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# Contrasting early successional dynamics of bacterial and fungal communities in recently deglaciated soils of the maritime Antarctic

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## Abstract

Although microorganisms are the very first colonizers of recently deglaciated soils even prior to plant colonization, the drivers and patterns of microbial community succession at early-successional stages remain poorly understood. The successional dynamics and assembly processes of bacterial and fungal communities were compared on a glacier foreland in the maritime Antarctic across the ~10-year soil-age gradient from bare soil to sparsely vegetated area. Bacterial communities shifted more rapidly than fungal communities in response to glacial retreat; species turnover (primarily the transition from glacier- to soil-favouring taxa) contributed greatly to bacterial beta diversity, but this pattern was less clear in fungi. Bacterial communities underwent more predictable (more deterministic) changes along the soil-age gradient, with compositional changes paralleling the direction of changes in soil physicochemical properties following deglaciation. In contrast, the compositional shift in fungal communities was less associated with changes in deglaciation-induced changes in soil geochemistry and most fungal taxa displayed mosaic abundance distribution across the landscape, suggesting that the successional dynamics of fungal communities are largely governed by stochastic processes. A co-occurrence network analysis revealed that biotic interactions between bacteria and fungi are very weak in early succession. Taken together, these results collectively suggest that bacterial and fungal communities in recently deglaciated soils are largely decoupled from each other during succession and exert very divergent trajectories of succession and assembly under different selective forces.

**KEYWORDS**
bacterial community, fungal community, glacier foreland, microbial ecology, microbial succession

  

## 1 | INTRODUCTION

The Antarctic Peninsula is one of the most rapidly warming regions in the Southern Hemisphere (Vaughan et al., 2003). The western and northern Antarctic Peninsula have experienced marked warming over the past half-century, with a rise in mean annual air temperatures of approximately +0.17–0.46°C per decade (Turner et al., 2019). Climate warming has led to the thinning and recession of numerous glaciers lying along the Antarctic Peninsula over the past half-century, and as a result, substantial terrain areas formerly underlain by glaciers have been newly exposed (Cook et al., 2005). A recent climate-modelling study predicted that there could be a threefold increase in ice-free areas in the Antarctic Peninsula by the end of the 21st century under the strongest climate-forcing scenario (Lee et al., 2017).

Newly exposed ground provides a suitable habitat for various pioneer species such as lichen, mosses, and microbes. Early colonizers facilitate the colonization and establishment of later colonists, and then progressive species turnover occurs over time. Ecological succession has been a fascinating research topic in ecology, and many ecological theories have been developed in the context of community succession (Clements, 1928; Connell & Slatyer, 1977; Walker & Chapin, 1987). Glacier forelands provide ideal landscapes for studying the patterns and processes of ecosystem succession (Walker, 1999). Many previous studies of ecological succession have focused on the colonization and community development of vascular plants (Cooper, 1923; Matthews & Whittaker, 1987). It was not until a couple of decades ago that microbial ecologists began to look at microbial dynamics in the glacier foreland (Brown & Jumpponen, 2014; Garrido-Benavent et al., 2020; Kim et al., 2017; Schutte et al., 2010). Despite recent efforts, the patterns and processes of microbial community succession at the very early successional stages prior to plant colonization have been largely overlooked, owing to their cryptic nature (Nemergut et al., 2007; Sattin et al., 2009). Microbial communities in recently exposed soils generally exert dramatic compositional shifts in a very short period of time (Schutte et al., 2010; Yoshitake et al., 2018). Nevertheless, most studies often set a longer time (or distance) interval along the chronosequence based on a macroecological perspective and rarely consider shorter community turnover times, that are more relevant to microbes (but see Bradley et al., 2016; Fernández-Martínez et al., 2017; and Garrido-Benavent et al., 2020), which often results in the limited understanding of the early-stage successional dynamics of microbial communities.

Successional dynamics of microbial communities have recently begun to be understood within the framework of community assembly mechanisms, as well as traditional concepts in succession studies (e.g., changes in species diversity and the rate of community turnover during succession). Bacterial and fungal communities followed distinct assembly trajectories along the soil chronosequence in glacier forelands (Brown & Jumpponen, 2014; Jiang et al., 2018). The establishment of plants served as a strong selection force that resulted in more deterministic community assembly for bacteria, but fungal assembly processes were consistently stochastic across the successional stages (Brown & Jumpponen, 2014). In unvegetated, very early successional soils, however, bacterial assembly processes appeared to be governed more by stochastic factors (Brown & Jumpponen, 2014), but the drivers of the differing community assembly patterns are unknown. A recent meta-analysis suggested that the presence of strong environmental filters (i.e., soil pH) rather than successional stages could be a major driving force controlling bacterial community assembly (Tripathi et al., 2018). General conclusions about the relative importance of community assembly mechanisms requires more results from a range of successional sites with varying successional timescales.

Microbial succession studies in glacier forelands have commonly been conducted via point-transect sampling, either parallel or perpendicular to the glacier snout line, across the soil-age gradient (Kim et al., 2017; Schmidt et al., 2008), whereas studies on plant succession often cover the entire landscape (Burga et al., 2010; Moreau et al., 2008). The "snapshot" sampling does not sufficiently account for a wide range of periglacial disturbances and overlooks the effects of spatial variation due to limited spatial coverage, which tends to result in incomplete conclusions or oversimplified views on successional dynamics solely as a function of time (Matthews, 1992). Irregular spatial sampling also hinders the use of more explicit spatial modelling approaches, such as the eigenfunction-based spatial filtering framework (Dray et al., 2006). In particular, although the spatial structure of the ecological community is strongly affected by directional spatial processes (e.g., deglaciation), spatial directionality or connectivity between sites has never been incorporated into community modelling. Aeolian dispersal is an allochthonous source of early colonizers and can also be an important driver of microbial community assembly in recently exposed terrain, especially in the case of strong directional processes (e.g., prevailing winds) (Cao et al., 2021). Proper variation partitioning of the effects of spatial relationships and environmental parameters on species distribution allows for better identification of key determinants of microbial community structure.

This study aimed to examine how the successional dynamics and assembly processes of bacterial and fungal communities differ during early successional stages on recently deglaciated terrain in the maritime Antarctic. Bacterial and fungal abundance was quantified by group-specific qPCR assay, and the community structure was investigated using MiSeq amplicon sequencing. To more explicitly account for the spatial information in the community model, a rectangular grid was constructed of regularly spaced points across a ~10-year soil-age gradient, and the effects of asymmetric directional spatial processes on microbial species distribution (e.g., the directional effects of glacial ice flow) were assessed using the asymmetric eigenvector maps (AEM) framework. The following specific questions were addressed: (i) Do patterns of compositional change and assembly trajectories differ between bacterial and fungal communities during succession? (ii) What are the major drivers of compositional shifts in bacterial and fungal communities along the soil-age gradient? (iii) To what extent do they interact over the course of succession?

