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Soil water content as a critical factor for stable bacterial community structure and degradative activity in maritime Antarctic soil

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Recent increases in air temperature across the Antarctic Peninsula may prolong the thawing period and directly affect the soil temperature (T_s) and volumetric soil water content (SWC) in maritime tundra. Under an 8°C soil warming scenario, two customized microcosm systems with maritime Antarctic soils were incubated to investigate the differential influence of SWC on the bacterial community and degradation activity of humic substances (HS), the largest constituent of soil organic carbon and a key component of the terrestrial ecosystem. When the microcosm soil (KS1-4Feb) was incubated for 90 days (T = 90) at a constant SWC of ~32%, the initial HS content (167.0 mg/g of dried soil) decreased to 156.0 mg (approximately 6.6% loss, $p < 0.05$). However, when another microcosm soil (KS1-4Apr) was incubated with SWCs that gradually decreased from 37% to 9% for T = 90, HS degradation was undetected. The low HS degradative activity persisted, even after the SWC was restored to 30% with water supply for an additional T = 30. Overall bacterial community structure remained relatively stable at a constant SWC setting (KS1-4Feb). In contrast, we saw marked shifts in the bacterial community structure with the changing SWC regimen (KS1-4Apr), suggesting that the soil bacterial communities are vulnerable to drying and re-wetting conditions. These microcosm experiments provide new information regarding the effects of constant SWC and higher T_s on bacterial communities for HS degradation in maritime Antarctic tundra soil.

Keywords: Antarctic tundra soil, bacterial composition, degradative activity, humic substances, microcosm

Introduction

Recent global warming is likely to lead to increased precipitation across maritime Antarctica (Horrocks *et al.*, 2020). Soil water content (SWC) is influenced, not only by precipitation, but also by the local microclimate, topography, and hydrologic reservoirs such as snow patches. Soil temperature (T_s) varies according to air temperature, incoming solar radiation, cloud, and snow cover (Mauro, 2004; Kowalewski *et al.*, 2006). The T_s and SWC are two critical environmental factors that individually or interactively influence microbial community structure and function (Lupatini *et al.*, 2019). SWC may determine microbial soil organic matter (SOM) decomposition rates by controlling the availability of nutrients, water, and oxygen (Glanville *et al.*, 2012). SWC can be suboptimal when the water content is either too low or too high (e.g., below 10% or over 35%), depending on the texture and composition of the soil (Seybold *et al.*, 2010; Wlostowski *et al.*, 2018). A high SWC decreases microbial degradation rates because of low oxygen supply; a low SWC decreases both microbial mobility and microbial degradative activity by reducing the diffusion of soluble substrates (Stres *et al.*, 2008). Microcosm-based experiments with tropical or subtropical soil have shown that SWC exerts more significant effects on bacterial diversity and structure compared to T_s (Supramaniam *et al.*, 2016; Lupatini *et al.*, 2019). However, microcosm or field studies have rarely been conducted to assess the relationship between T_s and SWC in cold environments such as soil in the maritime Antarctic tundra.

Tundra SOM contains both low-molecular weight (MW) compounds (e.g., simple and labile amino acids and organic acids), which are easily degraded by diverse soil microbes in a temperature-sensitive manner, and high-MW compounds (e.g., complex and recalcitrant lignin, cellulose, and humic substances [HS]), which are more resistant to microbial decomposition (although there is a discrepancy about their sensitivity to temperature increase) (Davidson and Janssens, 2006; Glanville *et al.*, 2012). The decomposition rate of high-MW organic carbons with complex structures and high activation energy can substantially increase with a small rise in temperature (Fierer *et al.*, 2005; Glanville *et al.*, 2012; Park *et al.*, 2015; Kim *et al.*, 2019). A laboratory study using Arctic tundra soil suggested that SWC increased due to climate change (higher temperature and precipitation), making high-MW compounds more susceptible to decomposition, and thus releasing more carbon into the atmosphere (Glanville *et al.*, 2012).

Generally, saprotrophic fungi are known to aerobically degrade high-MW HS, with soil bacteria playing supportive roles in initial HS breakdown and further catabolism of

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HS-derived small compounds (Lipczynska-Kochany, 2018). However, several bacterial strains with the ability to degrade HS have been isolated from various environments (including bipolar regions). The degradative activity and composition of these soil bacterial communities suggest that bacteria likely play significant roles in the entire HS degradation process-from depolymerization through mineralization (Kim *et al*., 2019). Although changes in water availability can cause considerable shifts in bacterial communities and activities, little is known about the effects of water content on bacterial community structure and HS degradative activity in maritime Antarctic tundra soil. In this study, laboratory microcosms of HS-rich Antarctic soils were incubated at a constant T_s of 8°C, and constant SWC was compared to gradually decreasing SWC.

