microalgae was transferred into sterile 15 mL Falcon tubes and frozen (-20 °C) until microscopic identification



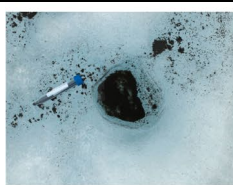

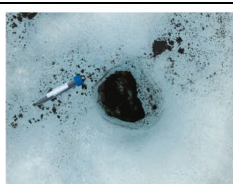

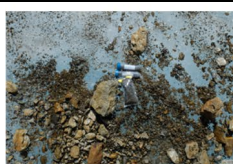
Supraglacial habitats (ID)	Description (and type)	Pictures
Bare ice (ICE)	Superficial ice layer (aquatic, compact)	
Snow (SNOW)	Snow and firn, i.e. partially compacted and re-crystallized snow (aquatic, partially compact)	
Water of cryoconite holes (CRYOw)	Water contained in cryoconite holes, i.e., small ponds filled with meltwater and with a powdery windblown dust - the cryoconite - at the bottom (aquatic, liquid)	
Bédière (BW)	Supraglacial streams originated from the melting of snow and ice (aquatic, liquid)	
Cryoconite in cryoconite holes (CRYO)	The cryoconite contained in cryoconite holes (terrestrial, in contact with water)	
Dirt cone (DC)	Convex structures with a core of ice covered by a layer of fine sediment (terrestrial, thick layer)	
Sparse cryoconite (SC)	Powdery windblown dust made of small rock particles, soot, and microbes deposited on ice and snow (terrestrial, thin layer)	

Table 1. Description of the supraglacial habitats sampled for algae in the Forni Glacier.

and counting. The remaining substrate pellet was rinsed, dried at 60 °C, and weighed to calculate the biovolume of taxa by dry weight of substrate (see the following subsection).

Algae identification and counting

All samples were thawed and homogenized, and algae counting was performed at 400× magnification under an IM35 inverted microscope following the Utermöhl method³⁹. Algal taxa were identified at the genus and species level when possible, using specific identification keys^{40,41}. Cell biovolume was estimated by assimilating

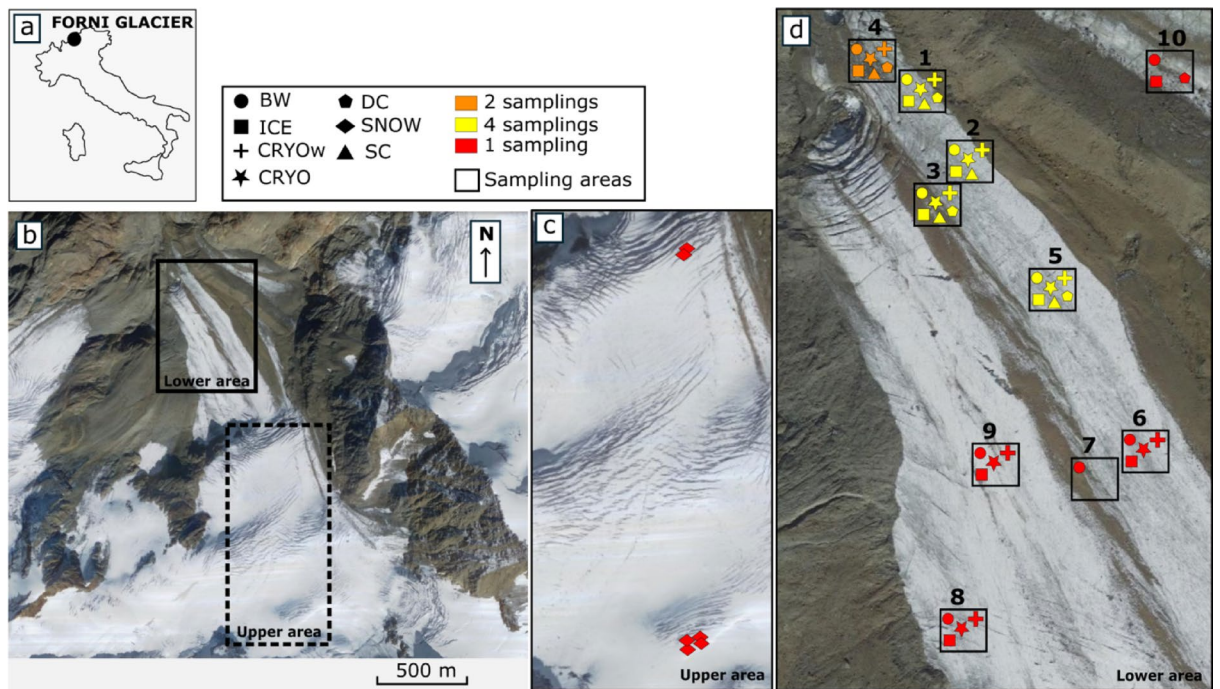


Fig. 1. Study area. (a) Location of the Forni Glacier in Italy; (b) Satellite image of the Forni Glacier with the area sampled on the glacier tongue (box) and the upper study area where snow samples were collected (dashed box); (c) Detail of the snow samplings on the upper area of the glacier; (d) Detail of the sampling areas on the glacier tongue with the 10 × 10 m sampling areas identified by numbers from 1 to 10. Each square represents an area and the symbols inside indicate the type of supraglacial habitat. The symbol colors (i.e., yellow, orange, red) indicate the number of sampling campaigns (see legend and Table S1). Satellite image from Google Earth.

each taxon to a simple geometric form, according to the literature^{42,43}. The final biovolume was obtained by multiplying the mean cell biovolume of each taxon (in μm^3) by its density, and expressed in $\mu\text{m}^3 \text{g}^{-1}$ of dry weight of sediment for the terrestrial habitats, and in $\mu\text{m}^3 \text{L}^{-1}$ of meltwater for the aquatic habitats. This study yielded a total of 115 measurements of algae biovolume and community composition, providing a comprehensive dataset to assess the spatial and temporal distribution of the algal biodiversity on the Forni Glacier (Tables S1 and S2).