## 2 | MATERIALS AND METHODS

### 2.1 | Study site and soil sampling

The study site was a recently deglaciated terrain located at the eastern coastal margin of the Barton Peninsula on King George Island (KGI) (62° 13′ 48″S, 58° 42′ 40″W). The Fourcade Glacier, a tidewater glacier draining into Potter Cove, has been retreating over the past 100 years (Ruckamp et al., 2011), and further recession is expected according to a recent multiyear glaciological observation (Falk et al., 2018). Satellite images revealed that the glacier terminus has retreated approximately 300 m from the coast over the past 27 years (Lee et al., 2017). Eleven successional stages (4–8 plots per stage) were reconstructed perpendicular to the direction of glacial ice flow, which was estimated by Unmanned Aerial Vehicle (UAV) images, and glacial striations remained on the surfaces of exposed rock fragments (Figure S1). The proglacial landscapes were grouped into two main categories according to land cover characteristics: the first half of the stages (stages 1–6) were composed mostly of barren rocks and soils, and the second half (stages 7–11) were sporadically occupied by several moss species such as *Bryum* sp., *Sanionia* sp., or *Ditrichum* sp., occurring mainly in protected soils between rock boulders (Figure S2). Vegetation cover was analysed from WorldView-3 (WV-3) satellite image acquired on 19 March 2016 with a spatial resolution of 1.2 m in multispectral bands (the satellite image was courtesy of the DigitalGlobe Foundation). To investigate vegetation cover in the sampling site normalized difference vegetation index (NDVI) known to be strongly correlated with Antarctic vegetation cover (Power et al., 2020) was calculated using two surface reflectance bands, that is, red and near-infrared 1 (NIR1), of the WV-3 image. Preprocessing and NDVI calculation of the WV-3 image were conducted using PCI Geomatica Banff (PCI Geomatics) and ENVI 5.6 (Harris Geospatial Solutions) software. The majority of the surfaces of rocks or gravels remaining in the moraines was occupied by crustose lichens, such as *Acarospora* spp., *Buellia* spp., *Caloplaca* spp., *Rhizocarpon* spp., and *Verrucaria* spp. In total, 93 soil samples (0–5 cm depth) were collected at regular intervals of a 10 × 10 m grid covering a 110 × 70 m quadrat area. Soil samples were carefully taken from sites minimally disturbed by glacier melt streams. Gravels larger than 3–4 cm in size were removed, and the remaining soils were passed through a 2-mm sieve. Soil samples were transported to the laboratory at King Sejong Station within 3 h and kept frozen at −20°C during shipment to the KOPRI laboratory in South Korea.

### 2.2 | Soil geochemistry and meteorological data

Soil physicochemical properties were determined following the procedures described previously (Kim et al., 2017) and detailed descriptions of results and methods are provided in Table S1 and the Supporting Information methods, respectively. The meteorological data for 2015–2018 were obtained from an automatic weather station (AWS) installed 50 m from the study site.

### 2.3 | Abundances of bacteria and fungi

Real-time quantitative PCR was performed to quantify the abundance of bacteria and fungi by using CFX96TM Real-time PCR Detection System (Bio-Rad). Bacterial 16S rRNA gene and fungal ITS region were targeted with the primer sets of 341F (5′-CCT ACG GGA GGC AGC AG-3′) and 797R (5′-GGA CTA CCA GGG TCT AAT CCT GTT-3′) for bacterial 16S rRNA gene (Muyzer et al., 1993; Nadkarni et al., 2002), and ITS1F (5′-CTT GGT CAT TTA GAG GAA GTA A-3′) and ITS4 (5′-TCC TCC GCT TAT TGA TAT GC-3′) for fungal ITS region (White et al., 1990), respectively. The two independent PCR mixtures for each DNA sample were prepared with 10 μl of LightCycler 480 SYBR Green I Master Mix (Roche Life Science), 1 μl each of forward and reverse primers (10 μM), approximately 20 ng of extracted DNA samples, and nuclease-free water was added up to the total volume of 25 μl. Negative control was prepared without extracted DNA samples. Three-step PCR was performed for amplification; initial denaturation at 95°C for 10 min followed by 40 cycles of denaturation at 95°C for 15 s, annealing at 50°C for 30 s, and extension at 72°C for 30 s. The standard curves were created using 10-fold dilution series of plasmids containing the bacterial 16S rRNA gene and fungal ITS region from environmental samples for bacterial and fungal communities, respectively.

### 2.4 | DNA extraction, amplicon sequencing, and community analysis

Soil DNA was extracted from 0.3 g of each soil sample using the DNeasy PowerSoil Kit (Qiagen) according to the manufacturer's instructions. Extracted DNA were amplified targeting 16S V4–V5 region (universal) using the primer pair, 515F (5′-GTGYCAGCMGCCGCGGTAA-3′) and 926R (5′-CCGYCAATTYMTTTRAGTTT-3′) (Parada et al., 2016), and fungal ITS2 region using the primer pair, ITS86F (5′-GTGAATCA TCGAATCTTTGAA) and ITS4R (5′-TCCTCCGCTTATTGATATGC-3′) (De Beeck et al., 2014). One-step PCR was performed using dual-indexed fusion primers, including Nextera P5/P7 adapters, i5/i7 indices, and target-specific forward/reverse primers (Comeau et al., 2017). The PCR conditions were as follows: initial denaturation for 30 s at 98°C, followed by 30 cycles of 98°C for 10 s, 55°C for 30 s, and 72°C for 30 s, and final extension for 4.5 min at 72°C. A total reaction volume of 25 μl was used for PCR, consisting of 5 μl (each primer 1 μM), 0.5 U of Phusion High-Fidelity DNA polymerase (Thermo Scientific, #F-530L), 0.5 μl of dNTPs (40 mM), and 5 μl of 5x Phusion HF PCR buffer. Sequencing library construction and amplicon sequencing (MiSeq 2 × 300 bp) were performed at Integrated Microbiome Resource (IMR), and more details on wet-lab protocols can be found at Microbiome Helper GitHub (https://github.com/LangilleLab/microbiome_helper/wiki/Microbiome-Amplicon-Sequencing-Workflow). Both 16S and ITS2 amplicon data were processed using the DADA2 algorithm (Callahan et al., 2016) to infer amplicon sequence variants (ASVs), and bioinformatic details are provided in the Supporting Information methods. Raw sequence data were

submitted to the NCBI Sequence Read Archive (SRA) database with the accession number PRJNA679688.

### 2.5 | Statistical analyses

To unbiasedly compare the degree of microbial richness between samples, ASV richness was calculated at equal sample coverage (coverage values of 0.999 for bacteria and 0.985 for fungi) using the estimateD function in the iNEXT R package (Hsieh et al., 2016). Bray-Curtis dissimilarities of all pairs of samples were calculated using the Hellinger-transformed ASV abundance matrix and visualized using nonmetric multidimensional scaling (NMDS). Permutational multivariate analysis of variance (PERMANOVA) was used to determine whether the microbial community structure differed significantly between bare (successional stage 1 to 6) and sparsely vegetated area (successional stages 7 to 11) using PRIMER6 (Anderson et al., 2008). A test for homogeneity of multivariate dispersions (Anderson et al., 2006) was performed in the vegan R package using the beta.disper function to assess whether there was any difference in within-group dispersion between bacterial and fungal communities and whether the differences in dispersion change over time. To perform spatially explicit ecological modelling of beta diversity, spatial explanatory variables were generated using a spatial eigenfunction approach. Both Moran's eigenvector maps (MEM) (Dray et al., 2006) and asymmetric eigenvector maps (AEM) (Figure S3) (Blanchet et al., 2008) were used to partition the effects of nondirectional spatial processes, and directional processes (i.e., the direction of deglaciation) on community variation, respectively. Variation partitioning approach was used to partition the community variation with environmental, spatial, and temporal components, and db-RDA was used for the community modelling of each fraction. R scripts and more detailed description about spatial analysis, variation partitioning, and db-RDA are provided in the Supporting information materials (Appendix S1).