Materials and Methods

Soil sampling and site description

A soil sampling site designated KS1 (= KGL04-03; 62°13′47″ S, 58°46′54″ W) was selected on Kaya Hill near the Korean Antarctic Research Station (King Sejong) on the Barton Peninsula in the maritime Antarctic (Fig. 1A). From 2014–2015, at a depth of 5 cm, the average hourly T_s ranged from -11.5°C to 2.0°C, with an average of -3.1°C, during winter (April to November). In summer (December to March), T_s ranged from -1.6°C to 14.2°C, with an average of 1.3°C. The average hourly SWC ranged from 0–45% (Fig. 1B). HS-rich tundra soils underneath moss (*Andreaea regularis* and *Sanionia uncinata*) and lichen (*Usnea aurantiaco-atra*) were collected from a depth of 0–20 cm in February 2016 (austral late summer, designated KS1-4Feb) and April 2016 (early winter, designated KS1-4Apr). Soil samples from three adjacent locations were pooled and homogenized in a plastic bag and stored at -20°C (Fig. 1C).

Microcosm experiment

Frozen soil samples were slowly thawed at 4°C in a refrigerator and then moved to two customized microcosm systems modified from a previously published model (Han *et al*., 2013). Each microcosm system consisted of a bottomless acrylic column (110-mm diameter; 200-mm height), holding 850 g of tundra soil on an autoclaved, 3-cm zeolite layer (Fig. 1D). The two microcosm systems were incubated at a target temperature of 8°C for 90 days (designated T = 90) to mimic the effects of increased T_s, assuming an approximate 5°C increase from a mean daily maximum temperature of 3.3 (± 3.2)°C from December to March in 2014–2015. During the incubation period, sterile water was continuously supplied as a 1.5-L single dose to KS1-4Feb soil through the bottom zeolite layer to maintain the water content of the initial soil sample. Water was not supplied to the KS1-4Apr soil, allowing it to dry slowly. After incubation of KS1-4Apr soil without water for T = 90, water was added, and incubation continued at 8°C for another T = 30. The T_s and SWC were continuously measured and recorded using a soil temperature sensor (S-TMB-M002, HOBO) and soil moisture sensor (S-SMC-M005, HOBO), respectively. Synthetic air (20.5% O_2 and 79.5% N_2) from a gas cylinder was supplied to the headspace of the microcosm system at a flow rate of 50 ml/min. At T = 30 intervals, the columns were opened, and a portion of the soil was removed for HS content and bacterial community analyses.

Physical and chemical analysis of soil

Two initial soil samples (T = 0), stored at -20°C, were dried at 45°C and passed through a 2-mm sieve. Soil pH was measured with a pH meter (Orion TM Star A215; Thermo Fisher Scientific) after mixing soil with deionized water (soil:water = 1:5 [w/v]), and soil electrical conductivity (Orion TM Star A215) was measured from the soil extract obtained by filtration of the soil suspension (soil:water = 1:5 [w/v]). Soil was ground to a fine powder using a ball mill and sieved through a 250-μm sieve before analyzing total carbon (TC) and total nitrogen (TN). TC and TN were measured using the combustion method (950°C) using an elemental analyzer (FlashEA 1112; Thermo Fisher Scientific).

Microbial biomass determination by phospholipid fatty acid analysis

Phospholipid fatty acids (PLFAs) were extracted from two initial soil samples (T = 0), which were stored at -20°C, and analyzed according to a procedure described by Quideau *et al*. (2016). Briefly, for total lipid extraction, 2.0 ml citrate buffer, 2.5 ml chloroform, 5.0 ml methanol, and 0.5 ml 1,2-dinonadecanoyl-*sn*-glycero-3-phosphocholine (0.1 mg/ml), as a phospholipid standard, were added to 1.0 g of freeze-dried soil in the order listed. Resulting total lipids were dissolved in 0.5 ml chloroform and separated into neutral lipids, glycolipids, and phospholipids using a solid-phase extraction column. The phospholipids were methylated with methanolic KOH to produce fatty acid methyl esters and separated by gas chromatography with flame ionization detection (Agilent Technologies). The peak area of each PLFA was identified and quantified relative to the surrogate standard (added to the soil sample) using Sherlock Mycobacterial Identification System 6.2B (MIDI Inc.). Standard fatty acid nomenclature was used: the prefixes Me-, cy-, i-, and a-, refer to methyl group, cyclopropane group, and iso- and anteiso-branched fatty acids, respectively. The sum of the following PLFAs was used as a measure of bacterial biomass: Gram-positive bacteria (i-C15:0, a-C15:0, i-C16:0, i-C17:0, a-C17:0), Gram-negative bacteria (C16:1ω5c, cy-C17:0), and actinomycetes (10Me-C17:0, 10Me-C18:0, 10Me-C19:0). Fungal biomass included C18:1ω9c and C18:3ω6c. Several other PLFAs were not included which were detected in rather small amounts and/or mixed with others (Frostegård and Bååth, 1996; Quideau *et al*., 2016).