Statistical analysis

All statistical analyses were performed with R 4.5.1⁴⁴ and are summarized in Figure S1.

Community and meteorological data characterization

The Shannon diversity index, the richness (number of taxa), and the evenness (Pielou index) were calculated at the species level using the *vegan* package⁴⁵ in R. Similarity percentage (SIMPER) analyses⁴⁶ were performed to estimate the similarity of the communities and the proportional contribution of the main taxonomic groups in the different supraglacial habitats and at the different sampling dates. Differences in meteorological data among the sampling periods have been tested using linear models, and variables were log-transformed in case of non-normal distribution of datapoints.

Variations in community composition

Variation in community composition among supraglacial habitats (7-level factor) and dates (4-level factor) was assessed by permutational multivariate analysis of variance (PERMANOVA) on Bray-Curtis dissimilarity matrices, which does not override agreement in the presence of species due to abundance differences^{47,48}. The analysis was performed with the R package *vegan*. The multivariate homogeneity of group dispersions was tested using the *betadisper* function. Pairwise comparisons among habitats and dates were performed with the same method while correcting p-values for multiple comparisons with the False Discovery Rate (FDR) procedure. The results were visualized by non-metric multidimensional scaling (NMDS), based on Bray-Curtis dissimilarity matrices⁴⁹. Both PERMANOVA and NMDS were performed on the relative biovolume of taxa to allow the comparison between terrestrial and aquatic habitats, which were measured in different units ($\mu\text{m}^3 \text{g}^{-1}$ and $\mu\text{m}^3 \text{L}^{-1}$, respectively).

Variations in algae biovolume and diversity

Spatial and temporal variation in algae biovolume and diversity was tested using linear mixed-effect models using the *lmerTest* package⁵⁰, with the area as a random factor to account for the potential non-independence of data from the same area. Pairwise comparisons of diversity and biovolume among dates and habitats were

performed with the *emmeans* package⁵¹. Since snow was sampled only once, we checked that this unbalanced sampling design did not bias our results by comparing the results of analyses with and without snow samples (details not shown).

Beta diversity

Beta diversity (BD), and local contribution of species and habitats to beta diversity (SCBD and LCBD, respectively), were assessed using the *adespatial* package⁵². First, we calculated the total beta diversity (quantitative form of the Jaccard coefficients) using the Podani's family⁵³. Then, we decomposed the total beta diversity into turnover and nestedness components, using the *beta.div.comp* function. For each component, the local contribution to beta diversity (LCBD) was calculated using Hellinger-transformed presence-absence data, resulting in values of $_{RichDiff}LCBD$ (turnover) and $_{Repl}LCBD$ (nestedness) for each habitat. $_{RichDiff}LCBD$, $_{Repl}LCBD$, and total LCBD were calculated using the *LCBD.comp* function. Finally, the *beta.div* function⁵⁴ was used to calculate the species contributions to beta diversity (SCBD indices for the species) and to test the significance of the LCBD indices (using random, independent permutations within the columns of the data matrix, $nperm = 999$).

Taxon-habitat associations

We performed an Indicator Species Analysis to identify algae taxa associated with one or more habitats ("indicator taxa" hereafter). This analysis was done using the *indicspecies* package⁵⁵ of R (multipatt function with 9,999 permutations). The function returns an "indicator value" (IndVal) index, which allows for assessing the strength of the association between species and site groups. Details of the IndVal calculation are available in the dedicated literature⁵⁵. We accounted for multiple testing by correcting p-values according to the FDR procedure. Indicator taxa with a $P_{FDR} < 0.05$ were considered significantly associated with a habitat or a combination of habitats. Habitats and indicator taxa associated with them were then represented in a network using the *igraph*⁵⁴ package in R.

Results

Community and meteorological data description

Overall, 17 algal taxa were observed in all the supraglacial habitats of the Forni Glacier, with a richness ranging from 1 to 9 taxa per site (mean \pm SE, 4.7 ± 0.2). The taxa belonged mainly to the class of the Zygnematophyceae (63% of the overall community), followed by Chlorophyceae (13%), Cyanophyceae (12%), Bacillariophyceae (i.e., diatoms) (4%), and Trebouxiophyceae (4%). The fungus *Chionaster nivalis*, belonging to the Bartheletiomycetes, was also observed in a notable proportion (3%).

The average incoming solar radiation differed significantly among the periods ($F_{3,167} = 34.3$, $P < 0.001$), with higher values in the beginning of the summer season than at the end in both years. In 2023, the average incoming solar radiation was slightly higher (187.27 ± 7.8 W m⁻² for the overall year) than in 2024 (166.78 ± 8.9 W m⁻² for the overall year) (Figure S2). The average temperature changed significantly during the study period ($F_{3,176} = 15.2$, $P < 0.001$) with a stable trend in 2023 and a decreasing trend across the summer season in 2024. The average temperature was 6.89 ± 0.27 °C in 2023 and 6.67 ± 0.46 °C in 2024. The average daily cumulated liquid precipitation did not differ among the sampling periods ($F_{3,167} = 2.57$, $P = 0.05$) and was 5.07 ± 1.2 mm in 2023 and 9.03 ± 1.3 mm in 2024. Despite the non-significant variation, precipitation shows higher values at the end of the summer season in both years, and the highest liquid precipitation in 2023 occurred on August 27 (59.6 mm), while in 2024 it occurred on September 8 (48.6 mm).

