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RESEARCH

Evidence for rapid ecosystem retrogression along a post-glacial chronosequence in Antarctica

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Abstract
Glacial retreat due to global warming is exposing large tracts of barren glacial sediments that are quickly colonized by CO_2-fixing microbial communities that can constitute the climax community in many high-Arctic, alpine, and Antarctic environments. Despite the potential importance of these processes, little is known about microbial community successional dynamics and rates of carbon (C) sequestration in environments where higher plants are slow or unable to establish. We analyzed microbial community succession and C and N accumulation in newly exposed sediments along an Antarctic glacial chronosequence where moss and microbial autotrophs are the dominant primary producers. During the first 4 years of succession (0 to 40 m from the glacier) algae (including diatoms) were the most relatively abundant eukaryotes, but by the second phase studied (8 to 12 years) moss amplicon sequence variants (ASVs) dominated. The rise in moss coincided with a significant buildup of C and N in the sediments. The final two phases of the successional sequence (16 to 20 and 26 to 30 years) were marked by declines in microbial species richness and moss relative abundance, that coincided with significant decreases in both total C and N. These retrogressive declines coincided with a large increase in relative abundance of predatory Vampyrellidae suggesting a possible mechanism for retrogression in this and perhaps other terrestrial ecosystems at the edge of the cryosphere. These findings have implications for understanding CO_2 sequestration and ecosystem succession in microbial-dominated regions of the cryobiosphere where large tracts of land are currently undergoing deglaciation.

Keywords Ecosystem retrogression · Carbon sequestration · Nitrogen fixation · Vampire amoebae · Cryobiosphere

Introduction

Retreat of glaciers has accelerated across most of the Earth in the last 100 years due to global warming linked to human activity (Marzeion et al. 2014). Following glacier retreat, newly exposed barren sediments are initially colonized by CO_2-fixing and N_2-fixing microbes, initiating pedogenesis and ecosystem succession. Ecosystem succession of post-glacial chronosequences has been studied for over 120 years leading to a relatively good understanding of the interplay between plant succession and pedogenesis (Mathews 1992). More recently many studies have shown that microbial communities can change dramatically and drive pedogenesis and buildup of soil carbon (C) and nutrients before the arrival of higher plants (Schmidt et al. 2008; Bradley et al. 2014). For example, N_2-fixing cyanobacteria can increase soil C and N concentrations well before the arrival of higher plants, especially in environments where plant colonization is very slow (Schmidt et al. 2008), but little is known about the factors controlling the rate of microbial succession in extreme Antarctic and high-elevation environments (Darcy et al. 2018).

Traditionally, succession is viewed as a progressive process in which there is a continuous increase in soil and biological development leading to a community with mature soils and a climax plant community. However, over longer periods of time (thousands of years), and in the absence of major disturbances, some plant-dominated ecosystems can enter retrogression, whereby primary productivity, species diversity, and other ecosystem properties decline (Wardle et al. 2004; Peltzer et al. 2010). Microbial communities have been shown to track retrogression of plant

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communities over very old chronosequences (Krüger et al. 2015; Teste et al. 2021), but retrogression has not been considered in microbial ecosystems in which plant succession is either very slow or absent. Slow or absent plant succession is quite common in the cryobiosphere, especially in extreme polar (Solon et al. 2021; Dragone et al. 2022) and high-elevation ecosystems (Nemergut et al. 2007; Vimercati et al. 2020), but the possibility of ecosystem retrogression has not been explored in such systems.