Extraction and quantification of HS

Initial soil samples and microcosm soil samples were completely dried at 60°C for five days and passed through a 1-mm sieve to remove debris. Dried soil (1 g) was mixed with 25 ml 0.5 N NaOH at room temperature overnight with continuous shaking. The NaOH extract was centrifuged twice at 6,000 × *g* for 10 min at 25°C. The supernatant was diluted 100-fold in 0.5 N NaOH and filtered through a 0.2-μm hydrophilic membrane (Advantec 13HP020AN Syringe Filters), and absorbance was measured at 350 nm. The concentrations of HS

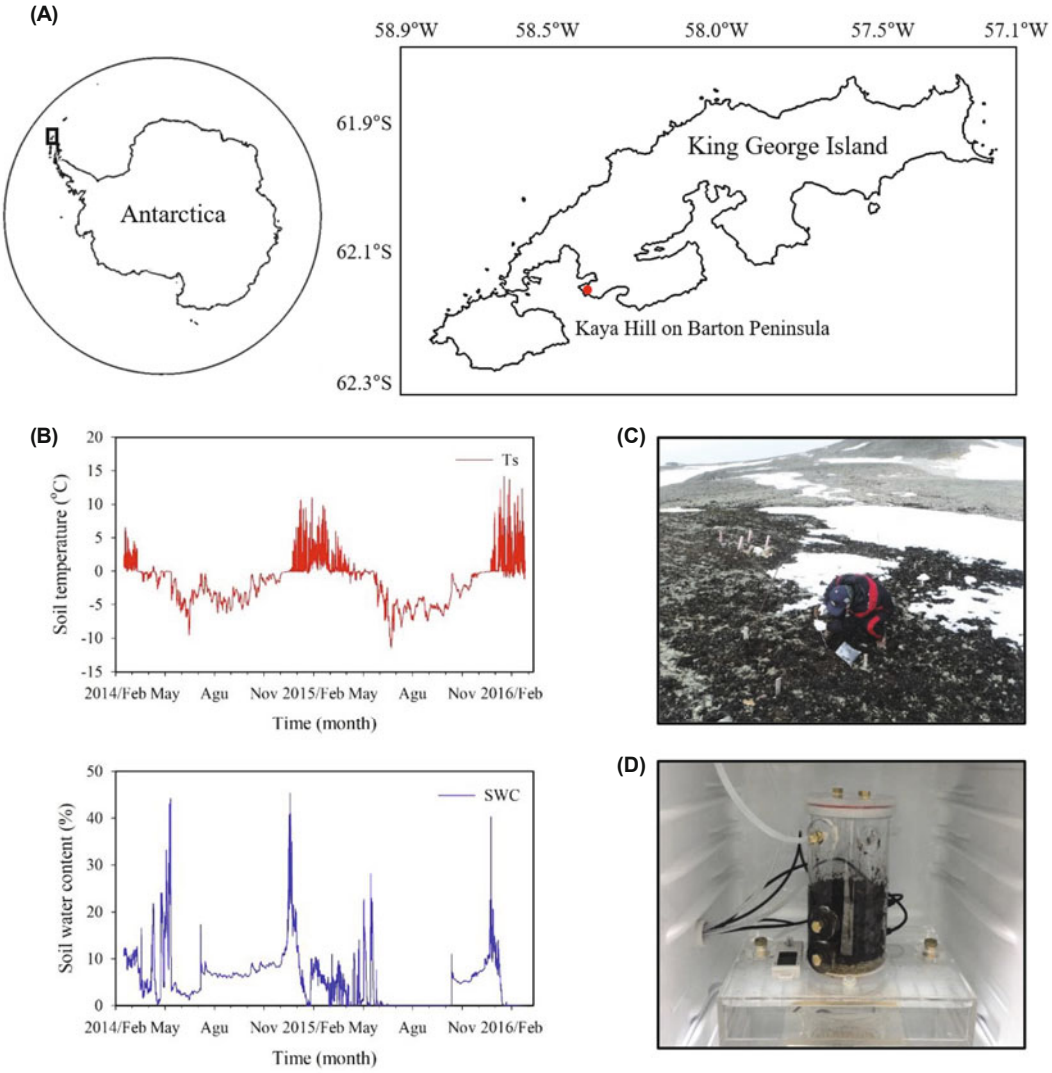

Fig. 1. **(A) Overview of Antarctica and a map of King George Island with the sampling location indicated in red, (B) Temporal variation of soil temperature (T_s) and soil water content (SWC); measured hourly from February 2014 to February 2016, (C) Photo of the sampling location (February 2016), and (D) Microcosm system with the bottomless acrylic column used for incubating maritime Antarctic tundra soils.**

were calculated against a standard curve of commercial humic acids (HA, a main component of HS; Sigma-Aldrich Cat. No. 53680) in 0.5 N NaOH (Badis *et al.*, 2009).

DNA extraction, PCR amplification, and sequencing

Total DNA was extracted from 0.3 g of each of initial soil samples and microcosm soil samples using the FastDNA Spin Kit for Soil (MP Biomedicals). Polymerase chain reaction (PCR) amplification using fusion primers (primer pair 341F/805R) targeted the V3-V4 region of the bacterial 16S ribosomal RNA (rRNA) gene (Fadrosh *et al.*, 2014). The PCR products were confirmed by 1% agarose gel electrophoresis, purified, and assessed for quality and product size. Sequencing was carried out at Chunlab, Inc. using a 2 × 250 bp Illumina MiSeq Sequencing System (Illumina).

Bioinformatic analysis

