frontiers in Earth Science

ORIGINAL RESEARCH
published: 17 February 2022
doi: 10.3389/feart.2022.740998

Spatial Distribution of Unique Biological Communities and Their Control Over Surface Reflectivity of the Stanley Glacier, Uganda

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Diverse microbes have been revealed to live in glaciers worldwide, but only a few biological studies were dedicated to glaciers in tropical Africa. These glaciers are shrinking rapidly and are expected to disappear shortly. In this study, we carried out biological and glaciological field observations on Stanley Glacier, the largest remaining glacier in the Rwenzori Mountains, Uganda, Africa. Microbial aggregates ranging from micrometer to centimeter in size were found on the glacier surface and contained moss and various types of Chlorophyta, among which a new endemic species of green alga. Concentrations of total impurities on the glacier surface, including microbial aggregates, varied spatially and decreased as altitude increased. The large microbial aggregates (larger than 4 cm in diameter) were found only at the glacier surface near the terminus and side margins, where the surface was less frequently covered with snow. It is also shown that the total organic matter on the glacier surface is determined by the timing of snow cover, which affects the quantity of solar radiation reaching the glacier ice surface. Furthermore, the total impurity content was negatively correlated with surface reflectivity, revealing their potential role in albedo reduction at the glacier surface through positive feedback between enhanced meltwater and increased biological growth.

Keywords: glacier ecosystem, tropical glacier, moss aggregation, psychrophile, Rwenzori mountains, albedo

OPEN ACCESS

Edited by:
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Specialty section:
This article was submitted to Cryospheric Sciences, a section of the journal Frontiers in Earth Science

Received: *14 July 2021*
Accepted: *19 January 2022*
Published: *17 February 2022*

Citation:
Uetake J, Samyn D, Anguma S and Takeuchi N (2022) Spatial Distribution of Unique Biological Communities and Their Control Over Surface Reflectivity of the Stanley Glacier, Uganda. Front. Earth Sci. 10:740998. doi: 10.3389/feart.2022.740998

INTRODUCTION

Glaciers and ice sheets are biological habitats hosting various forms of life (Boetius et al., 2015). Microbial communities on glaciers and ice sheets play essential roles in carbon (e.g., carbon fixation, carbon degradation) and nitrogen cycles (e.g., nitrogen fixation, nitrification, and denitrification) (Anesio et al., 2009; Telling et al., 2011), which are important for the activity not only of supra- or intra-glacier biota but also of downstream terrestrial and marine ecosystems (Lawson et al., 2014).

Due to climate change, African glaciers are shrinking very rapidly (Nicholson et al., 2013; Prinz et al., 2016) and are expected to disappear shortly (Taylor et al., 2006; Thompson et al., 2009). In the Rwenzori Mountains, located at the border between Uganda and the Democratic Republic of Congo in Eastern Africa, glacier wastage is thought to result from the combined effects of climate warming (Taylor et al., 2006) and changes in atmospheric moisture (i.e., decreased humidity and reduced cloudiness) (Mölg et al., 2006).