The relationship between pairwise community similarity and difference in successional stages was modelled by fitting negative exponential or power-law functions using the decay.model function in the betapart R package. To identify which processes result in differences in microbial community composition among sites, beta diversity was partitioned into abundance difference and replacement (species turnover) (Legendre, 2014). Bray-Curtis-based Podani families of indices (Podani & Schmera, 2011) were applied to an abundance matrix using the beta.div.comp function in the adespatial R package, and the resultant values were visualized using ternary diagrams in the ggtern R package. To determine the contribution of each species to beta diversity, total beta diversity was partitioned into species contributions to beta diversity (SCBD) indices, and the significance of the SCBD indices was tested with 999 permutations after Holm correction (Legendre & De Cáceres, 2013). To assess the microbial community assembly, we used a null modelling approach described by Stegen et al., (2013) and Dini-Antreote et al., (2015), and the details are provided in the Supporting Information methods. The spatial distribution of bacterial and fungal communities was generated by mapping NMDS axis 1 scores on sites through ordinary kriging interpolation approach in each 10 × 10 cm grid using ArcGIS 10.3 (ESRI) software.

### 2.6 | Co-occurrence network analysis

Cross-domain co-occurrences within- and between-taxonomic groups (e.g., bacteria-bacteria, bacteria-fungi, and fungi-fungi) were inferred using Sparse InversE covariance estimation for Ecological Association Inference (SPIEC-EASI) (Kurtz et al., 2015; Tipton et al., 2018). In order to reduce network complexity and achieve more reliable network inference, poorly represented ASVs were excluded and the analysis was restricted to ASVs present in at least 10% of samples. For example, the ASVs occurring in more than nine sites and those with relative abundance >1% of the total number of reads were used for network analysis. The final ASV data sets accounted for 84.0% and 86.8% of bacterial and fungal reads, respectively. We ran SPIEC-EASI with neighbourhood selection (MB) method, and a model selection scheme known as the stability approach to regularization selection (StARS) (Liu et al., 2010) was conducted using a variability threshold of 0.05%. The resultant network was visualized using the interactive platform Gephi v0.9.2 (Bastian et al., 2009). Additionally, the Pearson correlation coefficient was calculated between ASVs to examine the association within- and between-taxonomic groups.

## 3 | RESULTS

### 3.1 | Soil geochemistry and microbial abundance

Glacial retreat resulted in apparent shifts in soil physicochemical properties. Soil pH declined with soil age from pH 8.9 to 7.0, and WHC and clay content (%) also showed negative trends along the chronosequence (Figure S4). In contrast, the sand content (%) and the concentrations of SOC, TN, phosphate, and nitrate increased with soil age (Figure S4). Interestingly, certain variables showed contrasting patterns of change between barren and sparsely vegetated soils. Soil pH, SOC and TN contents, and phosphate and nitrate concentrations remained unchanged during the early half of the successional stages (mostly covered by barren soils), which was followed by rapid change of varying degrees during the late half of the stages (sparsely covered by mosses). Furthermore, these variables strongly covaried with each other along the soil-age gradient. Both bacterial and fungal abundances increased linearly with soil age, with abundances varying by three orders of magnitude within each stage (Figure 1a,b).

### 3.2 | Microbial taxa

In total, 2,347,341 prokaryotic 16S rRNA genes (10,871 ASVs) and 3,041,787 fungal ITS2 region (825 ASVs) sequences were obtained from 93 samples (Table S2). Bacterial communities were mostly

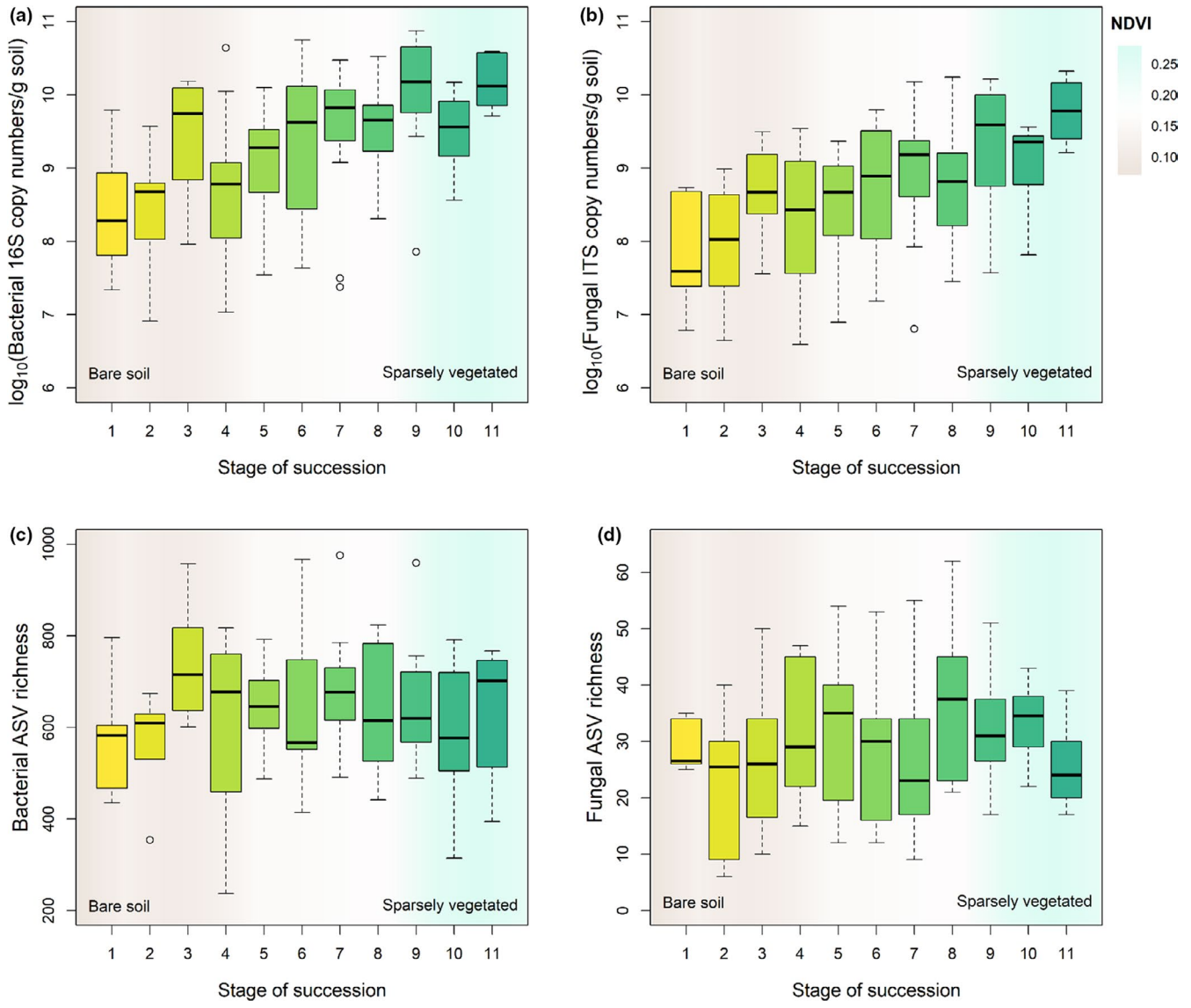


**FIGURE 1** Shifts in (a) bacterial and (b) fungal abundances and (c) bacterial and (d) fungal ASV richness along the soil-age gradient. Background colour gradient represents the mean NDVI values for sites belonging to each stage of succession [Colour figure can be viewed at wileyonlinelibrary.com]