Primers and adapter sequences were trimmed using Cutadapt v.1.15 (Martin, 2011), and filtered sequences were processed by the DADA2 algorithm (Callahan *et al.*, 2016), which resolves amplicon sequence variants (ASVs) with single-nucleotide resolution from 16S rRNA gene sequences. Resultant ASVs were then taxonomically assigned to genus-level phylotypes against the EzBiocloud database (May 2018) (Yoon *et al.*, 2017) for bacteria using the naïve Bayes classifier with a confidence threshold of 80% in mothur v.1.43.0 (Schloss *et al.*, 2009). Bray-Curtis dissimilarities were calculated using the Hellinger-transformed ASV matrix and visualized using principal coordinates analysis (PCoA). All plots were generated using basic functions in R version 3.5.1 (www. r-project.org) unless otherwise specified. Raw sequence data were submitted to the NCBI Sequence Read Archive database with an accession number of SRR11004813–SRR11004821.

Table 1. Chemical and physical soil characteristics

Sample	Incubation time (day)	Soil characteristics				
		pH	EC (μS/cm)	C%	N%	C/N
KS1-4Feb	T = 0	4.8	104.6	19.0	2.0	9.5
	T = 90	5.0	97.1	18.1	1.9	9.5
KS1-4Apr	T = 0	4.8	105.8	23.1	2.4	9.6
	T = 120	4.7	152.7	21.9	2.3	9.5

C, Carbon; EC, Electrical conductivity; N, Nitrogen; C/N, Carbon to Nitrogen ratio.

Table 2. Fungal and bacterial phospholipid-derived fatty acids

	Phospholipid fatty acids (mg/kg of soil)			
	KS1-4Feb		KS1-4Apr	
	T = 0	T = 90	T = 0	T = 120
Fungi	25.2	22.2	26.4	27.9
Bacteria	82.8	84.7	82.0	106.5
Gram+	58.7	56.9	52.8	70.0
Gram-	15.0	14.4	14.5	18.8
Actinomycete	9.1	13.4	14.7	17.7
Total	108.0	106.9	108.4	134.4
Ratio of fungal/bacterial biomass	0.3	0.3	0.3	0.3

Results

Soil characteristics

The soil chemical and physical properties were analyzed prior to conducting the microcosm experiments to initially compare the two T = 0 soil samples: the TC for KS1-4Feb was 19.0%, and the TC for KS1-4Apr was 23.1%. TN was 2.0% for KS1-4Feb versus 2.4% for KS1-4Apr, but the C/N ratio (9.6) and soil pH (4.8) were almost identical. At T = 90 sample of KS1-4Feb, the TC value decreased by approximately 1%. The same trend was noted in KS1-4Apr at T = 120 sample (Table 1). The carbon element loss might be attributed to the microbial consumption of SOM during the microcosm incubations.