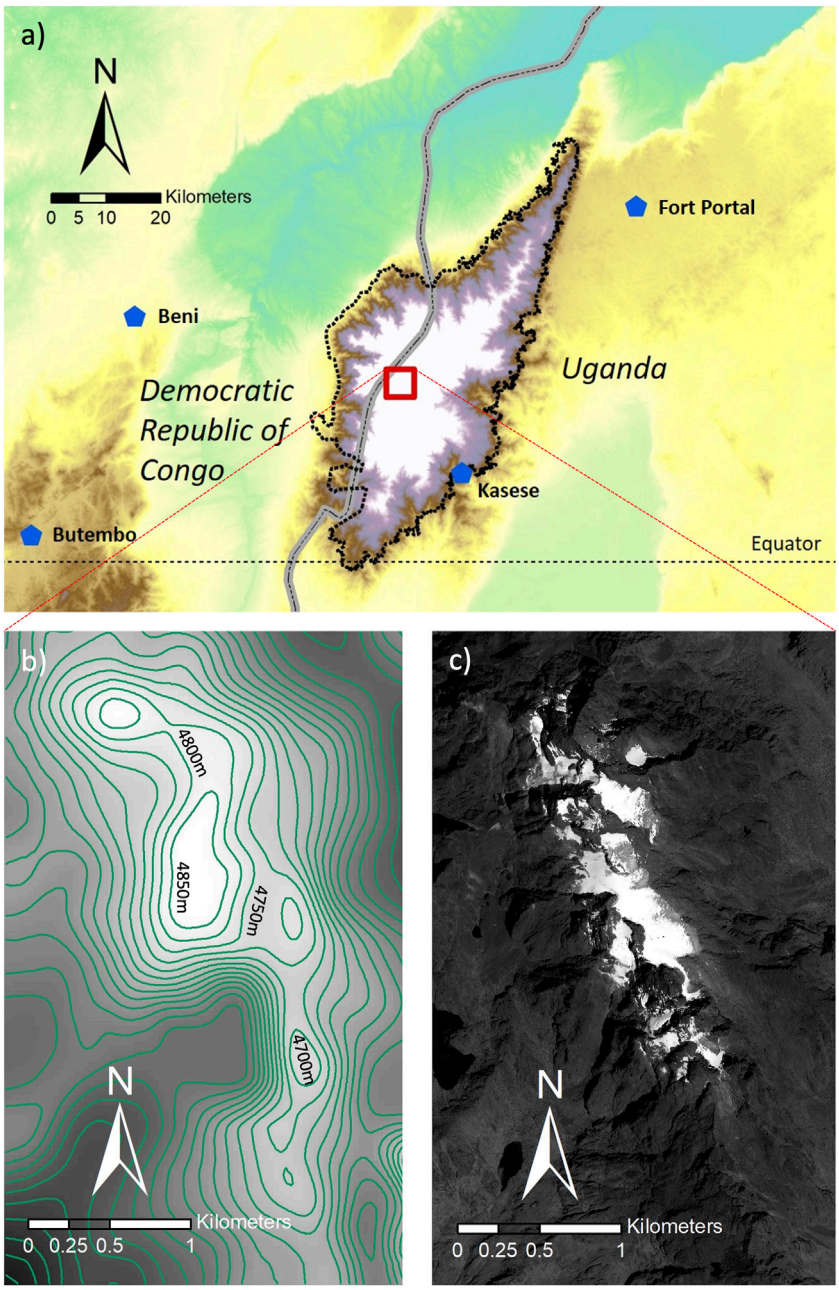

FIGURE 1 | (A) Map of the Rwenzori region (bold dotted contours) with national borders between Uganda and D.R. Congo (thick grey line); **(B)** DEM (SRTM) of Stanley Plateau area, with 50 m contour lines; **(C)** satellite image (Worldview) of Stanley Plateau area, with the same extent and scale as in **(B)**.

Snow and ice albedo constitutes another important factor controlling glacier volume evolution (Takeuchi, 2009; Takeuchi et al., 2015). Glacial micro-organisms have been recognized as important in this regard due to the darkening of their intracellular pigment at the snow or glacier surface (Lutz et al., 2016b; Tanaka et al., 2016; Yallop et al., 2012). Also, submillimeter to millimeter-sized biological aggregates known as "cryoconite granules" have similar effects, thereby reducing surface reflectivity (Cook et al., 2015). These granules are bound together through an extracellular polymeric substance produced by filamentous cyanobacteria (Langford et al., 2010; Uetake et al., 2019), forming a layered structure of microorganisms with complex biofilm (Smith et al., 2016; Takeuchi et al., 2010). The growth of cryoconite granules and subsequent reduction of glacier surface reflectivity and glacier melting has been reported in the Himalayas (Takeuchi et al., 2001a), Eastern Asia (Takeuchi et al., 2015), and Greenland (Takeuchi et al., 2018). The large-scale effect of these granules on water cycling in the Arctic has also been reported (Musilova et al., 2016).

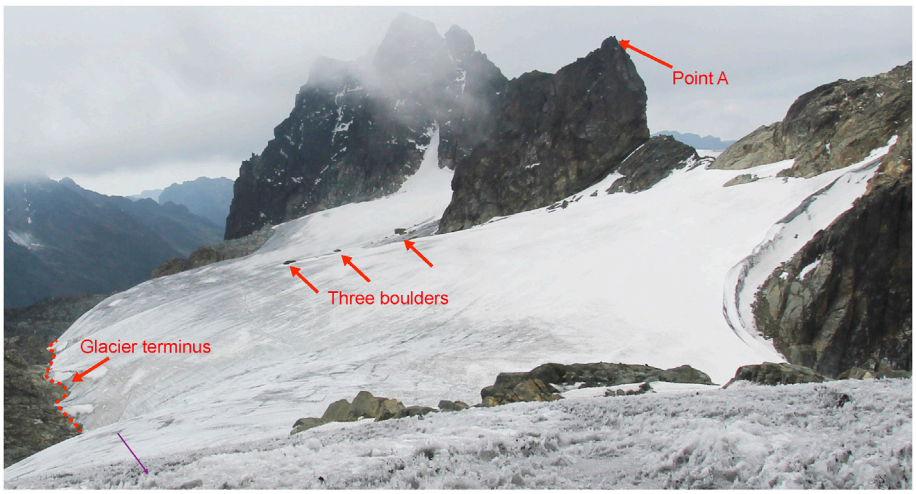

FIGURE 2 | General view of Stanley Glacier, Rwenzori mountains, looking southeastwards, from the 2012-ST3 sampling site (**Figure 3**). The image was taken in February 2012, 1 month after the Worldview satellite image shown in **Figures 1**, **3**. The position and direction of the photo are plotted on the same satellite image (**Figure 3**).

Although glacier shrinkage significantly impacts glacier ecosystems and periglacial downstream environments, only very few biological studies have been carried out in African glacierized regions: in Mt. Kilimanjaro (Vimercati et al., 2019), Mt. Kenya (Kuja et al., 2018) and Rwenzori Mountains (Uetake et al., 2014; Zawierucha et al., 2018). For example, on Stanley Glacier located in the Rwenzori Mountains at the border between Uganda and the Democratic Republic of Congo (DRC) (Uetake et al., 2014) described for the first time the existence of unique and relatively large (from micrometers to centimeters in size) biological aggregates made of moss. These aggregates were called "glacial moss gemmae aggregates" (GMGA), the term "gemma" referring to the cell components resulting from asexual reproduction. On the same glacier, Zawierucha et al. (2018) recently found new tardigrade species (*Adropion afroglacialis* sp. nov.), revealing unexpected biodiversity and activity in this poorly studied region of the world.