The present study focuses on a high-latitude, glacial chronosequence near Palmer Station on the Antarctic Peninsula and builds on previous work at this site (Strauss et al. 2012) by reanalyzing data from Vimercati et al. (2022) to better understand of the relationship between pedogenesis and microbial community succession along a 30-year chronosequence that is devoid of higher plants. Research at similar unvegetated chronosequences has hinted at retrogression prior to the invasion of higher plants (Bardgett et al. 2007; Schmidt et al. 2016). Several studies of Alaskan and European glaciers have shown a decline in soil carbon storage during the pre-plant phases of succession, but these declines were not preceded by a progressive phase of carbon accumulation and were likely due to heterotrophic utilization of supra-glacial carbon deposited during glacial melt (Schmidt et al. 2016), or use of ancient carbon in sediments from under the melting glacier (Bardgett et al. 2007; Hågvar and Ohlson 2013; Sattin et al. 2009). In contrast, we know of no examples of progressive succession followed by retrogression along a plant-free glacial chronosequence. However, progression followed by retrogression has been noted in shorter-term and temporary habitats, such as during the development and collapse of under-snow microbial communities (Schmidt et al. 2009), and during rise and fall of the dominant microbial groups during cold-food fermentations (Cho et al. 2006; Wolfe et al. 2014; Dysvik et al. 2020).

Studying the details of microbial successional and retrogression processes in the absence of higher plants is important given that the rate of glacial retreat is currently occurring on a timescale that is several orders of magnitude faster than the rate at which higher plants can colonize new substrate in many high-latitude and high-elevation environments (Knelman et al. 2014; Darcy et al. 2018; Zimmer et al. 2018; Reider and Schmidt 2021). Therefore, the ability of these new lands to stabilize and begin accumulating carbon as soil organic matter depends on microbial photo- and chemoautotrophs for the first decades to hundreds of years of ecosystem succession (Freeman et al. 2009; Schmidt et al. 2008, 2016). Here we report on the changes of microbial communities and C and N storage along a 30-year, post-glacial chronosequence on the Antarctic Peninsula that reveals a cycle of microbial succession followed by retrogression in the absence of higher plants.

Methods

Field site and sampling design

A full description and map of the study site can be found in Vimercati et al. (2022). The receding glacier is an extension of the Marr Ice Piedmont that covers most of Anvers Island, and the deglaciated chronosequence is just to the east of Palmer Station (64°46′ S, 64°04′ W) on a gently sloping terrace. This area started to become ice-free in the early 1960s and the glacier has retreated at an average rate of about 10 m year^{-1} over the past 60 years (Vimercati et al. 2022). The sampled area extends 300 m from the edge of the glacier, representing a soil chronosequence of approximately 30 years that is devoid of higher plants. Soil samples were taken from four discrete zones that each covered a distance interval of 40 m with an unsampled distance of 40 to 60 m between zones. Thus, the sampled zones were from 0 to 40 m, 80 to 120 m, 160 to 200 m, and 260 to 300 m. Within each zone, samples were taken every 20 m with 2 to 3 replicate samples taken within a 1 m distance from each other at each 20-m interval for a total of 27 samples. This type of clustered sampling scheme has provided a good estimation of spatial variability of soil and microbial parameters in similar ecosystems (King et al. 2008, 2010; Schmidt et al. 2016). Each soil sample (50–100 g) was collected using a sterile spatula from the top 4 cm of soil. Samples were stored at −20 °C at Palmer Station and during shipment to the University of Colorado at Boulder, where they were kept frozen until analyzed.