Spatial distribution in the supraglacial habitats

Biovolume and diversity index

The biovolume in aquatic habitats (i.e., BW, CRYOw, ICE, and SNOW) was on average $2,201 \pm 1,064$ μm^3 L⁻¹, while in terrestrial habitats (i.e., CRYO, DC, and SC) it averaged 593 ± 132 μm^3 g⁻¹ (Fig. 2a). In aquatic habitats, the maximum biovolume was observed in ICE, where it averaged $6,905 \pm 3,266$ μm^3 L⁻¹. This high biovolume was mainly due to the species *Mesotaneum berggrenii*, which reached a biovolume of $6,820$ μm^3 L⁻¹ in ICE (Figure S3). In terrestrial habitats, the maximum biovolume was found in SC, where it averaged 700 ± 307 μm^3 g⁻¹. The total algal biovolume differed significantly among the aquatic habitats ($F_{3,28} = 28.4$, $P < 0.001$) (Fig. 2a). The exceptions were for the comparisons BW - CRYOw, which did not differ from each other and showed lower biovolumes, and ICE - SNOW, which did not differ from each other and showed higher biovolumes (Table S3). The total biovolume of algae did not differ significantly among terrestrial habitats ($F_{2,12} = 0.42$, $P = 0.66$).

The Shannon index ranged between 0 and 1.71 per site (mean \pm SE, 0.73 ± 0.04), and differed significantly among the different supraglacial habitats ($F_{6,36} = 7.61$, $P < 0.001$) (Fig. 2b). SNOW significantly differed from ICE, CRYOw, and BW due to its higher diversity (mean \pm SE, 1.32 ± 0.11) (see the results of post-hoc comparisons in Table S4). The ICE habitat had the lowest mean value of the Shannon index (0.33 ± 0.07) and, although there was no significant difference in alpha diversity values between terrestrial habitats, the DC habitat had the highest mean value (1.13 ± 0.08). Algae evenness followed similar trends to Shannon diversity ($F_{6,40} = 7.65$, $P < 0.001$), with the highest values in SNOW (0.77 ± 0.02) and DC (0.66 ± 0.05) and the lowest in ICE (0.23 ± 0.05) (Figure S4a). Species richness also differed among habitats ($F_{6,105} = 21.7$, $P < 0.001$), with the highest values in SNOW (5.8 ± 0.8) and CRYO (6.7 ± 0.2) and the lowest in BW (3.2 ± 0.3) and CRYOw (3.4 ± 0.3) (Figure S4b).

Community composition

The community composition differed significantly among the supraglacial habitats ($F_{6,108} = 10.7$, $P < 0.001$) (Fig. 3a). More specifically, all the habitats differed from each other, except BW-CRYOw, BW-CRYO, BW-SC, CRYOw-CRYO, CRYOw-SC, and CRYO-SC (Table S5). The difference between SNOW and the other habitats was explained by a high proportion of the mucilage-forming colony of *Gloeocapsa* sp. (which represented 21% of

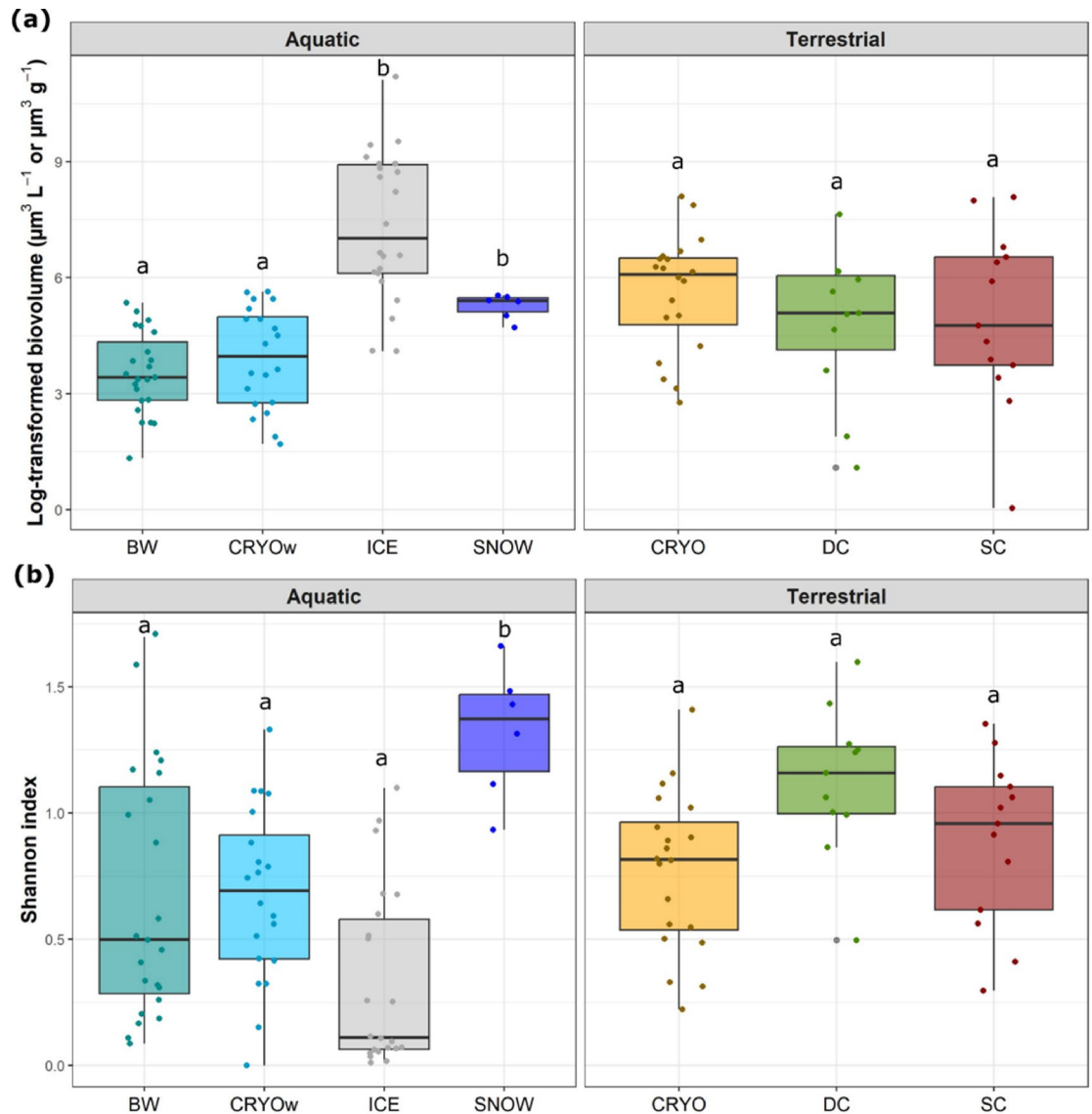


Fig. 2. Total biovolume of algae (a) and Shannon diversity index (b) in the different supraglacial habitats of the Forni glacier. Letters indicate if the supraglacial habitats within a type (terrestrial or aquatic) are significantly different (post-hoc pairwise comparison test).