In order to shed light on African glacier biodiversity and characterize the effect of supraglacial impurities on surface reflectivity, we sampled and analyzed the biological content of surface impurities from 17 sites across Stanley Glacier in the Rwenzori Mountains and described their spatial distribution and surface reflectivity. We first discuss here the factors affecting the growth of organisms on the glacier and, second, the effect of supraglacial impurities on the reflectivity of the glacier surface.

MATERIALS AND METHODS

Glacier Characteristics and Sampling Site

Stanley Glacier represents the largest glacier in the Rwenzori Mountains, flowing on the flank of Mount Stanley's second highest peak, Alexandra Peak (**Figures 1**, **2**). The area of the glacier was estimated to be 0.248 km^2 in February 2012 based on Worldview satellite imagery. The glacier flows southwards from 4,960 m to 4,770 m a.s.l. forming a plateau glacier called Stanley (or Elena) Glacier. According to a recent report, the glacier's area has now declined to less than 30% of its early 20th century area and is confined to the summit part of Mt Stanley (Samyn et al., 2017). We conducted field campaigns during the February month of four consecutive years between 2012 and 2015, during which snow and ice were collected at various sites on the glacier surface. In February 2012, surface ice and snow samples (10 × 10 × 5 cm) were collected for microscopic observation at three sites (2012 ST1 to 2012 ST3 in **Figure 3A**). In February 2015, surface ice and snow samples (10 × 10 × 5 cm) were collected for biological analysis at 17 sites selected 70–80 m apart across the glacier area. The samples were collected using an electric chainsaw (MUC250D, Makita, Japan) without any lubricants for ice and a stainless scoop for snow (**Figure 4**). Ice and snow samples were stored in the field into non-contaminating plastic bags until complete melting. These plastic bags were then hung in the camp, and supraglacial impurities settled at the bottom were carefully transferred into 100 or 5 ml plastic bottles for respective analyses. All 100 ml bottle samples were fixed using approximately 3% (final concentration) of 37% formaldehyde solution and transferred to the laboratory in Japan at environmental temperature for further size measurements. In contrast, the 5 ml bottle samples were kept cool during fieldwork and transportation, with plenty of ice in a large insulated container, for further morphological analysis in the laboratory.

Biogenic Material Size Sorting and Weighing

To characterize the impurities collected on the glacier surface, the 100 ml samples were sieved using stainless steel meshes and sorted into the following classes: Class 4,000 (with longest axis larger than 4,000 μm), Class 1,000 (1,000–3,999 μm), Class 250 (250–999 μm) and Class U250 (smaller than 250 μm). After size