Biogeochemical analyses

Total carbon (C) and nitrogen (N) concentration and isotopic analyses were performed in the Earth System Evolution Lab (EaSEL) at Iowa State University as described previously (Johnson et al. 2017; Schmidt et al. 2022). The samples were freeze-dried, crushed to a powder and 10% HCl was added to each sample to remove carbonates. Samples were sonicated and then centrifuged to remove the acid, 5 mL of DI water was added, and samples centrifuged again. Water was decanted, and this rinse step was repeated two more times. Samples were then dried at 70 °C overnight. Isotope signatures and concentrations of C and N were determined on a Thermo IsoLink Flash Elemental Analyzer attached to a Delta V Plus isotope ratio mass spectrometer. Samples were flash combusted at 1020 °C with an excess of oxygen (300 mL/min for 5 s) and a helium stream (140 mL/min) carried the combustion products over reagents to convert NOx and CO species to N_2 and CO_2. Samples were compared to external standards, including USGS62 (caffeine, $\delta^{15}N = 20.17‰$, $\delta^{13}C = -14.79‰$) and USGS42 (human hair, $\delta^{15}N = 8.05 \pm 0.1‰$, $\delta^{13}C = -21.09 \pm 0.1‰$) and to internal standards: peat ($\delta^{15}N = 4.24 \pm 0.1$, $\delta^{13}C = -28.17 \pm 0.1‰$) and urea ($\delta^{15}N = -2.73 \pm 0.1‰$, $\delta^{13}C = -37.14 \pm 0.1‰$). Analytical precision was 0.1‰, and reproducibility was 0.3‰ based on repeat analyses. Potential blank contributions were determined by running empty tin capsules and subtracting any influences from isotope and concentration values. Data are expressed in delta notation [$\delta = (R\ \text{sample}\ /R\ \text{standard} - 1) \cdot 1000$], where $R = {}^{13}C/{}^{12}C$, or ${}^{15}N/{}^{14}N$. The standards used were VPDB for $\delta^{13}C$ and atmospheric N_2 for $\delta^{15}N$. Differences in C, N, $\delta^{13}C$, and $\delta^{15}N$ values among the four successional zones were tested with analysis of variance followed by a Tukey post hoc test.

DNA extraction, sequencing and analyses

DNA was extracted from 0.5 g of soil using a PowerSoil® DNA Isolation Kit (MoBio Inc., Carlsbad, CA, USA) and DNA was quantified using a Qubit 3.0 fluorometer (Qubit, London, UK) with the Qubit dsDNA HS assay kit (Thermo Fisher Scientific). Bacterial and archaeal 16S rDNA was amplified using the 515F/806R primers, and eukaryotic 18S rDNA was amplified using the Euk1391f/EukBr primers according to the Earth Microbiome Project protocols (Porazinska et al. 2018). Amplified DNA was pooled, normalized to equimolar concentrations using SequalPrep Normalization Plate Kits (Invitrogen Corp., Carlsbad, CA, USA), barcoded and then sequenced using an Illumina MiSeq (2 × 150 bp chemistry) at the BioFrontiers Sequencing Core Facility at the University of Colorado at Boulder. DNA concentrations were Sequences have been deposited in the NCBI SRA database under project PRJNA836937.

Sequenced data were processed by first demultiplexing the data using idemp (https://github.com/yhwu/idemp) and trimming the primers with Cutadapt (Martin 2011). Quality plots were visually inspected and 16S rDNA forward and reverse reads were trimmed to 145 bp, while 18S rDNA forward and reverse reads were trimmed to 120 bp. The DADA2 pipeline (Callahan et al. 2016) was used to learn error rates, infer amplicon sequence variants (ASVs), merge sequences, filter out chimeras, and assign taxonomy. A naive Bayesian classifier trained on the SILVA 132 NR99 database (Quast et al. 2013) was used to assign taxonomy. The most abundant ASVs were verified by using BLAST (https://blast.ncbi.nlm.nih.gov). The "mctoolsr" R package was used to filter out chloroplasts, mitochondria, and eukaryotic reads from the 16S rDNA data and bacterial and archaeal reads from the 18S rDNA data (Leff 2017). Reads not assigned at least to the domain level were also removed. Fungal, algal, and moss reads were subset from total 18S rDNA sequences using the 'filter_taxa_from_input' function in the "mctoolsr" R package and analyzed separately. Search terms for taxa to keep at SILVA level 4 were 'Fungi' and 'uncultured_Chytridiomycota' (because "uncultured chytrids" were not designated as fungi in SILVA level 4 taxonomy) for fungal reads and 'Chloroplastida' and 'Ochrophyta' for algal reads, respectively. ASV tables were rarified to the number of sequences in the lowest populated sample (7756 for 16S rDNA, 3845 for 18S rDNA, Suppl. Figure 1). One sample was removed from the 18S rDNA dataset because of low number of reads. Differences in taxa relative abundances and ASV richness among the four successional zones were tested with analysis of variance followed by Tukey post hoc.