the community biovolume) and the fungus *Chionaster nivalis* (34% of the community biovolume) (Fig. 3b). The ICE habitat differed from the others for its high proportion of *Mesotaenium berggrenii* (93% of the community biovolume), while the dominance of green cyst-stages of the Chlamydomonadales explained the difference between DC and the other habitats. The relatively high proportion of *M. berggrenii*, as well as the presence of *Scotiella nivalis*, the red cyst-stages of the Chlamydomonadales, and *Oscillatoria* sp., explained the similarity in composition between BW, CRYOw, CRYO, and SC habitats. The dissimilarity between ICE and BW must be interpreted with caution, as the betadisper test showed a high difference in dispersion between these two groups.

Beta diversity

Total beta diversity was 0.435, and the majority of variation in algae composition was explained by richness difference (82.5%) rather than species replacement (17.4%) (Fig. 4). Among the seven supraglacial habitats, only SNOW contributed significantly to beta diversity ($P_{\text{adj}} = 0.028$). SNOW was characterized by the highest LCBD values (LCBD = 0.402) and a high replacement rate relative to the richness difference values. Terrestrial habitats (i.e., CRYO, DC, SC) also showed high replacement relative to richness difference values, while the opposite patterns were observed in BW, CRYOw, and ICE habitats. Algae species that contributed most to beta diversity (species contribution to beta diversity, SCBD) were *Mesotaenium berggrenii* (SCBD = 0.275), the green cyst of Chlamydomonadales (SCBD = 0.164), *Oscillatoria* sp. (SCBD = 0.158), and *Navicula gregaria* (SCBD = 0.122).