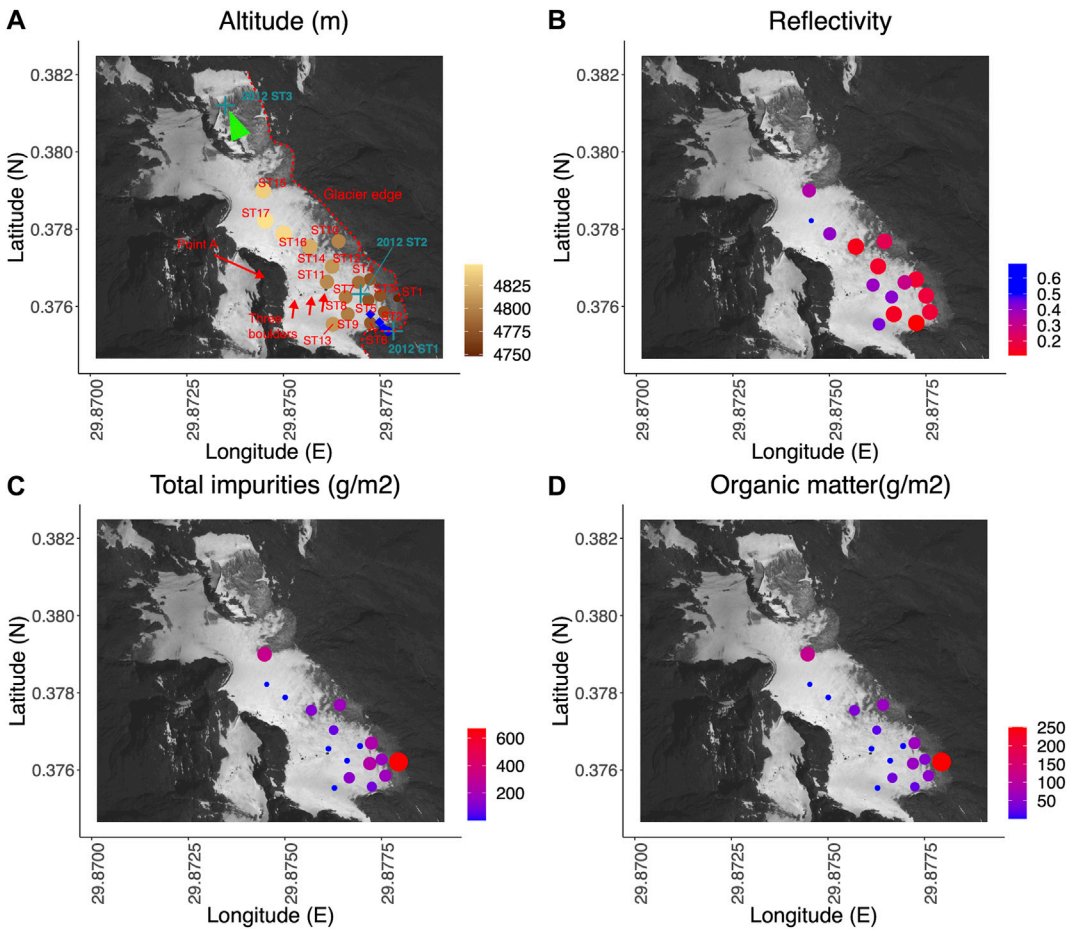

FIGURE 3 | Satellite image (Worldview) of sampling sites on Stanley Glacier in 22 January 2012 and spatial distribution of reflectivity and total impurities and organic matters. An overview picture of the corresponding sampling area is given in **Figure 3**. **(A)** Altitude of sampling sites in 2015 (circles), and site locations of snow depth measurements in 2013 (blue diamonds) and of phototroph collection in 2012 (teal green cross). The red dashed line indicates glacier terminus and margins on 22 January 2012; **(B)** reflectivity (spectral range: 353–1,008 nm); **(C)** total impurity content; **(D)** organic matter content. Point values (circles) are displayed through their respective color and size. Green triangle shows the position and angle of view used in **Figure 2**.

sorting, the total impurity content (organic matter + inorganic matter) of each sample was measured before homogenization and combusted at 850°C in the furnace of the NC analyzer (Sumigraph NC-22A, Sumika Ltd., Japan). Ignition loss (%) was calculated from the weight before and after combustion (Takeuchi et al., 2005a; Edwards et al., 2014). The amount of organic matter was estimated by multiplying the impurity content lost during combustion to the total impurity content. Both total impurity and organic matter contents were subsequently converted to weight per unit area (g m^{-2}). The weight per unit area threshold for accurate measurement was 0.056 g m^{-2}, and all samples with an ignition loss lower than this value were discarded from further analysis.

Microscopic Observations

Immediately after our samples arrived in the laboratory, the 5 ml bottle samples collected for morphological observation were analyzed using an optical microscope (FV1000: Olympus, Tokyo, Japan), focusing on the morphology of microbial cells, especially green algae and moss gemmae. In order to quantify their cell concentrations, the samples were diluted 12 to 60-fold with Milli-Q water and filtrated using a membrane filter (JGWP01300, Millipore) before the number of cells in the entire field of view were counted on each filter.

Surface Reflectivity and Snow Measurements

The glacier surface light spectrum (in the 344–1,051 nm range) was measured at all sites except ST1 and ST5 in February 2015 (**Figure 3B**) using a hand-held spectrometer (MS-720, EKO instruments, Japan) with a 25° field of view adapter from 10 cm above the measured surface (corresponding to about 15 cm^2 of measured surface area). The white reference for the spectrometer calibration was always kept horizontal against the glacier surface before each measurement. Surface reflectivity was calculated from the mean value of the measured spectrum (with a nominal wavelength ranging from 353 to 1,008 nm). In addition,

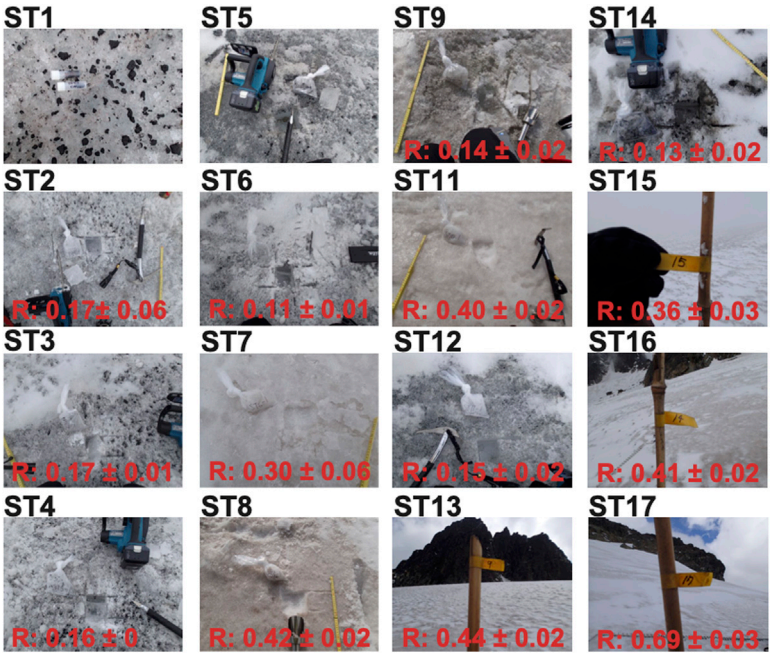

FIGURE 4 | Surface condition at each sampling site on Stanley Glacier. Measured reflectivity (R) is indicated with standard deviation at the bottom of each image (no reflectivity measurements were conducted at ST1 and ST5). All images were taken in February 2015.

snow depth was measured using an avalanche probe and a ruler on 10 February 2013, when most of the glacier surface was covered with temporary snow (**Supplementary Figure S1**).