Determination of microbial biomass

At T=0, the fungal and bacterial PLFA contents were de-

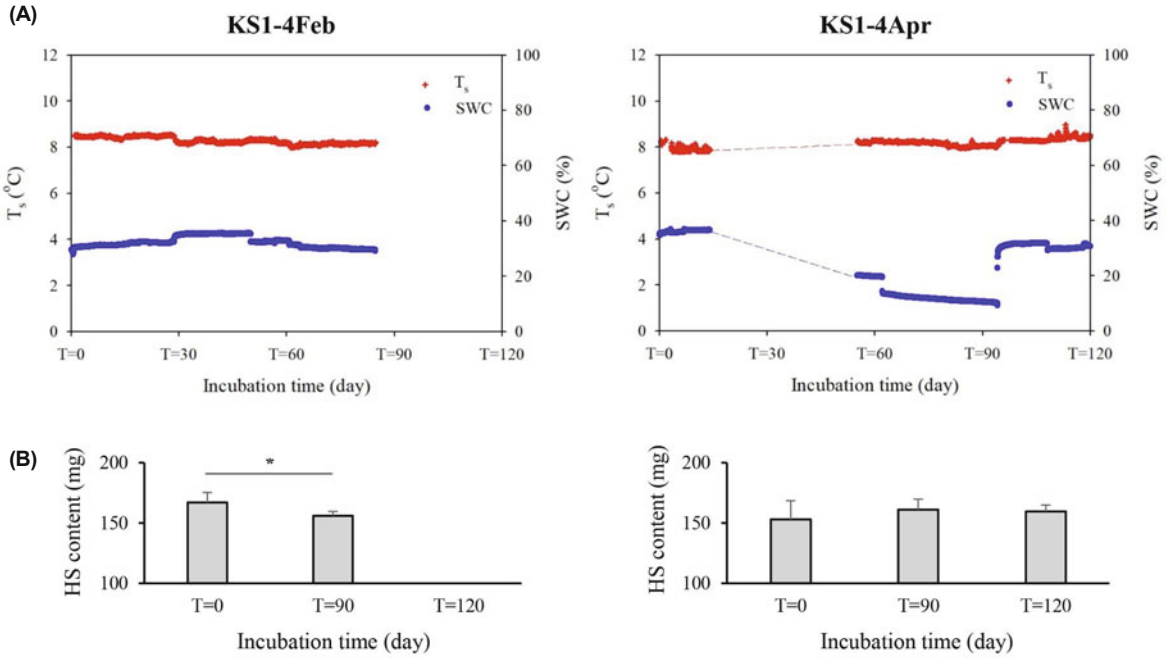

Fig. 2. **(A) Temporal variation of soil temperature (T_s) and soil water content (SWC) during microcosm incubation of KS1-4Feb and KS1-4Apr (Note: T_s and SWC for KS1-4Apr soil were not recorded for days 14–54 due to a power failure.), and (B) Changes in humic substances (HS) content.** * indicates significant differences ($p < 0.05$) between the treatments based on a one-way analysis of variance. Each error bar represents one standard deviation of five extraction replicates.

termined to be 25.2 and 82.8 mg/kg soil (total 108.0 mg/kg) in KS1-4Feb and 26.4 and 82.0 mg/kg soil (total 108.4 mg/kg) in KS1-4Apr. A ratio of fungal:bacterial biomass was 0.3 in both soils. These data indicated that the two soils were almost identical in the initial microbial communities despite the two-month time difference between samplings. The fungal and bacterial PLFA profiles were 22.2 and 84.7 mg/kg soil (106.9 mg/kg) for KS1-4Feb at T = 90. With respect to KS1-4Apr, the fungal and bacterial PLFA profiles were 27.9 and 106.5 mg/kg soil (134.4 mg/kg) at T = 120. Little change in KS1-4Feb biomass was detected at T = 90 when compared to that at T = 0, while a considerable change was present in KS1-4Apr biomass between T = 0 and T = 120. The biomass increase in KS1-4Apr is attributed to the increase in bacterial cell mass during the microcosm incubations. The initial ratios of fungal:bacterial biomass were steadily maintained in KS1-4Feb until T = 90 and in KS1-4Apr until T = 120 (Table 2).