represented by Proteobacteria (44.0 ± 6.9%), and to a lesser extent Bacteroidetes (15.4 ± 6.8%), Acidobacteria (10.1 ± 4.0%), Planctomycetes (8.3 ± 3.9%), and Actinobacteria (7.2 ± 3.2%) were similarly abundant across sites (Table S2). Given that very expansive metabolic versatility occurs at higher taxonomic ranks of bacteria, the changing patterns in the relative abundance of bacterial taxa were examined at lower taxonomic ranks (e.g., family or genus levels). Bacterial communities exhibited three distinct patterns of change in relative taxa abundance across the soil-age gradient. The first group was represented by sulphur-oxidizing chemolithotrophs, including *Thiobacillus* sp., Sulfuricellaceae, *Sulfuricaulis* sp., and Saprospiraceae (known for chemoorganotrophs). The higher relative abundance of these group members was maintained throughout the early-to-mid stages (stages 1–6), and then suddenly dropped and almost disappeared from stage 7, coinciding with the time that the land surface began to be covered by mosses to a large extent (Figure S5a). The second group showed a linearly decreasing trend of relative abundance along the age gradient. For example, the relative abundances of *Sphingomonas* sp., Gemmatimonadaceae, and an unknown Chloroflexi family (PAC002687_f) linearly decreased over time (Figure S5b). The third group consisted of bacterial taxa with increasing relative abundances in later successional stages. The relative abundances of Comamonadaceae (mostly represented by *Polaromonas* sp., 64.1%), and two Planctomycetes families (Gemmataceae and Planctomycetaceae) were initially very low but increased to varying degrees across the soil-age gradient (Figure S5C). Cyanobacteria were unevenly and patchily distributed across sites, with high variation in relative abundance in the range of 18.8%–0.02%. Most cyanobacterial sequences were assigned to *Microcoleus*, a filamentous, nonheterocystous genus. Archaeal

sequences consisted of only 0.06% of the total reads, and most of the archaeal sequences were assigned to unknown Thermoplasmata.

In contrast to bacteria, there were no distinguishable trends of relative abundance in fungal taxa following glacial retreat. Fungal communities were dominated mostly by two phyla, Ascomycota (57.3 ± 26.3%) and Mortierellomycota (32.9 ± 24.2%), followed by Basidiomycota (4.5 ± 5.0%) and Chytridiomycota (3.2 ± 5.2%) (Table S2). Members of Basidiomycota were mostly represented by psychrophilic yeasts such as *Glaciozyma*, *Phenoliferia*, *Leucosporidium*, and *Mrakia*. At the genus level, *Mortierella* (4.2 ± 10.9%) and various Ascomycota genera, including two lichenized fungal genera (*Verrucaria*, 9.5 ± 20.7% and *Austroplaca*, 5.3 ± 13.7%), *Thelebolus* (7.9 ± 15.2%), *Pseudogymnoascus* (5.3 ± 10.8%), and *Tetracladium* (1.0 ± 5.2%) were abundant across the sites (Table S2). Most fungal genera were patchily distributed across the sites with varying degrees of relative abundance (Figure S5D). *Verrucaria* and *Austroplaca* exhibited the contrasting spatial distribution following the direction of prevailing winds, and their occurrence was almost mutually exclusive across the sites (Figure S6).

### 3.3 | Microbial alpha- and beta-diversity

There were certain degrees of variation in ASV richness between different successional stages, but both bacterial and fungal richness overall did not significantly increase with the age of the soil (Figure 1c,d). The ASV richness of lower taxonomic ranks were further examined to determine the relative contribution of lower-ranked taxa to the total richness. The richness summary at the family and genus levels revealed that this apparent lack of a trend in bacterial richness was ascribed to a shift from glacier- to soil-favouring taxa. For example, the number of soil-favouring ASVs (e.g., Gemmataceae and Planctomycetaceae) markedly increased, while the number of glacier-favouring ASVs (e.g., Sphingomonadaceae and Saprospiraceae) consistently decreased along the soil-age gradient (Figure S7). There were no distinguishable patterns of fungal richness at lower taxonomic levels.

The rate of change in community structure along the soil-age gradient also differed among taxonomic groups. The bacterial community showed a steeper slope in the distance-decay relationship between community similarity and differences in successional stages, whereas fungal communities showed a relatively shallower slope, with considerable community overlapping between different successional stages (Figure S8). Both bacterial and fungal community structures shifted in the same direction along the soil-age gradient, almost paralleling the first NMDS axis (Figure 2a,b). The directional change in bacterial community structure following glacial retreat was relatively more apparent, and the pattern was well represented in its spatial distribution (Figure 2a,c). Conversely, fungal community structure changed rather less linearly along the soil-age gradient, thereby resulting in somewhat obscure directionality in community spatial distribution (Figure 2b,d). Both bacterial and fungal community structures differed significantly between different land cover types (base soil vs. sparsely vegetated), but the effects of land cover are stronger in bacterial communities than fungal communities (PERMANOVA; pseudo-$F = 5.9$, $p = .0001$ for bacteria, and pseudo-$F = 2.8$, $p = .0005$ for fungi). The comparison of multivariate dispersion between bacterial and fungal communities revealed that fungal communities were more loosely clustered at each successional stage than were bacterial communities, and there was no convergence in community structure across the age gradient for both bacteria and fungi (Figure 2a,b). To better explore the underlying mechanisms of the beta diversity patterns, the beta diversity of both bacterial and fungal communities was partitioned into two components: replacement and abundance difference. Bacterial beta diversity was determined more by the replacement process, whereas both the replacement and abundance difference components were equally important in determining fungal community structure (Figure 3a,b). The SCBD index was used to examine the microbial taxa that contributed primarily to the deglaciation-induced compositional changes. Higher scores in the SCBD indices composed of bacterial taxa, which exhibited greater responses to glacier-to-soil transition (Table S3). Among fungal ASVs with high SCBD scores, there were no fungal ASVs associated with directional changes in community structure following deglaciation.

The null model analysis based on βNTI was further used to examine how the relative influence of deterministic and stochastic assembly processes changes along the soil age gradient. Bacterial and fungal communities assembled very differently. Bacterial communities assembled in a more deterministic manner with a dominance of homogeneous selection ($\beta NTI < -2$), whereas fungal assembly processes were consistently stochastic ($|\beta NTI| < 2$ and $|RC_{bray}| < 0.95$) across the landscape (Figure 3c,d and Table S4).