Images of the Glacier

The satellite image (panchromatic band) used for glacio-biological mapping and shown in **Figures 1**, **3** was acquired by WorldView-1 (DigitalGlobe, United States) on 22 January 2012, and distributed to the authors by the Japan Space Imaging Corporation (http://www.spaceimaging.co.jp/en/, image ID: 1020010019691400). An overview picture was taken from the studied glacier area on 7 February 2012, from the upper part of Stanley Glacier (2012_ST3) and shown in **Figure 3**.

RESULTS

Microorganisms and Supraglacial Impurities on the Glacier

Optical microscopy revealed that the supraglacial impurities collected from all sites on Stanley Glacier contained mainly three major phototrophs, including moss gemmae of *Celatodon purpureus, Cylindrocystis brebissonii* and an unknown phototrophic organism (**Figure 5**). Three types of green algae were also observed, including red-pigmented green algae (**Figure 5**). The total cell concentration of the three most abundant taxa (*C. purpureus,* unidentified green alga, and *C. brebissonii*) shows a more significant value near the glacier terminus (2012-ST1: 450-5100, 1500-13350 and 2400-6600 cells/ml, respectively) and a lower value at the highest glacier site (2012-ST3: not detectable, 0-2.52 and 0.72-3.96 cells/ml) (**Figure 6**; **Supplementary Table S1**).

The same spatial pattern as for the total cell concentration was observed across the glacier in terms of total impurity content, which reflects the concentration of aggregates made up of the most abundant phototrophs, other microorganisms such as bacteria, and mineral dust. The mean total impurity content ranged from 0.06 to 801.0 gm^{-2} (mean SD: 143.8 ± 211.8 gm^{-2}), with the greatest and smallest concentrations occurring at the lowest site (669 ± 166 gm^{-2} at ST1) and the highest site (0.35 ± 0.33 gm^{-2} at ST17), respectively (**Supplementary Table S2**). The corresponding mean loss on ignition amounted to 33.2 ± 4.8%, whereas the mean total organic matter of impurities was of 46.3 ± 81.8 gm^{-2} (**Supplementary Figure S3**; **Supplementary Tables S3, S4**). Our measurements of the four different size fractions of impurities show that both total impurity and organic matter contents of Class 4,000 were the largest (total impurities: mean 65.93 gm^{-2}; organic matter: mean 22.34 gm^{-2}), followed by the smallest size class (Class U250) (total impurities: mean 35.40 gm^{-2}; organic matter: mean 10.53 gm^{-2}). The following ranking classes in terms of weight were Class 250 (total impurities: mean 32.56 gm^{-2}; organic matter: mean 10.21 gm^{-2}) and Class 1,000 (total impurities: mean 9.90 gm^{-2}; organic matter: mean 3.26 gm^{-2}) (**Supplementary Figure S3**).

Glacier Reflectivity

The surface reflectivity ranged from 0.10 to 0.73 (mean + -SD: 0.28 ± 0.16 gm^{-2}), with the lowest value at the terminus: ST6 and the highest at the snow-covered ST17 (**Figure 3B**, **Supplementary Table S5**). A correlation table and matrix