HS biodegradation during the microcosm incubation

Practically, KS1-4Feb soil was incubated at constant T_s of 8.3 (± 0.2)°C and constant SWC of 32 (± 2)% for T = 90. KS1-4Apr soil was incubated at 8.1 (± 0.2)°C for T = 120, but in the absence of supplied water, the SWC gradually decreased from 37% to 9% for the first T = 90. Upon rehydration, the SWC of KS1-4Apr soil increased to 30%, where it remained for the last T = 30 of the study (Fig. 2A). After T = 90 incubation, the HS content extracted from KS1-4Feb soil was 156.0 (± 3.5) mg/g of soil versus the initial HS level (100%) of 167.0 (± 8.4) mg/g of soil, an approximate 11.0 mg (6.6%, $p < 0.05$) decrease in HS during the incubation. This indicates that some HS was removed, possibly via a biologically mediated degradation process (Fig. 2B). In contrast, the KS1-4Apr soil microcosm maintained its initial HS level, 152.9 (± 15.5) mg/g of soil during the first T = 90. Additionally, we saw no change in HS levels after SWC was restored to 30%, indicating that HS degradation by the soil's indigenous microbes was negatively affected by gradual soil drying.

Changes in bacterial community composition during microcosm incubation

In total, 365,762 high-quality sequence reads were obtained from nine samples (four from KS1-4Feb and five from KS1-4Apr) with an average of 40,640 reads per sample. The resulting16S rRNA gene sequences spanned 33 bacterial phyla, dominated by Proteobacteria (19.9% in KS1-4Feb samples and 21.0% in KS1-4Apr samples), followed by Acidobacteria (14.0% and 17.8%), Actinobacteria (16.8% and 12.2%), Chloroflexi (12.2% and 15.5%), and candidate division AD3 (12.4% and 4.8%) (Fig. 3A). Interestingly, the fraction of candidate division AD3 slightly increased with the incubation time in both treatments. In the KS1-4Feb samples, where HS content decreased, Bacteroidetes increased in relative abundance, whereas the proportion in KS1-4Apr fluctuated with increasing incubation time. The changes in relative abundances of bacterial communities were also analyzed at lower taxonomic levels. Although we saw no discernible differences in bacterial phylum abundances between the two treatments, regardless of the different incubation conditions (i.e., the same T_s but different SWC), we observed dramatic changes in the relative abundance of certain bacterial taxa at the genus

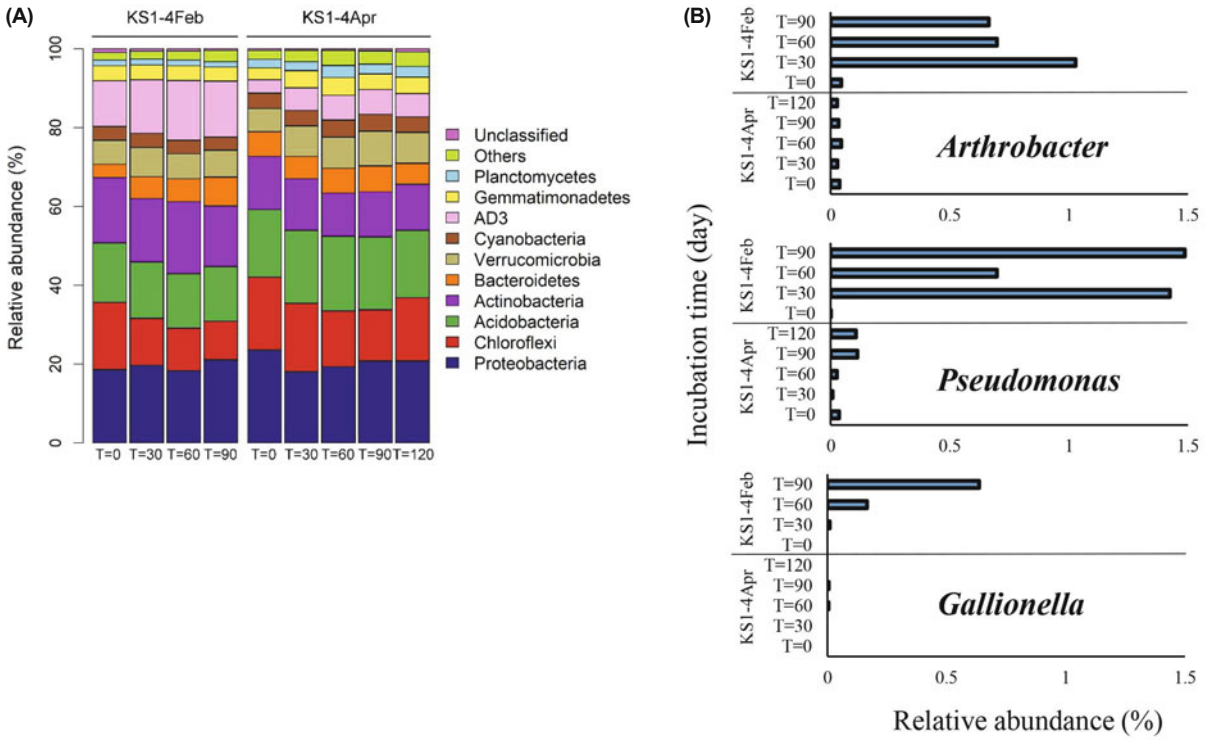

Fig. 3. (A) Comparison of bacterial phylum distribution throughout the incubation time. (B) Relative abundances of the major genera (%) detected during microcosm incubation.