### 3.4 | Key drivers of microbial beta-diversity

To identify the major drivers of the variation in bacterial and fungal community structures, the total community variation was partitioned with respect to environmental (edaphic properties), spatial (AEM and MEM variables), and temporal (soil age) components. The variation partitioning analysis revealed that the whole set of measured variables explained a larger proportion of variations in bacterial communities (25.2%) than those in fungal communities (18.4%) (Figure 4a,b). Edaphic properties played more important roles in determining the community structure of bacteria (18.2%) than that of fungi (7.7%), and among edaphic variables, soil pH was the primary driver of the variation in bacterial communities (10.4%) (Figure 4c). In bacterial communities, the majority of spatial variation was composed of directional spatial processes (AEM variables, 15.7%), and omnidirectional spatial processes (MEM variables, 5.7%) accounted for a lower proportion of the variation. The AEM model reflected most of the soil-age effect, with a large proportion (5.6%) of the edaphic component being jointly explained by AEM and soil age, suggesting that the environmental gradient is spatially structured in the direction of glacial retreat. The db-RDA plot also showed that the fitted site scores of AEM1 variable (paralleling the direction of glacial retreat) reflect

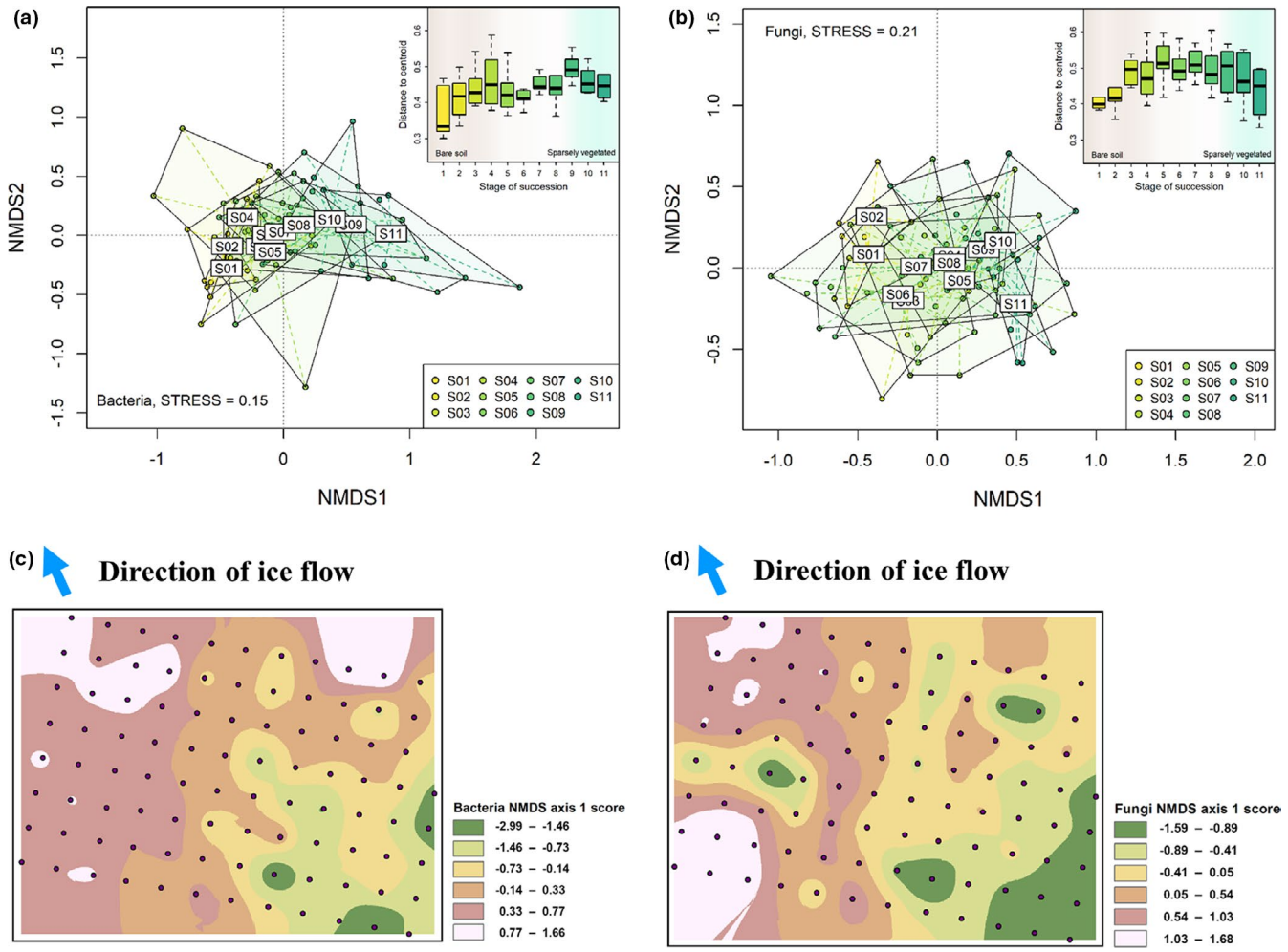


FIGURE 2 NMDS plots of (a) bacterial and (b) fungal communities and spatial mapping of (c) bacterial and (d) fungal communities using ordinary kriging interpolation of NMDS axis 1 scores and Jenks Natural Breaks algorithm (Jenks, 1967). Inset plots are boxplots of multivariate dispersions measured as the distance of sites to their group (successional stage) centroid [Colour figure can be viewed at wileyonlinelibrary.com]

the spatial patterns of the relative abundance of bacterial ASVs representatives of glacier-to-soil transition taxa (e.g., *Polaromonas* and *Sulfuricaulis* sp.) (Figure 4c). In fungal communities, directional spatial processes (AEM variables, 15.2%) played a key role in driving the variation of fungal community structure, and lower proportions were explained by edaphic (7.7%), omnidirectional spatial processes (MEM variables, 2.6%), and soil age (3.3%) components. In contrast to bacterial community, a relatively smaller proportion of variations (6.5%) was conjointly explained by edaphic and AEM components for fungal community (Figure 4b). Different from bacteria, there were no fungal ASVs whose spatial pattern of the relative abundance parallels the direction of AEM or MEM variables (Figure 4d).

### 3.5 | Biotic interactions within- and between-taxonomic groups

The co-occurrence network analysis was performed to test whether there are any strong biotic interactions within- and between-taxonomic groups (e.g., bacteria-bacteria, bacteria-fungi, and fungi-fungi) during succession. The total number of nodes (ASVs) and edges (interactions) used for the network analysis were 1,147 (1,042 for bacteria and 105 for fungi) and 9,986 (8,552 bacteria-bacteria, 1,267 bacteria-fungi, and 167 fungi-fungi), respectively. The co-occurrence network analysis resulted in a highly reduced number of bacterial-fungal connections (1.2% connectance), whereas intragroup members were more frequently associated with each other (1.6% and 3.1% connectance for bacteria-bacteria and fungi-fungi, respectively) (Table 1). When the network correlations were further validated using the Pearson correlation coefficient, much less frequent associations were also identified between bacteria and fungi compared to those between bacteria-bacteria and fungi-fungi (Table 1).