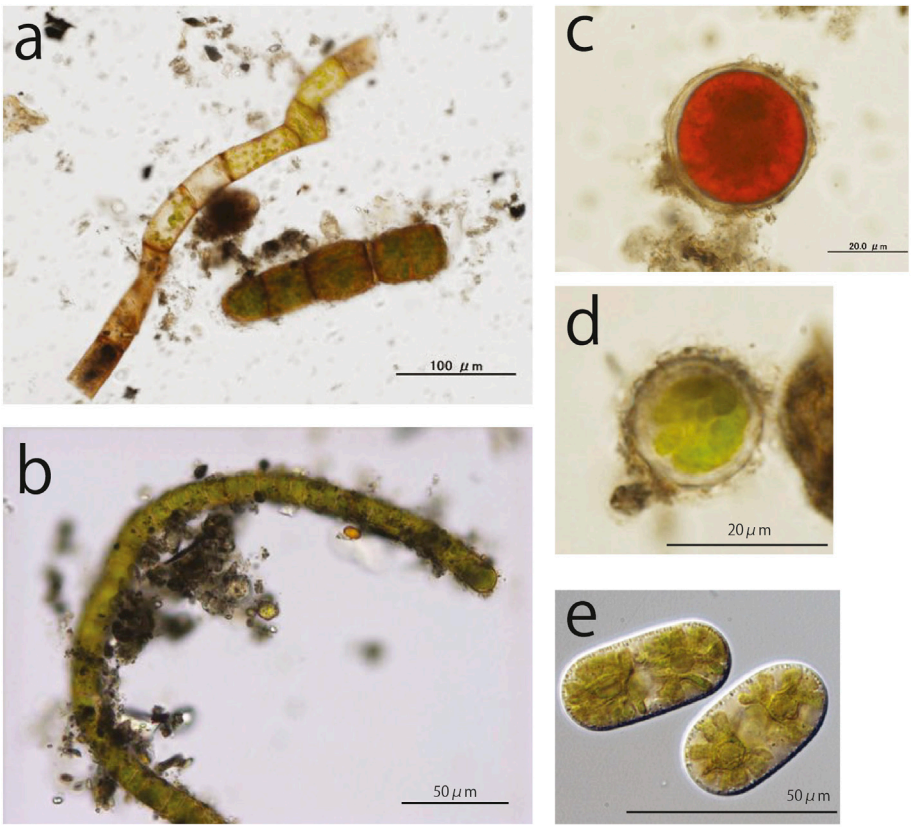

FIGURE 5 | Phototrophs (moss gemma and Chlorophyta) on Stanley Glacier surface: **(A)** *Celatodon purpureus,* **(B)** unidentified green algae, **(C)** snow red algae, **(D)** unidentified round, green algae, **(E)** *Cylindrocystis brebissonii.*

between the altitude, reflectivity, organic matter and total impurity content are shown in **Table 1** and **Supplementary Figure S2**. The concentration of total impurities (Impurity_Total) was negatively correlated (r = −0.52) with the reflectivity of the glacier surface (p = 0.05), whereas no significant correlation was found between the concentration of total organic matter (Organic_Total) and the glacier reflectivity (p = 0.11). In addition, the concentration of Class 4,000, which is the most abundant impurity fraction (45.9 and 48.2% of the total impurity and organic matter contents respectively), was not significantly correlated with reflectivity. However, the correlation coefficient between size fraction (for both total impurity and the organic matter contents) and reflectivity increased with decreasing size (**Table 1**).

DISCUSSION

A Unique Phototrophs Biodiversity

The unknown phototrophic organism shown in **Figure 5** presents novel taxonomic characteristics regarding its morphology. Due to logistical constrains, DNA-level identification of this type of organism was not possible within the context of the present work. However, some criteria, including cell size and the presence of chloroplast, suggest a strong likelihood to the green algae taxon. Since, first, the only occurrence of *C. purpureus* on a glacier has been reported from Stanley Glacier (Uetake et al., 2014), and, second, our unidentified filamentous alga has never been reported in any other region globally, these two phototrophic species can reasonably be considered as endemic of Rwenzori glacial environments in current knowledge. Two other types of green algae found on Stanley Glacier, including *Cylindrocystis brebissonii* and a red-pigmented alga, present similar morphological features as other algae commonly distributed on other glaciers worldwide (North America Hoham, 1975; Himalayas Yoshimura et al., 2000; Mueller and Pollard, 2004; Uetake et al., 2010; Yallop et al., 2012).

Factors Affecting the Biomass of Phototrophs

The concentration of these algal cells on Stanley Glacier surface decreases with elevation. Altitudinal variations of glacier microbes are commonly found in mountain glaciers (Segawa et al., 2010; Takeuchi, 2013; Takeuchi et al., 2005b, 2019; Uetake et al., 2010; Yoshimura et al., 1997). As air temperature decreases linearly with increasing elevation, seasonal snow cover melts faster at lower glacier elevation as a result of larger cumulated