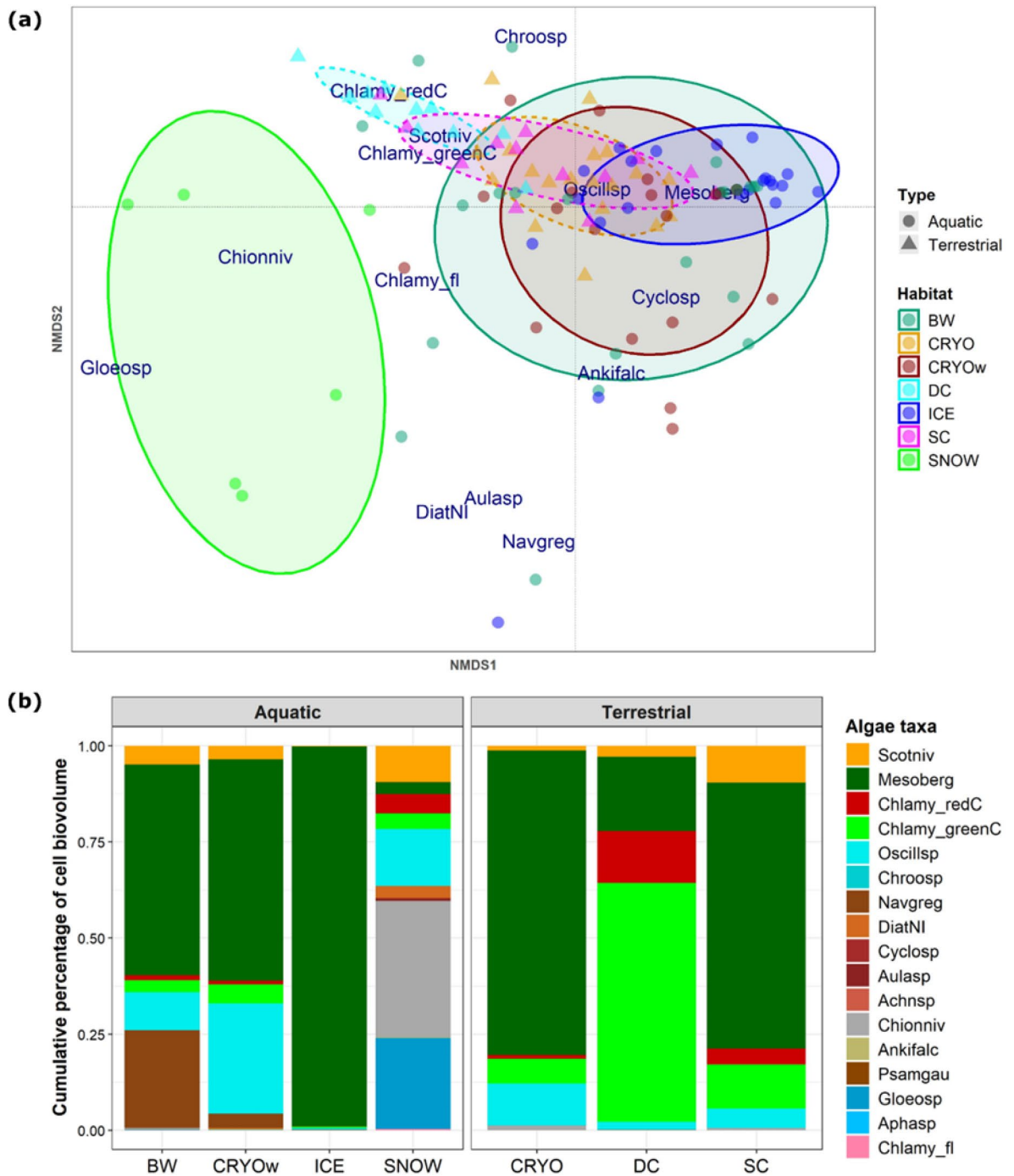


Fig. 3. (a) Ordination plot of the different algal species within the supraglacial habitats. The NMDS was performed on the relative biovolume of the algae taxa, based on the Bray-Curtis dissimilarity. The stress value of the NMDS was 0.12. Ellipses indicate 70% of the inertia. The dashed lines of the ellipses indicate the terrestrial habitats (SC, CRYO, DC), while the solid lines of the ellipses indicate the aquatic habitats (BW, CRYOw, ICE, SNOW). (b) Taxonomic composition of the algae taxa in the different supraglacial habitats. SC: sparse cryoconite, CRYO: cryoconite, DC: dirt cone, BW: bédrière, CRYOw: cryoconite water, ICE: bare ice, SNOW: snow. Scotniv: *Scotiella nivalis*, Mesoberg: *Mesotaenium berggrenii*, Chlamy_redC: Chlamydomonadales red cyst, Chlamy_greenC: Chlamydomonadales green cyst, Oscillsp: *Oscillatoria* sp., Chroosp: *Chroococcus* sp., Navgreg: *Navicula gregaria*, DiatNI: unclassified diatoms, Cyclosp: *Cyclotella* sp., Aulasp: *Aulacoseira* sp., Ach-nsp: *Achnanthydium* sp., Chionniv: *Chionaster nivalis*, Anki-falc: *Ankistrodesmus falcatus*, Psamgau: *Psammothidium gautii*, Gloeosp: *Gloeocapsa* sp., Aphasp: *Aphanocapsa* sp., Chlamy_fl: flagellated Chlamydomonadales.

addition, all terrestrial habitats (DC, SC, CRYO) presented at least one indicator taxon, which was not the case for aquatic habitats, as only ICE and SNOW had significantly associated indicator taxa.

Several taxa are specific indicators of aquatic habitats, such as diatoms, or *Gloeocapsa* sp. in SNOW, and others are specific indicators of terrestrial habitats, such as the green cysts of Chlamydomonadales. Other taxa are not specific and are indicators of both types of habitats, such as *Mesotaenium berggrenii*, the red cysts of Chlamydomonadales, and *Scotiella nivalis*. The species *Aulacoseira* sp. was recorded in only one sample of SNOW and five samples of ICE, with a p-value at the limit of significance ($P=0.046$), indicating that this result has to be interpreted with caution (Fig. 5a and b and Table S6). When we performed the Indicator Species Analysis on the types of habitats (terrestrial and aquatic), we found that *Scotiella nivalis* and the red cysts of Chlamydomonadales were significantly associated with terrestrial habitats (Fig. 5b and Table S7).

Temporal dynamics

Community biovolume and diversity

The biovolume of algae in aquatic habitats differed significantly among sampling dates ($F_{3,46} = 4.6$, $P=0.006$, Fig. 6). In particular, the algal biovolume was significantly higher in September 2023 than in July 2023 and July 2024 (see the results of post-hoc tests in Table S8). These differences were caused mainly by the higher