## 4 | DISCUSSION

The very early-stage successional dynamics and assembly processes of bacterial and fungal communities were examined in a recently

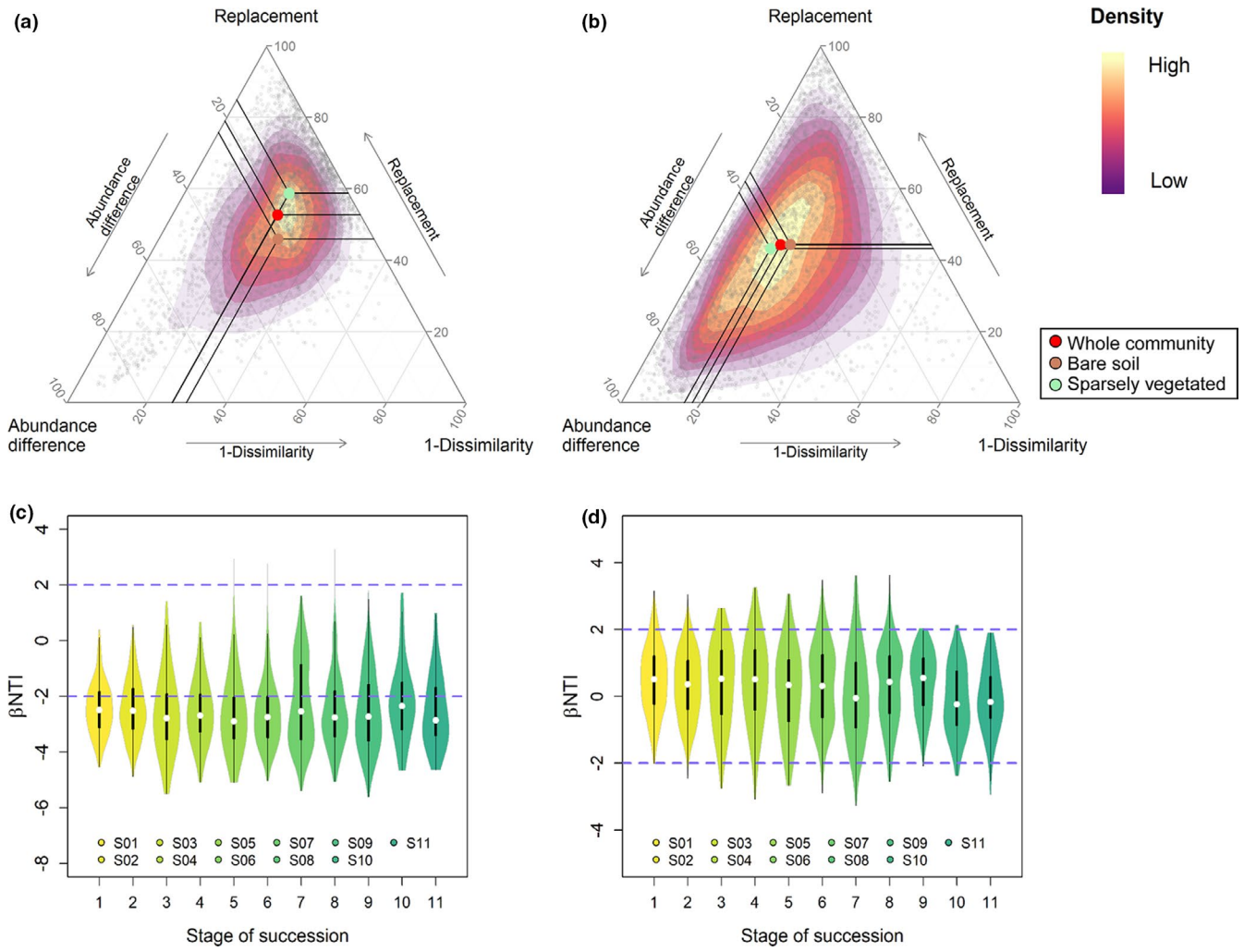


**FIGURE 3** Ternary diagrams representing the relative importance of replacement versus abundance difference components in (a) bacterial and (b) fungal beta-diversity, and the shifts in βNTI values along the successional stages for (c) bacterial and (d) fungal communities. The central dot in each (a) and (b) represents the centroid of similarity, replacement, and abundance difference components [Colour figure can be viewed at wileyonlinelibrary.com]

deglaciated terrain of maritime Antarctica at fine spatial and temporal scales. It should be noted that the site examined in this study spans the transition zone from bare soils (areas at approximately 60–80 m distance from the glacier snout) to sparsely vegetated area, and does not fully cover the entire chronosequence, especially sites in close proximity to the glacier terminus where microbial communities have often been found to be most different from those of the rest successional stages (Fernández-Martínez et al., 2017; Garrido-Benavent et al., 2020). Both bacterial and fungal communities displayed the same overall direction of compositional changes following glacial retreat, but the major drivers of beta diversity and assembly processes significantly differed from each other. Shifts in bacterial community structure were primarily governed by deterministic factors, mainly due to directional changes in soil physicochemical properties following glacial retreat. Phylogenetic null-modelling results based on βNTI also clearly showed the predominance of deterministic community-assembly patterns for bacterial communities during succession. Conversely, fungal communities were assembled mostly by stochastic factors, and community changes were largely unpredictable, which is well represented by looser within-stage community clustering, a high proportion of unexplained community variation, and a dominance of stochastic assembly processes throughout succession. These contrasting successional dynamics for bacteria and fungi are generally in line with the results of previous studies conducted in glacier forelands of other biomes (Brown & Jumpponen, 2014; Jiang et al., 2018). Schmidt et al., (2014) suggested several possible explanations for this divergent assembly pattern in terms of their differing physiological traits, dispersal abilities, and relationships with vegetation. Considering that the vegetation effect is limited in this freshly exposed site, this seemingly deterministic community assembly might result from the combination of metabolic versatility and unlimited dispersal ability of bacterial taxa. Alternatively, alkaline soil pH might result in a deterministic assembly pattern for bacteria because it imposes a stringent environmental filter on bacterial communities (Tripathi et al., 2018). The stronger role of stochastic processes in fungal community assembly may be