Results

Consistent with what is known about retrogression of plant communities, the Palmer glacial chronosequence showed an initial phase of progressive succession followed by retrogression in which stocks of soil nutrients declined (Figs. 1 and 2). Accumulation of soil C and N increased significantly between the initial (0–40 m) and second (80–120 m) zones, followed by a decline of both C and N in the final one or two zones of this chronosequence, and the final concentrations in zone 4 were statistically the same as in zone 1 for both C and N (Fig. 1). This parallel pattern of C and N fluctuations resulted in consistent C:N values across the entire chronosequence (Fig. 2) indicating non-N limited functioning of the microbial community; the overall C:N was 14.9 (SE 0.5) and it did not vary significantly between the four zones ($P = 0.24$).

Microbial diversity metrics also showed patterns indicative of progression followed by retrogression across the chronosequence (e.g. Suppl. Figure 2, 3). Focusing on phototroph diversity revealed that a rise and fall in moss (Fig. 3A) corresponded to the rise and fall of C and N patterns, whereas other phototrophs (cyanobacteria, algae and diatoms) did not track changes in C and N (Suppl. Figure 2a). The peak in moss relative abundance was also reflected in a significant increase in $\delta^{13}C$ and $\delta^{15}N$ values during the second stage of succession followed by a decline in $\delta^{13}C$ during the final two stages of succession (Suppl. Figure 4). Total ASV richness of both 16S and 18S datasets showed an initial increase between the first two successional zones but then declined after zone 2 for 16S and after stage 3 for 18S data (Suppl. Figure 3). In contrast, the final two stages of succession in the sampled chronosequence showed a significant increase in predatory Cercozoa (Vampyrellidae) (Fig. 3B) coinciding with the decline of relative abundance of moss. In contrast, fungi did not increase in relative abundance across the entire chronosequence (Suppl Fig. 2b).

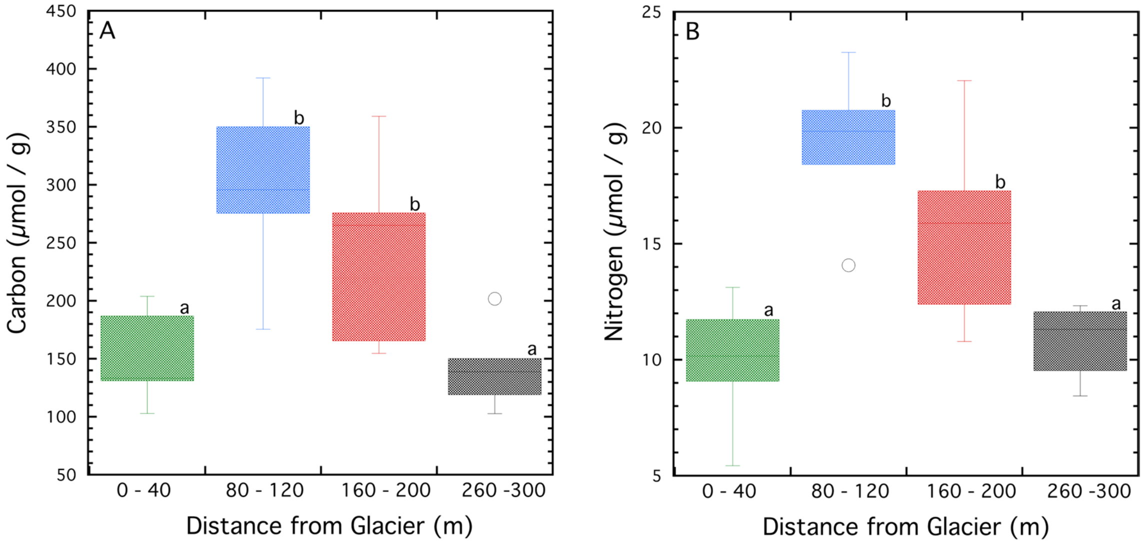

Fig. 1 Total organic C (**A**) and total N (**B**) of soils along the glacial chronosequence. Different lower-case letters indicate groups that are significantly different from each other ($P < 0.02$ for C and $P < 0.03$ for N). The colors represent the four discrete 40-m distance zones studied: green 0–40 m; blue 80–120 m, red 160–200 m, black 260–300 m