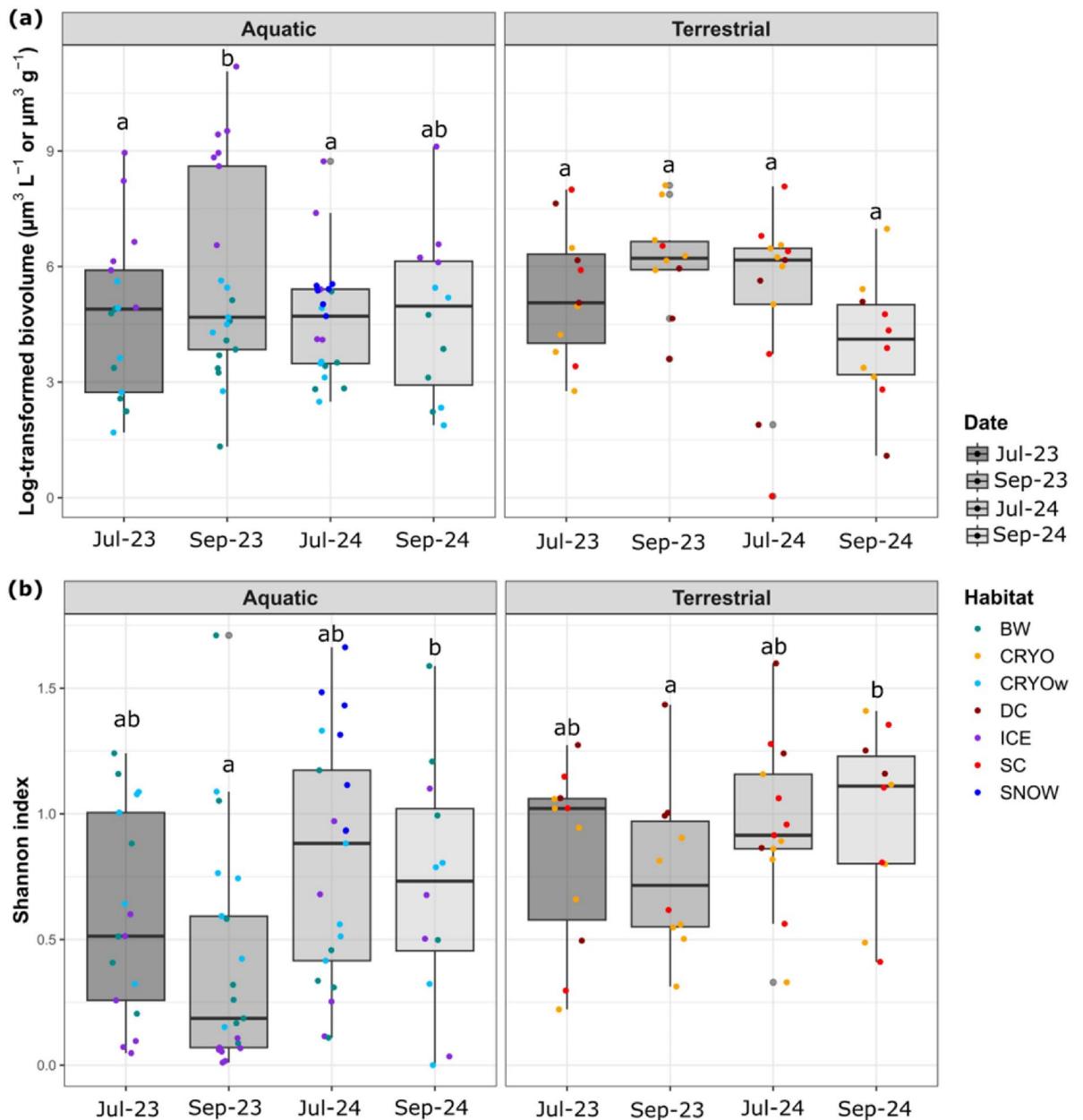


Fig. 6. Total biovolume of algae (a) and Shannon diversity index (b) at the different sampling dates. Different letters indicate sampling dates that differ significantly at post-hoc tests.

biovolume of the species *Mesotaenium berggrenii* in September 2023 than on the other dates, which averaged $5,712 \pm 3,471$ (mean \pm SE) $\mu\text{m}^3 \text{L}^{-1}$ in aquatic habitats in September 2023, while it was only $762 \pm 781 \mu\text{m}^3 \text{L}^{-1}$ in July 2023, $390 \pm 286 \mu\text{m}^3 \text{L}^{-1}$ in July 2024 and $897 \pm 744 \mu\text{m}^3 \text{L}^{-1}$ in September 2024. In terrestrial habitats, the algal biovolume did not significantly differ among sampling dates. The effect of the date on community composition was similar without the SNOW habitats.

The Shannon diversity differed significantly among the sampling dates ($F_{6,84} = 3.0$, $P=0.03$). In particular, the diversity was significantly lower in September 2023 than in September 2024 (see the results of post-hoc tests in Table S9).

Community composition

The community composition differed significantly among the sampling dates ($F_{3,111} = 2.75$, $P=0.003$). In particular, it differed between September 2023 and July 2024 and between September 2023 and September 2024 (see the results of post-hoc comparisons in Table S10). *M. berggrenii* represented a higher proportion of the community at the end of the summer season in both years, where it reached more than 90% of the total community (Figure S5). On the contrary, the red and green cysts of Chlamydomonadales were proportionally more abundant at the beginning of the summer season (together they reached 13% and 11% of the community in July 2023 and 2024, respectively, but only 1% and 4% in September 2023 and 2024). The species *Scotiella nivalis* reached higher proportions in 2024, where it represented more than 6% (July 2024) and 1% (September 2024) compared to 2023 (always $<0.5\%$ of the community). Diatoms, especially the species *Navicula gregaria*, progressively decreased across the years in aquatic habitats: in ICE, diatoms progressively decreased from July 2023 to September 2024; in CRYOw and BW, diatoms were less abundant in 2024 than in 2023 (Figure S6).

Discussion

Spatial dynamics of algal communities

Here, we present a description of the diversity of algal communities in different supraglacial habitats of an alpine glacier, and an estimate of the processes structuring these communities at the glacier scale (i.e., beta diversity). We found different algal communities in different supraglacial habitats characterized by diverse types of substrates. Supraglacial habitats on the Forni Glacier can be separated into two groups according to our results. On the one side are habitats characterized by a relatively high Shannon diversity, a high species richness, and a high contribution of species replacement to the total beta diversity. These habitats are SNOW, CRYO, DC, and SC to a lesser extent. On the other side are habitats characterized by a low Shannon diversity, a low species richness, and a high contribution of the richness difference to the total beta diversity. These habitats are ICE, CRYOw, and BW.

The high replacement relative to the difference in richness observed in SNOW indicates that a large number of algal taxa recorded in this habitat were not recorded in any other habitat⁵⁶. Furthermore, compared to other habitats, SNOW had the highest contribution to beta diversity, which is characterized by a large number of indicator taxa, some specific such as *Gloeocapsa* sp., and others less specific such as *Chionaster nivalis*, *Scotiella nivalis*, and diatom species. Since a high LCBD value indicates a site with a species composition that is very different from that of an average site and therefore unusual species combinations, these results support the hypothesis that the SNOW habitat should be considered of high conservation value⁵⁷. The species observed in SNOW represent a typical cryoseston community (snow algae and fungi) and have already been observed in other high-altitude snow fields^{58,59}, but their ecology and the reasons why these species co-occur in snow are still poorly understood. Previous studies have suggested syntrophic relationships between snow algae and fungi, where algae-associated microorganisms may utilize dissolved organic carbon (DOC) excreted by the algae⁶⁰. Algae, in turn, may benefit from the physical presence of the fungi that protect the algae against the high light conditions^{61,62}.

These results suggest that SNOW habitat acts as a “colonization site” at the glacier scale, hosting pioneer species, likely due to the highest contact of the SNOW with the atmosphere. The SNOW may thus capture a large number of atmospheric particles, including algae, but also probably nutrients⁶⁰, that directly deposit from the atmosphere on glacier surfaces with the snow and may provide favorable conditions for species development. Various ecological processes explain the difference in community structure and composition among the other supraglacial habitats (Fig. 7). First, we observed a high species replacement between SNOW and terrestrial sites (i.e., CRYO, DC, and SC). Interestingly, the combination formed by *Chionaster nivalis* and *Gloeocapsa* sp. in SNOW was replaced by the green cysts of the Chlamydomonadales in terrestrial habitats.