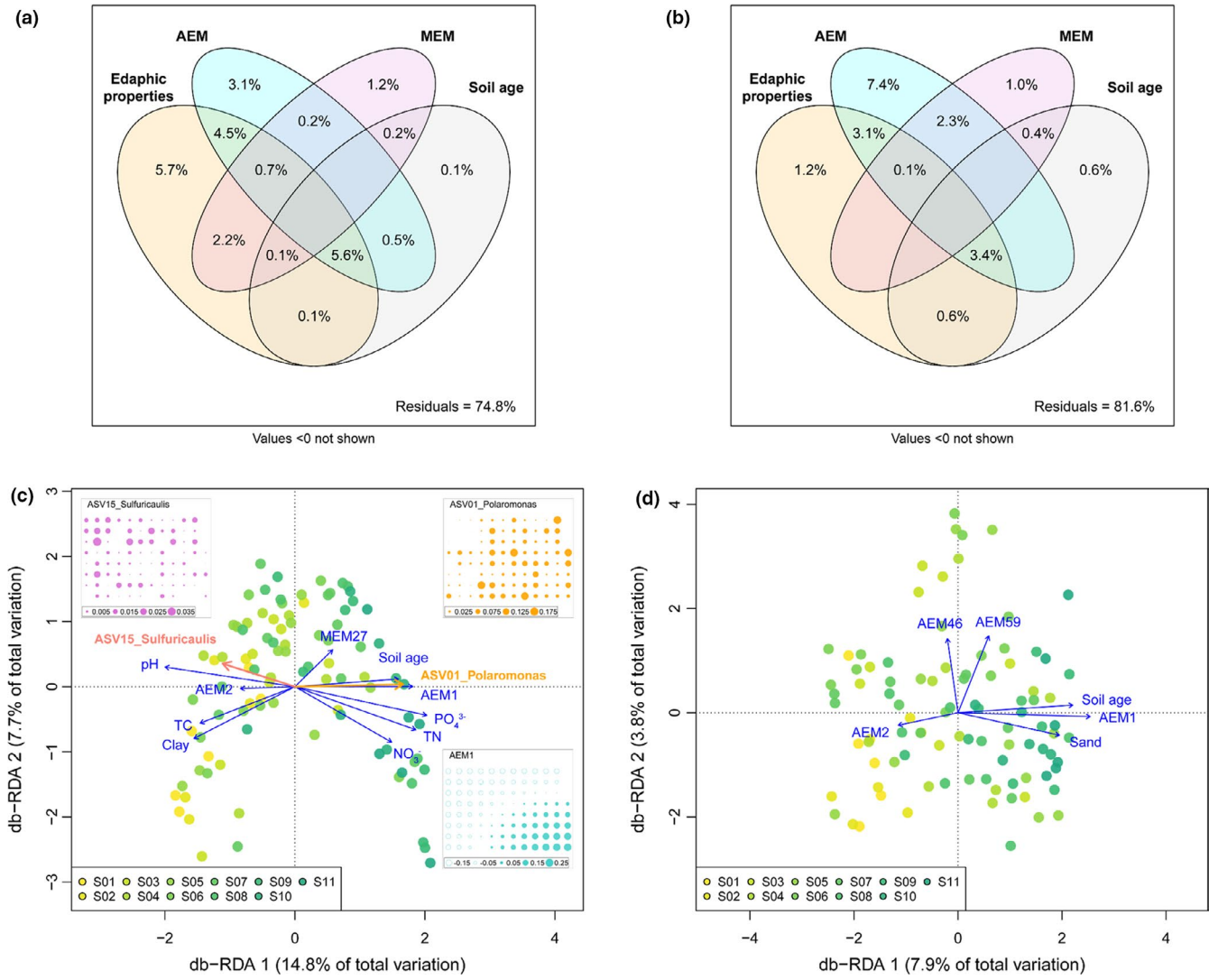


FIGURE 4 Venn diagrams representing variation partitioning results of (a) bacterial and (b) fungal community data, and db-RDA biplots of (c) bacterial and (d) fungal communities. Insets in (c) represent fitted site scores of the AEM1 variable and spatial mapping of the relative abundances of *Polaromonas* and *Sulfuricaulis* ASVs. Further description of the five spatial variables (AEM1, AEM2, AEM46, AEM59, and MEM27) and maps of their fitted site scores are shown in Figure S9 [Colour figure can be viewed at wileyonlinelibrary.com]

TABLE 1 Summary of the co-occurrence network and Pearson correlation between bacterial and fungal ASVs

| | Bacteria–bacteria | Bacteria–fungi | Fungi–fungi |
|---|---|---|---|
| Co-occurrence network (SPIEC-EASI) | | | |
| Number of nodes | 1,042 | – | 105 |
| Number of edges | 8,552 | 1,267 | 167 |
| Connectance[a] (%) | 1.6 | 1.2 | 3.1 |
| Pearson correlation ($r > .5$, $p < .05$) | | | |
| Number of ASVs | 1,042 | – | 105 |
| Number of correlations | 5,850 | 533 | 83 |
| Connectance[a] (%) | 1.1 | 0.5 | 1.5 |

[a]Connectance was calculated by dividing the number of connected edges by all possible links between members of the nodes.

ascribed to the geomorphological heterogeneity of the proglacial moraine. Given that the glacial till at this site was largely composed of rock fragments, wind-blown particles or propagules selectively arrived and accumulated in soil pockets between rocks and rock crevices or clefts, which probably led to a seemingly stochastic pattern. Most fungal taxa displayed nonuniform spatial distribution, and an extremely low content of organic matter was found across the landscape, so fungal taxa may have remained dormant in bare ground at the time of sampling (Jumpponen, 2003). Given that early-successional fungal taxa displayed distinct seasonal patterns in an alpine glacier foreland (Dresch et al., 2019), the potential influence of dormancy and seasonal variation in activity on fungal community assembly needs to be further investigated.

A majority of the bacterial taxa occurring in freshly exposed soils seem to be remnants of glacial residents because many of the taxa were also commonly detected in glacial environments. This

is consistent with a recent finding in the Damma glacier foreland, which showed that the vast majority of bacterial taxa in newly exposed soils originated from supra- or subglacial habitats rather than atmospheric deposition (Rime et al., 2016). More interestingly, both alpha- and beta-diversity partitioning results clearly showed evidence of a transition from bacterial taxa adapted to glacial conditions to those favouring edaphic environments. Many endogenous glacial taxa remaining closer to the glacier snout were rapidly replaced by typical soil taxa at later successional stages. The most striking example of this transition is the sulphur-oxidizing bacteria, whose relative abundance markedly changes at the border of bare ground and vegetated land. Iron or sulphur oxidation is essential for microbial primary production and mineral dissolution in subglacial environments (Boyd et al., 2014; Hamilton et al., 2013). The predominance of neutrophilic sulphur-oxidizing chemolithoautotrophs (*Thiobacillus*, *Sulfuricaulis*, and Sulfuricellaceae) in the early successional stage reflects that the sulphur oxidizers present in subglacial habitats still remained in freshly exposed soils after glacial retreat (Bradley et al., 2016). This is consistent with a recent finding that the oxidation of $FeS_2$ is also important in recently deglaciated soils of Midtre Lovénbreen (Borin et al., 2010; Mapelli et al., 2011). Although quantifying their relative contribution to the carbon and energy sources for other early colonizers is beyond the scope of this study, their dominance early in succession implies that they may be important primary producers in recently exposed soils with very low levels of organic carbon, before pioneer vegetation appears. Bacterial lineages (e.g., *Sphingomonas*, Gemmatimonadaceae, etc.) with their relative abundances linearly decreasing along the soil-age gradient may also be linked to habitat transition. Given that they have been commonly detected in en- or supraglacial environments such as cryoconite holes or subglacial sediment biofilms (Antony et al., 2016; Weisleitner et al., 2019, 2020), bacterial taxa thriving in endogenous glacial habitats may progressively diminish or disappear with habitat alteration. An increasing pattern in the relative abundance of soil- or organic matter-favouring taxa (e.g., Planctomycetaceae, Gemmataceae, etc.) toward later successional stages also supports this transition (Dedysh & Ivanova, 2018). Members of *Polaromonas* are thought to be globally dispersed in cold environments because they are commonly found in glacial habitats worldwide and are especially abundant in nonvegetated soils at the early successional stage (Darcy et al., 2011; Jiang et al., 2018; Kim et al., 2017; Sattin et al., 2009). Regarding their genetic potential to degrade versatile carbon substrates and their increasing relative abundance with organic carbon content, they may be metabolically active rather than dormant, and play important roles in the degradation of organic matter that has built up over the course of succession (Rime et al., 2016).