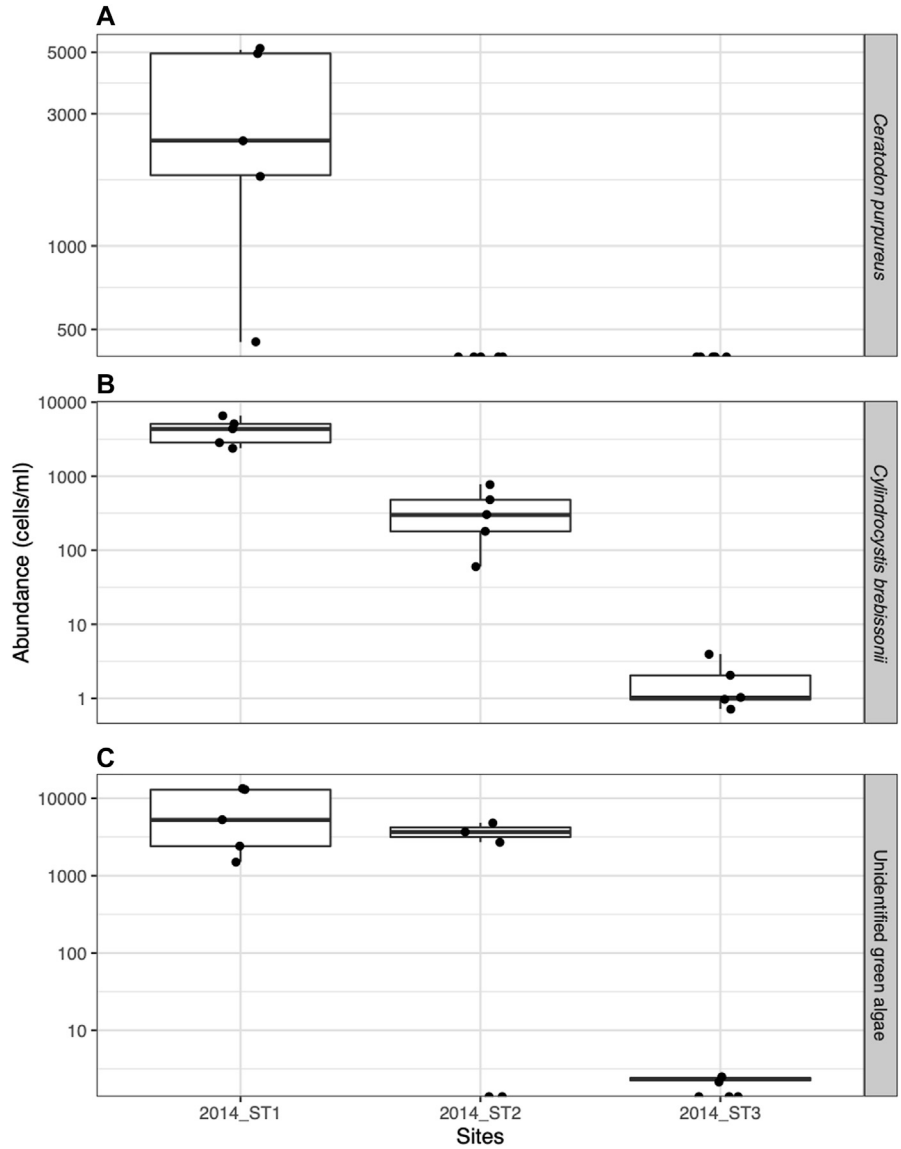

FIGURE 6 | Spatial variation of the cell concentration (cell count/ml) of phototrophs on Stanley Glacier: **(A)** *Celatodon purpureus,* **(B)** *Cylindrocystis brebissonii,* and **(C)** unidentified green algae).

solar radiation on the glacier ice surface, thereby inducing more optimum conditions for algal growth (Yoshimura et al., 1997). In February 2013, when most of the glacier surface was covered with snow despite the typically dry season period, snow depth gradually increased (from 0 to 0.8 m) with altitude (**Supplementary Figure S1**). Although the snow depth survey was conducted in limited areas and therefore only reflects a limited temporal pattern (blue diamond in **Figure 3A**), it is reasonable to consider that this altitudinal gradient of snow depth is likely to occur in other years.

Additionally, the area near the glacier terminus, including our lowest altitude sample (2012-ST1), was always free of snow cover during each of our February visits from 2012 to 2015, as exemplified on the 2012 satellite image in **Figure 3**. The presence of snow on the ice surface can significantly reduce light penetration through the snowpack (e.g., irradiance is reduced by one third under 5 cm snowpack, as shown by Pomeroy and Brun (2001), from which we assume as a corollary that the frequency of snowfall can constitute another factor leading to altitudinal changes in the distribution of phototrophs.

As a result of the snow depth altitudinal gradient, the solar radiation at the ice surface is likely to be strongest in the lowest area of the glacier, which is likely to promote the growth of phototrophs. Although the growth conditions of moss gemmae on glaciers have not yet been fully appraised, nutrient availability can be considered a limiting factor for phototrophs (Jones, 1991). Comparison of multiple glacier environments with varying geological settings also showed that the metabolic growth of

TABLE 1 | The Pearson correlation matrix between altitude, reflectivity, total impurity content and organic matter content. Each significance level (*p*-value) is associated to a symbol: <0.001: "***"; <0.01: "**"; <0.05: "*".

	Organic_Total	Organic_4,000	Organic_1,000	Organic_250	Organic_U250	Impurities_Total	Impurities_4,000	Impurities_1,000	Impurities_250	Impurities_U250
Altitude	−0.47	−0.44	−0.33	−0.25	−0.49*	−0.53*	−0.46	−0.35	−0.32	−0.48
Reflectivity	−0.43	−0.2	−0.48	−0.5	−0.63*	−0.52*	−0.24	−0.51*	−0.59*	−0.71**

green algae is promoted by the presence of nitrogen in sufficient concentration (Lutz et al., 2016a). For logistical reasons, nutrient concentration could not be measured in this study, however, previous glacier studies reported nutrient concentration as a secondary factor for growth compared to altitudinal change (Hodson et al., 2005; Yoshimura et al., 1997).

Effect of Impurities on the Reflectivity of Glacier Surface

Most of Stanley Glacier surface impurities consisted of aggregates of organic and inorganic material, including phototrophic and heterotrophic microorganisms together with mineral dust. The total impurity content on Stanley Glacier (143 ± 188 gm^{-2}) was significantly more extensive than those reported on glaciers in the Arctic (Takeuchi et al., 2014: 18.8 ± 21.6 gm^{-2}), in Russia (Takeuchi et al., 2015: 45.2 ± 12.0 gm^{-2}), in Patagonia (Takeuchi et al., 2001b: 38 gm^{-2} on average), in Alaska (Takeuchi, 2002: 23 gm^{-2} on average), and Caucasus Mountains (Kutuzov et al., 2021: 36 ± 38 gm^{-2}). However, it was lower than on Central Asian glaciers, where the greatest concentration of supraglacial impurity has been reported globally (Takeuchi et al., 2005: 292 ± 196 gm^{-2}; Takeuchi and Li, 2008: 335 ± 211 gm^{-2}). In terms of organic matter content, Stanley Glacier exhibited significantly larger values (46.3 ± 68.6 gm^{-2}) than Central Asian glaciers (Takeuchi et al., 2005: 25.4 ± 16.5 gm^{-2} and 8.6 ± 1.9%, Takeuchi and Li, 2008: 30.2 ± 15.6 gm^{-2} and 9.4 ± 1.6%) or any other glacier described in the literature [see, e.g., Edwards et al. (2014)]. Our results, therefore, point to relatively high impurity content and exceptionally high organic content at the surface of Stanley Glacier compared to other regions of the world.