The high occurrence of the cyst-like stages of Chlamydomonadales in terrestrial habitats is not completely surprising, as the life cycle of the snow algae should begin with a resting state on the snow-free surface following snowmelt in summer^{61–63}. In addition, it has been demonstrated that high absorbed solar radiation and high temperatures⁶⁴, as those associated with terrestrial substrates, promote the resting stage of snow algae that synthesizes large amounts of astaxanthin⁶⁵. Thus, a species replacement occurred in terrestrial habitats, where species richness remained high, but the algae community was composed of species more adapted to the specific environmental conditions of the terrestrial substrates. Algae community structure differed among the terrestrial habitats, with a higher proportion of Cyanobacteria (especially *Oscillatoria* sp.) and *Mesotaenium berggrenii* in CRYO and SC. This observed difference may be explained by the sediment grain size of the substrates, as previous studies demonstrated that the finest texture of cryoconite (2–30% of the coarse fraction) and the water content caused differences in algae composition⁶⁶.

The other aquatic habitats (i.e., CRYOw, ICE, and BW) were characterized by a lower species number and a higher contribution of richness difference to community variability. These results indicate that in CRYOw, ICE, and BW, the changes in community composition are mainly related to species loss and that these habitats are a subset of the algae species at richer sites, i.e., SNOW. Some taxa were still associated with aquatic habitats, such as

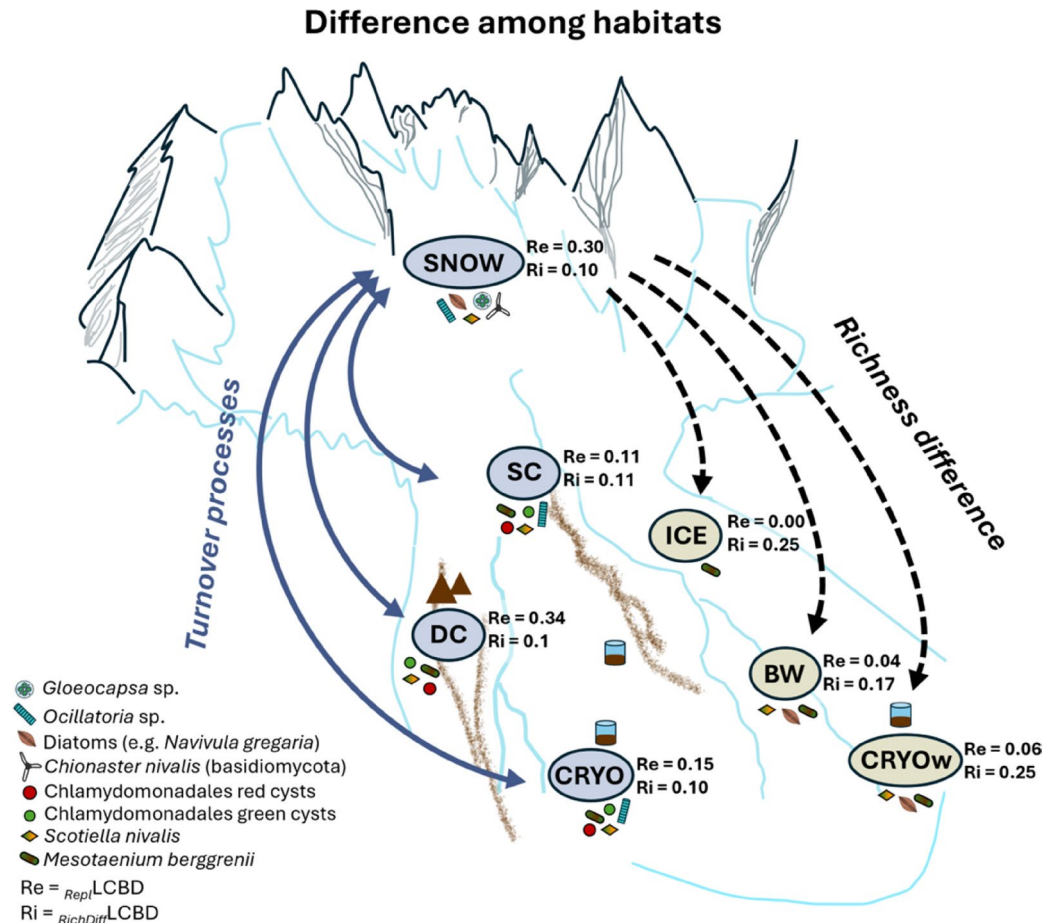


Fig. 7. Synthesis of the spatial dynamics of algal communities among the supraglacial habitats of the Forni Glacier. Re and Ri indicate respectively whether habitats with a unique composition show changes related to spatial replacement of species or species gain/loss. In habitats with high Re ($Re_{ReplLCBD}$) and low Ri ($Ri_{RichDiffLCBD}$), changes in composition are mainly related to spatial replacement of species, while in habitats with high Ri and low Re, changes in composition are mainly related to species gain/loss. Blue-grey sites are the sites with the highest species richness, while yellow-grey sites are the sites with the lowest species richness. Brown triangles represent the dirt cones (DC), brown lines represent the sparse cryoconite (SC), cylinders represent the cryoconite holes fill with cryoconite (brown part, CRYO) and water (blue part, CRYOW), and blue lines represent the bédrières (BW). SNOW, CRYOW, ICE, and BW are aquatic habitats while CRYO, SC and DC are terrestrial habitats.

diatoms, and more generalist species were also observed, such as the Zygnematophyceae *Mesotaenium berggrenii*. A striking ecological question concerns why *M. berggrenii*, despite being present in all the microhabitats, largely dominated on bare ice. The presence in its vacuoles of purpurogallin carboxylic acid-6-O-b-D-glucopyranoside can be seen as an adaptation to the high UV irradiation levels associated to bare ice⁶⁷. In addition, *M. berggrenii* should perform better at temperatures close to the freezing point than other species present on the glacier, which could give it a competitive advantage on bare ice⁶⁸. Likely, a combination of several factors, such as the amount of available water, low temperature, and high UV levels, explains the greater occurrence of *M. berggrenii* on ICE. Another explanation could be that the phenolic compound present in the vacuoles of *M. berggrenii* might act as a chemical defense against grazers crossing the glacier ice (notably, the abundant springtail *Vertagopus glacialis* on the Forni Glacier¹², like, for example, phenolic compounds in marine kelp, which are active against herbivores⁶⁷). Thus, the decrease in species richness observed in BW, CRYOW, and ICE may be due to species thinning causing nestedness, or to other ecological processes⁵⁷.