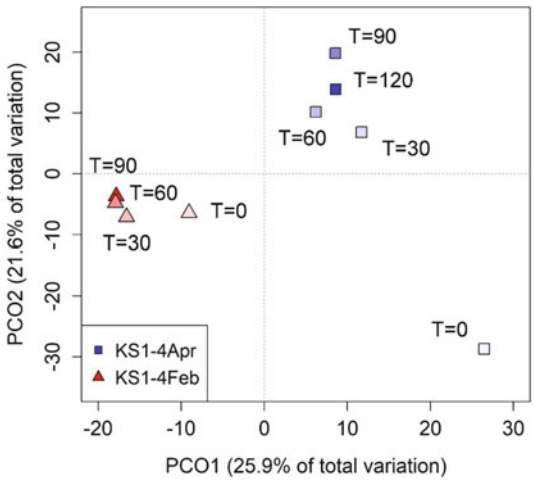

Fig. 4. **PCoA plot of the bacterial community showing the shifting patterns in community composition throughout the incubation time.**

level. The relative abundances of three genera (*Arthrobacter*, *Pseudomonas*, and *Gallionella*) clearly increased in KS1-4Feb samples compared with KS1-4Apr samples (Fig. 3B). For example, *Arthrobacter* (phylum Actinobacteria; class Actinobacteria_c), obligate aerobes commonly found in soils and studied for bioremediation, increased in relative abundance approximately 15-fold (from 0.045% at T = 0 to 0.664% at T = 90). The highest increase in the relative abundance (743-fold, from 0.002% to 1.486%) was *Pseudomonas* (phylum Proteobacteria; class Gammaproteobacteria), aerobes with substantial metabolic diversity in a wide variety of ecological niches. The abundance of iron-oxidizing chemolithotrophic *Gallionella* (phylum Proteobacteria; class Betaproteobacteria) changed significantly (from 0% to 0.637%) during the incubation period of T = 90.

We observed directional shifts in bacterial community composition throughout the incubation time in both treatments, but the extent of compositional changes was different (Fig. 4). At the ASV level, we found pronounced community changes in KS1-4Apr samples, with the most significant shift observed during the first T = 30. In contrast, the bacterial community structure was only slightly altered in KS1-4Feb samples. The bacterial community of KS1-4Apr at T=120 reverted to that of earlier samples (e.g., T = 30 and T = 60 samples) after the original SWC was restored.

Discussion

An enormous amount of organic carbon is stored in the polar tundra due to low-level microbial degradative activity that results from long-term low T_s. HS are highly complex, aromatic heteropolymers, constituting up to 70% of total SOM in natural environments including the tundra (Lipczynska-Kochany, 2018). Over the past several decades, the Arctic and Antarctic have undergone rapid warming, and the increased air temperature has likely expanded the thawing period, thus directly affecting T_s and SWC in the tundra soil. Because the individual effects of T_s and SWC on microbial HS degradation are still poorly understood, even less is known about their combined impact on degradative activity for polymeric HS in the heterogeneous tundra soil.

Rainfall, snowmelt, and glacier melt in summer are significant sources of water supply for the maritime Antarctic tundra soil. The rising air temperature increases the number of rainy days and length of the melting season, thus increasing the water supply to soil microbes. SWC is different depending on the soil types and topographic slopes and results in different microbial responses. On average, the sampling site KS1, which is rich in SOM (including HS), is continuously supplied with water from melting snow during the summer season, but some parts begin to gradually dry owing to gentle slope (Fig. 1B). Since KS1-4Feb and KS1-4Apr soils were collected in different months, the soil properties, particularly SWC, might be different. Presumably, the indigenous microbial communities have already adapted to the changing SWC. Indeed, we confirmed a small difference between TC and TN values at T = 0, but the C/N ratio and soil pH were almost identical (Table 1). In microbial community analyses at T = 0, the total microbial PLFA contents and ratios of fungal: bacterial biomass were almost identical to each other (Table 2), with no discernible differences in bacterial phylum abundances between the two soils (Fig. 3A). When considering the heterogeneity and dynamics of tundra soil, we concluded that these slight differences would not impact our microcosm experiments. Our laboratory-based approach is important for studying microbial community responses (especially HS degradation) to changing SWC in natural Antarctic tundra soil.