Contrary to that of bacterial communities, the glacier-to-soil transition of fungal taxa is not clear. Most fungal taxa displayed non-uniform spatial distribution with high variation in relative abundance, and there was no apparent sign of species replacement from glacier- to soil-favouring taxa. Many of the fungal taxa abundant at this site seem to occur in a broad range of cold habitats in polar regions. For example, members of *Mortierella*, the most dominant genus at this site, are commonly found in various Antarctic habitats such as soil, mosses, and permafrost (da Silva et al., 2020; Gomes et al., 2018; Melo et al., 2014; Newsham et al., 2018). Biological granite weathering and organic acid release by *Mortierella* species isolated from the unvegetated foreland of the Damma glacier have been reported (Brunner et al., 2011), and certain species can grow at 0°C (Onofri et al., 2004), supporting their predominance in the proglacial bare soils of Antarctica. Two Leotiomycetes genera (*Tetracladium* and *Pseudogymnoascus*) and various psychrophilic basidiomycete yeasts are also abundant at this site. Representatives of the genus *Pseudogymnoascus* have often been reported in cold habitats of alpine, Arctic, and Antarctic regions (Garrido-Benavent et al., 2020; Perini et al., 2019; Santos et al., 2020). Psychrophilic basidiomycete yeasts are globally widespread in the cryosphere and preferentially detected in barren soils near the glacier snout (Dresch et al., 2019; Rime et al., 2015). *Tetracladium* is an aquatic hyphomycetes genus often found in Antarctica and is one of the most abundant fungal genera in the sparsely vegetated moraine of alpine glaciers (Dresch et al., 2019). Given that aeroaquatic fungal species inhabiting cryoconite holes or melt water flow can also colonize proglacial soils or the roots of pioneering plants (Edwards et al., 2013), the saprobic Ascomycota and basidiomycete yeasts found at this site may be remnants of glacial resident fungi (Dresch et al., 2019).

Most fungal taxa displayed seemingly random patterns of occurrence, but the spatial distribution of two lichenized fungi clearly showed evidence of dispersal limitation, presumably by prevailing winds. Both lichenized fungal taxa (*Verrucaria* and *Austroplaca*) are typical of saxicolous or terricolous crustose lichens. *Verrucaria* encompass many species with cosmopolitan distribution (Galloway, 2008; Index Fungorum, 2019) and many of them were preferentially found on the surfaces of rocks near freshwater or sea water sources in the KGI (Olech, 2004), suggesting that lichen propagules may be dispersed from the inland area of the KGI by the prevailing westerlies. The majority of known *Austroplaca* species are confined to the high-latitude region in the Southern Hemisphere, and some are endemic to the Antarctic continent (Arup et al., 2013). Given that members of *Austroplaca* are frequently found on rocky coastal shores in Antarctica, wind dispersal by easterlies from the ocean might result in a skewed distribution toward the coastal area. More interestingly, a very conspicuous checkerboard distribution (mutually exclusive patterns of co-occurrence between species) between them was observed across the landscape. A likely explanation for this pattern is that priority effects occurring via niche preemption (early-arriving species inhibit the colonization of later colonists) may play an important role in determining their spatial distribution (Fukami, 2015).

The AEM framework has been successfully applied to situations in which species distribution is strongly influenced by directional spatial (e.g., fluvial processes in river or ocean) (Blanchet et al., 2011) or temporal processes (e.g., time series data) (Legendre & Gauthier, 2014). The present study showed that the directional spatial structure of microbial communities following glacial retreat can also be better explained by AEM spatial modelling. A large proportion of the shared fraction between AEM, soil age, and edaphic properties

showed that the spatial structure of bacterial communities is produced mostly by directional spatial processes, and a large proportion of measured edaphic properties are also spatially structured in a directional manner. Conversely, AEM variables were less jointly explained by edaphic properties for fungal communities. A large proportion of AEM (3.1% for bacteria and 7.4% for fungi) uniquely explained the community variation, suggesting that directional processes due to unmeasured environmental or climatic factors still remained. A likely source for the unmeasured directional process is wind because the direction of the prevailing winds generally parallels that of glacial retreat at this site (Figure S6).

A co-occurrence network analysis revealed very weak biotic interactions between bacteria and fungi at this site. Microbial succession studies on glacier forelands have mostly focused on a single taxonomic group (i.e., bacteria) (Kim et al., 2017; Nemergut et al., 2007; Schutte et al., 2010). Although several studies have examined multiple taxonomic groups together, emphasis was placed on describing the similarity or dissimilarity in community characteristics between different groups (Brown & Jumpponen, 2014; Rime et al., 2015). The biotic interactions between different microbial groups during succession have rarely been studied (Jiang et al., 2018; Mapelli et al., 2018). A potential reason for the lack of bacterial-fungal interactions is a stark difference in their physiologies; bacteria possess a broad range of metabolic capabilities, but fungi are only capable of heterotrophic lifestyles. The presence of bacterial taxa with versatile microbial metabolisms (e.g., chemolithotrophs, heterotrophs, phototrophs, etc.) in these nutrient-poor soils of recently deglaciated sites supports this.

## 5 | CONCLUSIONS

This study illustrates that bacterial and fungal communities underwent distinct early-successional trajectories in recently deglaciated soils of the retreating Fourcade glacier in the maritime Antarctic. Shifts in bacterial community structure were primarily determined by directional changes in soil geochemical properties following glacial retreat, which is evidenced by the spatial directionality in community structure and the more important role of species replacement in generating beta diversity. There was a clear transition from bacterial taxa thriving in glacial habitats to those favouring edaphic conditions during succession. Unlike bacterial communities, shifts in fungal community structure appeared to be less associated with changes in deglaciation-induced soil geochemistry and seemingly stochastic patterns in community composition and assembly. A highly reduced co-occurrence relationship between bacterial and fungal ASVs implies that bacterial and fungal communities independently respond to glacial retreat without cross-domain associations early in succession at this site. The decoupled relationship and differing drivers of beta diversity between bacterial and fungal communities will help to provide a better mechanistic understanding of how belowground microbial communities establish and develop in newly deglaciated areas of Antarctica.

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## AUTHOR CONTRIBUTIONS

Mincheol Kim designed the study and wrote the manuscript. Hyeryeon Gyeong analysed data and wrote the manuscripts with Mincheol Kim. Binu Mani Tripathi assisted with analysis and interpretation to assess the microbial community assembly process. Chang-Uk Hyun collected and processed satellite image and NDVI data for sampling sites. Jeongeun Yun, Jinhyun Kim, and Hojeong Kang performed the real-time quantitative PCR experiments. Seok Cheol Kim, Ji Hee Kim, and Sanghee Kim contributed to gathering and transportation samples. All authors discussed the results and contributed to the final manuscript.

## OPEN RESEARCH BADGES

This article has earned an Open Data Badge for making publicly available the digitally-shareable data necessary to reproduce the reported results. The data is available at https://doi.org/10.5061/dryad.hdr7sqvh8 and Appendix S1.

## DATA AVAILABILITY STATEMENT

Raw 16S and ITS2 amplicon sequence data have been made available at the NCBI Sequence Read Archive (SRA) database under BioProject ID PRJNA679688. Additional data (e.g. information of sampling sites, soil physicochemical properties and summary of sequencing results) are available at: Dryad doi: https://doi.org/10.5061/dryad.hdr7sqvh8.

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## SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

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