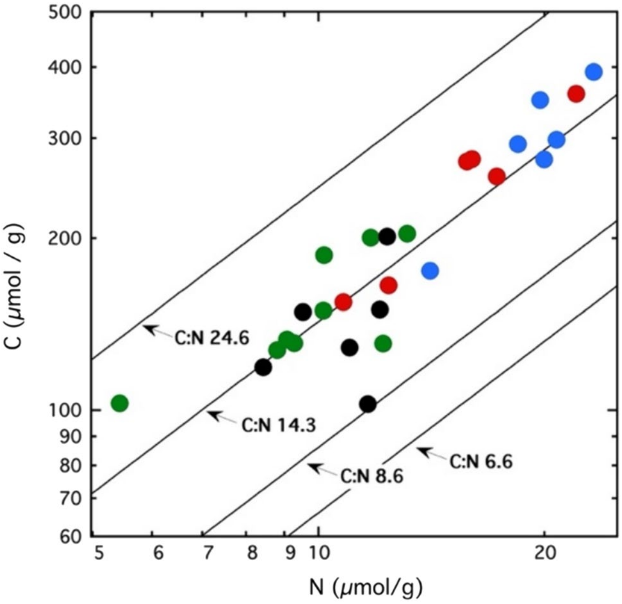

Fig. 2 Log–log plot of soil C:N along the glacial chronosequence. The bottom two lines represents the “Redfield ratio” of 8.6 and 6.6 for microbes in soils and seawater, respectively. The middle line represents the global mean for the C:N of soil organic matter of 14.3 (Cleveland and Liptzin 2007) and the top line is the mean C:N of very dry “soils” in the Dry Valleys of Antarctica (Burkins et al. 2001; Schmidt et al. 2022). The colored symbols represent the four discrete 40-m distance zones studied: green 0–40 m; blue 80–120 m, red 160–200 m, black 260–300 m

Discussion

Traditionally the microbial phase of primary succession following glacial retreat has been assumed to be a progressive process that facilitates the eventual establishment of a climax community of higher plants. While this view holds true for many mesic climate zones such as Europe, coastal Alaska, and New Zealand (Raffl et al. 2006; Frey et al. 2013; Mainetti et al. 2021), many areas currently undergoing rapid glacial retreat are in climate zones where the microbial phase of succession can be prolonged for decades to hundreds of years (Nemergut et al. 2007; Schmidt et al. 2008), or where succession to higher plants never occurs (Solon et al. 2018, 2021; Vimercati et al. 2020). The current study was done at a site that is intermediate in climate between those most extreme sites and very mesic sites and demonstrates a clear pattern of progression followed by retrogression as indicated by both biogeochemical (Figs. 1, 2) and microbial diversity (Fig. 3) metrics. It is important to note that the diversity data presented in this paper are all relative abundance data, so some caution is warranted when interpreting these data in terms of absolute changes.

The decline in moss relative abundance (Fig. 3A) and the lack of evidence of moss growth after zone 2, is important since paleo and contemporary evidence indicates that mosses are the climax phototrophs at this and similar sites on the Antarctic Peninsula (Boy et al. 2016; Groff et al. 2023). In more mesic systems moss are often important as a transitional phase in succession between a microbially dominated system and one dominated by higher plants (Bueno de Mesquita et al. 2017). But in this system, plant colonization