Several factors can explain the lower diversity and richness observed in BW, ICE, and CRYOW, such as abiotic factors (i.e., temperature or nutrient availability) and biotic factors (i.e., competition and dispersal capacity)^{69,70}. Another explanation could be a difference in mutualist interactions between algae and bacteria. Indeed, it has been shown that beneficial interactions exist between bacteria and algae in harsh environments⁷¹, with algal growth stimulated by the release of essential minerals, vitamins, auxins, and quorum-sensing signaling molecules by bacteria^{72–74}. Furthermore, variations in bacterial community composition have been demonstrated among different supraglacial habitats (snow, ice, meltwater, soil)^{28,75,76}, and higher bacterial diversity and more complex interaction networks (relationships in co-occurrence networks based in Pearson's correlation coefficient) have been observed in soils compared to other habitats⁷⁷. We thus suggest that ICE, BW, and CRYOW could host lower

bacterial diversity that could facilitate algae to a lower extent compared to terrestrial substrates. This explanation is coherent with the observed differences in diversity and richness of algae between CRYO and CRYOw. Finally, ICE, BW, and CRYOw are the most “unstable” habitats and thus the most affected by glacial melt, which may make it harder for newly colonizers to survive.

Temporal variability in algal communities

Our results revealed that algal biomass, diversity, and species composition on the Forni Glacier showed significant intra- and inter-annual variation. In particular, the algal community changed more in aquatic habitats, and this variability in algal biovolume and diversity was mainly driven by the algal bloom in the ICE samples. Indeed, the quantity of *M. berggrenii* increased substantially in ICE in late summer, with the highest values reached in September 2023, increasing the total biovolume and decreasing the Shannon diversity index. Previous studies on the Greenland Ice Sheet revealed a significant linear relationship between average Zygnematophyceae biomass on surface ice and time since snow line retreat^{26,78}. Always on the Greenland Ice Sheet, it has been demonstrated that algal abundance (especially *M. berggrenii*) was moderated by rainfall events⁷⁹, as studies revealed a positive correlation between the number of days since the last precipitation event and algal abundance, and attributed this effect to the flushing of algae during rainfall events. However, the factors driving a greater frequency of Zygnematophyceae in some samples and periods remain largely unclear. In our study, precipitation was higher in 2023 than in 2024 (cumulated liquid precipitation during the studied period was 482 and 299 mm, respectively), with a peak of almost 60 mm at the end of August 2023 when highest values of algal abundances were recorded, which contradicts what was found on the Greenland Ice Sheet. However, it can also be assumed that snowfall events promote the algae transport and deposition on the glacier surface⁸⁰. In addition, air temperatures were more stable in 2023 than in 2024, which could promote the development of *M. berggrenii*. Finally, the sampling was performed later in the ablation season in 2023 than in 2024, which could also explain a difference in the development of the snow algae. A difference in diatom biovolume was also observed across the years, with higher biovolumes observed in 2023 than in 2024. In 2024, air temperature, incoming solar radiation, and liquid precipitation were slightly lower, which could result in slower colonization processes and less favorable conditions for diatom development. Differences in the colonization of the bare ice due to variability in seeding processes could also explain the temporal variation of algal development, as suggested in another study⁸¹ for bacterial communities.

Conclusion

Despite their potential importance for surface albedo, carbon cycle, and global biodiversity patterns, few studies have characterized the algal communities in all supraglacial habitats on a same glacier. Our results revealed that the algal biovolume, diversity, and community composition varied among habitats, years, and months on the Forni Glacier. More specifically, we showed that different ecological processes structured the algae communities among the different supraglacial habitats.

Even though regional disparities exist in glacier responses to climate warming, recent studies show an overall consistent pattern of glacial retreat, surface lowering, and ice mass lost over the entire European Alps, with an average loss rate between 2000 and 2014 of approximately -39 km^2 per year⁸². The Forni Glacier is no exception, exhibiting a thinning and retreat between 4.28 ± 1.46 and 4.55 ± 0.24 m per year between 2007 and 2022^{83,84}. These trends indicate that, under continuous warming, further loss of glacier ice and snow is inevitable. As a consequence, the habitats that sustain the highest levels of glacial biodiversity are disappearing, threatening the extinction of glacier-specialist taxa. Such biodiversity loss could have cascading effects on adjacent high-altitude ecosystems that depend on glacier-derived resources.

Understanding the biological and ecological processes occurring in these rapidly vanishing environments is therefore urgent. If we fail to study them now, we risk not only losing unique biodiversity but also missing an invaluable opportunity to uncover fundamental ecological mechanisms governing life under extreme conditions, insights that could inform our understanding of ecosystem resilience under future climate scenarios.

Our study demonstrates that high-resolution investigations of single glaciers across multiple habitats provide critical insights into the factors shaping community dynamics and ecosystem function. Nevertheless, to achieve a broader understanding, coordinated efforts combining classical microscopy with molecular and functional analyses are needed. Expanding such integrative studies across different glaciers and temporal scales will be key to identifying the thresholds of ecological changes and improving predictions of how glacier ecosystems will evolve under accelerating climate change.

Data availability

Data are available on the following <https://doi.org/10.5281/zenodo.16939622>.

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Author contributions

F.D.: Conceptualization, Data curation, Formal analysis, Investigation, Methodology, Resources, Software, Visualization, Writing (original draft preparation). R.A. and A.F.: Funding acquisition, Project administration, Resources, Supervision, Validation, Writing (review and editing). A.A., G.D., F.F., A.F., D.F., M.G., V.L., T.L., F.S.M., V.N., F.P., A.S., M. S., L. M.T., B.V., L.V., and M.C.: Resources, Validation, Writing (review and editing). B.L.: Conceptualization, Resources, Supervision, Validation, Writing (review and editing).

Declarations

Competing interests

The authors declare no competing interests.

Additional information

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