Our microcosm experiments with the SOM-rich soil samples showed that a constant SWC of 32 (± 2)% helped to maintain microbial community stability during the T = 90 incubation period. Two community-level analyses, PLFA for microbial (fungal and bacterial) biomass change (Table 2) and PCoA for bacterial compositional change (Fig. 4), support our claims. The constant SWC along with the applied summer seasonal T_s led to higher HS degradative activity (Fig. 2B). SWC typically ranges from 15% to 35%, and most soils are water-saturated at 35%. Many studies suggest that the optimal SWCs for microbial degradative activities vary in a range of 8–25% depending on organic materials and environmental conditions (Stres *et al.*, 2008; Yadav and Hassanizadeh, 2011). Considering HS loss in the microcosm system with KS1-4Feb, the constant SWC of ~32% is still amenable for microbial aerobic decomposition of Antarctic tundra HS. In contrast, gradual drying from 37% to 9% for T = 90 and then rewetting to ~30% for T = 30, resulted in a considerable change in the microbial biomass and a dynamic change in bacterial community structure during T = 120.

The changing SWC likely destabilized the microbial community composition and function, which led to an undetectable HS decomposition rate despite the same T_s. These data indicate that the combination of increased T_s and constant water supply (as a result of rising temperatures) promotes HS decomposition, which, in turn, enhances microbial nutrient uptake and growth. We evaluated the combined effects of T_s and SWC changes on the bacterial communities in the soil ecosystem. During HS degradation in KS1-4Feb, the relative abundance of Bacteroidetes (some of which are litter-asso-

ciated bacteria with a broad substrate range; Brabcova *et al.*, 2016) increased with longer incubation times, implying that Bacteroidetes are involved in HS degradation. In contrast, the proportion of Bacteroidetes fluctuated in KS1-4Apr without HS degradation activity (Fig. 3A), which suggests that Bacteroidetes strains might be vulnerable to the changes in SWCs. Their role in the maritime tundra, especially in HS degradation, remains to be determined.

Until recently, few studies had evaluated the effects of changing T_s and SWC, individually or combined, on the microbial decomposition of HS from polar tundra soils. In one study, Alaskan HS-rich soil was incubated at 5°C (mimicking the thawing period temperature of approximately 5.6°C) and the initial SWC maintained. After a T = 99 incubation, the content of HS significantly decreased to 48%. During the incubation, the relative abundance of the bacterial phylum Proteobacteria and archaeal phylum Euryarchaeota increased, suggesting their involvement in HS degradation in an Arctic sampling site (Park *et al.*, 2015). In another example, a passive warming experiment using an open-top chamber was performed in the Antarctic's King George Island for three years. The increases of T_s and SWC (approximately 0.8°C and 8%, respectively) inside the chambers minimally affected the bacterial and archaeal communities, whereas they significantly altered the fungal community, with an increased abundance of the heterotrophic fungal Ascomycota. Despite their effects on the microbial communities, however, the increase in T_s and SWC did not induce any significant changes in the content and structure of HS in the King George Island Antarctic site (Kim *et al.*, 2018). Previous reports contrast with our results for HS degradation rates and microbial community changes in the following ways: (1) considerable HS degradation with a relative increase of specific bacterial phyla at 8°C and constant SWC and (2) undetectable HS degradation together with unchanged or abruptly changed bacterial community at 8°C and decreasing SWC content. Soil properties, including TC content, T_s, and SWC, differed between the previously reported experiments and our experiments, which may account for the different microbial responses.

It is generally accepted that soil bacteria are directly involved in HS degradation, even in cold environments. Degradation includes both the depolymerization of HS and the further catabolism of HS-derived small compounds. Indeed, several cold-adapted bacterial strains were isolated for their ability to degrade HS under adequate physiological conditions and characterized for their degradative activity. However, information on HS degraders and their degradation pathways at the single-species level or active bacterial consortia remain limited until now (Kim *et al.*, 2019). Our findings provide new insights into the changes in bacterial communities and HS degradation rates in tundra soil that has been undergoing rapid warming. They also indicate that, in addition to T_s, SWC changes should also be considered as an important factor that directly affects the microbial structure and function in the Antarctic tundra ecosystem.

Acknowledgments

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Conflict of Interest

We have no conflict of interest to report.

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