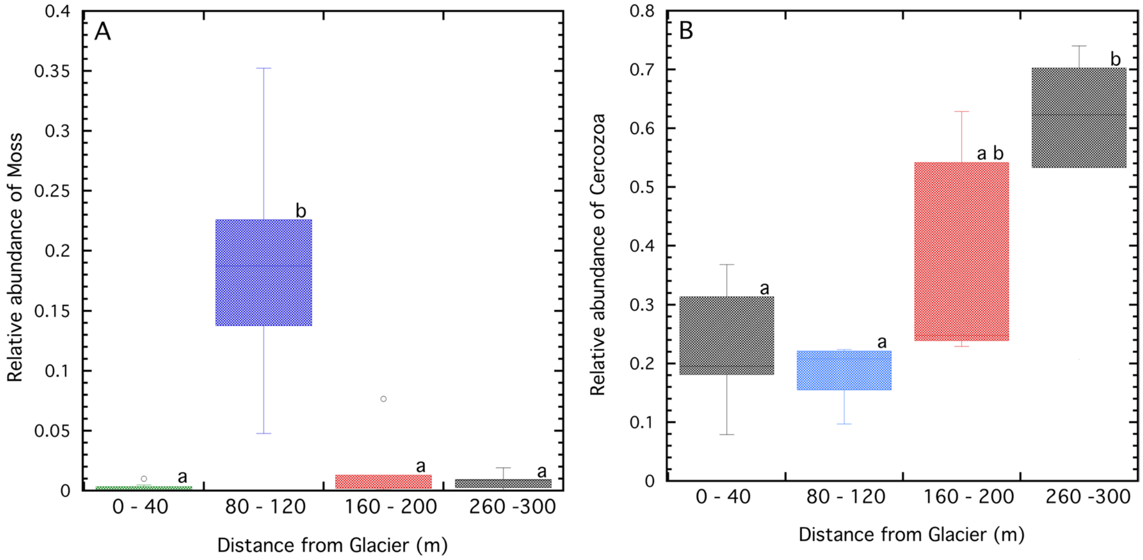

Fig. 3 Relative abundances of the moss ASVs peaked in the second successional stage and then declined (**A**), whereas relative abundance of predatory Cercozoa (**B**), mostly in the Vampyrellidae family increased in the later stages, coinciding with decreases in moss

may be limited by the relatively harsh climate; the only two vascular plant species near this site occur patchily closer to the coast in areas fertilized by birds and marine mammals (Komárková et al. 1985; Otero et al. 2013; Boy et al. 2016). In addition, no higher plants were observed along the studied chronosequence, indicating that higher plants are not involved in the first 30 years of succession at this site. In contrast, the rise and fall of the moss ASVs along the chronosequence (Fig. 3A) coincided with the rise and fall of total C and N pools in the soil (Figs. 1, 2), indicating that mosses were likely driving soil development during the initial progressive phase of succession along the chronosequence as has been suggested in previous studies (Prietzel et al. 2019). The rise and fall of moss also coincided with a rise and fall in δ^{13}C values. However, moss δ^{13}C values are fairly species specific for Antarctic mosses, ranging from about −23‰ to −27‰ (Galimov 2000; Bramley-Alves et al. 2016) and there are no published δ^{13}C for microscopic Antarctic terrestrial algae, so further work would be needed to understand the up and down shifts in δ^{13}C along the studied chronosequence.

The results of this study have important implications for the potential of newly forming soils in the cryobiosphere to sequester atmospheric CO_2. The initial rise in soil carbon storage from zone 1 to zone 2 was quite robust and brought organic C levels up to a concentration about an order of magnitude higher than typical dry soils of Taylor Valley, Antarctica (Burkins et al. 2001; Schmidt et al. 2022). However, all the gain in C was lost during retrogression (stages 3 and 4), bringing C stocks back down to their original post-glacial levels (Figs. 1, 2). In contrast, most post-glacial chronosequences in mesic systems do not show this decline in C storage during microbial succession (Bradley et al. 2014), but soil carbon gains are minimal in more extreme sites of the cryobiosphere such as high-elevation sites in central Alaska and in the high Andes even after 50 years of succession (Nemergut et al. 2007; Schmidt et al. 2016). At those sites, severe nutrient limitation is likely the reason for minimal C gains by the soil (Darcy et al. 2018), but little work has been done to assess which nutrients are limiting to photosynthetic microbes (including moss) on the Antarctic Peninsula (Chong et al. 2009, 2015; Newsham et al. 2019).