The total impurity and organic matter contents were spatially variable (**Figure 3**, **Supplementary Figure S3**). In particular, both the total impurity and organic matter contents of the smallest size fraction significantly decreased with altitude (**Supplementary Figure S2**), except at the "high altitude" glacier marginal sites (including ST9, ST10, ST14, and ST15) where total impurity and organic matter contents were relatively larger than elsewhere on the glacier. In the vicinity of the glacier terminus (ST1, ST2, ST3, ST5), at the side margins (ST4) and at high altitude glacier marginal sites (ST9, ST10, ST14, ST15), the total organic matter content was especially large and to our knowledge larger than any other record values [e.g., 30.2 gm^{-2} Takeuchi and Li (2008)]. This can be attributed to the presence of GMGAs in high concentrations since the fraction of Class 4,000 to the total organic matter content is also generally high at these sites (except ST5, ST9, and ST 14) (**Supplementary Figure S3B**). Most of the high GMGA concentration sites (ST1, ST2, ST3, ST4, ST10, ST15) were located in the darker ice area identified on the satellite image acquired in January 2012 (**Figure 3**) and on the field picture taken 1 month later (**Figure 2**). The snow cover at these sites is less frequent throughout the year, thereby favoring the growth of phototrophs compared to other areas.

As can be seen from **Figures 3**, **4**, the impurity content as well as their size distribution vary from site to site across the glacier surface. Although the impurity content on the glacier surface was well recognized as an important factor leading to the reduction of glacier reflectivity, both the total amount of impurities and their size distribution should also be considered in that regard, owing to the negative correlation observed between size fraction of impurities and glacier reflectivity. It is interesting to note that the largest size fraction (Class 4,000), which was associated with the largest measured impurity content due to the presence of moss aggregates, did not correlate well with ice surface reflectivity. Conversely, the correlation coefficients between the finer size fractions (i.e. Class 250 and Class U250) and reflectivity were relatively large (**Table 1**; **Supplementary Figure S2**). These findings support the fact that, despite their low ratio in organic matter, small and homogeneously spread impurities (e.g., ST9 in **Figure 4**) were probably more effective in reducing albedo than large and scattered GMGAs (e.g., ST2, ST3, and ST4 in **Figure 4**). These finer size fractions are likely to provide vital ground for the development process of the larger aggregates.

CONCLUSION

Based on its taxonomic characteristics, a new species of green algae, endemic of Rwenzori glacial environments in Africa, was discovered within the present work. Together with another endemic species of moss previously reported by the authors, more ubiquitous green alga taxa were also observed, suggesting a high degree of microbial diversity. Our measurements of total impurity concentration at the surface of Stanley Glacier point to exceptionally high organic content compared to other regions of the world. An inverse relationship was found between the surface reflectivity and the total impurity content. Our work supports previous findings suggesting that supraglacial impurities, including microbial aggregates, effectively reduce albedo and are likely to promote snow and ice melting at the glacier surface. In turn, albedo reduction possibly has a positive feedback effect on glacial microbial communities due to enhanced meltwater availability and increased solar radiation absorption. A size effect was also observed on glacier reflectivity by microbial impurities, with finely distributed granules having a stronger impact on surface albedo reduction than larger moss aggregates. In the framework of further investigations, we suggest focusing on moss generation processes such as the growth of

phototrophs and their subsequent detachment/aggregating mechanisms in order to better understand the spatial distribution evolution of the various impurity size fractions and their respective impact on glacier reflectivity.

DATA AVAILABILITY STATEMENT

The original contributions presented in the study are included in the article/**Supplementary Material**, further inquiries can be directed to the corresponding author.

AUTHOR CONTRIBUTIONS

JU designed research; JU, DS, and SA performed field research; JU analyzed data; and JU, DS, and NT wrote the paper.

FUNDING

JU.acknowledges support from a Grant-in-Aid for Young Scientists (B; Grant agreement #25740012) from the Ministry of Education, Culture, Sports, Science and Technology of Japan. DS acknowledges support from a Marie Curie fellowship of the European Commission (H2020-EU.1.3.2.; Grant agreement #656847) and Fonds Ernest Solvay (Belgium). NT acknowledges support from a Grant-in-Aid for Scientific Research (A; Grant agreement #19H01143) from the Ministry of Education, Culture, Sports, Science and Technology of Japan.

ACKNOWLEDGMENTS

The field research was supported by the Uganda Wildlife Authority, the Uganda National Council for Science and Technology. In addition, the authors would like to thank A. Wada of the Greenleaf Tourist Club for management of local transportation in Uganda. We also thank the guides and porters of the Rwenzori Mountaineering Service for guidance and transportation of research equipment, Y. Tsuji, for operating the NC analyzer.

SUPPLEMENTARY MATERIAL

The Supplementary Material for this article can be found online at: https://www.frontiersin.org/articles/10.3389/feart.2022.740998/full#supplementary-material

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