While nutrient limitation is a potential cause of retrogression in this study and studies of plant retrogression (Peltzer et al. 2010), alternative explanations are also possible (such as soil waterlogging) as discussed elsewhere for plant retrogression (Gaxiola et al. 2010; Coomes et al. 2013). Soil waterlogging is not a likely explanation in this study since soil water contents are consistent across the four zones of this chronosequence (Vimercati et al. 2022). A possible explanation for retrogression in the current study is the dramatic rise in the relative abundance of members of the Cercozoa in stages 3 and 4 (Fig. 3B). More than 95% of the cercozoan sequences were of one ASV (ASV 1) in the Vampyrellidae, an aptly named family of cercozoans that parasitize a range of microbial eukaryotes (Hess and Suthaus 2022). Members of the Vampyrellidae have been implicated in catastrophic crashes of photosynthetic communities in several aquatic systems (Gong et al. 2015; Carney et al. 2016), but to date their ecological roles in terrestrial systems have not been explored, despite their prevalence in other extreme cryosphere soil systems (Solon et al. 2018; Vimercati et al. 2019; Thompson et al. 2020). Although there is no direct evidence demonstrating moss predation by vampire Cercozoa in the present study, high levels of moss grazing by soil invertebrates have been noted early in succession, especially at high-elevation glacial forefronts in Norway (Hågvar 2012; Flø and Hågvar 2013). Likewise, a rise in relative abundance of predatory/parasitic microbes has been linked to retrogression of microbial communities during succession on cheese rinds during the cheese ripening processes (Wolfe et al. 2014). Obviously more work is needed to understand the role of vampire Cercozoa and other parasites and grazers during ecosystem retrogression of microbial communities in Antarctica.

Perhaps the most surprising aspect of the current study is that this ecosystem underwent both succession and retrogression in a seemingly rapid span of 30 years. However, 30 years is a very long time in the microbial world, even in cold systems. Other cold microbial ecosystems such as cold-fermented foods (Cho et al. 2006) and under-snow, and high-elevation peri-glacial environments (Schmidt et al. 2007; Knelman et al. 2014) have been shown to undergo substantial successional changes over spans of weeks to months. It could be that retrogressive microbial processes have been missed in most studies of primary succession due to minimal sampling during the earliest stages of ecosystem succession in studies that examine succession over hundreds to thousands of years. Nonetheless, retrogression of microbial-driven processes are likely very important in the cryobiosphere, especially in systems where higher plants are unlikely to thrive. More work is still needed to understand succession of microbial communities in the emerging terrestrial cryobiosphere.

The present study also highlights the need for more mechanistic studies of the factors (other than cold and aridity), such as predation/parasitism, that may limit ecosystem development in the terrestrial cryosphere. Recent *in situ* and field fertilization studies in the high-Andes, central Alaska Range, and Rocky Mountains indicate that phosphorus limitation, rather than cold and aridity, is limiting ecosystem succession and C accumulation following glacial retreat (Knelman et al. 2014; Darcy et al. 2018; Bueno de Mesquita et al. 2020). Similar studies are needed in Antarctic and high-Arctic glacial environments to determine what nutrients are most limiting to microbial and plant succession following glacial retreat and how nutrient limitation may interact with the types of predator–prey interactions hinted at in the current study. Nonetheless, the current study is an advance towards understanding the initial stages of pedogenesis and ecosystem succession following glacial melting in an environment where higher plants do not dominate long-term ecosystem development.

Supplementary Information The online version contains supplementary material available at https://doi.org/10.1007/s00300-024-03279-0.

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Author contributions LV and SKS conceived and designed research. LV, BWJ, JNR and SKS carried out laboratory and field work. CPB, BWJ, SKS and AJS analyzed data. SKS wrote the manuscript. All authors read, edited, and approved the manuscript.

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Data availability Sequence data that support the findings of this study have been deposited in the NCBI SRA database under project PRJNA836937.

Declarations

Competing interests The authors declare no competing interests.

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